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Shrub persistence and increased grass mortality in response to drought in dryland systems

Daniel E. Winkler[1] | Jayne Belnap[1] | David Hoover[2] | Sasha C. Reed[1] | Michael C. Duniway[1]

[1]U.S. Geological Survey, Southwest Biological Science Center, Moab, Utah

[2]Rangeland Resources & Systems Research Unit, U.S. Department of Agriculture, Agricultural Research Service, Fort Collins, Colorado

Correspondence
Daniel E. Winkler, U.S. Geological Survey, Southwest Biological Science Center, Moab, UT 84532.
Email: dwinkler@usgs.gov

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Abstract

Droughts in the southwest United States have led to major forest and grassland die-off events in recent decades, suggesting plant community and ecosystem shifts are imminent as native perennial grass populations are replaced by shrub- and invasive plant-dominated systems. These patterns are similar to those observed in arid and semiarid systems around the globe, but our ability to predict which species will experience increased drought-induced mortality in response to climate change remains limited. We investigated meteorological drought-induced mortality of nine dominant plant species in the Colorado Plateau Desert by experimentally imposing a year-round 35% precipitation reduction for eight continuous years. We distributed experimental plots across numerous plant, soil, and parent material types, resulting in 40 distinct sites across a 4,500 km^2 region of the Colorado Plateau Desert. For all 8 years, we tracked c. 400 individual plants and evaluated mortality responses to treatments within and across species, and through time. We also examined the influence of abiotic and biotic site factors in driving mortality responses. Overall, high mortality trends were driven by dominant grass species, including *Achnatherum hymenoides*, *Pleuraphis jamesii*, and *Sporobolus cryptandrus*. Responses varied widely from year to year and dominant shrub species were generally resistant to meteorological drought, likely due to their ability to access deeper soil water. Importantly, mortality increased in the presence of invasive species regardless of treatment, and native plant die-off occurred even under ambient conditions, suggesting that recent climate changes are already negatively impacting dominant species in these systems. Results from this long-term drought experiment suggest major shifts in community composition and, as a result, ecosystem function. Patterns also show that, across multiple soil and plant community types, native perennial grass species may be replaced by shrubs and invasive annuals in the Colorado Plateau Desert.

KEYWORDS

Bromus tectorum, cheatgrass, climate change, graminoids, grass, parent material, perennials, populations, *Salsola*, shrubs

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1 | INTRODUCTION

The increasing prevalence of meteorological drought (hereafter "drought") in the western United States has negatively impacted nearly all native biological systems (Easterling et al., 2000), resulting in widespread tree and native grass die-offs (Allen & Breshears, 1998; Anderegg, Anderegg, Abatzoglou, Hausladen, & Berry, 2013; Breshears et al., 2005; Munson, Belnap, Schelz, Moran, & Carolin, 2011; Scott, Hamerlynck, Jenerette, Moran, & Barron-Gafford, 2010), an increased frequency and intensity of wildfires (Littell, McKenzie, Peterson, & Westerling, 2009; Westerling & Swetnam, 2003), changes in woody shrub encroachment (Archer, Schimel, & Holland, 1995; D'Odorico, Okin, & Bestelmeyer, 2012; Grover & Musick, 1990), net carbon loss from systems (Barger et al., 2011; Scott, Jenerette, Potts, & Huxman, 2009), and an increased pervasiveness of invasive species (DiTomaso, 2000). Future climate scenarios suggest extreme droughts will become more common, characterized as "extreme" due to their duration, intensity, or both (Cayan et al., 2010; Cook, Ault, & Smerdon, 2015; Cook, Woodhouse, Eakin, Meko, & Stahle, 2004; Seager et al., 2007). Drought impacts are exacerbated in the southwestern United States where dryland systems are inherently water-limited and have been drastically altered by human land-use impacts for well over a century (Breshears et al., 2005; Madany & West, 1983; Neff et al., 2008; Williams et al., 2010). Further, it is likely that some systems in the southwest have already reached tipping points where mortality of long-lived species will have lasting impacts on plant and associated animal communities for decades or longer (Browning & Archer, 2011; Miriti, Rodríguez-Buriticá, Wright, & Howe, 2007; but see Peters, Yao, Sala, & Anderson, 2012). This pattern of drought impacts has been observed elsewhere around the globe (e.g., Caldeira et al., 2015; Dietze & Moorcroft, 2011; Fensham, Fairfax, & Archer, 2005; Lioubimtseva, Cole, Adams, & Kapustin, 2005; Rice, Matzner, Byer, & Brown, 2004; Stokes, Ash, & Howden, 2008) and is not restricted to water-limited systems (Allen et al., 2010; Ash, McIvor, Mott, & Andrew, 1997; Lopez & Kursar, 2007; Michaelian, Hogg, Hall, & Arsenault, 2011).

Drought-induced mortality is commonly hard to predict, given that the severity of drought can vary due to the often unknown impacts of subtle interannual climate variability, species-specific drought tolerances, and the interaction of drought and demographic processes (Hawkes, 2000; Koepke, Kolb, & Adams, 2010; Lopez & Kursar, 2007; McDowell et al., 2011, 2008; Mueller et al., 2005; Pratt et al., 2014). This is especially true in long-lived perennial plant species that often have morphological and physiological strategies that help individuals withstand short-term drought (<5 years; Barbeta, Ogaya, & Peñuelas, 2013; Hoover, Duniway, & Belnap, 2015; Koepke et al., 2010; McAuliffe & Hamerlynck, 2010; McDowell et al., 2008). These include, but are not limited to, maintaining rooting structures to access deep soil or groundwater during periods of stress (Breshears et al., 2009; Giordano, Guevara, Boccalandro, Sartor, & Villagra, 2011; Schenk & Jackson, 2002), seasonal deciduousness, and dormancy during dry periods (Comstock & Ehleringer, 1992; Ehleringer & Sanquist, 2018). Drought can also interact with natural senescence of long-lived, aging populations (Bowers & Turner, 2001; Miriti et al., 2007), making it a challenge to disentangle direct drought impacts from natural episodic population turnover (Bowers, 2005; Miriti et al., 2007; Winkler, Conver, Huxman, & Swann, 2018). However, drought can also alter population and community structure by increasing mortality in younger individuals, thereby influencing the ability of species to recruit new individuals into populations (Conver, Foley, Winkler, & Swann, 2017; Granda, Escudero, & Valladares, 2014; Padilla & Pugnaire, 2007). Identifying which species are most susceptible to drought and will thus experience widespread mortality under future climate remains a challenge, because documented occurrences of these events are typically observed in either a single species (Bowers & Turner, 2001; Breshears et al., 2005) or are focused on plant functional groups to estimate general trends (Peng et al., 2011; Van Mantgem & Stephenson, 2007; Williams et al., 2013).

Our ability to predict drought-related mortality is further complicated by the fact that the responses of species and individual plants to drought can also be strongly influenced by abiotic and biotic factors, including edaphic properties and competition with invasive plants (Gitlin et al., 2006). Species often differ in drought-avoidance strategies that can interact with soil ecohydrological processes and biogeochemical cycling and, as a result, determine which species can withstand the negative impacts of drought (Fernandez-Illescas, Porporato, Laio, & Rodriguez-Iturbe, 2001; Grossiord et al., 2018; Koepke et al., 2010; Schwinning, Starr, & Ehleringer, 2005; Sperry & Hacke, 2002). Biotic interactions in dryland systems may also affect drought vulnerability through facilitation or competition, which can reduce or exacerbate soil moisture stress (Butterfield, Betancourt, Turner, & Briggs, 2010; Carrillo-Garcia, De La Luz, Bashan, & Bethlenfalvay, 1999; McCluney et al., 2012). For example, invasive species can take advantage of systems experiencing drought in order to ensure their colonization and spread (Alpert, Bone, & Holzapfel, 2000; MacDougall & Turkington, 2005; Winkler, Gremer, Chapin, Kao, & Huxman, 2018), thereby increasing competition for already limited resources (DeFalco, Bryla, Smith-Longozo, & Nowak, 2003; Everard, Seabloom, Harpole, & Mazancourt, 2009).

Vegetation in the Colorado Plateau Desert may be especially vulnerable to future drought impacts given that there has already been an increase in anomalously dry years (Cook et al., 2015). This increasing aridity is occurring simultaneously with increasing temperature, further reducing soil water availability (Seager et al., 2007; Wuebbles, Fahey, & Hibbard, 2017) and resulting in major forest die-offs and shifts in community composition (Allen & Breshears, 1998; Breshears et al., 2005; Munson et al., 2011; Swetnam & Betancourt, 1998). These and related studies suggest that an increase in woody shrubs and a decrease in native perennial grasses is likely to occur under future conditions (Hoover et al., 2015; Hoover, Duniway, & Belnap, 2017; Munson et al., 2011; Wertin, Reed, & Belnap, 2015). However, long-term population studies on dominant plant species have not been utilized to predict and quantify mortality of individuals

through time or over a period of prolonged drought. Additionally, few studies to date have examined the combined effects of multiple abiotic and biotic factors on individual responses to drought.

Nonetheless, the remaining challenge is to forecast which species will be most vulnerable to drought-induced mortality and what these events will mean for ecosystems. Experimental droughts can resolve some of these issues by allowing the measurement of multiple targeted species across climatically variable years (Adams et al., 2009; Hoover, Wilcox, & Young, 2018). We experimentally investigated meteorological drought-induced mortality of nine dominant plant species in the Colorado Plateau Desert by imposing a year-round 35% precipitation reduction for eight continuous years across 40 sites spanning plant community and soil types common on the Colorado Plateau. More than 400 individual plants were tracked throughout the duration of the experiment and mortality data were evaluated in the context of the relative contribution of treatments, interannual climate variability, and species identity to determine drought susceptibility in these dryland systems. We also examined the importance of multiple abiotic and biotic factors in driving responses to drought. We tested whether drought susceptibility varies by abiotic site factors including elevation, soil depth, and parent material, as well as biotic interactions with biological soil crusts (biocrusts) and invasive plant species. We hypothesized that long-term drought would negatively influence all species, but that the magnitude would vary according to species-level differences in drought tolerance. Finally, we predicted that the presence of biocrusts would reduce the negative impacts of drought (facilitation) while the presence of invasive species would increase the negative impacts of drought (competition), providing broader implications for how Colorado Plateau landscapes are currently changing and how they will respond to future climate change.

2 | MATERIALS AND METHODS

2.1 | Study site

Our research sites are located in the Colorado Plateau Desert in southeastern Utah (Figure 1). The Colorado Plateau Desert is one of North America's five major deserts and encompasses nearly 340,000 km^2 of land in Utah, Colorado, New Mexico, and Arizona (Schwinning, Belnap, Bowling, & Ehleringer, 2008; Winkler, Backer, et al., 2018). The climate is characterized as a cold, arid to semiarid dryland, with a wide variety of soil types and associated plant communities, driven primarily by elevation gradients (ranging from 600 to 3,353 m a.s.l.), variation in geological substrates (parent materials), and geomorphology (Duniway et al., 2016). Precipitation in the desert is bimodal, with cool season moisture originating from Pacific Ocean systems and warm season moisture originating from the North American Monsoon (Hereford & Webb, 1992). The annual precipitation ranges from 130 to 350 mm depending on location and elevation in the region. Because soil water on the Colorado Plateau is primarily recharged during the cool season when evapotranspiration is low, peak productivity typically occurs in mid- to late spring when temperatures are warm and soil moisture is still accessible to plants at a wide range of soil depths (Comstock & Ehleringer, 1992; Summer et al., 2009).

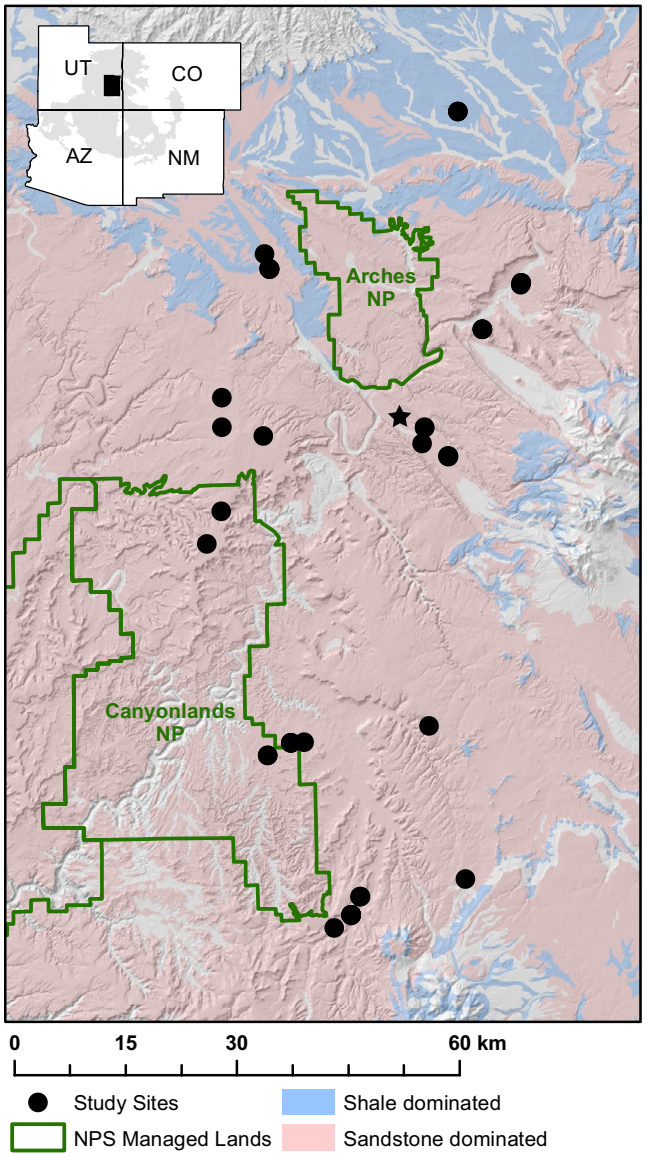

FIGURE 1 Map of experimental study sites (black circles) with National Park (NP) Service lands (green borders) and Moab, Utah (star) shown for reference. The inset in the upper left shows the location of the study area (black box) within the Colorado Plateau (gray-shaded area) stretching across Utah, Colorado, New Mexico, and Arizona

Plant species on the Colorado Plateau are well-tuned to variable and ephemeral precipitation (Comstock & Ehleringer, 1992) and, over the past 10,000 years, have responded to climate variability similar to that of today (Coats, Cole, & Mead, 2008). Mosaics of vegetation dot the landscape, following the large abiotic gradients on the Plateau (Bunting, Munson, & Villarreal, 2017). High-elevation sites on the Plateau are typically dominated by pinyon and juniper species while low-elevation plant communities (typically below 1,600 m), where this study was focused, are dominated by shrub

species, including *Coleogyne ramosissima*, *Ephedra viridis*, *Atriplex* spp., and perennial grass species, including *Achnatherum hymenoides*, *Pleuraphis jamesii*, and *Hesperostipa comata* among others (Bunting et al., 2017; Munson, Duniway, & Johanson, 2016).

2.2 | Sampling design and measurements

We established 40 experimental sites in 2010 that spanned a range of plant community types, elevations, and parent materials across a 4,500 km^2 region of the Colorado Plateau in southeastern Utah (Figure 1; Table 1; Table S1). Thirty of the sites were located on public or private lands open to grazing and, thus, fences were erected in 2010 to exclude domestic livestock. This activity resulted in all 30 previously grazed sites being dominated by poorly developed biocrusts. Each site consisted of two 1.5 × 2 m plots that were randomly assigned to either control (ambient precipitation) or meteorological drought (35% precipitation reduction) treatments. We selected this drought level as a conservative estimate of what plants may realistically experience in conjunction with increasing temperature by 2,100 (Cook et al., 2015). Rainfall reductions were achieved year-round using passive rainfall removal shelters. These shelters were constructed to be significantly larger than the plots: shelters were 2.3 × 3.1 m to create a ca. 0.5 m buffer around the sides of each plot. Shelters consisted of slanted roofs made of V-shaped acrylic strips that intercepted 35% of precipitation. Roofs were sloped by 10° and were approximately 1 m tall at the short end. Captured rainfall was removed from the plot using a series of gutters. All plots were hydrologically isolated for the top 30 cm using vinyl flashing placed 20 cm from the outer edge of each plot and buried to a depth of 30 cm around each plot. Treatments began in 2011, resulting in eight continuous years of experimental drought as of 2018.

We permanently tagged 401 individual plants, representing 9 target shrub and perennial grass species, in order to track survival and mortality through time (Table 1). Species represented multiple functional groups, and cover classes were chosen across our experiment based on their presence in a minimum of 10 replicates (control and drought) across the sites. Target shrub species included *Atriplex corrugata*, *C. ramosissima*, *E. viridis*, *Krascheninnikovia lanata*, and cactus *Opuntia* spp. (*Opuntia* species included *O. polyacantha* and *O. phaeacantha* which were combined for analyses). Target grass species included *A. hymenoides*, *Hesperostipa comata*, *P. jamesii*, and *Sporobolus cryptandrus* (Table 1). Individuals were tracked annually and plant status (dead or alive) was recorded at peak productivity (typically in April or May each year). We permanently tagged new plants whenever previously tagged individuals in a plot died. We ensured all newly tagged individuals existed in the plots before treatments began using plot photographs from when the study began. Individuals marked dead were tracked for additional years since dormancy can sometimes occur and plants can green-up in subsequent years. Of the 401 tracked individuals, 25 appeared dead but re-greened in the following year and this occurred in 6 of the 9 target species. We tested for potential error introduced by 2018 data by correcting data, removing either the mean or maximum number of individuals of each species that re-greened during the experiment, and found no effect. Thus, raw mortality data were used in all analyses. Ground cover of biocrusts (i.e., lichens, moss, darkly pigmented cyanobacteria, lightly pigmented cyanobacteria) and foliar cover of invasive species (*Bromus tectorum* and *Salsola tragus*) was visually estimated as a percentage in each plot using four 75 × 100 cm survey grids. Plant cover was recorded only for those parts of the plants that were alive and green. For example, branches and senesced leaves were not included in cover estimates.

Precipitation data were obtained from NOAA's National Climatic Data Center (http://www.ncdc.noaa.gov) from a station located within our drought experiment study area (station id: USC00425733). Additionally, daily precipitation amounts were obtained using tipping bucket rain gauges (Rainew 111; RainWise Inc., Trenton, ME) installed as a subset of our sites, with data logged hourly (Table S3).

TABLE 1 Target species, number of individuals sampled (n), plant functional types (PFT), and parent materials where species were sampled

Species	*n*	PFT	Parent material
Achnatherum hymenoides	78	C_3 grass	Sandstone, shale
Atriplex corrugata	26	C_4 shrub	Shale
Coleogyne ramosissima	47	C_3 shrub	Sandstone
Ephedra viridis	36	C_3 shrub	Sandstone
Hesperostipa comata	59	C_3 grass	Sandstone
Krascheninnikovia lanata	25	C_3 shrub	Sandstone, shale
Opuntia spp.	21	CAM cactus	Sandstone
Pleuraphis jamesii	90	C_4 grass	Sandstone, shale
Sporobouls cryptandrus	19	C_4 grass	Sandstone

2.3 | Statistical analyses

We used an information theoretic approach using generalized linear models to determine the combination of factors that best predicted mortality (Aho, Derryberry, & Peterson, 2014; Barber & Ogle, 2014; Burnham & Anderson, 2014). We included treatment, year, and species as fixed effects in our first-order models to test for treatment effects on mortality while accounting for the influence of interannual climate variability and species-level differences. Models also included individual plant ID nested within site as random effects to account for pseudo-replication across sites and tagged individuals. This also accounted for uneven sample sizes for any given species in any given year, including potential effects of adding newly tagged individuals throughout the study. We tested for the predictive ability of each main effect by comparing the full model with simpler variants and the change in Akaike information criterion corrected for small sample sizes for each model (ΔAIC_c; Johnson & Omland, 2004; Aho et al., 2014). We used ΔAIC_c to compute Akaike weights (w_i) as a measure of the relative likelihood that a given model was the best of all models. We calculated marginal r^2 to estimate the predictive power of explanatory variables for the best model (Nakagawa & Schielzeth, 2013).

We continued with a second set of models by adding abiotic variables including elevation (m), soil depth (shallow or deep), and parent material as additional explanatory variables to the best-fit model. For statistical analyses, we grouped the parent materials into two general classes, (a) shale dominated and (b) sandstone dominated (Figure 1; see Hoover et al., 2015 for more details). We then built a final set of models by adding biotic variables including cover of biocrusts (i.e., lichens, moss, and darkly pigmented cyanobacteria) and invasive species cover to the previous best-fit model. This final set of predictive variables was subsequently used on individual year and species models to test differences in mortality between treatments and years, as well as the influence of abiotic and biotic variables identified as important in model comparisons. We did this by employing the ANOVA function in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2013) to obtain *p* values using *F* statistics and Satterthwaite approximations for degrees of freedom. Last, we visualized the relationship between the probability of survival and invasive species cover in each treatment to examine the influence of invasives on drought-susceptibility. We corrected model convergence issues by optimizing model algorithms using the BOBYQA optimizer function (Powell, 2009). All models were built using the nlme package in R 3.3.2 (Pinheiro, Bates, DebRoy, & Sarkar, 2018; R Core Team, 2014). We also summarized ambient climate conditions using data obtained from NOAA's National Climatic Data Center (http://www.ncdc.noaa.gov) from a station located within our drought experiment study area (station id: USC00425733) and report seasonal rainfall totals for a subset of our sites throughout the duration of the experiment.

3 | RESULTS

Mortality was best predicted by treatment, year, and species identity (AIC_c = −370.88; marginal r^2 = 0.19; Table 2). Models with an interaction between treatment and year, or without individual predictor variables were worse at predicting mortality (ΔAIC_c = 10.72–230.94; Table 2). Compared to our first models, subsequent models were improved by including parent material (AIC_c = −371.97), though predictive power was only slightly improved (marginal r^2 = 0.20; Table 3). Additionally, models that included elevation and/or soil depth were worse at predicting mortality (ΔAIC_c = 1.10–19.69; Table 3). Models were further improved by including invasive species cover (AIC_c = −372.60) though, again, predictive power was only slightly improved (marginal r^2 = 0.21; Table 4). Models with biocrust cover were worse at predicting mortality and, as a result, were excluded from our final models (ΔAIC_c = 6.59–18.98; Table 4).

Drought treatment effects differed from year to year but tended to increase species-level mortality especially during or immediately following a year with below-average precipitation (Figure 2; Tables S2 and S3). Overall, mortality was higher in drought treatments, with ca. 10%–20% higher mortality compared to ambient treatments (Figure 2). Mortality more than doubled in 2013 ($F = 5.58_{(1,276)}$, $p = 0.02$), 2014 ($F = 6.69_{(1,250)}$, $p = 0.01$), and 2018 ($F = 31.02_{(1,328)}$, $p < 0.001$). Zero mortality was observed in ambient treatments in 2017 but c. 5% mortality was observed in drought treatments on average ($F = 6.43_{(1,261)}$, $p = 0.01$). Mortality was significantly higher in ambient plots in 2012 ($F = 5.00_{(1,289)}$, $p = 0.02$), though the difference between treatments was minimal (Figure 2).

Our four target grass species all saw increased mortality in drought treatments across all years (Figure 3), and the extent of drought varied strongly by species. *A. hymenoides* was most sensitive to drought, with nearly 30% mortality on average ($F = 26.04_{(1,70)}$, $p < 0.0001$; Figure 3).

TABLE 2 Results of linear mixed-effects models predicting 2011–2018 mortality (binary response as alive or dead) with treatment (tmt), year (yr), their interaction, and species (sp) as fixed effects

Model	*k*	AIC_c	ΔAIC_c	w_i
tmt * yr + sp	23	−360.16	10.72	<0.01
tmt + yr + sp	**16**	**−370.88**	**0.00**	**0.99**
tmt + yr	8	−326.60	44.28	0
tmt + sp	9	−202.96	167.92	0
yr + sp	15	−354.19	16.58	0
tmt	1	−153.50	217.39	0
yr	7	−315.30	55.58	0
sp	8	−183.62	187.26	0
Intercept	0	−139.94	230.94	0

Note: Site and individual plant ID are included as nested random effects. AIC_c are Akaike information criterion values corrected for small sample sizes. w_i are Akaike weights, which indicate the probability of each model being the best fit (shown in bold font) relative to others shown.

TABLE 3 Results of generalized linear mixed-effects models predicting 2011–2018 mortality (binary response as alive or dead) with treatment (tmt), year (yr), species (sp), elevation (elev), soil depth (soil), and parent material (pm) as fixed effects

Model	*k*	AIC_c	ΔAIC_c	w_i
tmt + yr + sp + elev + soil + pm	19	−352.28	19.69	0
tmt + yr + sp + elev + soil	18	−355.78	16.18	0
tmt + yr + sp + elev + pm	18	−358.82	13.14	<0.01
tmt + yr + sp + soil + pm	18	−365.77	6.12	0.03
tmt + yr + sp + elev	17	−362.22	9.75	<0.01
tmt + yr + sp + soil	17	−365.20	6.77	0.02
tmt + yr + sp + pm	**17**	**−371.97**	**0.00**	**0.60**
tmt + yr + sp	16	−370.88	1.10	0.35

Note: Site and individual plant ID are included as nested random effects. AIC_c are Akaike information criterion values corrected for small sample sizes. w_i are Akaike weights, which indicate the probability of each model being the best fit (shown in bold font) relative to others shown.

However, *A. hymenoides* also experienced upwards of 20% mortality in ambient treatments on average. Additionally, *A. hymenoides* was sensitive to year effects ($F = 17.74_{(7,259)}$, $p < 0.0001$; Figure 4; Table 5), with mortality varying from year to year. *H. comata* saw low levels of mortality in ambient treatments but experienced 10%–20% mortality in drought treatments ($F = 5.94_{(1,51)}$, $p = 0.02$; Figure 3; Table 5). Individual year effects on *H. comata* were clear ($F = 3.28_{(7,305)}$, $p < 0.01$; Figure 4; Table 5), with mortality occurring in drought treatments 2013–2015 and 2018, and marginally in ambient treatments in 2014. *P. jamesii* also experienced higher levels of mortality in drought treatments compared to ambient ($F = 4.28_{(1,488)}$, $p = 0.04$; Figure 3; Table 5), which also varied by year ($F = 10.32_{(7,488)}$, $p < 0.0001$; Figure 4; Table 5). Mortality in *P. jamesii* occurred in drought treatments in nearly all years but also occurred in ambient treatments, primarily during years that saw below-average precipitation (Figure 4; Table 5; Table S1). *S. cryptandrus* was the sole grass species to only experience mortality in drought treatments ($F = 7.00_{(1,16)}$, $p = 0.02$; Figure 3; Table 5), with ca. 25%–30% mortality occurring across all years of the experiment. Year effects on *S. cryptandrus* were marginally significant and mortality only occurred in 2013, 2014, and 2018 ($F = 2.00_{(7,79)}$, $p = 0.06$; Figure 4; Table 5).

TABLE 4 Results of generalized linear mixed-effects models predicting 2011–2018 mortality (binary response as alive or dead) with treatment (tmt), year (yr), species (sp), parent material (pm), % cover of biological soil crusts (crust), and % cover of invasives (invas) as fixed effects

Model	k	AIC_c	ΔAIC_c	w_i
tmt + yr + sp + pm + crust + invas	19	−360.65	11.95	<0.01
tmt + yr + sp + pm + crust	18	−353.62	18.98	<0.01
tmt + yr + sp + pm + invas	**18**	**−372.60**	**0.00**	**0.96**
tmt + yr + sp + pm	17	−366.01	6.59	0.04

Note: Site and individual plant ID are included as nested random effects. AIC_c are Akaike information criterion values corrected for small sample sizes. w_i are Akaike weights, which indicate the probability of each model being the best fit (shown in bold font) relative to others shown.

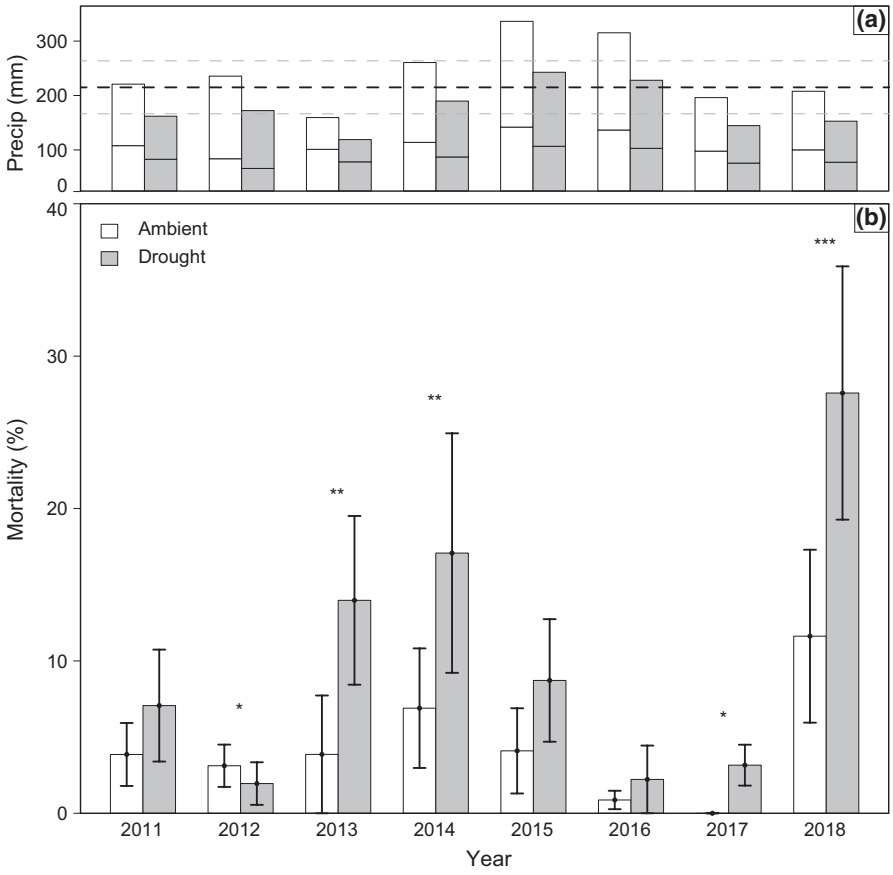

FIGURE 2 (a) Previous year's precipitation (mm) by season for ambient (white bars) and drought (gray bars) treatments for each year of the experiment. Each bar is split into a top and bottom section by a solid horizontal line: the bottom section is cool season precipitation (includes Nov–April), while the top section is warm season precipitation (includes May–October). The dashed lines indicate the historic average precipitation (black dashed line), and dry or wet years as 25th and 75th percentiles (gray dashed lines; 1900–2018). Precipitation data were obtained from NOAA's National Climatic Data Center (http://www.ncdc.noaa.gov) from a station located in Moab, Utah (station id: USC00425733). (b) Mean (±*SEM*) mortality for each year (2011–2018) as a percentage of the total number of individuals in ambient (white bars) and drought (gray bars) treatments across all target species and sites. Asterisks indicate significant differences between treatments in a given year based on linear mixed-effect models with an $\alpha = 0.05$ (*$p = 0.05$, **$p < 0.01$, ***$p < 0.001$)

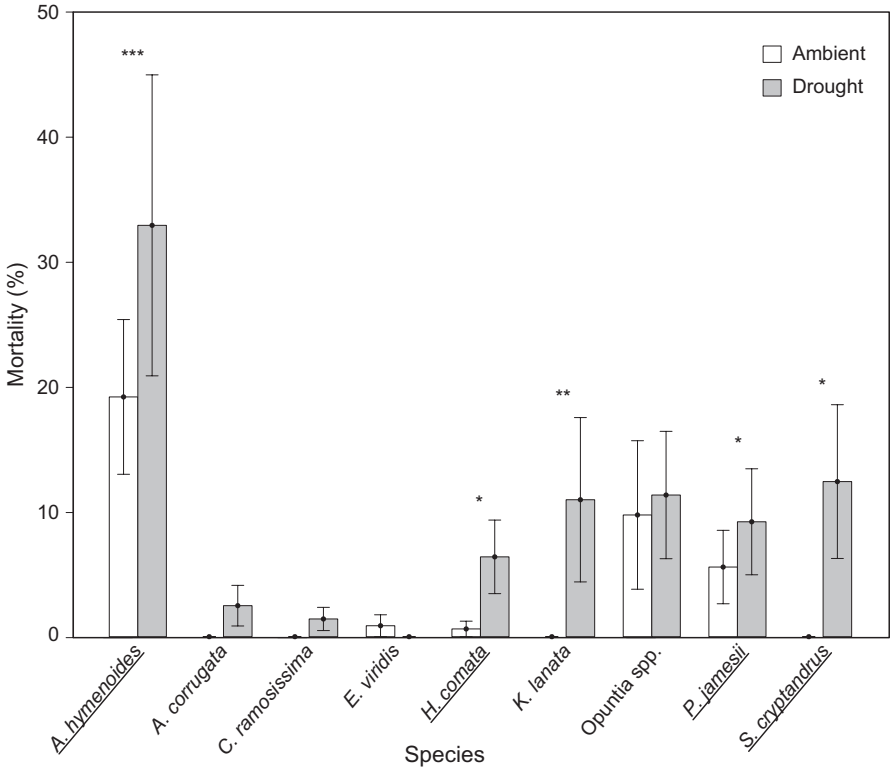

FIGURE 3 Mean (± *SEM*) mortality for each target species (grass species names are underlined) as a percentage in ambient (white bars) and drought (gray bars) treatments across all years of the experiment. Asterisks indicate significant differences between treatments based on linear mixed-effect models with an $\alpha = 0.05$ (*$p = 0.05$, **$p < 0.01$, ***$p < 0.001$)

Nearly all shrub species were resistant to meteorological drought treatments (Figure 3; Table 5), but *K. lanata* saw greater than 10% mortality on average in drought treatments ($F = 9.31_{(1,20)}$, $p < 0.01$; Figure 3; Table 5). Year effects were also clear for *K. lanata* ($F = 3.28_{(7,151)}$, $p < 0.01$; Table 5), with a majority of its mortality occurring during years with below-average precipitation (Figure 4; Table 5; Tables S2 and S3). Other shrub species experienced mortality in drought treatments, though this varied by year and species identity (Figures 3 and 4). This included *At. corrugata* and *C. ramosissima* that only experienced mortality in drought treatments (Figure 4), though these responses were not significant (*At. corrugata*, $F = 1.31_{(1,21)}$, $p = 0.27$; *C. ramosissima*, $F = 1.27_{(1,39)}$, $p = 0.27$; Table 5). *E. viridis* saw nonsignificant levels of mortality in ambient treatments ($F = 1.06_{(1,30)}$, $p = 0.31$; Figure 3; Table 5) but only in 2018 (Figure 4). The shrub-like cactus *Opuntia* spp. also experienced mortality in both ambient and drought treatments but responses were nearly equal ($F = 0.36_{(1,16)}$, $p = 0.56$; Figure 3; Table 5). However, year effects on *Opuntia* spp. mortality were significant ($F = 3.69_{(1,16)}$, $p < 0.01$; Figure 4; Table 5). Approximately 10% mortality occurred in 2011, 2012, and 2014 in ambient treatments while 10%–20% mortality occurred in 2013, 2014, and 2015 in drought treatments (Figure 4). Both ambient and drought treatments saw upwards of 30%–40% *Opuntia* spp. mortality in the driest year, 2018 (Figure 4; Tables S2 and S3).

Invasive species cover was negatively correlated with target shrub and grass species survival in general (Table 4; Figure 5). Overall, compared with plots that had no invasive cover, the probability of surviving was c. 10% lower in drought treatments when invasive species cover was minimal (Figure 5) and was c. 20% lower at the highest levels of invasive species cover, though these differences were not significant. This relationship was largely driven by *A. hymenoides*' negative response to invasive species cover ($F = 11.09_{(1,259)}$, $p < 0.01$; Table 5) regardless of treatment. Mortality in all other species did not appear to be directly influenced by invasives (Table 5).

4 | DISCUSSION

Identifying which plant species are vulnerable to drought-induced mortality under climate change is a major challenge in ecology. Drylands cover more than 40% of the terrestrial Earth surface (Prăvălie, 2016) and have experienced large morality events related to drought in recent decades (e.g., Breshears et al., 2005; Ehleringer & Sandquist, 2018; Jacobsen & Pratt, 2018). Although episodic mortality has been observed in shrubs and grasses, a majority of the die-offs have been observed and studied in tree species, leaving drought thresholds for grasses and shrubs relatively poorly understood. We conducted an 8 year drought experiment to test the tolerances of dominant shrub and grass species to a prolonged meteorological drought, tracking ca. 400 individual plants in 40 sites spanning 4,500 km^2 of Colorado Plateau Desert. Our models of mortality responses to drought were largely driven by interannual climate variability and species identity. Further, our results suggest mortality of dominant plant species is likely to occur under future drought scenarios and that this will primarily be manifest in native grass species. In contrast, dominant shrub species were generally resistant to drought treatments (in terms of mortality, they likely did not experience ecological drought).

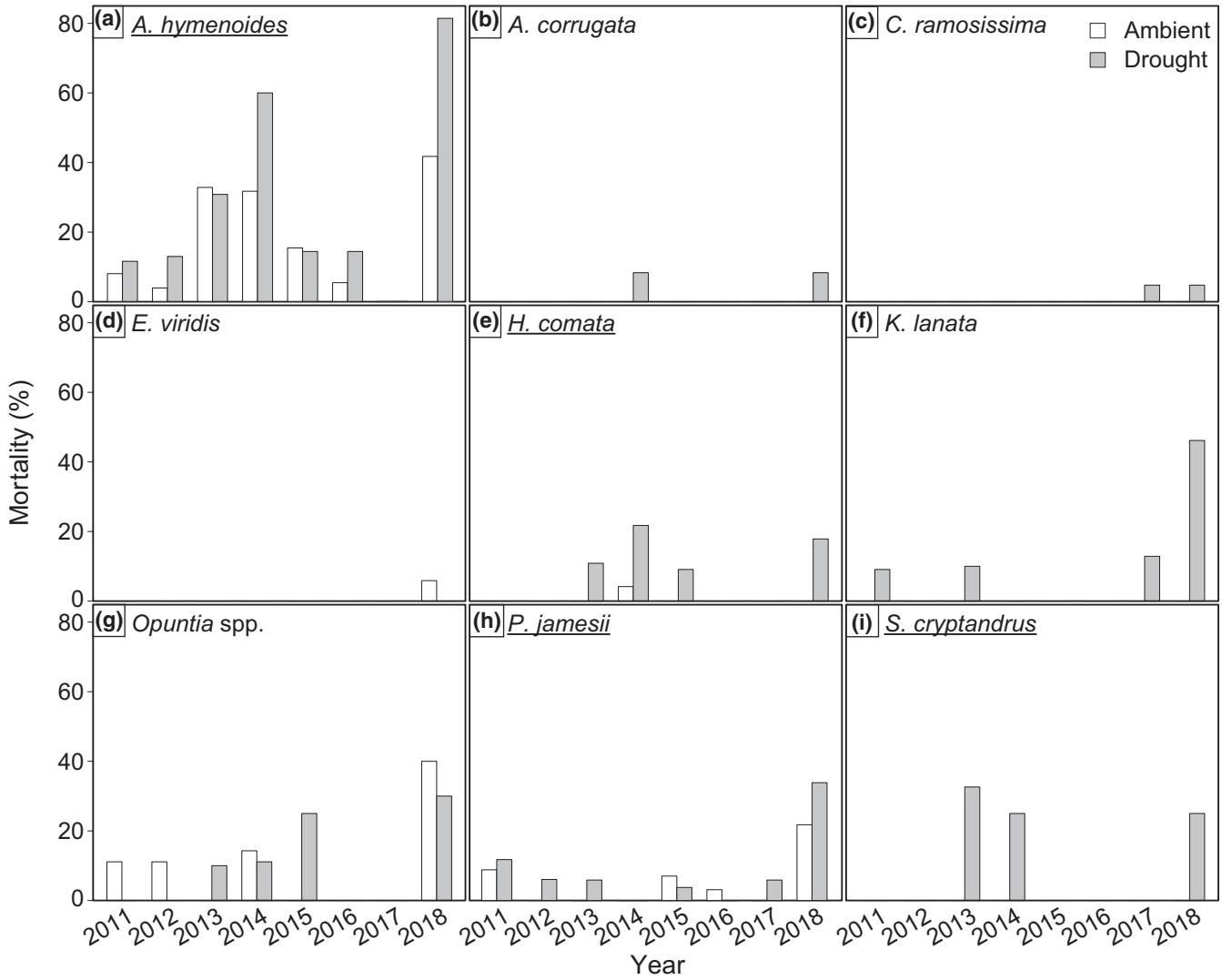

FIGURE 4 Species-level mortality as a percentage each year in ambient (white bars) and drought (gray bars) treatments (grass species names are underlined). Target species include (a) *Achnatherum hymenoides*, (b) *Atriplex corrugata*, (c) *Coleogyne ramosissima*, (d) *Ephedra viridis*, (e) *Hesperostipa comata*, (f) *Krascheninnikovia lanata*, (g) *Opuntia* spp., (h) *Pleuraphis jamesii*, and (i) *Sporobolus cryptandrus*

TABLE 5 Final species-level linear mixed-effects model results for fixed effects including treatment, year, parent material, and invasive species cover

	Treatment		Year		Parent material		Invasives cover	
Model	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Achnatherum hymenoides	**26.04 (1,70)**	**<0.0001**	**17.74 (7,259)**	**<0.0001**	0.50 (1,8)	0.51	**11.09 (1,259)**	**<0.01**
Atriplex corrugata	1.31 (1,21)	0.27	0.96 (7,153)	0.50	–	–	1.05 (1,153)	0.31
Coleogyne ramosissima	1.27 (1,39)	0.27	0.97 (7,315)	0.45	–	–	0.03 (1,315)	0.87
Ephedra viridis	1.06 (1,30)	0.31	0.94 (7,223)	0.47	–	–	0.07 (1,223)	0.79
Hesperostipa comata	**5.94 (1,51)**	**0.02**	**3.28 (7,305)**	**<0.01**	–	–	0.01 (1,305)	0.96
Krascheninnikovia lanata	**9.31 (1,20)**	**<0.01**	**4.21 (7,151)**	**<0.001**	2.23 (1,2)	0.27	0.98 (1,151)	0.32
Opuntia spp.	0.36 (1,16)	0.56	**3.08 (7,103)**	**<0.01**	–	–	0.02 (1,103)	0.89
Pleuraphis jamesii	**4.28 (1,488)**	**0.04**	**10.32 (1,488)**	**<0.0001**	2.83 (1,11)	0.12	0.84 (1,488)	0.36
Sporobolus cryptandrus	**7.00 (1,16)**	**0.02**	**2.00 (7,79)**	**0.06**	–	–	0.71 (1,79)	0.40

Note: *F* statistics including degrees of freedom (parenthetically) are reported with *p* values. Values showing significant differences at $\alpha = 0.05$ are shown in bold font.

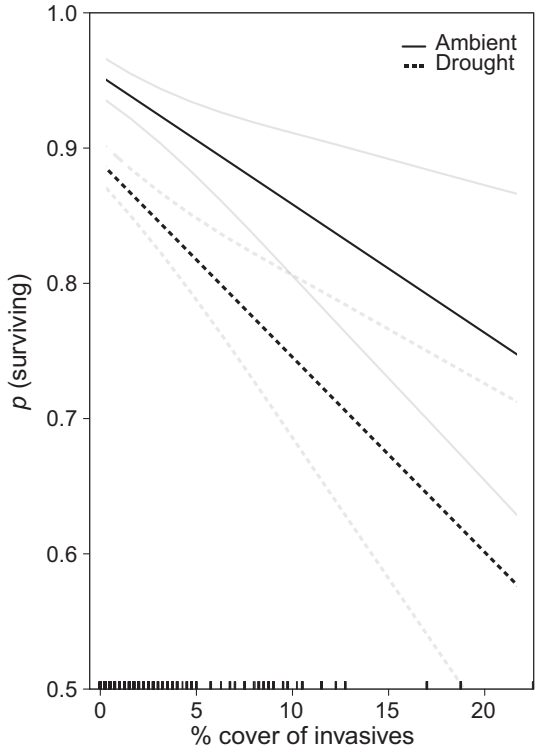

FIGURE 5 The probability (*p*) of surviving in relation to invasive species cover (%) in ambient (solid lines) and drought (dashed lines) treatments across all years and species. Probabilities are based on linear mixed model estimates with 95% confidence intervals plotted as gray lines. Tick marks indicate observed invasive species cover values. An interaction between treatment and year did not improve models and suggests mortality (especially of *Achnatherum hymenoides*; Table 5) was higher with increasing invasive cover regardless of treatment

Our experimental results are valuable not only because they represent a long-term, multispecies assessment of mortality across numerous common plant and soil types, but also because the data suggest important differences in mortality thresholds. Some species responded strongly to interannual climate variability under ambient conditions, with mortality exacerbated by experimental meteorological drought for several species (e.g., *A. hymenoides*, *H. comata*, *P. jamesii*). Other species experienced mortality only under the imposed experimental drought (e.g., *S. cryptandrus*), lending insight into more expansive changes to community composition with the more frequent and severe droughts expected in the Colorado Plateau's future (Cook et al., 2015).

Drought impacts differed widely from year to year, likely due to interannual variation in precipitation. Interannual climate variability is well-established as a major factor in explaining perennial species responses to drought (Anderegg, Anderegg, & Berry, 2013; Lopez & Kursar, 2007; McAuliffe & Hamerlynck, 2010; Vicente-Serrano et al., 2013), and here too, we observed large variation in mortality among years (Figure 2; Tables S2 and S3). A majority of studies use long-term monitoring data to estimate drought impacts on plant populations, most of which do not track individuals and sample only intermittently (e.g., Turner, 1990; Mueller et al., 2005; Okin, Dong, Willis, Gillespie, & MacDonald, 2018; but see Winkler, Conver, et al., 2018). Thus, there is a clear need to disentangle the effects of short-term climate variability (i.e., extreme drought events that may occur during a growing season) from chronic drought effects to predict future mortality events (Hawkes, 2000). Our long-term drought experiment is one of the first to track individuals of different species throughout a continuous period, capturing ambient changes as well as responses to chronic reductions in precipitation. The long-term experimental drought resulted in 30% mortality on average across species after 8 years of treatments, a stark difference from the less than 10% mortality observed in the first year of the experiment or the 2%–3% mortality during wetter years when treatments saw minimal effects. Even short-term drought experiments have shown strong effects on plant mortality (Adams et al., 2009; Hoover et al., 2015, 2017; Munson, Bunting, Bradford, Butterfield, & Gremer, 2018; O'Brien, Aviles, & Powers, 2018), but our study suggests that additional, and potentially cumulative effects, may go unnoticed without additional years of data.

The greatest mortality observed was for the C_3 grass *A. hymenoides*, which showed nearly 20% mortality in ambient treatments (Figure 3) and 50% increase in mortality with experimental drought imposed. These results complement long-term observational studies for the Colorado Plateau that suggest a strong decline of C_3 grasses such as *A. hymenoides* (Munson et al., 2011). *A. hymenoides* is a critical source of forage for domestic livestock and wildlife in the Colorado Plateau Desert, yet the results from our study suggest a low drought threshold for this plant, indicating the species may continue to see strong population declines in response to the increased drought predicted for the Southwest (Cook et al., 2015). This low tolerance may be the result of decreased physiological performance in response to drought that has been shown to ultimately reduce *A. hymenoides* carbon gain and decrease cover, and is likely related to the shallow root profiles of these graminoid species (Hoover et al., 2017; Wan, Sosebee, & McMichael, 1993).

Earlier results from our experiment suggested C_4 grass species may be resistant to drought impacts (Hoover et al., 2015, 2017), but additional years of treatments now reveal that all the dominant native grass species studied here are susceptible. This has important implications for the wildlife and livestock that depend upon grass as forage. The eventual mortality of *P. jamesii* after 8 years of the drought treatments suggest that either a threshold was crossed since the years included in the previous studies (2014) and the years include here (up through 2018) or the cumulative effects of chronic drought required an additional four years to be revealed (Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007; Ogle & Reynolds, 2004; Pedersen, 1998). *S. cryptandrus*, another common C_4 grass, was relatively resistant to drought, both natural and experimental, except in 3 years where drought treatments resulted in marked plant mortality. *S. cryptandrus* is well known to be highly drought tolerant (Mueller & Weaver, 1942; Teague, Dowhower, & Waggoner, 2004; Wan et al., 1993) and the fact that *S. cryptandrus* did not show mortality in ambient treatments and that mortality occurred in drought treatments only in below average annual precipitation years (Figure 2; Tables S2 and S3) suggests a *S. cryptandrus* drought threshold approximates current conditions.

Unlike our target native grass species, four of the five shrub species we studied showed little or no mortality in response to meteorological drought, even after 8 years of treatment. This confirms expectations based on previous observational studies that shrub presence will likely continue to increase in the Southwest (Archer et al., 1995; Munson et al., 2011), though drought treatments are causing some declines in shrub cover in this study (Hoover et al., 2015). Shrubs in general are more drought tolerant than grass species due to their more extensive and deeper root structures (Comstock & Ehleringer, 1992; Ehleringer & Cook, 1991; Toft, 1995) and, thus, can likely access deeper soil water during periods of meteorological drought.

Patterns of shrub expansion are not confined to the Colorado Plateau Desert and have been documented in semiarid and arid systems across the globe (D'Odorico et al., 2012; Fensham et al., 2005; Houghton, Hackler, & Lawrence, 1999; Moleele, Ringrose, Matheson, & Vanderpost, 2002; Throop & Archer, 2008). In our current study, *E. viridis* was among the species most resistant to our drought treatments, a finding also supported by observational studies (Munson et al., 2011). Interestingly, *E. viridis* is the only gymnosperm in our study, with evergreen stems, different hydraulic architecture than the other shrubs (Tyree, Davis, & Cochard, 1994), as well as lower transpiration rates (Comstock & Ehleringer, 1992). *E. viridis* also maintains a distribution into substantially warmer, drier regions than our other focal species (Hollander & Vander Wall, 2009). These traits may give *E. viridis* and other shrubs that can remain active all year (e.g., *C. ramosissima*; Summers et al., 2009; Meyer & Pendleton, 2015) a competitive advantage over other species that are dormant during much of the winter (Lin, Phillips, & Ehleringer, 1996).

We saw no signs of *C. ramosissima* experiencing ecological drought in our treatments. This drought resilience is likely explained by the species' relatively extensive rooting profile allowing it to access reserves of soil moisture, especially in deeper soils (Ehleringer, Phillips, Schuster, & Sandquist, 1991; Lei & Walker, 1997; Wallace & Romney, 1972). *C. ramosissima* also has the ability to split into clonal fragments as a potential mechanism to avoid whole-plant mortality (Schenk, 1999) and this may further explain results from our experiment. Although a majority of *C. ramosissima*'s roots are located at 10–30 cm depth (Bowns, 1973), our plot design did not contain infrastructure to isolate plots below this lower depth and, thus, individuals may have been able to access available soil moisture not influenced by our treatments. Shrubs themselves have differing rooting profiles that can confer an advantage or disadvantage during periods of drought; including the ability to osmotically adjust tissues to prevent desiccation or cavitation (Hacke, Sperry, & Pittermann, 2000; Scholz, Bucci, Arias, Meinzer, & Goldstein, 2012). This may explain the mortality observed in *K. lanata*, which has the shallowest rooting profile of the shrubs we studied (Bonham & Mack, 1990). Little is known about the physiological ecology of *K. lanata* but, similar to most of the grass species we studied, this shrub serves an important forage crop in much of the western United States. (Wang, Bai, Low, & Tanino, 2006). *K. lanata* was resistant to treatments through the first 6 years of our experiment but experienced significant mortality in drought treatments in 2017 and 2018, potentially evidencing delayed drought-induced mortality (Nepstad et al., 2007; Ogle et al., 2015; Ogle & Reynolds, 2004) as was seen in our C_4 grass species.

Importantly, we also found that mortality was heightened in the presence of invasive species, with increasing rates of mortality occurring with increasing invasive species cover (Figure 5). The most common invasive plant at our study sites was *Bromus tectorum* (cheatgrass), which has an overlapping growth and flowering phenology with *A. hymenoides* (DeFalco, Fernandez, & Nowak, 2007). *B. tectorum* abundance may have resulted in increased competition for limited available soil moisture or other resources that germinating *B. tectorum* seedlings were able to capture in our drought treatments, especially in 2013–2014 and 2018 when mortality was highest in *A. hymenoides*. Indeed, during drought, reduced access to such resources caused by increased competition with invasive plants could quickly push plants past a mortality threshold (Everard et al., 2009). It is important to note that our inference for invasive effects is somewhat limited due to the patchy nature of invasive species in our study plots. Despite this, the relationships between invasion and mortality for some species were notably strong. Annual invasive species in the southwest United States have been shown to be more drought tolerant than natives due to their ability to utilize water resources faster and more efficiently (DeFalco et al., 2003; Holzapfel & Mahall, 1999; Kimball, Angert, Huxman, & Venable, 2011). As a result, invasives may be better equipped to positively respond to climate change while inherently being well adapted to climate variability through avoidance strategies (Diez et al., 2012; Seabloom, Harpole, Reichman, & Tilman, 2003; Smith et al., 2000). Based on the strong patterns observed here and the likelihood of enhanced invasive success and competition with drought, the interactive relationships between invasive species, native plant strategies, and drought warrant further inquiry in drylands.

We also assessed the potential role of biocrusts in affecting plant responses to drought, but did not observe any effects of biocrusts in our experiment. Due to the grazing history of our sites, most had soils dominated by bare ground and poorly developed biocrusts (i.e., low biomass of lichens and moss; Belnap, 1995, 2002). A long history of surface disturbing land uses on the Colorado Plateau Desert has resulted in the common occurrence of these poorly developed biocrust communities (Duniway, Geiger, Minnick, Phillips, & Belnap, 2018). In the data analyzed here, there was not enough variation in biocrust cover or developmental stage to determine their functional role in drought mitigation or exacerbation. Biocrusts have the potential to help dictate system responses to climatic change (Reed et al., 2016) and future work is needed to elucidate these interactions.

In addition to evaluating biotic interactions, we observed abiotic influences on plant mortality. For example, models that included parent materials were better at predicting mortality across all species; however, this relationship only slightly improved predictive power. Other studies have shown that soil type and parent material can interact with drought to determine species responses (Harper, Smettem, Carter, & McGrath, 2009; Koepke et al., 2010;

Sperry & Hacke, 2002), but none of our species-level models revealed a clear relationship between parent material and mortality. We attribute this weak effect of parent material (and no detectable importance of soil depth and elevation) to the deterministic association of soils and climate in structuring species and community distributions on the Colorado Plateau (Duniway et al., 2016). That is, species are generally well adapted to the soils and climate at which they occur, even under the long-term moderate drought imposed here. This is similar to previous results that show parent materials are important for mitigating drought in our study area, but the effect size of soils and parent material is smaller than expected (Hoover et al., 2015, 2017).

Overall, we show that drought-induced mortality of several dominant plant species in the Colorado Plateau Desert will likely occur in response to future climates and will vary substantially by species. Our results suggest that major shifts in community composition will likely continue in response to drought and that native perennial grass species may be replaced by other functional types, including dominant shrubs or invasive annuals in the Colorado Plateau Desert. We also show that substantial mortality has already occurred in response to recent, ambient drought conditions: native grass species were particularly sensitive to both ambient and long-term experimental drought, which has potential consequences for shifting ecosystem function and carbon balance in this water-limited system (Gitlin et al., 2006; Scott, Biederman, Hamerlynck, & Barron-Gafford, 2015). This predicted change also has implications for resource managers selecting native plant species to use for restoration and reclamation purposes (Doherty, Butterfield, & Wood, 2017; Shackelford et al., 2013; Winkler, Backer, et al., 2018) as restoration efforts using perennial grasses may have limited success in drier climates compared to those using shrubs. Future studies would benefit from focusing on the interactive role abiotic and biotic factors play in determining plant population responses to drought-induced mortality. Studies are also needed to uncover the role of ecological memory of past stressors in determining current and future responses (Ogle et al., 2015). Additionally, studies on the Colorado Plateau should examine the potential interactive effects of drought and warmer temperatures that have been shown in some systems to significantly affect mortality and system response (Adams et al., 2009; Breshears et al., 2005; Grossiord et al., 2018).

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ORCID

Daniel E. Winkler https://orcid.org/0000-0003-4825-9073
David Hoover https://orcid.org/0000-0002-9326-9791

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SUPPORTING INFORMATION

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

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