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LETTER

Small-scale water deficits after wildfires create long-lasting ecological impacts

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Abstract

Ecological droughts are deficits in soil–water availability that induce threshold-like ecosystem responses, such as causing altered or degraded plant-community conditions, which can be exceedingly difficult to reverse. However, 'ecological drought' can be difficult to define, let alone to quantify, especially at spatial and temporal scales relevant to land managers. This is despite a growing need to integrate drought-related factors into management decisions as climate changes result in precipitation instability in many semi-arid ecosystems. We asked whether success in restoration seedings of the foundational species big sagebrush (*Artemisia tridentata*) was related to estimated water deficit, using the SoilWat2 model and data from >600 plots located in previously burned areas in the western United States. Water deficit was characterized by: (1) the standardized precipitation-evapotranspiration index (SPEI), a coarse-scale drought index, and (2) the number of days with wet and warm conditions in the near-surface soil, where seeds and seedlings germinate and emerge (i.e. days with 0–5 cm deep soil water potential >−2.5 MPa and temperature above 0 °C). SPEI, a widely used drought index, was not predictive of whether sagebrush had reestablished. In contrast, wet-warm days elicited a critical drought threshold response, with successfully reestablished sites having experienced seven more wet-warm days than unsuccessful sites during the first March following summer wildfire and restoration. Thus, seemingly small-scale and short-term changes in water availability and temperature can contribute to major ecosystem shifts, as many of these sites remained shrubless two decades later. These findings help clarify the definition of ecological drought for a foundational species and its imperiled semi-arid ecosystem. Drought is well known to affect the occurrence of wildfires, but drought in the year(s) after fire can determine whether fire causes long-lasting, negative impacts on ecosystems.

Introduction

Moisture deficit is one of the key ways that climate variability affects ecological processes, populations, community composition and successes or failures of land management interventions, such as restoration of native vegetation. However, there is little guidance on how to determine when water deficit becomes ecologically impactful and thus constitutes 'ecological drought' (Slette *et al* 2019, Zang *et al* 2019). Drought has traditionally been defined as a deficit in precipitation relative to evapotranspiration (i.e. meteorological drought), shortage of water pools on earth (i.e. hydrological drought), or water deficits affecting human needs (i.e. agricultural or socioeconomic drought; Wilhite and Glantz 1985, Crausbay *et al* 2017). Ecological drought is a deficit in water availability that causes ecosystems to cross adaptive

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thresholds, resulting in major changes in their structure and function (Crausbay *et al* 2017, Snyder *et al* 2019). Even though the duration and magnitude of a water deficit causing threshold-like change must be known for a particular ecosystem or community in order to designate and predict ecological drought, there are few examples of ecological drought being resolutely (i.e. highly-resolved to a specific time, soil-depth, and soil–water availability) quantified in ways that are spatially and temporally robust and thus, generalizable.

'Drought' has traditionally been identified by meteorological or hydrological drought indices such as Palmer Drought Severity Index (PDSI), Standardized Precipitation Index (SPI), and more recently, by the Standardized Precipitation Evapotranspiration Index (SPEI) (Alley 1984, Beguería *et al* 2010, Vicente-Serrano *et al* 2012). Vicente-Serrano *et al* (2012) empirically compared these three indices to one another and determined that SPEI was more flexible on shorter time scales than PDSI (i.e. monthly) and it could better identify drought impacts than SPI, owing to SPEI's inclusion of water outputs in evapotranspiration. However, quantifying ecological drought using site-level condition data (e.g. edaphic properties, vegetation structure, etc) from meteorological/hydrological drought indices can result in mischaracterizing the severity and impact of ecological drought.

Drought indices have been found to be correlated with certain coarse-scale shifts in ecosystem productivity, such as annual net primary productivity (ANPP) at the regional scale, which has provided understanding of climate effects on seasonal plant responses (Ruppert *et al* 2015). However, temporary reductions in ecosystem productivity do not constitute threshold-like changes if they are reversible, which is often the case when vegetation composition remains intact. Therefore, these types of changes do not qualify as ecological drought. In contrast, loss of dominant species in a plant community does constitute a threshold change if the loss is permanent or long-term (Bestelmeyer *et al* 2018, Law *et al* 2018). Drought indices do not relate well at the individual plot or local community scale, and thus are poor predictors of within-season plant responses and demographic processes such as germination, establishment, or mortality, which can lead to restructuring of plant communities. To better define and understand ecological drought, we must first identify the ecologically-relevant and biophysically meaningful metrics of water deficit that lead to demographic success or failure of a given plant species.

One biophysically relevant metric that directly relates to water deficit and plant survival is water potential. This metric provides a concise means of quantifying the availability of water to plants and other organisms (Campbell and Norman 1998), especially when it is measured at specific places and times where plants have critical interactions with soil and air (Breshears *et al* 2009, Roundy *et al* 2018). Using soil–water potential to define and quantify ecological drought should facilitate detection of water availability thresholds that influence key plant demographic transitions. Several studies have addressed threshold responses to variability in soil–water potential at the individual plant-, plot-, or site-level (e.g. Adams *et al* 2009, Breshears *et al* 2009, Roundy *et al* 2018), but few of these studies addressed threshold responses at the population-level (i.e. whole-stand) or across a species' range.

Ecological droughts may be most likely to induce rapid change in plant communities recovering from disturbance, whether the recovery is natural or augmented by restoration. In certain ecosystems, plant germination and initial seedling survival are both sensitive to water deficits. These demographic bottlenecks can limit post-restoration plant establishment, particularly in drylands such as sagebrush steppe (James *et al* 2011, 2019, Kildisheva *et al* 2016). Restoration seedings in sagebrush ecosystems often fail in part due to soil–water deficits (i.e. ecological drought) during critical germination or emergence periods (Gornish *et al* 2015, Germino *et al* 2018). However, few studies have quantified the daily soil-surface conditions that most likely affect the demographic success of seeds and seedlings (but see Roundy *et al* 2018, James *et al* 2019 for examples involving grass species). Soil-surface moisture can become uncoupled from weather station-measured rain, atmospheric vapor pressure deficit, and bulk soil volumetric water content due to solar and terrestrial radiation balances at the soil surface—especially during the spring plant-emergence period. Nonetheless, current approaches for assessing demographic responses to soil–water availability tend to use climate variables such as annual evapotranspiration, seasonal water supply, or climatic water deficit (Dilts *et al* 2015). To date, no studies have attempted to define or quantify ecological drought, which could be a major driver in restoration failure or success.

Weather and 'drought' impacts on restoration are of particular interest in western North America, where only about half of the ~1000 000 km^2 once dominated by big sagebrush (*Artemesia tridentata* Nutt) and perennial bunchgrass communities remains. Sagebrush populations or stands have been steadily extirpated when wildfires, induced by exotic annual grasses, burn repeatedly and at increasingly larger extents (Brooks *et al* 2004, Balch *et al* 2013). Without major intervention, the remaining sagebrush steppe is at risk of ecosystem degradation and conversion to annual grasslands. Managers of these landscapes often seed after fire with mixtures of sagebrush and other shrubs, perennial grasses, and forbs to stabilize the soil, compete with exotic annual grasses, and rehabilitate wildlife habitat (Pilliod *et al* 2017b). These restoration efforts and investments have been substantial in recent decades due to increased fire frequencies, with hundreds of thousands of hectares seeded annually at large

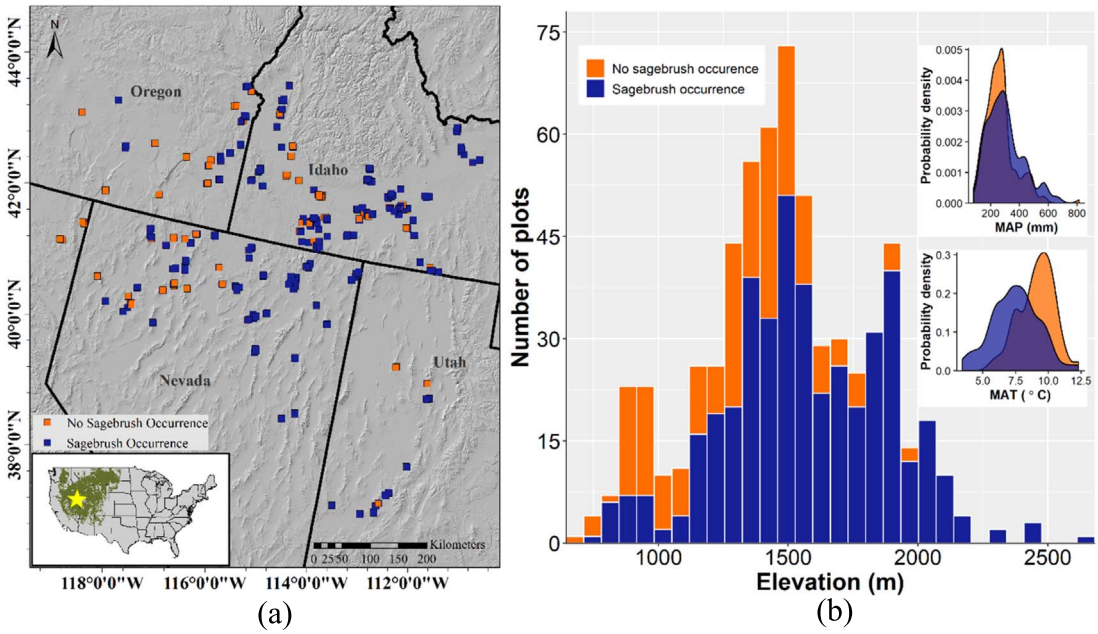

Figure 1. Map of 627 sagebrush sampling sites in the western United States of America (a), distribution of elevation (stacked histogram), mean annual precipitation (MAP) and mean annual temperature (MAT) (b). Sites with sagebrush present are in blue and sites where sagebrush was not detected are in orange.

costs (Pilliod *et al* 2017b). Thus, understanding the drivers that lead to seeding success is a priority for land management organizations in dryland ecosystems as outlined in the US Integrated Rangeland Fire Management Strategy (http://integratedrangelandfiremanagementstrategy.org/).

Here, we use a data set of sagebrush occupancy, SPEI, and simulations of soil–water potential from 627 plots that were seeded after wildfires across the Great Basin over the last ~40 years (figure 1) to investigate the influence of ecological drought on restoration outcomes. We asked whether successful and unsuccessful sagebrush seedings (i.e. plots with and without sagebrush years to decades after seeding) could be related to either the SPEI index or to soil–water potential in the specific times and locations (soil surfaces) where seeds and seedlings emerge and face strong selection and mortality. We focus on the month of March, when sagebrush typically germinate and emerge, and when soil water is typically at or below soil–water potential thresholds of −2.5 MPa and soil temperatures are typically above 0 °C (Meyer and Monsen, 1992, DiChristina and Germino 2006, Schlaepfer *et al* 2014). To further guide our attempt to quantify ecological drought we hypothesized that: (1) SPEI, a commonly used drought index, would be a useful predictor of plot-level big sagebrush establishment, which we infer based on its presence years after fire and seeding, and (2) soil–water potentials, modeled from weather data, provide a more robust means of quantifying the magnitude and duration of water deficit that constitutes ecological drought for sagebrush.

Methods

Plot locations and sampling

Sagebrush abundance was measured between 2011 and 2016 on 627 plots across the Great Basin (figure 1). Each plot burned once between 1976 and 2008 prior to our sampling. Plots were seeded with big sagebrush in the fall or winter after fire, as documented in federal agency records contained in the Land Treatment Digital Library (Pilliod and Welty 2013). Of the 627 plots, 452 were placed in randomly selected in burned-treated areas and the other 175 were placed in sites identified by the Bureau of Land Management cooperators as having successful post-restoration sagebrush establishment. We used an additional 127 random plots that burned once between 2009–2015 and were subsequently seeded during the following fall or winter with big sagebrush for statistical model validation.

Three 50 m AIM style belt transects were used to quantify sagebrush density in each plot (Herrick *et al* 2005), although the analysis here focuses on sagebrush occupancy (present or not detected). The central start point was randomly determined and the three transects proceeded away from this central point at an event 120° separation for a length of 50 m each. The width of the belt transects was variable to provide a balance of sampling time allocated per plot relative to the relative abundance of sagebrush. Transects were set at 6 m wide by default, but widths were reduced to 4 m, 2 m, or 1 m if observers expected to detect more than 20, 50, or 70 individual plants per transect, respectively.

SPEI calculation

Pre-emergence drought severity was estimated at every plot using the SPEI (Vicente-Serrano et al 2010, Beguería and Vicente-Serrano 2013) for the periods including 1, 2, 3, and 6 months prior to seedling emergence, which was assumed to be March. SPEI is calculated on a monthly basis from a climatic water balance that incorporates moisture deficit or surplus across a user-defined time scale and is adjusted to a log-logistic probability distribution. The SPEI averaging periods were determined from analyses of SPEI computation lengths, soil depths and corresponding R^2 values (unpublished data). SPEI was calculated at each plot using the 'SPEI' package in R (Beguería and Vicente-Serrano 2013), using values of precipitation and potential evapotranspiration extracted from the University of Idaho Gridded Surface Meteorological Dataset (gridMET; Abatzoglou 2013) for 1979–2014 at a 4 km resolution. Because the meteorological data are only available from 1979–2014, we were unable to use the 6 earliest burned plots for this analysis; hence our sample size was $N = 621$ for the SPEI-based model.

Ecohydrological modeling

Soil–water availability was simulated from measured and estimated inputs for each plot using SOILWAT2 (Version 3.2.2, Schlaepfer and Murphy 2018), a daily time-step, multiple soil layer, process-based, simulation model of ecosystem water balance (Schlaepfer *et al* 2012, Bradford *et al* 2014). SOILWAT2 uses weather data and soil properties (i.e. texture) at each soil layer, and monthly vegetation (live and dead biomass, litter, and active root profile) to simulate daily water balance processes. We used the Livneh (1915–2008, 6 km resolution) and PRISM (2009–2015; 4 km resolution) daily weather datasets to extract daily temperature (minimum and maximum) and precipitation, as well as the monthly normals of cloud cover, wind speed and relative humidity, which were downscaled to daily values for input into SOILWAT2 (Livneh (2014), PRISM Climate Group 2017). Livneh data were used for the 627 model development plots and PRISM data were used for the 127 validation plots so that weather data corresponded with respective post-fire time periods. Plot specific soil properties and characteristics were obtained for each plot through a combination of field sampling and use of the SSURGO national database where field sampling data were not available (Soil Survey Staff 2017). The field sampling for soil data consisted of recording soil depth and determining soil texture for each plot (Barnard *et al* 2019). We analyzed soil texture at 0–10 cm depth for 335 plots in this study using the Bouyocous hydrometer method including peroxide pre-treatment and extended settling time for detection of clays. At each plot four soil subsamples were taken for analysis, which were then averaged together for input into SoilWat2. Nearly all sagebrush establishment after fire results from seeds that germinate during spring (March) in the year after fire, when adequate surface moisture and suitable air and soil temperatures coincide and cover of other plant species is still absent or scarce (Schlaepfer *et al* 2014, Germino *et al* 2018). Our analyses focused on this time period (March) and assumed 0% cover of other plant species. We also focused on the thin, near-surface soil-layer (0–5 cm) where sagebrush seeds germinate and emerge.

Analyses

All analyses and figures were completed in RStudio (R Core Team 2019). SPEI is calculated on a monthly basis, meaning that the calculation considers at least the previous 30 d. Thus, to determine if sagebrush occurrence (presence or not detected) could be explained by variation in SPEI among the plots, we needed to consider the duration for which SPEI was calculated prior to the presumed March germination and emergence period. We ran a binomial generalized linear mixed model (GLMM) to relate sagebrush occupancy (binary response variable) to the SPEI values (continuous, fixed effects predictor variable) for each SPEI monthly calculation (1, 2, 3, or 6 month(s)), with plot ID as a random effect ($\alpha = 0.05$; lme4 R package, Bates *et al* 2015).

The second analysis was a logistic regression GLMM of the 627 plots to relate sagebrush occupancy (response variable) to March near-surface soil–water potentials, March soil temperatures, and elevation (explanatory variables). Soil–water potential and soil temperature were each averaged across March to provide mean March values for each plot. We included plot ID as a random effect in the binomial logistic regression GLMM ($\alpha = 0.05$; lme4 R package). Results from this model were used to predict the probability of sagebrush establishment using the 127-plot validation dataset.

In the final analysis, we used a gamma log-link function GLMM to assess the relationship between simulated soil–water potentials (absolute values of SWP as the response variable) and the fixed effects of sagebrush occurrence (binary, present or not detected), soil temperature, and elevation (both scaled to improve model convergence), plus the random effects of plot ID and Julian calendar day in March for which soil water data were simulated. The plot ID and calendar day factors were included to explain variability across space and time. We parameterized the GLMM with data from all 627 plots and then validated the model using our 127 validation plots and the same gamma log-link GLMM structure. Due to the complex model covariance structure we could not predict the probability of each validation plot being occupied using the original GLMM, however were able to assess whether the GLMM model estimates, levels of significance, and model residuals were similar when

parameterized with validation plots (Wegner and Olden 2012).

We quantified the duration of ecological drought using two different approaches. First, we calculated the mean temperature and water availability for each day in March, separately for plots that were occupied by sagebrush and for plots where sagebrush was not detected. Second, for each plot, we tallied the number of days with soil temperatures above an *a priori* threshold of 0 °C and soil water potentials less than an *a priori* threshold of −2.5 MPa. These *a priori* thresholds were based on thermal requirements for germination (Meyer and Monsen 1992) and based on xylem water potentials that cause net photosynthesis to be zero or less in sagebrush seedlings establishing in the first-year post-fire (DiChristina and Germino 2006). We quantified ecological drought for the 627 model development plots as well as the 127 validation plots and examined the difference in number of days between the two data sets.

Results

SPEI did not differ between plots based on sagebrush occupancy, regardless of whether SPEI was calculated using values from 1, 2, 3, or 6 m prior to the March post-fire (figure 2).

Sagebrush was present at 69% of the 627 plots used to parameterize the models and at 57% of the 127 validation plots. In the logistic regression model, mean March soil–water availability was not a significant predictor of sagebrush occurrence (figure 3). However, increases in soil temperature significantly reduced the probability of sagebrush establishment (figure 3; $P = 0.002$) and sites with higher elevation had significantly greater probability of sagebrush occurrence (figure 3; $P < 0.001$). Moreover, we found that *daily* soil–water availability at the soil-surface during the narrow March window following each post-fire seeding was a strong predictor of sagebrush occupancy (figure 4; $P < 0.001$; table 1). Increased soil temperatures reduced soil–water availability, whereas increases in elevation increased soil–water availability (table 1; $P < 0.001$ and $P < 0.001$ respectively). Running the same gamma log-link GLMM with the 127 validation plots resulted in similar coefficients and model residuals as were obtained for the full model using the 627 plots. Plots occupied by sagebrush had greater soil–water availability than unoccupied plots (figure 4; $P = 0.046$; table 1), and soil temperature was negatively related to soil–water availability (figure 4; $P < 0.001$; table 1). Elevation was not a significant predictor in the gamma log-link GLMM parameterized with the 127 validation plots, though elevation was a significant factor in the GLMM parameterized with the 627 plots. The explained variance improved for the 127 validation plots compared to the 627 plots ($R^2 = 0.35$, $R^2 = 0.13$ respectively; table 1).

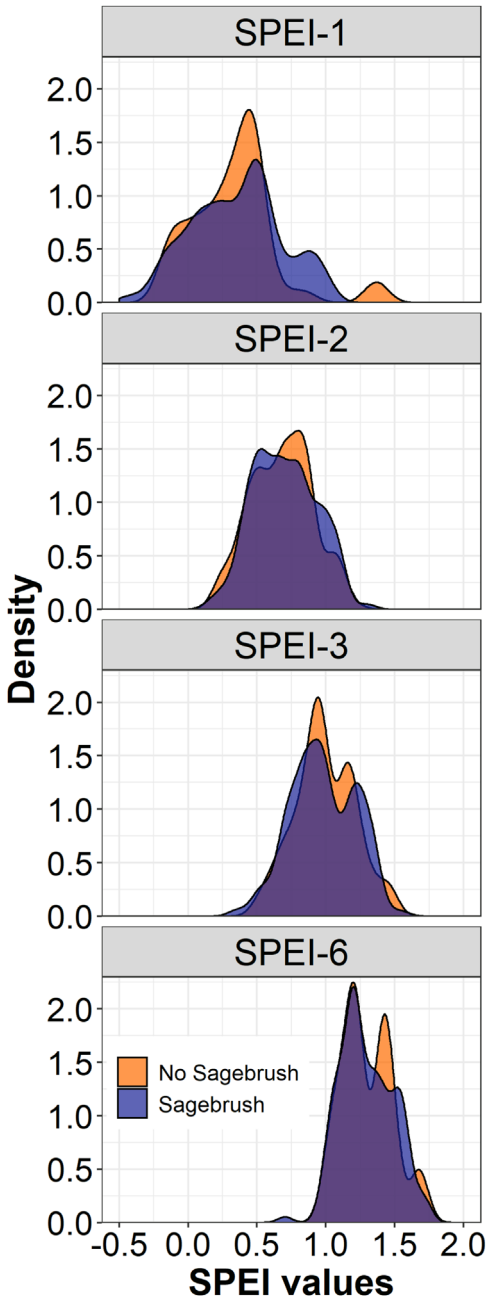

Figure 2. Density of plots for each SPEI (standardized precipitation evapotranspiration index) value for sites with sagebrush present (blue) and sites with sagebrush not detected (orange). Four different antecedent timescales of SPEI relative to March were calculated (1, 2, 3, 6 months).

Of the 627 plots, those with sagebrush present had an average of 23 d during the March following fire and seeding in which mean daily water availability and temperatures of soil were >−2.5 MPa and >0 °C, respectively, compared to an average of 16 d for plots where sagebrush was not detected ($\Delta = 7$ d). In contrast, analysis of our 127 validation plots revealed that

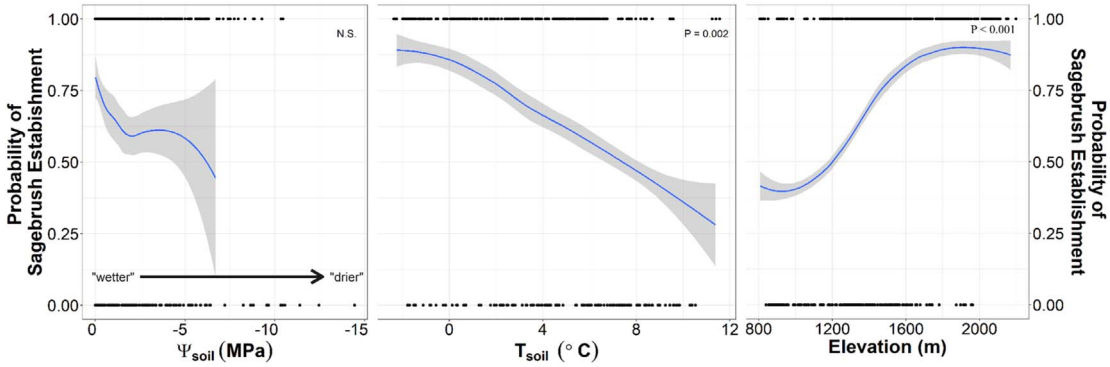

Figure 3. Probability of sagebrush seedling establishment as a function of monthly soil–water availability, soil temperature and elevation. Gray region in the 95% CI and points show data used to fit the model.

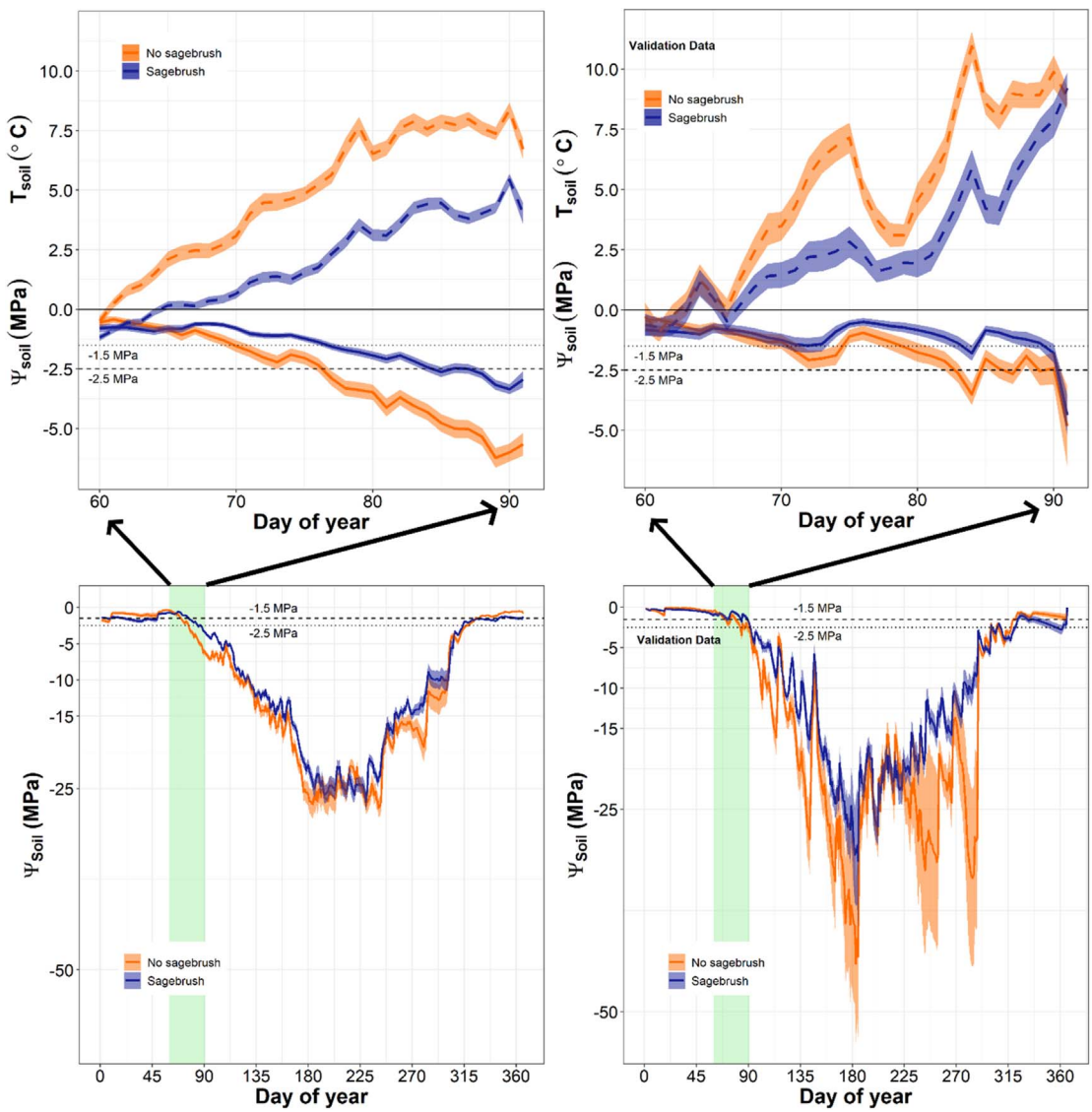

Figure 4. Mean differences in water potential (lower panels and lower half of top panels) and temperature (top of upper panels) in the soil surface (0–5 cm) in the year following fire and seeding, for sites that did or did not have sagebrush during observations made in 2011–2016) (blue and orange, respectively). The green box indicates the critical germination and emergence period in March, which is zoomed into in the top panels. Two water potential thresholds are highlighted, including the nominal permanent wilting point (−1.5 MPa), and the point at which photosynthesis in seedlings ceases (−2.5 MPa). In the upper panels, solid lines represent soil–water potentials and dashed lines are soil temperatures. The two panels on the left represent 627 plots, while the two right panels represent 127 plots used for validating statistical models.

Table 1. Two generalized mixed-effects models: (1) logistic regression GLMM with sagebrush presence as the response variable; (2) Gamma log-link GLMM with soil–water availability as the response variable. The gamma log-link GLMM has two datasets present: 1) original data that had 627 plots, and (2) validation data that had 127 plots. To compare effectiveness of the GLMM an R^2 value is listed. Model variable significance is represented through bolded values ($\alpha = 0.05$).

		Estimate	Std. error	*P* value	R^2
Logistic regression GLMM					
Response variable: sagebrush presence					
Original data ($N = 627$)					
	(Intercept)	**1.49**	**0.21**	**< 0.001**	
	Soil–water availability	0.04	0.05	0.402	
	Soil temperature	**−0.14**	**0.04**	**0.002**	
	Elevation	**0.74**	**0.15**	**< 0.001**	
Gamma log-link GLMM					
Response variable: soil–water availability					
Original data ($N = 627$)					0.13
	Intercept	**−0.71**	**0.20**	**< 0.001**	
	Sagebrush Present	**−0.67**	**0.19**	**< 0.001**	
	scaled Soil Temperature	**0.70**	**0.01**	**< 0.001**	
	scaled Elevation	**−0.45**	**0.09**	**< 0.001**	
Validation data ($N = 127$)					0.35
	Intercept	−0.50	0.27	0.064	
	Sagebrush Present	**−0.68**	**0.34**	**0.046**	
	scaled Soil Temperature	**0.56**	**0.03**	**< 0.001**	
	scaled Elevation	−0.30	0.17	0.076	

plots where sagebrush was present averaged 26 d meeting these criteria, compared to an average of 24 d for plots where sagebrush was not detected ($\Delta = 2$ d).

Discussion

Defining and then quantifying ecological drought requires relating soil–water availability to plant responses, and here we demonstrate this using a large dataset of post-fire seeding outcomes for big sagebrush in the Great Basin. Counter to expectations, we found that early spring SPEI did not predict post-fire and restoration sagebrush occupancy (figure 2). Thus, we conclude that SPEI is likely unsuited to quantify ecological drought for our application. However, in support of our second hypothesis, daily soil–water availability during March, a direct measure of water availability for plants, was useful in quantifying ecological drought as it pertains to sagebrush in the Great Basin (figure 4, lower panel). Daily soil–water availability combined with soil temperature was important for understanding when ecological drought conditions were met (figure 4 upper panel), whereas similar metrics, measured on a monthly-scale, were not predictive (figure 3). To our knowledge, this is the first time that daily soil–water availability and soil temperature have been used to identify the duration (i.e. less than 7 d) of water deficit capable of leading to a demographic bottleneck of sagebrush establishment, ultimately qualifying as an ecological drought. The influence of short-term ecological drought on sagebrush restoration success has clear implications for understanding how climate change may affect sagebrush population dynamics in the Great Basin (Shriver *et al* 2019).

Ecological droughts are often thought of in terms of months or years rather than days. However, more frequent, short-term droughts can have profound negative impacts on plant survival (Adams *et al* 2009). Although we assessed sagebrush occupancy years later, our data suggest that initial sagebrush germination and emergence success is dictated by daily water availability and temperatures of soil in the first March post-fire. Our results are similar to those of James *et al* (2019), who found increased soil temperatures reduce the establishment of seedlings in the Great Basin (figure 3). Similarly, James *et al* (2019) and Young *et al* (2019) also did not find a correlation between a climatic drought variable, monthly climatic water deficit (CWD = potential evapotranspiration/actual evapotranspiration), and seedling establishment (figure 2). Climatic variables (i.e. those based on monthly or yearly timeframes) may be too coarse for predicting seedling establishment because of the narrow temporal windows associated with establishment. This suggests that daily environmental conditions are needed to understand seedling bottlenecks.

In the Great Basin, soil water-availability during early spring is critical for native plant species to germinate, emerge, and establish. Water deficits during this critical time period results in decreased establishment success (James *et al* 2011, Roundy *et al* 2018). In the near-future (i.e. 2050), climate conditions are

predicted to include increases in daytime minimum temperatures by 2 °C as well as increases in winter precipitation in the form of rain (Palmquist *et al* 2016, Brabec *et al* 2017, Snyder *et al* 2019). Our results suggest that a 2 °C increase in daytime minimum temperatures would cause a ~13% reduction in sagebrush establishment probability (figure 3). An increase in springtime temperatures would also dry soil surfaces faster, potentially leading to establishment failure (current study; Shriver *et al* 2018) if increased temperatures are not accompanied by increased March precipitation. Warmer and wetter winter conditions will also favor exotic-annual grass establishment (Concilio *et al* 2013, Compagnoni and Adler 2014), which can increase wildfire prevalence in the Great Basin (Abatzoglou and Kolden 2011, Bradley *et al* 2016, Pilliod *et al* 2017a).

Climate change and specifically drought will impact both fire occurrence and perhaps more critically, ecosystem recovery, especially reestablishment of foundational perennial species, in the Great Basin. Germination and emergence will likely occur earlier in the late winter or early spring, potentially shifting the 'window' of establishment when water-availability and temperature conditions are each more suitable. However, it is difficult to predict if the temporal 'window,' during which suitable temperature and water availability overlap for seedling establishment, will become longer or shorter. Warmer winter conditions could eliminate snow from the soil surface, causing more, or stronger, freeze-thaw events that reduce seedling establishment because of frozen soils and a lack of available soil–water (Gornish *et al* 2015). Thus, restoration of semi-arid landscapes may become even more necessary (because of reduced natural re-establishment) and more difficult because of climate change, though improvements in weather forecasting can help mitigate the impacts on restoration investments (Hardegree *et al* 2018). Understanding how ecological droughts impact different plant life stages and species is critical for determining restoration potential for sites. We suggest that ecologists evaluate the use of soil–water availability in appropriate spatio-temporal scales, especially at time periods when critical demographic transitions occur, as a means to define and quantify ecological drought. This approach gives mechanistic insights into how plant populations and communities will change because of soil–water deficits.

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Data availability

The data that support the findings of this study are openly available at doi:10.5066/P9LDKQE2.

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References

Abatzoglou J T and Kolden C A 2011 Climate change in western US deserts: potential for increased wildfire and invasive annual grasses *Rangeland Ecol. Manage.* **64** 471–8

Abatzoglou J T 2013 Development of gridded surface meterological data for ecological applications and modelling *Int. J. Climatol.* **33** 121–31

Adams H D, Guardiola-Claramonte M, Barron-Gafford G A, Camilo Villegas J, Breshears D D, Zou C B, Troch P A and Huxman T E 2009 Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought *Proc. Natl Acad. Sci.* **106** 7063–6

Alley W M 1984 The Palmer drought severity index: limitations and assumptions *J. Clim. Appl. Meteorol.* **23** 1100–9

Balch J K, Bradley B A, D'Antonio C M and Gómez-Dans J 2013 Introduced annual grass increases regional fire activity across the arid western USA (1980–2009) *Glob. Change Biol.* **19** 173–83

Barnard D M, Germino M J, Arkle R S, Bradford J B, Duniway M C, Pilliod D S, Pyke D A, Shriver R K and Welty J L 2019 Soil characteristics are associated with gradients of big sagebrush canopy structure after disturbance *Ecosphere* **10** 1–12

Bates D, Maechler M, Bolker B and Walker S 2015 Fitting linear mixed-effects models using lme4 *J. Stat. Softw.* **67** 1–48

Beguería S and Vicente-Serrano S M 2013 SPEI: calculation of the standardized precipitation-evapotranspiration index. R package version 1.6

Beguería S, Vicente-Serrano S M and Angulo-Martínez M 2010 A multiscalar global drought dataset: the SPEIbase: a new gridded product for the analysis of drought variability and impacts *Bull. Am. Meteorol. Soc.* **91** 1351–4

Bestelmeyer B T, Peters D P C, Archer S R, Browning D M, Okin G S, Schooley R L and Webb N P 2018 The grassland-shrubland

regime shift in the southwester United States: misconceptions and their implications for management *Bioscience* **68** 678–90
Brabec M M, Germino M J and Richardson B A 2017 Climate adaptation and post-fire restoration of a foundational perennial in cold desert: insights from intraspecific variation in response to weather *J. Appl. Ecol.* **54** 293–302
Bradford J B, Schlaepfer D R and Lauenroth W K 2014 Ecohydrology of adjacent sagebrush and lodgepole pine ecosystems: the consequences of climate change and disturbance *Ecosystems* **17** 590–605
Bradley B A, Curtis C A and Chambers J C 2016 *Bromus* response to climate and projected changes with climate change *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US: Causes, Consequences, and Management Implications* ed M J Germino (Cham: Springer) pp 257–74
Breshears D D, Myers O B, Meyer C W, Barnes F J, Zou C B, Allen C D, McDowell N G and Pockman W T 2009 Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements *Front. Ecol. Environ.* **7** 185–9
Brooks M L, D'Antonio C M, Richardson D M, Grace J B, Keeley J E, DiTomaso J M, Hobbs R J, Pellant M and Pyke D 2004 Effects of invasive alien plants on fire regimes *BioScience* **54** 677–88
Campbell G S and Norman J M 1998 *An Introduction to Environmental Biophysics* (New York: Springer)
Compagnoni A and Adler P B 2014 Warming, competition, and *Bromus tectorum* population growth across an elevation gradient *Ecosphere* **5** 1–34
Concilio A L, Loik M E and Belnap J 2013 Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin *Glob. Change Biol.* **19** 161–72
Crausbay S D, Ramirez A R, Carter S L, Cross M S, Hall K R, Bathke D J and Sanford T 2017 Defining ecological drought for the twenty-first century *Bull. Am. Meteorol. Soc.* **98** 2543–50
DiChristina K and Germino M 2006 Correlation of neighborhood relationships, carbon assimilation, and water status of sagebrush seedlings establishing after fire *West. North Am. Naturalist* **66** 441–9
Dilts T E, Weisberg P J, Dencker C M and Chambers J C 2015 Functionally relevant climate variables for arid lands: a climatic water deficit approach for modelling desert shrub distributions *J. Biogeogr.* **42** 1986–97
Germino M J, Barnard D M, Davidson B E, Arkle R S, Pilliod D S, Fisk M R and Applestein C 2018 Thresholds and hotspots for shrub restoration following heterogeneous megafire *Landscape Ecol.* **33** 1177–94
Gornish E S, Aanderud Z T, Sheley R L, Rinella M J, Svejcar T, Englund S D and James J J 2015 Altered snowfall and soil disturbance influence the early life stage transitions and recruitment of a native and invasive grass in a cold desert *Glob. Change Biol.* **177** 595–606
Hardegree S P, Abatzoglou J T, Brunson M W, Germino M J, Hegewisch K C, Moffet C A, Pilliod D S, Roundy B A, Boehm A R and Meredith G R 2018 Weather-centric rangeland revegetation planning *Rangeland Ecol. Manage.* **71** 1–11
Herrick J E, Van Zee J W, Havstad K M, Burkett L M and Whitford W G 2005 *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems* (Las Cruces, NM: USDA-ARS Jornada Experimental Range)
James J J, Sheley R L, Leger E A, Adler P B, Hardegree S P, Gornish E S and Rinella M J 2019 Increased soil temperatures and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration *J. Appl. Ecol.* **56** 2609–19
James J J, Svejcar T J and Rinella M J 2011 Demographic processes limiting seedling recruitment in arid grassland restoration *J. Appl. Ecol.* **48** 961–9
Kildisheva O A, Erickson T E, Merritt D J and Dixon K W 2016 Setting the scene for dryland recovery: an overview and key findings from a workshop targeting seed-based restoration *Restor. Ecol.* **24** S36–42
Law D J, Adams H D, Breshears D D, Cobb N S, Bradford J B, Zou C B, Field J P, Gardea A A, Williams A P and Huxman T E 2018 Bioclimatic envelopes for individual demographic events driven by extremes: plant mortality from drought and warming *Int. J. Plant Sci.* **180** 53–62
Livneh B 2014 A long-term hydrologically based dataset of land surface fluxes and states for the conterminous United States: updates and extensions *J. Clim.* **27** 478–86
Meyer S E and Monsen S B 1992 Big sagebrush germination patterns: subspecies and population differences *J. Range Manage.* **45** 87–93
Palmquist K A, Schlaepfer D R, Bradford J B and Lauenroth W K 2016 Mid-latitude shrub steppe plant communities: climate change consequences for soil water resources *Ecology* **97** 2342–54
Pilliod D S and Welty J L 2013 Land treatment digital library: US geological survey data series 806 (https://doi.org/10.3133/ds806)
Pilliod D S, Welty J L and Arkle R S 2017a Refining the cheatgrass-fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends *Ecolo. Evol.* **7** 8126–51
Pilliod D S, Welty J L and Toevs G R 2017b Seventy-five years of vegetation treatments on public rangelands in the Great Basin of North America *Rangelands* **39** 1–9
PRISM Climate Group 2017 Oregon State University (https://prism.oregonstate.edu) (accessed 2017)
R Core Team 2019 R: a language and environment for statistical computing *R Foundation for Statistical Computing* (Vienna, Austria) (https://R-project.org/)
Roundy B A, Chambers J C, Pyke D A, Miller R F, Tausch R J, Schupp E W, Rau B and Gruell T 2018 Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability *Ecosphere* **9** 1–27
Ruppert J C, Harmoney K, Henkin Z, Snyman H A, Sternberg M, Willms W and Linstädter A 2015 Quantifying drylands' drought resistance and recovery: the importance of drought intensity, dominant life history and grazing regime *Glob. Change Biol.* **21** 1258–70
Schlaepfer D R, Lauenroth W K and Bradford J B 2012 Ecohydrological niche of sagebrush ecosystems *Ecohydrology* **5** 453–66
Schlaepfer D R, Lauenroth W K and Bradford J B 2014 Natural regeneration processes in big sagebrush (*Artemesia tridentata*) *Rangeland Ecol. Manage.* **67** 344–57
Schlaepfer D R and Murphy R 2018 rSOILWAT2: An Ecohydrological Ecosystem-Scale Water Balance Simulation Model. R package version 2.3.2.
Shriver R K, Andrews C M, Arkle R S, Barnard D, Duniway M C, Germino M J, Pilliod D S, Pyke D A, Welty J L and Bradford J B 2019 Transient population dynamics impede resilience and drive ecosystem transformation after disturbance *Ecol. Lett.* **22** 1357–66
Shriver R K, Andrews C M, Pilliod D S, Arkle R S, Welty J L, Germino M J, Duniway M C, Pyke D A and Bradford J B 2018 Adapting management to a changing world: warm temperatures, dry soil, and interannual variability limit restoration success of dominant woody shrub in temperate drylands *Glob. Change Biol.* **24** 4972–82
Slette I J, Post A K, Awad M, Even T, Punzalan A, Williams S, Smith M D and Knapp A K 2019 How ecologists define drought, and why we should do better *Glob. Change Biol.* **25** 3193–200
Snyder K A, Evers L, Chambers J C, Dunham J, Bradford J B and Loik M E 2019 Effects of changing climate of hydrological cycle in cold desert ecosystems of the great basin and columbia plateau *Rangeland Ecol. Manage.* **72** 1–12
Soil Survey Staff 2017 Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey (https://websoilsurvey.nrcs.usda.gov/) (accessed 2017)
Vicente-Serrano S M, Beguería S, Lorenzo-Lacruz J, Camarero J J, López-Moreno J I, Azorin-Molina C, Revuelto J,

Morán-Tejeda E and Sanchez-Lorenzo A 2012 Performance of drought indices for ecological, agricultural, and hydrological applications *Earth Interact.* **16** 1–12

Vicente-Serrano S M, Beguería S and López-Moreno J I 2010 A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index *J. Clim.* **23** 1696–718

Wegner S J and Olden J D 2012 Assessing transferability of ecological models: an underappreciated aspect of statistical validation *Methods Ecol. Evol.* **3** 260–7

Wilhite D A and Glantz M H 1985 Understanding the drought phenomenon: the role of definitions *Water Int.* **10** 111–20

Young D J N, Werner C M, Welch K R, Young T P, Safford H D and Latimer A M 2019 Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion *Ecology* **100** e02571

Zang C S, Buras A, Esquivel-Muelbert A, Jump A S, Rigling A and Rammig A 2019 Standardized drought indices in ecological research: why one size does not fit all *Glob. Change Biol.* **26** 322–4