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Interannual variation in climate contributes to contingency in post-fire restoration outcomes in seeded sagebrush steppe

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Abstract

Interannual variation, especially weather, is an often-cited reason for restoration "failures"; yet its importance is difficult to experimentally isolate across broad spatiotemporal extents, due to correlations between weather and site characteristics. We examined post-fire treatments within sagebrush-steppe ecosystems to ask: (1) Is weather following seeding efforts a primary reason why restoration outcomes depart from predictions? and (2) Does the management-relevance of weather differ across space and with time since treatment? Our analysis quantified range-wide patterns of sagebrush (*Artemisia* spp.) recovery, by integrating long-term records of restoration and annual vegetation cover estimates from satellite imagery following thousands of post-fire seeding treatments from 1984 to 2005. Across the Great Basin, sagebrush growth increased in wetter, cooler springs; however, the importance of spring weather varied with sites' long-term climates, suggesting differing ecophysiological limitations across sagebrush's range. Incorporation of spring weather, including from the "planting year," improved predictions of sagebrush recovery, but these advances were small compared to contributions of time-invariant site characteristics. Given extreme weather conditions threatening this ecosystem, explicit consideration of weather could improve the allocation of management resources, such as by identifying areas requiring repeated treatments; but improved forecasts of shifting mean conditions with climate change may more significantly aid the prediction of sagebrush recovery.

KEYWORDS

Artemisia, historical contingency, horseshoe prior, restoration seeding, weather, wildfire, year effects

1 | INTRODUCTION

The outcomes of ecological restoration are often unpredictable, and vastly different population or community trajectories can emerge when the same treatments are applied to similar sites (Brudvig, 2011; Crouzeilles et al., 2016; Suding, 2011). Low predictive power in restoration ecology poses a challenge to the conservation of biodiversity and ecosystem functions in degraded habitats, and the sources of this variability remain poorly understood (Brudvig et al., 2017; Dietze, 2017). In part, disparities in restoration outcomes may be caused by interannual weather variation, which can alter assembling communities via its influence on initial propagule arrival, establishment, and other subsequent ecological filters (Chase, 2007; Chesson, 2000; Fukami et al., 2005; Myers & Harms, 2009; Seabloom, 2011). Resource managers consider weather conditions during and after plantings (Hardegree et al., 2018), and conditions during the treatment year may be correlated with restoration success (sometimes referred to as "initiation" or "year" effects; Brudvig et al., 2017, Stuble, Fick, & Young, 2017; Stuble, Zefferman, et al., 2017, Groves & Brudvig, 2019, Groves et al., 2020, Werner et al., 2020).

Despite these considerations, the relative importance of weather in predicting restoration outcomes remains poorly understood over broad spatiotemporal extents (Brudvig et al., 2017). One of the key reasons the knowledge gap persists is that interannual weather variation is rarely explicitly addressed in ecological experimental designs (~3%–5% of studies examined in Vaughn & Young, 2010 and Werner et al., 2020). Moreover, the few experiments that are replicated in time and thus able to isolate the effects of weather are, by necessity, small in their geographic scope (Werner et al., 2020). In contrast, datasets spanning larger spatial extents are often limited in the temporal resolution of their observations, recording aggregate outcomes of multiple years or life-history stages. Weather measurements can be highly correlated over weeks and years; thus, larger-scale studies that utilize infrequent observations (e.g., restoration outcomes observed several years following treatment) may fail to distinguish the effects of a particular year's conditions from longer-term climate drivers or other correlated, time-invariant site characteristics (Fernández-Martínez et al., 2015; Groves & Brudvig, 2019).

The tendency of studies to not formally consider interannual weather variation has hindered the incorporation of ecologically significant weather effects (e.g. "ecological drought"; Crausbay et al., 2017) into restoration planning at management-relevant scales. For instance, retrospective analyses identifying spatiotemporal variation in the barriers to restoration could improve treatment design (Copeland et al., 2021) or identify areas that experienced inopportune post-restoration conditions to inform the strategic deployment of beneficial follow-up treatments (Shriver et al., 2018). However, these applications hinge on addressing a key experimental gap in restoration: Is weather a widespread driver of why restoration outcomes differ from expectations? And if so, how transferrable are these effects are in space (i.e., at new sites) and time (i.e., across years)?

Here, we examine the influence of weather on predictions of restoration outcomes on Bureau of Land Management (BLM) lands across a broad spatiotemporal extent, focusing on shrub recovery in an imperiled dryland ecosystem characterized by variable precipitation and temperature. Sagebrush-steppe (dominated by *Artemisia* spp., especially big sagebrush, *Artemisia tridentata*) once covered nearly 1,000,000 km^2 of western North America and is a critical habitat component for numerous species of conservation concern; however, its range has been reduced by half due to land-use, climate change, conifer encroachment, and invasion of exotic annual grasses, such as *Bromus tectorum* (cheatgrass; Miller et al., 2011; Shi et al., 2018). Cheatgrass reduces fire return intervals and locally eradicates fire-sensitive sagebrush shrubs (Balch et al., 2013). This has motivated large-scale investments into sagebrush restoration, primarily through the broadcasting of seeds in recently burned areas (Pilliod & Welty, 2013; Pilliod, Welty, & Toevs, 2017). While these treatments constitute one of the largest conservation efforts to restore native species globally, their success is highly variable and often low (e.g., Arkle et al., 2014; Davies et al., 2013; Davies & Bates, 2017; Eiswerth et al., 2009; Knutson et al., 2014; Pyke et al., 2013).

Soil moisture and factors that control it, such as antecedent snowpack, previous or current-years precipitation, and temperatures, are key drivers of the establishment and growth of sagebrush shrubs in field-based studies (Brabec et al., 2017; Nelson et al., 2013; O et al., 2020; Schlaepfer et al., 2014a; Shriver et al., 2018; Tredennick et al., 2016). Weather, especially during the year following seeding, is often cited as a primary cause of variation in restoration success in sagebrush steppe; however, these effects are difficult to isolate at management-relevant scales, as past studies of the drivers of restoration success are often subject to tradeoffs in temporal resolution and spatial extent (Germino et al. 2018; Applestein et al. 2018). Recent computational advances have enabled the estimation of the cover of plant functional groups from satellite imagery, providing spatially continuous and temporally replicated retrospective data that could advance the detection of widely generalizable weather effects in restoration (Rigge et al., 2020).

In this work, we quantify the extent to which the inclusion of weather covariates improves landscape-scale prediction of the recovery of sagebrush steppe ecosystems' foundational taxa (*Artemisia* spp.), which represents a widespread conservation challenge across western North America. We integrate a long-term dataset of restoration reseeding actions and remotely sensed estimates of sagebrush cover following wildfires over 20 years across the western United States (Figure 1), which provide a unique opportunity to explore variation in the predictive importance of

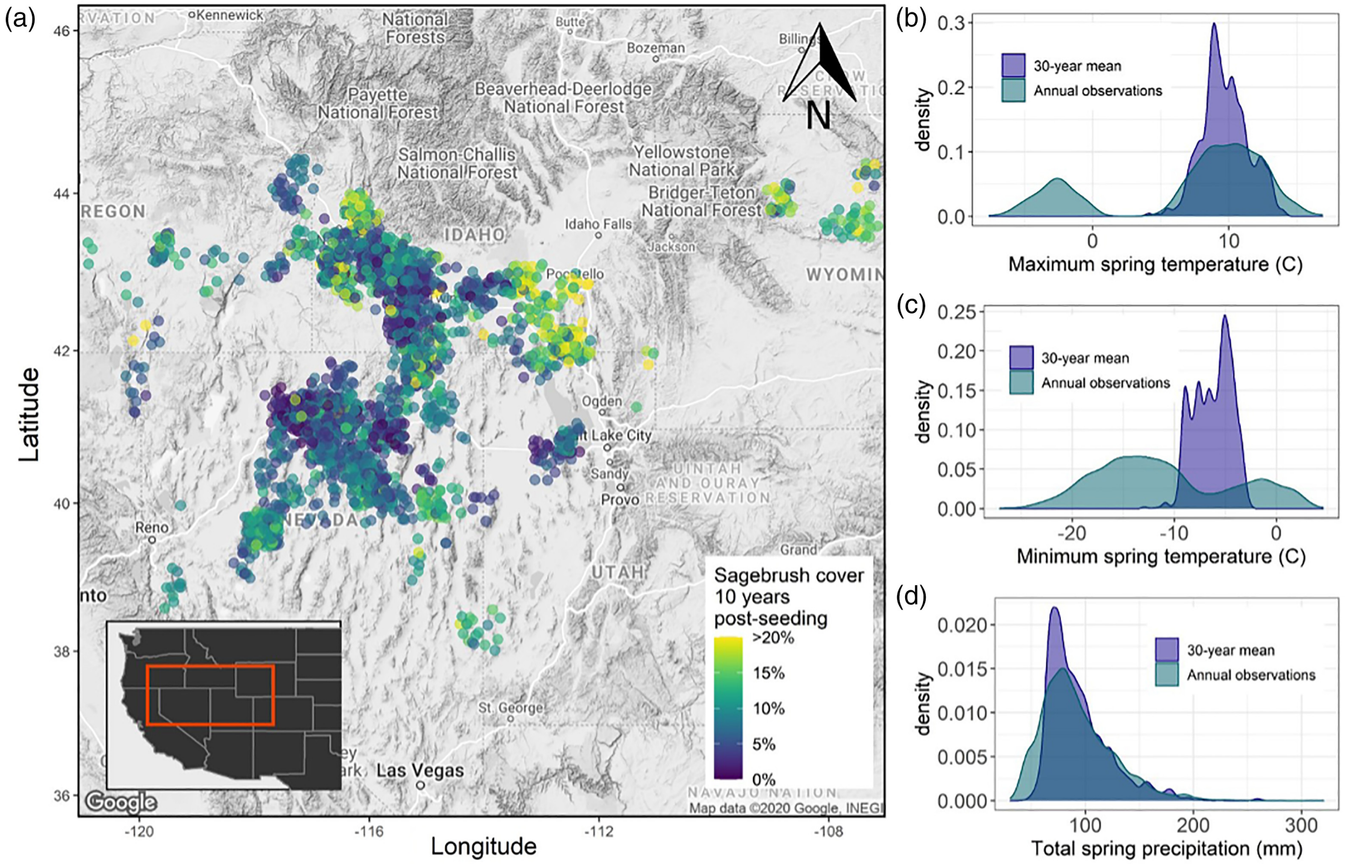


FIGURE 1 (a) Locations of 2726 sites that received seeding treatments following fires between 1984 and 2005, based on the Land Treatment Digital Library. Points indicate centroids of spatially contiguous clusters of pixels and have been slightly offset to reduce overlap. Point color reflects sites' mean sagebrush cover 10 years following treatment. (b–d) the range of 30-year mean spring (February–April) climate conditions for these sites (in blue), compared to the annual weather conditions (in teal) observed in the first 4 years following fire.

interannual weather in restoration over a wide extent. We addressed the following research questions about the predictive importance and management-related transferability of impacts of interannual variation:

1. To what extent does weather improve predictions of restoration outcomes at new sites, beyond the information provided by long-term climatic and static biophysical characteristics?
2. Do the weather conditions during the first year after treatment have a disproportionate impact on restoration outcomes (e.g., initiation "year effects"), compared to subsequent years following seeding?
3. Do the impacts of weather vary spatially, across the climatic range of treated sagebrush steppe ecosystems?

Retrospective analyses that explicitly quantify the impacts of interannual variation in restoration will be essential to improving treatment designs via adaptive management, prioritizing sites, and enhancing the prediction of highly variable ecological outcomes.

2 | METHODS

To address questions 1 and 2, we compared the predictive accuracy of Bayesian sparse models that only assessed static variables (such as long-term climate and time-invariant biophysical characteristics) to those that also included sources of interannual variation (weather variables from the first 4 years following the fire, as well as other possible "planting year" effects). We addressed question 3 using a multilevel autoregressive model of yearly changes in sagebrush cover during the first 4 years following fire and seeding. Given the strong correlation between annual weather and long-term climate variables, examining yearly changes in cover allowed for the identification of correlations between a single season's weather conditions and a single year's outcome.

2.1 | Data extraction

Sagebrush cover was extracted at 30-m pixel resolution from the USGS Rangeland Condition Monitoring

Assessment and Projection (RCMAP, formerly known as the National Land Cover Database's "Back in Time" Sagebrush Rangeland Fractional Component), which provides estimates of functional group cover for each year from 1984 to 2018 across the Great Basin (Homer et al., 2015; Rigge et al., 2020). More details about RCMAP and its field validation can be found in Supporting Information S1. Our analysis focused on areas that burned only once between 1984 and 2005 and were subsequently seeded with at least one *Artemisia* species, using either aerial or ground seeding approaches. We identified areas that had been seeded only once following the fire, using the Land Treatment Digital Library (LTDL, Pilliod & Welty, 2013), a catalog of management actions on BLM lands in the western United States, which constitute nearly 60% of the Great Basin region (Pilliod, Welty, & Toevs, 2017). We extracted or calculated elevation, slope (U.S. Geological Survey, 2017), topographic wetness index (TWI) (Beven & Kirkby, 1979), heat load (McCune & Keon, 2002), and Level-III ecoregion (US EPA 2019) for each pixel.

To increase computational tractability over our large study area, we identified clusters of spatially contiguous pixels with the multivariate clustering algorithm in ArcGIS Pro (ESRI, Redlands CA), using criteria for elevation, heat load, TWI, ecoregion, and slope (Supporting Information S1). This process resulted in 2726 site clusters across 170 fires between 1984 and 2005. To confirm that variation within clusters was minimized, we verified that the relative standard error for elevation was less than 20% within a cluster. The median cluster size was 205 pixels (mean = 831.5, SD = 1897.1). We calculated cluster-level means and standard deviations for each dependent variable and for sagebrush cover, which was the response variable in this analysis.

Though numerous weather periods have been demonstrated to impact sagebrush recovery, we focused on temperature minima, temperature maxima, and total precipitation during February–April, which have been commonly investigated for their influence on establishment and growth by determining snowmelt, germination timing, post-germination freezing events, and soil moisture availability for seedlings before the onset of summer drought (Brabec et al., 2017; Nelson et al., 2013; O'Connor et al., 2020; Schlaepfer et al., 2014a; Shriver et al., 2018). Using the raster and ncdf4 packages in R (Hijmans & van Etten, 2012; Pierce, 2019), we extracted February–April variables for total precipitation, absolute minimum temperature, and mean maximum temperatures for the first 4 years after the fire, as well as February–April 30-year averages for each of these parameters from the gridMet modeled meteorological dataset (Abatzoglou, 2013). GridMet contains daily, high-spatial resolution (4-km) climate estimates for the contiguous United States from 1979 to the present. Weather deviations were calculated as the residual between each year's February–April observations and 30-year normal conditions for that month. Throughout the text we refer to these as "spring" weather variables, indicating that this period describes the start of the growing season when sagebrush seeds tend to germinate.

2.2 | Questions 1 and 2: Impacts of interannual variation and the initiation year on predicting restoration outcomes

To assess whether annual spring weather variables improved predictions of sagebrush cover, we developed a set of five Bayesian "sparse" models. Sparsity-inducing horseshoe priors were adopted to avoid overfitting and effectively reduce the set of numerous highly correlated biophysical and spring weather variables (>0.7) that could not be chosen solely by our knowledge of the system (Carvalho et al., 2009). Regularizing horseshoe priors have the effect of "selecting" among large variable sets by shrinking negligible effect sizes, allowing only a subset of the variables to have large positive or negative parameter values. Rather than reducing the variable set through traditional model selection, horseshoe priors achieve a similar outcome using two parameters: a global parameter that generally draws coefficients toward zero, while local scale parameters with half-Cauchy priors allow larger estimates to "escape" shrinkage (Piironen & Vehtari, 2017).

While horseshoe priors may be used as a means of selecting relevant variables on their own, we fit five separate models to directly quantify the changes in predictive error associated with the addition of each set of new covariates (Tables 1 and 2). Each successive model parsed the extent to which static biophysical variables (Model 1), mean spring climate (Model 2), time-varying spring weather variables (Models 3–4), and other "initiation year" effects (Model 5) improved the prediction of sagebrush cover at new sites, a decade after treatment occurred (see Table 1 for specific covariates included). If the impacts of spring planting year weather conditions (*Question 2*) had distinct predictive importance, we expected to see improved out-of-sample predictive accuracy (metrics described below) for Model 3, compared to Models 1 and 2, which contained only static biophysical characteristics and long-term climate variables. If post-treatment weather beyond the planting year was additionally important to sagebrush recovery (*Question 1*), we expected to see improved predictive accuracy for Model 4, relative to Model 3. If additional characteristics of the

TABLE 1 Description of variables included in models of post-treatment sagebrush cover

Category	Variables	Included in:
Time-invariant biophysical site characteristics	• Slope (°) • Elevation (m) • Heat load (index) • Surviving, post-fire sagebrush cover before restoration (%) • Level III Ecoregion (categorical, 7 in this dataset)	Models 1, 2, 3, 4, and 5
Long-term mean spring climate	• 30-year mean for February–April mean maximum temperature (°C) • 30-year mean for absolute minimum February–April temperature (°C) • 30-year mean for total February–April precipitation (mm)	Models 2, 3, 4, 5
Spring weather following treatment	Annual deviations (for Years 1–4 post-treatment) of the following variables from the calculated 30-year means: • February–April mean maximum temperature (°C) • Absolute minimum February–April temperature (°C) • Total February–April precipitation (mm)	Variables for Year 1 in Model 3 Variables for Years 1–4 in Models 4 and 5
Fire/seeding year	• Varying intercept for the year in which fires occurred	Model 5

TABLE 2 Comparison of out-of-sample predictive performance for models of remotely sensed sagebrush cover that incorporate time-invariant biophysical variables, long-term (30 years) climate averages, and annual weather deviations

		Out-of-sample predictive performance		
Model	**Variables included**	**Out-of-sample Bayesian R^2**	**ΔELPD**	**SE ΔELPD**
Model 5	Spring weather, climate, and time-invariant biophysical variables, with varying intercept for fire/seeding year	0.69	0.00	0.00
Model 4	All spring weather (years 1–4), climate, and time-invariant biophysical variables	0.67	−40.49	10.10
Model 3	Year 1 spring weather, climate, and time-invariant biophysical variables	0.61	−235.59	21.91
Model 2	Long-term (30 years) climate and time-invariant biophysical variables	0.59	−273.79	23.07
Model 1	Time-invariant biophysical variables only	0.55	−338.41	25.61

Note: Bayesian-R^2 is reported as the mean value from the full set of posterior predictions generated. The change in the expected log pointwise predictive density (ΔELPD) for a new dataset indicates the difference between the model with the highest estimated predictive accuracy (for which ΔELPD = 0) and other models. More negative ΔELPD values indicate decreased relative predictive accuracy, with associated standard errors (SE).

treatment year, beyond spring weather, were important, we expected to see additional gains in prediction for Model 5.

To account for the measurement error inherent in clustering groups of remotely sensed estimates, we modeled the observed mean sagebrush cover (y_{observed}) for each site as normally distributed around the unknown true value (y_{true}, with mean μ_i and standard deviation σ) with a standard deviation equal to the standard error for each site (σ_{err}). In general, these models were specified as:

$$y_{\text{observed}[i]} \sim TNormal\left(y_{\text{true}[i]}, \sigma_{err[i]}\right)$$

$$y_{\text{true}[i]} \sim TNormal(\alpha + \boldsymbol{X_i} \cdot \boldsymbol{\beta}, \sigma)$$

$$\beta_j \sim Normal\left(0, \tau \cdot \widetilde{\lambda}_j\right), \widetilde{\lambda}_j = \frac{c\lambda_j}{\sqrt{c^2 + \tau^2 \lambda^2_j}}$$

$$\lambda_j \sim halfCauchy(0, 1)$$

$$\tau \sim halfCauchy(0, 1)$$

$$c^2 \sim Inverse\ Gamma\left(\frac{\nu}{2}, \frac{\nu}{2} s^2\right)$$

where $\boldsymbol{\beta}$ represents a vector of j parameters for the matrix of included variables $\boldsymbol{X_i}$ (described in Table 1); τ and λ represent global and local scale parameters for the horseshoe priors; c represents a regularization parameter; and N is the number of observations. The integration of inverse-gamma and half-Cauchy distributions effectively regularizes slopes (that exceed the global scale) by a Student's-T prior with scale s and degrees of freedom ν. Based on the discussion provided in Piironen and Vehtari (2017) and recommendations in the *brms* package (Bürkner, 2017), ν and s^2 were assigned values of 4 and 2, respectively. We defined the ratio of non-zero to zero parameters as 1:4 to identify a tractable subset of variables for planning restoration actions. Model 5 additionally contained a varying intercept for the treatment year.

2.3 | Question 3: Effects of weather on annual growth of sagebrush and their spatial variation

To isolate the effects of specific weather variables on post-treatment sagebrush recovery and examine spatial variation in these effects, we developed a Bayesian multilevel autoregressive model of annual changes in sagebrush cover at reseeded sites for the first 4 years following the fire ($n = 8157$ observations at 2726 sites). Covariates were included to isolate the effects of (1) 30-year mean February–April mean maximum temperature, minimum temperature, and total precipitation conditions; (2) annual deviations from these long-term averages; and (3) interaction terms between climate and weather variables to quantify spatial variation in the effects of weather across sites. We included quadratic terms for climate variables to capture non-linear responses to temperature and precipitation. The model also contained a temporally autoregressive term for sagebrush cover in the previous timestep (*prev)* and varying intercept components for time since fire (α_{TSF}) and site identity (α_{site}) to reflect repeated measures of sites. The model employed a truncated normal distribution bounded at 0 and 100 (to match the structure of the sagebrush percent cover estimates) and a measurement error term, similar to the models described above. The model was specified as:

$$y_{\text{observed}[i]} \sim TNormal\left(y_{\text{true}[i]}, \sigma_{err[i]}\right)$$

$$y_{\text{true}[i]} \sim TNormal(\mu_i, \sigma)$$

$$\mu_i = \overline{\alpha} + \alpha_{TSF[i]} + \alpha_{site[i]} + \gamma * prev_i + C_i\beta + W_i\partial + (C_i * W_i)\rho$$

$$\alpha_{TSF} \sim Normal(0, \sigma_{TSF})$$

$$\alpha_{site} \sim Normal(0, \sigma_{\text{site}})$$

where individual observations (i) are nested separately within sites (*site*) and years since fire (*TSF*). $\overline{\alpha}$ represents the mean intercept. $\boldsymbol{\beta}, \partial$, and $\boldsymbol{\rho}$ indicate vectors of parameters associated with climate variables (matrix $\boldsymbol{C}$), weather variables (matrix $\boldsymbol{W}$), and their interaction. Correlations between included variables were <0.6. We applied the weakly informative standard priors used in the *brms* package.

2.4 | Model fit, comparison, and predictive performance

Variables were centered and scaled by 1 standard deviation. Models were estimated using the language Stan and the *brms* package in R, using a Markov Chain Monte Carlo sampler with four chains, each with 2000 iterations and 1000 warmup iterations (Bürkner, 2017; Stan Development Team, 2020). We assessed effective sample size and model convergence, indicated by Gelman–Rubin statistics close to 1 and stable, well-mixed chains (Stan Development Team, 2020). Parameter estimates with 90% credible intervals that did not contain zero were considered to have non-zero effects on the response variable (Stan Development Team, 2020). We assessed model fit by calculating Bayesian-R^2 values (Gelman et al., 2019) and examining visualizations of posterior predictive fit (Supporting Information S2).

To assess predictive performance, we reserved 33% of the data to calculate out-of-sample Bayesian-R^2 from each model, in addition to calculating the estimated expected log pointwise predictive density for a new

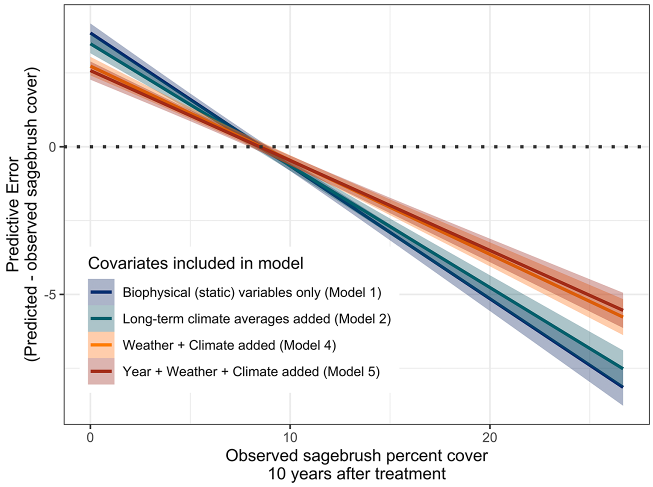


FIGURE 2 Comparison of the mean predictive error between models of sagebrush recovery that contained only time-invariant biophysical and long-term climate variables (shown in blue and teal) and models that incorporated sources of interannual variation (shown in orange and red), across levels of sagebrush cover 10 years after treatment. Trend lines indicate linear regressions for individual observations of predictive error and sagebrush cover, with 95% credible intervals. Predictive error was calculated as the difference between the model's prediction and the observed sagebrush cover value. Lines closer to the dashed line (predictive error = 0) indicate improved average model accuracy.

dataset from the fitted model (ELPD, Vehtari et al., 2016). In model comparison, larger ELPD values indicate improved predictive performance.

The use of remotely sensed data incurs inherent tradeoffs, between the spatiotemporal scope and the measurement error inherent in the use of remotely sensed datasets. We examined the sensitivity of our models' predictions to possible measurement errors, using field validation data (Applestein & Germino, 2021; the process is described in Supporting Information S2). Model code can be found via Github: https://github.com/absimler/restoration-weather.

3 | RESULTS

3.1 | Question 1: Impacts of interannual variation on prediction of long-term restoration outcomes

Static, biophysical, and long-term climate variables captured a large amount of the variation in test datasets (Table 2; Out-of-sample $R^2 = 0.55$ for a model containing static variables alone; 0.59 for a model also containing long-term climate averages). Sagebrush cover measured 10 years after seeding was greater at steeper, higher-elevation sites, and decreased with increasing heat load (Supporting Information S3, Figure S1). Long-term sagebrush recovery was also greater in the Wyoming Basin and Idaho Batholith ecoregions and lower in the Northern and Central Basin, compared to other zones (Supporting Information S3, Figure S1).

However, the inclusion of weather variables from the 4 years following the fire improved the predictive performance of the model of sagebrush cover a decade after reseeding, compared to models containing static, biophysical features and long-term climate averages alone (Figure 2, Table 2; ΔOut-of-sample $R^2 = 0.08$; ΔELPD $= -273.79$, SE $= 23.07$, with negative ΔELPD values indicating improved relative predictive performance). Models that incorporated interannual variation reduced overprediction at lower values of sagebrush cover and underprediction at high values of sagebrush cover (Figure 2).

3.2 | Question 2: Importance of “initiation” year for predicting restoration outcomes

Inclusion of weather variables from only the first year following fire also resulted in small gains in out-of-sample prediction, compared to models containing static biophysical and climate characteristics (Table 2; ΔOut-of-sample $R^2 = 0.02$; ΔELPD $= -103.2$, SE $= 15.4$). However, this model's predictive accuracy was considerably lower than the model containing weather effects for the first 4 years post-fire (Table 2). Incorporating a varying intercept for the year in which a fire occurred and in which the site was reseeded also minorly improved prediction, compared to the model containing all spring weather covariates (Table 1; ΔOut-of-sample $R^2 = 0.02$, ΔELPD $= -40.49$, SE $= 10.10$; Figure 6), indicating additional possible long-term effects of planting year.

Posterior parameter estimates for all predictive models can be found in Supporting Information S3. Within-sample Bayesian-R^2 values for the models of sagebrush cover a decade after treatment ranged from 0.50 (for Model 1) to 0.67 (for Model 5).

3.3 | Question 3: Effects of weather on annual growth of sagebrush and their spatial variation

Interannual increases in sagebrush cover in the first 4 years following the fire were greatest at sites with intermediate mean spring precipitation (172 mm), generally cooler average spring maximum temperatures (7.6°C), and colder absolute minimum (−12.8°C) temperatures

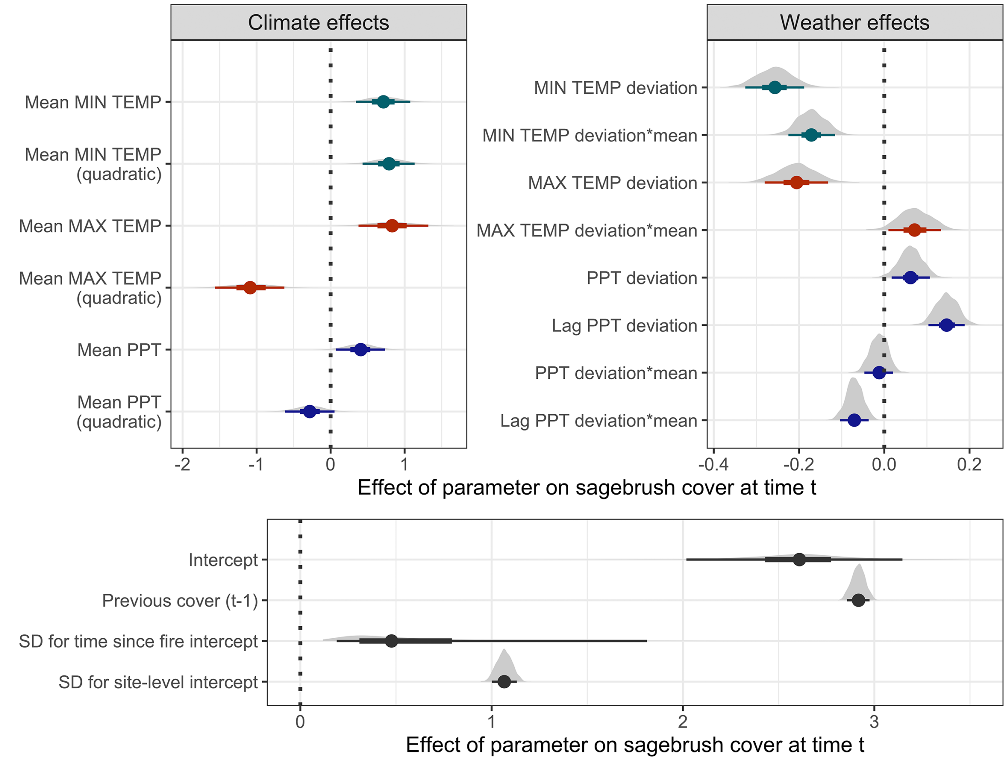


FIGURE 3 Parameter estimates for the effects of climate, weather, and other variables on annual changes in sagebrush cover over the first four years following fire. Climate effects included sites' 30-year means for spring minimum temperatures (MIN TEMP in teal), maximum temperatures (MAX TEMP in red), and total precipitation (PPT in blue). Weather effects included each spring's deviation from each long-term climate variable, in addition to a lagged deviation effect for precipitation in the preceding year. Climate-weather interactions are indicated as deviation × mean. Dots indicate median parameter estimates with associated 50% (thick lines) and 90% (thick lines) credible intervals, with the full posterior distribution shown in grey. Parameters with 90% credible intervals that did not include zero (indicated by the dotted line) were considered to have nonzero effects on the response.

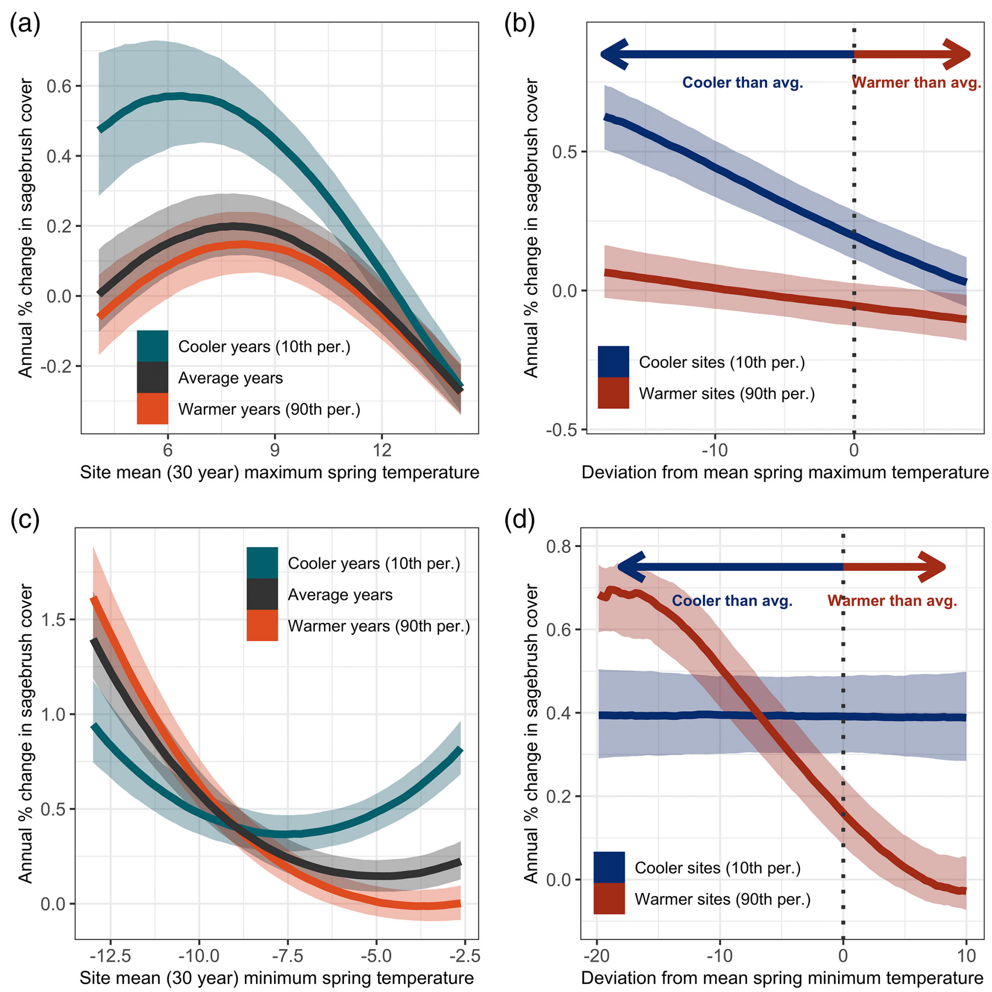
(Figures 3–5). Beyond the effects of long-term climate, annual changes in sagebrush cover generally increased in wetter and cooler years across treated BLM lands within the Great Basin, compared to sites' long-term climatic means (Figure 3).

However, the size and direction of weather effects exhibited substantial spatial variation across the climatic range of treated sagebrush systems (Figures 4 and 5). Years with lower maximum spring temperatures resulted in increased sagebrush growth in cover (+61%) at cooler sites but had weaker effects (+9%) at the warmest sites (Figure 4a,b). By comparison, in years with lower minimum temperatures, annual percent growth in cover increased by 68% at warmer sites, but changed negligibly (−2%) at cooler sites (Figure 4c,d). Years with greater precipitation were consistently correlated with increased change in sagebrush cover across both arid and wet sites (Figure 5a,b) but lagged precipitation effects were stronger at drier sites (Δ94%), compared to sites with generally wetter spring conditions (Δ33%, Figure 5c,d). The model of annual changes in sagebrush cover had a within-sample R^2 of 0.86 and an out-of-sample R^2 of 0.80.

4 | DISCUSSION

Our ability to predict ecological responses to restoration will be improved if we can first understand and explain the ecological outcomes of past treatments, especially at broad spatiotemporal scales (Brudvig et al., 2017). Here, we find that landscape-scale patterns of post-treatment sagebrush cover are related to and predicted by spring weather prevailing in the first few years after restoration interventions on BLM lands. The inclusion of spring weather improved predictions of post-fire seeding outcomes compared to models based only on time-invariant site characteristics, including climate averages (Table 2, Figure 2); however, the importance of weather differed across the climatic range of the burned, treated sagebrush steppe ecosystems examined here (Figures 3–5), suggesting that the management implications of weather

FIGURE 4 Marginal effects of interannual variation in spring maximum (a,b) and minimum (c,d) temperatures on annual percent sagebrush growth in the first four years following fire (with 50% credible intervals shown in shaded bands). Annual percent change ((New–Previous)/Previous) has been calculated for the median value of preceding year sagebrush cover, and other variables have been held at their means. Panels a and c illustrate the effects of cooler (10th percentile, in teal) or warmer (90th percentile, in orange) years, relative to a site's 30-year mean temperature conditions (in grey). Panels b and d illustrate effects of annual weather deviations at sites that are cooler (10th percentile, in blue) or warmer (90th percentile, in red) on average.



effects may have limited transferability across space and time.

4.1 | Impacts of spring weather on prediction of post-treatment sagebrush cover

Inclusion of spring weather variables improved out-of-sample predictions of long-term sagebrush recovery on BLM lands; however, static biophysical factors, such as heat load and slope, captured much of the variation in dryland shrub cover (Tables 1 and 2; Davies et al., 2011; Knutson et al., 2014; Pyke et al., 2013). We propose that the increased out-of-sample accuracy (of ∼8–10%) associated with the inclusion of spring weather and other "year" effects indicates an appreciable improvement in the prediction of outcomes that requires further investigation, particularly given (1) the substantial investment in sagebrush restoration across the Great Basin, (2) urgent risks posed for declining sagebrush-dependent wildlife species, and that (3) no existing model provides satisfactory predictions of sagebrush recovery (Knutson et al., 2014; Pyke et al., 2013). Though current weather forecasts may not skillfully predict spring conditions at the time of fall seedings, the effects of interannual variation quantified in this study have several possible management applications on BLM lands. For instance, retrospective analysis of the past year's weather conditions can be used to identify areas urgently requiring follow-up seedings, which have been demonstrated to improve the probability of sagebrush establishment in burned areas (Shriver et al., 2018). Further, the importance of weather effects significantly varied across the examined range of seeded sagebrush steppe ecosystems (Figures 3–5), suggesting that restoration practitioners could apply this information to prioritize sites where outcomes may be more consistently predictable or allocate funding across several planting years, to minimize risks at variable sites.

However, the substantial variation captured by time-invariant and long-term characteristics (Table 2) may further inform restoration prioritization. These results suggest that, with climate change, accurate forecasting of

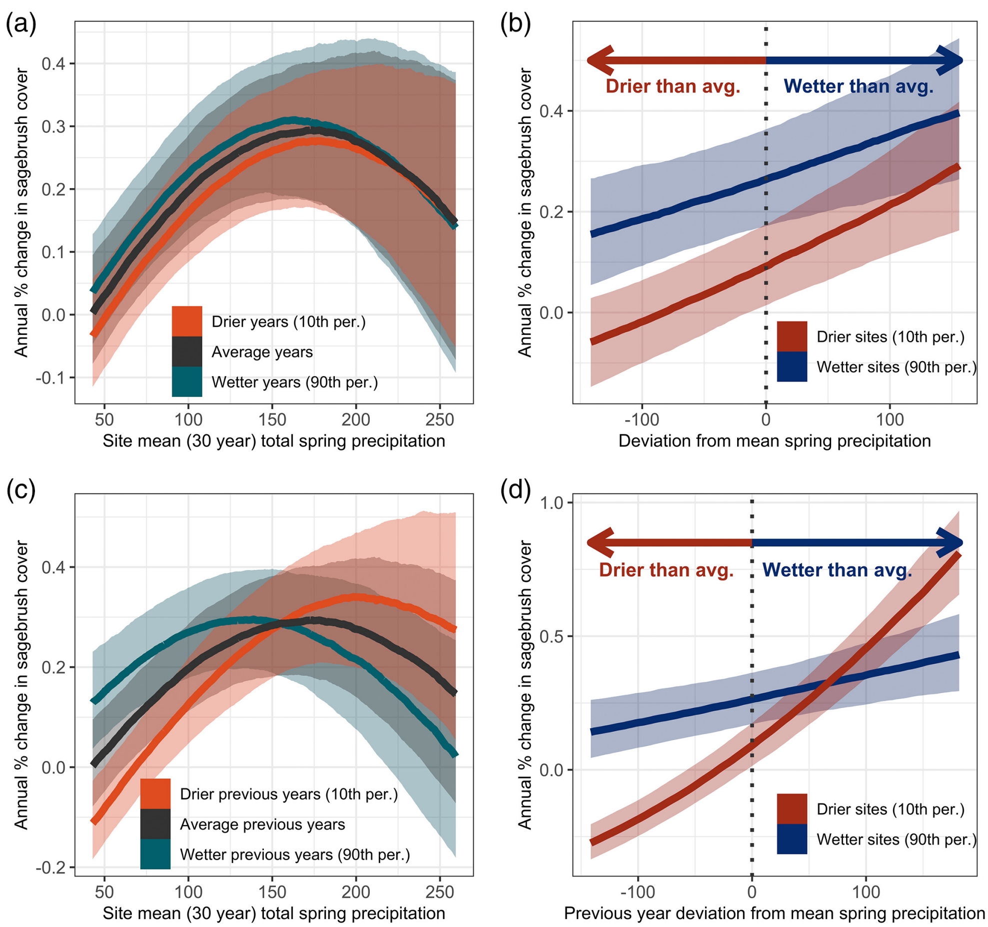


FIGURE 5 Predicted effects of interannual variation in spring precipitation for the current (a,b) and preceding (c,d) years on annual percent sagebrush growth in the first four years following fire (with 50% credible intervals shown in shaded bands). Annual percent change ((Current − Previous)/Previous) has been calculated for the median value of preceding year sagebrush cover, and other variables have been held at their means. Panels a and c illustrate the effects of drier (10th percentile, in orange) or wetter (90th percentile, in teal) years, relative to a site's 30-year mean precipitation (in grey). Panels b and d illustrate effects of annual weather deviations at sites that are drier (10th percentile, in red) or wetter (90th percentile, in blue) on average.

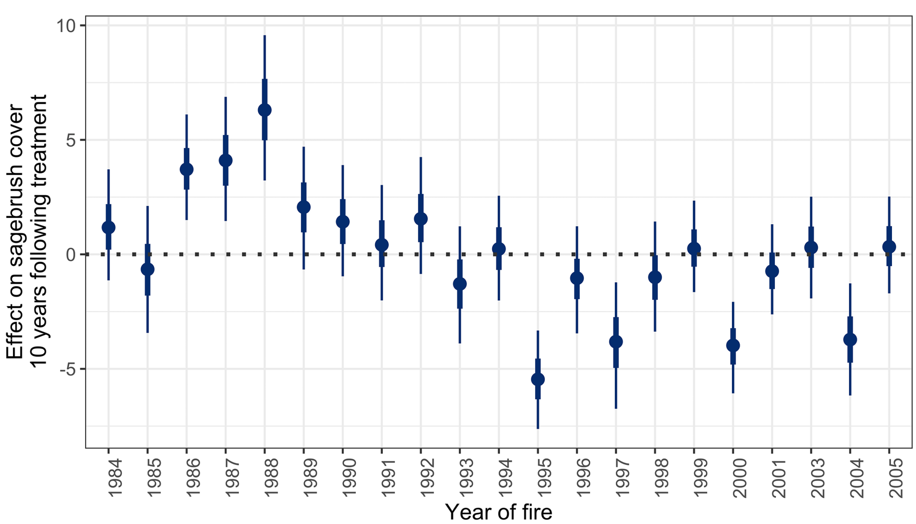


FIGURE 6 Varying intercept components for the effect of the year in which post-fire restoration seeding occurred on remotely sensed sagebrush cover (10 years following fire) in a model containing weather, climate, and biophysical site covariates; 50% and 90% credible intervals for each fire year's deviation from the mean intercept are indicated by thick and thin lines, with median estimates indicated by dots.

shifting mean conditions at sites may capture more of the variation in sagebrush recovery in this ecosystem than in spring weather. Targeted site selection based on expected mean climate conditions, rather than the selection of suitable years for treatment, may more effectively minimize losses in restoration investment. Management applications that leverage interannual variation must also weigh the inferential benefits of using more temporally resolved covariates against the analytical costs, especially given that the predictive value of weather may not be equal across all sites (Figures 4 and 5) and all densities of sagebrush (Figure 2). For instance, at lower sagebrush densities, interannual variation may result in the difference between predicting modest levels of recovery and complete recruitment failure, compared to high sagebrush densities, where the management-relevance of modest overprediction may be less consequential (Figure 2).

4.2 | Impacts of initiation year conditions on post-treatment sagebrush recovery

Existing studies of interannual weather variation in restoration frequently focus on the effects of planting years in particular (referred to as "year effects"; Groves et al., 2020; Stuble, Fick, & Young, 2017; Vaughn & Young, 2010; Werner et al., 2020). Planting year conditions may drive species arrival, niche preemption, and early niche modification, generating "historical contingencies" in community structure (Fukami, 2015). The addition of weather covariates from the first spring following seeding improved the prediction of sagebrush cover 10 years following treatment, suggesting that initiation year conditions may indeed leave long-lasting imprints on restoration outcomes (Table 2). However, we found that this improvement was minor, and that predictive performance continued to increase as additional weather covariates (from post-fire years 2–4) were added (Table 2). Our findings suggest that management-relevant variability in sagebrush recovery may emerge at other points along with these populations' trajectories beyond the planting year. These effects may be owed additional consideration in both analysis and experimental design. It is also possible that initiation year weather may have greater predictive importance in determining other ecological patterns, such as sagebrush establishment or community assembly (which were outside of the scope of this remotely sensed dataset; Supporting Information S2), compared to population growth (Fukami, 2015).

Across BLM lands within the Great Basin, we also found that certain reseeding years exhibited substantially lower or higher sagebrush cover in the decade following reseeding, beyond what was predicted by spring weather, climate, and biophysical variables (Table 2, Figure 6). Other time-varying social or ecological factors, such as the timing and locations of particular megafires, shifts in firefighting activities, variation in post-fire seeding practices (related to budgets and agency policy changes), yearly differences in grazing by native ungulates and livestock (Davies et al., 2020; Manier & Hobbs, 2007), or variation in remote sensing of sagebrush cover (Shi et al., 2020) could all contribute to these region-wide differences in sagebrush cover on seeded BLM lands. Further, other aspects of initiation year weather not considered in this study could contribute to the dominance of undesired invasive species overseeded natives (e.g., in grasslands, Bakker et al., 2003) or variation in competition with other rangeland plants (Hall et al., 1999; Rinella et al., 2015, 2016).

4.3 | Spatial variation in the influence of spring weather on sagebrush recovery

The relationships between spring weather and sagebrush growth, detected by coarse-scale remotely sensed data, reflect ecophysiological mechanisms identified in past field-based studies of sagebrush. Mean temperatures, spring precipitation, and late-winter snowpack retention have been linked to the occurrence and growth of reseeded sagebrush, primarily by influencing soil–water availability, specifically in the early stages of sagebrush development (Apodaca et al., 2017; Applestein et al., 2021; Nelson et al., 2013; O'Connor et al., 2020; Schlaepfer et al., 2014b). The overall negative effects of maximum and minimum temperatures detected here indicate a role for water deficit in influencing sagebrush recovery at a larger scale (Figures 3 and 4), as these factors drive the phenology of spring snowmelt, recharge, soil moisture, and seedling success during subsequent periods of summer drought. The positive effect of the previous year's precipitation also suggests that fluctuations in deeper soil water resources may additionally drive the growth of taprooted sagebrush shrubs that have survived initial establishment filters (as detected in past studies; Pilliod, Welty, & Arkle, 2017; Tredennick et al., 2016).

However, the effects of weather varied with sites' mean temperature and precipitation conditions, possibly reflecting shifting physiological constraints across sagebrush's range (Figures 4 and 5). At warm sites, reduced minimum temperatures may facilitate increased growth (Figure 4C,D) by prolonging the period during which soil water potential stays above thresholds relevant for germination, establishment, and growth; whereas, at cooler sites, lower temperature minima may inhibit snowmelt and the initiation of growing conditions (O'Connor et al., 2020). At the hottest sites, annual deviations in maximum temperature may be less likely to prolong soil moisture in ecologically significant ways, resulting in similar (and largely negative) changes in sagebrush cover across years (Figure 4A,B). Increased spring precipitation resulted in spatially consistent increases in sagebrush growth (Figure 5), but lagged precipitation effects were stronger in drier climates, possibly indicating increased variability in deeper soil water availability at these sites (Schlaepfer et al., 2012). Together these results provide evidence that the barriers to sagebrush restoration vary in space (along climate gradients) and in time (with annual weather conditions; Copeland et al., 2021). However, effect sizes for these variables were influenced by our focus on treated BLM lands, which may be more ecologically degraded and experience generally drier, warmer conditions, compared to the full extent of sagebrush steppe ecosystems (Reid et al., 2018; Simler-Williamson & Germino, 2022).

Spatial variation in the importance of weather suggests that the predictability of restoration outcomes may vary with the severity or nature of the environmental factors constraining community recovery (as proposed by Brudvig et al., 2017). Further, our findings emphasize that the weather effects detected by smaller-scale studies may not translate to improved prediction or management across large landscapes (Applestein et al., 2021). Considerations about the transferability of studies (given their environmental context) are particularly important considering that restoration treatments may be disproportionately applied to more stressful or degraded sites, compared to the full climatic range of sagebrush steppe ecosystems (Reid et al., 2018; Simler-Williamson & Germino, 2022).

4.4 | Toward prediction in restoration science

Future work should aim to explicitly isolate the extent to which weather conditions improve the prediction of restoration outcomes at new sites in management-relevant ways (Applestein et al., 2021), rather than explaining within-sample effects. In addition to temporal replication of treatments, datasets with frequent observations may be key to isolating the management relevance of annual weather, compared to long-term climate, given high correlations between these variables (Groves et al., 2020). An additional challenge inherent in the study of weather is that there is a myriad of possible variable combinations and temporal windows to consider, including lag effects (Ogle et al., 2015). In light of these large candidate variable sets, "sparse" models (e.g., Piironen & Vehtari, 2017) may be powerful approaches to minimize overfitting and achieve a model size more realistic for management use (Dietze, 2017).

Future conditions in the Great Basin are predicted to be warmer with more variable precipitation (Palmquist et al., 2016), invasive annual grasses continue to spread across western North America, and associated fire frequencies are expected to increase (Fusco et al., 2019). Therefore, "favorable" restoration years and suitable mean site conditions (Schlaepfer et al., 2014a) may become rarer regionally, as the total area requiring restoration intervention expands, possibly without a comparable increase in resources for restoration. These rapidly changing constraints underscore the need for studies that explicitly isolate the predictive importance of weather, relative to long-term shifts in mean conditions, to inform the effective use of limited restoration resources.

AUTHOR CONTRIBUTIONS

Matthew J. Germino supervised the project, including procuring funding. Cara Applestein coordinated spatial datasets and extraction of weather data, and Allison B. Simler-Williamson and Cara Applestein collaborated on the analysis with input from Matthew J. Germino. All authors co-developed the research questions and contributed to the manuscript text.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

DATA AVAILABILITYSTATEMENT

This analysis was developed using the Land Treatment Digital Library (https://ltdl.wr.usgs.gov/), the RCMAP sagebrush cover time series (https://www.mrlc.gov/data-services-page), and GridMet surface meteorological data (https://www.climatologylab.org/gridmet.html), in conjunction with other publicly-available data cited in the text. The processed set of treated sites are provided via Dryad: https://doi.org/10.25338/B87H16.

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REFERENCES

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, *33*(1), 121–131. https://doi.org/10.1002/joc.3413

Apodaca, L. F., Devitt, D. A., & Fenstermaker, L. F. (2017). Assessing growth response to climate in a Great Basin big sagebrush (*Artemisia tridentata*) plant community. *Dendrochronologia*, *45*, 52–61. https://doi.org/10.1016/j.dendro.2017.06.007

Applestein, C., Caughlin, T. T., & Germino, M. J. (2021). Weather affects post-fire recovery of sagebrush-steppe communities and model transferability among sites. *Ecosphere*, *12*(4), e03446e03446. https://doi.org/10.1002/ecs2.3446

Applestein, C., & Germino, M. J. (2021). Detecting shrub recovery in sagebrush steppe: Comparing Landsat-derived maps with field data on historical wildfires. *Fire Ecology*, *17*(1), 1–11. https://doi.org/10.1186/s42408-021-00091-7

Arkle, R. S., Pilliod, D. S., Hanser, S. E., Brooks, M. L., Chambers, J. C., Grace, J. B., Knutson, K. C., Pyke, D. A., Welty, J. L., & Wirth, T. A. (2014). Quantifying restoration effectiveness using multi-scale habitat models: Implications for sage-grouse in the Great Basin. *Ecosphere*, *5*(3), 1–32. https://doi.org/10.1890/ES13-00278.1

Bakker, J. D., Wilson, S. D., Christian, J. M., Li, X., Ambrose, L. G., & Waddington, J. (2003). Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, *13*(1), 137–153. https://doi.org/10.1890/1051-0761(2003)013[0137:COGROY]2.0.CO;2

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology*, *19*(1), 173–183. https://doi.org/10.1111/gcb.12046

Beven, K. J., & Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin*, *24*(1), 43–69. https://doi.org/10.1080/02626667909491834

Brabec, M. M., Germino, M. J., & Richardson, B. A. (2017). Climate adaption and post-fire restoration of a foundational perennial in cold desert: Insights from intraspecific variation in response to weather. *Journal of Applied Ecology*, *54*(1), 293–302. https://doi.org/10.1111/1365-2664.12679

Brudvig, L. A. (2011). The restoration of biodiversity: Where has research been and where does it need to go? *American Journal of Botany*, *98*(3), 549–558. https://doi.org/10.3732/ajb.1000285

Brudvig, L. A., Barak, R. S., Bauer, J. T., Caughlin, T. T., Laughlin, D. C., Larios, L., Matthews, J. W., Stuble, K. L., Turley, N. E., & Zirbel, C. R. (2017). Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology*, *54*(4), 1018–1027. https://doi.org/10.1111/1365-2664.12938

Bürkner, P. C. (2017). BRMS: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Carvalho, C. M., Polson, N. G., & Scott, J. G. (2009). Handling sparsity via the horseshoe. *Journal of Machine Learning Research*, *5*, 73–80.

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(44), 17430–17434. https://doi.org/10.1073/pnas.0704350104

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Copeland, S. M., Baughman, O. W., Boyd, C. S., Davies, K. W., Kerby, J., Kildisheva, O. A., & Svejcar, T. (2021). Improving restoration success through a precision restoration framework. *Restoration Ecology*, *29*(2), 1–8. https://doi.org/10.1111/rec.13348

Crausbay, S. D., Ramirez, A. R., Carter, S. L., Cross, M. S., Hall, K. R., Bathke, D. J., Betancourt, J. L., Colt, S., Cravens, A. E., Dalton, M. S., Dunham, J. B., Hay, L. E., Hayes, M. J., McEvoy, J., McNutt, C. A., Moritz, M. A., Nislow, K. H., Raheem, N., & Sanford, T. (2017). Defining ecological drought for the twenty-first century. *Bulletin of the American Meteorological Society*, *98*(12), 2543–2550. https://doi.org/10.1175/BAMS-D-16-0292.1

Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V., & Rey Benayas, J. M. (2016). A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, *7*, 1–8. https://doi.org/10.1038/ncomms11666

Davies, K. W., & Bates, J. D. (2017). Restoring big sagebrush after controlling encroaching western juniper with fire: Aspect and subspecies effects. *Restoration Ecology*, *25*(1), 33–41. https://doi.org/10.1111/rec.12375

Davies, K. W., Bates, J. D., & Boyd, C. S. (2020). Response of planted sagebrush seedlings to cattle grazing applied to decrease fire probability. *Rangeland Ecology & Management*, *73*(5), 629–635. https://doi.org/10.1016/j.rama.2020.05.002

Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., Svejcar, T. J., & Gregg, M. A. (2011). Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation*, *144*(11), 2573–2584. https://doi.org/10.1016/j.biocon.2011.07.016

Davies, K. W., Boyd, C. S., & Nafus, A. M. (2013). Restoring the sagebrush component in crested wheatgrass-dominated communities. *Rangeland Ecology & Management*, *66*(4), 472–478. https://doi.org/10.2111/REM-D-12-00145.1

Dietze, M. C. (2017). Prediction in ecology: A first-principles framework: A. *Ecological Applications*, *27*(7), 2048–2060. https://doi.org/10.1002/eap.1589

Eiswerth, M. E., Krauter, K., Swanson, S. R., & Zielinski, M. (2009). Post-fire seeding on Wyoming big sagebrush ecological sites: Regression analyses of seeded nonnative and native species densities. *Journal of Environmental Management*, *90*(2), 1320–1325. https://doi.org/10.1016/j.jenvman.2008.07.009

Fernández-Martínez, M., Garbulsky, M., Peñuelas, J., Peguero, G., & Espelta, J. M. (2015). Temporal trends in the enhanced vegetation index and spring weather predict seed production in Mediterranean oaks. *Plant Ecology*, *216*(8), 1061–1072. https://doi.org/10.1007/s11258-015-0489-1

Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340

Fukami, T., Bezemer, T. M., Mortimer, S. R., & Van Der Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290. https://doi.org/10.1111/j.1461-0248.2005.00829.x

Fusco, E. J., Finn, J. T., Balch, J. K., Chelsea Nagy, R., & Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(47), 23594–23599. https://doi.org/10.1073/pnas.1908253116

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. *American Statistician*, *73*(3), 307–309. https://doi.org/10.1080/00031305.2018.1549100

Groves, A. M., Bauer, J. T., & Brudvig, L. A. (2020). Lasting signature of planting year weather on restored grasslands. *Scientific Reports*, *10*(1), 1–10. https://doi.org/10.1038/s41598-020-62123-7

Groves, A. M., & Brudvig, L. A. (2019). Interannual variation in precipitation and other planting conditions impacts seedling establishment in sown plant communities. *Restoration Ecology*, *27*(1), 128–137. https://doi.org/10.1111/rec.12708

Hall, D. B., Anderson, V. J., & Monsen, S. B. (1999). *Competitive effects of Bluebunch wheatgrass, crested wheatgrass, and Cheatgrass on antelope bitterbrush seedling emergence and survival. RMRS-RP-16*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.1093/oseo/instance.00010394

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., & Meredith, G. R. (2018). Weather-centric rangeland revegetation planning. *Rangeland Ecology & Management*, *71*(1), 1–11. https://doi.org/10.1016/j.rama.2017.07.003

Hijmans, R. J., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. R Package version.

Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N., Wickham, J., & Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States-representing a decade of land cover change information Landsat-based mapping project. *Photogrammetric Engineering & Remote Sensing*, *81*(5), 345–354. https://doi.org/10.14358/PERS.81.5.345

Knutson, K. C., Pyke, D. A., Wirth, T. A., Arkle, R. S., Pilliod, D. S., Brooks, M. L., Chambers, J. C., & Grace, J. B. (2014). Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology*, *51*(5), 1414–1424. https://doi.org/10.1111/1365-2664.12309

Manier, D. J., & Hobbs, N. T. (2007). Large herbivores in sagebrush steppe ecosystems: Livestock and wild ungulates influence structure and function. *Oecologia*, *152*(4), 739–750. https://doi.org/10.1007/s00442-007-0689-z

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, *13*(4), 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

Miller, R. F., Knick S. T., Pyke D. A., Meinke C. W., Hanser S. E., Wisdom M. J., & Hild A. L. (2011). Characteristics of sagebrush habitats and limitations to long- term conservation. In S. T. Knick and J. W. Connelly (Eds)., *Greater Sage-Grouse: Ecology and conservation of landscape species and its habitats* (pp. 146–184). University of California Press, Berkeley, CA.

Myers, J. A., & Harms, K. E. (2009). Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecology Letters*, *12*(11), 1250–1260. https://doi.org/10.1111/j.1461-0248.2009.01373.x

Nelson, Z. J., Weisberg, P. J., & Kitchen, S. G. (2013). Influence of climate and environment on post-fire recovery of mountain big sagebrush. *International Journal of Wildland Fire*, *23*(1), 131–142. https://doi.org/10.1071/WF13012

O'Connor, R. C., Germino, M. J., Barnard, D. M., Andrews, C. M., Bradford, J. B., Pilliod, D. S., Arkle, R. S., & Shriver, R. K. (2020). Small-scale water deficits after wildfires create long-lasting ecological impacts. *Environmental Research Letters*, *15* (4), 1–10. https://doi.org/10.1088/1748-9326/ab79e4

Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., Loik, M. E., & Tissue, D. T. (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*, *18*(3), 221–235. https://doi.org/10.1111/ele.12399

Palmquist, K. A., Schlaepfer, D. R., Bradford, J. B., & Lauenroth, W. K. (2016). Mid-latitude shrub steppe plant communities: Climate change consequences for soil water resources. *Ecology*, *97*(9), 2342–2354. https://doi.org/10.1002/ecy.1457

Pierce, D. (2019). ncdf4: Interface to Unidata netCDF.

Piironen, J., & Vehtari, A. (2017). Sparsity information and regularization in the horseshoe and other shrinkage priors. *Electronic Journal of Statistics*, *11*(2), 5018–5051. https://doi.org/10.1214/17-EJS1337SI

Pilliod, D. S., & Welty, J. L. (2013). *Land treatment digital library*. US Geological Survey. https://doi.org/10.3133/ds806

Pilliod, D. S., Welty, J. L., & Arkle, R. S. (2017). Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution*, *7*(19), 8126–8151. https://doi.org/10.1002/ece3.3414

Pilliod, D. S., Welty, J. L., & Toevs, G. R. (2017). Seventy-five years of vegetation treatments on public rangelands in the Great Basin of North America. *Rangelands*, *39*(1), 1–9. https://doi.org/10.1016/j.rala.2016.12.001

Pyke, D. A., Wirth, T. A., & Beyers, J. L. (2013). Does seeding after wildfires in rangelands reduce erosion or invasive species? *Restoration Ecology*, *21*(4), 415–421. https://doi.org/10.1111/rec.12021

Reid, J. L., Fagan, M. E., & Zahawi, R. A. (2018). Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. *Science Advances*, *4*(5), 1–4. https://doi.org/10.1126/sciadv.aas9143

Rigge, M., Homer, C., Cleeves, L., Meyer, D. K., Bunde, B., Shi, H., Xian, G., Schell, S., & Bobo, M. (2020). Quantifying western U.S. rangelands as fractional components with multi-resolution remote sensing and in situ data. *Remote Sensing*, *12*(3), 1–26. https://doi.org/10.3390/rs12030412

Rinella, M. J., Espeland, E. K., & Moffatt, B. J. (2016). Studying long-term, large-scale grassland restoration outcomes to improve seeding methods and reveal knowledge gaps. *Journal of Applied Ecology*, *53*(5), 1565–1574. https://doi.org/10.1111/1365-2664.12722

Rinella, M. J., Hammond, D. H., Bryant, A. M., & Kozar, B. J. (2015). High precipitation and seeded species competition reduce seeded shrub establishment during dryland restoration. *Ecological Applications*, *25*(4), 1044–1053.

Schlaepfer, D. R., Lauenroth, W. K., & Bradford, J. B. (2014a). Modeling regeneration responses of big sagebrush (Artemisia tridentata) to abiotic conditions. *Ecological Modelling*, *286*, 66–77. https://doi.org/10.1016/j.ecolmodel.2014.04.021

Schlaepfer, D. R., Lauenroth, W. K., & Bradford, J. B. (2014b). Natural regeneration processes in big sagebrush (Artemisia tridentata). *Rangeland Ecology & Management*, *67*(4), 344–357. https://doi.org/10.2111/REM-D-13-00079.1

Seabloom, E. W. (2011). Spatial and temporal variability in propagule limitation of California native grasses. *Oikos*, *120*(2), 291–301. https://doi.org/10.1111/j.1600-0706.2010.18781.x

Shi, H., Homer, C., Rigge, M., Postma, K., & Xian, G. (2020). Analyzing vegetation change in a sagebrush ecosystem using long-term field observations and Landsat imagery in Wyoming. *Ecosphere*, *11*(12), 1–20. https://doi.org/10.1002/ecs2.3311

Shi, H., Rigge, M., Homer, C. G., Xian, G., Meyer, D. K., & Bunde, B. (2018). Historical cover trends in a sagebrush steppe ecosystem from 1985 to 2013: Links with climate, disturbance, and management. *Ecosystems*, *21*(5), 913–929. https://doi.org/10.1007/s10021-017-0191-3

Shriver, R. K., Andrews, C. M., Pilliod, D. S., Arkle, R. S., Welty, J. L., Germino, M. J., Duniway, M. C., Pyke, D. A., & Bradford, J. B. (2018). Adapting management to a changing world: Warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands. *Global Change Biology*, *24*(10), 4972–4982. https://doi.org/10.1111/gcb.14374

Simler-Williamson, A. B., & Germino, M. J. (2022). *Statistical consideration of nonrandom treatment applications reveals region-wide benefits of a widespread post-fire restoration action*. Nature Communications, Accepted.

Stan Development Team. (2020). RStan: the R interface to Stan. Retrieved from http://mc-stan.org

Stuble, K. L., Fick, S. E., & Young, T. P. (2017). Every restoration is unique: Testing year effects and site effects as drivers of initial restoration trajectories. *Journal of Applied Ecology*, *54*(4), 1051–1057. https://doi.org/10.1111/1365-2664.12861

Stuble, K. L., Zefferman, E. P., Wolf, K. M., Vaughn, K. J., & Young, T. P. (2017). Outside the envelope: Rare events disrupt the relationship between climate factors and species interactions. *Ecology*, *98*(6), 1623–1630. https://doi.org/10.1002/ecy.1820

Suding, K. (2011). Understanding successes and failures in restoration ecology. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Tredennick, A. T., Hooten, M. B., Aldridge, C. L., Homer, C. G., Kleinhesselink, A. R., & Adler, P. B. (2016). Forecasting climate change impacts on plant populations over large spatial extents. *Ecosphere*, *7*(10), 1–16. https://doi.org/10.1002/ecs2.1525

U.S. Geological Survey. (2017). *1/3rd arc-second Digital Elevation Models (DEMs)—USGS National Map 3DEP Downloadable Data Collection.* U.S. Geological Survey.

Vaughn, K. J., & Young, T. P. (2010). Contingent conclusions: Year of initiation influences ecological field experiments, but temporal replication is rare. *Restoration Ecology*, *18*(Suppl. 1), 59–64. https://doi.org/10.1111/j.1526-100X.2010.00714.x

Vehtari, A., Gelman, A., & Gabry, J. (2016). loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. Retrieved from https://cran.r-project.org/package=loo.

Werner, C. M., Stuble, K. L., Groves, A. M., & Young, T. P. (2020). Year effects: Interannual variation as a driver of community assembly dynamics. *Ecology*. https://doi.org/10.1002/ecy.3104

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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