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Weather affects post-fire recovery of sagebrush-steppe communities and model transferability among sites

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Abstract. Altered climate, including weather extremes, can cause major shifts in vegetative recovery after disturbances. Predictive models that can identify the separate and combined temporal effects of disturbance and weather on plant communities and that are transferable among sites are needed to guide vulnerability assessments and management interventions. We asked how functional group abundance responded to time since fire and antecedent weather, if long-term vegetation trajectories were better explained by initial post-fire weather conditions or by general five-year antecedent weather, and if weather effects helped predict post-fire vegetation abundances at a new site. We parameterized models using a 30-yr vegetation monitoring dataset from burned and unburned areas of the Orchard Training Area (OCTC) of southern Idaho, USA, and monthly PRISM data, and assessed model transferability on an independent dataset from the well-sampled Soda wildfire area along the Idaho/Oregon border. Sagebrush density increased with lower mean air temperature of the coldest month and slightly increased with higher mean air temperature of the hottest month, and with higher maximum January–June precipitation. Perennial grass cover increased in relation to higher precipitation, measured annually in the first four years after fire and/or in September–November the year of fire. Annual grass increased in relation to higher March–May precipitation in the year after fire, but not with September–November precipitation in the year of fire. Initial post-fire weather conditions explained 1% more variation in sagebrush density than recent antecedent 5-yr weather did but did not explain additional variation in perennial or annual grass cover. Inclusion of weather variables increased transferability of models for predicting perennial and annual grass cover from the OCTC to the Soda wildfire regardless of the time period in which weather was considered. In contrast, inclusion of weather variables did not affect transferability of the forecasts of post-fire sagebrush density from the OCTC to the Soda site. Although model transferability may be improved by including weather covariates when predicting post-fire vegetation recovery, predictions may be surprisingly unaffected by the temporal windows in which coarse-scale gridded weather data are considered.

Key words: annual grass; fire; perennial grass; post-fire weather; sagebrush; sagebrush-steppe; weather variability.

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Introduction

Changing global patterns of precipitation and temperature are impacting vegetation dynamics by modifying habitat suitability and disturbance regimes (Cramer et al. 2001, Griffiths et al. 2015, Kim et al. 2018). Hotter and drier conditions in the western United State are expected to increase the frequency, severity, and size of wildfires (McKenzie et al. 2004, Abatzoglou and Kolden 2011). Fire has the potential to spur much more rapid rates of change in species composition than altered weather patterns alone (Dale et al. 2001, McKenzie et al. 2004). In many ecosystems, fire disturbances combined with weather conditions are affecting recovery of key foundational native species (Keeley et al. 2005, Nelson et al. 2014, Meng et al. 2015). Understanding how initial post-fire recovery and recruitment will affect long-term trajectories of certain functional groups, in light of weather patterns, is critical to understanding how the combination of weather and fire influence the vegetative composition of ecosystems (Keane et al. 2013).

Parameterizing weather in explanatory or predictive models can be particularly challenging because there are a myriad of weather variables which can be aggregated over any time frame. In many ecosystems, post-disturbance recruitment occurs episodically during periods of favorable weather conditions (Enright et al. 2015). Favorable weather conditions for recruitment may not be known a priori, and major community composition changes in response to weather variability can lag behind extreme events, only realized after cumulative seasons of weather conditions deviating from average (Ogle and Reynolds 2004, Wu et al. 2015). Vegetative community structure at any point in time will reflect past weather events (Anderson and Inouye 2001, Ogle et al. 2015, Wilson et al. 2017). Forecasting future vegetation responses to climate change will require quantifying the relative importance of short-term vs. longer-term weather effects for shaping plant communities.

Sagebrush steppe occupies a vast, sparsely populated, ~500,000 km^2 area of western North America that includes high variability in climate, soils, disturbances, and other factors affecting plant communities (Chambers et al. 2014, McIver and Brunson 2014). Most field-based information about vegetation responses to climate and other drivers in sagebrush steppe has come from a relatively small number of locations and areas compared to this vast domain (Nelson et al. 2014, Shinneman and McIlroy 2016). Thus, knowing the generalizability of plant community and environment relationships is critical for science and management applications in sagebrush steppe (McIver and Brunson 2014). Plant-environment models trained using site-specific data can be tested for generalizability by assessing accuracy of predictions made at different sites (Wenger and Olden 2012). Such tests are a priority need in ecology (Houlahan et al. 2017, Dietze et al. 2018). Developing ecological forecasts for restoration science will also enable transfer of knowledge from highly studied sites to sites in need of land management (Brudvig et al. 2017).

Sagebrush-steppe ecosystems provide an excellent focal system in which to consider the interplay of disturbance and climate variability. Weather at specific time periods after fire is critically important in determining whether a plant community is invaded by exotic annual grass vs. re-established with sagebrush or perennial grass (Lesica et al. 2007, Hardegree et al. 2012, Nelson et al. 2014). After burning of sagebrush steppe, exotic annual grasses compete with perennial native species for soil water or other soil resources (Melgoza et al. 1990, DiCristina and Germino 2006). Furthermore, sagebrush establishment after fire can be highly episodic, and both winter and spring precipitation are important for new seedling establishment (Nelson et al. 2014, Houlahan et al. 2017, Shriver et al. 2019). Although establishment the year directly after fire is important, sagebrush may take advantage of high precipitation for several years after fire occurrence (Lesica et al. 2007, Nelson et al. 2014). Following establishment, most sagebrush seedling mortality occurs in the first year (Donovan and Ehleringer 1991, Owens and Norton 1992), with a previous study finding that minimum spring temperatures can be a limiting factor of sagebrush survival (Brabec et al. 2017). There is also evidence that sagebrush communities display a lagged response to weather: Both Anderson and Inouye (2001) and Pilliod et al. (2017) found that precipitation three or four years earlier was positively correlated with sagebrush or native herbaceous cover. These observations suggest that consideration of time lags could improve analyses of vegetation-water relationships.

We analyzed the relative importance of weather patterns on cover of exotic annual and perennial grasses and density of sagebrush as they varied annually over a nearly 30-yr observation period on a large landscape where multiple fires had occurred. We sought to determine how annual and perennial grass cover and sagebrush density responded to time since fire and antecedent weather using a model comparison approach that included tests of model fit, as well as transferability. Our questions were as follows:

1. How do the dominant sagebrush-steppe functional groups (perennial grass, annual grass, and sagebrush) respond to time since fire and antecedent weather conditions—either during specific post-fire windows or during a general antecedent 5-yr period?
2. Do post-fire weather conditions during specific recruitment windows leave a lasting impact on long-term vegetation trajectories or is functional group dominance more a product of recent weather, regardless of post-fire conditions?
3. Does consideration of post-fire weather or recent 5-yr weather help predict post-fire outcomes at a new site?

Materials and Methods

Sites

Data used to parameterize models were collected between 1989 and 2017 from monitoring plots spread across approximately 108,000 ha on the Orchard Combat Training Center (OCTC) located in the Morley Nelson Snake River Birds of Prey National Conservation Area in Southwestern Idaho (Fig. 1). Approximately half of the plots burned at least once between 1957 and 2014. We only included data records where monitoring occurred in consecutive years because our analysis was on year-to-year change. The dominant sagebrush type in this system is Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*).

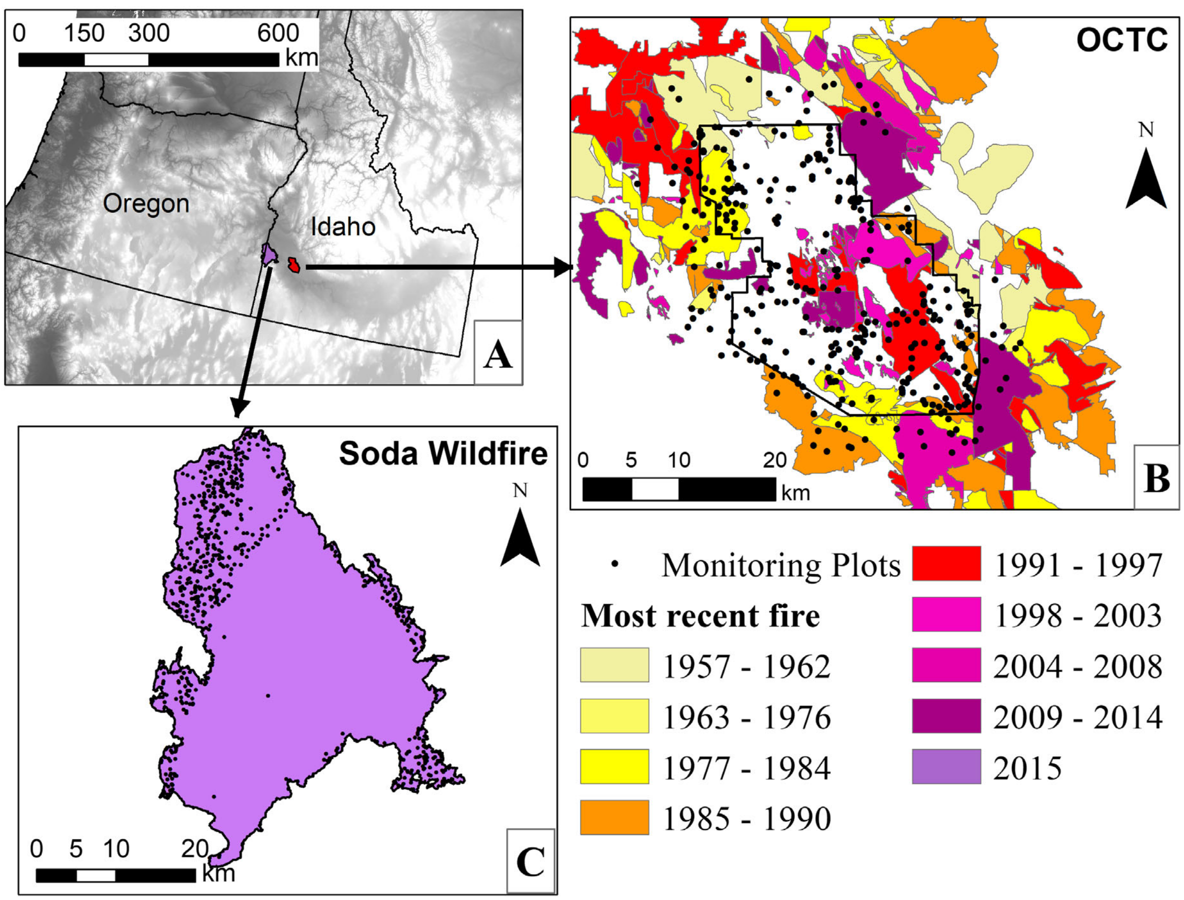

Fig. 1. Location of the Orchard Combat Training Center (OCTC), where data for model parameterization were collected, and Soda wildfire, where data for model validation were collected, are shown relative to elevation (panel A; darker shades are lower elevation based on the USGS digital elevation model). The distribution of sampling plots and fire histories are shown for OCTC in panel (B) and the Soda fire area in panel (C).

Bluebunch wheatgrass (*Psuedoroegneria spicata*) and Sandberg's bluegrass (*Poa secunda*) were the dominant bunchgrass species. According to land manager records, only 6% of plots had recorded seedlings of any type (primarily big sagebrush or shadscale, *Atriplex* sp.), and only two plots have seedlings recorded within 5 yr of fire. Elevation ranges from 862 and 1066 m (U.S. Geological Survey's Digital Elevation Model, 30-m pixel). Average annual precipitation (between 1989 and 2017) ranged from 199 to 307 mm, and average monthly temperature was between 10°C and 12°C (PRISM 2017). A total of 6478 plot-year entries were included in analysis.

Data for model transferability tests came from the Soda wildfire (burned in 2015) for monitoring done 2016–2018 and only 2017 and 2018 data were used to incorporate the previous year's density or cover data as a model input. The eastern edge of the Soda wildfire site is approximately 25 km from the OCTC across the Snake River (Fig. 1). Areas that were seeded by managers with sagebrush were excluded from this analysis because removing these areas from this analysis primarily left lower elevation areas that were more comparable in elevation and other site conditions to the OCTC. The dominant sagebrush type in this system is Wyoming big sagebrush with some low sagebrush (*A. arbuscula*). Low sagebrush were excluded from analysis. Bluebunch wheatgrass and Sandberg's bluegrass were the dominant bunchgrass species. Among the plots included in the test dataset, about 5% and 7% were drill seeded or aerially seeded with perennial grass, respectively. The total number of plot-year entries included was 698. Elevation for the test plots selected on the Soda wildfire ranged from 747 to 1692 m (U.S. Geological Survey's Digital Elevation Model, 30-m pixel). Average annual precipitation (between 2016 and 2018) ranged from 238 to 473 mm, and average monthly temperature was between 8°C and 11°C (PRISM 2017).

Data collection

At the OCTC, cover data for perennial and annual grasses were derived from line point intercept monitoring (LPI). Density of sagebrush (plants/m^2) came from belt transects ranging from 100 to 1400 m^2.

At the Soda wildfire, cover data for perennial and annual grasses were derived from grid-point intercept (GPI) from overhead photographs (Applestein et al. 2018). We quantified sagebrush density using a frequency-density method. First, we counted individuals in a 1-m^2 quadrat, and if three individuals were not found, we moved outwards in circular plots with radiuses of 5.5, 9, 13, and 18 m until we found at least three individuals within the incremental area. Then, we completed counting all the individual plants in that radius to determine density. Density was calculated as the number of individuals over the area searched (to obtain plants/m^2).

Calculation of climate and landscape variables

For OCTC and Soda data, we calculated the following from 800-m resolution PRISM data from 1957 to 2018 by plot: monthly precipitation, mean daily temperature by month, maximum daily temperature by month, and minimum daily temperature by month. Time since fire was derived by extracting the date of the last fire on record from the Land Treatment Digital Library database in the Great Basin (Pilliod and Welty 2013). If there was no record of the last fire, we assumed that the last fire was more than 100 yr prior and coded this as such in the input data.

Annual and perennial grass cover were treated as continuous variables, and sagebrush density was treated as an ordinal variable. We transformed exotic annual grass and perennial grass cover as suggested by Smithson and Verkuilen (2006) to remove 0 and 1 values, which cannot be fit with a beta-distribution. The transformation is given as

$$y^n = \frac{y'(n-1)+0.5}{n}$$

where n is the sample size, y' is the original data point, and y^n is the transformed data point. We then modeled transformed grass cover values with a beta-distributed random variable using a logit link function. Density of sagebrush (number/m^2) was binned into one of five possible categories: 0, <0.5, 0.5–1, 1–5, and >5 plants/m^2 and modeled via ordinal regression (using the cumulative distribution with logit link). We chose to bin sagebrush density rather than model it directly because exact counts are more likely to be site-specific, whereas density bins are likely to be more generalizable across different sites. A previous assessment comparing plant cover measured as a continuous vs. ordinal variable found that using ordinal categories did not result in a significant loss of information (Irvine et al. 2019).

Model parameterization

We compared models of vegetative functional group density or cover as predicted by (1) no weather or fire effects (landscape effects only), (2) landscape and fire effects only (time since fire), (3) landscape and antecedent weather effects (with or without time since fire). We parameterized antecedent weather variability in two ways. First, we built a model that included weather variables selected a priori during specific time windows in the first several years after fire with the assumption that weather during these time periods would have lasting impacts on functional group density or cover. Secondly, we built models that included weather variables within the most recent five years, allowing the data to determine important time windows.

Cover of the target functional groups were estimated using Bayesian generalized linear models (GLMs) fit in STAN (a no-U-turn sampler) via the brms package in R (Bürkner 2017, R Core Team 2017). We also explored fitting generalized additive models (GAMs), which do not make assumptions about the linearity of response curves, but GAM model errors were higher than the GLM errors so we report on the GLMs here for the final analysis. To better interpret covariate effects and facilitate model convergence, we standardized covariates (but not response variables) using the scale package in R, which subtracts the mean from each value and divides by the standard deviation. Additional covariates (elevation, percent sand, percent clay) were incorporated into all models because they are known to affect the habitat suitability of a site for sagebrush (Schlaepfer et al. 2012, Nelson et al. 2014). These covariates were not strongly correlated with each other (Appendix S1: Table S1). All models included an autoregressive term (density or cover from the previous time step). Model convergence was assessed by rhat values and visual checks of the posterior predictive distributions (calculation given by Brooks and Gelman 1998).

We set uninformative priors for the models from the brms package. These were as follows: normal(0,1) for all parameters except for the beta dispersion parameter, Φ, for which gamma (0.01,0.01) was used.

The models are as follows

$$A_{pt} \sim \mathrm{Beta}(\mu_t^{\mathrm{a}}, \Phi^{\mathrm{a}})$$

where A_{pt} is the observed annual grass cover at year t and plot p, μ_t^{a} is the overall mean annual grass cover in year t, Φ^{a} is the annual grass dispersion parameter.

$$P_{pt} \sim \mathrm{Beta}(\mu_t^{\mathrm{p}}, \Phi^{\mathrm{p}})$$

where P_{pt} is the observed perennial grass cover at year t and plot p, μ_t^{p} is the overall mean perennial grass cover in year t, Φ^{p} is the perennial grass dispersion parameter.

$$q_{pt} = \Pr\{S_{pt} > k | X_{pt}\} = \sum_{k+1}^{5} p_{ptk}$$

where S_{pt} is the observed sagebrush density category and $k = 1, \ldots, 5$, which corresponds to $S = 0$, $0 < S < 0.5$, $0.5 < S < 1$, $1 < S < 5$, and $S > 5$, respectively. q_{pt} is the probability that a plot p during year t has a sagebrush density greater than that defined by k, p_{ptk} is the probability that a plot has a sagebrush density in category k, given X_{pt} covariates at plot p and year t. This parameterization reflects a cumulative logistic regression where the calculation of the probability of a given density category takes into consideration the probability of any of the other density categories occurring.

μ_t^{a}, μ_t^{p}, and q_{pt} (annual grass cover, perennial grass cover, and sagebrush density category, respectively) are calculated using different covariates for each model, where superscript $^{\mathrm{a}}$ denotes annual grass cover covariates, superscript $^{\mathrm{p}}$ denotes perennial grass cover covariates, and superscript $^{\mathrm{s}}$ denotes sagebrush density covariates. A_{pt-1} stands for annual grass cover at plot p one year before time t, P_{pt-1} stands for perennial grass cover at plot p one year before time t, and S_{pt-1} stands for sagebrush density category at plot p one year before time t. All models include terms β0, β1, β2, and β3, which are coefficients for elevation (elev), percent sand (sand), percent clay (clay), and the previous year's cover/density, respectively.

Model 0: null model

The null model served as a baseline with which to compare the time since fire and weather effects models with the null hypothesis that neither weather conditions nor time-since-fire covariates improve predictions of post-fire vegetative outcomes. The null model considered the year-to-year change in sagebrush, annual grass, and perennial grass cover with fixed landscape covariates (elevation, percent sand, percent clay) but no fire or weather variables. μ_t^a, μ_t^p, and q_{pt} (annual grass cover, perennial grass cover, and sagebrush density category) are calculated as such:

$$\mathrm{logit}(\mu_t^a) = a^a + \beta 0^a \times \mathrm{Elev} + \beta 1^a \times \mathrm{Sand} + \beta 2^a \times \mathrm{Clay} + \beta 3^a \times A_{pt-1}$$

$$\mathrm{logit}(\mu_t^p) = a^p + \beta 0^p \times \mathrm{Elev} + \beta 1^p \times \mathrm{Sand} + \beta 2^p \times \mathrm{Clay} + \beta 3^p \times P_{pt-1}$$

$$\mathrm{logit}(q_{pt}) = a^s + \beta 0^s \times \mathrm{Elev} + \beta 1^s \times \mathrm{Sand} + \beta 2^s \times \mathrm{Clay} + \beta 3^s \times S_{pt-1}.$$

Model 1: time since fire

The time-since-fire model was similar to the null model in that it tested if post-fire vegetative outcomes could be predicted purely with time since fire and landscape covariates but no inclusion of weather variables. The model considered the year-to-year change in sagebrush, annual grass cover, and perennial grass cover as a function of time since fire with no consideration for weather variables. μ_t^a, μ_t^p, and q_{pt} (annual grass cover, perennial grass cover, and sagebrush density category) are calculated as such:

$$\mathrm{logit}(\mu_t^a) = a^a + \beta 0^a \times \mathrm{Elev} + \beta 1^a \times \mathrm{Sand} + \beta 2^a \times \mathrm{Clay} + \beta 3^a \times A_{pt-1} + \beta 4^a \times \mathrm{Yrs}$$

$$\mathrm{logit}(\mu_t^p) = a^p + \beta 0^p \times \mathrm{Elev} + \beta 1^p \times \mathrm{Sand} + \beta 2^p \times \mathrm{Clay} + \beta 3^p \times P_{pt-1} + \beta 4^p \times \mathrm{Yrs}$$

$$\mathrm{logit}(q_{pt}) = a^s + \beta 0^s \times \mathrm{Elev} + \beta 1^s \times \mathrm{Sand} + \beta 2^s \times \mathrm{Clay} + \beta 3^s \times S_{pt-1} + \beta 4^s \times \mathrm{Yrs}$$

where β4 is the coefficient for time since fire (yrs).

Model 2: time since fire and post-fire weather events

The second model tested how time since fire and weather covariates in the first several years after fire would affect post-fire vegetation recovery. We hypothesized that pre-selected weather variables during specific time windows in the first several years after fire would have lasting impacts on functional group density or cover. We only included plots that burned from 1900 to 2016 for this analysis (n = 5374). A previous analysis of weather variable effects on vegetation at the OCTC found no relationship between temperature and cheatgrass or native herbaceous cover (Pilliod et al. 2017), so we did not include temperature variables for the annual or perennial grass cover models. The two climate variables used for testing annual grass cover were fall and spring precipitation the year following fire since Bradley et al. (2016) identified these variables as directly affecting annual grass growth and biomass. Native perennial grass cover, specifically bluebunch wheatgrass and Sandberg's bluegrass, is positively correlated with higher fall and total annual precipitation (Anderson and Inouye 2001, Adler et al. 2009). Consequently, we tested fall and total annual precipitation on the year-to-year variation in perennial grass cover. Furthermore, because Anderson and Inouye (2001) identified a four-year lag for precipitation effects on total perennial grass cover, we included average annual precipitation for the first four years following fire.

We selected climate variables for sagebrush based on factors known to be important specifically for seedling recruitment and initial survival; these included average winter/spring precipitation (Shriver et al. 2019), maximum precipitation January–June, spring temperature (Brabec et al. 2017), mean temperature of the coldest month, and mean temperature of the hottest month. All of these variables were assessed during the first four years after the fire. μ_t^a, μ_t^p, and q_{pt} (annual grass cover, perennial grass cover, and sagebrush density category) are calculated as such:

$$\mathrm{logit}(\mu_t^a) = a^a + \beta 0^a \times \mathrm{Elev} + \beta 1^a \times \mathrm{Sand} + \beta 2^a \times \mathrm{Clay} + \beta 3^a \times A_{pt-1} + \beta 4^a \times \mathrm{Yrs} + \beta 5^a \times \mathrm{MMPYr1} + \beta 6^a \times \mathrm{SNPYr0}$$

$$\mathrm{logit}(\mu_t^p) = a^p + \beta 0^p \times \mathrm{Elev} + \beta 1^p \times \mathrm{Sand} + \beta 2^p \times \mathrm{Clay} + \beta 3^p \times P_{pt-1} + \beta 4^p \times \mathrm{Yrs} + \beta 6^p \times \mathrm{SNPYr0} + \beta 7^p \times \mathrm{APYr14}$$

$$\begin{aligned}\mathrm{logit}(q_{pt}) &= a^s + \beta0^s \times \mathrm{Elev} + \beta1^s \times \mathrm{Sand} + \beta2^s \\ &\quad \times \mathrm{Clay} + \beta3^s \times S_{pt-1} + \beta4^s \times \mathrm{Yrs} \\ &\quad + \beta8^s \times \mathrm{JAP14} + \beta9^s \times \mathrm{JJP14} + \beta10^s \\ &\quad \times \mathrm{MJT14} + \beta11^s \times \mathrm{MnCMn14} \\ &\quad + \beta12^s \times \mathrm{MxHMn14}\end{aligned}$$

where β5 is the coefficient for March–May precipitation in the first year after fire (MMPYr1), β6 is the coefficient for September–November precipitation in the year of fire SNPYr0, β7 is the coefficient for annual precipitation years one through four after fire APYr14, β8 is the coefficient for mean January–April precipitation years one through four after fire (JAP14), β9 is the coefficient for the maximum January–June precipitation years one through four after fire JJP14, β10 is the coefficient for the mean March–June precipitation in years one through four after fire (MJT14), β11 is the coefficient for the mean temperature of the coldest month in years one through four after fire (McCMn14), and β12 is the coefficient for the mean temperature of the hottest month in years one through four after fire (MxHMn14).

Model 3: recent five-year weather using random forests to weigh the importance of weather during antecedent months

The third model used a moving window approach to assess how antecedent weather at certain times of the year affects density or cover of sagebrush, annual grasses, and perennial grasses with no hypothesis concerning what times of year would have the most impact (Fig. 2). We allowed the data to inform which weather windows affected functional group density or cover. Our approach is conceptually

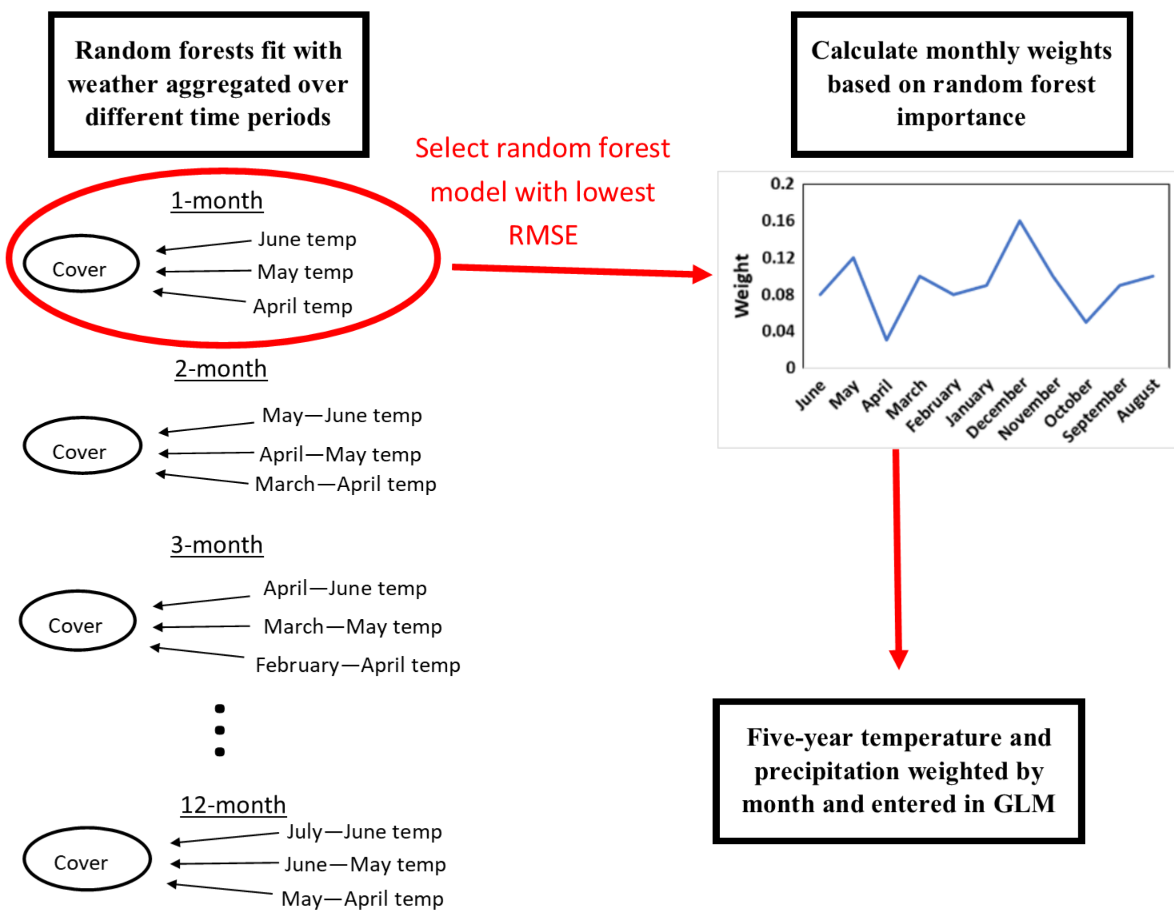

Fig. 2. Conceptual example of analysis used to fit models 3 and 4. Only temperature is shown as an example on the diagram, although precipitation was also included.

similar to the ecological memory models fit by Ogle et al. (2015), but with weather weights calculated via random forest importance instead of from a fitted Dirichlet distribution. Deriving monthly weather weights from this distribution makes the assumption that there is a point in time in the past that is most important for predicting current plant responses and that the importance of weather events before or after this point declines along a specified parametric curve. We anticipated that there might be multiple spikes of importance during times of the year that were particularly important to plant growth and that using a method with sufficient flexibility to represent these spikes would help to determine certain periods of time that had the most impact on current plant density or cover.

Random forests

To determine how to weigh specific time periods of past weather, we fit random forests to predict the response variables (annual grass, perennial grass, and sagebrush density) from summed monthly precipitation and average monthly temperature combined across different time period lengths. A similar technique to identify temporal lags and time period lengths has previously been used for looking at climate effects in a remote sensing context (Lamberty et al. 2012). Random forests were trained using the caret package in R using the parRF model.

In the first step, we fit random forests with monthly precipitation and monthly average temperature as the independent variables aggregated over 1-, 2-, 3-, 4-, 5-, 6-, or 12-month time periods. In each iteration, all five years of previous weather data were included but the window length determined the level of temporal aggregation (for instance, the random forest with 1-month windows included a variable for each month in the five-year time period, whereas the random forest with 6-month windows included an averaged variable for each overlapping 6-month time period). The random forest with the lowest out-of-bag (OOB) root mean square error (RMSE) was selected (for all three functional groups, it was the 1-month time period random forest). OOB is the prediction error on average of each sample predicted by those trees which did not use the sample for training. In the second step, importance values for each of these 1-month time periods were then calculated using the varImp function in the caret package (Kuhn 2012). Monthly weights were calculated scaled based on variable importance values from the random forest with all weights summing to 1. In the final step, cumulative five-year average temperature and monthly precipitation were calculated using monthly weights. A conceptual example of this method is shown in Fig. 2. To facilitate model-fitting in random forest models, we considered sagebrush density as a continuous response variable for this step.

Full GLM model using monthly weights derived from random forest

We assigned proportional weights to each window relative to the importance of each window from the random forest with all weights equaling 1 (this was done separately for each functional group). μ_t^{a}, μ_t^{p}, and q_{pt} (annual grass cover, perennial grass cover, and sagebrush density category) in the final model are thus defined as:

$$
\begin{aligned}
\operatorname{logit}(\mu_t^{\mathrm{a}}) = {} & a^{\mathrm{a}} + \beta 0^{\mathrm{a}} \times \mathrm{Elev} + \beta 1^{\mathrm{a}} \times \mathrm{Sand} \\
& + \beta 2^{\mathrm{a}} \times \mathrm{Clay} + \beta 3^{\mathrm{a}} \times A_{pt-1} \\
& + \beta 13^{\mathrm{a}} \times \textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{a}} + \beta 14^{\mathrm{a}} \\
& \times {}_{-}\textstyle\sum^{i=1} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{a}} \times \beta 15^{\mathrm{a}} \\
& \times \operatorname{int}\left(\textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{a}}, \textstyle\sum_{i=1}^{n} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{a}}\right)
\end{aligned}
$$

$$
\begin{aligned}
\operatorname{logit}(\mu_t^{\mathrm{p}}) = {} & a^{\mathrm{p}} + \beta 0^{\mathrm{p}} \times \mathrm{Elev} + \beta 1^{\mathrm{p}} \times \mathrm{Sand} \\
& + \beta 2^{\mathrm{p}} \times \mathrm{Clay} + \beta 3^{\mathrm{p}} \times P_{pt-1} \\
& + \beta 13^{\mathrm{p}} \times \textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{p}} + \beta 14^{\mathrm{p}} \\
& \times \textstyle\sum_{i=1}^{n} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{p}} \times \beta 15^{\mathrm{p}} \\
& \times \operatorname{int}\left(\textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{p}}, \textstyle\sum_{i=1}^{n} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{p}}\right)
\end{aligned}
$$

$$
\begin{aligned}
\operatorname{logit}(q_{pt}) = {} & a^{\mathrm{s}} + \beta 0^{\mathrm{s}} \times \mathrm{Elev} + \beta 1^{\mathrm{s}} \times \mathrm{Sand} + \beta 2^{\mathrm{s}} \\
& \times \mathrm{Clay} + \beta 3^{\mathrm{s}} \times S_{pt-1} \\
& + \beta 13^{\mathrm{s}} \times \textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{s}} + \beta 14^{\mathrm{s}} \\
& \times \textstyle\sum_{i=1}^{n} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{s}} \times \beta 15^{\mathrm{s}} \\
& \times \operatorname{int}\left(\textstyle\sum_{i=1}^{n} \mathrm{ppt} \times \mathrm{wp}_i^{\mathrm{s}}, \textstyle\sum_{i=1}^{n} \mathrm{tmp} \times \mathrm{wt}_i^{\mathrm{s}}\right)
\end{aligned}
$$

where wp_i is the month-specific and functional group-specific precipitation weight and wt_i is the month-specific and functional group-specific temperature weight. β13 is the coefficient of the weighted sum of precipitation ($\sum_{i=1}^{n}$ppt), β14 is the coefficient of the weighted sum of temperature ($\sum_{i=1}^{n}$tmp) and β15 is the coefficient of an interaction term between precipitation and mean monthly temperature (int).

Model 4: time since fire and recent five-year weather using random forests to weigh the importance of weather during antecedent months

Model 4 was the same as model 3, but with an added term for time since fire (β4 × Yrs) for each functional group, in order to test if including timing of fire as a covariate (but not specifically post-fire weather conditions) improved predictions of post-fire outcomes in a recent weather model.

Model fit and significance of effect sizes

We assessed model fit using leave-one-out (loo) cross-validation from the brms package (Bürkner 2017). For annual and perennial grass cover, we evaluated model fit using RMSE (root mean squared error), NRMSE (normalized root mean squared error), and squared bias. RMSE is calculated as

$$\mathrm{RMSE} = \left[\frac{\sum_{i=1}^{n}(P_i - A_i)^2}{n}\right]^{0.5}$$

where n is the sample size, P_i is the predicted value, and A_i is the actual value (Willmott 1981). NRMSE is calculated by dividing the RMSE by the range of the observed response variable. For sagebrush density, probability predictions were made for each density category and the category with the highest probability was taken to be the density prediction. From these predictions, we calculated a confusion matrix and evaluated model fit using overall accuracy, and Cohen's kappa (referred to just as kappa hereafter) using the caret package in R (Kuhn 2012). Kappa is calculated as

$$\mathrm{kappa} = \frac{P_\mathrm{o} - P_\mathrm{e}}{1 - P_\mathrm{e}}$$

where P_e is the chance of proportional agreement between the predicted and actual data and P_o is the actual proportional agreement between the predicted and actual data for categorical variables (Cohen 1960).

To determine the significance of effect sizes, we used the bayestestR package to calculate the probability of direction (pd, or maximum probability of effect; Makowski et al. 2019). The pd is correlated with frequentist P values where pd values of 0.95, 0.975, 0.995, and 0.9995 are approximately equivalent to two-sided P values of 0.1, 0.05, 0.01, and 0.001, respectively. For the purposes of this analysis, we define a significant effect size as one with a pd of 0.975 or greater.

Model transferability

We calculated predictions of each model for the 2017 and 2018 Soda wildfire data and then calculated error metrics as described above in the previous section. Comparing the transferability of each model allowed us to assess our last question of whether post-fire weather or recent antecedent 5-yr weather helped predict post-fire outcomes.

Results

Vegetation responses to time since fire and antecedent weather

Model 1: time since fire.—Annual grass cover increased by a small amount (1.5% over 100 yr, pd = 1, Table 1) and perennial grass cover did not change with time since fire (pd = 0.73, Table 2). Sagebrush density was more likely to increase with time since fire (13% more likely to have density higher than 0 plants/m^2 over 100 yr, pd = 1, Table 3). However, including time since fire did not improve fit (model 0 vs. model 1 comparison between NRMSE, Table 4).

Model 2: time since fire and historical post-fire weather events.—Annual grass cover increased by 3.7% as March–May precipitation in the year after fire increased from 31.2 to 146 mm (pd = 1, Fig. 3A, Table 1), but not significantly with September–November precipitation in the year of fire (pd = 0.91, Table 1). Perennial grass cover increased by 14% as mean annual precipitation increased from 160.1 to 415.7 mm in the first four years after fire (pd = 1, Fig. 3C, Table 2) and increased by 2.6% as September–November precipitation in the year of fire increased from 20.9 to 152.7 mm (pd = 1, Table 2, Fig. 3B).

In the OCTC data, sagebrush density was negatively related to mean temperature of the coldest month (34% higher probability of no

Table 1. Modeled marginal responses of annual grass cover to spatial or temporal predictors across the range of each predictor.

Covariate	Minimum covariate value	Maximum covariate estimate	Estimate of change in cover	l-95% CI	u-95% CI	pd
Model 0: Null model						
Prior year's annual grass cover (%)	0	98	70.11	68.06	72.07	*1.00*
% Clay	7.5	37.5	71.48	68.73	73.89	0.86
% Sand	11.4	67.3	72.7	70	75.2	*0.99*
Elevation (m)	862.7	1065.6	72.1	69.6	74.4	*0.98*
Model 1: Time since fire						
Prior year's annual grass cover (%)	0	98	71.98	69.98	73.85	*1.00*
% Clay	7.5	37.5	2.68	2.1	3.33	0.94
% Sand	11.4	67.3	3.27	2.39	4.21	*0.99*
Elevation (m)	862.68	1065.58	2.55	2.25	2.89	0.95
Time since fire (yr)	1	100	1.5	1.54	1.45	*1.00*
Prior year's annual grass cover (%)	0	98	73.04	70.44	75.4	*1.00*
Model 2: Post-fire weather effects						
% Clay	7.5	37.5	4.55	3.66	5.52	0.85
% Sand	11.4	67.3	6	4.8	7.33	*1.00*
Elevation (m)	862.68	1065.58	3.73	3.21	4.31	0.55
Time since fire (yr)	1	100	4.33	4.03	4.62	*0.99*
March–May ppt (year after fire)	31.2	145.7	3.66	3.39	3.94	*1.00*
September–November ppt (year of fire)	20.9	152.7	4.54	3.82	5.34	0.91
Model 3: Recent five-year weather						
Prior year's annual grass cover (%)	0	0.98	78.34	76.21	80.26	*1.00*
% Clay	7.5	37.5	8.64	7.41	9.97	0.94
% Sand	11.4	67.3	12.07	10.24	14.18	*0.99*
Elevation (m)	862.68	1065.58	3.34	2.8	3.85	0.95
Weighted mean temp	9.71	11.78	2.54	1.47	4.02	*1.00*
Weighted mean precip	13.79	32.35	9.01	8.2	9.9	*1.00*
Model 4: Time since fire + recent five-year weather						
Prior year's annual grass cover (%)	0	98	78.45	76.25	80.36	*1.00*
% Clay	7.5	37.5	8.95	7.67	10.27	0.51
% Sand	11.4	67.3	12.26	10.47	14.3	*1.00*
Elevation (m)	862.68	1065.58	3.15	2.69	3.69	*1.00*
Time since fire (yr)	1	100	10.15	9.26	11.05	*1.00*
Weighted mean temp	9.71	11.78	2.63	1.5	3.97	*1.00*
Weighted mean precip	13.79	32.35	8.92	8.1	9.73	*1.00*

Notes: Estimates are the median of the posterior probability distribution, l-95% CI stands for the lower 95% credible interval and the u-95% CI standards for the upper 95% credible interval. The abbreviation pd is the probability of direction (the Bayesian equivalent of a frequentist *p* value, where 0.975 is equivalent to 0.05 *p* value). Estimate of change in cover is the amount of change in cover of the functional group predicted between the maximum and minimum covariate value. Positive values mean an increase in cover and negative values mean a decrease in. Significant pd values (≥0.975) are italicized.

sagebrush present at 1°C vs. −5.4°C, pd = 1, Fig. 4B, Table 3) and slightly positively related to mean temperature of the hottest month in the first four years after fire (34% higher probability of sagebrush density >0 at 27.01°C, pd = 0.99, Table 3, Fig. 4C). There was a 30% higher probability of sagebrush density >0 as maximum January–June precipitation in the first four years after fire increased from 77.2 to 325.3 mm (pd = 0.99, Table 3, Fig. 4A).

Model 3: recent five-year weather using random forests to weigh the importance of different months.— All three functional groups showed increases in cover or density with increased precipitation weighted by month over the five years preceding each observation (Fig. 5A–C, Tables 1–3). Both annual and perennial grass cover increased by 2.5% and 8%, respectively, as prior 5-yr mean temperature weighted by increased by from ~9.6°C to 11.8°C (pd = 1 for both, Tables 1, 2).

Table 2. Modeled marginal responses of perennial grass cover to spatial or temporal predictors across the range of each predictor.

Covariate	Minimum covariate value	Maximum covariate estimate	Estimate of change in cover	l-95% CI	u-95% CI	pd
Model 0: Null model						
Prior year's perennial grass cover (%)	0	83	64.44	62.14	66.59	*1.00*
% Clay	7.5	37.5	−1.7	−2.08	−1.29	*0.99*
% Sand	11.4	67.3	1.3	0.33	2.38	0.96
Elevation (m)	862.68	1065.58	14.22	13.11	15.38	*1.00*
Model 1: Time since fire						
Prior year's perennial grass cover (%)	0	83	64.16	61.85	66.31	*1.00*
% Clay	7.5	37.5	−1.89	−2.19	−1.59	*0.99*
% Sand	11.4	67.3	1.08	0.25	2.01	0.96
Elevation (m)	862.68	1065.58	14.15	13.06	15.27	*1.00*
Time since fire (yr)	1	100	−0.19	−0.07	−0.31	0.73
Model 2: Post-fire weather effects						
Prior year perennial grass cover (%)	0	83	58.38	55.55	61.12	*1.00*
% Clay	7.5	37.5	−1.68	−2.09	−1.24	*0.98*
% Sand	11.4	67.3	1.8	0.81	2.89	*0.99*
Elevation (m)	862.68	1065.58	6.25	5.42	7.19	*1.00*
Time since fire (yr)	1	100	−1.63	−1.5	−1.76	*1.00*
Average annual precip (4 yr post-fire)	160.1	415.7	14.38	13.09	15.74	*1.00*
September–November ppt (year of fire)	20.9	152.7	2.63	2.02	3.31	*1.00*
Model 3: Recent five-year weather						
Prior year's perennial grass cover (%)	0	83	63.96	61.57	66.19	*1.00*
% Clay	7.5	37.5	−2.12	−2.47	−1.73	*0.99*
% Sand	11.4	67.3	0.83	−0.14	1.81	0.96
Elevation (m)	862.68	1065.58	12.84	11.71	14.16	*1.00*
Weighted mean temp	9.61	11.76	7.99	7.22	8.73	*1.00*
Weighted mean precip	13.53	31.57	10.68	9.82	11.54	*1.00*
Model 4: Time since fire + recent five-year weather						
Prior year's perennial grass cover (%)	0	83	63.84	61.53	66.11	*1.00*
% Clay	7.5	37.5	−2.16	−2.54	−1.77	*1.00*
% Sand	11.4	67.3	0.78	−0.17	1.77	0.86
Elevation (m)	862.68	1065.58	13.02	11.77	14.28	*1.00*
Time since fire (yr)	1	100	−0.35	−0.2	−0.47	0.87
Weighted mean temp	9.61	11.76	7.99	7.24	8.85	*1.00*
Weighted mean precip	13.53	31.57	10.84	9.98	11.75	*1.00*

Notes: Estimates are the median of the posterior probability distribution, l-95% CI stands for the lower 95% credible interval and the u-95% CI standards for the upper 95% credible interval. The abbreviation pd is the probability of direction (the Bayesian equivalent of a frequentist p value, where 0.975 is equivalent to 0.05 p value). Estimate of change in cover is the amount of change in cover of the functional group predicted between the maximum and minimum covariate value. Positive values mean an increase in cover and negative values mean a decrease in. Significant pd values (≥0.975) are italicized.

Sagebrush density was not significantly affected by mean temperature weighed by month (pd = 0.96, Table 3).

Model 4: time since fire and recent five-year weather using random forests to weigh the importance of different months.—Adding a term to model 3 to incorporate time since fire did not result in any appreciable changes to the effect sizes of weighted averages of precipitation and temperature on functional group density or cover.

Do post-fire weather conditions or recent five-year weather better explain functional group abundances? Model fit

The models which included weather had very similar accuracy to the null no-weather model, which underscores the importance of considering and comparing hypothesis-driven models with null effect models when trying to predict future vegetation composition dynamics (Harvey et al. 1983). With a one exception, functional group

Table 3. Modeled marginal responses of sagebrush abundance to spatial or temporal predictors across the range of each predictor.

Covariate	Minimum covariate value	Maximum covariate value	Cat 1 (0 plants/ m^2)	Cat 2 (<0.5 plants/ m^2)	Cat 3 (>0.5–1.0 plants/ m^2)	Cat 4 (1–5 plants/ m^2)	Cat 5 (>5 plants/ m^2)	pd
Model 0: Null model								
Prior year's sagebrush category	1	5	−93%	−7%	0%	66%	34%	*1.00*
% Clay	7.5	37.5	−9%	8%	1%	0%	0%	0.94
% Sand	11.4	67.3	1%	−1%	0%	0%	0%	0.59
Elevation	862.68	1065.58	−17%	15%	2%	0%	0%	*1.00*
Model 1: Time since fire								
Prior year's sagebrush category	1	5	−93%	−7%	0%	69%	31%	*1.00*
% Clay	7.5	37.5	−12%	11%	1%	0%	0%	*0.99*
% Sand	11.4	67.3	−2%	2%	0%	0%	0%	0.68
Elevation (m)	862.68	1065.58	−16%	14%	2%	0%	0%	*1.00*
Time since fire (yr)	1	100	−13%	12%	1%	0%	0%	*1.00*
Model 2: Post-fire weather effects								
Prior year's sagebrush category	1	5	−94%	−6%	0%	75%	25%	*1.00*
% Clay	7.5	37.5	−11%	10%	1%	0%	0%	0.95
% Sand	11.4	67.3	−6%	5%	0%	0%	0%	0.84
Elevation (m)	862.68	1065.58	−20%	19%	1%	0%	0%	*0.99*
Time since fire (yr)	1	100	−23%	21%	1%	0%	0%	*1.00*
Max January–June ppt (4 yr post-fire)	77.2	325.3	−30%	28%	1%	0%	0%	*0.99*
Mean temp coldest month (4 yr post-fire)	−5.4	1	34%	−32%	−2%	0%	0%	*1.00*
Mean temp hottest month (4 yr post-fire)	21.8	27.01	−34%	31%	2%	0%	0%	*0.99*
Mean January–April precip (4 yr post-fire)	58.95	180.1	16%	−15%	−1%	0%	0%	0.92
Mean March–June temp (4 yr post-fire)	10.46	14.12	−2%	2%	0%	0%	0%	0.59
Model 3: Recent five-year weather								
Prior year's sagebrush category	1	5	−93%	−7%	0%	68%	32%	*1.00*
% Clay	7.5	37.5	−6%	5%	1%	0%	0%	*1.00*
% Sand	11.4	67.3	−1%	1%	0%	0%	0%	0.56
Elevation (m)	862.68	1065.58	−7%	6%	1%	0%	0%	0.88
Weighted mean temp	9.25	11.29	11%	−10%	−1%	0%	0%	0.96
Weighted mean precip	13.43	32.14	−17%	15%	2%	0%	0%	*1.00*
Model 4: Time since fire + recent five-year weather								
Prior year's sagebrush 2category	1	5	−93%	−7%	0%	72%	28%	*1.00*
% Clay	7.5	37.5	−9%	8%	1%	0%	0%	0.96
% Sand	11.4	67.3	−4%	4%	0%	0%	0%	0.81
Elevation	862.68	1065.58	−5%	5%	0%	0%	0%	0.82
Time since fire (yr)	1	100	−14%	13%	1%	0%	0%	*1.00*

(Table 3. Continued.)

Covariate	Minimum covariate value	Maximum covariate value	Cat 1 (0 plants/m^2)	Cat 2 (<0.5 plants/m^2)	Cat 3 (>0.5–1.0 plants/m^2)	Cat 4 (1–5 plants/m^2)	Cat 5 (>5 plants/m^2)	pd
Weighted mean temp	9.25	11.29	9%	−8%	−1%	0%	0%	0.93
Weighted mean precip	13.43	32.14	−20%	18%	2%	0%	0%	*1.00*

Notes: Estimates are the median of the posterior probability distribution, l-95% CI stands for the lower 95% credible interval and the u-95% CI standards for the upper 95% credible interval. The abbreviation pd is the probability of direction (the Bayesian equivalent of a frequentist *p* value, where 0.975 is equivalent to 0.05 *p* value). The change in the probability of occurrence of each density category predicted between the maximum and minimum covariate values is given. Positive values mean an increase in density and negative values mean a decrease in density. Significant pd values (≥0.975) are italicized.

abundances overall were no better explained by post-fire weather conditions during specific intervals than they were by recent five-year antecedent weather (Tables 4, 5). Model 2 (post-fire weather events) was 1% more accurate at predicting sagebrush density class than the other models. The models that included weather at all (either post-fire or recent 5-yr weather) were better at predicting perennial grass cover by 1% (as measured by a decrease in NRMSE) over the models which did not include weather (models 0 and 1) and the five-year recent weather (3–4) were 1% better at predicting annual grass compared to the others (Table 4).

Does consideration of post-fire weather or recent weather help predict post-fire outcomes at a new site? Model transferability

No model emerged as most transferable over all of the three plant functional groups, indicating no consistent landscape, disturbance, or weather drivers in post-fire abundances across all functional groups. Instead, transferability varied among the plant types. The models that included weather (2–4) were better at predicting perennial grass (by 7–10% decrease in NRMSE) and annual grass (by 1–4% decrease in NRMSE) cover on the Soda wildfire than the models which did not include weather (models 0 and 1; Table 5). The differences in model transferability between the two different weather parameterizations (model 2, post-fire weather events; and model 3, five-year weather) when predicting perennial or annual grass cover were minimal: 1% error for perennial grass, 2% error for annual grass (Table 5). No model was more transferable than any other for predicting sagebrush density.

Discussion

We sought to assess how time since fire and antecedent weather affected long-term functional

Table 4. Model fit metrics: error for grass cover values and accuracy of sagebrush density class (from by leave-one-out cross validation on the OCTC dataset) for each generalized additive model.

Model	Sagebrush density class			Perennial grass cover			Annual grass cover		
	Overall accuracy	Kappa	*P*	RMSE	NRMSE	Bias	RMSE	NRMSE	Bias
Model 0: Null model	90%	0.83	<0.0001	0.12	14%	0.004	0.14	15%	0.001
Model 1: Time since fire	90%	0.83	<0.0001	0.12	14%	0.004	0.14	15%	0.001
Model 2: Post-fire weather events	91%	0.84	<0.0001	0.12	14%	0.003	0.14	14%	0.000
Model 3: Recent five-year weather	90%	0.83	<0.0001	0.12	13%	0.004	0.14	14%	0.001
Model 4: Time since fire + recent five-year weather	90%	0.83	<0.0001	0.12	13%	0.004	0.14	14%	0.001

Notes: For annual and perennial grass cover, root mean squared error (RMSE) and normalized root mean squared error (NMSE), calculated by dividing the RMSE by the range of the observed response variable, as given. For sagebrush density class, overall accuracy, kappa, and *P* values are given.

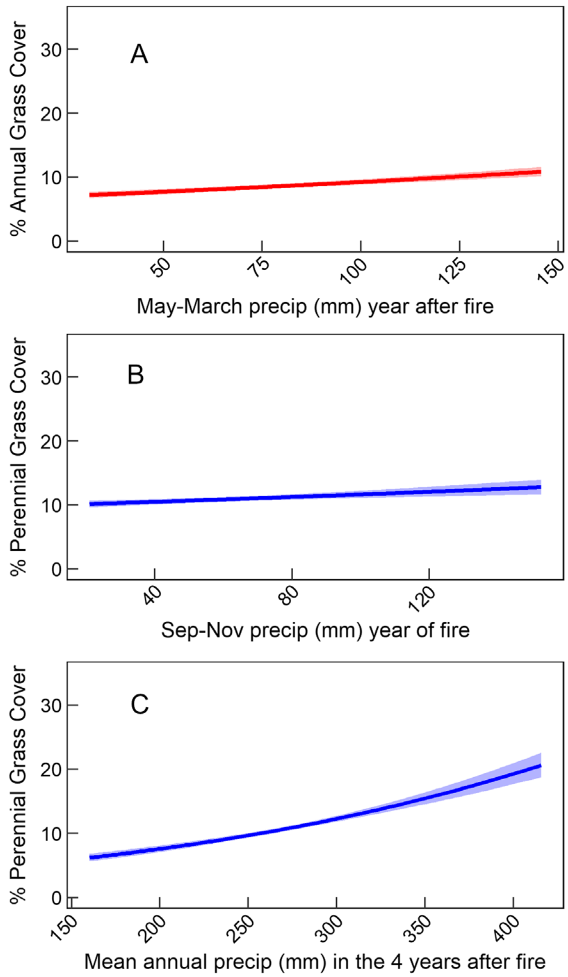

Fig. 3. Marginal effects from model 2 of three post-fire weather covariates on annual grass cover and perennial grass cover. Precipitation (precip) is given in millimeters (mm). The center line shows the median of the posterior probability distribution, the shaded ribbons show the 95% credible interval.

group abundances, and how sensitive within-site and across-site predictions of abundance were to weather during specific post-fire windows or in general antecedent five-year period. We found mostly positive relationships between post-fire precipitation and abundance of all functional groups, and mixed effects of temperature. Post-fire weather in specific time periods critical for recruitment did not explain long-term vegetation trajectories better than did recent five-year weather conditions, although incorporating weather during either time period improved perennial and annual grass cover predictions at a new site.

Vegetation responses

Post-fire precipitation is a key factor directing plant community development following fire disturbances (Shryock et al. 2015, Young et al. 2019, McIlroy and Shinneman 2020). Indeed, we found that post-fire precipitation had significant positive effects on abundances of all three functional groups. As expected, sagebrush density increased with maximum Jan-June precipitation in the first four years after fire (post-fire weather model, Model 2) and with precipitation in the preceding 5 yr (recent five-year weather models), which may be indicative of drought thresholds on seedling establishment, such as the threshold of −2.5 MPa in mean soil-water availability in the March after fire found by O'Connor et al. (2020). A previous study found a relationship between fall precipitation and cheatgrass (the most common annual grass species in the western USA) outside of a specific post-fire context (Bradley et al. 2016). We found that annual grass cover increased with precipitation in the spring of the year after fire but not with fall precipitation in the year of fire (post-fire weather model). This may reflect the fact that fire usually reduces the annual grass seedbank (Pyke 1994), and thus propagule arrival to a burned site could be delayed. There was a positive effect of post-fire fall precipitation on perennial grass cover, which indicates a different life cycle strategy between annual and perennial species. Perennial grasses can frequently resprout after fire (Wright and Bailey 1982) and can immediately take advantage of available soil moisture. Indeed, perennial grass cover increased with precipitation during all of the time periods analyzed. This finding is consistent with previous research that has indicated that precipitation is strongly related to germination and cover of perennial grasses (Pilliod et al. 2017, James et al. 2019). Furthermore, Adler et al. (2009) found that survival of several common perennial bunchgrass species was 90% or higher after 3–4 yr, so both seedlings and resprouts that emerge during critical post-fire time periods are likely to subsist long after fire.

Freezing temperatures during critical growing periods can reduce sagebrush seedling establishment and survival (Brabec et al. 2017). However

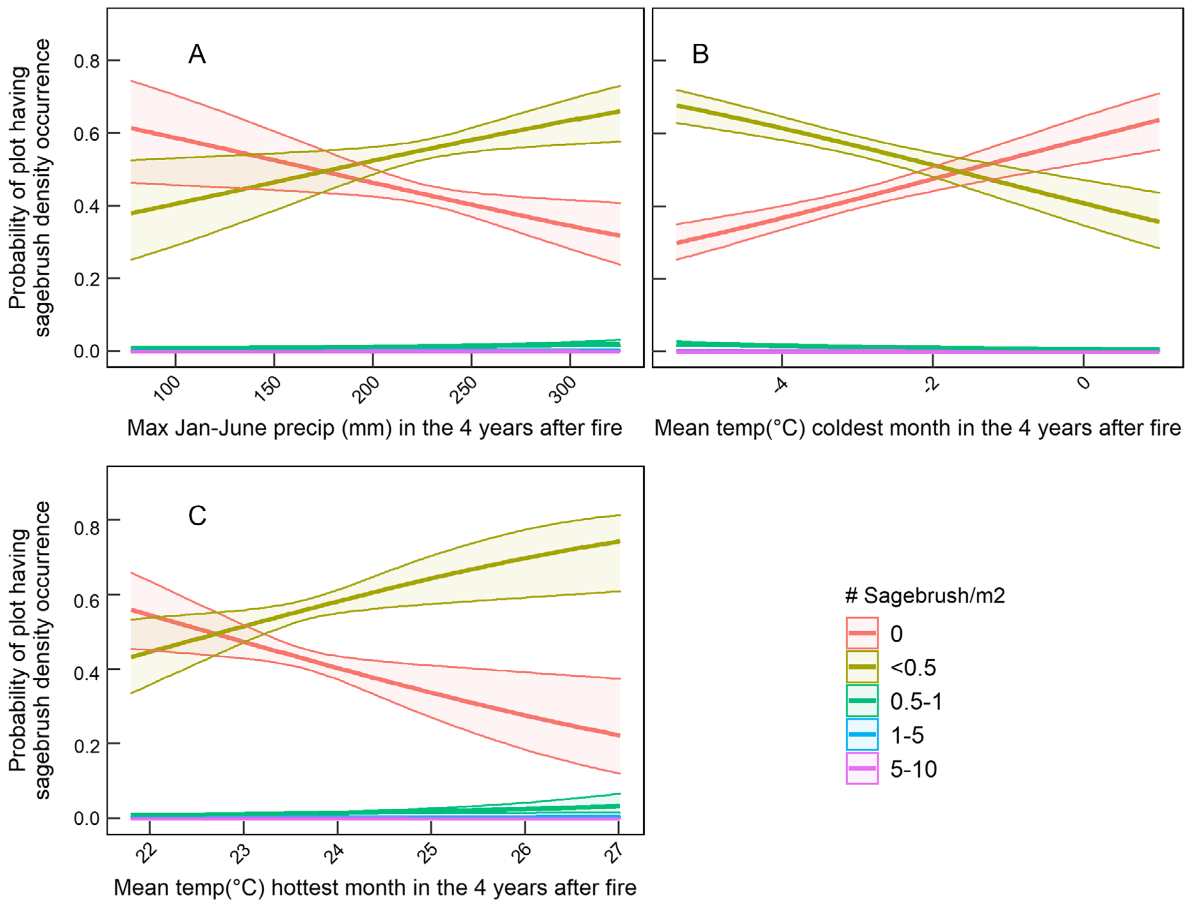

Fig. 4. Marginal effects from model 2 of post-fire weather covariates on the probability of a plot having sagebrush density in a certain category (given as number of sagebrush per m^2). Precip stands for precipitation and is measured in millimeters (mm). Temp stands temperature and is measured in degrees celsius (°C).

contrary to Brabec et al. (2017), we observed an increase in sagebrush density in relation with lower mean temperature of the coldest month and higher mean temperatures in the hottest month in the first four years after fire. The OCTC has a relatively warm climate for sagebrush and low winter temperatures may be less of a selective factor here than in colder climates (Lazarus et al. 2019). The lack of an effect of mean monthly temperature (from the five-year weather model) on sagebrush density is consistent with the findings of Brabec et al. (2017) and Kleinhesselink and Adler (2018), who suggest that temperature extremes are more often the limiting factor for establishment. However, weather effects on sagebrush seedling establishment and early survival may not translate into long-term effects on population dynamics because of size structure effects (Shriver et al. 2019) and negative density dependence (Chu and Adler 2015) and because susceptibly to minimum temperature appears to decrease as plants age (Germino et al. 2019).

We modeled year-to-year change in grass cover or sagebrush density class, and incremental change each year was generally small. In particular, shifts from one sagebrush density class to another may occur more slowly than the temporal resolution and focus of our models, ultimately diminishing change detection. This finding is in agreement with Anderson and Holte (1981), who reported negligible change in shrub density in relatively undisturbed sagebrush steppe over a 9-yr period of time, even as precipitation varied year-to-year. Sagebrush cover in

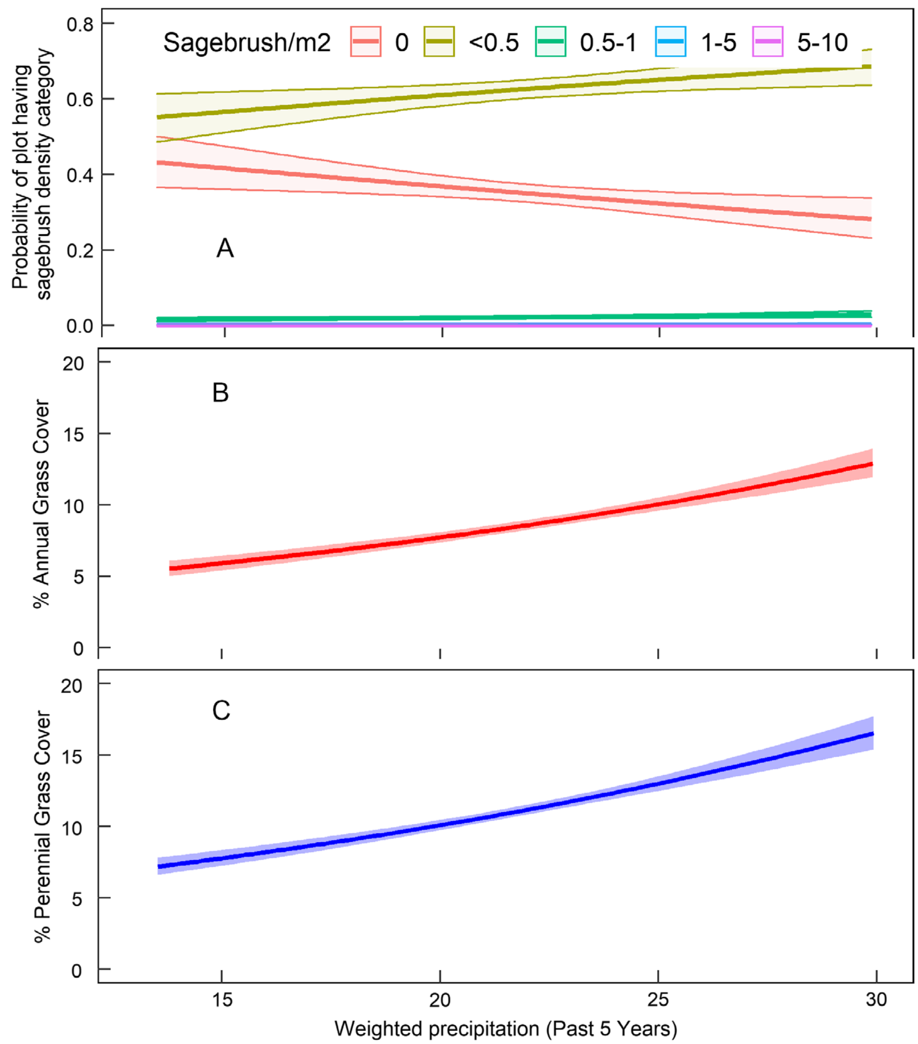

Fig. 5. Marginal effects of average monthly precipitation in the most recent five years weighted by random forest-derived importances (from model 3). Effects are shown on sagebrush density category (top), annual grass cover (% AG Cover, middle), and perennial grass cover (% PG Cover, bottom). Precipitation is given in millimeters (mm). The center line shows the median of the posterior probability distribution, the shaded ribbons show the 95% credible intervals.

that study did increase with precipitation, suggesting that established plants may display greater response to weather variability (i.e., growth or shedding of biomass) without concomitant changes in recruitment or mortality.

Explanatory factors for post-fire vegetation recovery: How does weather fit in?

Our coarse-scale consideration of weather provided only marginal gains in explaining long-term vegetation trajectories, nor did it reveal that weather during specific post-fire recruitment periods had a lasting impact relative to the effects of antecedent weather at any time before or after fire. Variation in vegetation over time can frequently be partly accounted for by temporal autocorrelation. For instance, in remote sensing vegetation cover trend analysis, normalized difference vegetation index (NDVI) in prior months or years can be used to better predict future NDVI (Fernández-Manso et al. 2011, Adeyeri et al. 2017). The fact that our null model that only

Table 5. Transferability error for grass cover values and accuracy of sagebrush density class (from validation error on the Soda Wildfire dataset) for each generalized linear model.

	Sagebrush density class			Perennial grass cover			Annual grass cover		
Model	Overall accuracy	Kappa	*P*	RMSE	NRMSE	Bias	RMSE	NRMSE	Bias
Model 0: Null model	89%	0.71	<0.0001	0.42	55%	−0.27	0.36	36%	−0.02
Model 1: Time since fire	89%	0.71	<0.0001	0.42	55%	−0.27	0.35	35%	−0.01
Model 2: Post-fire weather events	89%	0.71	<0.0001	0.35	45%	−0.20	0.34	34%	−0.02
Model 3: Recent five-year weather	89%	0.71	<0.0001	0.35	46%	−0.21	0.32	32%	0.07
Model 4: Time since fire + recent five-year weather	89%	0.71	<0.0001	0.36	47%	−0.21	0.32	32%	0.07

Notes: For annual and perennial grass cover, root mean squared error (RMSE) and normalized root mean squared error (NMSE), calculated by dividing the RMSE by the range of the observed response variable, as given. For sagebrush density class, overall accuracy, kappa, and *P* values are given.

incorporated landscape variables performed nearly as well as our models that included weather suggests that a significant amount of variation in future vegetative trajectories can be explained by knowing past abundances.

Generalizing weather effects on post-fire vegetation recovery across sites

There has been a recent call in ecology to develop and apply iterative forecasting approaches in predicting ecosystem responses to disturbance and changing climate, especially near-term forecasting (Dietze et al. 2018). Our findings suggest that although including weather covariates may improve transferability of predictions of post-fire vegetation recovery for some functional groups, predictions may not be sensitive to the choice of weather variables when the weather data is spatially and temporarily coarse. We used PRISM data for this study, which is the most readily available and frequently used weather dataset but also has a coarse spatial scale of 250-m pixel sizes and is available only in monthly increments (PRISM 2017). Previous studies have shown that microsite vegetative structure and topographic position can change the suitability for perennial seedling establishment in semiarid ecosystems (Franzese et al. 2009, Boyd and Davies 2010), which means that local conditions may moderate larger scale weather effects. Furthermore, soil moisture thresholds for plant establishment or survival can occur on the scale of days, rather than months, as shown for sagebrush (O'Connor et al. 2020). The choice of weather variable parametrization may increase in importance as data becomes more fine-scale, both temporally and spatially.

The approach we used illustrates how ecological forecasting can be applied to restoration ecology, including leveraging data from highly studied sites to inform predictions at sites with limited data. These sorts of studies can help fill in the gap for management-applicable predictions on a useful temporal and spatial scale; many ecological forecasts currently rely on long-term simulations at regional scales (Pouyat et al. 2010, Dietze et al. 2018), despite a land manager need for near-term predictions at a local scale (Dilling and Lemos 2011). Our analysis found that weather effects (either post-fire or recent antecedent) were more important for predicting post-fire perennial and annual grass cover at a new site than they were for explaining variability at a single site.

Our analysis did not directly address weather effects on specific post-fire demographic stages. Future analyses could consider other population dynamics which may affect longer-term outcomes, such as size structure or negative density dependence (Chu and Adler 2015, Shriver et al. 2019). Furthermore, we only present two ways of considering the temporal dynamics of weather variability (i.e., post-fire weather during the growing season or recent antecedent five-year weather) here but acknowledge that other temporal windows or weather variables (such as soil-water deficit, temperature extremes) could be considered.

Conclusions

While we consistently found some effects of precipitation on vegetation recovery, the temporal dynamics of weather variation in relation to time since fire were not important for predicting annual or perennial grass cover or sagebrush density at a new site, at least for the models we tested that relied on coarse-scale weather data. Coarse-scale seasonal weather forecasts may provide some utility for predicting whether precipitation will be sufficient for successful vegetation recovery after fire. However, developing models with finer-scale weather data (i.e., daily, such as in O'Connor et al. 2020) will be an important next step for leveraging our methods to forecast vegetation dynamics. Land managers often have to make decisions on post-fire management treatments without site-specific knowledge of the subject plant communities, and model predictions is one of the only ways the information can be obtained. We have shown a method of transferring information at one area affected by historic fires to predict outcomes at another burned area, and our basic approach could be adopted for similar applications made elsewhere. The information gained could be useful for helping to predict both post-fire restoration outcomes, or other applications such as fire vulnerability based on fuel predictions. Long-term monitoring in particular can provide important information about weather variability for transferring quantitative forecasts from well-studied sites to new sites.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3446/full