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Episodic occurrence of favourable weather constrains recovery of a cold desert shrubland after fire

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Abstract

1. Key to the long-term resilience of dryland ecosystems is the recovery of foundation plant species following disturbance. In ecosystems with high interannual weather variability, understanding the influence of short-term environmental conditions on establishment of foundation species is essential for identifying vulnerable landscapes and developing restoration strategies. We asked how annual environmental conditions affect post-fire establishment of *Artemisia tridentata*, a shrub species that dominates landscapes across much of the western United States, and evaluated the influence of episodic establishment on population recovery.
2. We collected *A. tridentata* stem samples from 33 plots in 12 prescribed fire sites that burned 8–11 years before sampling. We determined individual establishment years using annual growth rings. We measured seasonal soil environmental conditions at the study sites and asked if these conditions predicted annual establishment density. We then evaluated whether establishment patterns could be predicted by site-level climate or dominant subspecies. Finally, we tested the effect of the magnitude and frequency of post-fire establishment episodes on long-term population recovery.
3. Annual post-fire recruitment of *A. tridentata* was driven by the episodic availability of spring soil moisture. Annual establishment was highest with wetter spring soils (relative influence [RI] = 19.4%) and later seasonal dry-down (RI = 11.8%) in the year of establishment. Establishment density declined greatly 4 to 5 years after fire (RI = 17.1%). Post-fire establishment patterns were poorly predicted by site-level mean climate (marginal $R^2 \le 0.18$) and dominant subspecies (marginal $R^2 \le 0.43$).
4. Population recovery reflected the magnitude, but not the frequency, of early post-fire establishment pulses. Post-fire *A. tridentata* density and cover (measured 8–11 years after fire) were more strongly related to the magnitude of the largest establishment pulse than to establishment frequency, suggesting that population recovery may occur with a single favourable establishment year.
5. *Synthesis and applications*. This study demonstrates the importance of episodic periods of favourable weather for long-term plant population recovery following

disturbance. Management strategies that increase opportunities for seed availability to coincide with favourable weather conditions, such as retaining unburned patches or repeated seeding treatments, can improve restoration outcomes in high-priority areas.

KEYWORDS
annual weather conditions, big sagebrush, ecological restoration, favourable weather, plant establishment, post-fire recovery, prescribed fire, resource pulses

1 | INTRODUCTION

Altered disturbance regimes, shifting climate and non-native plant invasions are resulting in the transformation of dryland ecosystems around the globe (Maestre et al., 2016). Key to long-term resilience of dryland ecosystems is recovery of foundation plant species following disturbance. Foundation plant species typically dominate an ecosystem's structure and influence ecosystem processes and the distribution and abundance of a wide range of community members, and thus play a disproportionate role in ecosystem recovery (Brown et al., 2001). Spatial differences in mean environmental conditions, such as along climatic gradients, are important predictors of recovery potential (Arnan et al., 2007; Shryock et al., 2015). In many dryland environments, however, year-to-year fluctuations in weather can exceed spatial differences among climate zones (Loik et al., 2004) and exert strong effects on biological processes (Schwinning & Sala, 2004). In ecosystems with high interannual weather variability, a greater understanding of the influence of short-term environmental conditions on the rate and trajectory of foundation species' recovery after disturbance can be used to inform restoration strategies by identifying landscapes that are vulnerable to disturbance and climate change.

Globally, the invasion of non-native plants has altered fire regimes and, in some cases, initiated grass-fire cycles resulting in the loss of foundation species (Brooks et al., 2004). Understanding foundation species' responses to fire is necessary for the conservation of native habitats in the context of altered fire regimes. Resource pulses are a critical driver of ecosystem dynamics in drylands, where the amount and timing of precipitation vary greatly from year to year (Schwinning & Sala, 2004). Dryland ecosystems are typically resource-limited, and plant population processes—including seed production, establishment and growth—often fluctuate in response to resource pulses driven by interannual weather conditions (Petrie et al., 2017; Redmond et al., 2012, 2017). Overall shifts towards warmer and drier conditions in the future are expected to impact population dynamics of dryland plant species (e.g. Miranda et al., 2009; Renwick et al., 2018), yet interannual variability in weather can create complex trends despite linear shifts in mean conditions (de Elía et al., 2013; Malanson et al., 2017). Continuous multi-year observations of plant demographic responses can provide powerful insights into how populations and communities may respond to the interacting effects of climate and disturbance regime changes (Kleinhesselink & Adler, 2018).

In cold deserts of the western United States, *Artemisia tridentata* Nutt. (big sagebrush) is a foundation shrub species that characterizes multiple ecological types across tens of millions of ha (Davies et al., 2011). The interacting effects of increasing wildfire, annual grass invasions and land use have led to widespread loss of sagebrush ecosystems in recent decades (Fusco et al., 2019). Fire often facilitates invasion of non-native annual grasses such as *Bromus tectorum* (cheatgrass), leading to shortened grass-fire cycles and resulting in transformation of native ecosystems to annual grass-dominated landscapes (Bradley et al., 2018). Following fire, a central management objective is reestablishment of sagebrush species, which are critical habitat elements for Greater sage-grouse and other species of conservation concern (Coates et al., 2016). However, most sagebrush taxa, including the widespread species *A. tridentata*, are not adapted to fire and do not resprout. Post-fire recovery must occur through seeds, which have short-distance dispersal and very limited (1–2 years) viability in the soil seed bank (Wijayratne & Pyke, 2012). To promote post-fire *A. tridentata* recovery in large burns where seed dispersal is limited, land managers have invested heavily in seeding treatments (Pilliod et al., 2017). However, post-fire seeding efforts are often unsuccessful at increasing *A. tridentata* cover (Arkle et al., 2014; Knutson et al., 2014), indicating that seed availability alone does not ensure recovery.

As for many dryland plants, *A. tridentata* recruitment is driven largely by soil water availability (Schlaepfer et al., 2014). Cold deserts of the western U.S. have a winter-dominated precipitation regime, and soil moisture typically peaks in late winter before gradually declining (Shriver et al., 2018). Long-term regeneration success of *A. tridentata* in large burned areas is strongly related to spring soil moisture in the first year after fire (Nelson et al., 2014) or after post-fire seeding (Shriver et al., 2018), indicating that successful establishment requires favourable weather conditions coincident with the short period of seed viability. Wet-thermal models show that germination of dryland species relies on accumulation of warm and wet conditions in near-surface soils (Cline, Roundy, & Christensen, 2018). Near-surface soils tend to be much warmer in burned sites than in unburned sites, allowing germination requirements to be met more quickly during wet spring periods, yet hotter and drier conditions in late spring can increase seedling mortality risk (Cline, Roundy, Hardegree, et al., 2018). Freeze-thaw cycles may also constrain survival of early-germinating seedlings

(Roundy & Madsen, 2016). Recruitment may be further limited by competition from other plants (Chambers et al., 2017), resulting in a short post-fire window for establishment before resources are redistributed among plants recovering from or colonizing after fire (Ziegenhagen & Miller, 2009). These drivers of establishment vary annually, and although climate projections indicate reduced regeneration in hotter and drier areas (Schlaepfer et al., 2015), it is unlikely that establishment patterns can be accurately predicted from mean climate variables (Miranda et al., 2009).

The long-term population implications of short-term regeneration success are critically important for restoration but poorly understood. In ecosystems with extremely infrequent favourable conditions for recruitment, population recovery may be driven by a single establishment event, indicating pulse-driven population dynamics (Chesson et al., 2004). However, multiple establishment events have a cumulative effect on population size (Wiegand et al., 2004), and more frequent establishment events may result in larger populations, buffering population losses from seedling mortality by spreading the risk across multiple years (Shriver et al., 2019). Dendroecological studies reconstruct past regeneration events, facilitating insight into the dynamics that have produced extant communities and providing opportunities for connecting short-term regeneration events and long-term population responses.

Here, we investigated how seasonal environmental conditions affect annual *A. tridentata* establishment and evaluated the influence of episodic establishment patterns on post-fire population recovery. We combined dendroecological methods, soil environmental data and vegetation measurements from prescribed fires spanning broad environmental gradients to ask: (a) How does post-fire *A. tridentata* establishment respond to seasonal environmental conditions and time since fire? We hypothesized that establishment would be greatest in years with high spring soil water availability and more likely immediately after fire, before competition with other plants and seedbank depletion inhibits establishment. (b) Can temporal patterns of *A. tridentata* establishment be predicted based on mean climate? We hypothesized that drier sites would have more variable establishment patterns and smaller establishment peaks, reflecting a lower likelihood of favourable conditions for recruitment. (c) How is post-fire *A. tridentata* population recovery influenced by temporal patterns of post-fire establishment? We hypothesized that cover and density would be highest in sites with larger establishment peaks and with more frequent establishment events, but that the influence of establishment frequency would be strongest. Identifying the drivers of post-fire establishment and influences on population recovery will help managers identify vulnerable portions of the landscape and prioritize interventions.

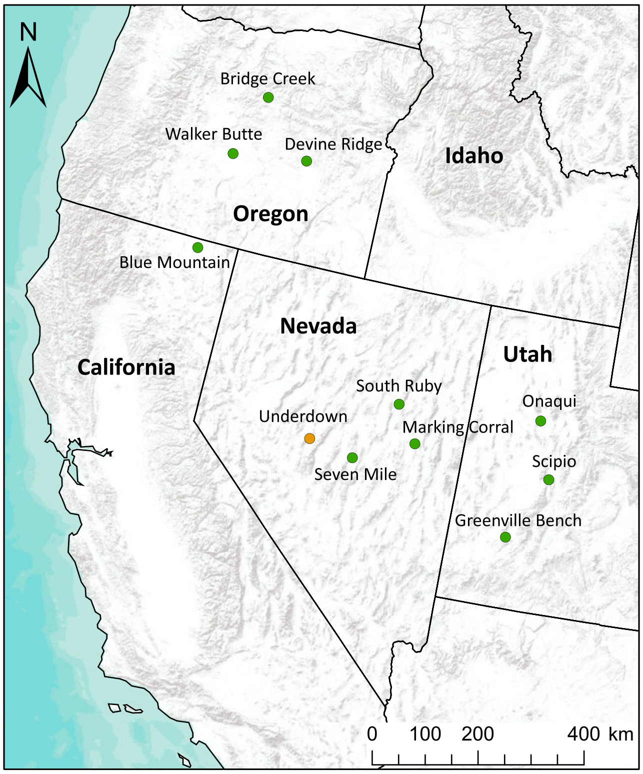

FIGURE 1 Map of the study sites in the Intermountain West, USA. Green circles indicate sites that are part of the SageSTEP network. The orange circle indicates the location of the Underdown Canyon Demonstration Area (two sites)

2 | MATERIALS AND METHODS

2.1 | Study site locations

Our study took place in 12 prescribed burn sites across the Intermountain West of the United States (Figure 1). Study sites were part of two experimental networks in ecosystems co-dominated by pinyon-juniper (*Pinus* and *Juniperus* species) woodlands and *A. tridentata* shrublands. Underdown Canyon (two sites) is a Demonstration Area established to study ecological effects of prescribed fire across a local elevational gradient (Urza et al., 2017, 2019). The Sagebrush Steppe Treatment Evaluation Project (SageSTEP; 10 sites) is a long-term regional-scale study examining effects of multiple fuel treatments (McIver & Brunson, 2014).

Sites were distributed across a broad geographical area encompassing a range of edaphic and climatic gradients and contained three subspecies of *A. tridentata* (Table 1). Prescribed fire treatments were implemented between 2004 and 2009 using a 'stagger-start' design that increases variability in post-treatment weather and thus reduces potential for restricted inferences (Loughin, 2006). Study sites were fenced to prevent livestock grazing and no post-fire seeding or planting treatments were implemented. Post-treatment weather across the region was variable, characterized by longer periods of drought punctuated by infrequent cool, wet years (Roundy et al., 2014, 2020).

2.2 | Field methods

We collected data in 2015 (Underdown) and 2017 (SageSTEP) on post-fire *A. tridentata* density and cover and obtained stem samples

TABLE 1 Characteristics of the 12 study sites, including year burned, the *Artemisia tridentata* subspecies present at the site, and environmental attributes

Site	Year burned	*Artemisia tridentata* subspecies	Elevation (m)[a]	Annual precipitation (mm)[b]	Mean annual temperature (°C)[b]	Annual climatic water deficit (mm)[c]
	Mean ± *SE*					
SageSTEP network						
Blue Mountain, CA (BM)	2007	*vaseyana*	1,494	454 ± 21.2	7.6 ± 0.11	218 ± 8.2
Bridge Creek, OR (BC)	2006	*tridentata*	909	306 ± 13.5	9.8 ± 0.13	373 ± 8.9
Devine Ridge, OR (DR)	2007	*vaseyana*	1,508	373 ± 15.1	6.0 ± 0.16	237 ± 7.2
Greenville Bench, UT (GR)	2007	*wyomingensis*	1,851	330 ± 13.3	9.5 ± 0.11	326 ± 7.8
Marking Corral, NV (MC)	2006	*wyomingensis*	2,205	315 ± 12.7	6.8 ± 0.12	277 ± 7.3
Onaqui, UT (OJ)	2006	*wyomingensis*	1,707	319 ± 14.2	9.0 ± 0.14	350 ± 8.3
Scipio, UT (SC)	2007	*wyomingensis*	1,742	394 ± 13.5	9.7 ± 0.13	373 ± 8.3
Seven Mile, NV (SV)	2007	*wyomingensis*	2,256	265 ± 11.6	7.0 ± 0.12	316 ± 8.3
South Ruby, NV (SR)	2008	*wyomingensis*	2,011	317 ± 14.4	7.7 ± 0.12	321 ± 7.4
Walker Butte, OR (WB)	2006	*vaseyana*	1,416	261 ± 12.9	6.6 ± 0.12	287 ± 7.7
Underdown Canyon Demonstration Area						
Underdown Mid, NV (NM)	2004	*vaseyana*	2,170	333 ± 17.8	7.4 ± 0.12	228 ± 7.4
Underdown Upper, NV (NU)	2004	*vaseyana*	2,305	395 ± 17.8	6.7 ± 0.12	202 ± 7.0

[a] Mean elevation of sampling plots.

[b] 30-year record from 1981 to 2010 (PRISM Climate Group, 2016).

[c] 30-year record from 1981 to 2010 (Dilts et al., 2015).

for determining establishment dates. We randomly located sampling plots within prescribed burn perimeters. Three sampling plots were established at each site, except Scipio and Bridge Creek, where smaller burn areas restricted sampling to one and two plots respectively. Our final sampling design included 33 plots across 12 sites.

We measured shrub cover by species using the canopy gap intercept method (Herrick et al., 2017). We recorded shrub canopies along 6-m transects extending radially in 8 cardinal and ordinal directions from plot centre. *Artemisia tridentata* stem samples were then collected from variable-radius plots. The plot radius was based on a target sample size of five samples for each year between burning and sampling (number of years between burning and sampling varied among sites). Collection plots were expanded radially until the target sample size was met, cutting all *A. tridentata* individuals below the root crown for a complete demographic profile. If the target sample size was not met within a 6-m radius, up to two additional plots were established at nearby randomized locations, and all samples and measurements were pooled within plot clusters.

2.3 | Laboratory methods

A total of 2,004 *A. tridentata* stem samples were collected. Samples were cross-sectioned with a band saw to expose the pith at the junction of root crown and stem. Stem samples were then processed using standard dendrochronological techniques (Stokes & Smiley, 1968). We used annual ring counts to determine establishment year because the young age of the samples precluded cross-dating and minimized chances of drought-induced missing rings. Annual growth rings were counted under a stereomicroscope by two individuals, and samples for which the independent ring counts disagreed were re-examined. For samples that did not include the pith ($n = 25$), we overlaid concentric circles to estimate the number of missing years (Nelson et al., 2014). For analyses of post-fire establishment, we removed samples that established prior to the year of burning ($n = 415$) or in the year of sampling ($n = 83$). In total, we used 1,506 *A. tridentata* individuals in post-fire analyses.

2.4 | Soil environmental data

Soil temperature and water availability were measured in each burned site. Soil temperature was recorded using thermocouples and soil water matric potential was measured using gypsum blocks, at multiple soil depths: 1–3, 13–15 and 28–30 cm. Data microloggers were programmed to read sensors every 60 s and store hourly averages. Sites were instrumented immediately after burn treatments, and with the exception of small data gaps resulting from sensor malfunctions, data on soil temperature and water availability were collected through the year of sampling. Hourly measurements were used to calculate a suite of seasonal variables associated with plant growth and cover (Roundy et al., 2014). Further details on soil environmental data are in Roundy et al. (2018) and Chambers et al. (2007).

2.5 | Statistical analyses

2.5.1 | Drivers of annual post-fire establishment

We modelled annual *A. tridentata* establishment density as a function of time since fire and soil environmental conditions. Annual establishment density represents the number of *A. tridentata* individuals that established in each calendar year in each plot, scaled to density (ha^{-1}). We used generalized boosted regression trees because they were appropriate for modelling nonlinear relationships in our dataset (Elith et al., 2008) and have previously been used to model post-fire seedling recruitment (e.g. Christopoulou et al., 2014; Johnstone et al., 2010). We focused on soil environmental predictors that represent water availability during spring and early summer (Table 2), which are critical seasons for *A. tridentata* recruitment (Shriver et al., 2018). As soil measurements in different depths were highly correlated, we used measurements from a single depth to reduce potential effects of collinearity on the interpretation of individual variable effects. We used near-surface soil measurements (1–3-cm depth), which were more strongly correlated with establishment than deeper soil measurements and were consistent with prior work on germination and early seedling survival (e.g. Cline, Roundy, Hardegree, et al., 2018).

The model was fit in R version 3.5.2 (R Core Team, 2018), using the *gbm.step* function in the DISMO package (Hijmans et al., 2017) and the *gbm* function in the GBM package (Greenwell et al., 2019). The model was defined with 10-fold cross-validation, bag fraction of 0.5, complexity of 3, and learning rate of 0.003 to achieve the recommended 1,000 trees per model (Elith et al., 2008). Effects were interpreted by examining relative influence and plotting partial dependencies for individual predictor variables.

2.5.2 | Temporal patterns of post-fire establishment across regional climatic gradients

For each plot ($N = 33$), we used annual establishment density (plants/ha) from the first 8 post-fire years to calculate metrics of temporal patterns of post-fire *A. tridentata* establishment. Median establishment represented a typical post-fire year, maximum establishment represented the largest establishment peak, CV of establishment represented interannual variation, and the proportion of years with establishment represented the frequency of establishment events. Median, maximum and CV were $\log_{10}$-transformed prior to analysis.

Artemisia tridentata subspecies are strongly stratified by climate, precluding the presence of subspecies and climate as explanatory variables in the same models. Thus, we used linear mixed effects

TABLE 2 List of predictor variables used in the boosted regression tree model predicting annual *Artemisia tridentata* establishment. Variables represent conditions in the year of establishment, except for those named 'year + 1', which represent conditions in the year following establishment. Spring = March through June; Summer = July through August; Winter = December through February, assigned to the subsequent calendar year

Variable name	Units	Interpretation	Description
Time since fire	Years	Time since fire	Years since the prescribed fire occurred
Spring wet days Spring wet days, year + 1 Summer wet days Summer wet days, year + 1	Days	Soil water availability	Number of days when soil water matric potential was > −1.5 MPa
Spring degree days Spring degree days, year + 1 Summer degree days Summer degree days, year + 1	°C	Soil temperature	Sum of all hourly temperatures >0°C
Start of dry period	Day of year	Timing of summer soil dry-down	First day of the longest spring/summer period in which soil water matric potential was < −1.5 MPa
Winter frost free days	Days	Freeze-thaw effects	Number of days for which soil temperature was >0°C

models to compare two alternative sets of predictors: a suite of climatic normals (climate model) or dominant subspecies of *A. tridentata* (subspecies model). In climate models, we predicted each establishment metric as a function of site-level climate variables (1981–2010 normals): annual precipitation, mean annual temperature and spring climatic water deficit. Annual precipitation and temperature were from 30-year-normal gridded PRISM climate data (PRISM Climate Group, 2016). Spring climatic water deficit (March-June; from Dilts et al., 2015) was calculated using a Thornthwaite water balance model (Lutz et al., 2010) that incorporates monthly temperature and precipitation, elevation and soil water storage. Pairwise correlations (Pearson's *r*) between climatic predictor variables were <0.61. In subspecies models, we predicted each establishment metric as a function of the dominant *A. tridentata* subspecies (factor with three levels: *A.t. tridentata* [$n = 2$], *A.t. wyomingensis* [$n = 16$], and *A.t. vaseyana* [$n = 15$]). For both climate and subspecies models, the density of residual pre-fire *A. tridentata* (i.e. individuals that established before the fire; ha^{-1}) was included as a predictor variable to represent effects on seed availability and species interactions. Site was included as a random intercept to account for spatial clustering of plot observations.

Models were built in R package LME4 (Bates et al., 2015). We scaled climatic predictor variables (*z*-score) and reported standardized parameter coefficient estimates. 95% confidence intervals were estimated for all fixed effects using the *confint* function with bootstrapping in LME4. Marginal and conditional R^2 values were calculated using the *r.squaredGLMM* function in the MuMIn package (Barton, 2015).

2.5.3 | Importance of temporal patterns of post-fire establishment for long-term population recovery

To evaluate importance of temporal patterns of post-fire establishment on population recovery, we modelled total post-fire *A. tridentata* density and cover as a function of post-fire establishment metrics, controlling for time since fire and dominant subspecies. Post-fire *A. tridentata* density is the total number of *A. tridentata* individuals that established after burning in each plot, scaled to density (ha^{-1}), and represents the size of the post-fire population. Cover is the percent of the plot area covered by *A. tridentata* canopy cover, and represents the availability of sagebrush habitat. The correlation (Pearson's *r*) between post-fire density and cover was 0.49. We used linear mixed effects models to predict post-fire density (ha^{-1}) and cover (%; log_{10}-transformed). Fixed effects included metrics representing the abundance (median and maximum) and frequency (proportion of establishment years) of post-fire establishment, calculated for each plot as described above. Fixed effects also included time since fire (ranging from 8 to 11 years), residual *A. tridentata* density, and dominant subspecies. Pairwise correlations (Pearson's *r*) between continuous fixed effects were <0.6. Site was included as a random intercept to account for spatial clustering of plot observations. Models and outputs were produced as described in the previous section.

3 | RESULTS

3.1 | Drivers of annual post-fire establishment

Eighty percent of dated *A. tridentata* individuals established after the prescribed fires. However, all 12 sites, and 28 of 33 sampling plots, contained residual individuals that established pre-fire. Post-fire *A. tridentata* establishment was highly episodic for all sites, with non-uniform patterns of establishment density across post-fire years (see Figure S1 in Supporting Information). Considering all possible establishment years across sampling plots, 50% of establishment occurred in only 11% of possible plot-year combinations, and 34% of possible plot-year combinations had no observed establishment.

Model results (cross-validated AUC = 0.917) suggest that *A. tridentata* establishment was primarily driven by spring soil water availability in the year of establishment. Three of the four highest-ranked predictor variables represented various measures of spring soil moisture. Establishment density was greatest in years with wetter spring soils, represented by a higher number of spring wet days (Figure 2a). Similarly, establishment density was greatest in years with a later soil dry-down, indicated by the start of the spring/summer dry period (Figure 2c), and with cooler springs, indicated by lower spring degree days (Figure 2d). Time since fire was the variable with the second-highest relative influence. Establishment density was greatest immediately after fire, declining in a threshold-like manner 4 to 5 years after fire (Figure 2b). Summer conditions, winter frost-free days, and all variables from the year following establishment were weak predictors (Figure 2e–j).

3.2 | Temporal patterns of post-fire establishment across regional climatic gradients

Temporal patterns of *A. tridentata* establishment in the 8 years following fire were weakly related to site-level climate and dominant subspecies (Table 3). Median annual establishment, CV of annual establishment, and the proportion of years with establishment were not significantly related to any tested climatic variables or to residual *A. tridentata* density, but the relatively large contribution of the random intercept terms indicated an important role of site characteristics that were not represented by climatic variables included in the models. Maximum annual post-fire establishment, which represented the magnitude of the largest establishment pulse, was greater in sites with higher annual precipitation ($\beta = 1.50$; 95% CI = 1.01–2.23; Table 3). Neither mean climate, subspecies, residual *A. tridentata* density, nor site random effect explained much variation in maximum establishment density (conditional $R^2 = 0.12$ [climate model] and 0.07 [subspecies model]), indicating high variability within and among sites. Plots with *A. t.* ssp. *tridentata* had significantly lower median establishment, higher establishment CV, and a lower proportion of establishment years than other subspecies (Table 3). This subspecies occurred at only two plots at one site (Bridge Creek) and had median establishment densities of 0 (see Figure S1).

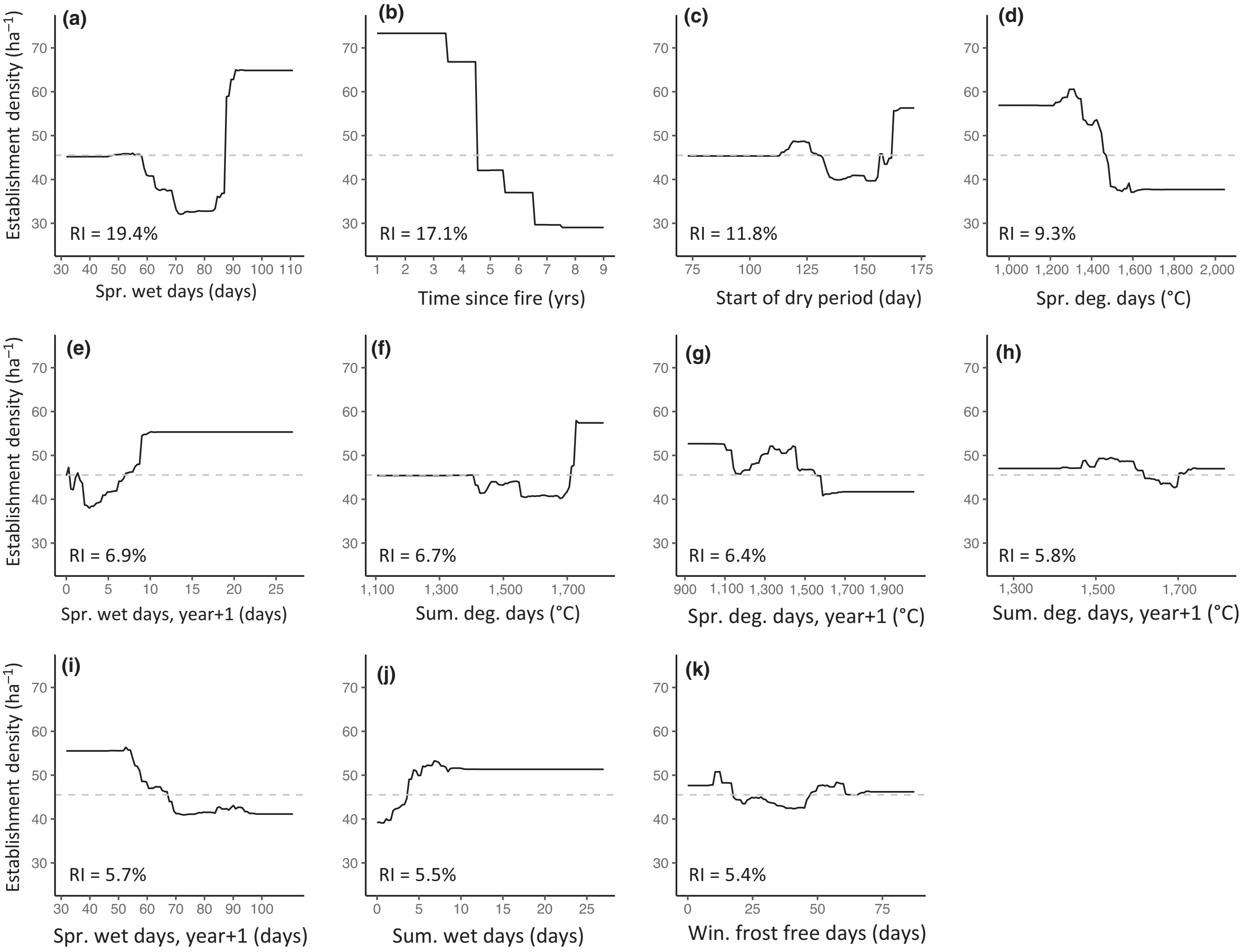

FIGURE 2 Partial dependency plots for variables in a boosted regression tree predicting annual *A. tridentata* establishment density (ha^{-1}). Each panel (a–k) shows the relationship between establishment density and a single predictor variable, ordered by decreasing relative influence (RI). Partial dependency plots (black solid lines) represent the estimated marginal effect of a variable on the response when all other variables are held at their average. Grey dashed lines indicate median establishment density across all plots and years. Predictor variables represent conditions in the year of establishment, except for those named 'year + 1', which represent conditions in the year following establishment (i.e. conditions experienced by a 1-year-old plant)

3.3 | Importance of temporal patterns of post-fire establishment for long-term population recovery

Total post-fire *A. tridentata* density and cover were most strongly predicted by the magnitude of the largest post-fire establishment year (maximum annual establishment; Table 4; Figure 3). Density was predicted to be approximately four times greater in plots with the highest maximum annual establishment (β = 219.9; 95% CI = 167.2–280.4; Figure 3a). Density was also positively related to median annual establishment (β = 212.0; 95% CI = 150.0–275.3). Cover was predicted to more than double with a 1-*SD* increase of maximum establishment (odds ratio; β = 2.17; 95% CI = 1.55–3.15; Figure 3b). Contrary to expectations, the frequency of post-fire establishment (proportion of years with establishment) was not associated with *A. tridentata* density (β = −53.7; 95% CI = −128.4–10.2) or cover (β = 0.77; 95% CI = 0.46–1.29). Time since fire was positively related to cover (β = 1.46; 95% CI = 1.02–2.10), but was not predictive of post-fire density (β = 3.8; 95% CI = −48.4–64.5). Residual *A. tridentata* density had a positive effect on *A. tridentata* cover (β = 2.18; 95% CI = 1.52–3.19) but was not predictive of total post-fire density (β = 44.8; 95% CI = −7.5–97.4). Total post-fire density did not differ among dominant *A. tridentata* subspecies (Figure 3c), but plots with *A. t. vaseyana* had higher cover than plots with *A. t. wyomingensis*after accounting for covariate effects (Figure 3d). Temporal patterns of post-fire establishment were more predictive of density (marginal R^2 = 0.91) than of cover (marginal R^2 = 0.70; Table 4).

4 | DISCUSSION

Our results highlight the importance of infrequent periods of favourable conditions for determining recruitment and long-term plant population dynamics following disturbance. Post-fire *A. tridentata* recruitment was driven by episodic availability of spring soil moisture,

TABLE 3 Results from alternative models predicting plot-level establishment metrics in the first 8 years after fire as a function of climate normals (climate model) or dominant subspecies of *Artemisia tridentata* (subspecies model). Site was included as a random intercept. Shown are estimated regression coefficients (β), with 95% confidence intervals (CI) calculated from parametric bootstrapping listed parenthetically. Continuous fixed effects bolded if 95% CI did not overlap 1 (models of median, maximum and CV establishment density) or did not overlap 0 (model of proportion of establishment years)

	Metrics of establishment magnitude		***Metrics of establishment frequency***	
	Median annual establishment (log$_{10}$)[b]	**Maximum annual establishment (log$_{10}$)[b]**	**CV annual establishment (log$_{10}$)[b]**	**Proportion of years with establishment**
	β (95% CI)			
Climate model predictors				
Intercept	24.7 (11.2–56.6)	141.8 (108.4–186.9)	1.10 (0.95–1.29)	0.73 (0.62–0.84)
Annual precipitation[a]	2.16 (0.66–5.90)	**1.50 (1.01–2.23)**	0.88 (0.69–1.12)	0.08 (−0.09–0.23)
Mean annual temperature[a]	0.51 (0.18–1.45)	0.82 (0.53–1.16)	1.23 (0.97–1.54)	−0.10 (−0.27–0.06)
Spring climatic water deficit[a]	2.50 (0.63–8.90)	1.33 (0.78–2.31)	0.79 (0.58–1.06)	0.07 (−0.14–0.30)
Residual *A. tridentata* density[a]	1.16 (0.64–1.94)	1.07 (0.76–1.51)	0.97 (0.86–1.09)	0.02 (−0.07–0.09)
Marginal R^2	0.13	0.12	0.18	0.11
Conditional R^2	0.56	0.12	0.67	0.59
Subspecies model predictors				
ssp. *Tridentata*[c]	0.04 (−0.9–5.9)	64.0 (22.0–196.2)	2.43 (1.65–3.59)	0.26 (0.00–0.56)
ssp. *Wyomingensis*[c]	38.5 (17.0–79.7)	146.5 (94.9–229.1)	0.99 (0.86–1.16)	0.73 (0.62–0.85)
ssp. *Vaseyana*[c]	23.9 (9.83–52.5)	152.4 (101.6–241.3)	1.09 (0.93–1.30)	0.81 (0.68–0.92)
Residual *A. tridentata* density[a]	1.06 (0.64–1.69)	1.08 (0.76–1.52)	1.00 (0.90–1.10)	0.02 (−0.06–0.09)
Marginal R^2	0.35	0.07	0.42	0.34
Conditional R^2	0.49	0.07	0.59	0.51

[a] Continuous predictor variables have been standardized.

[b] For continuous predictors of log$_{10}$-transformed response variables, coefficient estimates are back-transformed and presented as odds ratios such that each increase in the predictor variable by 1 *SD* multiplies the expected value of the response by β.

[c] Absolute factor estimates provided for *A. tridentata* subspp. categories.

and population recovery was associated with the magnitude, but not frequency, of post-fire establishment pulses. Temporal patterns of establishment were poorly predicted by site-level climate or dominant subspecies.

4.1 | Post-fire recruitment driven by episodic availability of spring soil moisture

Spring soil water availability is a primary driver of perennial plant establishment in cold desert ecosystems that experience winter-dominated precipitation followed by a gradual decline in soil moisture (Hardegree et al., 2016; James et al., 2019). Specifically, for *A. tridentata*, episodic establishment was promoted by wetter and cooler spring soil conditions and a later start of the seasonal dry-down in the year of establishment. Although warmer temperatures can promote germination (Cline, Roundy, & Christensen, 2018) and increase seedling biomass accumulation (Schlaepfer et al., 2014), we found that recruitment was associated with cooler spring temperatures. Decreased plant community transpiration resulting from cooler temperatures may prolong onset of soil water stress during the seasonal dry-down process, and mean annual temperature was found to be more important than precipitation in range-wide models of *A. tridentata* dynamics (Kleinhesselink & Adler, 2018; Renwick et al., 2018). Freeze-thaw cycles may constrain survival of early-germinating seedlings (Roundy & Madsen, 2016), but we observed no influence of winter frost-free days on establishment. Effects of soil environmental conditions beyond the year of seedling establishment were negligible, indicating that first-year seedling survival is limited by harsh abiotic conditions and is the primary bottleneck to *A. tridentata* recruitment. However, we were not able to quantify the effect of extreme climatic events, which have the potential to cause ecological impacts such as widespread mortality across age classes (Miriti et al., 2007; Petrie et al., 2020).

Fires typically produce resource pulses that result in short establishment windows before resources are used by competing residual and newly established plants (Jentsch & White, 2019). We found a 4–5-year window for post-fire *A. tridentata*

TABLE 4 Results from models predicting total post-fire *Artemisia tridentata* density and cover as a function of plot-level temporal patterns of establishment. Site was included as a random intercept. Shown are estimated regression coefficients (β), with 95% confidence intervals (CI) calculated from parametric bootstrapping listed parenthetically. Fixed effects bolded where 95% CI did not overlap 0 (density model) or did not overlap 1 (cover model)

	Post-fire *A. tridentata* density (ha^{-1})	*A. tridentata* cover (%; log_{10})[a]
Predictor	**β (95% CI)**	
Median annual establishment[b]	**212.0 (150.0–275.3)**	1.39 (0.90–2.02)
Maximum annual establishment[b]	**219.9 (167.3–280.4)**	**2.17 (1.55–3.15)**
Proportion of establishment yrs[b]	−53.7 (−128.4–10.2)	0.77 (0.46–1.29)
Yrs since fire[b]	3.8 (−48.4–64.5)	**1.46 (1.02–2.10)**
Residual *A. tridentata*[b]	44.8 (−7.5–97.4)	**2.18 (1.52–3.19)**
A. tridentata ssp. *Tridentata*[c]	378.3 (131.1–630.0)	0.76 (0.15–4.02)
A. tridentata ssp. *Wyomingensis*[c]	543.7 (465.5–628.3)	1.03 (0.59–1.66)
A. tridentata ssp. *Vaseyana*[c]	599.4 (508.9–679.1)	5.10 (2.91–8.57)
Marginal R^2	0.91	0.70
Conditional R^2	0.92	0.71

[a] Coefficient estimates are back-transformed from the $\log_{10}$ scale. For continuous predictor variables, each one-unit increase in the predictor variable multiplies the expected value of the response by β.

[b] Continuous predictor variables have been standardized, and regression coefficients give the effect of a change of 1 *SD*.

[c] Absolute factor estimates provided for *A. tridentata* subspp. categories.

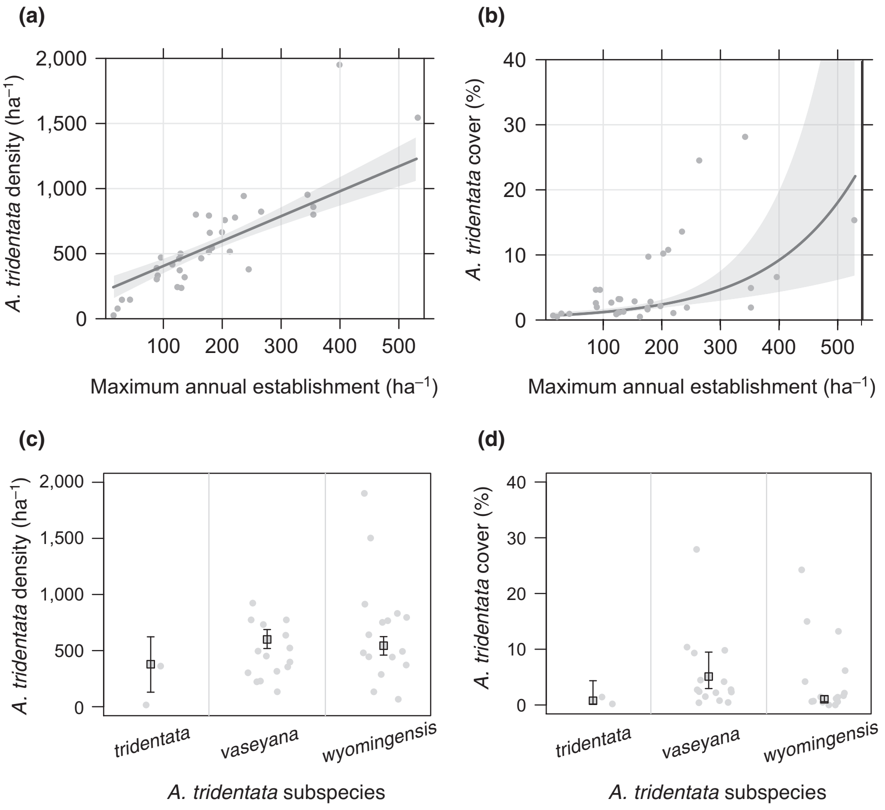

FIGURE 3 Partial effect plots for models predicting post-fire *Artemisia tridentata* density (a, c) and cover (b, d). Marginal effect of maximum annual establishment on post-fire *A. tridentata* (a) density (β [95% CI] = 209.1 [147.4–267.7]) and (b) cover ($\log_{10}$; β [95% CI] = 2.40 [1.48–4.07]). Marginal estimates of post-fire (c) density and (d) cover by subspecies. Lines represent the coefficient mean estimate ±95% confidence interval. Sampling occurred between 8 and 11 years after fire, and both density and cover models included time since fire and residual *A. tridentata* density as covariates, with a random intercept for site

establishment, after which recruitment may have been limited by competition from other species that were increasing in abundance (Freund et al., 2021). This observed window of establishment is longer than previously suggested (Wijayratne & Pyke, 2012; Ziegenhagen & Miller, 2009). Most sampling plots contained residual *A. tridentata* individuals that had established prior to burning and survived the fire, and although the abundance of residual *A. tridentata* was not a significant predictor of establishment metrics, these surviving plants likely provided an important seed source throughout the post-fire period (Turner et al., 1998). Patchy burns are common for prescribed fires, which typically burn under conservative weather windows. Our study sites had heterogeneous tree, shrub and herbaceous cover (Chambers et al., 2014; Urza et al., 2017) and thus discontinuous fuel loadings that likely limited fire spread. In higher-severity burns with no surviving adult *A. tridentata*, the window of establishment is likely narrowed to 1 or 2 years after fire before depletion of viable seeds in the soil seedbank (Wijayratne & Pyke, 2012). The observation of a 4–5-year window for establishment suggests that residual *A. tridentata* provided a continuous post-fire seed source that, compared to the soil seedbank alone, extended the opportunity for post-fire recruitment. Our findings underscore the importance of disturbance refugia—locations that experience less severe disturbance than the surrounding landscape, such as unburned patches—for contributing to post-disturbance recovery (Krawchuk et al., 2020).

Interannual variability may strongly influence ecosystem responses to climate change (Werner et al., 2020). Climate projections indicate declining snowpack, warming temperatures and increased variability in soil water availability in cold deserts of the western U.S. (Klos et al., 2014; Palmquist et al., 2016; Schlaepfer et al., 2012). Multiple modelling studies predict climate-induced reductions in *A. tridentata* recruitment, with the greatest losses in drier locations (Renwick et al., 2018; Schlaepfer et al., 2015). Our sites did not include the driest *A. tridentata* habitats. However, we found that both the magnitude (median and maximum) and variability (CV and frequency) of establishment were poorly predicted by mean climatic conditions, and that even typically dry sites experienced large pulses of establishment. Thus, interannual variability in climate may help buffer recruitment dynamics against short-term effects of climate change, as long as there is reasonable probability of favourable conditions during the post-fire window for establishment. For example, interannual variability in precipitation has been shown to increase the resilience of Iberian semi-arid plant communities to changing rainfall patterns (Miranda et al., 2011).

4.2 | Post-fire population recovery reflects the magnitude, but not frequency, of early establishment pulses

Post-disturbance community recovery is sensitive to both the magnitude and frequency of episodic establishment events (Chesson et al., 2004). While population recovery may be driven by single establishment events, population dynamics of perennial plants tend to reflect the cumulative effects of multiple pulses occurring over time (Chesson et al., 2004). Contrary to our expectations, total post-fire *A. tridentata* density, which represents the size of the population that established after fire, was well predicted by the magnitude of the largest establishment pulse but was not related to the frequency of establishment events. The lack of a relationship between post-fire density and time since fire (8–11 years after fire) means that the population size did not change over that time period and suggests that demographic processes such as recruitment and mortality had largely stabilized by the time of sampling. Canopy cover, which represents sagebrush habitat, was less strongly related to post-fire establishment pulses, although *A. tridentata* cover was higher in sites with a larger peak of maximum annual establishment. Cover was also positively associated with time since fire, which, given the finding of a consistent population size over time, likely reflects age-related plant growth rather than recruitment. Residual *A. tridentata* density was positively related to cover; however, because cover measurements included both pre-fire and post-fire individuals, we cannot infer whether the effect is due to an influence on seed availability or simply because the surviving plants comprised a substantial amount of canopy cover.

The strong relationship between post-fire density and maximum annual establishment suggests that population recovery is possible with a single favourable year within the 4–5-year post-fire establishment window. However, we did not explore potentially important effects of post-fire recruitment frequency on population and habitat structure. For example, *A. tridentata* recruitment pulses are often followed by steep population declines because seedlings have low survival probabilities, and early post-fire stands are susceptible to extirpation (Chambers et al., 2017; Shriver et al., 2019). Multiple establishment episodes may buffer the risk of population loss by increasing the probability that seedling cohorts will survive subsequent conditions. To better understand post-fire population recovery, research is needed on how specific demographic processes—including seed production, seedling mortality and growth—respond individually to interannual weather and interactions with neighbouring plants (Chesson et al., 2004).

4.3 | Management implications

Our results suggest opportunities for improving management outcomes and promoting conservation of ecosystems losing foundation species due to altered fire regimes. In the western U.S., the Bureau of Land Management seeded thousands of km^2 with *A. tridentata* after fires during recent decades (Pilliod et al., 2017). Although seeding can successfully promote post-fire *A. tridentata* recovery in some circumstances (Germino et al., 2018; Ott et al., 2017; Urza et al., 2019), outcomes of landscape-scale seeding treatments are often poor (Knutson et al., 2014). A better understanding of the factors determining establishment of obligate seeders, like sagebrush, can be used to effectively prioritize resources for restoration of disturbed landscapes.

Our study showed that a residual seed source can promote establishment of an obligate seeder during years with favourable weather conditions for up to 5 years after fire. *Artemisia tridentata* seeds have a short period of viability and are not likely to survive fire (Wijayratne & Pyke, 2012), and residual, seed-producing individuals are critical to continuous post-fire seed availability. Thus, recovery may be improved by fire management strategies that leave fine-scale mosaics of unburned patches, within incomplete-burn prescribed fires and throughout fire interiors during wildfire suppression operations.

Our results also suggest that the window of opportunity for post-fire seeding in the interior of larger fires may be longer than previously thought. In drier portions of the landscape, restoration treatments can be timed so seed availability coincides with favourable weather and results in successful establishment. Seasonal weather forecasts are becoming more available (Bradford et al., 2018; Hardegree et al., 2018) and can help ensure seeding is implemented in years when favourable conditions (e.g. wet, cool springs) will promote establishment. Additionally, repeated seeding in multiple successive years may improve restoration success in high-priority areas by increasing the odds that seed availability coincides with favourable conditions for establishment (Davies et al., 2018; Shriver et al., 2018; Wilson et al., 2004). Planned repeated seeding may decrease market uncertainties for the seed industry and enable increases in availability of locally-adapted seed sources when coupled with proper seed storage (Brabec et al., 2015). A stable seed market would also help alleviate the current temporal mismatch of available commercial seed sources and large fire years when post-fire restoration needs are high (Camhi et al., 2019). Our study contributes to the growing body of evidence that infrequent periods of soil water availability are a major driver of post-disturbance recovery and highlights the importance of developing management strategies grounded in the underlying ecology of foundation plant species.

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AUTHORS' CONTRIBUTIONS

A.K.U., P.J.W., J.C.C. and S.G.K. conceived the ideas and designed the methodology; A.K.U., P.J.W., D.B., S.G.K. and B.A.R. collected the data; D.B. and A.K.U. analysed the data; A.K.U. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.jh9w0vtbk (Urza et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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