Ecosystems (2026) 29:24
https://doi.org/10.1007/s10021-025-01043-x

ECOSYSTEMS
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ORIGINAL ARTICLE

Loss of Ecosystem Resistance to Invasion after Wildfire Facilitated by a Pulse of Soil Nitrogen Availability: Experimental Evidence in the Burned Sagebrush Steppe

Toby M. Maxwell,[1,2,3]* Matthew J. Germino,[2] and Marie-Anne de Graaff[1]

[1]*Department of Biology, Boise State University, 1910 University Drive, Boise, Idaho 83725, USA;* [2]*U.S. Geological Survey, Forest, Rangeland, and Ecosystem Science Center, 230 N Collins Road, Boise, Idaho 83702, USA;* [3]*Oregon State University – Cascades, Natural Resources and Environmental Sciences, 1500 SW Chandler Ave, Bend, Oregon 97702, USA*

Abstract

The impacts of climate shifts on ecosystems dominated by long-lived perennials are likely most pronounced during community reassembly after disturbances such as fire and confounded by interactions between disturbances and plant community composition. A 30-year-experimental hydroclimate manipulation of multiple sagebrush steppe communities was completely consumed by a 2019 wildfire, providing an opportunity to evaluate effects of precipitation deficit on ecosystem recovery. Ambient precipitation was doubled for 23 years via irrigation in winter or summer in grassland or shrub–steppe communities until 2016. Plots that had received irrigation thus experienced drought for three years preceding and continuing after the fire. These landscapes are vulnerable to invasion by exotic annuals such as *Bromus tectorum L.* (cheatgrass) that promote wildfire occurrence, which favors even greater invasion levels. Thus, we asked whether patterns of invasion after the compound disturbance of drought and fire related to the long-term pre-fire climate and plant community structure. Established theory led to the prediction that plant communities developed under wetter climates would have greater resistance to invasion. The most resistant plots were the most arid (that is, never irrigated control plots with no drought) which had the least pre-fire canopy cover of shrubs and nitrogen-fixing forbs and greater proportional cover of perennial bunchgrasses. Plots that developed under winter irrigation had greater cover of shrubs and N-fixing forbs, corresponding to pulses of plant available soil nitrogen that were 8.2-fold greater than pre-fire levels, compared to a 0.20-fold post-fire reduction in soil nitrogen observed in the ambient plots. Nitrogen pulses and invasion were most evident in the inter-canopy

Received 31 July 2025; accepted 22 December 2025;
published online 20 January 2026

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-025-01043-x.

Author Contributions MJG conceived of and designed the original experiment and performed the pre-fire research; TMM, MJG, and MAdG conceived of and designed the post-fire study. TMM performed the post-fire research and analyzed the data. TMM, MJG, and MAdG wrote the paper.

**Corresponding author; e-mail:* toby.maxwell@osucascades.edu

bare-soil patches ('interspaces') and were least evident where perennial grasses were most abundant. Long-term hydroclimate altered pre-fire plant community composition in ways that affected post-fire resistance to invasion such that the combined effects of fire and water deficit led to greater than expected invasion in wetter regions that are conventionally considered resistant to invasion and resilient to wildfire.

Key words: soil nitrogen; *Bromus tectorum*; nutrient cycling; resilience; resistance; sagebrush steppe; pulse; ecohydrology; experimental; wildfire.

Highlights

- Arid plots considered least resistant to invasion by annuals were most resistant.
- A post-fire pulse of soil N linked to pre-fire N-fixers and shrubs drove invasion.
- Perennial grasses increased resistance by reducing plant available soil N.

Introduction

Plant community resistance to exotic-plant invasion following a disturbance such as wildfire is difficult to predict in a changing climate because prevailing weather and historical climate can have strong and differing effects on community reassembly and invasibility (Parks and others 2015; Applestein and others 2021; Jiao and others 2021). Wildfire–climate interactions are particularly relevant to understanding post-fire resistance to invasion in the predominantly perennial, semiarid sagebrush steppe of the Western USA, where warmer and drier conditions are exacerbating invasion by exotic annuals (EAs, for example, *Bromus tectorum L.*, cheatgrass) after fire (Taylor and others 2014; Bradley and others 2018; Smith and others 2021). These EAs can increase wildfire occurrence or severity beyond the adaptive capacity of the native perennial community, in turn favoring EAs over native perennials in the post-fire environment (Brooks and others 2004; Boyd and others 2015a; Bradley and others 2018). A key outcome of EA invasion is to create a positive feedback loop known as the exotic-annual-grass fire cycle (D'Antonio and Vitousek 1992) which threatens wildlife, carbon stocks, and productivity across tens of millions of hectares of drylands in the Western USA, and in tropical and Austral drylands (Germino and others 2016; Nagy and others 2021; Doherty and others 2022; Mahood and others 2022; Maxwell and Germino 2022; Maxwell and others 2024).

Considerable variation in hydroclimate occurs across the domain of sagebrush steppe in semiarid North America, where mean annual precipitation can vary from 200–600 mm and seasonality varies from some summer precipitation in the east to nearly none in the western part of the range (Cook and Irwin 1992; Goodrich and others 1999). Interannual climate variability is also considerable, and wet–dry cycles can strongly affect the occurrence of disturbances such as fire and the conditions affecting community reassembly (Hatchett and others 2016; Millar and others 2019; Werner and others 2020). Increasing aridity exacerbates invasion and fire and its effect may become most evident when long-lived perennial communities are affected by catastrophic disturbances such as stand replacing wildfires, as has been shown in the sagebrush steppe (O'Connor and others 2020; Jiao and others 2021; Daramola and Xu 2022). Short-term responses of EAs to wildfire can also drive long-term recovery patterns of whole communities (Germino and others 2022a).

In sagebrush steppe, resistance to invasion is considered to be greater in areas with wetter or cooler soil moisture or temperature regimes and more summer precipitation, with few localized exceptions (Bradley 2009; Chambers and others 2014; Taylor and others 2014; Larson and others 2017). We define resistance as the tendency of ecosystems to maintain their plant community structure after a disturbance (Holling 1973; Folke and others 2004; DeRose and Long 2014). Resistance to cheatgrass invasion has appeared greater in cooler or wetter sites, due in part to greater abundance and vigor of perennial herbs in those settings along with low-temperature inhibition of cheatgrass (Chambers and others 2007, 2014; Bradley 2009). Warmer and drier conditions and more frequent droughts are forecast for the region (Snyder and others 2019). Therefore, there is a need to experimentally test whether plant communities that were established in a wetter climate will retain their expected resistance to invasion after fire in a drier climate and/or under drought.

The hypothesized mechanism for greater resistance in wetter and/or cooler parts of the sagebrush steppe is that greater use of soil water and nutrients by resprouting perennial herbs after fire preempt soil resource availability to invading species (Chambers and others 2007, 2014). A better

understanding of the mechanisms that control post-fire soil resource availability could help explain where, when, and why resistance should deviate from predictions based on established soil moisture and temperature regimes (Davis and others 2000; Vasquez and others 2008; Chambers and others 2014; Kainrath and others 2022). However, assessing the influence of soil resource availability on resistance is particularly difficult in drylands because heterogenous spatial patterning of vegetation and harsh climate conditions, which together lead to patchy and flashy nutrient and water cycling (Cui and Caldwell 1997; Austin and others 2004; Bechtold and Inouye 2007; McAbee and others 2017).

We addressed the need for improved mechanistic understanding of resistance with a rare opportunity that arose following a 2019 wildfire that burned a long-term climate-manipulation study in the sagebrush steppe of the Eastern Snake River Plain at the Idaho National Laboratory, USA. Starting in 1993 and up to three years prior to the 2019 wildfire, mean annual precipitation was doubled through supplemental irrigation in winter or summer compared to control plots which received no extra water. The additional precipitation altered the ambient soil moisture regime (that is, 'hydroclimate') from aridic (dry year-round) to xeric (winter-wet) or ustic (summer-wet) conditions, with low, intermediate, and high expected resistance to EAs, respectively. The experiment also manipulated initial plant community composition through planting and seeding of bare soils with either native shrub–steppe vegetation or with perennial bunchgrasses. The experimental treatments created distinct plant communities and affected soil carbon and nitrogen cycling among plot types (Germino and Reinhardt 2014; Campos and others 2017; McAbee and others 2017; Huber and others 2019).

To our knowledge, this study provides the first experimental test of resistance theory in the sagebrush steppe done with a natural wildfire and experimental variation in soil hydroclimate. Most other evidence comes from uncontrolled observations of plant communities over time, in some cases with experimental removal of native species (for example, Chambers and others 2007; Prevéy and others 2010). Our experimental treatments and pre-fire data allowed us to test for causal effects of climate and pre-fire plant community composition on resistance (Figure 1D) and soil resource availability (Figure 1E) and to evaluate whether and how key components of the pre-fire plant community related to post-fire resistance to invasion (Figure 1F). Specifically, we hypothesized that post-fire resistance to EA invasion would be greater with: 1) lesser cover of nitrogen-fixing plants in the pre-fire plant community, which can create hotspots of soil nitrogen that promote invasion (as in Maron and Connors 1996); 2) lesser cover of fire intolerant shrubs that, when burned lead to resource rich, bare-soil patches that could be entry points for invasion (Bechtold and Inouye 2007; Hoover and Germino 2012; Germino and others 2018; Arkle and others 2022); and 3) greater cover of perennial grasses, which recover quickly after wildfire and thus can pre-empt acquisition of soil resources by EAs. The data and theoretical developments presented in this study can be used to improve predictions of invasion after disturbance across the nearly 100 million ha of heavily managed sagebrush steppe landscape, and the many other ecosystems affected by exotic annual invasions, drought, and wildfire globally (D'Antonio and Vitousek 1992).

Methods

Ecohydrology Experimental Design and Site History

Mean annual temperature and precipitation are 5.5 °C and 210 mm, respectively, at the experimental site and the local soil temperature and moisture regimes were frigid and aridic, respectively. For this study, we focused on 54 of the 72 8 × 8-m plots configured in three replicated blocks having all combinations of:

1) Three hydroclimates hereafter referred to as 'ambient,' or 'winter-wet' or 'summer-wet,' corresponding to ambient environmental conditions, or a doubling (+ 200 mm water) of annual water inputs via supplemental irrigations in winter or summer, respectively, from 1993 through 2016.
2) Two community types: perennial grassland (that is, a crested wheatgrass monoculture), or a diverse native sagebrush steppe assemblage.

Ambient, winter-wet or summer-wet hydroclimate treatments corresponded to aridic, xeric, or ustic, soil moisture classifications, respectively, and all plots, including un-irrigated, 'ambient' plots, had identical irrigation hose infrastructure. The plots were established by excavating and backfilling blocks of 6 subplots each with a homogenized loamy soil to 0.5, 1, or 2-m depths, but soil depth had mostly no, or occasionally only weak effects on resistance to EAs and thus were not considered,

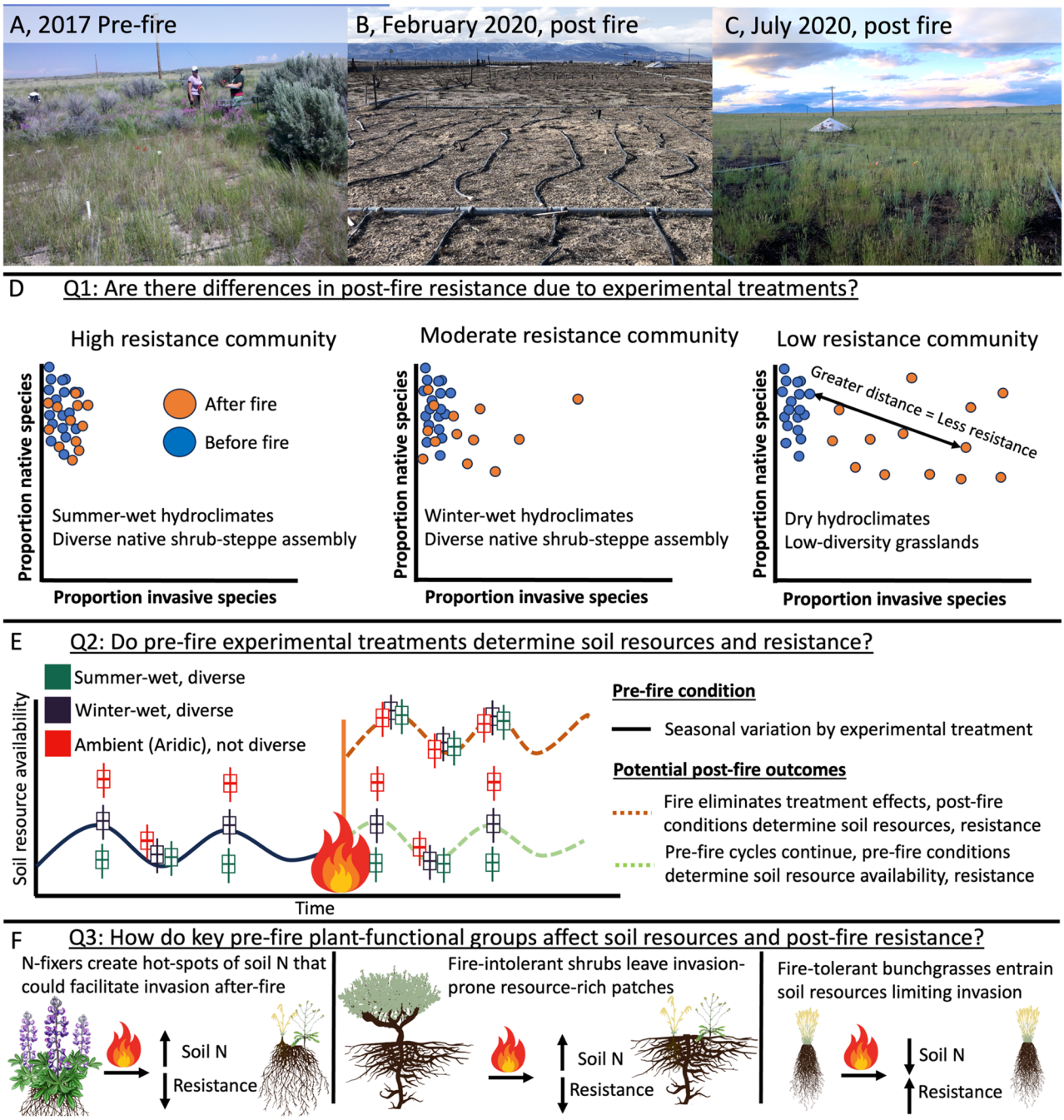


Figure 1. Images of the long-term ecohydrology experiment before the July 2019 Sheep fire (A), or during the following winter (B), and or summer (C). Note the abundance of shrubs in the pre-fire image. Irrigation hoses were present in all plots, including non-irrigated ambient control plots to control for potential microsite effects. Hypothetical scenarios are shown for high or low resistance to invasion according to our resistance metric (D), and strong or weak legacy effects of the pre-fire experimental treatments (E). Legacy effects are strong when post-fire patterns of nitrogen cycling correspond to pre-fire experimental treatments (dashed green line), or weak when post-fire patterns cease to reflect pre-fire plant community and climate conditions and more closely match post-fire weather and plant community (dashed orange line). Hypotheses are visualized for the effects of key components of the pre-fire plant community—that is, nitrogen-fixing forbs, perennial shrubs, and perennial bunchgrasses—on resistance (F). Photograph credits: Matthew Germino (A,B); Toby Maxwell (C).

that is, soil depth was included as a random effect in our models. For more information on the design of the original experiment see Anderson and Forman (2003).

Plots that were watered for the 23 years leading up to the cessation of irrigation in 2016 were considered to be under soil water deficit in the years before (Fall 2017-July 2019) and after the fire (August 2019-onward), whereas control plots had the same 'ambient' (aridic) soil moisture regime throughout the experiment and before/after the fire. Ambient precipitation was slightly greater than the long-term average of 210 mm in the years prior to the wildfire (that is, 230, 231, 221, 262 mm in 2016–2019, respectively), below-average for two years following the wildfire (106 and 178 mm in 2020 and 2021, respectively) and above average in 2022, the final year of this study (241 mm). 'Drought' was considered to be the effect of the irrigation cessation, and not the below-average water years that occurred in 2020 and 2021.

The experiment burned along with 48,000 ha of surrounding sagebrush steppe in the 2019 Sheep Fire, and all above-ground biomass was consumed (Figure 1B). Our sampling timing thereafter occurred in spring 2020 when COVID-19 regulations allowed.

Plant Community

Plant cover that intercepted a narrow pin lowered to ground was recorded at all levels of the canopy for 144 points per plot in 2016 using grid-point intercept or 100 points per plot in 2020–2022 using line-point intercept, with measurements made at peak productivity and excluding the outer 1-m buffer inside of plot edges.

In 2022, plant density was counted in each plot at random locations within two strata, the inter-canopy ('interspace') areas between established perennials and the 'whole plot' which included the entire measured area (that is, inter- and sub-canopy). Interspaces were primarily bare soil but were still defined as interspaces if they had newly germinated seedlings and/or annual plants. We randomly selected six interspace soil patches at least 1 m from the edge of each plot and counted the density and identity of any germinating plants and similarly counted germinating and mature plants in an adjacent 1-m^2 area for 'whole plot' plant density. Interspaces were at least 10 × 10 cm and always bordered by established perennials. Interspace area was estimated by measuring the longest axis of the interspace between any two bordering perennial plants and the perpendicular axis, and multiplying the two measurements, that is, assuming rectangular interspace dimensions. All plants were counted within interspace or whole plot areas to the species level except for native annual forbs which were classified as a group.

Resistance

To quantify resistance to EA plant invasion, we calculated the relative cover of perennial and exotic herbaceous plant cover (Eqs. 1, and 2 below).

$$\text{Perennial grass index} : P_i = \frac{P}{P+H} \quad (1)$$

$$\text{Exotic herbaceous annual index} : E_i = \frac{E}{E+N} \quad (2)$$

P is the total cover of perennial grasses, H is the total cover of non-perennial-grass species (forbs, annual grasses, shrubs), E is the total cover of exotic herbaceous annuals, and N is the total cover of native herbaceous species. Resistance was calculated as a function of the Euclidean distance between pre- and post-fire experimental plot values in P-E index space (Figure 1D, see Wainwright and others 2020 for details). All pre-fire points were from the most recent pre-fire plant community survey taken in 2016, while post-fire index values were calculated for each plot for 2020, 2021, and 2022. Resistance was expressed as the negative value of the Euclidean distance so that a more positive value indicated greater resistance—that is, a greater distance between pre- and post-fire plant communities in P-E index space would be more negative and thus indicated lower resistance (Figure 1D). A maximum resistance value of zero would indicate no invasion.

Soil Inorganic Nitrogen and Water Content

Soils were sampled in 2020 and 2021 at times that aligned with 1) the spring green up when soil N and water were expected to be most available, 2) peak biomass when competition for soil resources was expected to be greatest, and 3) post-senescence when perennial plants were dormant. We used a stratified-random sampling approach to account for the spatial heterogeneity of vegetation and the associated inter-canopy areas between perennial canopies (that is, 'interspaces'). Soils were sampled from 0 to 10 cm in all plots in 3 randomly selected interspaces and under the canopy of the largest crested wheatgrass plant that bordered each interspace (that is, 'under-plant' microsites). Interspaces

and associated plants were randomly selected (and therefore different) at each sampling event. Three soil samples from each microsite-type per plot were aggregated per sampling event, stored on ice in a cooler in the field, and then frozen at -20 °C within 24 h until processing and analysis.

Nitrate and ammonium concentrations were quantified from soils sieved to 2 mm. Approximately, 12 g of soil was placed in 40 mL of 2 M-potassium chloride (KCl) was shaken for 45 min, then filtered through Cytiva Whatman grade 1 (11 µm) filter paper, frozen, and analyzed in bulk colorometrically (BioTek Synergy Mx plate reader, Winooski, VT, USA) using vanadium chloride and indophenol assays for nitrate and ammonium, respectively (Verdouw and others 1978; Doane and Horwáth 2003). Soil inorganic nitrogen (hereafter 'soil N') data are presented as the sum of nitrate- and ammonium-derived nitrogen.

Volumetric water content (VWC) was measured every week during summer 2020 and approximately monthly at times that matched soil sampling in summer 2021 in four randomly selected interspace- or under-plant microsites using a Hydrosense II soil moisture sensor with 12 cm tines (Campbell Scientific, Logan, Utah, USA).

Leaf Sampling and Elemental Analysis

In 2020, individual crested wheatgrass plants were marked and their leaves sampled in 2020 and 2021. Crested wheatgrass was chosen because of its ubiquity and abundance among all plots. Plants were chosen by first identifying the largest interspace in each plot and then randomly selecting 4 individual plants that bordered each interspace. Sampled leaves were dried for 48 h at 60 °C, crushed to a powder, weighed to 0.0001 mg accuracy, and analyzed for total carbon and nitrogen content on a Costech EA 4010 elemental analyzer at the U.S. Geological Survey soil–plant interactions lab in Boise, ID.

Statistics

Significant differences in resistance between the experimental treatments were determined using general linear models with least significant difference tests to assess for differences between group means at $p < 0.05$ (Figure 2). Differences in soil N or water content due to the experimental treatments were assessed using generalized linear mixed effects models with gamma distributions and a log link function using the package *glmmTMB* in R (Tables 1, S1, S2, Brooks and others 2017). A type III ANOVA of the model was used to generate chi

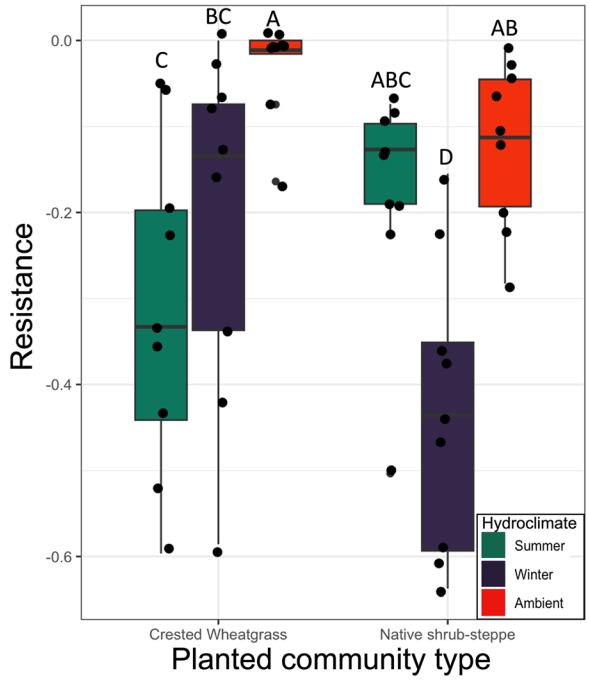


Figure 2. Differences in resistance to invasive plants among experimentally planted community types (x axis groupings) and pre-fire hydroclimates (colors), with significant differences between all treatment combinations indicated by letters above each box (LSD test, $p < 0.05$). More negative values indicate less resistance, such that zero resistance is the most resistant to invasion that a plot could be. Resistance is a unitless value that is a function of pre- to post-fire perennial compared to invasive herbaceous plant cover where greater bunchgrass cover and/or lower invasive herbaceous cover in the post-fire plant community would increase the resistance of a plot (Eqs. 1 and 2, Figure 1).

square tests of statistical significance for the main effects of the experimental treatments and interactions within them on soil N and water content (Table 1). There were no deviations from normality or trends between predicted and residual values for the models as determined by the *simulateResiduals* function from the package *Dharma* in R (Hartig 2016).

To assess if any components of the pre-fire plant community were linked to post-fire EA resistance by soil nitrogen availability, we asked whether N-fixer, shrub, or perennial grass canopy cover related to soil nitrogen content at each sampling time point (Figure 5 A, B, C). To do so, we used generalized linear mixed effects models with the experimental treatments, plot ID, and year as random effects (Figure 5, Table S3). Significant differences between estimated effects of plant functional type on soil N at a particular date were determined using

Table 1. Type 3 ANOVA Results for Mixed Effects Models that Tested for Experimental Treatment Effects on Interspace Soil Inorganic N and Volumetric Water Content

Variable	Soil inorganic N		Volumetric water content	
	Random effects: Soil depth, plot ID			
	Chisq	$P >$ Chisq	Chisq	Pr > Chisq
(Intercept)	33.0	< 0.0001	1788	< 0.0001
Irrigation treatment	5.08	0.079	0.026	0.99
Planted vegetation community	1.0	0.32	0.53	0.44
Sampling date	107	< 0.0001	1408	< 0.0001
Irrigation treatment: Planted vegetation	9.05	0.011	0.79	0.67
Irrigation: Sampling date	7.51	0.68	23.6	0.0088

the *plot_slopes* function in the *marginaleffects* package in R (Arel-Bundock and others 2024, Figure 5 D, E, F).

A structural equation model (SEM) was developed based on the a priori hypotheses that the experimental treatments and functional plant community components would affect resistance (Figures 1D, E, F). The SEM tested the hypothesis that pre-fire N-fixer, shrub, and perennial bunchgrass cover would affect resistance, and that their effects should be mediated by soil properties (Figures 1F, 6, Table S4, (Maron and Connors 1996; Bechtold and Inouye 2007; Chambers and others 2007)). We distinguished perennial grass cover and crested wheatgrass cover in the SEM because previous observational evidence suggests that crested wheatgrass may have unique traits that affect soil N availability (for example, Blank and Morgan 2012a). The SEM included annual measures of plant cover for each functional group, resistance, plot-scale average interspace size, and leaf nitrogen content. The model included three annual measures of soil N for each of 54 plots for 2020 and 2021. The models within the SEM were run with *glmmTMB* in R (see Figure 6, Table S4 for details, Brooks and others 2017). Block ID was included in a version of the models as a random effect but often prevented model convergence and explained negligible variance and so was removed from all models. All models were conditioned on differences in plot-scale total canopy cover by including it as a co-variate (Table S4). To simplify the visualization in Figure 6, Table S4, paths were omitted that were not significant ($p > 0.10$) or not relevant to our hypotheses (Figure 1E, F). Data in the model were standardized to a mean of zero and standard deviation of one, allowing for comparison of coefficients and accurate quantification of effect sizes of paths in the model. Goodness of fit was assessed by Fisher's C which was 5.075 and Chi-squared which was 1.634, with $p = 0.80$ and 0.75, respectively, indicating that that hypothesized model structure was supported by the data.

To test for the effect of the soil N pulse (Figure 4A, B) on resistance for the first three years after the fire, we built individual regression models, testing for the effect of the soil N pulse as well as pre-fire N-fixer, shrub, and perennial bunchgrass cover on resistance for each year of the study (Figure 7A, B, C, D). We also constructed a generalized linear mixed effects model that included all these variables, thereby controlling for any co-variation, of each component variable on resistance (Figure 7 E, F, G, H, Table S5). To assess co-variation and thus mechanistic links among the dependent variables in the combined model, it was re-run but without N-fixers and then again without N-fixers or shrubs (Table S5). Note that resistance is reported here for the 2022 sampling in which plant community measurements were adequate to calculate resistance, but this time point was not included in other models (for example, Figures 5 and 6, Tables S1, 2, 3) because soil N was not sampled in 2022. Thus, we assessed how the soil N pulse and pre-fire community conditions affected long-term (3-year) resistance outcomes. Model residuals were normally distributed, and there was no correlation between model predicted and residual values.

Results

Experimental Treatment Effects on Plant Community Composition, Density, and Resistance

Pre-fire foliar cover of N-fixers, shrubs, and perennial bunchgrasses varied between the experimental hydroclimate and planted community treatments (Figure S1). The greatest pre-fire N-fixer

and shrub cover occurred in winter-wet native shrub–steppe planted plots (41%, 37.5%, respectively) where shrub cover was eightfold greater than in any other treatment combination (Figure S1). Pre-fire perennial grass cover was greatest (79.2%) in summer-wet native planted plots, which also had the greatest cover of rhizomatous grasses and sedges (Figure S1). N-fixer, shrub, and perennial grass cover were least in ambient plots (mean ± SE of 0.17 ± 0.17%, 2.6 ± 0.90%, and 40 ± 1.3%, respectively); intermediate in summer-wet plots (10% ± 0.019, 3.9 ± 0.66% and 47 ± 3.5%, respectively); and maximum in winter-wet plots (13% ± 0.029, 11.7 ± 2.6%, and 47 ± 3.5%, respectively, Figure S1).

In the first year after the wildfire (2020) three years of drought, followed by fire led to plant communities in which shrubs and N-fixers were mostly absent (Figure S1). Compared to pre-fire levels, post-fire N-fixer cover decreased by 9.5% and 10.1% in summer- and winter-wet plots, respectively, but increased by 0.4% in ambient plots. In irrigated and control plots, N-fixer cover decreased by a mean of 6.4% from before to after fire, regardless of planted community. Shrub mortality was nearly 100% in the first year after the fire, and the few resprouting shrubs were rabbitbrush (*Ericameria nauseosa*) which had the greatest, albeit minimal, cover in ambient-crested wheatgrass planted plots (mean ± SE of 0.25 ± 0.18%). Perennial grass cover was relatively unaffected by the fire, increasing by 2.9% in grassland plots and 10.6% in native shrub–steppe plots (Figure S1). Perennial grass cover was 4.6%, 2.6%, and 14.4% greater in ambient-, winter-, and summer-wet plots, respectively, in 2020 compared to the 2016 pre-fire plant survey.

Post-fire resistance to EA invasion varied according to long-term pre-fire hydroclimate (irrigation treatments), and hydroclimate effects on resistance depended on the original planted community type (native shrub–steppe or perennial grassland, Figure 2). The least resistance (that is, most invasion) was observed in plots that received irrigation, especially in winter (Figure 2, LSD test $p < 0.05$). Plots that received only ambient precipitation and were never irrigated had the greatest post-fire resistance to invasion (closest to zero, Figure 2), followed by summer, and winter hydroclimate plots (mean ± SE of − 0.070 ± 0.045, − 0.24 ± 0.031, − 0.30 ± 0.044, respectively, $p < 0.05$). Experimentally planted crested wheatgrass grasslands had greater resistance than native shrub–steppe planted plots (mean ± SE of − 0.16 ± 0.030, − 0.24 ± 0.042, respectively, $p < 0.05$).

The density of EAs (plants/m^2) was greater in the interspace microsites compared to the whole plot and the difference was most pronounced in winter-wet plots where invaders were 1.44–4.2-fold denser in interspaces (Figure 3). Exotic annual *Bromus* species, mostly cheatgrass, were dominant among the exotic species in winter-wet plots that had been planted with native shrub–steppe vegetation and tap-rooted forbs were most common among the other plot types.

Soil Nitrogen Content

Plots that were originally planted with native shrub–steppe vegetation had 1.14 to 1.96-fold greater plant available soil nitrogen (hereafter soil N) in interspace soils than crested wheatgrass planted plots (Table S2). The effect of the hydroclimate on soil N depended on whether a plot was planted as a perennial grassland or native shrub–steppe ($p < 0.011$, Table 1, S1) leading to post-fire soil N that was 1.21–2.06-fold greater in previously irrigated, compared to ambient plots (Table S2). Winter-wet native shrub–steppe plots had the greatest measured soil N values, but average soil N was greater across all time points in summer-wet plots (that is, Tables S1, S2).

A pulse of soil N was observed on June 30, 2020—the first post-fire soil sampling (Figure 4). The magnitude of the N pulse depended on the planted community and hydroclimate and was greatest in winter-wet native shrub–steppe planted plots, which had an 8.18-fold increase in soil N compared to pre-fire levels. No pulse was observed in ambient crested wheatgrass planted plots, which had an 0.78-fold reduction in soil N. Soil N was positively associated with pre-fire N-fixer, shrub, and perennial grass cover, with the strongest correlations at the first sampling point after the fire—that is, June 2020 (1.69 ± 0.51, $p = 0.0008$; 1.65 ± 0.61, $p = 0.0071$; 0.95 ± 0.26, $p = 0.0003$; respectively, Figure 5, Table S3). The correlation between soil N and pre-fire perennial grass cover changed signs from positive at the first sampling point, to negative two weeks later at the second sampling point (effect size of − 0.71 ± 0.35, $p < 0.0001$, Figure 5, Table S3).

Leaf N Content

Leaf N content of crested wheatgrass plants (hereafter 'leaf N') ranged from 0.67–1.6% depending on the sampling year, hydroclimate, and vegetation treatments (Figure S2). Leaf N was 1.43-fold

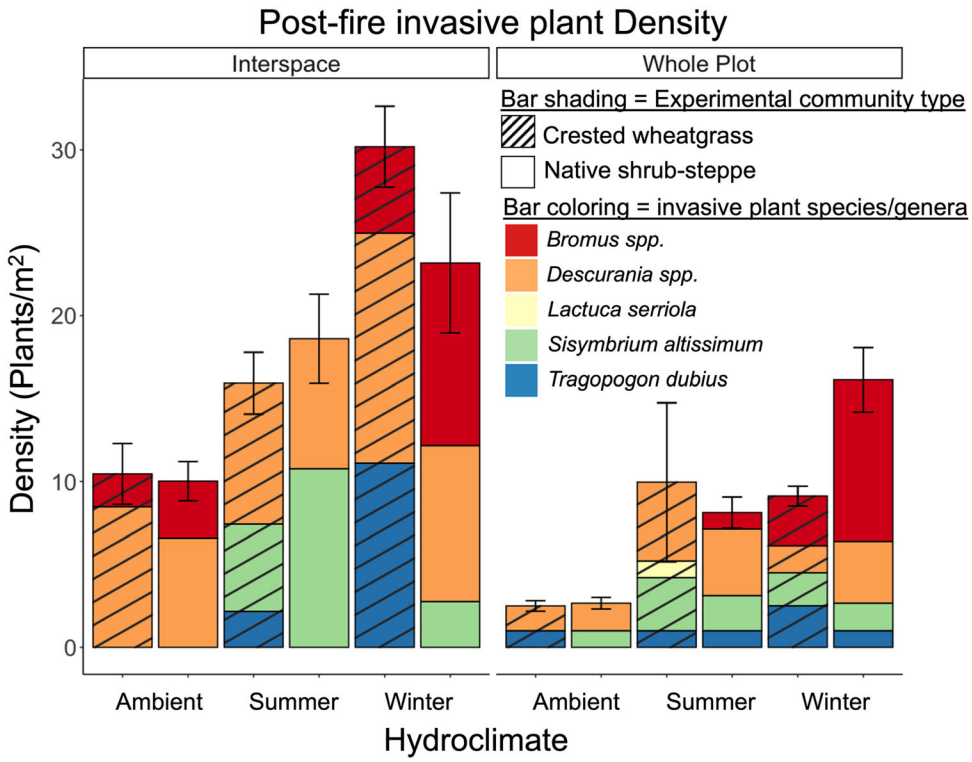


Figure 3. Density of invasive plants in spring 2022 according to experimentally planted community (shading), hydroclimate (x axis groupings), and microsite (left and right panels). Error bars are standard error of $n = 9$ replicate plots of the sum total density of exotic invasive plants (that is, the value at the top of the bar) for each treatment combination and the height of the constituent bars for each species that make up a bar are average values across the 9 plots. *Bromus* species are exotic annual grasses, and all other species are short-lived (annual or biennial), tap-rooted forbs.

greater in the second year after the fire—2021—compared to 2020 and 1.42- and 1.50-fold greater in summer compared to winter or ambient plots on average. Native shrub–steppe planted plots had 1.24-fold greater leaf N content than crested wheatgrass planted plots, and the effects of planted community and hydroclimate on leaf N were independent (that is, there was no interaction).

Structural Equation Modeling: Soil Properties and Leaf N as Moderators of Pre-Fire Plant Community Effects on Post-Fire Resistance

Our structural equation model (SEM) confirmed that ambient-, summer- and winter-wet hydroclimate treatments had strong direct effects on both soil N (− 0.085, + 0.26, − 0.16, respectively) and resistance (+ 0.28, − 0.24 and − 0.06, respectively, Figure 6, Table S4). The SEM provided evidence to support our three hypothesized mechanisms by showing that: 1) pre-fire N-fixer cover had the strongest effect on resistance, and the effect was negative (− 0.46), 2) greater pre-fire shrub canopy cover decreased resistance both directly (effect size − 0.26) and indirectly by creating larger bare-soil patches (effect size 0.43), and 3) greater pre-fire perennial grass cover increased resistance (effect size 0.32), while cover of the perennial crested wheatgrass had no direct effect on resistance after conditioning on the overall perennial grass effect (Figure 6, Table S4). Perennial grass cover and crested wheatgrass cover had independent direct effects on leaf N (0.26, − 0.38, respectively), which mediated their effects on resistance (Figure 6). However, indirect effects of perennial grasses on resistance via their effect on leaf N were minor (0.013 and -0.019 for perennial bunchgrasses and crested wheatgrass, respectively) because of the small effect of leaf N on resistance.

Direct effects of pre-fire N-fixer, shrub, and perennial bunchgrass cover on resistance (-0.46, − 0.26, 0.32, respectively) were stronger than direct effects of post-fire soil N, interspace area, and bunchgrass leaf N (0.030, − 0.04, 0.050, respectively). Thus, indirect effect sizes (calculated by multiplying the coefficients along a given path)

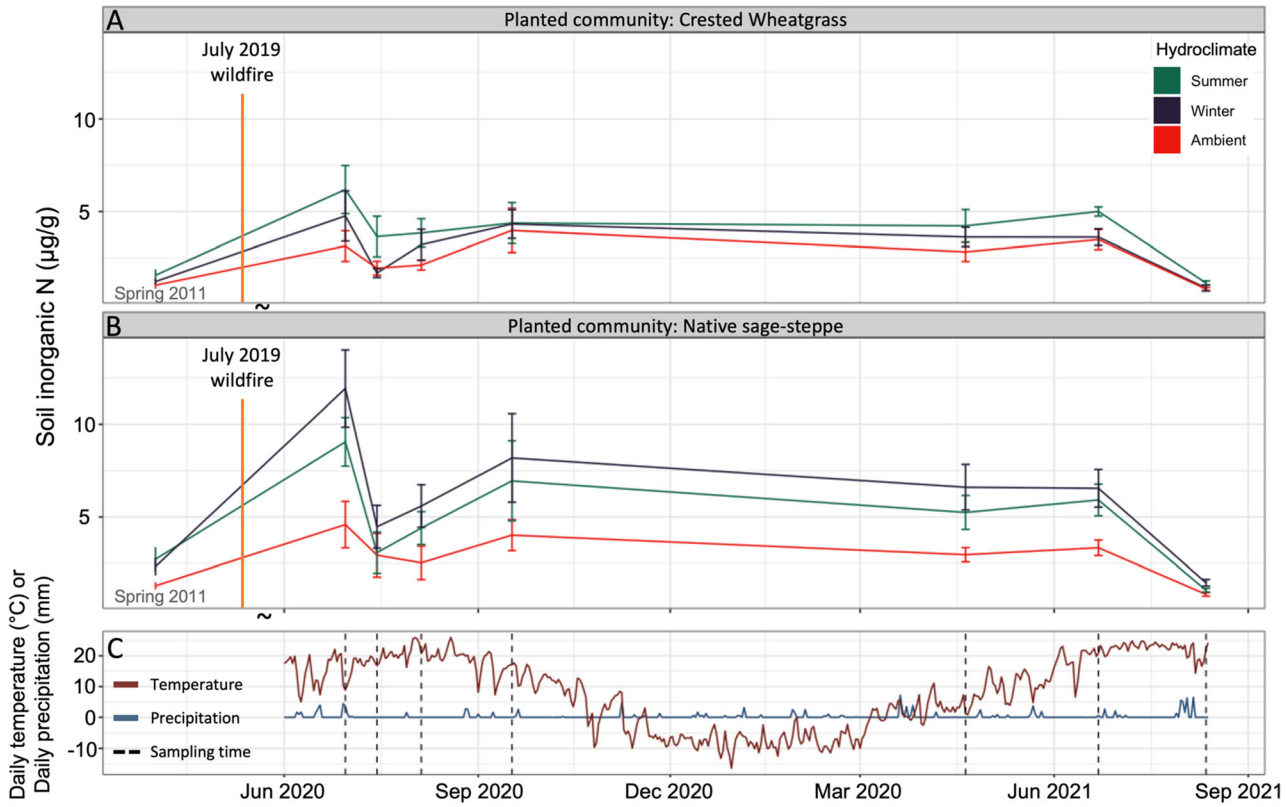


Figure 4. Temporal trends of total soil inorganic nitrogen for crested wheatgrass (A) and native sage-steppe planted communities (B) and prism-derived daily temperature (red) and precipitation (blue) values (C). Hydroclimate treatments are represented by colored lines (within A, B) where summer, winter, and ambient hydroclimates are green, purple, and red, respectively. The time series starts with the most recent measurement prior to the 2019 wildfire (Spring 2011) and includes 7 post-fire measurements of soil inorganic N from this most recent phase of the experiment. Error bars and points are the mean ± SE of $n = 9$ plots. Note that the x-axis values are not proportional to time until the beginning of the post-fire experiment in June 2020.

were small compared to the direct effects of the pre-fire plant community on post-fire resistance. When tested as fixed effects, the planted vegetation experimental treatment was not statistically significant in the SEM, and thus is not visually represented, but was included in the model as a random effect (Table S4).

Relationship Between Resistance and Soil Resources

The snapshot measurements of soil water content did not vary among the experimental treatments (Tables 1, S1), thus, soil water was excluded from further analysis. Soil N was greater the first spring (June 2020) after the fire than at any other time and correlated directly to the pre-fire shrub and N-fixer composition at that time point (Figure 5, Table 1, S1, S3). Soil N during the first spring after the fire also correlated strongly and inversely to post-fire resistance to invasion for three years post-fire (that is, the duration of this study; Figure 7A, Table S5). Pre-fire N-fixer and shrub canopy cover were inversely associated with resistance, and perennial bunchgrass cover was directly correlated to resistance each year of the study (Figure 7 B, C, D). Generalized linear mixed effects models revealed that the effect of soil N on resistance was mostly explained by variation in pre-fire shrub, N-fixer, and perennial bunchgrass cover (Figure 7A vs Figure 7E, Table S5). Soil N had a direct effect on resistance that, while not significant, trended from negative to positive over the first three years after the fire (Figure 7E). The effect of pre-fire N-fixer and shrub cover on resistance remained significant and relatively consistent in effect size between years of the study after controlling for the experimental treatment effects, soil N content, and perennial grass cover (Figure 7 F, G). Soil N and perennial grass effects on resistance were significant in models that did not include N-fixer-, or N-

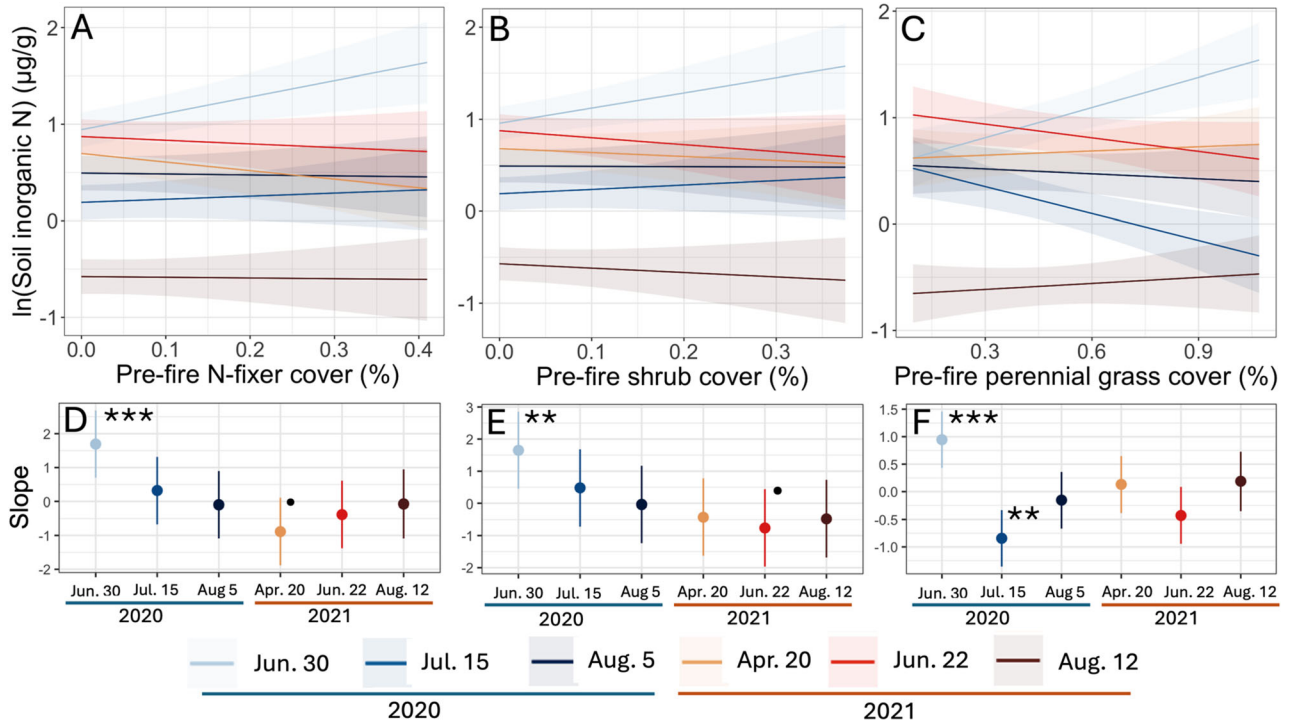


Figure 5. Predicted conditional responses and corresponding slopes for the relationship between soil inorganic N and Pre-fire N-fixer cover (A, D), Pre-fire perennial grass cover (B, E), and Pre-fire shrub cover (C, E). Each line (A, B, C) or point (D, E, F) corresponds to a specific date shown at the top in colors with a cool, blue colors for 2020 dates and warm, red colors for 2021. Shaded ribbons around each line of predicted values (A, B, C) or error bars (D, E, F) represent 95% confidence intervals. Asterisks in D, E, F represent slope values that are significantly different from zero (***$p < 0.001$, **$P < 0.01$, * < 0.05, $P < 0.10$).

fixer- and shrub cover (Table S4, right-hand 2 columns) indicating covariance.

Discussion

Overview

Our experimental study design enabled us to test for the effects of long-term hydroclimate and pre-fire plant community type and composition on post-fire resistance to invasion by exotic annuals in droughted, regionally representative (that is, summer- vs winter-wet) perennial bunchgrass- and shrub-dominated communities of the sagebrush steppe (Figure 1). The greater resistance of ambient (arid climate) compared to winter- or summer-wet plots (Figure 2) was surprising because established theory and land management guidelines would suggest that wetter sagebrush steppe communities should have greater resistance to invasion (Chambers and others 2007, 2014, 2019, 2023, Figure 1D). The reversal of expected patterns of resistance likely related to the effects of fire combined with the 3-year drought imposed on summer- and winter-wet plots, prior to and following the fire. The inverted resistance occurred despite similar, or greater, pre-fire perennial grass cover and post-fire perennial grass recovery and lesser amount of post-fire bare soil, and thus perceived greater community resistance to invasion in summer- and winter-wet compared to ambient plots (Figure S1, Chambers and others 2007, 2014).

To explain our observation of the unexpected hydroclimate-resistance relationship, we investigated how soil resource availability varied within and between the experimental irrigation and vegetation planting treatments and how any differences therein related to the pre-fire plant community composition and post-disturbance resistance to invasion. The rationale for our approach stems from the 'soil resource hypothesis' which states that when soil resource supply exceeds demand, that the probability of change in the plant community increases—that is, invasion is more likely (Davis and others 2000; Funk and Vitousek 2007). Because invasion after the fire occurred predominantly in interspace microsites (Figure 3), we focused our analysis on how soil resources in interspaces related to pre-fire plant

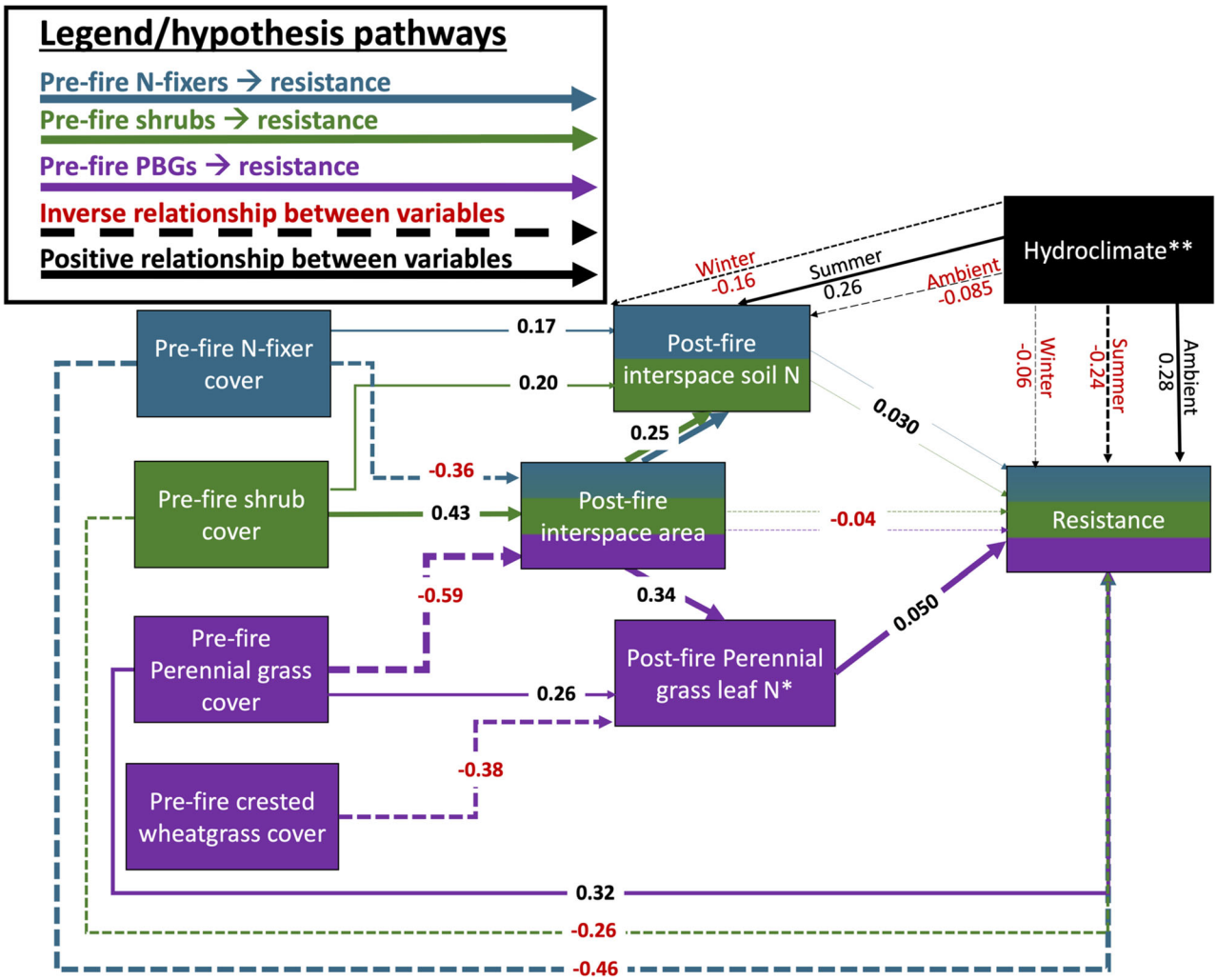


Figure 6. Structural equation model assessing the effects of pre-fire plant community composition on resistance as mediated by soil and leaf traits. Dashed arrows with red text or solid arrows with black text/numbers refer to negative or positive effects, respectively. Colored paths correspond to parts of the model that address each hypothesis that was posed in the introduction of this manuscript, as shown in the color-coded key in the upper left. Standardized correlation coefficients are shown for each relationship with negative correlations in red accompanied by dashed arrows. The entire model can be found in Table S3 and indirect effects may be calculated by multiplying the coefficients along any path because the values were standardized to a mean of zero and a standard deviation of one.

community conditions in search of a mechanism that could explain the unexpected patterns of post-fire resistance to invasion.

Our data revealed a strong effect of a post-fire soil N pulse on resistance to EAs that lasted for at least three years (Figure 7A, Table S5). EAs in the sagebrush steppe have been shown to rapidly entrain soil N (Vasquez and others 2008; Witwicki and others 2013; Slate and others 2022), and our data suggest that when pre-fire shrub- and N-fixer cover is high, that soils will have elevated N and larger, un-occupied interspaces that can facilitate a rapid response of EAs, corresponding to the magnitude of N pulse (Figures 5, 6, 7). This observation is supported by related research in the sagebrush steppe which reported greater invasion and fewer perennial grass roots in larger bare-soil interspaces (Reisner and others 2013; Germino and others 2019). Our results also align with recent research showing that drought, as occurred in our less-resistant-previously irrigated plots, supports plant-soil feedbacks that reinforce invasion by maintaining elevated soil N (Strain and others 2025). Overall, our results showed that native or resident plant communities that entrain soil resource pulses should be more resistant to invasion after fire, and that pre-fire shrub- and N-fixer cover increased the magnitude of the pulse (Figure 7), while perennial

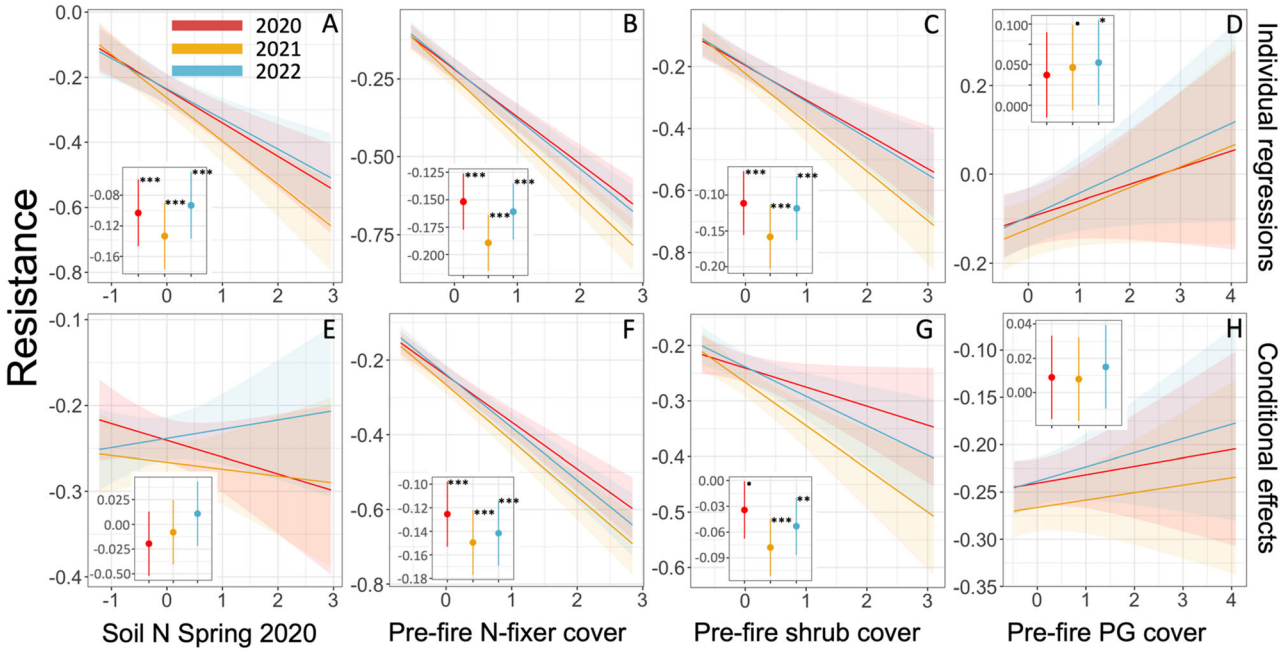


Figure 7. Linear regressions of resistance to EA invaders as a function of soil N during the spring after the wildfire (A), pre-fire N-fixers (B) and pre-fire shrubs (C), and pre-fire perennial grass cover for each year of the experiment. The relationship between each variable and resistance for 2020, 2021, and 2022 is represented by red, yellow, and blue lines, respectively, with shaded ribbons for each line that represent 95% confidence intervals. Conditional effects for all combinations of each variable and year (E, F, G, H) were derived from a generalized linear mixed effects model that included all variables (soil N, pre-fire N-fixer cover, pre-fire shrub cover and pre-fire perennial bunchgrass cover) each interacting with year and with random slopes for the experimental treatments and plot ID (raw model results found in Table S5). Paired plots are embedded within each pane that indicate the slope of each line within each pane. Asterisks in inset plots represent slope values that are significantly different from zero (***$p < 0.001$, **$P < 0.01$, * < 0.05, $P < 0.10$).

grass cover attenuated it as predicted by previous studies (Chambers and others 2007; Blank and Morgan 2012b).

Our experimental results also highlight the sensitivity of soil and plant processes to weather (Figure 4). A significant drop in soil N occurred from July–August 2021 associated with a precipitation event just prior to soil sampling. This weather event likely stimulated germination and green up of the vegetation, leading to N uptake and the observed soil N-reductions. In contrast, in September 2020, an end-of-season soil N increase occurred after a series of smaller rain events that likely only wetted the soil only enough to stimulate microbial N-mineralization but not plant uptake. Thus, historical climate regime, planted community, and weather all combined to generate unique plant-soil interactions that may facilitate or resist invasion.

Although we observed EA invasion, EA cover was not near or above threshold cover levels (that is, ~ 20%) that are nominally considered by the vegetation managers to be indicative of degraded habitat quality and risks toward plant community conversion to EA dominance (Germino and others 2022a, 2022b; Smith and others 2025). EA cover on our plots was similar to cover in the surrounding region (Bagchi and others 2017), and density of invasive plants (plants/m2) was comparable to levels observed in unburned areas between 1950 and 1995 in the surrounding region (Anderson and Inouye 2001). Relatively low EA cover and density indicate that, on average, the large 2019 Sheep fire did not stimulate an invasion event similar to the severe post-fire invasions observed over many millions of acres of warmer soil climate regimes in the sagebrush steppe (D'Antonio and Vitousek 1992; Doherty and others 2022). Nonetheless, patterns of post-fire EA establishment varied among the pre-fire hydroclimatic regimes and depended on the planted community, resulting in 'hotspots' of initial invasion that could be harbingers of more widespread invasion (Germino and others 2022a, 2022b).

We propose three candidate mechanisms for reduced resistance in plots that developed under wetter pre-fire soil moisture regimes: 1) Irrigated

plots had greater pre-fire foliar cover of N-fixing native perennial forbs, which may have created hotspots of soil fertility had reduced resistance to EA invasion after fire (as in Maron and Conners, 1996); 2) plots with wetter pre-fire hydroclimates also had greater pre-fire sagebrush cover, larger sagebrush individuals (Reinhardt and others 2019) and were under drought (that is, had 50% reduction of water inputs for three years prior to and following the fire due to the irrigation shut-off), which likely led to greater fuel connectivity, drier vegetation, and greater burn severity, and thus larger interspaces that were resource rich and prone to invasion after the fire (Germino and others 2019; Mahood and others 2022); and/or 3) Ambient (never irrigated) plots that were historically more arid, but were not subject to drought prior to and following the fire had fewer shrubs (Figure S1) and thus the perennial grass communities in those plots were less water stressed, less affected by fire (as expected, Boyd and others 2015), and thus were able to attenuate the post-fire soil N pulse to levels that increased resistance to EA invasion. We discuss each of these mechanisms in the sections that follow.

Pre-Fire Presence of N-Fixers Facilitated Post-Fire EA Invasion by Enriching Plant Available Soil N

Our data provide evidence for a causal link between the greater capacity of winter- and summer-wet climates to support a more robust N-fixer community compared to our ambient plots (50% drier, 'aridic' hydroclimate), leading to a greater post-fire soil N pulse and EA invasion (Figures 4, 6, 7, S1, Table S4). N-fixers increase soil N by as much as 2.4 g N/m^2/year in sagebrush steppe ecosystems (Goergen and others 2009), equaling annual additions of 6% of the total soil N in our plots (based on a total N assessment, Huber 2017), but concentrated in microsites associated with the N-fixers (Maron and Connors 1996). Our results show that pre-fire N-fixer cover directly corresponded to the magnitude of N pulse observed (Figure 5), suggesting that while N-fixers do support productivity of these low-fertility ecosystems, that they can also negatively affect resistance to invasion (Figures 6, 7B, 7F, Table S5). Thus, pre-fire N-fixer cover may be a useful predictor of plant community resistance to EA invasion, although that effect should depend on shrub cover and the recovery of perennial grasses (Figures 6, 7A, Table S5). Previous studies offer support for this mechanism where, for example, hotspots of N created by previous occupation of N-fixers were readily invaded by exotic weeds in coastal California and Hawaii, USA (Maron and Connors 1996; Carino and Daehler 2002).

The one other study of post-fire impacts of N-fixers on plant community recovery after fire in the Great Basin occurred in an area with patchy EAs and found that pre-fire *Lupinus* N-fixers facilitated post-fire native perennial grasses and forbs by enriching interspace microsites with soil N after fire (Goergen and Chambers 2009, 2012). We observed a consistent and strong effect of greater pre-fire N-fixer cover, which was to decrease resistance to invasion for three years post-fire (Figure 7F). Soil N in our experiment had a variable effect on resistance where greater soil N facilitated invasion (decreased resistance) in the first year but increased resistance to invasion in the third year after fire (Figure 7E). This could relate to multi-year timescales required for robust perennial grass recovery which led to a variable perennial grass-soil N relationship over time (Figure S1, 5F), whether N-fixers enable EA invasion or enhance the growth of native perennials appears to be context and time dependent. More generally, N-fixers are known to alter primary succession in other low-fertility ecosystems via facilitating establishment of other perennials, such as following retreat of glaciers in Alaska, USA (Fastie 1995) or volcanic eruptions in Washington, USA (Morris and Wood 1989).

Greater Pre-Fire Shrub Canopy Cover was Associated with Increased Post-Fire Soil N Availability and Reduced Resistance to EA Invasion

A mechanistic explanation for why plots that had greater pre-fire shrub cover were also most vulnerable to invasion was revealed by our SEM (Figure 6). Specifically, plots that had greater pre-fire shrub cover had larger interspaces after the fire which facilitated invasion (that is, resistance was lower, Figure 6). Greater shrub cover and larger interspaces led to greater soil N content, which we expected would decrease resistance, but the SEM showed a very weak and positive soil N-resistance relationship. Our mixed effects models revealed that the effect of soil N on resistance depended on the time of measurement, thus the generalized soil N—resistance effects were not mechanistically insightful. The theorized negative effects of soil N on resistance were obscured in the SEM due to its covariance with shrub and N-fixer cover and interspace size, and further, may have been offset by the robust recovery of perennial grass commu-

nities that could benefit from greater soil N, increasing resistance (Figures 5, 6, 7, S1, Table S5). Models that explicitly focused on the June 30th, 2020 soil N pulse revealed that the magnitude of the pulse corresponded to pre-fire shrub and N-fixer cover, and further showed that greater shrub cover negatively affected resistance because of its positive effect on post-fire soil N (Figure 7, Table S5).

It is well established that rapid rates of nutrient cycling under desert shrub canopies generate islands of soil fertility with greater nutrient and water content than the adjacent bare-soil interspaces, and that these islands can persist for years after shrub removal (Bechtold and Inouye 2007). While these 'fertile islands' may be the best locations for shrub re-establishment (Arkle and others 2022), they also are vulnerable to EA invasions, as revealed by a soil-transplant experiment (Hoover and Germino 2012), and in this study under field conditions (Figure 3). When sagebrush-dominated communities burn, their post-fire resistance is related to perennial grass recovery (Chambers and others 2007, 2014). However, if shrubs are large or dense enough, increased heating from their combustion in wildfire increases burn intensity under shrub canopies, leading to greater mortality of bunchgrasses under or near them, an effect that is exacerbated under drought conditions (Boyd and others 2015a; Hulet and others 2015). This leads to burned shrub microsites with increased resource supply and decreased uptake, due to few or no resprouting perennials, which creates an opportunity for increased germination and post-fire invasion, that is, confirming the soil resource hypothesis (Davis and others 2000).

We propose that the larger pre-fire shrub volumes in our summer- and winter-wet plots (and especially in the winter-wet native shrub–steppe plots, Figure S1, Germino and Reinhart, 2014) combined with three years of imposed drought (that is, irrigation cessation) likely led to higher intensity burning, which, in turn, increased mortality of the perennial grass understory, leading to large, nutrient rich, and poorly resistant burned shrub microsites where EAs could establish. Importantly, we found greater establishment of EAs in plant communities that would be considered highly resistant to invasion due to their greater productivity and diverse communities that arose from their development in a wetter climate, but that were under drought stress before and after the fire (Figures 2, 3, S1). Thus, we found that three years of drought can reduce the post-fire resistance to invasion of an ecosystem that is generally considered to have a low likelihood of invasion.

Perennial Grasses Provided Resistance to Invasion by Outcompeting Exotic Annuals for Soil N

Observational and experimental glasshouse studies have shown that perennial grasses in semiarid landscapes are key to resisting EA invasions because they recover quickly after wildfire and can outcompete germinating EAs for nutrients, moisture, and light (Bookman and Mack 1983; Humphrey and Schupp 2004; Chambers and others 2007; Vasquez and others 2008). Our experimental results provide concise evidence for the capacity of perennial grasses to entrain soil N by showing that, while pre-fire perennial grass cover was positively associated with a soil N pulse, there was a switch to a negative perennial grass-soil N association within just 2 weeks (Figure 5 C, F). The directional shift of this effect coincided with a significant and rapid reduction in soil N content (Figure 4) which suggests that that pre-fire perennial grass cover may be predictive of a plant community's capacity to rapidly entrain pulses of soil resources that can otherwise facilitate EA invasion (Figure 7). Thus, any management that significantly diminishes perennial grass abundance or vigor and favors shrub abundance (for example, overgrazing, Cooper 1953; Laycock 1967) would likely increase the magnitude of a post-fire soil N pulse, reducing post-fire resistance to invasion in these ecosystems. Importantly, our results do not suggest that shrubs are incompatible with post-fire resistance to invasion, but, for example, in the case of a near closed-canopy shrubland, greater fire severity that affects bunchgrass mortality (for example, Boyd and others 2015c) could harm resistance to invasion even in areas considered to have high resistance to invasion. More research is needed to understand how shrub and perennial grass density interact with climate, drought and fire to affect post-fire resistance.

Larger bare-soil interspaces had greater soil N content and plots with greater pre-fire perennial grass cover had smaller interspaces (Figure 6), which is consistent with the expectation that smaller interspace sizes enhance post-fire perennial grass recovery, uptake of soil N, and resistance to EA establishment (Figures 4, 6, 7). The link between perennial grasses and interspace size is supported by past research in post-fire sagebrush steppe landscapes which showed that lateral roots of bunchgrasses were scarcer in larger basal gaps,

while EAs were more abundant (Germino and others 2019). Interspace size may be an easily observed expression of the balance of soil resource supply and uptake in these semiarid ecosystems, especially after a disturbance, which is consistent with the 'soil resource hypothesis' (Davis and others 2000). More research is needed to assess whether thresholds in interspace size may exist that could be used improve predictions of resistance to invasion after fire and provide targets for bare-soil interspace size and cover for managers.

Conclusions

Diverse and productive plant communities provide vital ecosystem services to drylands such as wildlife habitat, carbon storage and cultural value. However, dominance of native species that lack adaptation to frequent disturbance and leave fertile hotspots after disturbance is problematic when and where exotic invaders complicate native plant recovery. Notably, both altered disturbance regimes and exotic species are increasing simultaneously across many drylands and other ecosystem types, globally. In our experiment which assessed combined drought and fire responses of two common sagebrush steppe plant community types in three regionally representative hydroclimates, greater pre-fire cover of foundational shrubs or N-fixers decreased post-fire resistance to invasion and thereby detracted from resistance to invasion after a compound disturbance of drought and fire. Sagebrush steppe communities that can recover and control soil resources in the first growing season after a fire are less vulnerable to invasion that could eventually be compounded by annual grass fire feedbacks that culminate in conversion of perennial ecosystems into annual grasslands.

Importantly, the historically wetter and more diverse communities that were anticipated to be most resistant to invasion in our experiment were less resistant than ambient, non-droughted plots. Our results showed that this reversal of expected patterns of resistance could be attributed to the greater density of N-fixing forbs and fire intolerant shrubs that led to larger bare-soil interspaces and a greater post-fire pulse of soil N. The resistance-reversal also related to the compound disturbance of drought coinciding with fire, which likely increased mortality of perennial grasses under shrub canopies that otherwise could have conveyed resistance to invasion after the fire. The disturbance-recovery (that is, resistance and resilience) patterns of these ecosystems could only be understood by considering the interactions between historical climate, contemporary weather, and plant community composition and could not be predicted from generalized characteristics such as whether the plant community developed in a wetter climate.

ACKNOWLEDGEMENTS

The authors thank Sophie Steppe, Austin Davis, and Logan Brauer for help with field sampling, Ashley Leavell, Jayna Thompson, Olivia Tabor, Cora Pirie, Amy Woody, Sophie Steppe, and Molly Long for assistance with sample preparation and analysis in the lab. We thank Amy Forman for logistical support and access to the INL. Keith Reinhardt and many other field technicians helped maintain the irrigations, and Maria Pacioretty assisted in pre-fire data collection. We also thank Monica Turner (EIC) and David Perry (SME) at Ecosystems and the anonymous reviewers, who gave many rounds of thoughtful feedback. Funding was provided to all authors by the US National Science Foundation (NSF DEB #2037660, 2019). Pre-fire research was funded by the US Climate Science Center (2012) and US National Science Foundation awards to MJG (2005-2011). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

FUNDING

Division of Environmental Biology, NSF DEB #2037660

DATA AVAILABILITY

Data is available via the Oregon State University ScholarsArchive at https://ir.library.oregonstate.edu/concern/datasets/000007993 or https://doi.org/10.7267/000007993.

Declarations

Conflict of Interest The authors declare no conflict of interest.

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REFERENCES

Anderson J, Forman A. 2003. Evapotranspiration caps for the idaho national engineering and environmental laboratory: A summary of research and recommendations. https://inl.gov/content/uploads/2023/08/PCBESummaryweb.pdf. Last accessed 13/05/2024

Anderson JE, Inouye RS. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol Monogr 71:531–556.

Applestein C, Caughlin TT, Germino MJ. 2021. Weather affects post-fire recovery of sagebrush-steppe communities and model transferability among sites. Ecosphere 12:e03446.

Arel-Bundock V, Greifer N, Heiss A. 2024. How to interpret statistical models using **marginaleffects** for *R* and *Python*. J Stat Softw 111. https://www.jstatsoft.org/v111/i09/. Last accessed 18/04/2025

Arkle RS, Pilliod DS, Germino MJ, Jeffries MI, Welty JL. 2022. Reestablishing a foundational species: Limitations on post-wildfire sagebrush seedling establishment. Ecosphere 13:e4195.

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235.

Bagchi S, Singh NJ, Briske DD, Bestelmeyer BT, McClaran MP, Murthy K. 2017. Quantifying long-term plant community dynamics with movement models: implications for ecological resilience. Ecol Appl 27:1514–1528.

Bechtold HA, Inouye RS. 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. J Arid Environ 71:122–132.

Blank RR, Morgan T. 2012a. Mineral nitrogen in a crested wheatgrass stand: implications for suppression of cheatgrass. Rangel Ecol Manag 65(1):101–104.

Blank RR, Morgan T. 2012b. Suppression of *Bromus tectorum* L. by Established Perennial Grasses: Potential Mechanisms—Part One. Appl Environ Soil Sci 2012:1–9.

Bookman PA, Mack RN. 1983. Competition between Bromus tectorum L. and Poa pratensis L.: the role of light. Oecologia 57:406–411.

Boyd CS, Davies KW, Hulet A. 2015a. Predicting fire-based perennial bunchgrass mortality in big sagebrush plant communities. Int J Wildland Fire 24:527.

Bradley BA. 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Glob Change Biol 15:196–208.

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu M-N. 2018. Cheatgrass (Bromus tectorum) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biol Invasions 20:1493–1506.

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTOMASO JM, Hobbs RJ, Pellant M, Pyke D. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677.

Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M, Bolker B M. 2017. glmmTMB Balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378.

Campos X, Germino M, De Graaff M-A. 2017. Enhanced precipitation promotes decomposition and soil C stabilization in semiarid ecosystems, but seasonal timing of wetting matters. Plant Soil.

Carino DA, Daehler CC. 2002. Can inconspicuous legumes facilitate alien grass invasions? Partridge peas and fountain grass in Hawai'i. Ecography 25:33–41.

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A. 2007. What makes great basin sagebrush ecosystems invasible BY *bromus tectorum*? Ecol Monogr 77:117–145.

Chambers JC, Bradley BA, Brown CS, D'Antonio C, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA. 2014. Resilience to stress and disturbance, and resistance to Bromus tectorum L. Invasion in Cold Desert Shrublands of Western North America. Ecosystems 17:360–375.

Chambers JC, Brooks ML, Germino MJ, Maestas JD, Board DI, Jones MO, Allred BW. 2019. Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. Front Ecol Evol 7:185.

Chambers JC, Brown JL, Bradford JB, Doherty KE, Crist MR, Schlaepfer DR, Urza AK, Short KC. 2023. Combining resilience and resistance with threat-based approaches for prioritizing management actions in sagebrush ecosystems. Conserv Sci Pract 5:e13021.

Cook JG, Irwin LL. 1992. Climate-vegetation Relationships between the Great Plains and Great Basin. Am Midl Nat 127:316.

Cooper HW. 1953. Amounts of big sagebrush in plant communities near tensleep, wyoming, as affected by grazing treatment. Ecology 34:186–189.

Cui M, Caldwell MM. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. Plant Soil 191:291–299.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87.

Daramola MT, Xu M. 2022. Recent changes in global dryland temperature and precipitation. Int J Climatol 42:1267–1282.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534.

DeRose RJ, Long JN. 2014. Resistance and resilience: A conceptual framework for silviculture. For Sci 60:1205–1212.

Doane TA, Horwáth WR. 2003. Spectrophotometric determination of nitrate with a single reagent. Anal Lett 36:2713–2722.

Doherty K, Theobald DM, Bradford JB, Wiechman LA, Bedrosian G, Boyd CS, Cahill M, Coates PS, Creutzberg MK, Crist MR, Finn SP, Kumar AV, Littlefield CE, Maestas JD, Prentice KL, Prochazka BG, Remington TE, Sparklin WD, Tull JC, Wurtzebach Z, Zeller KA. 2022. A sagebrush conservation

design to proactively restore america's sagebrush biome. U.S. Geological Survey

Fastie CL. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at glacier bay, alaska. Ecology 76:1899–1916.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annu Rev Ecol Evol Syst 35:557–581.

Funk JL, Vitousek PM. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081.

Germino MJ, Reinhardt K. 2014. Desert shrub responses to experimental modification of precipitation seasonality and soil depth: relationship to the two-layer hypothesis and ecohydrological niche. Jones R, editor. J Ecol 102:989–997.

Germino MJ, Barnard DM, Davidson BE, Arkle RS, Pilliod DS, Fisk MR, Applestein C. 2018. Thresholds and hotspots for shrub restoration following a heterogeneous megafire. Landsc Ecol 33:1177–1194.

Germino MJ, Fisk MR, Applestein C. 2019. Bunchgrass root abundances and their relationship to resistance and resilience of burned shrub-steppe landscape. Rangel Ecol Manag 72:783–790.

Germino MJ, Kluender CR, Anthony CR. 2022a. Plant community trajectories following livestock exclusion for conservation vary and hinge on initial invasion and soil-biocrust conditions in shrub steppe. Conserv Sci Pract 4:e12838.

Germino MJ, Torma P, Fisk MR, Applestein CV. 2022b. Monitoring for adaptive management of burned sagebrush-steppe rangelands: addressing variability and uncertainty on the 2015 Soda Megafire. Rangelands 44:99–110.

Germino MJ, Belnap J, Stark JM, Allen EB, Rau BM. 2016. Ecosystem impacts of exotic annual invaders in the genus bromus. In: Germino mj, chambers jc, brown cs, editors. exotic brome-grasses in arid and semiarid ecosystems of the western us. springer series on environmental management. Cham: Springer International Publishing. pp 61–95. http://link.springer.com/https://doi.org/10.1007/978-3-319-24930-8_3. Last accessed 20/10/2023

Goergen EM, Chambers JC. 2009. Influence of a native legume on soil N and plant response following prescribed fire in sagebrush steppe. Int J Wildland Fire 18:665.

Goergen E, Chambers JC. 2012. Facilitation and interference of seedling establishment by a native legume before and after wildfire. Oecologia 168:199–211.

Goergen E, Chambers JC, Blank R. 2009. Effects of water and nitrogen availability on nitrogen contribution by the legume, Lupinus argenteus Pursh. Appl Soil Ecol 42:200–208.

Goodrich S, McArthur ED, Winward A. 1999. Sagebrush ecotones and average annual precipitation. In: USDA Forest Service Proceedings RMRS-P-11. pp 88–94.

Hartig F. 2016. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hatchett BJ, Boyle DP, Garner CB, Kaplan ML, Putnam AE, Bassett SD. 2016. Magnitude and frequency of wet years under a megadrought climate in the western Great Basin, USA. Quat Sci Rev 152:197–202.

Holling CS. 1973. Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23.

Hoover AN, Germino MJ. 2012. A common-garden study of resource-island effects on a native and an exotic, annual grass after fire. Rangel Ecol Manag 65:160–170.

Huber DP, Lohse KA, Commendador A, Joy S, Aho K, Finney B, Germino MJ. 2019. Vegetation and precipitation shifts interact to alter organic and inorganic carbon storage in cold desert soils. Ecosphere 10:e02655.

Huber DP. 2017. Precipitation timing and control volumes regulate carbon and nutrient cycling in cold desert soils.

Hulet A, Boyd CS, Davies KW, Svejcar TJ. 2015. Prefire (Preemptive) Management to Decrease Fire-Induced Bunchgrass Mortality and Reduce Reliance on Postfire Seeding. Rangel Ecol Manag 68:437–444.

Humphrey LD, Schupp EW. 2004. Competition as a barrier to establishment of a native perennial grass (Elymus elymoides) in alien annual grass (Bromus tectorum) communities. J Arid Environ 58:405–422.

Jiao W, Wang L, Smith WK, Chang Q, Wang H, D'Odorico P. 2021. Observed increasing water constraint on vegetation growth over the last three decades. Nat Commun 12:3777.

Kainrath NB, Dijkstra P, Gehring CA, Updike C, Grady KC. 2022. Water as the key to sagebrush restoration success in cheatgrass-invaded ecosystems. Restor Ecol 30:e13473.

Kay Strain M, Leger EA, Blaszczak JR, Hoyos HA, Arizmendi K, Hanan EJ. 2025. Root Exudation by an Annual Grass Modifies Soil Biogeochemical Cycling: A Mechanism for Invasion. Ecosystems 28:60.

Larson CD, Lehnhoff EA, Rew LJ. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. Oecologia 185:763–774.

Laycock WA. 1967. How Heavy Grazing and Protection Affect Sagebrush-Grass Ranges. J Range Manag 20:206.

Mahood AL, Jones RO, Board DI, Balch JK, Chambers JC. 2022. Interannual climate variability mediates changes in carbon and nitrogen pools caused by annual grass invasion in a semiarid shrubland. Glob Change Biol 28:267–284.

Maron JL, Connors PG. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia 105:302–312.

Maxwell TM, Germino MJ. 2022. The effects of cheatgrass invasion on US Great Basin carbon storage depend on interactions between plant community composition, precipitation seasonality, and soil climate regime. J Appl Ecol 59:2863–2873.

Maxwell TM, Quicke HE, Price SJ, Germino MJ. 2024. Annual grass invasions and wildfire deplete ecosystem carbon storage by >50% to resistant base levels. Commun Earth Environ 5:669.

McAbee K, Reinhardt K, Germino MJ, Bosworth A. 2017. Response of aboveground carbon balance to long-term, experimental enhancements in precipitation seasonality is contingent on plant community type in cold-desert rangelands. Oecologia 183:861–874.

Millar CI, Charlet DA, Delany DL, King JC, Westfall RD. 2019. Shifts of demography and growth in limber pine forests of the Great Basin, USA, across 4000 yr of climate variability. Quat Res 91:691–704.

Morris WF, Wood DM. 1989. The Role of Lupine in Succession on Mount St. Helens: Facilitation or Inhibition? Ecology 70:697–703.

Nagy RC, Fusco EJ, Balch JK, Finn JT, Mahood A, Allen JM, Bradley BA. 2021. A synthesis of the effects of cheatgrass invasion on US Great Basin carbon storage. Macinnis-Ng C, editor. J Appl Ecol 58:327–337.

O'Connor RC, Germino MJ, Barnard DM, Andrews CM, Bradford JB, Pilliod DS, Arkle RS, Shriver RK. 2020. Small-scale water deficits after wildfires create long-lasting ecological impacts. Environ Res Lett 15:044001.

Parks SA, Holsinger LM, Miller C, Nelson CR. 2015. Wildland fire as a self-regulating mechanism: the role of previous burns and weather in limiting fire progression. Ecol Appl 25:1478–1492.

Prevéy JS, Germino MJ, Huntly NJ, Inouye RS. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. Plant Ecol 207:39–51.

Reinhardt K, McAbee K, Germino MJ. 2019. Changes in structure and physiological functioning due to experimentally enhanced precipitation seasonality in a widespread shrub species. Plant Ecol 220:199–211.

Reisner MD, Grace JB, Pyke DA, Doescher PS. 2013. Conditions favouring B *romus tectorum* dominance of endangered sagebrush steppe ecosystems. Sheppard A, editor. J Appl Ecol 50:1039–1049.

Slate ML, Matallana-Mejia N, Aromin A, Callaway RM. 2022. Nitrogen addition, but not pulse frequency, shifts competitive interactions in favor of exotic invasive plant species. Biol Invasions 24:3109–3118.

Smith JT, Allred BW, Boyd CS, Davies KW, Jones MO, Kleinhesselink AR, Maestas JD, Morford SL, Naugle DE. 2021. The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. Divers Distrib 28:83–96.

Smith KT, Mealor BA, Merkle JA. 2025. Mule Deer Response to Invasive Annual Grasses: Implications for Strategic Management in Sagebrush Priority Areas. Rangel Ecol Manag 103:128–137.

Snyder KA, Evers L, Chambers JC, Dunham J, Bradford JB, Loik ME. 2019. Effects of Changing Climate on the Hydrological Cycle in Cold Desert Ecosystems of the Great Basin and Columbia Plateau. Rangel Ecol Manag 72:1–12.

Taylor K, Brummer T, Rew LJ, Lavin M, Maxwell BD. 2014. Bromus tectorum Response to Fire Varies with Climate Conditions. Ecosystems 17:960–973.

Vasquez E, Sheley R, Svejcar T. 2008. Nitrogen Enhances the Competitive Ability of Cheatgrass (Bromus tectorum) Relative to Native Grasses. Invasive Plant Sci Manag 1:287–295.

Verdouw H, Van Echteld CJA, Dekkers EMJ. 1978. Ammonia determination based on indophenol formation with sodium salicylate. Water Res 12:399–402.

Werner CM, Stuble KL, Groves AM, Young TP. 2020. Year effects: Interannual variation as a driver of community assembly dynamics. Ecology 101:e03104.

Witwicki DL, Doescher PS, Pyke DA, DeCrappeo NM, Perakis SS. 2013. Nitrogen limitation, 15N tracer retention, and growth response in intact and Bromus tectorum-invaded Artemisia tridentata ssp. wyomingensis communities. Oecologia 171:1013–1023.