



Using Satellite Remote Sensing to Assess Shrubland Vegetation Responses to Large-Scale Juniper Removal in the Northern Great Basin ☆☆☆

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ARTICLE INFO

Article history:

Received 26 January 2024

Revised 10 May 2024

Accepted 8 August 2024

Key Words:

Bromus tectorum

Juniperus spp.

Restoration

Sagebrush

Tree removal

Woody encroachment

ABSTRACT

Woody encroachment into grasslands and shrublands disrupts ecosystem processes and reduces biodiversity. Tree removal is a widespread strategy to restore ecosystem services and biodiversity in impacted landscapes. However, tree removal can also increase the risk of invasion by exotic annual grasses. In western North America, juniper (*Juniperus spp.*) encroachment threatens the ecological integrity of intact sagebrush (*Artemisia tridentata*) shrublands. We used remote sensing to track vegetation changes following juniper removals on 288 parcels totaling 106 333 ha in southern Idaho, USA. We also analyzed vegetation changes following 64 wildfires that burned 152 611 ha of nearby rangeland during the same period. We matched areas within removals and wildfires to similar undisturbed areas, and then used causal impact analysis to estimate the effects of the disturbances. Juniper removals resulted in sustained reduction of tree cover and increased perennial forb and grass cover across nearly all sites, achieving key management goals. Based on the metrics evaluated, juniper removal was more effective than wildfire in delivering long-term restoration in this sagebrush system. However, juniper treatments also stimulated temporary undesirable increases in annual grasses and forbs, indicating the need for additional management to achieve durable conservation outcomes. Intensive mechanical methods initially reduced shrub cover in some treatments, but shrubs recovered to near pre-treatment levels within 7 years. Using a recently-developed metric of ecological integrity for sagebrush ecosystems, we show that these large, long-term projects halted or reversed degradation attributed to juniper expansion, demonstrating that restoration can improve the trajectory of ecosystems when implemented at scale.

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Introduction

The expansion of woodlands into grasslands and shrublands is a global phenomenon that alters the structure, function, and biodiversity of rangelands (Archer et al., 2017; Nackley et al., 2017; Stevens et al., 2017). Woodland expansion contributes to numerous undesired outcomes in rangelands, including the extirpation of

grassland and shrubland wildlife, reduced forage for wildlife and livestock, and in some cases, diminished water storage and delivery (Huxman et al. 2005; Archer et al. 2017). Land managers have increasingly turned to tree removal to bolster valued ecosystem services and protect rangeland-obligate flora and fauna (Archer et al. 2011; Ratajczak et al. 2012; Baruch-Murdo et al. 2013).

Across the sagebrush biome of western North America, Pinyon pines (*Pinus spp.*) and juniper (*Juniperus spp.*) are native, widespread, and rapidly expanding into historically treeless sagebrush and grassland systems (Romme et al. 2009). This expansion has been ongoing since the mid 19th century and is linked to regional climatic changes, the introduction of domestic livestock by European settlers, and the replacement of indigenous land

☆ State of the Sagebrush published in Rangeland Ecology & Management.

☆☆ This work was supported by USDA Natural Resources Conservation Service's Working Lands for Wildlife and USDA Agricultural Research Service.

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stewardship practices with a policy of aggressive fire suppression (Tausch et al., 1981; Miller et al. 1995).

The widespread expansion of pinyon-juniper (PJ) woodlands is a major threat to the sagebrush biome and the biodiversity it supports (Davies et al., 2011). Satellite remote sensing indicates tree cover in western U.S. shrubland ecosystems has increased by more than 1.8 million ha over the past 30 years and continues to accelerate (Morford et al., 2022). According to a recently-published analysis, which proposed a composite index of ecological integrity (hereafter Sagebrush Ecological Integrity or SEI) to track contemporary change in sagebrush ecosystems, expansion of PJ woodlands was responsible for 21% of contemporary (since 1990) declines in SEI across the sagebrush biome, impacts second only to the continued expansion of annual invasive grasses such as cheatgrass (*Bromus tectorum*; Doherty et al., 2022).

Tree removal projects in the sagebrush biome are commonly used to enhance herbaceous plant communities and restore shrubland habitat for wildlife such as the greater sage-grouse (*Centrocercus urophasianus*; Olsen et al., 2021b) and mule deer (*Odocoileus hemionus*; Bergman et al., 2014; Johnston and Anderson, 2023). Between 2009 and 2019, some 707 500 ha of the sagebrush biome received conifer treatments from a variety of federal to local land management agencies; however, most of these treatments were not spatially coordinated to address unified conservation priorities at landscape to biome scales (Mozelewski et al., this issue). As a result, some treatments have been placed in locations where potential conservation outcomes were limited, or in areas where treatments conflicted with other biodiversity and habitat goals, such as the preservation of intact PJ woodlands for declining pinyon jay (*Gymnorhinus cyanocephalus*) populations (Boone et al., 2021; Tack et al., 2023).

In 2010, the USDA Natural Resources Conservation Service (NRCS) Sage Grouse Initiative (SGI) began implementing a spatially-targeted conifer removal program to restore sage-grouse habitat. Sage-grouse have experienced widespread population declines over the past half century and are highly sensitive to the presence of trees. Sage-grouse avoid trees (Coates et al., 2017; Severson et al., 2017; Olsen et al., 2021a), suffer lower survival when they move through tree-encroached landscapes (Coates et al., 2017; Prochazka et al., 2017), and abandon their communal breeding grounds at even low levels of tree canopy cover (~4%; Baruch-Mordo et al., 2013). The SGI approach targeted conifer removal projects to watersheds and landscapes with large, continuous areas of intact (i.e., “core”) sage-grouse habitat where local stakeholders demonstrated willingness to implement tree removal projects at scale. This “Defend the Core” approach to conservation implementation (Maestas et al., 2022) clusters tree removal treatments within or immediately adjacent to core sage-grouse habitat, strategically targeting sagebrush rangelands in the early phases of encroachment where treatment is less expensive and more likely to yield desired outcomes (Roundy et al., 2014a). The SGI spatial targeting and clustering approach is linked to better conservation outcomes than dispersed treatments (Naugle et al. this issue), positive demographic responses for sage-grouse (Olsen et al., 2021b), and fewer potential conflicts with competing biodiversity priorities (Tack et al., 2023). However, the effectiveness of the targeted SGI approach on vegetation outcomes and the durability of conifer removal treatments in maintaining tree-free sagebrush systems remains largely untested, particularly at watershed and landscape scales.

Assessing the long-term effectiveness and identifying potential ecological risks of conifer removal treatments are essential steps in evaluating treatment success and improving program implementation to achieve durable conservation outcomes. Local and regional assessments in the sagebrush biome show that conifer removal effectively reduces tree cover for one to two decades and in-

creases cover of perennial forbs, grasses, and shrubs (Davies et al., 2019; Fick et al., 2022). However, tree removal treatments can also inadvertently increase abundance of undesirable invasive annual grasses (Redmond et al., 2014; Bates et al., 2017; Williams et al., 2017). In the context of maintaining ecological integrity of sagebrush systems, tree removal projects can curb one problem while exacerbating another, thereby falling short of fully restoring ecosystem function and protecting biodiversity.

Here, we evaluate the efficacy of large-scale conifer removal projects in southern Idaho, USA. We used remotely sensed vegetation data to track multi-year changes in rangeland vegetation cover following mechanical removal of junipers on 288 public and private rangeland parcels across >100 000 ha. We contrasted the effects of mechanical conifer removal with those of 64 nearby wildfires, which collectively burned >150 000 ha of rangeland in the region over the same period. Our objectives were to quantify post-treatment changes in vegetation, evaluate treatment effectiveness, compare vegetation outcomes of mechanical removal and wildfire disturbance, and to determine the net effect of extensive conifer removal on landscape-scale ecological integrity.

Methods

Study area and juniper removal programs

Our analysis examines juniper removal treatments to improve sage-grouse habitat across two project areas in southern Idaho, totaling approximately 106 333 ha (Fig. 1, Table 1). Implementing these projects involved collaboration among numerous stakeholders including the Bureau of Land Management (BLM), Idaho Department of Lands, Idaho Fish & Game, Idaho's Governor's Office of Species Conservation, USDA Natural Resources Conservation Service (NRCS), private landowners, and the United States Fish and Wildlife Service. Treated parcels in this analysis span private and public lands. NRCS obtained permission from landowners to include their private land parcels in this analysis, though not all landowners participated; roughly 5 700 ha of treatments on private lands were not included, comprising roughly 4% of all treated lands.

The Owyhee project area, located in Idaho's southwest corner within the Northern Basin and Range ecoregion (Fig. 1A), primarily targeted the removal of western juniper (*J. occidentalis* Hook.). This was achieved through chainsaw cutting followed by lopping and limbing (hereafter cut-and-lop) to ensure slash heights under 1.2 m (4 ft; Fig. 2A). On public lands, select areas near roads and private residences and heavier slash accumulations underwent a one-season curing process before consideration for prescribed burning. Post-treatment burning of slash was not systematically monitored on private lands and occurred with some regularity. Additionally, a smaller portion of the project area (695 hectares, <1%) received mastication treatments (grinding the tree using a motorized implement on a wheeled or tracked vehicle, Fig. 2B). No prescribed fire occurred after mastication treatments. Notably, no systemic seeding efforts of grasses or forbs occurred with juniper removal in this project area. Treatments in the Owyhee project area began in 2004, increased during 2012–2018, and accelerated again in 2019 with the publishing of the Bruneau-Owyhee Sage-grouse Habitat Project Record of Decision by the BLM (BLM, 2019). This analysis follows Owyhee juniper treatments conducted from 2004 through 2020 across 87 836 ha. Treatments continue as of 2024.

The Burley project area is situated in south-central Idaho along the Nevada and Utah borders and falls within the Northern Basin and Range and Snake River Plain ecoregions (Fig. 1B). Here, management focused primarily on the removal of Utah juniper (*J. os-*

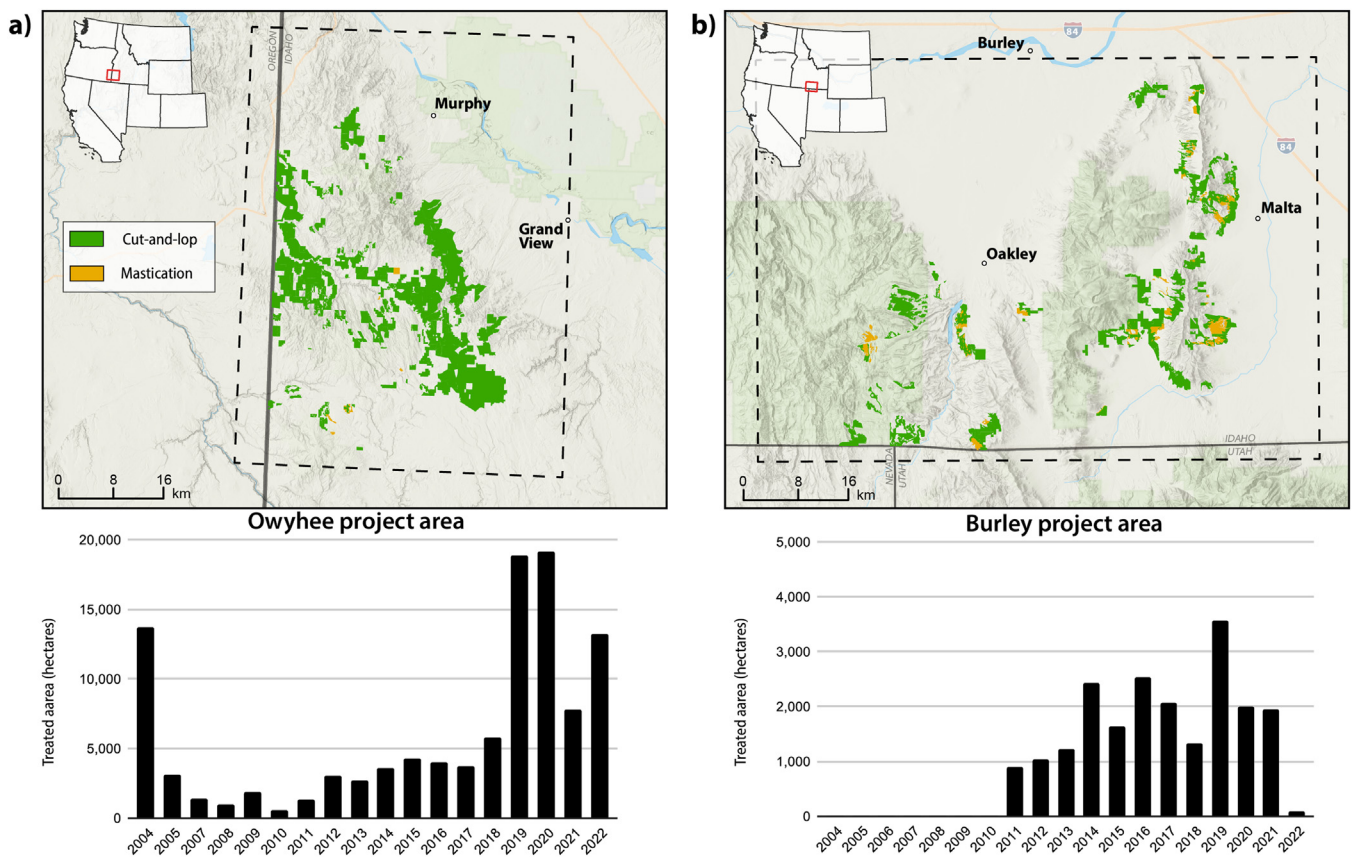


Figure 1. Project area and juniper treatment volumes by year for (A) Owyhee and (B) Burley regions. Map insets show the location of each study region within western North America using a red rectangle. Note the difference in scales between the maps. Only treatments conducted through 2020 were included in the analysis.

Table 1

Number and size of treatment and wildfire areas analyzed within the Burley and Owyhee project areas. Analyzed treatments and wildfires occurred between 2004 and 2020.

Project area	Treatment	Areas (ha)	Polygons (n)
Burley	Cut-and-lop	15 681	49
	Mastication	2 816	34
	Wildfire	48 955	27
Owyhee	Cut-and-lop	87 079	193
	Mastication	757	12
	Wildfire	103 656	37
Total		258 944	352

teosperma (Torr.) Little), with a total treated area of 18 497 ha from 2011 to 2020. Treatment methods consisted of cut-and-lop (covering 85% of area) and mastication (15% of area). Cut-and-lop involved trimming branches so that the remaining slash stood no more than 0.6 m (2 ft) above ground. Prior to mastication, grasses were seeded at a minimum application rate of 9 kg ha⁻¹. Notably, no post-treatment burning was completed in this project area. As of 2024, juniper removal treatments continue, with federal public lands projects being directed by the Burley Landscape Sage-Grouse Habitat Restoration II Environmental Assessment (BLM 2017).

Across these project areas, treatments were designed to restore and expand sage-grouse habitat, and thus were targeted in areas where junipers were in early phases of encroaching into otherwise intact sagebrush-dominated shrublands. Using the LANDFIRE Biophysical Setting spatial data (version 1.4.0; LANDFIRE, 2018), we determined that three biophysical settings made up the large majority of treated areas: Inter-Mountain Basins Montane Sagebrush Steppe (39.5%), Great Basin Xeric Mixed Sagebrush Shrubland

(33.8%), and Inter-Mountain Basins Big Sagebrush Steppe (14.8%). Rocky Mountain Montane Riparian Systems (3%), Rocky Mountain Aspen Forest and Woodland (2.7%), and Columbia Plateau Western Juniper Woodland and Savanna (2%) occurred in small, scattered patches within treatment polygons. The remaining 4.2% of the polygons was occupied by 32 other biophysical settings individually comprising <1% of the total area.

Spatial treatment and wildfire data

We digitized maps of juniper removal treatments using data from federal, state, and private land managers, employing ESRI ArcMap and ESRI ArcGIS Pro. Each treatment polygon in our spatial database identified a landowner, juniper treatment method, and treatment date. For polygons without a treatment date, we used Sentinel-2 satellite imagery to identify the year and month that juniper removal was completed. A total of 219 ha (<0.2%) of treatments were excluded due to incomplete treatment information.

We assembled a spatial database of areas burned by wildland fires using the Monitoring Trends in Burn Severity product (MTBS; Eidenshink et al., 2007). This database was then merged with the juniper treatment polygons to form a comprehensive dataset of disturbances in each project area. We included fires between 2011 and 2020 in the Burley project area, and 2004 to 2020 for the Owyhee project area. We omitted wildfires larger than 20 234 ha (50 000 ac; n=8, totaling 505 931 ha) because these fires were significantly larger (more than two orders of magnitude) than the areas treated mechanically.

After combining data on wildfire and juniper treatments, we screened both datasets to eliminate areas experiencing >1 disturbance or treatment event. Portions of treatment polygons that

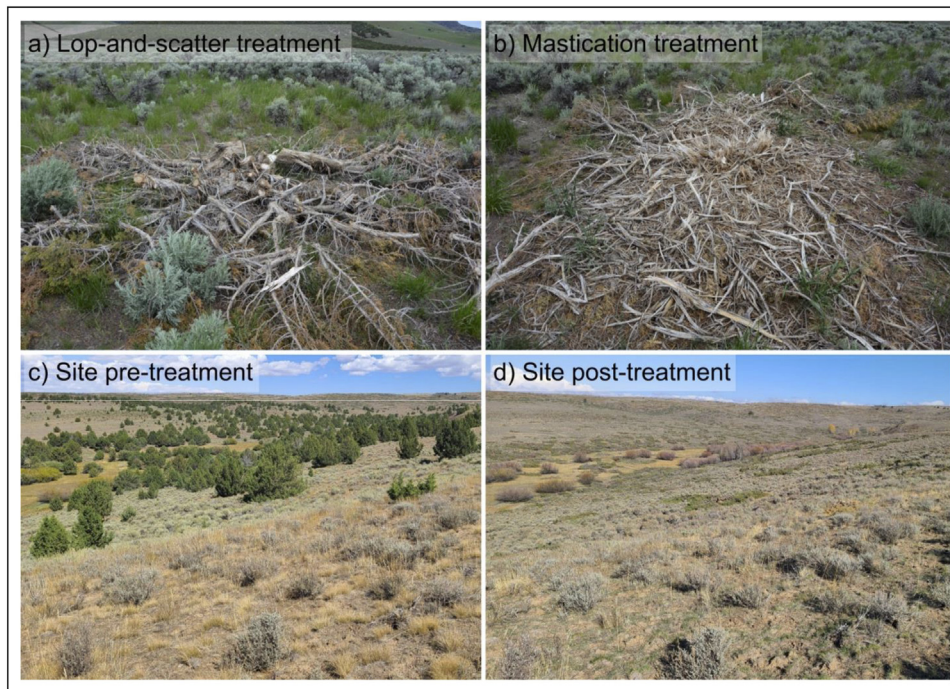


Figure 2. Juniper management from our study sides demonstrating (A) cut-and-lop and (B) mastication treatments 7 months post-treatment. Panels c and d show the Pole Creek unit in the Owyhee project area (N42.598°, W116.513°) prior to and after cut-and-lop treatments in 2023. Photo Credit: Connor D. White.

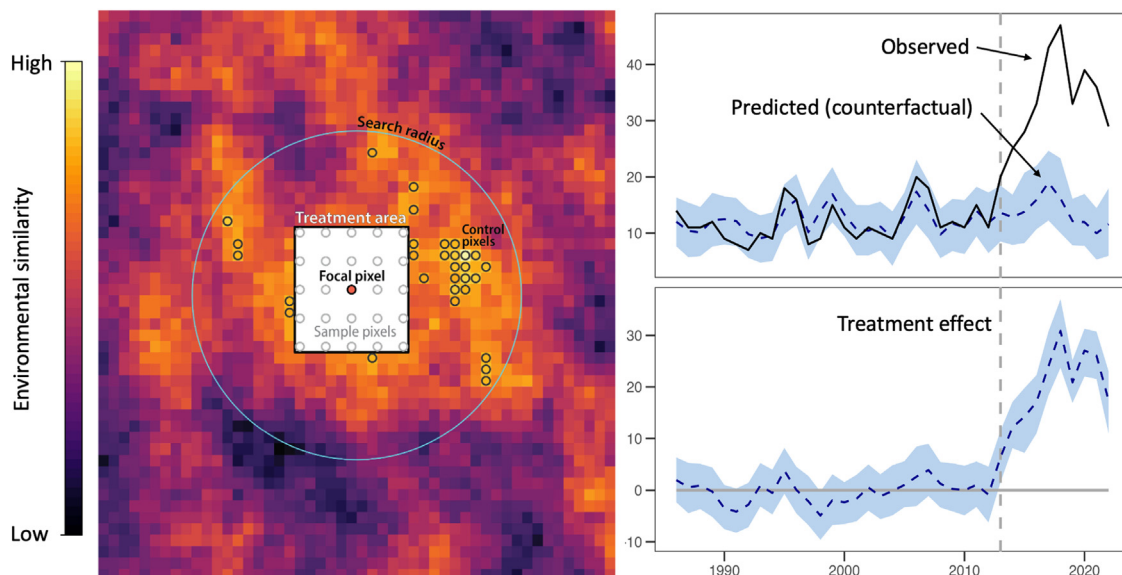


Figure 3. (Left panel) Conceptual model of sample point matching and causal impact analysis used in this analysis. Each sample point within an event (treatment area or wildfire; depicted here as a white square) is matched with 30 environmentally similar, undisturbed points outside of the event. The upper right panel illustrates how a Bayesian structural time series model is trained to predict cover (dashed line is the prediction, blue ribbon is the 95% credible interval) at the sample point based on cover at matched control points during the pre-treatment period (area left of dashed vertical line). The estimated treatment effect (lower right) is the difference between the counterfactual predictions and observations during the post-treatment period (right side of dashed vertical line).

burned at any point during the MTBS period of record (1984–2020) or had >1 recorded treatment over the course of the study period, and portions of wildfire perimeters that experienced >1 fire during the study period, were removed from the analysis. After screening, our dataset included 352 distinct spatial units spanning 258 944 ha (Table 1). All treated areas and wildfires are shown in Fig. S1 in supplemental materials (available online at [insert URL here]).

Vegetation data and environmentally matched control points

In the Burley region, we established a grid of sample points at 90-m grid intervals within the areas that underwent juniper removal or were burned in wildfire (hereafter “events”). For each sample point, we then identified environmentally similar control points in nearby areas not impacted by juniper treatments or wildfire (Fig. 3). Our method of selecting control points was a modification of that used in Fick et al. (2021; 2022) and consisted of extracting a set of soil, vegetation, and topographic variables (de-

scribed in Table S1) for each sample point and potential control points in undisturbed areas within 5 000 m. We then used Gower's distance (Gower, 1971) to calculate the environmental similarity of each undisturbed point to the sample point and selected the 30 most similar undisturbed points to serve as controls. We used the same methods for the Owyhee region but used a larger 180-m grid for sampling.

Before analyzing the wildfire areas, we first excluded elevations not represented in the mechanically treated areas and removed areas where the pre-disturbance tree cover exceeded the maximum observed in the treated regions. Tree cover data was sourced from the Rangeland Analysis Platform version 3 (hereafter RAP; Allred et al., 2021). We calculated pre-disturbance tree cover as the average cover from 2000 to 2009 for Burley and from 1993 to 2002 for Owyhee. Additionally, we excluded non-rangeland areas, fields of hay or alfalfa, and idle cropland using the National Land Cover Database (Dewitz, 2023) and the USDA National Agricultural Statistics Service Cropland Data Layer (USDA National Agricultural Statistics Service, 2020).

Lastly, to filter out any disturbances that were not explicitly mapped as tree-removal treatments or wildfires in the datasets available to us, we used the LandTrendr algorithm (Kennedy et al., 2010; 2018) in Google Earth Engine (Gorelick et al., 2017) to find areas of abrupt vegetation loss between 1991 and 2023 in each project area. We used the default parameters in Kennedy et al. (2018) applied to Normalized Burn Ratio (NBR: $[(NIR - SWIR2)/(SWIR2 + NIR)]$) and masked out clouds, shadows, snow, and water. We excluded control points that exhibited abrupt vegetation loss, (i.e. disturbances with a duration of <3 years) in the post-treatment period. This resulted in the exclusion of <2% of control points, with a minimal (<1%) loss of treatment points because each treatment point was matched to 20–30 control points.

Counterfactual vegetation cover

For each sample point and its environmentally matched control points, we extracted time series of cover estimates (1986–2022) for annual herbaceous, perennial herbaceous, shrubs, and trees from RAP. We refer to the time series of cover data before and after conifer removal or wildfire as the “pre-treatment” and “post-treatment” respectively. Using the pre-treatment time series of cover from the 30 control points as predictors, we trained Bayesian structural time series (BSTS) models to predict annual changes in pre-treatment cover at each sample point (Brodersen et al., 2015). Following the approach of Fick et al. (2021), these predictions were then extended to the post-treatment period to produce a counterfactual time series of cover for each sample point (Fig. 3). This counterfactual time series represents the expected vegetation cover in the absence of treatment and can be compared directly to the observed cover following treatment as a measure of treatment impact (Fick et al. 2022). We fit the BSTS models using the “bsts” (Scott, 2024) and “CausalImpact” (Brodersen et al., 2015) packages in R (R Core Team, 2023). To assess the accuracy of the fitted models at each sample point, we calculated Pearson's correlation, r , between the observed and predicted cover values during the pre-treatment period.

Modeling treatment effects

We used the difference between the counterfactual cover predictions and observed vegetation cover to measure the effect of conifer treatment or wildfire on vegetation at each sample point in each year (hereafter “treatment effect”). We used linear mixed effects models, fitted with the “lme4” package (Bates et al., 2015)

in R, to model treatment effects (dependent variable) as a function of treatment type, time since treatment, and two additional variables related to the context or setting of the sampled pixel. Treatment type (*treatment*) was a factor indicating wildfire, mastication treatment, or cut-and-lop treatment. In this analysis, we pooled all cut-and-lop treatments without regard to follow-up burning. To explore the effects of follow-up prescribed burning in the Owyhee project area, we provide an additional analysis in Appendix 2 in supplemental materials. We grouped the data into five time periods (*period*) relative to the year of treatment/disturbance: pre-disturbance (1–3 years pre-disturbance), immediate (0–1 years post-disturbance), short-term (2–4 years post-disturbance), mid-term (5–7 years post-disturbance), and long-term (>7 years post-disturbance). We proposed two categorical variables describing the context of each sampled pixel: *project* (Burley or Owyhee) and encroachment phase (*phase*). The pre-disturbance tree cover estimates (described in the section *Vegetation data and environmentally matched control points*) were used to assign each sampled pixel to a pre-treatment encroachment phase (<1% canopy cover, phase I = 1–10% canopy cover, phase II = 10–30% canopy cover, and phase III > 30% canopy cover), as in Miller et al. (2005). The Pearson's correlation (r), quantifying the pre-treatment agreement between the observed cover and BSTS model predictions (see above), was used to weight each observation, such that pixels whose behavior more closely matched BSTS model predictions were given higher weight in the mixed effects model. Pixels with $r < 0.5$ were omitted, resulting in the omission of approximately 0.1–2% of sampled pixels across plant functional types. To reduce computation time, we subsampled pixels such that each unique encroachment phase/event combination was represented by a maximum of 20 pixels. We selected model structures separately for each plant functional type in a two-step procedure following Zuur et al. (2009).

First, we selected from among four candidate random effects structures, using the restricted maximum likelihood to fit models and selecting the best-fitting structure with Akaike's information criterion corrected for small sample size (AIC_c). Minimally, we included random intercepts for the sampled point or *pixel*, nested within the unique treatment or wildfire *event*, nested within the *project* area to account for the repeated measures and hierarchical nature of the sampling schema (specified as (1|*project/event/pixel*) in lme4 formula syntax). Other candidate random effects structures included random year effects at various levels of the spatial hierarchy (i.e., at the event level, project level, or global; see Table S2). In this step, all models included fixed effects of *treatment*, *period*, and *phase* plus their interactions (i.e., a saturated model).

After determining the most supported random effects structure, we then selected from among two competing fixed effects model structures. Candidate models included effects of *treatment*, *period*, and either *phase* or *project*, as well as interactions among all three factors (i.e., three-way interactions). In this step, candidate models were fit using maximum likelihood and ranked with AIC_c (Zuur et al. 2009).

Once the random and fixed effects structures were chosen, models were re-fit using the restricted maximum likelihood (Zuur et al. 2009) and the “emmeans” package (Lenth, 2024) was used to extract point estimates and 95% confidence intervals of marginal predictions for each combination of factor levels. A flow-chart illustrating the steps of the treatment effects analysis is provided in Figure S2 in supplemental materials.

Assessing landscape-scale outcomes with sagebrush ecological integrity

We used the sagebrush ecological integrity (SEI) suite of products from the Sagebrush Conservation Design (Doherty et al., 2022)

to assess the extent to which the Burley and Owyhee conifer removal projects yielded ecologically meaningful outcomes at the landscape scale. The SEI spatial products quantify the relative integrity of sagebrush shrublands across the extent of the biome, and include a continuous quantitative metric (SEI) and a discretized version of that continuous metric which categorizes rangelands into core sagebrush areas (CSA), growth opportunity areas (GOA), and other rangeland areas (ORA). SEI is the spatially-smoothed product of 5 component factors, each placed on a common scale using expert-derived nonlinear transformations that describe how variation in each component is related to the overall health of the sagebrush ecosystem. The rescaled “Q values” ranged from 0 to 1, with values near 1 indicating desirable conditions (Doherty et al., 2022). Thus, positive ecosystem attributes (sagebrush and perennial herbaceous plants) are scaled such that high cover results in Q values near 1, while threats (human modification, annual herbaceous plants, and trees) are scaled such that high cover results in Q values near 0. We defined the landscape for each project area by buffering all management treatments by 2 km and drawing a minimum convex hull around the buffered treatments. Within this convex hull, we masked out non-rangeland land cover (i.e., forests and persistent woodlands, croplands, open water, developed areas) and rangelands outside the range of elevations represented in the treatment polygons. For each project landscape, we then calculated the mean of each component Q value in each SEI period (1998–2001, 2003–2006, 2008–2011, 2013–2016, 2017–2020). All data processing was conducted in Google Earth Engine via the Javascript code editor.

Results

Model selection

After removing sample points that experienced multiple disturbance events, those with insufficient numbers of undisturbed control points nearby, and points where pre-treatment observed cover had a low correlation with BSTS model predictions ($r < 0.5$; indicative of poor fit of the counterfactual model), we modeled treatment effects among 306 unique events: 224 cut-and-lop treatments, 38 mastication treatments, and 44 wildfires. Final sample sizes after subsampling were as follows: AFG = 9 564 pixels; PFG = 9 563 pixels; SHR = 9 570 pixels; TRE = 9 522 pixels. Across all plant functional types except annual forbs and grasses, the most supported model structure included random intercepts for *pixel* within *event* within *project*, and for *event* within *project* within *year* (i.e., $(1|project/event/pixel) + (1|year/project/event)$; Table S2). For annual forbs and grasses, the estimated variance among projects was zero, producing a singular model fit. Therefore, we pooled across project areas, re-coded events to keep them unique across projects, and re-fit models with random effects structures lacking the *project*-level intercept $((1|event/pixel) + (1|year/project/event))$. The most supported fixed effects structure for all plant functional types was the 3-way interaction among *phase*, *treatment*, and *period* (Table S3).

Trees

The magnitude of treatment effects on trees increased predictably across phases, reflecting the fact that effect sizes were directly proportional to tree cover at the time of treatment. Both management treatments produced persistent effects which remained nearly unchanged between the short- (2–4 years) and long-term (>7) post-treatment periods. Wildfire had significant but smaller effects on tree cover across all encroachment phases except <1% cover, and wildfire treatment effects in phase III sites began to

decline in magnitude after 2–4 years post-treatment (Fig. 4; also see Fig. S3).

Perennial forbs and grasses

Management treatments increased perennial forb and grass cover across all post-treatment periods and phases, except in sites with <1% pre-treatment tree cover in the last period (>7 years post-treatment), where the 95% confidence interval around the estimated mean treatment effect overlapped zero for cut-and-lop. For both cut-and-lop and mastication, greater responses were observed among later encroachment phases. Perennial forbs and grasses also responded positively to wildfire, but after an initial decline (0–1 year post-treatment) in areas experiencing earlier phases of encroachment (<1% and phase I). Generally, treatment effects stabilized after the 2–4 years period. However, in areas with phase III encroachment, both management treatments, but not wildfire, continued to show increasing positive effects across all periods (Fig. 4).

Shrubs

Both cut-and-lop and mastication treatments increased shrub cover in later encroachment phases (phases II and III), but had either a neutral (cut-and-lop) or a small negative (mastication) effect among earlier phases (Fig. 4). Shrub cover was strongly reduced by wildfire where tree cover was low, nearly unchanged in phase II, and increased in phase III (Fig. 4). Similar to perennial forbs and grasses, positive treatment effects in phase III sites continued to increase in magnitude across all periods for both management treatments, but not wildfire (Fig. 4).

Annual forbs and grasses

Annual forb and grass cover increased with all treatments, but with a short lag in the case of wildfire (Fig. 4). Mastication generally produced the largest increases in annual cover, but wildfire had larger long-term (>7 years) effects among minimally-encroached (<1% cover) and phase II sites. Cut-and-lop produced the smallest increase in annual cover over the medium- to long-term except in phase III woodlands, where the response was intermediate between wildfire and mastication. Treatment effects among management treatments were almost uniformly larger among later phases of tree encroachment, while effects of wildfire were less clearly related to pre-treatment tree cover. In management treatments, treatment effects on annuals peaked in either the 2–4 or 5–7 years post-treatment period before declining in the >7 year post-treatment period (Fig. 4).

Landscape-scale treatment effectiveness (SEI)

Sagebrush, perennial herbaceous, and human modification components were relatively stable since 2001. Tree Q values declined (indicating increasing tree cover) from 2001 to the mid 2010s in both project areas but then stabilized (Owyhee) or reversed course (Burley) as a result of conifer removal treatments that scaled up dramatically after 2010 and wildfires. Annual herbaceous Q values were the most limiting component and also the most variable through time, reflecting the high sensitivity of annual plants to fluctuation in precipitation.

Discussion

Our remote sensing-based analysis of 288 juniper removal treatments covering 106 333 ha in the Northern Basin and Range ecoregion of southern Idaho and conducted over a 17-year period

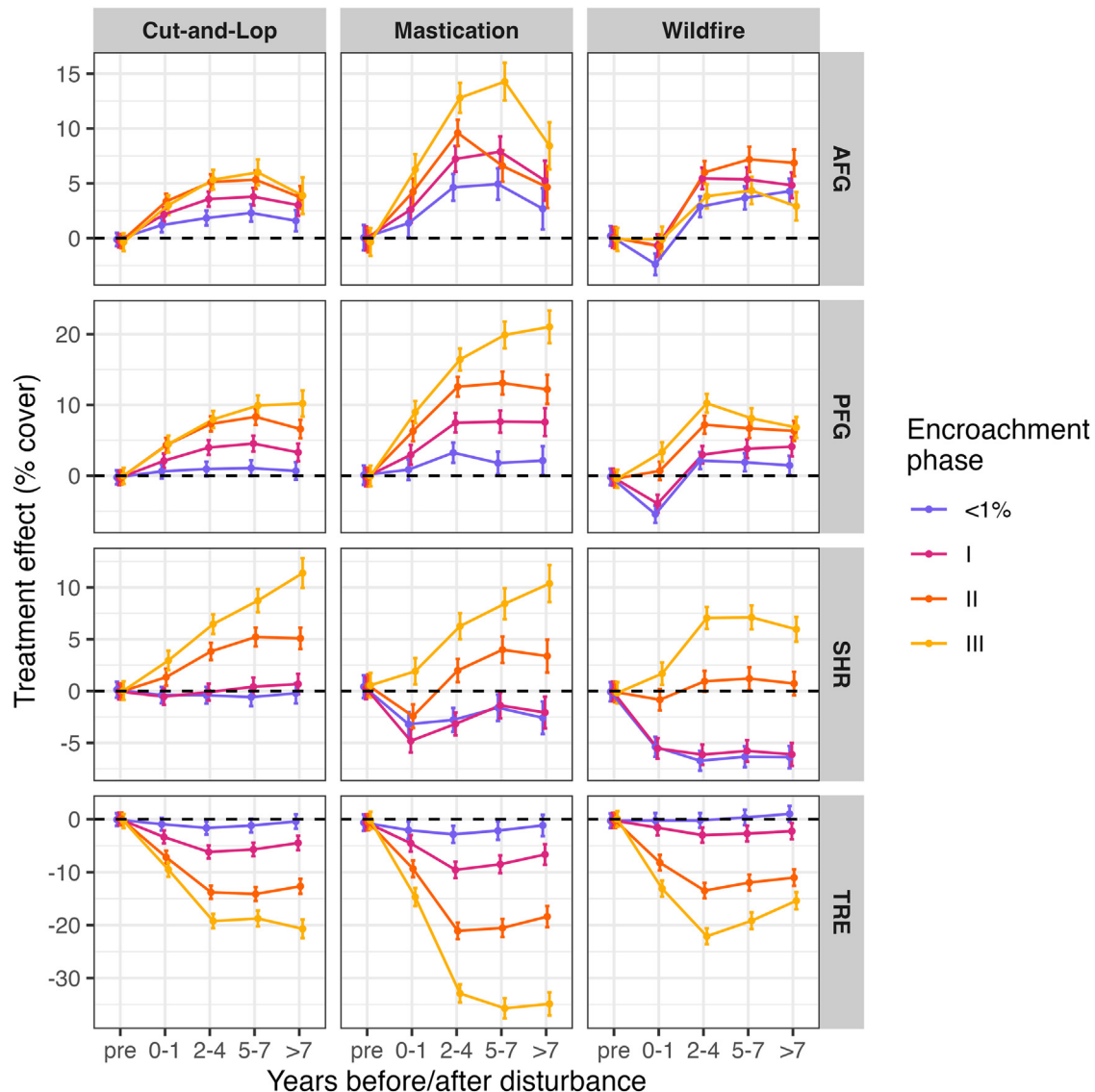


Figure 4. Effects of conifer removal treatments and wildfire over four different time periods on annual (AFG), perennial (PFG), shrub (SHR) and tree (TRE) cover in southern Idaho. Sampled points were stratified by pre-treatment (or pre-fire) conifer encroachment phase, where phase I = 1–10% canopy cover, phase II = 10–30% canopy cover, and phase III > 30% canopy cover. Points and error bars show estimated marginal means and 95% confidence intervals derived from the mixed-effects models fit separately for each cover type.

provides new evidence that sustained, focused implementation of tree removal treatments can effectively address the second leading driver of sagebrush ecosystem degradation: conifer encroachment (Doherty et al., 2022; Mozelewski et al., this issue). Across all phases of encroachment, treatments yielded >7 years of conifer suppression and increased cover of perennial forbs and grasses—a functional group that plays a key role in sagebrush ecosystem functions such as resistance to invasion and resilience to disturbance (Chambers et al., 2007, 2014). Among later phases of encroachment, treatments significantly increased shrub cover. These positive outcomes were, however, frequently accompanied by increases in cover of undesirable annual herbaceous vegetation, highlighting the need for managers to simultaneously address multiple ecosystem threats to maximize the efficacy of treatments.

Our findings provide encouraging evidence for partners implementing the Sagebrush Conservation Design (Doherty et al., 2022) that properly targeted and implemented juniper treatments can contribute to biome-wide goals to defend and grow high-value sagebrush ecosystems. Similar to the private lands analy-

sis by Naugle et al. (this issue), we show targeted juniper removal halted (Owyhee) or reversed (Burley) steady declines in Sagebrush Ecological Integrity across both public and private lands (Fig. 5). Collectively, these findings demonstrate what can be achieved in geographies where “community readiness” (Wollstein et al., this issue) fosters cross-boundary, landscape-scale restoration. Our results support biome-wide spatial prioritization that targets conifer management in areas of lower invasive annual grass risk (Reinhardt et al., this issue) with the growing recognition that ongoing juniper management in the Great Basin may need to be coupled with invasive grass control to enable projects to maintain or return to core status (Bates et al., 2017; Naugle et al., this issue).

Responses of major plant functional groups were similar to those documented by Fick et al. (2022), who introduced the analytical framework used here to assess outcomes of 302 PJ treatments in the Colorado Plateau. They found that both hand and mechanical tree removal treatments increased the cover of perennial forbs and grasses, shrubs, and annual forbs and grasses, with minor differences among treatment methods. Similar to our findings,

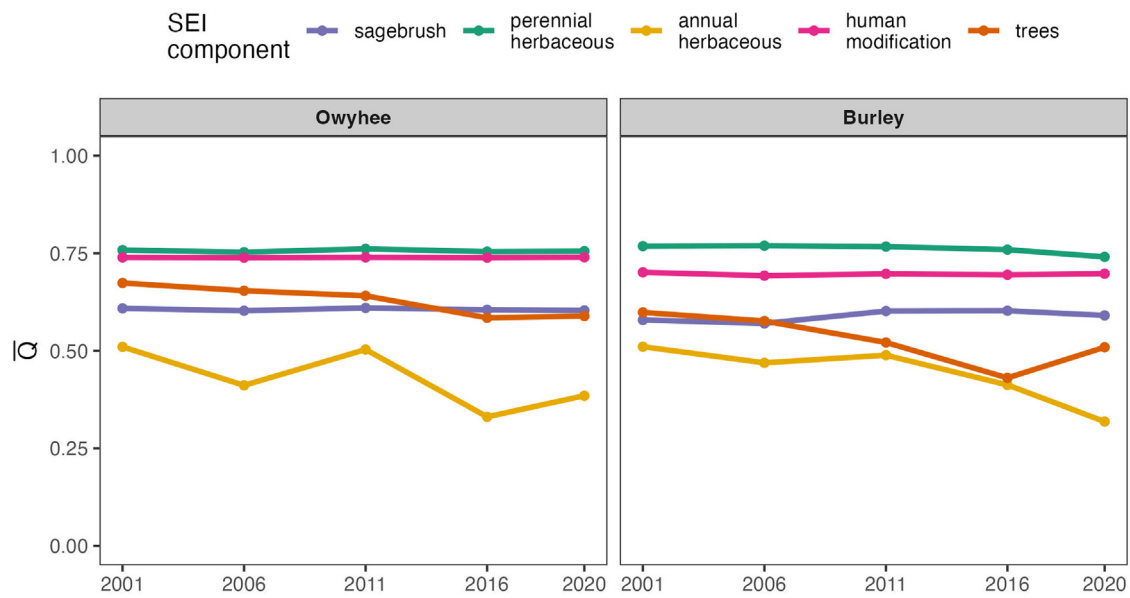


Figure 5. Average value of SEI component Q values (see methods text) within the Owyhee and Burley conifer removal project landscapes.

the magnitude of responses of understory functional groups were positively related to pre-treatment tree cover (Fick et al., 2022). A notable divergence with their findings was the relatively larger treatment effects on annual forb and grass cover. This may simply reflect regional differences in suitability for the dominant invasive annual grasses affecting sagebrush ecosystems; the Northern Basin and Range ecoregion is among those most impacted by invasive annual grasses in the western U.S. (Hak and Comer, 2020). Significantly, our research not only aligns with the conclusions of Fick et al. (2022) but also extends their insights on juniper removal effectiveness to a broader swath of the sagebrush biome. If coarse plant functional group cover suffices for key outcome assessment, Fick et al.'s (2022) counterfactual time series approach offers a scalable and powerful method to retroactively analyze management effectiveness.

Our study reinforces the durable, positive effect of conifer removal on perennial forbs and grasses consistently demonstrated in previous studies. Field research shows that tree removal increases water and nutrient availability (Bates et al., 2000; Young et al., 2013; Roundy et al., 2014b; Bates and Davies, 2017), generally resulting in increased perennial herbaceous vegetation and shrub cover (Ross et al., 2012; Roundy et al., 2014a, 2014b; Miller et al., 2014; Stephens et al., 2016; Havrilla et al., 2017; Ernst-Brock et al., 2019; Freund et al., 2021; Nigro et al., 2023; Williams et al., 2020, 2019, 2017). Positive treatment effects on herbaceous vegetation may take several growing seasons to emerge (e.g., Havrilla et al., 2017), but the effects are often persistent. We did observe a modest decline in the effect size on perennial forbs and grasses >7 year post-treatment in cut-and-lop treatments among phase I and II sites, but treatment effects remained significantly positive (Fig. 4). Pre-treatment seeding, which did not occur among cut-and-lop treatments, may be at least partly responsible for the larger and more persistent increases in perennial herbaceous vegetation among mastication treatments. Similarly, Fick et al. (2022) reported lasting positive effects of hand and mastication treatments on perennial forb and grass cover measured up to 15 years after treatment. Studies extending beyond a decade post-treatment are scarce, yet they offer important insights into the long-term efficacy of juniper management. For instance, Bates et al. (2017) found significantly higher density and biomass of perennial grasses 25 years after treatment in Oregon. Similarly, in west-

ern Nevada, Ernst-Brock et al. (2019) found a durable increase in perennial cover 32 years after treatment when juniper removal was combined with grass seeding.

The results also show that the effect of juniper removal on shrub cover varies depending on encroachment phase. Shrubs responded positively to both removal treatments when applied to phase II and III sites; however, shrub cover was either unaffected (cut-and-lop) or reduced slightly (mastication) following treatment among sites in earlier phases of encroachment. This may reflect that phase <1% and phase I sites were treated before trees significantly suppressed shrub cover. Reduction of shrub cover in mastication treatments (approximately 3–5% immediately following treatment, stabilizing to ~1.5–2.5% 5–7 years post-treatment) likely reflects plant mortality or canopy damage caused by the heavy, tracked vehicles used to implement these treatments. Importantly, the magnitude of treatment-induced shrub reductions was substantially smaller than the reductions associated with wildfire, which is especially destructive to non-resprouting shrubs like sagebrush (Fig. 4). Moreover, shrub cover in mastication treatments appeared to recover to near pre-treatment levels within several years, whereas shrub cover remained persistently low following wildfire (Fig. 6). Median shrub cover ≥7 years post-treatment was similar among management treatments, at 20% for cut-and-lop and 19% for mastication, but only 12% for wildfire (Fig. 6).

Consistent with previous studies in juniper and PJ systems (Ernst-Brock et al., 2019; Freund et al., 2021; e.g., Miller et al., 2014; Roundy et al., 2014a; Havrilla et al., 2017; Williams et al., 2017), juniper removal treatments increased annual forb and grass cover, which in this region is a reliable indicator of invasive annual grasses such as *B. tectorum* and *Taeniatherum caput-medusae* (see Smith et al., 2023). We found that the impact of juniper treatments on annual cover was larger among sites in later phases of encroachment, similar to patterns observed in other sagebrush ecosystems (Bates et al., 2013; Williams et al., 2017). Site-level response of invasive annual grasses to tree removal depends on a number of factors, including pre-treatment infestation, pre-treatment abundance of competitors (especially perennial grasses), responses of competitors to the treatment, and soil temperature and moisture regimes (Davies et al., 2019; Williams et al., 2017). The larger increases in annual cover among later phases of encroachment may result from weakened perennial herbaceous

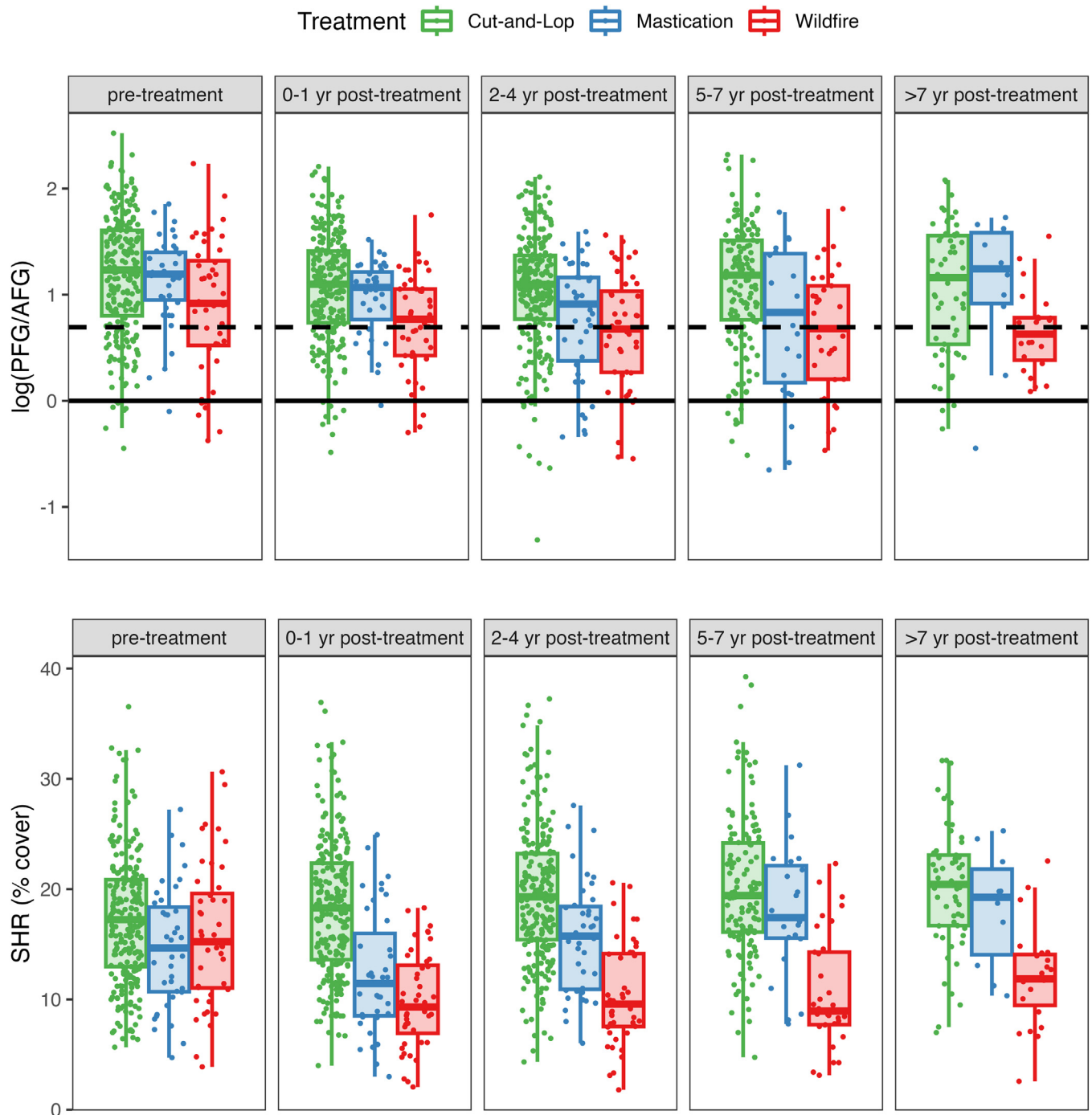


Figure 6. Ratio of perennial to annual herbaceous cover (log scale) over time among tree removal treatments and wildfires (top row). Values above the solid horizontal line indicate perennial cover > annual cover, whereas values below zero indicate annual cover > perennial cover. Points above the dashed line have perennial cover that is more than double that of annual cover. Bottom row shows average shrub cover over time among tree removal treatments and wildfires. For all plots, a point represents average cover at the event level.

communities in those sites and the greater amount of soil disturbance associated with treatments in heavier tree cover. For example, mastication elicited a larger response in annual forb and grass cover than cut-and-lop within a given phase in our study area, consistent with findings from sagebrush communities across Utah and the Colorado Plateau (Monaco and Gunnell, 2020; Fick et al., 2022). These observations are consistent with treatment-related soil disturbance playing a role in moderating the response of annuals, but they do not rule out other differences be-

tween hand and mechanical treatments that may also contribute to varying outcomes.

To understand the implications for the observed increase in annual cover, the results must be interpreted in the context of other treatment effects. Perennial and annual herbaceous plants both benefit from access to the same resource pool when trees are removed, and both increase simultaneously following treatment (Fig. 4; Bates et al., 2000). The net outcome may therefore be neutral or even positive for perennial dominance, especially if native perennials are positioned to gradually outcompete annuals for

these resources over time (Ellsworth et al., 2024). Post-treatment successional dynamics will vary depending on site-specific factors such as pre-treatment community composition, weather, and climate (Roundy et al., 2018). Due to the recency of the treatments examined in this study, our ability to assess effects beyond about 10 years after treatments is limited. However, over the temporal period of our data, there is little indication that treatments have tipped the balance in favor of annuals. In Figure 6, we show that perennials have maintained higher cover than annuals among the overwhelming majority of cut-and-lop and mastication treatments, and perennial cover exceeded annual cover by a factor of >2 in more than half of treatments in every post-treatment period. This stability is even more notable when you consider the broader trends toward increasing dominance of annuals across cold desert ecoregions of the western U. S. (Smith et al., 2022; Kleinhesselink et al., 2023), a phenomenon affecting disturbed and undisturbed vegetation communities alike (Pyke et al., 2022; Smith et al., 2023).

Nevertheless, increased cover of annuals is an undesirable side effect of treatments that can undermine the durability of positive conservation outcomes, for example, by increasing the probability of wildfire (Fusco et al., 2019; Smith et al., 2022) and preventing full recovery to core sagebrush status (Naugle et al., this issue). Our findings suggest managers in this region should anticipate increases in invasive annual grasses after juniper removal treatments and should implement steps to mitigate this impact. Grazing management adjustments to target annual grasses are a low-cost option that may be effective in some settings (Davies et al., 2021; 2022). Pre-treatment seeding of native perennials is a strategy commonly employed to mitigate secondary invasion by invasive annuals and previous work supports the effectiveness of this practice (Bybee et al., 2016; Havrilla et al., 2017). In our study, pre-treatment seeding was implemented in most of the mastication treatments, but our findings suggest that additional mitigation is warranted, particularly for mechanical tree removals performed during later stages of encroachment. Herbicide application to directly control invasive annual grasses and deplete their seed-bank will likely be necessary to more fully mitigate annual grass responses (Sebastian et al., 2017; Courkamp et al., 2022).

Although a cursory glance at Figure 4 would suggest wildfire produces smaller and more transient reductions in tree cover than management treatments, these patterns in the means may obscure a spatially heterogeneous response. Wildfire scars, as mapped by MTBS fire perimeters, can include significant internal variation in burn severity, including unburned patches (Kolden et al., 2012). Because we sampled wildfire perimeters irrespective of burn severity, unburned and low-severity burned patches are represented in our sample. Additional analysis revealed that although tree cover remained quite low in the majority of sampled wildfire pixels (reflected by the median), more patches of residual tree cover remained—and grew in size and density—within wildfire perimeters compared to management treatments (Fig. S3). We speculate that wildfire, though a patchy burning process, leaves more residual trees on the landscape which may in turn expose a larger area to propagule pressure, resulting in faster recovery through recruitment. We note, however, that this may not apply to prescribed fire treatments conducted specifically to target trees. Research indicates that the treatment longevity of prescribed fire is often greater than that of cutting (Davies et al., 2019) and prescribed burns are carefully planned to minimize undesired impacts on understory soils and plants, such as burning during cool seasons.

Implications

Our research joins an extensive body of evidence supporting the effectiveness of juniper removal projects in attaining desired

vegetation outcomes in sagebrush restoration projects (Bates et al., 2000; Miller et al., 2014; Roundy et al., 2014a; Bybee et al., 2016; Williams et al., 2017; Monaco and Gunnell, 2020; Wozniak et al., 2020; Freund et al., 2021; Fick et al., 2022). Our evaluation of remotely sensed data reinforces the efficacy of juniper removal in reducing tree cover and enhancing perennial forbs and grasses but highlights a critical trade-off: the unintended increase of invasive annual grasses observed among most restoration sites. Managers applying juniper management in parts of the sagebrush biome where invasive annual grasses are prevalent should adopt comprehensive strategies that include both preventative and remedial measures to control invasive annual grasses. Additional research comparing the effectiveness of seeding, herbicide treatment, or a combination of these treatments, is also needed to support management. Our results generally support the 'Defend the Core' strategy (Maestas et al., 2022) for project targeting, which prioritizes sagebrush-restoration efforts in lightly encroached areas with robust, intact understories, particularly in areas not affected by invasive annual grasses (Reinhardt et al., this issue). This approach minimizes risks associated with intensive mechanical treatments, such as unintended disturbance to desirable shrubs and the establishment of invasive annual grasses, reducing the need for expensive post-treatment rehabilitation (Taylor et al., 2013).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Joseph T. Smith: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Andrew R. Kleinhesselink:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Jeremy D. Maestas:** Conceptualization, Data curation, Writing – original draft, Writing – review & editing. **Scott L. Morford:** Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **David E. Naugle:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Connor D. White:** Data curation, Writing – original draft, Writing – review & editing.

Acknowledgments

This project was supported by BLM Montana/Dakotas as well as Partnering to Conserve Sagebrush Rangelands, a partnership between BLM and the Intermountain West Joint Venture. We thank Tate Walters and Connie Tharp with the Natural Resources Conservation Service and private landowners in the project areas for assistance with assembling and providing permission to include private lands data in this analysis. We thank Kristopher Mueller for his assistance in producing figures. We are grateful to the two anonymous reviewers whose constructive feedback substantially improved the manuscript. The findings and conclusions presented in this paper are those of the authors and do not necessarily reflect the views of the USDA Natural Resources Conservation Service. The funding agency has provided financial sponsorship to make this work open access and had no influence or involvement over the review or approval of any content.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.rama.2024.08.010](https://doi.org/10.1016/j.rama.2024.08.010).

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