

SPECIAL FEATURE:
SAGEBRUSH STEPPE TREATMENT EVALUATION PROJECT

Sagebrush recovery patterns after fuel treatments mediated by disturbance type and plant functional group interactions

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Abstract. Fire and fuel management is a high priority in North American sagebrush ecosystems where the expansion of piñon and juniper trees and the invasion of nonnative annual grasses are altering fire regimes and resulting in loss of sagebrush species and habitat. We evaluated 10-yr effects of woody fuel treatments on sagebrush recruitment and plant functional group interactions using Sagebrush Steppe Treatment Evaluation Project data. We used mixed-effects ANOVAs to examine treatment effects on sagebrush density and cover and perennial and annual grass cover in expansion woodlands (prescribed fire and cut-and-leave) and annual grass invasion areas (prescribed fire, mowing, tebuthiuron herbicide application). We used piecewise structural equation models to evaluate interactions among sagebrush seedling density, juvenile and adult density, and cover and perennial and annual grass cover. Fuel treatments were equated to pulse or press disturbances varying in resource release and subsequent intra- and interspecific interactions. Prescribed fire, a high magnitude pulse disturbance with more severe effects in warm and dry sites, reduced sagebrush cover and decoupled associations among sagebrush seedlings, juvenile and adult density, and cover indicating changed population structure. Cutting and leaving trees, a low magnitude pulse disturbance in cooler and moister woodlands, increased sagebrush density and cover and generally had lesser effects on sagebrush intraspecific associations. Mowing, a moderate magnitude pulse disturbance, and tebuthiuron herbicide application, a multiyear press disturbance, reduced sagebrush cover and disrupted intraspecific relationships. Competitive release increased cover of perennial grass in all treatments but tebuthiuron. Annual grass increased in all treatments, especially prescribed fire and tebuthiuron. Annual and perennial grass interactions with sagebrush were generally rare, but in woodland treatments perennial grass suppressed annual grass through year 6. Treatments in cooler and moister woodland sites had more positive effects on sagebrush recruitment and perennial grass cover, less negative effects on sagebrush intraspecific interactions, and smaller increases in annual grass cover indicating potential increases in resilience to fire. In warmer and drier invasion sites, reductions in woody fuels resulted in lack of sagebrush recruitment, disruption of sagebrush intraspecific interactions, and progressive increases in annual grass indicating reduced resilience to fire and resistance to invaders.

Key words: annual grass invasion; *Artemisia tridentata*; *Bromus tectorum*; fuel treatment; piñon and juniper; resilience to disturbance; resistance to invasion; sagebrush recruitment; Special Feature: Sagebrush Steppe Treatment Evaluation Project; woodland expansion.

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INTRODUCTION

The Great Basin of North America is a 541,727-km² cold desert dominated by sagebrush (*Artemisia* spp.) shrubland where changes in composition and structure of native vegetation coupled with invasion of nonnative annual plants are driving rapid transformations. Invasion and expansion of nonnative invasive annual grasses, especially cheatgrass (*Bromus tectorum* L.), at low-to-mid-elevations, are resulting in annual grass–fire cycles (Bradley et al. 2018, Chambers et al. 2019). Expansion and infilling of piñon and juniper trees at mid-to-high elevations are causing depletion of understory species and increased risk of high-severity fire (Miller et al. 2019). Fire and fuel management has become a high priority due to escalating risks not only to human life, property, and economic resources, but also to sagebrush habitats and the species that depend on them (USDOI 2015).

A primary objective of fire and fuel management is to increase ecological resilience (recovery potential) to disturbance and resistance to invasive annual plants as a means of decreasing fire severity and extent and preventing development of invasive plant–fire cycles (Reinhardt et al. 2008, Valdecantos et al. 2008, Stephens et al. 2016). Management actions have focused on decreasing woody species (shrubs and/or trees) to reduce fuel loads and continuity and increase perennial native herbaceous species capable of surviving wildfire and competing with annual invaders. As more species become threatened by loss of sagebrush habitat, maintaining sagebrush density and cover has become increasingly important (Coates et al. 2016).

A major limitation to maintaining sagebrush populations following both fuel treatments and post-fire rehabilitation is sagebrush seedling establishment and population recruitment (Knutson et al. 2014, Brabec et al. 2015). Big sagebrush (*Artemisia tridentata*) subspecies are obligate seeders that are killed by fire and characterized by

relatively small, short-lived seed (2–3 yr) with low average dispersal distances (1–2 m; Schlaepfer et al. 2014). Mortality of small sagebrush size classes (seedlings and juveniles) is typically very high, and recruitment into the population over time is often low (Ziegenhagen and Miller 2009, Shriver et al. 2019). In these dryland ecosystems, recruitment requires alignment of soil temperature and soil water availability and is promoted by low temperatures and high soil moisture in spring (Shriver et al. 2018, 2019). At landscape scales, recruitment is typically greater at higher elevations with cooler temperatures and more available soil moisture than at lower elevations with warmer and drier conditions (Condon et al. 2011, Chambers et al. 2017, Shriver et al. 2019), but local variation occurs due to effects of soils and topography (Germino et al. 2018).

The rate and magnitude of sagebrush population and plant community recovery after disturbance depend on post-disturbance vegetation composition and structure, amount and timing of resource release, and subsequent intra- and interspecific interactions (Mitchell et al. 2017, Adler et al. 2018, Jentsch and White 2019). Similar to other types of disturbances, fuel treatments can be characterized as (1) pulse events of short duration and varying magnitude that result in abrupt changes in ecological attributes and processes or (2) longer-term presses of relatively low magnitude that result in more gradual change (Jentsch and White 2019). Amount and timing of resource release are strongly mediated by disturbance characteristics. In expansion woodlands and cheatgrass invasion sites, prescribed fire results in a short duration, disturbance pulse of moderate-to-high magnitude that causes mortality of fire-intolerant woody vegetation. Soil nutrients increase immediately after treatment (Stubbs and Pyke 2005, Rau et al. 2007, 2014, Bates and Davies 2017) and can remain elevated for four or more years afterward depending on microsite (Rau et al. 2007, Bates and Davies

2017). Soil water availability also increases and can remain elevated for over a decade after tree removal depending on year and season (Roundy et al. 2018, 2020).

In contrast, mechanical treatments to remove woody biomass (fuel) typically result in a disturbance pulse of low-to-intermediate magnitude. In sagebrush ecosystems experiencing woodland expansion, trees are often cut down or shredded, while shrub cover is maintained (Cline et al. 2010, Young et al. 2013b, Roundy et al. 2018). In dense sagebrush stands with potential for annual grass invasion, shrub cover is typically reduced through mowing treatments or herbicide applications (Davies et al. 2012, Pyke et al. 2014). Reducing shrub cover in dense sagebrush stands can result in a pulse or press disturbance depending on timing and amount of shrub mortality caused by the treatment. All treatments generally increase soil nutrient availability (Rau et al. 2014, Bates and Davies 2017), but increases in seasonal availability of soil water are more pronounced for tree removal in areas experiencing woodland expansion than for shrub reduction in annual grass invasion sites (Young et al. 2013a, Rau et al. 2014, Roundy et al. 2018). Depending on treatment type, lag times can occur due to uptake of soil water and nutrients by residual native species (Bates and Davies 2017) or annual grass (Rau et al. 2014, Williams et al. 2017).

Intra- and interspecific interactions influence sagebrush population processes following disturbance and are affected by residual vegetation (Mitchell et al. 2017, Roundy et al. 2018) and competitive release (Adler et al. 2018). Disturbances that remove both adult and juvenile plants, like prescribed fire, alter sagebrush population processes. Age class structure shifts to the smallest individuals, which have the highest mortality rates (Shriver et al. 2019). In the absence of a persistent seed source, populations may fail to increase over time due to short-lived seeds and episodic establishment (Allen et al. 2008, Wijayratne and Pyke 2012). Mechanical tree removal in woodland expansion sites results in resource release and increased sagebrush growth and cover (Bates and Davies 2016, Williams et al. 2017) and may increase both seed production and population recruitment. Population increase depends on site conditions and longer-term

weather patterns due to highly specific soil temperature and moisture requirements for establishment (Schlaepfer et al. 2014). In dense sagebrush stands, mechanical or herbicide treatment decreases sagebrush cover and density (Davies et al. 2012, Pyke et al. 2014) and may depress both seed production and population recruitment for several years (Germain et al. 2018).

Interspecific interactions can range from positive to negative and are strongly mediated by traits of dominant species in sagebrush communities (Reichenberger and Pyke 1990, Davies et al. 2012). In the absence of disturbance, large, adult sagebrush can facilitate bunchgrass reproductive potential, particularly under drought conditions (Swanson et al. 2020). Positive interactions also can occur between adult sagebrush and native forbs, that is, *Penstemon palmeri* (Poulos et al. 2014). However, little information exists about interactions of adult sagebrush with either grasses or forbs following fuel treatments.

Competitive release following removal of one or more species from a community provides an intuitive measure of the strength of interspecific competition (Adler et al. 2018). Perennial grasses typically increase over time following prescribed fire and mechanical treatment, particularly on more mesic sites (Bates and Davies 2016, Williams et al. 2017), where they are strong competitors for resources and can reduce sagebrush population recruitment (McAdoo et al. 2013, Chambers et al. 2017). Annual grasses are also strong competitors that can reduce sagebrush recruitment (McAdoo et al. 2013, Davidson et al. 2019). However, perennial grass is often negatively associated with annual grass and can effectively suppress its establishment, growth (Chambers et al. 2007), and cover (Davies 2008, Chambers et al. 2014b, Bansal and Sheley 2016) across a range of site conditions.

The long-term Sagebrush Treatment Evaluation Project (SageSTEP) provides an opportunity to evaluate the effects of woody fuel treatments on sagebrush recovery patterns and plant functional group interactions. SageSTEP was established in 2006 to evaluate the effectiveness of fuel treatments on sagebrush plant communities experiencing tree expansion and cheatgrass invasion (McIver and Brunson 2014). The multisite experimental framework includes study

locations that are broadly distributed across sagebrush ecosystems in the Great Basin region of the western United States. Ten or more years of data are now available on sagebrush recovery patterns for woody fuel treatments that have different initial effects on plant functional groups. We examined treatment effects on sagebrush density and cover and the dominant herbaceous functional groups—perennial and annual grass cover. We then evaluated how relationships among sagebrush seedling density, juvenile and adult density and cover, and perennial and annual grass cover covary over time during recovery using piecewise structural equation models (SEMs). We hypothesized that (1) treatments that remove all plant cover such as prescribed fire disrupt relationships among sagebrush density and cover and alter interactions with perennial and annual grasses; (2) mechanical treatments that remove trees without affecting sagebrush increase sagebrush density and cover and annual and perennial grass cover; and (3) treatments that preferentially reduce sagebrush cover or cover and density, such as mowing or tebuthiuron application, respectively, alter feedbacks among sagebrush density and cover and facilitate increases in annual and perennial grass cover. We discuss management implications of treatment outcomes for sagebrush and ecosystem recovery.

METHODS

Study area

We used 17 SageSTEP sites arrayed across the Intermountain West in the States of Idaho, Nevada, Oregon, Utah, Washington, and California. Eleven sites were experiencing woodland expansion and were characterized by big sagebrush (Chambers et al. 2014b, McIver and Brunson 2014). Sites characterized by Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) had blue bunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) and needlegrasses (*Achnatherum* sp.) in the understory, loamy, and typically skeletal soils, and mesic/aridic to xeric soil temperature/moisture regimes. Sites characterized by mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) had Idaho fescue (*Festuca idahoensis* Elmer) and blue bunch wheatgrass in the

understory and loamy soils or mollic epipedons, and frigid/xeric soil regimes. Criteria used to select woodland expansion sites were as follows: (1) Dominant shrub was big sagebrush; (2) piñon and/or juniper was currently expanding into the site; (3) no evidence of stands being dominated previously by mature piñon or juniper; (4) soils were loams; (5) native grasses and forbs were present in the understory; and (6) introduced species were not a dominant component.

Six sites lacked woodland expansion but were threatened by cheatgrass invasion and were characterized by Wyoming big sagebrush (Pyke et al. 2014). Subdominants on these sites were blue bunch wheatgrass or Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth). Soils were loams, soil temperature regimes were mesic to frigid, and soil moisture regimes were aridic to xeric. Criteria used to select cheatgrass invasion sites were as follows: (1) Dominant shrub was Wyoming big sagebrush; (2) soils were loams; and (3) cheatgrass invasion had occurred, but native grasses and forbs were still present in the understory.

Experimental design and treatments

The study design was a randomized complete block with each of the 17 sites representing a block. For each of the eleven sites exhibiting tree expansion, three 8- to 20-ha treatment plots were established depending on site uniformity and topography. Each treatment plot contained 15 measurement subplots that were 0.1 ha (33 × 30 m) in size and located to include the range of tree cover on the site. One of three treatments was randomly assigned to each treatment plot in the block—control, mechanical, and prescribed fire. Treatments were applied in 2006, 2007, and 2009 for the woodland expansion sites in a stagger-start design (Loughin 2006). A stagger-start design alleviates the effects of starting an experiment under the same set of climate conditions so that results can be applied over broader inference space. Burning and cut-and-leave treatments were applied at each site in the same year to form a statistical block. Prescribed fire was applied between August and early November, and tree cutting was implemented between September and November. In the mechanical treatment, all trees >2 m tall were cut and left on the ground. Tree canopies were

reduced to <5% in burn plots and <1% in cut-and-leave plots (Miller et al. 2014).

The six cheatgrass invasion sites varied in size from roughly 120 to 325 ha. Four treatment plots that were 20–81 ha in size were established at each cheatgrass invasion site. Each treatment plot contained 6–9 measurement subplots that were 0.1 ha (33 × 30 m) in size and located to cover a range of perennial grass cover. Control, prescribed fire, mowing, or tebuthiuron herbicide treatments were randomly assigned to each treatment plot in the block. Treatments were applied once and were implemented in 2006, 2007, and 2008 using a stagger-start design (Loughin 2006), with start dates varying among sites. Prescribed fire was applied in October following mowing and tebuthiuron treatments on all sites except Moses Coulee, which received mowing and tebuthiuron in winter 2008/2009 followed by prescribed fire in September 2009. In the same treatment year, sagebrush was mowed with a rotary blade to a height of ~35 cm and tebuthiuron was applied at a rate of 1.68 kg/ha. Shrub cover was reduced from an average of 26–4% by fire and from 20% to 8% by mowing (Pyke et al. 2014).

Measurements

Data were collected from each subplot on all 17 sites during the growing season immediately prior to treatment application (year 0), in years 1, 2, and 3 after treatments (Miller et al. 2014, Pyke et al. 2014), and in years 6 and 10 yr after treatments. Within each subplot, plant cover was sampled at 0.5-m intervals along five, 30-m transects ($n = 300$ points/subplot) using the line-point intercept method (Herrick et al. 2005). Herbaceous plant cover was sampled as foliar cover and was summed for annual grasses (primarily *B. tectorum*) and perennial grass (primarily *P. spicata* and *Achnatherum* spp. in sites dominated by Wyoming big sagebrush and *F. idahoensis* and *P. spicata* in sites dominated by mountain big sagebrush). Sagebrush canopy cover was sampled by recording a hit as a direct contact or point falling within the live canopy perimeter. Sagebrush seedling (shrubs <5 cm tall) density, referred to as seedling density (SDL) hereafter, was counted in 1/4-m² quadrats placed every 2 m along the three central 30-m transects ($n = 45$). Juvenile and adult sagebrush density, referred to as juvenile and adult density (DEN) hereafter,

was a count of all individuals >5 cm tall in three, 2 × 30 m rectangular belt transects. Pretreatment tree cover was measured as the sum of aerial crown cover (A) for each tree >0.5 m tall in the subplot, using the formula $A = \pi (D1 \times D2)/4$, where $D1$ is the longest crown diameter and $D2$ is the perpendicular crown diameter.

Data analyses

Treatment effect.—To evaluate the changes from pretreatment (year 0) to year 1 and year 10 after treatment, we used a simple mixed-effects analysis of variance with treatment, time since treatment, and their interaction as the fixed effects and site as the random effect. We evaluated distributions of residuals from models and used $\log_e$ plus one transformations to satisfy model assumptions of normality and homogeneity of variance. We illustrated the changes by graphing the median and interquartile range as boxplots. We used the *lmer* function of the R package *lme4* (Bates et al. 2015) to examine treatment effects on sagebrush juvenile and adult density, sagebrush cover, and annual and perennial grass cover. Separate analyses were performed for each site type (woodland and cheatgrass sites) because treatments and conditions differed between the two site types. We calculated the estimated marginal means (least-squares means) using the *emmeans* package (Searle et al. 1980, Lenth et al. 2020) to compare differences among treatments and years.

Associations affecting sagebrush over time after treatment.—To better understand how sagebrush seedling density, juvenile and adult density, and cover interacted with each other and the two other dominant functional groups (annual and perennial grasses) over time, we used piecewise SEMs (Lefcheck 2016). The piecewise SEMs were implemented with the component models as linear mixed-effects models for five time steps (years 0–1, 1–2, 2–3, 3–6, and 6–10). Significant ($P < 0.05$) associations between variables were presented in the SEMs as standardized path coefficients for each time step. We evaluated distributions of residuals from models and used $\log_e$ plus one transformations to satisfy model assumptions of normality and homogeneity of variance. Site was included as a random effect in each piece of the SEM.

The conceptual model illustrates hypothesized associations between variables over time. The

interpretation of modeled associations was based on our understanding of the population processes and intraspecific and functional group interactions that affect sagebrush populations over time (Fig. 1). The sagebrush portion of the conceptual model evaluated year-to-year changes in sagebrush seedling density, juvenile and adult density, and cover states. Path 1 was the association of seedling density at time (t) with seedling density at time ($t + 1$; path 1) and was influenced by processes such as seedling survival and recruitment to juvenile and adult

size between time steps. The association of juvenile and adult density with itself between time steps (path 2) was influenced by processes such as juvenile and adult survival between time steps. The association of sagebrush seedling density at time (t) with juvenile and adult density at time ($t + 1$; path 3) was influenced by processes such as seedling establishment and recruitment to the juvenile and adult size. The association of sagebrush cover at time (t) with seedling density at time ($t + 1$; path 4) was influenced by processes such as the integrated effects of seed

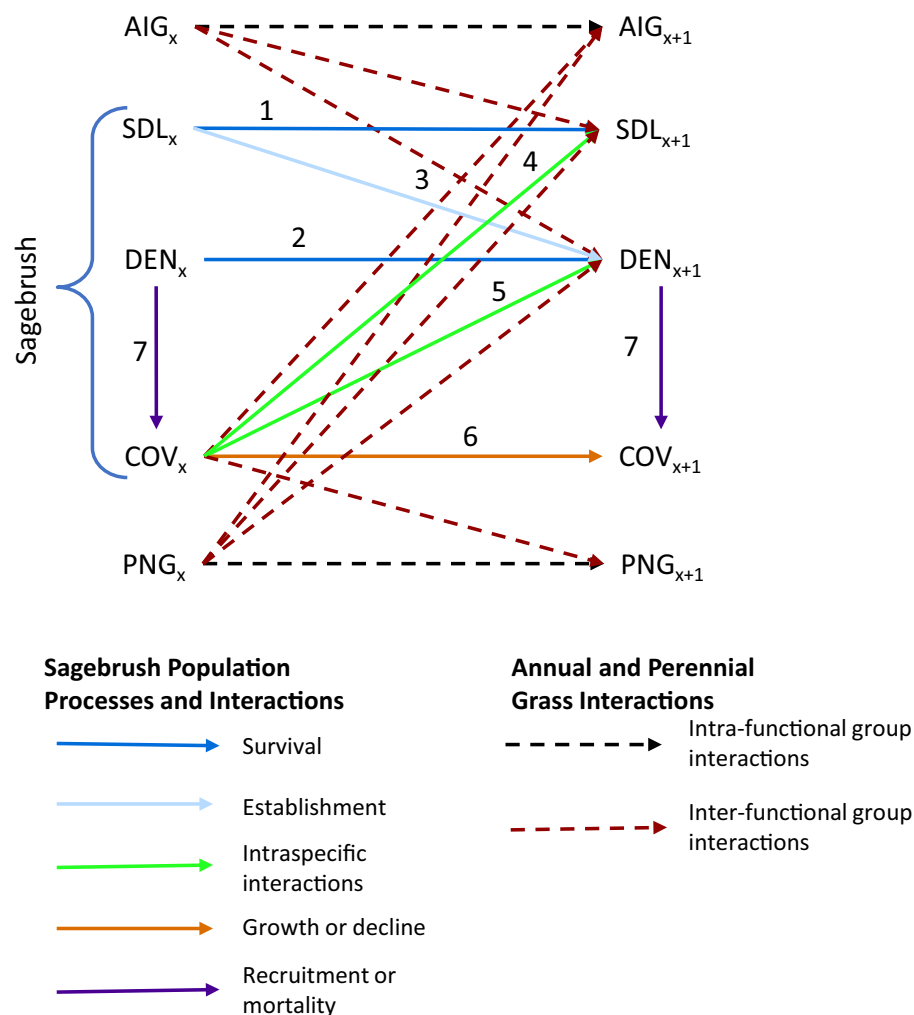


Fig. 1. Conceptual model of sagebrush population processes and interactions, annual and perennial grass interactions with sagebrush, and annual and perennial grass interactions with each other. Abbreviations are AGR, annual invasive grass; SDL, sagebrush seedling density; DEN, sagebrush juvenile and adult density; COV, sagebrush cover; PNG, perennial grass cover.

production on seedling recruitment and intraspecific competition or facilitation with adult sagebrush on seedlings. The association of sagebrush cover at time (t) with juvenile and adult density at time ($t + 1$; path 5) was influenced by processes such as the integrated effects of seed production and intraspecific competition or facilitation between juvenile and adult sagebrush. Sagebrush cover variation was partitioned between variation associated with the last time period's cover (path 6) and variation associated with the current year's density (path 7). The amount of variation that is associated with the last time period's cover was influenced by processes such as growth or decline of existing sagebrush. The amount of variation that is associated with the current year's juvenile and adult density can be indirectly related to recruitment and mortality. Finally, the association of both annual grass and perennial grass cover in time (t) with sagebrush seedling density and juvenile and adult density in time ($t + 1$) was influenced by processes such as inter-functional group competition and facilitation.

We modeled the dominant functional groups, annual and perennial grasses, based on cover. The associations of the prior time step with the current time step were influenced by processes such as intra-functional group competition. The effects of sagebrush cover and perennial grass cover on annual grass cover were influenced by processes such as inter-functional group competition. Similarly, the association of perennial grass between time steps was influenced by processes such as intra-functional group competition and population dynamics, while the association of perennial grass with sagebrush cover between time steps was influenced by processes such as inter-functional group competition.

For sites with woodland expansion, tree cover was included as a variable during the first time step only (pretreatment to first post-treatment year) because treatments (prescribed fire or mechanical) effectively removed most trees and any effect of trees thereafter was indirect. In untreated controls, tree cover was included only in the first time step to keep the models comparable. The association of tree cover with the other variables was intended to account for known effects of tree cover on post-treatment interactions.

RESULTS

A high degree of variability existed among subplots within sites as indicated by subplot trajectories over time (Figs. 2–8) and among sites as indicated by box plots of the different treatment combinations (Appendix S1: Figs. S1, S2). Despite this variability, ANOVA results were highly significant for treatment, time since treatment, and the treatment-by-time interaction not only for sagebrush juvenile and adult density and cover but also for annual grass and perennial grass cover (Appendix S1: Table S1).

Woodland expansion sites

Treatment effects.—In control plots, both sagebrush juvenile and adult density and cover were less in year 10 than prior to treatment or in year 1 (Fig. 2b, c; Appendix S1: Fig. S1a, b). Annual grass cover was lower than pretreatment levels in year 1 but increased over time and in year 10 was greater than pretreatment or year 1 levels (Fig. 2a; Appendix S1: Fig. S1c). Perennial grass cover was also lower than pretreatment levels in year 1 but had returned to pretreatment levels in year 10 (Fig. 2d; Appendix S1: Fig. S1d).

The reduction in tree cover in the burn and mechanical treatments averaged 86% (range 63–100%) and 99% (range 96–100%), respectively, across the 11 sites, indicating that treatments were effective in accomplishing tree removal objectives (Miller et al. 2014). In year 10, mean tree cover remained low in both treatments.

In prescribed fire plots, sagebrush juvenile and adult density and cover were significantly reduced the first year after fire (Fig. 3b, c; Appendix S1: Fig. S1a, b). Both median values (Fig. 3b, c) and ANOVA results indicated that juvenile and adult densities increased relative to year 1 but were still less than control and pretreatment levels ten years after burning (Appendix S1: Fig. S1a). Annual grass cover decreased the first year after burning but increased progressively over time (Fig. 3a) and was higher than in any other treatment combination in year 10 (Appendix S1: Fig. S1c). Perennial grass cover decreased the first year after prescribed fire, but by year 10 was greater than either control and pretreatment plots (Fig. 3d; Appendix S1: Fig. S1d).

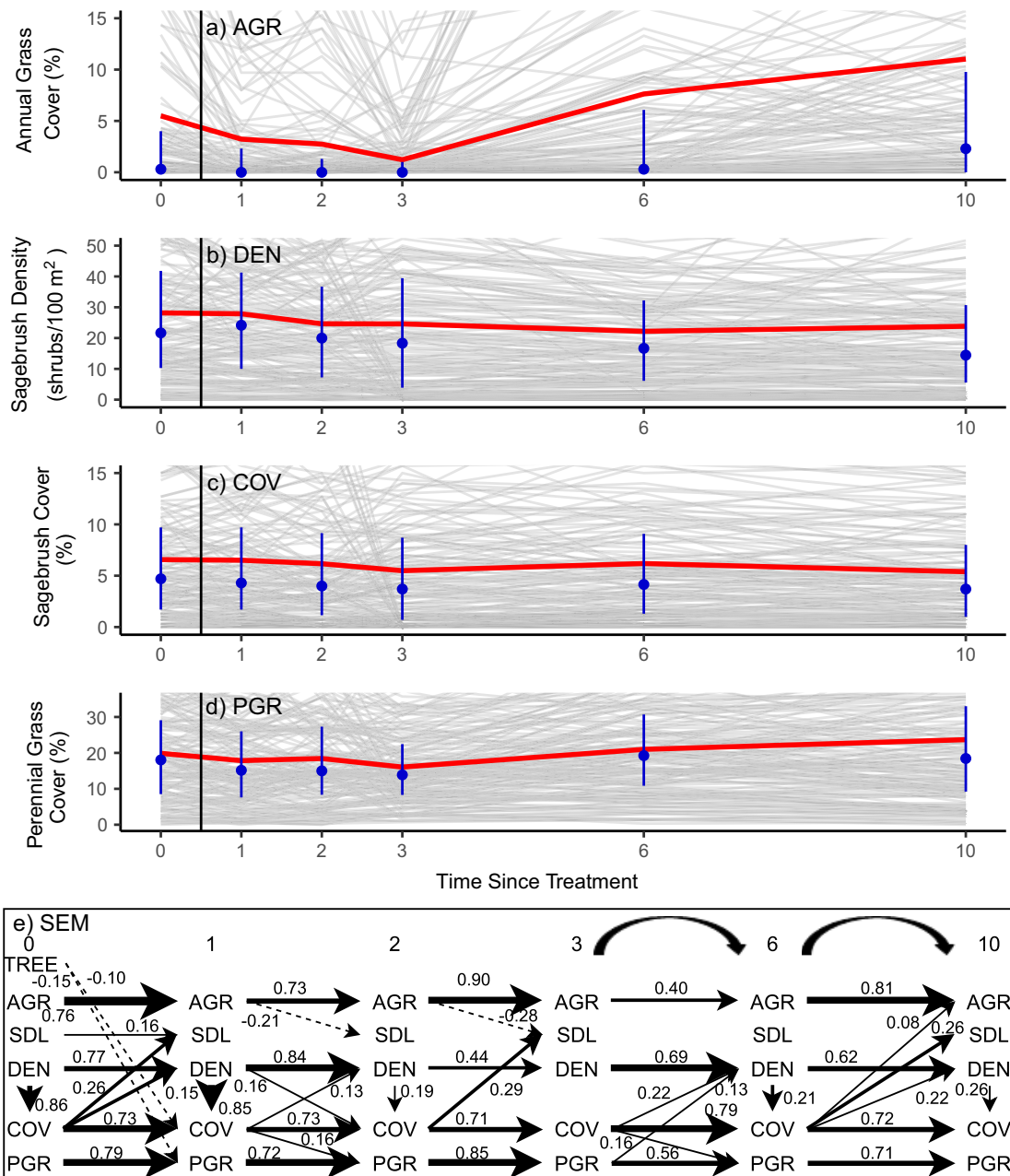


Fig. 2. Control plots in the woodland expansion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) and tree cover pretreatment (TREE) were included in the SEM.

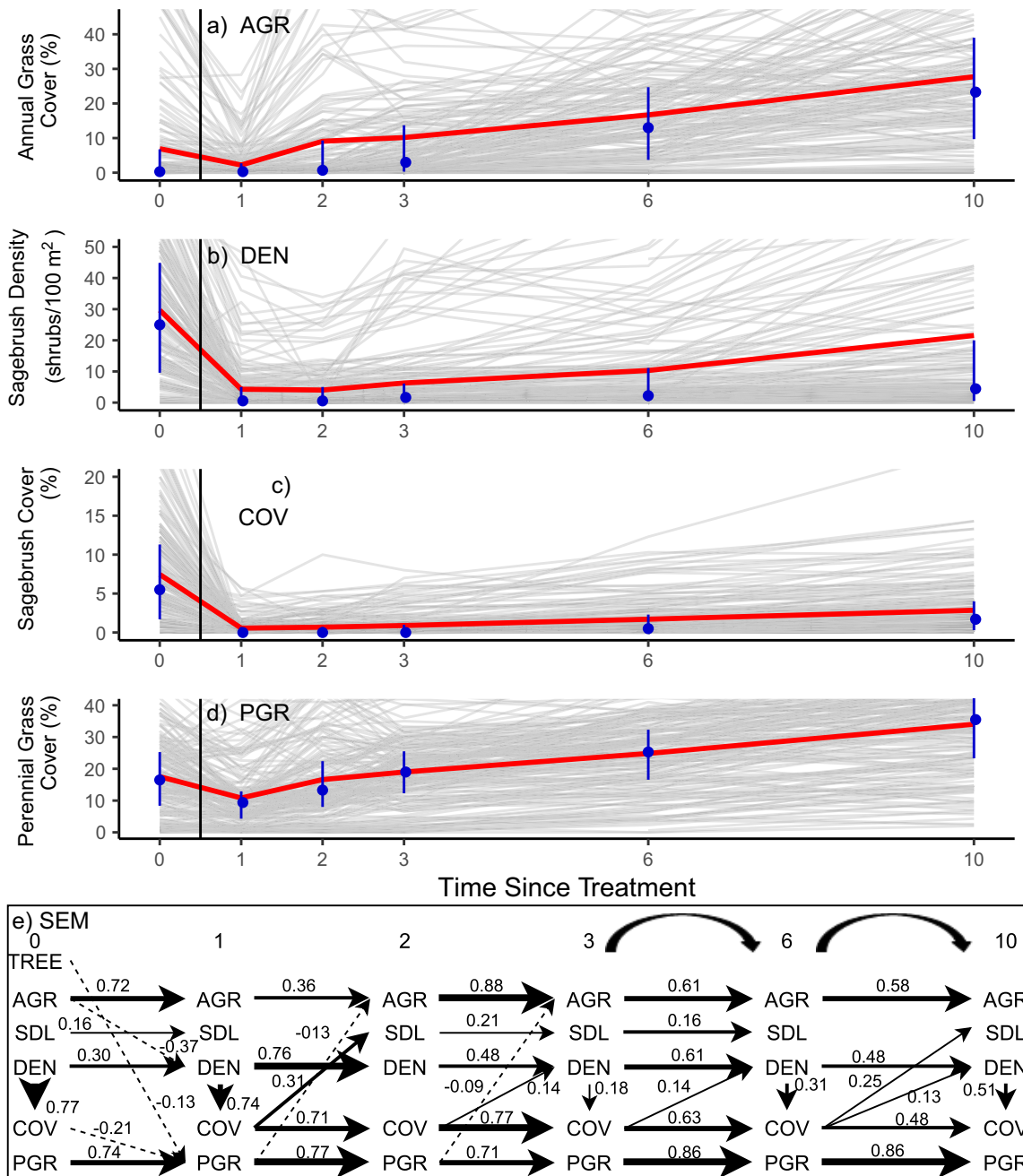


Fig. 3. Fire treatment plots in the woodland expansion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) and tree cover pretreatment (TREE) were included in the SEM.

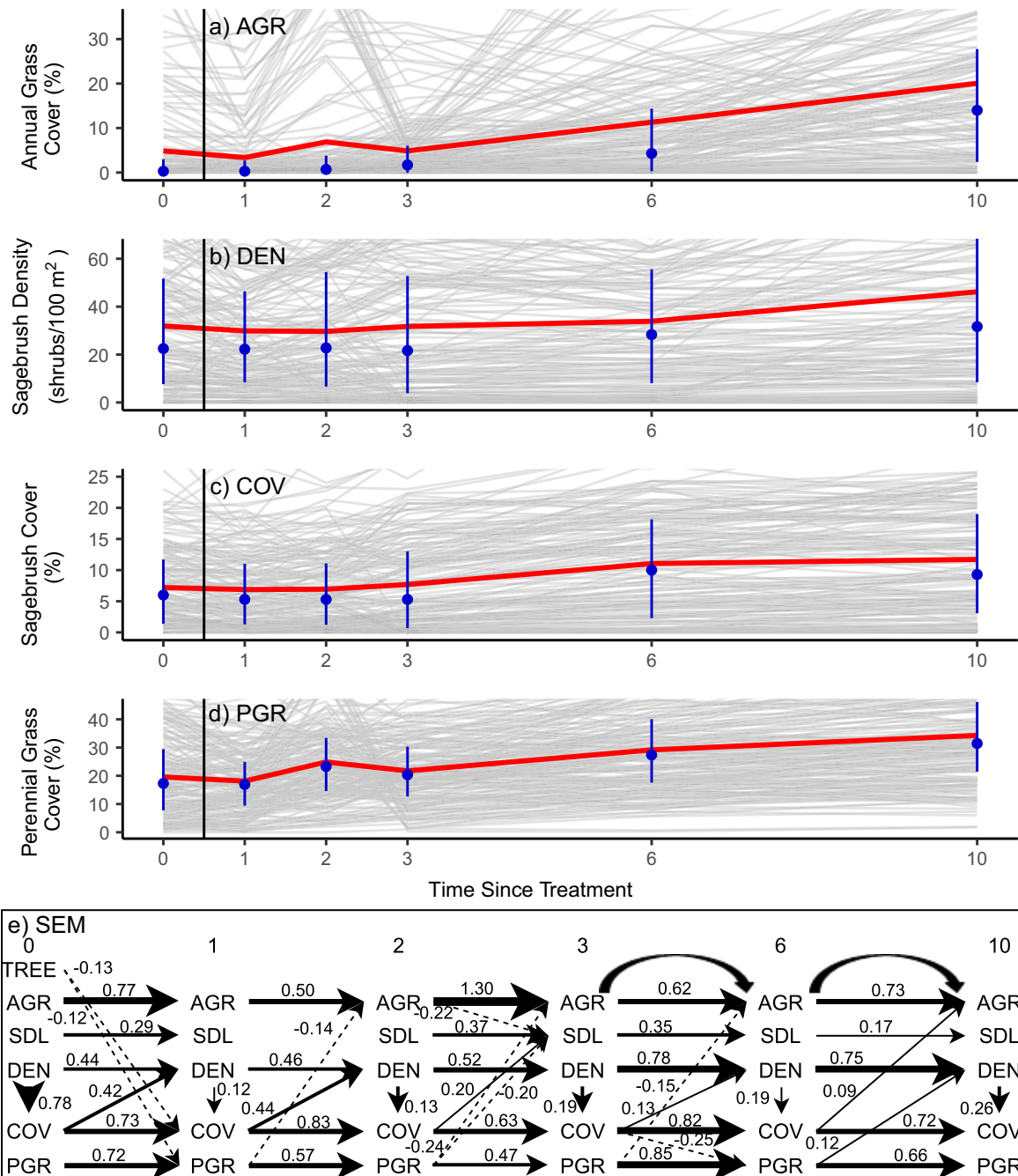


Fig. 4. Mechanical treatment plots in the woodland expansion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) and tree cover pretreatment (TREE) were included in the SEM.

In mechanical plots, little change occurred in sagebrush juvenile and adult density and cover in the first years after treatment, but in year 10 both density and cover were higher in the mechanical treatment than any other treatment combination (Fig. 4b, c; Appendix S1: Fig. S1a, b). While annual grass cover showed little change initially, by year 10 it had increased significantly and was only slightly less than in prescribed fire plots (Fig. 4a; Appendix S1: Fig. S1c). Similarly, perennial grass cover showed little initial change, but increased over time and by year 10 was as great as in prescribed fire plots (Fig. 4d; Appendix S1: Fig. S1d).

Associations affecting sagebrush over time after treatment.—Structural equation model results for control and mechanical plots indicate slight negative effects of initial tree cover on sagebrush cover in the following year (Figs. 2e, 4e). In addition, in control, fire, and mechanical plots initial tree cover had negative effects on perennial grass in the initial time step (Figs. 2e, 3e, 4e).

In control plots, sagebrush cover was positively related to sagebrush seedling or juvenile and adult density at all time steps (Fig. 2e). As expected, sagebrush juvenile and adult density was positively related to sagebrush cover in most time steps, but the strength of the association varied over time. Sagebrush cover had a slight positive association with perennial grass in years 1–2 and 3–6 and a positive association with annual grass cover in years 6–10. Annual grass cover was negatively related to sagebrush seedling density in years 1–2 and 2–3.

In prescribed fire plots, the positive association of sagebrush cover with itself among years was lost after burning as a result of fire-caused mortality, and in year 1, sagebrush juvenile and adult density was not associated with prefire cover (Fig. 3e). In addition, sagebrush cover had a negative association with perennial grass cover the first year after burning. The positive association of sagebrush cover with itself was regained in years 1–2, and sagebrush cover was positively related to sagebrush seedling or juvenile and adult density in all following time steps. Notably, perennial grass cover was negatively related to annual grass cover in years 1–2 and 2–3 on prescribed fire plots. However, annual grass cover had a negative effect on sagebrush juvenile and adult density in the initial time step.

In mechanical plots, sagebrush cover was positively associated with seedling density or juvenile and adult density in all but the final step (Fig. 4e). However, sagebrush cover was negatively related to perennial grass cover in years 3–6. Perennial grass cover was negatively related to sagebrush seedling density in years 2–3 and to annual grass cover in years 1–2, 2–3, and 3–6. Annual grass cover was negatively associated with seedling density in years 2–3.

Cheatgrass invasion sites

Treatment effects.—In control plots sagebrush juvenile and adult density varied over time, but neither juvenile and adult density nor cover differed from pretreatment or year 1 values in year 10 (Fig. 5b, c; Appendix S1: Fig. S2a, b). Similar to woodland plots, annual grass cover increased over time and year 10 values were higher than initial values (Fig. 5a; Appendix S1: Fig. S2c). In contrast, perennial grass cover did not increase over time (Fig. 5d; Appendix S1: Fig. S2d).

In prescribed fire plots, sagebrush juvenile and adult density and cover were greatly reduced by fire. Ten years after burning, cover had not increased and was lower than in any other treatment (Fig. 6b, c; Appendix S1: Fig. S2b). Juvenile and adult density was higher in year 10 than in year 1, but year 10 values were less than in any other treatment combination (Appendix S1: Fig. S2a). Annual grass cover increased over time, and year 10 means were greater than all treatment combinations except tebuthiuron application (Fig. 6a; Appendix S1: Fig. S2c). Perennial grass cover was reduced the first year after burning but by year 10 was higher than pretreatment or year 1 levels and exceeded levels in tebuthiuron plots (Fig. 6d; Appendix S1: Fig. S2d).

In mowed plots, treatment reduced sagebrush cover but not juvenile and adult density. In year 10, juvenile and adult densities were similar to pretreatment (Fig. 7b, c; Appendix S1: Fig. S2a). Sagebrush cover was lower than pretreatment and similar to tebuthiuron plots. Annual grass cover varied over time (Fig. 7a) and although it was higher in year 10 than pretreatment, it was lower than in prescribed fire and tebuthiuron plots (Appendix S1: Fig. S2c). Perennial grass cover increased over time and after 10 yr was higher than in any other treatment, except prescribed fire (Fig. 7d; Appendix S1: Fig. S2d).

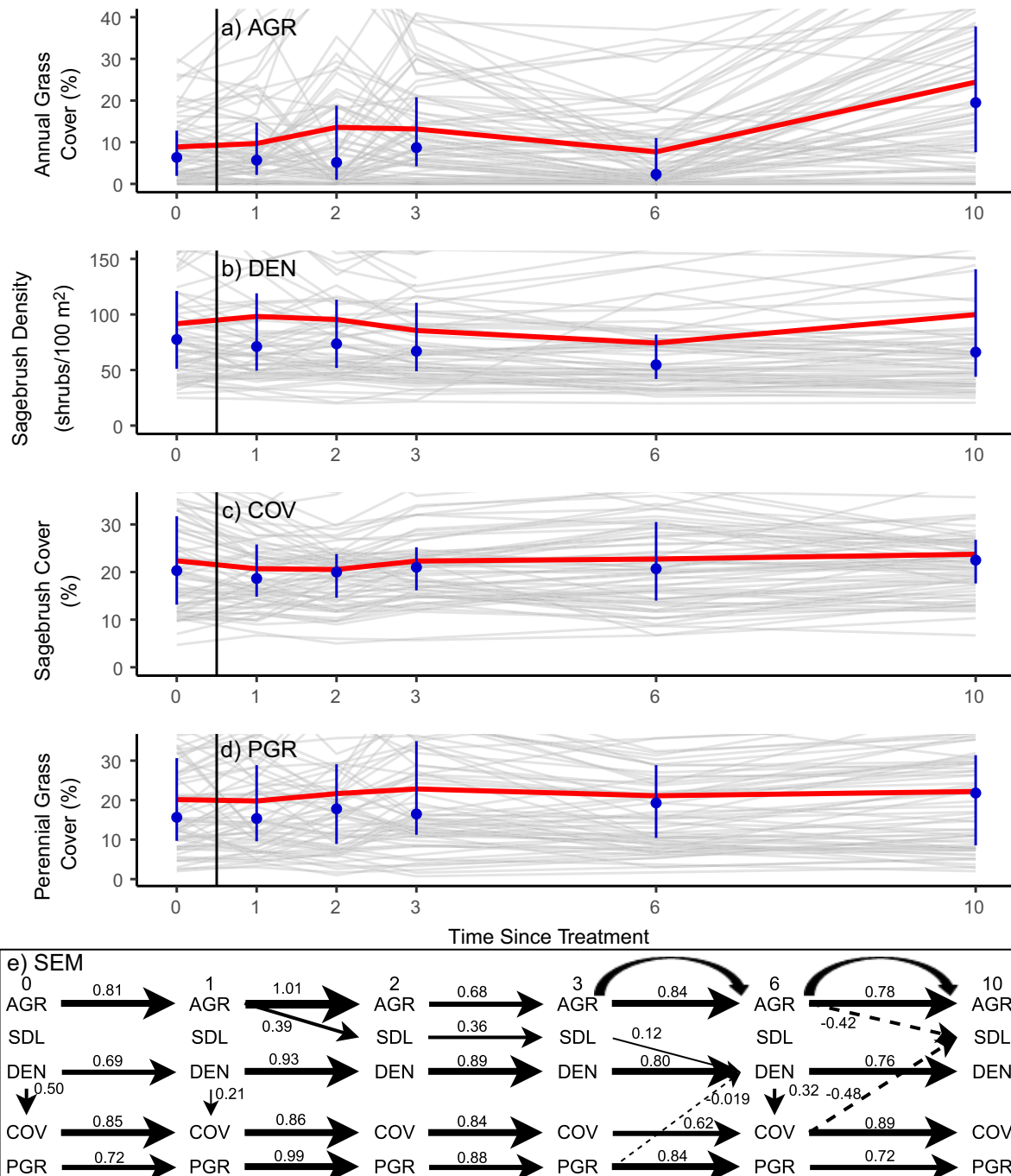


Fig. 5. Control plots in the cheatgrass invasion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) was included in the SEM.

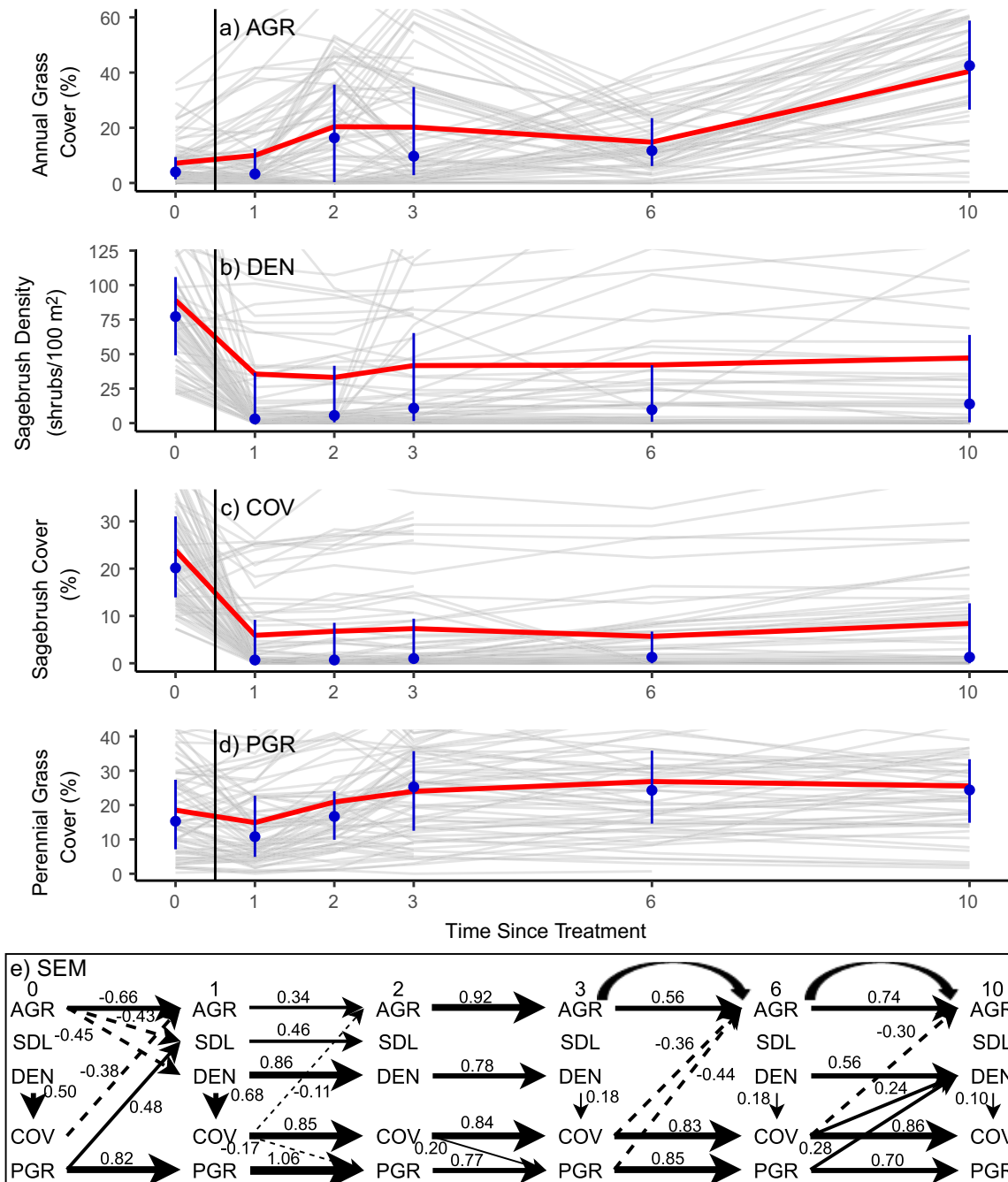


Fig. 6. Fire treatment plots in the cheatgrass invasion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) was included in the SEM.

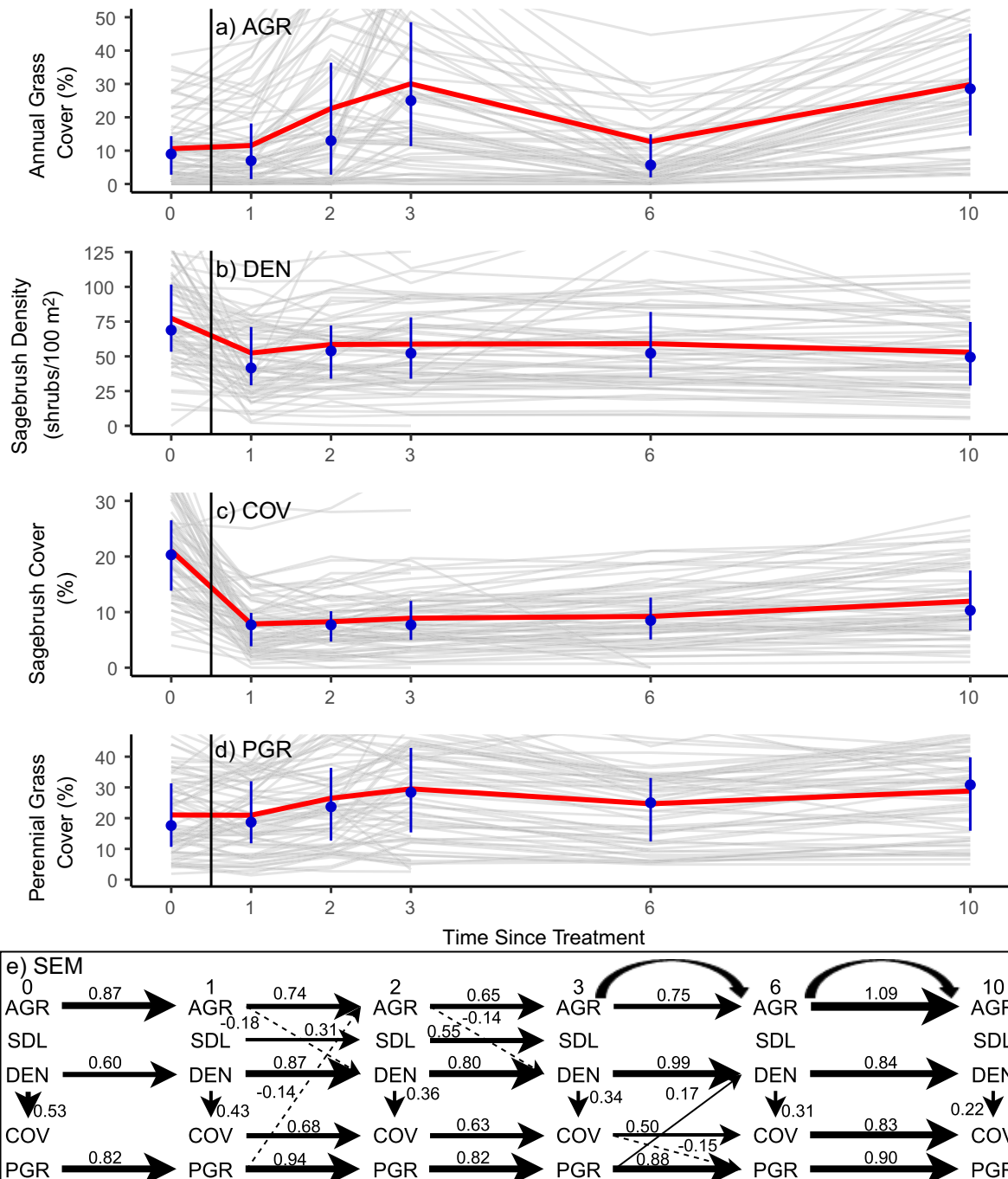


Fig. 7. Mowing treatment plots in the cheatgrass invasion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the medians, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) was included in the SEM.

In tebuthiuron plots, sagebrush juvenile and adult density and cover decreased more slowly in response to treatment, but by year 10 both density and cover were less than pretreatment and year 1 (Fig. 8b, c; Appendix S1: Fig. S2a, b). Annual grass cover also increased more slowly over time but by year 10 was as high as prescribed fire (Fig. 8a; Appendix S1: Fig. S2c). Perennial grass cover increased over time but was still less than any other treatment in year 10 (Fig. 8d; Appendix S1: Fig. S2d).

Associations affecting sagebrush over time after treatment.—In contrast to woodland control plots, in cheatgrass invasion control plots sagebrush cover had no positive associations with sagebrush seedling density or juvenile and adult density in any time step (Fig. 5e). Sagebrush seedling density was positively associated with juvenile and adult density in years 3–6, but sagebrush cover was negatively related to seedling density in years 6–10. Annual grass cover was positively associated with sagebrush seedling density in years 1–2 but negatively associated with seedling density in years 6–10. Perennial grass cover had a slight negative association with sagebrush juvenile and adult density in years 3–6.

In prescribed fire plots, the positive associations between pretreatment and year 1 sagebrush seedling density, juvenile and adult density, and cover were lost indicating significant disruption of sagebrush population dynamics (Fig. 6e). Sagebrush seedling density was associated with itself only in years 1–2. In addition, sagebrush cover was not associated with seedling density and was positively related to juvenile and adult density only in years 6–10. Sagebrush cover had negative associations with annual grass cover in all years except 2–3, and perennial grass cover was also negatively related to annual grass in years 3–6.

In mowed plots, the positive associations between pretreatment and year 1 sagebrush cover were lost in year 1 but were regained in subsequent years (Fig. 7e). No relationships existed between sagebrush cover and juvenile and adult density or seedling density in any of the time steps (Fig. 7e). Annual grass cover was negatively related to sagebrush juvenile and adult density in years 1–2 and 2–3. Perennial grass cover had a negative association with

annual grass in years 1–2, but positive association with sagebrush juvenile and adult density in years 3–6.

In tebuthiuron plots, sagebrush cover was positively associated with juvenile and adult density and negatively associated with perennial grass cover prior to treatment effects in year 0–1 (Fig. 8e). No other associations were detected for sagebrush cover until years 3–6 and 6–10 when it was positively associated with juvenile and adult density and negatively associated with annual grass cover. In years 6–10, sagebrush cover was also positively associated with perennial grass. Annual grass cover was negatively related to sagebrush juvenile and adult density in both the initial time step and in years 6–10.

DISCUSSION

Intra- and interspecific interactions differ among site types

The SEM results indicated clear differences in population processes and interactions within control plots in woodland expansion and cheatgrass invasion sites. Woodland expansion into sagebrush ecosystems can be equated to a long-term press disturbance of low magnitude and long duration (Jentsch and White 2019) in which trees negatively affect the dominant functional groups (Miller et al. 2000). We observed negative associations of trees with sagebrush cover or perennial grass cover in the first time step for all treatments in woodland expansion sites. Resource release and increased cover of sagebrush or herbaceous species following prescribed fire and mechanical treatment indicate that trees are strong competitors for soil water and nutrients (Rau et al. 2007, Bates and Davies 2017, Roundy et al. 2020). Perennial grasses also compete for resources and can further reduce sagebrush seedling establishment and population recruitment (Reichenberger and Pyke 1990, McAdoo et al. 2013, Chambers et al. 2017). Despite this, sagebrush cover in woodland expansion control plots was positively related to sagebrush seedling or juvenile and adult density at all time steps and interactions with perennial grass were positive. These positive interactions may result from decreases in species densities and cover over time and increases in intra- and interspecific interdependence due to the long-term press of

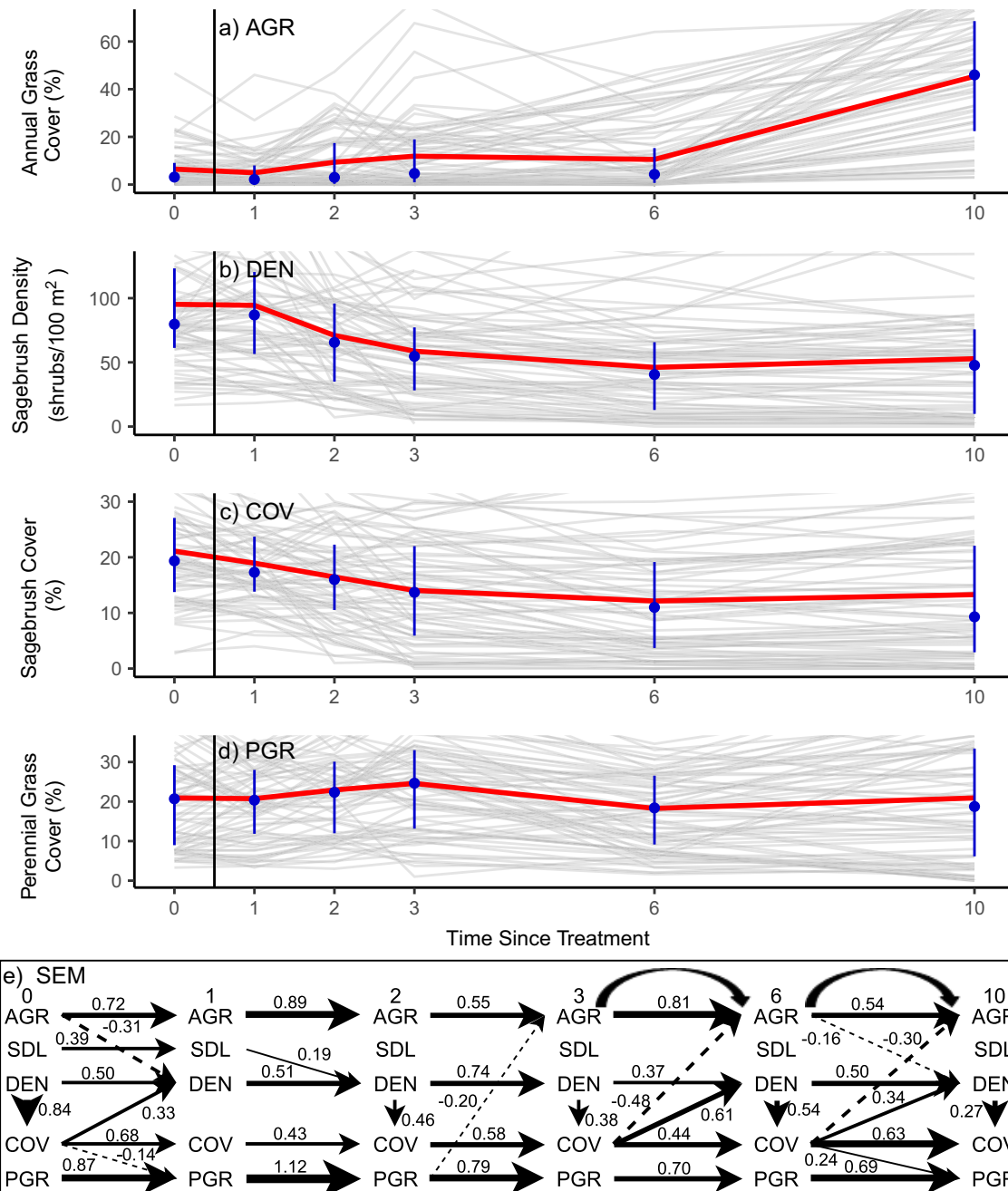


Fig. 8. Tebuthiuron treatment plots in the cheatgrass invasion sites over the experimental time frame: (a) annual invasive grass cover (AGR), (b) sagebrush juvenile and adult density (DEN), (c) sagebrush cover (COV), (d) perennial grass cover (PGR), and (e) the resulting structural equation model (SEM) fit to the data. In panels (a–d), gray lines are the measured values for each subplot in the experiment. Red lines are the mean values. Blue dots are the median, and blue lines represent the interquartile ranges. In panel (e), solid and dashed arrows indicate significant positive or negative relationships, respectively, and are labeled with their standardized path coefficients. In addition to the variables illustrated in panels (a–d), seedling density (SDL) was included in the SEM.

trees. Also, greater and less variable precipitation coupled with higher productivity on cooler and moister woodland sites (Roundy et al. 2018) may result in more consistent feedbacks among population processes and help to maintain sagebrush populations during initial phases of tree expansion.

Annual grasses are also strong competitors that reduce seedling establishment and population recruitment of sagebrush (McAdoo et al. 2013, Davidson et al. 2019) and perennial grass (Humphrey and Schupp 2004). In cheatgrass expansion controls, annual grass cover was related to sagebrush density in only two time steps and was not related to perennial grass cover. Annual grass did not appear to result in a long-term press on native perennial species perhaps due to high variability in biomass, density, and cover among years (Mack and Pyke 1983) and thus competitive interactions. Sagebrush cover had no positive relationships with seedling density or juvenile and adult density or perennial grass. In warm and dry sites, sagebrush population processes are strongly influenced by growing season temperatures and soil moisture availability and low recruitment rates are common (Shriver et al. 2018, 2019). Our results indicate less consistent feedbacks among population processes in general on these sites.

Livestock grazing can alter population processes and intra- and interspecific interactions (Condon and Pyke 2018). Exclusion of livestock likely contributed to increases in perennial or annual grass in both woodland expansion and cheatgrass invasion control plots over time. The higher levels of annual and perennial grass likely influenced competitive interactions among interfunctional groups within the two site types and thus the SEM results.

Prescribed fire disrupts sagebrush and functional group interactions

Prescribed fire was analogous to a pulse disturbance of short duration and high magnitude (Jentsch and White 2019) and had lasting effects on sagebrush population processes and functional group interactions. The positive associations between pretreatment and year 1 sagebrush seedling density, juvenile and adult density, and cover were decoupled immediately after fire due to plant mortality in both site types. Although

most intraspecific associations were regained within 2–3 yr after treatment in woodland plots, these relationships were sporadic in cheatgrass invasion plots. Greater available soil moisture, such as occurs on higher elevation woodland expansion sites (Roundy et al. 2018), typically results in higher sagebrush survival probabilities, growth rates, and recruitment than on relatively dry sites (Germino et al. 2018, Shriver et al. 2019). Sagebrush juvenile and adult densities were highly variable within both site types illustrating the importance of site conditions (Chambers et al. 2017) and yearly differences in temperature and soil water for recruitment (Shriver et al. 2018).

Low sagebrush cover despite increases in juvenile and adult densities on many sites indicated that most individuals were small-sized. In a regional analysis of sagebrush demography, annual survival probabilities of smaller individuals (5–15 cm in height) were about 10%, while those of the largest size class (>75 cm) approached 100% (Shriver et al. 2019). Also, larger plants were predicted to produce far more seed and more recruits (Shriver et al. 2019). Our prescribed fires were patchy, and residual sagebrush plants likely resulted in persistent sagebrush seed sources.

Prescribed fire resulted in major changes in intra-functional group interactions over time. In expansion of woodland sites, pretreatment sagebrush cover was negatively associated with perennial grass, which was negatively associated with annual grass in subsequent time steps. Thus, high levels of prefire sagebrush cover were indirectly associated with higher post-fire annual grass cover. Resource release due to tree and sagebrush mortality on burned plots can last 3 or more years for available soil nitrogen and phosphorus depending on microsite (Stubbs and Pyke 2005, Rau et al. 2007, 2014, Bates and Davies 2017) and over a decade for available soil water depending on season and year (Cline et al. 2018, Roundy et al. 2020). This increase was likely the primary cause of increased annual and perennial grass cover and suppression of sagebrush intraspecific interactions through year 10. Higher annual and perennial grass cover in control plots relative to pretreatment in year 10 indicates that higher levels of precipitation during the year 10 measurement period (B. A. Roundy, *unpublished*

data) may also have played a role. However, year 10 cover of annual and perennial grasses in treated plots exceeded that in control plots in both woodland expansion and cheatgrass invasion sites.

Negative effects of perennial grass on sagebrush seedling establishment and recruitment across environmental gradients (Chambers et al. 2017) and on annual grass cover on relatively warm and dry sites (Davies 2008, Bansal and Sheley 2016) are common following fuel treatments (Chambers et al. 2014b, Urza et al. 2019). In cheatgrass invasion sites, annual grass exhibited much larger increases than perennial grass, and negative associations between perennial and annual grasses occurred only through years 3–6. Annual grass also increased over time in woodland expansion plots, but negative effects of perennial grass on annual grass were lost in the final time steps. This suggests that a threshold of annual grass invasion exists beyond which perennial grass no longer suppresses annual grass.

Mechanically removing trees increases sagebrush recovery but alters functional group interactions

The cut-and-leave treatment in woodland expansion sites resulted in a pulse disturbance of short duration and low magnitude with more rapid and greater recovery than other treatments (Jentsch and White 2019). Sagebrush cover and density interactions following treatment were similar to controls in most years, and sagebrush cover and juvenile and adult density increased over time. Increased population recruitment may be attributed in part to higher soil water availability during late spring on mechanical plots (Roundy et al. 2020) and residual sagebrush, which provided a consistent seed source. Other studies of mechanical treatments report variable sagebrush recruitment (Bates and Davies 2017) undoubtedly due to high specificity for both site (Germino et al. 2018) and weather conditions (Shriver et al. 2018). As in burned plots, sagebrush size structure likely differed from mature communities and intraspecific competition may result in thinning over time (Shriver et al. 2019).

Intra-functional group interactions differed over time. Annual and perennial grass exhibited a steep initial increase in years 1–2 after treatment. Both functional groups are strong

competitors with sagebrush seedlings (Rinella et al. 2015, Germino et al. 2018) and had negative associations with seedling or juvenile and adult density in years 2–3. Perennial grass had the previously observed negative relationship with annual grass (Chambers et al. 2014b) initially, but no effect in the final time step when annual grass increased significantly. Despite large increases in sagebrush cover and density indicating seedling recruitment, the increases in annual and perennial grass indicate that longer-term population recruitment may be limited by intra-functional group competitive interactions.

Reducing sagebrush alters intraspecific feedbacks and facilitates annual and perennial grass

Sagebrush mowing was analogous to a pulse disturbance of short duration and low-to-intermediate magnitude (Jentsch and White 2019). Mowing resulted not only in an immediate decrease in sagebrush cover (Pyke et al. 2014, Swanson et al. 2016) but also density due to plant mortality as observed elsewhere (Davies et al. 2011, Davies and Bates 2014). Resource release following treatment (Davies et al. 2011, Rau et al. 2014) resulted in a steep increase in annual and perennial grasses with the greatest number of both interspecific and intra-functional group interactions occurring in years 1–2 and 2–3. Once resources were repartitioned in this dryland system, inter-functional group interactions appeared to decrease.

In contrast to mowing, tebuthiuron treatment resulted in a multiyear press on sagebrush. Continuous decreases in sagebrush cover and juvenile and adult density occurred through year 6 due to low application rates of tebuthiuron (Olson and Whitson 2002, Pyke et al. 2014). Although available soil nitrogen was elevated for the first two years after tebuthiuron application (Rau et al. 2014), annual grass did not increase across treatment plots until years 6–10. Delayed sagebrush mortality coupled with the increase in annual grass resulted in strong negative associations between sagebrush and annual grass in the last two time steps, and these interactions may continue into the future.

Management implications

The type of fuel treatment and environmental conditions of the site had major effects on post-

treatment sagebrush density and cover. Prescribed fire was the most severe treatment resulting in highly variable but generally low sagebrush recruitment and cover in both site types 10 yr later. High variability in site conditions across the SageSTEP network coupled with yearly differences in soil water availability, reduced seed availability, and more extreme conditions for seedling establishment after fire help explain these results (Schlaepfer et al. 2014, Roundy et al. 2018, 2020). Sagebrush recruitment is typically greater at higher elevations in relatively cool and moist sites than at lower elevations in warmer and drier sites (Chambers et al. 2017, Shriver et al. 2019). Restricting prescribed fire to cooler and moister sites may increase the probability of sagebrush establishment (Germino et al. 2018, Shriver et al. 2019) and resistance to invasive annual grass (Chambers et al. 2014a, b). Burns that leave patches of intact sagebrush can provide seed sources and ameliorate site conditions. Monitoring sagebrush densities in the first one to two years after prescribed fire may help determine the need to seed. In areas lacking initial sagebrush establishment, seeding adapted ecotypes of sagebrush in the first two years after fire may support sagebrush recruitment prior to large increases in competitive grasses.

Cutting and leaving trees was the only treatment that did not remove or reduce sagebrush and that resulted in higher sagebrush density and cover than pretreatment. Relatively cooler and moister conditions in woodland sites along with increased soil water availability after tree removal (Roundy et al. 2018, 2020), persistent seed sources, and smaller increases in annual grass help explain these results. Restricting mechanical treatments to sites within the woodlands that have low-to-moderate tree cover and sufficient perennial herbaceous species for recovery can help maintain sagebrush habitat and increase perennial grasses and forbs (Miller et al. 2014, Bates and Davies 2017, Roundy et al. 2018). Because more tree seedlings may survive mechanical than prescribed fire treatments, cut-and-leave treatments may need to be retreated sooner than prescribed fire treatments (Davies et al. 2019).

Mowing and tebuthiuron application had the desired effect of reducing sagebrush fuel and 10 yr after treatment had similar sagebrush cover and density. On these relatively warm and dry

sites, juvenile and adult density and cover remained consistently low after the initial decline indicating a lack of recruitment. Competition with annual grass after both treatments and with perennial grass after mowing undoubtedly had negative effects on sagebrush recruitment. Shorter-term studies indicate that mowing results in more favorable effects on perennial grasses and smaller increases in annual grasses in cooler and moister mountain big sagebrush (Davies et al. 2011) than warmer and drier Wyoming big sagebrush communities (Davies and Bates 2014). In our Wyoming big sagebrush, cheatgrass invasion sites mowing resulted in higher perennial grass than other treatments and lower annual grass in all but controls. Similar to other longer-term studies of tebuthiuron treatments in Wyoming big sagebrush, annual grass cover increased several folds but perennial grass did not increase (Blumenthal et al. 2006). Although both treatments reduced woody fuels, fine fuel and fuel continuity were increased. In annual grass invasion sites in general, potential benefits of woody fuel reduction were largely negated by lack of sagebrush recruitment and progressive increases in annual grass. On many sites, these treatments likely resulted in a decrease in resilience to fire and resistance to invaders.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3450/full>