



National Headquarters

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December 9, 2020

William Dunkelberger
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Humboldt-Toiyabe National Forest
1200 Franklin Way
Sparks, Nevada 89431

Re: Scoping Comments, Humboldt-Toiyabe National Forest Forestwide Prescribed Fire Restoration Project

Dear Mr. Dunkelberger:

Thank you for considering the following scoping comments on the Humboldt-Toiyabe National Forest's proposed Prescribed Fire Restoration Project. Defenders of Wildlife (Defenders) is a national non-profit conservation organization with 1.8 million members and supporters in the U.S., and over 3,000 in Nevada, and is dedicated to protecting all wild animals and plants in their natural communities. To this end, Defenders uses science, public education and participation, media, legislative advocacy, litigation, and proactive on-the-ground solutions in order to impede the accelerating rate of extinction of species, associated loss of biological diversity, and habitat alteration and destruction.

Defenders generally agrees that prescribed fire is an important tool for restoring natural fire regimes to ecosystems. However, we strongly oppose approving this project with a programmatic categorical exclusion (CX) under the National Environmental Policy Act (NEPA).

The Forest Service is proposing to adopt a CX to "increase the pace and scale of prescribed burning"¹ on the Humboldt-Toiyabe National Forest (HTNF). The project would enable multiple prescribed burning projects each year up to 10,000 acres with an objective of treating up to 100,000 acres annually. Using a CX for a proposed action of this scale is inappropriate and likely not in accordance with the NEPA.

The Forest Service should prepare an Environmental Assessment or Environmental Impact Statement to analyze the effects of the proposed project

The CX may not be lawful as a programmatic effort to significantly increase the agency's management footprint. CXs are intended to be used for "small," "insignificant," and "routine" projects, *Sierra Club v. Bosworth*, 510 F.3d 1016, 1027 (9th Cir. 2007), not large landscape-level projects. Such projects likely

¹ Dunkelberger, W.A. 2020. Letter: Forest-wide Prescribed Fire Restoration Project. Humboldt-Toiyabe National Forest. November 9. Pg. 1.

have direct, indirect, and/or cumulative effects because they are not by definition “insignificant” or “routine.”

NEPA aims to improve the quality of the human environment by relying on sound science and public engagement to reduce and mitigate harmful environmental impacts. NEPA protects against unnecessary and avoidable harm that, if federal agencies were not required to take a “hard look” at when planning management actions, would accumulate and result in permanent impacts to wildlife, water quality, cultural resources, and other natural resources.

It’s hard to imagine that the proposed action would not have significant impacts to the HTNF’s wildlife, including 12 species federally protected under the Endangered Species Act and over 100 Regional Forester Sensitive Species, and other natural and cultural resources and values. For example, applying prescribed burning in sagebrush ecosystems has been shown to have significant detrimental impacts on the sagebrush vegetative community and associated species. Knick et al. 2005; Ellsworth and Kauffman 2010; Ellsworth and Kauffman 2017. While the HTNF’s scoping proposed action document indicates an understanding of these issues, the impacts of prescribed burning activities must be assessed in an EA or EIS.

To determine whether the proposed project’s impacts may be “significant,” the Forest Service should first prepare an Environmental Assessment (EA). 40 C.F.R. §§ 1501.4, 1508.9. If the EA reveals that “the agency’s action may have a significant effect upon the . . . environment, an EIS [Environmental Impact Statement] must be prepared.” *Nat’l Parks & Conservation Ass’n v. Babbitt*, 241 F.3d 722, 730 (9th Cir. 2001) (internal quotations omitted). If the agency determines that no significant impacts are possible, it must still adequately explain its decision by supplying a “convincing statement of reasons” why the action’s effects are insignificant. *Blue Mountains Biodiversity Project v. Blackwood*, 161 F.3d 1208, 1212 (9th Cir. 1998).

Using an EA to authorize this project would enable public engagement in compliance with NEPA and the spirit of democracy

The Forest Service must provide for public engagement on projects undertaken with an EA or EIS but not for those undertaken with a CX. Public engagement is often responsible for important improvements in project design and implementation. Sometimes these improvements are incorporated through additional alternatives, modification of the proposed action, or the addition of mitigation commitments, while other times they are adopted as a result of appeal or adjudication. The point is that without the benefit of the EA or EIS process, the shortcomings of the projects would not have been revealed or addressed.

The Forest Service must consult with the U.S. Fish and Wildlife Service to identify potential harms to species listed as threatened or endangered under the Endangered Species Act

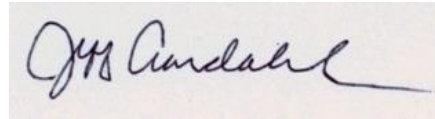
Under Section 7 of the Endangered Species Act and its implementing regulations each federal agency, in consultation with the Services must insure that any action authorized, funded, or carried out by the agency is not likely to (1) jeopardize the continued existence of any threatened or endangered species

or (2) result in the destruction or adverse modification of the critical habitat of such species. 16 U.S.C. § 1536(a). Agency “action” is broadly defined to include actions that may directly or indirectly cause modifications to the land, water, or air, and actions that are intended to conserve listed species or their habitat, specifically including, as here, “the promulgation of regulations.” 50 C.F.R. § 402.02(b). Under the Services’ joint regulations implementing the ESA, an action agency such as Forest Service must initiate consultation under Section 7 whenever its discretionary action “may affect” a listed species or critical habitat. 50 C.F.R. § 402.14(a); see also *Ass’n of Home Builders v. Defenders of Wildlife*, 551 U.S. 644 (2007).

Sincerely,



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See Attachments:

- Ellsworth, L. M., & Kauffman, J. B. (2017). Plant community response to prescribed fire varies by pre-fire condition and season of burn in mountain big sagebrush ecosystems. *Journal of Arid Environments*, 144, 74-80.
- Ellsworth, L. M., & Kauffman, J. B. (2010). Native bunchgrass response to prescribed fire in ungrazed mountain big sagebrush ecosystems. *Fire Ecology*, 6(3), 86-96
- Knick, S. T., Holmes, A. L., & Miller, R. F. (2005). The role of fire in structuring sagebrush habitats and bird communities. *Studies in Avian Biology*, 30, 63.

RESEARCH ARTICLE

NATIVE BUNCHGRASS RESPONSE TO PRESCRIBED FIRE IN UNGRAZED MOUNTAIN BIG SAGEBRUSH ECOSYSTEMS

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ABSTRACT

Fire was historically a dominant ecological process throughout mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) ecosystems of western North America, and the native biota have developed many adaptations to persist in a regime typified by frequent fires. Following spring and fall prescribed fires conducted in sites of different ecological conditions at the Lava Beds National Monument, California, USA, we examined the reproductive, density, and cover responses of four native bunchgrasses: bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). High rates of survival and fire-enhanced flowering were measured following fires. Thurber's needlegrass density decreased following spring burns in sites dominated by cheatgrass (*Bromus tectorum* L.) (from 3.3 plants m⁻² to 0.8 plants m⁻²; $P < 0.05$). Density of bluebunch wheatgrass decreased following spring fires (from 3.7 plants m⁻² to 1.9 plants m⁻²; $P = 0.02$) and cover was reduced in both spring and fall burn treatments ($P = 0.04$) in native dominated sites. Fire-enhanced flowering (increases in reproductive efforts) occurred in bluebunch wheatgrass in cheatgrass dominated sites (244% increase in reproductive culms following fire), native dominated sites (350% increase), and woody encroachment sites (500% increase) sites following fall fires. These results show that these native bunchgrasses positively respond to prescribed fire through increases in reproductive efforts and high rates of survival following fires. This suggests that fire can be an important tool for the restoration and conservation of these fire adapted bunchgrasses.

Keywords: *Artemisia tridentata*, *Bromus tectorum*, bunchgrass, cheatgrass, fire return interval, mountain big sagebrush, prescribed fire, *Pseudoroegneria spicata*, rangeland restoration

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INTRODUCTION

Dramatic changes in vegetation structure and composition have occurred in the Great Basin of North America due to human activities including fire suppression, livestock grazing, increased ignitions by Native Americans, and the introduction of non-native plant and animal species. Prior to Euro-American settlement, stand replacing fires were frequent, occurring at intervals of less than 30 years in mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) ecosystems (Young and Evans 1981, Miller and Rose 1999, Miller *et al.* 2000). The Great Basin has experienced two general shifts in structure related to changes in fire regimes. Low-elevation areas subject to frequent human disturbances became susceptible to increased fire frequency and invasion and dominance by exotic grasses (D'Antonio and Vitousek 1996, Brooks and Pyke 2001). During the 1900s, fire frequency decreased in wetter or higher elevation areas due to fire exclusion and livestock grazing (Miller and Tausch 2001), resulting in expansion of western juniper (*Juniperus occidentalis* Hook.) and a reduction of native bunchgrasses and forbs (Miller and Rose 1999). Prior to Euro-American settlement, expansion of western juniper was believed to have been limited by fire, drought, and competition with grasses (Kilgore 1981). The introduction of domestic grazing animals in these areas decreased the amount of fine fuels necessary for fire spread (Kauffman and Sapsis 1989), and western juniper increased in range under the longer fire-return interval (Miller *et al.* 1994). The current rate and extent of western juniper encroachment onto sites formerly occupied by bunchgrasses and sagebrush has exceeded rates of expansion from the preceding 5000 years (Miller and Wigand 1994). Restoration and maintenance of native plant communities in mountain big sagebrush systems may require a reintroduction of fires that have shaped its development.

Plant communities in the Great Basin developed in response to a natural fire regime, and the biota evolved adaptations to persist within its natural range of fire return (Kauffman *et al.* 1997, Pendergrass *et al.* 1999, Wroblewski and Kauffman 2002). Individual survival as well as increased reproductive effort through fire-enhanced flowering may facilitate recovery of these plant communities following fire (Kauffman 1990). Increased flowering has been observed following fire in grasses of high deserts east of the Oregon Cascades (Sapsis 1990). Uresk *et al.* (1976) reported increased vegetative growth in bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) following wildfire, but no difference in number of reproductive culms.

In this study, we examined the effects of prescribed fire on ungrazed mountain big sagebrush ecosystems in three different ecological conditions (cheatgrass [*Bromus tectorum* L.] dominated, native dominated, and juniper dominated) at Lava Beds National Monument, California, USA. We sought to answer the following research questions: 1) Is there a change in reproductive effort, cover, or density of native bunchgrass species following prescribed fire in ungrazed mountain big sagebrush plant communities? 2) Is there a differential effect of prescribed fire on native bunchgrass species due to the season of burn? 3) Is the response of these species to fire different in sites with a different current plant composition (native, cheatgrass, juniper)? We hypothesized that: 1) reproductive effort would increase in bunchgrass species in the year following prescribed fire, and that bunchgrass densities would not change significantly following fire, but cover would be decreased in the first post-fire year; 2) plants burned in the fall would have fewer reductions in cover and density than those burned in the spring due to lower intensity burns that occurred after the active growing season had passed; and 3) bunchgrasses in sites dominated by native plants with an intact fire return interval would demonstrate a greater

reproductive effort and no reduction in cover and density as compared to bunchgrasses in sites where the plant communities have been altered by fire suppression and invasion of exotic plants.

METHODS

Study Area

The study was conducted at Lava Beds National Monument, 77 km southeast of Klamath Falls, Oregon, USA (Figure 1). This area ranges in elevation from 1228 m along the shore of Tule Lake to 1725 m at its highest point (Erhard 1979). The climate is cool and semi-arid; the average annual precipitation is 39 cm (Miller *et al.* 2003), and the average temperature ranges from -1°C in January to

20°C in July (Erhard 1979). Most naturally ignited fires occur from July to September, when dry thunderstorms often coincide with high temperatures and low fuel moisture contents. Soils are of volcanic origin, and shallow with basaltic outcrops (Erhard 1979). Lava Beds National Monument was chosen for this study due to an existing plant community gradient from cheatgrass dominated in the lowest elevation site, native dominated at mid-elevation where access is difficult, and juniper dominated at the highest elevation near the monument headquarters, where fire has been suppressed. We chose three sites that are classified as mountain big sagebrush-bluebunch wheatgrass-Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) habitat type (Erhard 1979), but with variation in plant composition, land use history, soils, and microtopography (Figure 2). Historically, fire return intervals were likely about 50 yr (± 20 yr) (Miller *et al.* 2003), and were of moderate to high severity, limiting encroachment of western juniper.

At the lowest elevation site (Gillems Camp; elevation: 1234 m to 1244 m), the plant communities were dominated by a continuous cover of cheatgrass, with rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), Thurber's needlegrass, and squirreltail (*Elymus elymoides* [Raf.] Swezey) also common. Because of the close proximity to water, these areas were likely heavily grazed by domestic livestock prior to monument establishment. Soils are classified in the Bakeoven family (Luckow and Ahuja 2001), which are well-drained very cobbly fine sandy loams.

The Fleener Chimneys site (elevation: 1341 m to 1362 m) is presumed to have been grazed less intensively than the Gillems Camp site due to its distance from water and difficulty of terrain (i.e., lava flows that limit domestic ungulate movement from water to this site). Plant communities are dominated by native vegetation including mountain big sagebrush, native bunchgrasses (bluebunch wheatgrass,

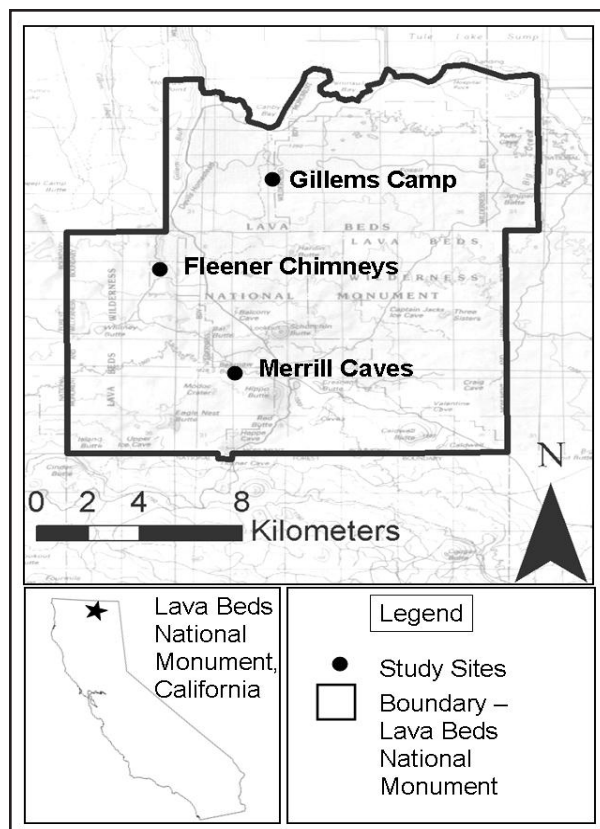


Figure 1. Study was conducted at the Lava Beds National Monument, California, USA, in mountain big sagebrush ecosystems.



Figure 2. Sampling locations represent areas of different ecological conditions within mountain big sagebrush communities at the Lava Beds National Monument, California, USA: a) Gillem's Camp, dominated by invasive cheatgrass with history of livestock grazing; b) Fleener Chimneys, intact site dominated by mountain big sagebrush and native bunchgrass; and c) Merrill Caves, dominated by western juniper with native understory.

Thurber's needlegrass, squirreltail, Idaho fescue [*Festuca idahoensis* Elmer]) and native forbs (spiny phlox [*Phlox hoodii* Richardson], threadleaf phacelia [*Phacelia linearis* {Pursh} Holz.], common yarrow [*Achillea millefolium* L.]). Soils are classified in the Searles association and are gravelly sandy loams (Luckow and Ahuja 2001). Few non-native plants occur on these sites, and there has been minimal encroachment by western juniper.

At the highest elevation site (Merrill Caves; elevation: 1451 m to 1472 m), fire suppression has resulted in the encroachment of western juniper, with a high cover of trees and shrubs (mountain big sagebrush, antelope bitterbrush [*Purshia tridentata* {Pursh} DC], curl-leaf mountain mahogany [*Cercocarpus ledifolius* Nutt.]). Soils are in the Searles association, with frequent rocky outcroppings. Frequent understory species include bluebunch wheatgrass, squirreltail, threadleaf phacelia, tapertip hawksbeard (*Crepis acuminata* Nutt.), and sulphur-flower buckwheat (*Eriogonum umbellatum* Torr.). There were few cheatgrass individuals, as well as a low incidence of other exotic plants at this site.

Lava flows throughout the National Monument act as natural fuel breaks as well as livestock barriers, and contribute to a diverse land use and fire history. Management personnel at Lava Beds National Monument have demonstrated a commitment to restoration of native plant communities, structure, and ecosystem function. Livestock grazing was removed from all areas of the National Monument by the mid 1970s, and plant communities have responded positively to the release from this disturbance (Erhard 1979, Martin *et al.* 1980, Olsen *et al.* 1980). Native herbivores, notably mule deer (*Odocoileus hemionus* Rafinesque) and pronghorn (*Antilocapra americana* [Ord]) continue to occupy all areas within the monument.

Experimental Design and Bunchgrass Sampling

The experiment was established as a randomized block design. Five experimental blocks were established at each of the three sites. Each block contained three 0.40 ha (1 ac) treatment plots in which either a spring burn, fall burn, or control treatment was applied. Spring burns at Fleener Chimneys and Gillems Camp were conducted on 25 June 2003. Due to weather constraints during 2003, spring burns at Merrill Caves were not conducted. Fall burns at all three sites took place on 12 November 2003. Temperature was higher and relative humidity was lower during the spring burns compared to fall burns, and we saw some differences in resultant fire behavior measures (flame lengths, rate of spread, etc.; Kauffman *et al.* 2006). Both spring and fall fires burned in a mosaic pattern, burning some areas and leaving small patches unburned.

Density of bunchgrass individuals was calculated from microplot measurements along five 20-meter permanent transects within each treatment plot. Each transect contained two 30 × 60 cm microplots ($n = 50$ for each treatment by site combination) at fixed locations along the transect, in which all bunchgrass individuals were identified to species. Measurements of bunchgrass density were made during the active growing season immediately preceding spring fires (June 2003, pre-fire) and one year following fires (July 2004, post-fire).

Percent cover of bunchgrasses was also quantified in 30 × 60 cm microplots along permanent sampling transects. Pre-fire cover was measured in late June 2003, and post-fire cover was measured in early July 2004, during the active growing season. Change following fire was analyzed at the microplot level and averaged for each transect.

We quantified reproductive effort of the most abundant native bunchgrasses (bluebunch wheatgrass, squirreltail, and Thurber's needlegrass) following fall fires. In each plot, the

number of flowering culms of at least 15 individuals of each species was counted as they were encountered along a 20 × 1 meter belt transect. Measurements were taken during peak flowering of plants (late in the growing season). Measurements were taken in late June 2003 (pre-fire) and early July 2004 (post fire).

Statistical Analysis

Fixed effects Analysis of Variance (ANOVA) models were used to determine whether there was an effect of fire treatment on bunchgrass cover, density, and reproductive effort after controlling for the site and the blocked design. The interaction of site and treatment was evaluated in the model to assess whether there was a different effect of the fire treatment depending on the site. Because the spring fire treatment was not applied at the Merrill Caves site, the site × treatment combination was removed from the analysis and two balanced two-way ANOVAs were used. One model included all three sites and two treatments (control, fall) as well as the site by treatment interaction. A second model included the Fleener and Gillems sites and all fire and control treatments (control, fall, spring), as well as the site by treatment interaction. A multiple comparison test (Tukey) was used if the *F*-test for treatment effect was significant at the $P < 0.05$ significance level. All statistical analyses were performed using SPSS 10.0 for Windows (SPSS, IBM Corporation, Somers, New York, USA).

RESULTS

Gillems Camp

At the low-elevation, cheatgrass dominated site, shortened fire return intervals, increased disturbance, and a continuous fuel load has resulted in a landscape dominated by non-native annual grass (33% to 41% cheatgrass cover

before fire) (Ellsworth 2006). The continuous fuel load provided for high fuel consumption (spring fires, 89% consumption from 6.89 Mg ha⁻¹ to 0.74 Mg ha⁻¹; fall, 81% combustion from 6.55 Mg ha⁻¹ to 1.24 Mg ha⁻¹) (Kauffman *et al.* 2006). Although the prescribed fires were of high intensity with high levels of fuel consumption (Table 1), density of squirreltail, Sandberg bluegrass, and bluebunch wheatgrass did not decline. Spring fires resulted in a decrease in density of Thurber's needlegrass from 3.3 to 0.8 plants per m² (site × treatment effect: $P < 0.05$), but there was no change following fall fires. There was no significant increase in flowering of squirreltail following fires. In contrast, there was a significant increase in flowering of Thurber's needlegrass following fall fires compared to unburned controls ($P < 0.01$; Figure 3). Fire-enhanced flowering was observed in bluebunch wheatgrass following fall burns (Figure 4) and this effect was most pronounced at the Gillems Camp site. Flowering culms increased from 9 to 31 per plant in fall fire plots, compared to an increase from 9 to 18 culms per plant in unburned controls (treatment effect: $P < 0.01$; site × treatment effect: $P < 0.01$). There was

no significant change in cover of native bunchgrass species following prescribed fires or in unburned controls (Figure 5).

Fleener Chimneys

At the native dominated site, cheatgrass cover was minimal (0.5% to 2% cover before fire), and there was an intact native bunchgrass and shrub component (16% average shrub cover) with interspersed bare ground prior to burns. Fires were patchy and resulted in a mosaic burn pattern (Table 1). Fall fires were much lower in intensity and severity than spring fires, resulting in less consumption of fuel and a patchier burn response. Fuel loads in spring fires were reduced from 9.98 Mg ha⁻¹ to 2.16 Mg ha⁻¹; fuels in fall burns were reduced from 8.98 Mg ha⁻¹ to 5.96 Mg ha⁻¹. Density of bluebunch wheatgrass was reduced following spring fires (from 3.7 plants per m² to 1.9 plants per m²; $P = 0.02$) and cover (Figure 5) was reduced in both spring (7% decrease) and fall (5% decrease) burn treatments ($P = 0.04$). Fire treatments had no significant effects on cover or density of Thurber's needlegrass, squirreltail, or Sandberg bluegrass in the first post-fire year.

Table 1. Weather, fire behavior, and fuel consumption was measured during spring (June 2003) and fall (November 2003) prescribed fires at Lava Beds National Monument, California, USA (taken from Kauffman *et al.* 2006).

	Gillems Camp		Fleener Chimneys		Merrill Caves
	Spring	Fall	Spring	Fall	Fall
Weather (min-max)					
Temperature (°C)	17-28	7-12	14-24	6-11	8-16
Relative humidity (%)	28-53	41-55	30-54	53-60	30-68
Wind speed (m s ⁻¹)	1-2	0-3	1-4	0-2	0-3
Fine fuel moisture (%)	6-10	8-9	5-10	10-11	7-12
Fire behavior (min-max)					
Rate of spread (m s ⁻¹)	0.04-0.07	0.01-0.46	0.01-0.05	0.04-0.41	0.00-0.03
Flame length (m)	0.3-3.0	0.1-3.7	0.2-1.5	0.2-1.8	0.3-4.6
Fuel consumption (mean ± 1 SE)					
Fine surface fuels (Mg ha ⁻¹)	2.00 ± 0.36	2.63 ± 0.29	0.35 ± 0.18	1.06 ± 1.21	1.36 ± 0.87
Total fuels (Mg ha ⁻¹)	6.15 ± 1.27	5.31 ± 1.51	5.50 ± 2.31	3.02 ± 1.48	12.11 ± 6.18

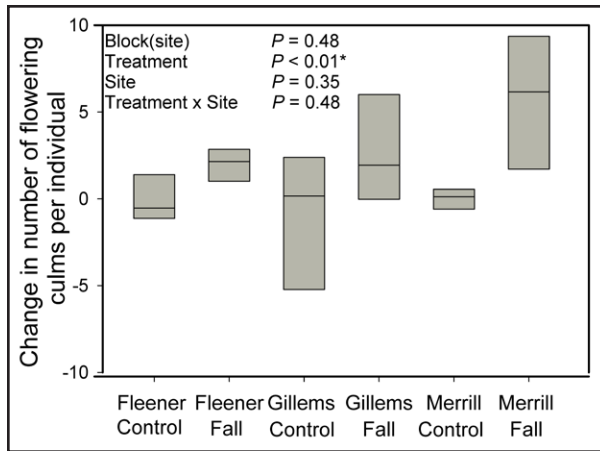


Figure 3. Reproductive effort (number of flowering culms per plant) of Thurber's needlegrass was measured following fall prescribed fires and in unburned control plots in mountain big sagebrush systems at the Lava Beds National Monument, California, USA. Upper bounds of boxes indicate the seventy-fifth percentile, and lower bounds indicate the twenty-fifth percentile. Line within each box indicates the median. *P*-values are results of fixed effects ANOVA model. Asterisks denote statistical significance at $\alpha = 0.05$ for model terms.

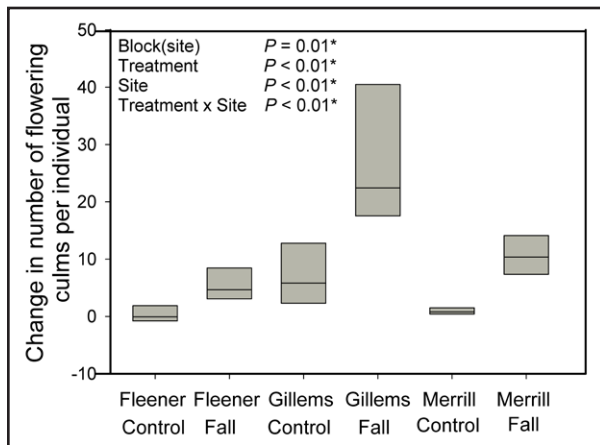


Figure 4. Reproductive effort (number of flowering culms per plant) of bluebunch wheatgrass was measured following fall prescribed fires and in unburned control plots in mountain big sagebrush systems at the Lava Beds National Monument, California, USA. Upper bounds of boxes indicate the seventy-fifth percentile, and lower bounds indicate the twenty-fifth percentile. Line within each box indicates the median. *P*-values are results of fixed effects ANOVA model. Asterisks denote statistical significance at $\alpha = 0.05$ for model terms.

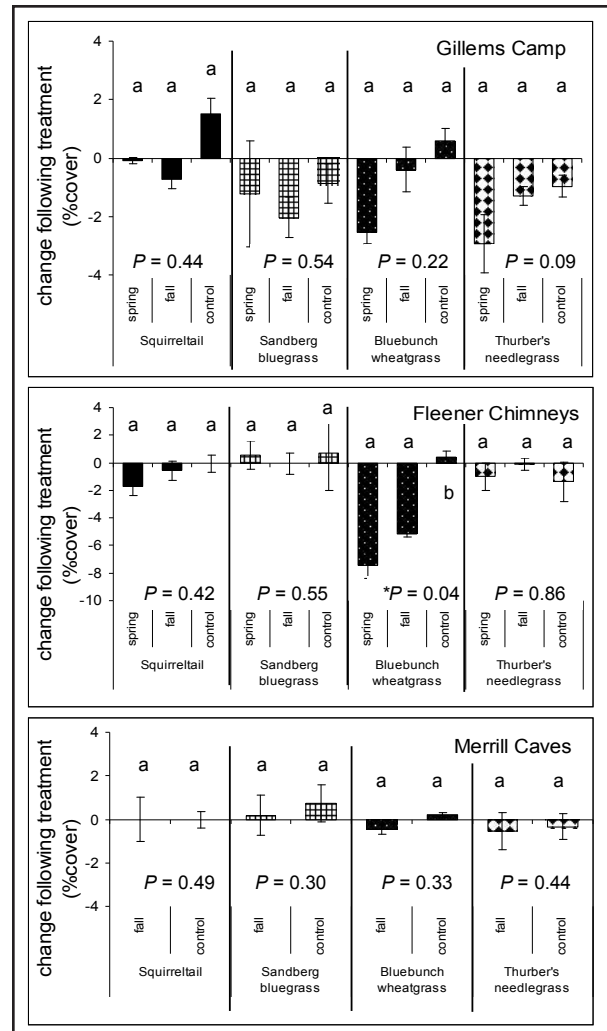


Figure 5. Change in cover of native bunchgrass species following spring (June 2003) and fall (November 2003) prescribed fire treatments and controls at Lava Beds National Monument, California, USA. Data were collected prior to spring fires (2003) and in July 2004. Bars are mean values for differences in cover and error bars are one standard error. *P*-values are results of fixed effects ANOVA model. Asterisks denote statistical significance at $\alpha = 0.05$.

Fire-enhanced flowering was apparent in bluebunch wheatgrass and Thurber's needlegrass plants the year following fall burns. Reproductive culms increased from 2 per individual before fire to 9 per individual in the first post-fire year (treatment effect: $P < 0.01$; Figure 4) in bluebunch wheatgrass and from 0.02 to 4 flowering culms per Thurber's needlegrass individual following fall burns (treatment effect: $P <$

0.01; Figure 3). There was no evidence of fire-enhanced flowering in squirreltail.

Merrill Caves

At the site characterized by western juniper dominance, high fire consumption rates were measured (a fuels reduction of 21.62 Mg ha⁻¹ to 9.51 Mg ha⁻¹ in fall burn plots). Understory fuels burned in a mosaic pattern, with some unburned islands remaining following the prescribed fires. Bunchgrass density and cover (Figure 5) did not significantly change following fall fires for any species studied. Fire-enhanced flowering was observed following fall fires in bluebunch wheatgrass and Thurber's needlegrass (Figures 3 and 4). Fall fires resulted in significant increases in flowering for bluebunch wheatgrass from 2 flowering culms per individual before fire and 12 flowering culms the year following fire (treatment effect: $P < 0.01$). Increases in reproductive effort following fall fire was also measured in Thurber's needlegrass (from 1 flowering culm to 7 flowering culms; $P < 0.01$). There was no evidence of fire-enhanced flowering in squirreltail at this site.

DISCUSSION

Our results suggest that native bunchgrass species in ungrazed mountain big sagebrush ecosystems at Lava Beds National Monument are well adapted to surviving fire and reproducing in the post-fire environment. Fire did not result in the significant decrease in density or cover of most bunchgrass species. Where significant reductions in density or cover were measured, there were also increases in post-fire flowering for the affected species, suggesting a capacity for resilience of these species following fire.

Fire in the sagebrush ecosystem functions structurally to decrease woody vegetation and shift the plant community towards an herbaceous, grass-dominated state (D'Antonio and Vitousek 1992). In the absence of shrub and

juniper cover, grasses and forbs are able to utilize available nutrient resources and colonize microsites previously occupied by woody species. In other sagebrush ecosystems, fire has been shown to stimulate vegetative growth of bunchgrass species (Sapsis 1990), as well as enhance sexual reproduction of bunchgrasses (Kauffman and Sapsis 1989) and broad-leaved herbs (Wroblewski and Kauffman 2002).

While the abundance of native plants at the Gillems Camp site had increased since measurements by Erhard (1979), there was still a dominance of invasive annuals such as cheatgrass and tumble mustard (*Sisymbrium altissimum* L.). Nevertheless, there was a low mortality of the native bunchgrasses and significant post-fire flowering. The removal of sheep and cattle grazing within the national monument in 1974 initiated a trend toward reestablishment of native plants in the monument, decreasing the dominance of cheatgrass that was evident in the late 1970s (Erhard 1979). Although the reintroduction of the natural fire regime is a logical approach to the restoration of sagebrush ecosystems that have been degraded by anthropogenic disturbance, it is difficult to predict the response of the native flora to fire where there is a strong presence of highly competitive annuals. This study suggests that the native grasses should be able to persist following fire in mountain big sagebrush communities at Lava Beds National Monument, even in the more degraded areas.

In sites where natives dominate, we hypothesized that native plants would respond positively to prescribed fire. Prior to fire, the Fleener Chimneys site was dominated by sagebrush, perennial bunchgrasses, and native forbs. The increase in reproductive effort and high survival of all studied bunchgrass species at this site suggests that they are well adapted to fire survival under these environmental conditions and that prescribed fire would have few detrimental effects. Although our results show some significant changes in cover and density for studied species, this may largely be a transient immediate post-fire effect, and warrants

further monitoring. Other studies have shown that in relatively intact native bunchgrass communities, fire resulted in an immediate reduction in density, followed by an increase in subsequent years, largely due to seedling success in a post-burn environment (Sapsis 1990). Sapsis (1990) also found that increased seedling establishment of bluebunch wheatgrass and Idaho fescue following prescribed burns was characteristic of native bunchgrass communities at John Day Fossil Beds National Monument, Oregon, USA.

Higher intensity spring fires resulted in greater decreases in cover and density than lower intensity fall burns. The weather during spring burns was warmer and drier, resulting in lower fine fuel moistures, but patchy vegetation structure prevented the fire from spreading quickly (Table 1; Kauffman *et al.* 2006). With the reintroduction of fire, we found that reproductive efforts in the native bunchgrasses increased more in the burned plots than in the unburned controls. This may be a response to greater resource availability (water, nutrients, light availability) in the post-fire environment. Cover and density of native bunchgrasses were fairly constant before and after burns, indicating that these native plants will persist if the natural disturbance interval is maintained.

Native plants in sagebrush ecosystems have been shown to respond positively to fire in previous studies in which plants had been released from domestic grazing pressure. In mountain big sagebrush communities of Lava Beds National Monument following removal of domestic cattle, Champlin (1983) observed significant increases in basal area of bluebunch wheatgrass and Sandberg bluegrass two years after burning. Conversely, he found decreases in basal area of Thurber's needlegrass immedi-

ately following fire. In an area where domestic grazing had been eliminated 15 years previously, Sapsis (1990) found that both fall and spring burning reduced the frequency of invasive annual grasses in basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*)-bluebunch wheatgrass communities at John Day Fossil Beds National Monument, and increased reproductive effort of perennial grasses following fall burns. Wright and Klemmedson (1965) found that early summer burns damaged squirreltail and Thurber's needlegrass, but that only Thurber's needlegrass was harmed by late summer burning. Sandberg bluegrass was not affected by either season of burn. In Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities in eastern Oregon, Davies and Bates (2008) found that the cover and density of Thurber's needlegrass was no different than in adjacent unburned areas two years following fire.

The results of this study and others (Sapsis 1990, Wroblesky and Kauffman 2002) suggest that in ungrazed systems of various conditions that are managed for restoration of native ecosystem diversity, native grass species can survive fire and even benefit from conditions present in post-fire environments. Lower intensity fall fires provided more positive post-fire effects than spring fires, suggesting that it is more advantageous to apply prescribed fires when the active growing season has passed and fires are easier for managers to control. While a need for longer term monitoring following prescribed fire is imperative, initial post-fire response suggests that fire-adapted species will respond positively to prescribed fire when applied within the natural range of variability.

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Plant community response to prescribed fire varies by pre-fire condition and season of burn in mountain big sagebrush ecosystems



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ABSTRACT

Artemisia tridentata ssp. *vaseyana* ecosystems evolved with periodic fire, but invasive grasses, conifer encroachment, fire suppression, and climate change have resulted in altered fire regimes and plant communities. Post-fire increases in invasive annual grasses such as *Bromus tectorum* and reductions in native vegetation are common across the sagebrush steppe. Where fire has been excluded though, there are increases in the native tree *Juniperus occidentalis*, which outcompetes the native understory. We applied prescribed fire in spring and fall at three sites (native-dominated, *B. tectorum*-dominated, and *J. occidentalis*-dominated). We documented 65% survival of *A. tridentata* following fall burns and 33% survival following spring burns in native-dominated plots, with evidence of post-fire sprouting in *Purshia tridentata* and *Tetradymia canescens*. At the *B. tectorum*-dominated site, shrub cover was reduced to <1%. Fires at the *J. occidentalis* site were discontinuous, resulting in ~50% mortality of trees and shrubs, with little resprouting. Native herbaceous vegetation persisted following fires, with no increases in *B. tectorum*. There were higher plant survival rates following fall fires and native-dominated sites than in spring burns or where exotics dominated. These results show that burn season and prefire condition are important considerations when evaluating management alternatives in *A. tridentata* ssp. *vaseyana* ecosystems.

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1. Introduction

Fire is a critical part of ecosystem function in the vegetation communities of the sagebrush steppe (Miller et al., 2013). Anthropogenic alterations including urbanization, domestic livestock grazing, fire suppression, and introduction of exotic plants, however, have modified plant community assemblages and altered disturbance regimes (Miller and Eddleman, 2000; West, 2000). Additionally, increasing pressure to protect late-successional habitats for sagebrush-obligate species (Dahlgren et al., 2015; Murphy et al., 2013) and a rapidly changing climate further complicate fire management and planning efforts (Westerling et al., 2006).

Prior to Euro-American settlement, fires occurred approximately every 15–25 years in *Artemisia tridentata* ssp. *vaseyana* communities, and were often stand-replacement events (Miller and Rose, 1995). Lightning-ignited fires were common in late summer. In addition, indigenous groups used fire to maintain

desirable native food plants, for increased crop productivity, and to manage game species (Griffin, 2002; Shinn, 1980). Following settlement of the western United States by Euro-Americans, fire was used excessively, and combined with the introduction of livestock, resulted in degraded rangelands (Young and Blank, 1995). In response to these practices, policies were established by the early 1900's discouraging planned ignitions and requiring the suppression of wildfire (Clark and Starkey, 1990).

Plant community composition is impacted by altering fire regimes, as species better adapted to the new regime – often invasive and early successional species – thrive in the altered environment. In the sagebrush steppe, two circumstances arising from altered fire regimes are prevalent. Low elevation areas with low resilience due to low precipitation and warm soil moisture regimes (Miller et al., 2013) which were overgrazed by domestic livestock or otherwise degraded became susceptible to invasion (Chambers et al., 2007, 2014) by *Bromus tectorum* and other invasive grasses (Boyte and Wylie, 2016). These grasses have increased the potential for fires by providing a continuous, dry fuel source and lengthening the fire season (Paysen et al., 2000). Increased disturbances increase susceptibility to exotic invasion, and perpetuate a cycle of positive

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feedbacks between increased invasion and frequent fire (D'Antonio and Vitousek, 1992).

In contrast, fire return intervals in higher elevations of the Great Basin have been lengthened by fire suppression and removal of fine fuels by domestic livestock grazing (Burkhardt and Tisdale, 1976; Miller and Tausch, 2000). Prior to Euro-American settlement, expansion of *Juniperus occidentalis* (western juniper) is believed to have been limited by frequent fires, drought, and competition with grasses (Kilgore, 1981). Fire exclusion by suppression and reduction of fine fuels due to livestock grazing have contributed to expansion because young junipers (<3 m) do not often survive fire (Bunting, 1984). A fire return interval of ~50 years, longer than that often reported for this mesic end of the sagebrush steppe, is frequent enough to limit juniper expansion (Burkhardt and Tisdale, 1976). The current rate of *J. occidentalis* encroachment into bunchgrass and sagebrush sites exceeds rates of expansion from the 5000 years preceding (Miller and Wigand, 1994). Restoration in this ecosystem may require incorporating fire's natural role to maintain native plant communities and return structure and function to the ecosystem (Davies et al., 2011).

Plant species in the Great Basin have developed strategies to persist within the natural fire regime (Ellsworth and Kauffman, 2010; Wroblewski and Kauffman, 2003). Re-introduction of fire into intact *A. tridentata* ssp. *vaseyana* systems may maintain or restore native composition and structure (Pyle and Crawford, 1996). However, where invasive grasses are a dominant ecosystem component and anthropogenic influences have resulted in the loss of native species, fire may perpetuate or increase invasive dominance (Chambers et al., 2007), at least in the short term (Ellsworth et al., 2016; Miller et al., 2013).

Season of burn may be an important determinant of plant response to fire. Most naturally ignited fires in the sagebrush steppe coincide with frequent dry lightning during summer and early fall, but most prescribed fires are set late in the fall, after fuel moisture increases and likelihood of fire escape is reduced (Miller et al., 2013). Further, it is expected that fires that occur in the fall, after the active growing season, result in less direct mortality than growing season fires because live, moist plant tissue is more subject to heat-induced mortality than dormant tissue (Wright and Klemmedson, 1965). Direct comparisons between seasonal impacts of fire on individual plant species and plant communities are difficult and conclusions often inconsistent due to the confounding impacts of fire intensity and severity, weather conditions before and during prescribed burns, and the logistical challenges of implementing prescribed burning during the active fire season (Kauffman and Martin, 1990; Pyle and Crawford, 1996; Wright and Klemmedson, 1965). Where direct comparisons between seasons of burn have been made (i.e., Ellsworth and Kauffman, 2010; Pyle and Crawford, 1996; Wright and Klemmedson, 1965), results are highly variable and focus on individual plant mortality rather than plant community response. In this study, we quantified the differences in plant community composition following spring and fall prescribed fire treatments in sites differing in fire and disturbance history, elevation, and pre-fire plant composition, but all mapped as the same *A. tridentata* ssp. *vaseyana* plant community type (Erhard, 1979). The response of landscapes to fire is dependent upon on the condition of the site, the existing plant composition, and the soil seedbank which will generate postfire vegetation (Davies et al., 2008; Ellsworth and Kauffman, 2013). Our objective was to quantify vegetation compositional shifts following spring and fall prescribed fire in *A. tridentata* ssp. *vaseyana* ecosystems in different ecological conditions: 1) native-dominated- little past fire suppression or anthropogenic degradation 2) *B. tectorum*-invaded- intensive historic use and increase in fire frequency and 3) juniper-dominated- light historic land use but with successful fire suppression. We

hypothesized: 1) at all sites, fire would reduce woody species resulting in a postfire dominance of herbaceous vegetation; 2) native forbs and perennial bunchgrasses would respond more favorably to prescribed fires in the pristine and juniper dominated sites than in the *B. tectorum*-invaded site; 3) fall fires will result in increased cover of perennial bunchgrasses and native forbs than spring fires; and 4) more shrub cover will be retained after fall fires than spring fires due to increased heterogeneity of burn response during cooler weather. To test these hypotheses, we applied three prescribed burn treatments (spring, fall, unburned control) in a randomized block design in each of the three sites of differing ecological condition (native, *B. tectorum*-invaded, and juniper-dominated).

2. Methods

2.1. Study site

The study sites were located within the Lava Beds National Monument, California, 77 km southeast of Klamath Falls, Oregon. This area ranges in elevation from 1228 m along the shore of Tule Lake in the northeast to 1725 m at the southwest corner (Erhard, 1979). The climate is cool and semi-arid, with an average annual precipitation of 39 cm (Miller et al., 2003) and a mean temperature range from -1° C in January to 20° C in July. Most natural fires occur from July to September, when dry thunderstorms often coincide with high temperatures and low fuel moisture contents. The geology of the monument is unique, with basaltic lava flows and cinder cones scattered across the landscape. The monument is located on the north face of Medicine Lake shield volcano, which has erupted periodically over the last 500,000 years, and most recently erupted approximately 1100 years BP. Soils are of volcanic origin, shallow with basaltic outcrops (Erhard, 1979).

Five experimental blocks were established at each of three sites (Gillems Camp, Fleener Chimneys, and Merrill Caves; Fig. 1) at the Lava Beds National Monument. Sites were mapped as the same *Artemisia tridentata* ssp. *vaseyana* community type (Erhard, 1979) but with different land use histories and current species composition. Fleener Chimneys (pristine site) was dominated by native perennial grasses and forbs, with predominately *A. tridentata* ssp. *vaseyana*, *Tetradymia canescens* and *Purshia tridentata* in the overstory. There was a significant lava flow between this site and water, which likely limited historic domestic grazing. Merrill Caves (juniper-dominated site) was characterized by an overstory of *J. occidentalis*, with mostly native forbs and bunchgrasses in the herbaceous layer, and a reduction in the shrub layer. This site was also far away from surface water but close to the Monument headquarters, necessitating fire suppression in the area for structure protection. Gillems Camp (*B. tectorum*-invaded site) was located near the historic shore of Tule lake, had a history of degradation by domestic livestock grazing, and was dominated by *B. tectorum* and native bunchgrasses with a sparse cover of woody vegetation, principally *Ericameria nauseosa* (grey rabbitbrush).

We employed a randomized block design at each site to conduct the experiments. Each block (5 per site) contained three plots (each a minimum size of 0.25 ha) in which a spring and a fall prescribed fire treatment as well as an unburned control were randomly assigned. For each combination of site and season of burn, there were five replicate burn plots for a total of 30 burn plots (plus 15 unburned controls). There was a 5-m burned buffer around all burned plots.

Spring burns at Fleener Chimneys and Gillems Camp were conducted in June 2003. Due to weather constraints during 2003, spring burns at Merrill Caves were not conducted until June, 2004. Fall burns at all sites were conducted in November 2003. Each fire

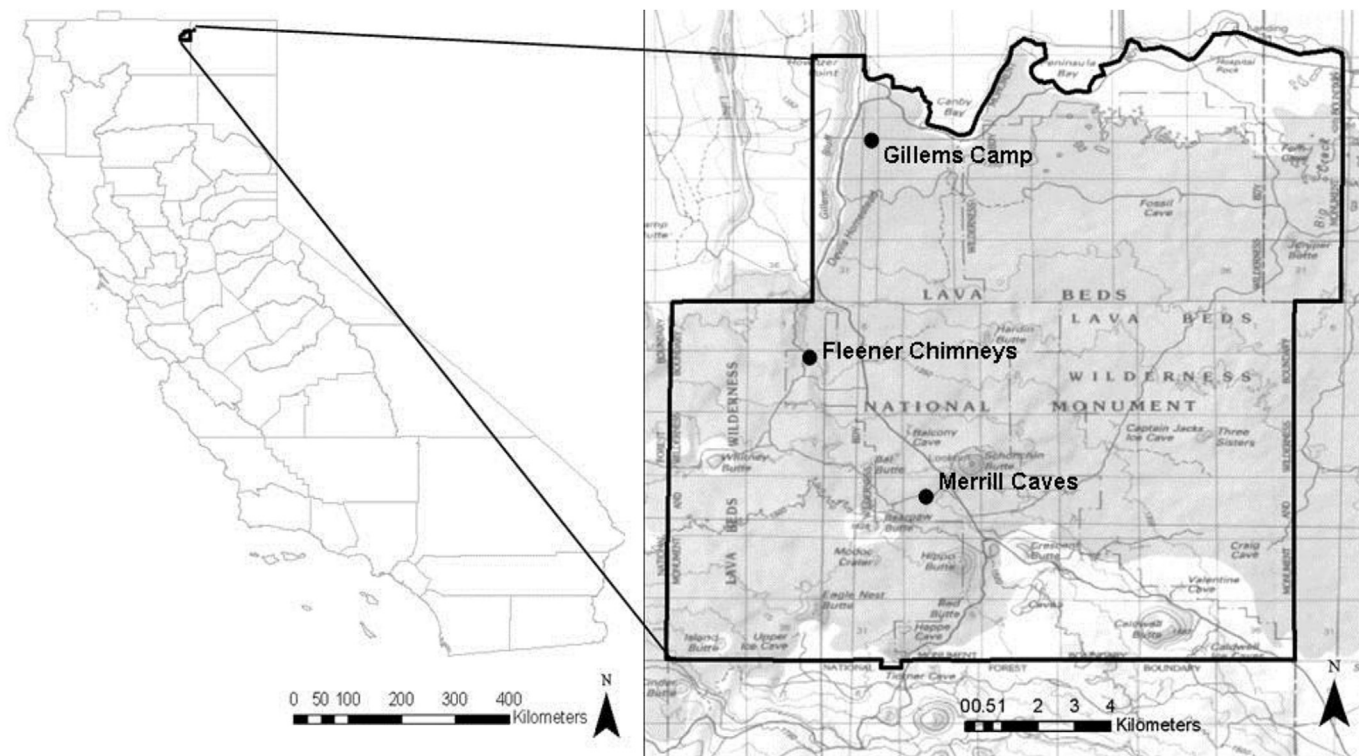


Fig. 1. *Artemisia tridentata* ssp. *vaseyana* study sites at Lava Beds National Monument, California, USA. Gillems Camp is a *Bromus tectorum*-invaded site; Fleener Chimneys is in pristine, native-dominated condition; Merrill Caves is characterized by dominance of *Juniperus occidentalis*.

was ignited independently as a backfire along the fireline using a drip torch. Where fuels were discontinuous, additional spot ignitions were used to facilitate fire spread. Although environmental conditions (temperature, relative humidity) were warmer and drier during the spring burns than during fall burns, it did not result in significantly different fire behavior measures (see Ellsworth and Kauffman, 2010). Both spring and fall fires burned in a mosaic pattern, burning some areas and leaving others unburned. As temperatures increased and relative humidity decreased throughout the days of the burns, rate of spread, flame lengths, and fireline intensity increased.

2.2. Vegetation community sampling and analysis

Cover of herbaceous vegetation was quantified in 30 × 30 × 60 cm microplots (N = 150 for each treatment by site combination) at established locations along permanent transects. Vegetation cover was quantified in July 2002 (prefire, spring treatments) and 2003 (prefire, fall and control treatments) and again in June–July, 2004 (1 year post-fire [1YPF]). Herbaceous cover for spring burns at Merrill Caves was not collected 1 YPF due to the later year of burn. Every individual herbaceous plant rooted within each microplot was identified, and cover (%) was estimated. For shrub species, cover was measured in five 1 m by 20 m subplots, adjacent to permanent transects in each plot. Prefire shrub cover was measured in June 2003 and burned plots were measured again in June 2004. Shrub cover in control plots was not remeasured and assumed to remain fairly constant between sample years. Individual shrubs were counted and summed across burn treatment plots prefire (2003) and 1YPF (2004) to estimate survival and sprouting of commonly occurring shrubs (*A. tridentata*, *E. nauseosa*, *C. viscidiflorus*, *P. tridentata*, and *T. canescens*).

Analysis of variance (ANOVA) was used to determine whether

there was a treatment (spring burn, fall burn, or control) or year (prefire, 1 YPF) effect on cover of vegetation functional groups (*B. tectorum*, native forb, shrub, and perennial bunchgrass). Post-hoc multiple comparisons with a Tukey correction factor were performed following significant analyses to determine differences between time periods and determine whether there was a differential change over time between treatments (interaction term). Where sample size of individual shrubs was adequate (≥ 40 individuals per site*treatment combination), two-sample t-tests were used to determine whether there was a difference in shrub survival (% of original live shrubs) and basal resprouting (% of topkilled shrubs) between spring and fall burn treatments for each shrub species. Analyses were considered significant at $\alpha < 0.05$ and suggestive at $0.05 \leq \alpha < 0.10$. IBM SPSS Version 23 (IBM SPSS, Inc., Chicago, IL) was used for univariate analyses.

Multivariate analyses were used to test for differences in plant community composition following spring and fall burn treatments. Multi-Response Permutation Procedures for blocked data (MRBP) were used to evaluate the strength of *a priori* groupings of species assemblages at each site by testing the null hypothesis of no difference between control and fire treatment groups following fire treatments. Indicator species analysis (Dufrene and Legendre, 1997) was used to identify species that were unique to each treatment group at each site. This analysis generates an indicator value (IV) for each species present based on species abundance and relative frequency of each species. Indicator values were then tested for significance using a Monte Carlo randomization test (McCune et al., 2002). All species which occurred in fewer than two sample plots were deleted from the analysis, resulting in 62 species remaining which reduced noise in the data. Plant community data were transformed using a square root transformation (McCune et al., 2002), which improved the distribution of the data. All multivariate statistics were performed using PC-ORD, Version 6.

3. Results

3.1. Native-dominated site (Fleener Chimneys)

Prescribed fires at Fleener Chimneys were difficult to ignite, carried poorly, and resulted in a heterogeneous burn pattern, particularly during fall burns, which had lower temperatures and higher relative humidities than spring fires (Ellsworth and Kauffman, 2010). Prior to burns, mean shrub cover at this site was 30% (SE = 3%) across treatment and control plots. Many shrubs were purposefully ignited, resulting in high mortality of shrubs (Table 1) and a decrease in post fire shrub cover to 6% cover (SE = 1%) in spring burn treatments and 18% cover (SE = 3%) in fall burn treatments (treatment, $P = 0.62$; time, $P < 0.01$; treatment*time, $P = 0.04$; Fig. 2). There was 33% mean survival (SE = 20%) of *A. tridentata* ssp. *vaseyana* individuals in spring burns and 65% mean survival in fall burns (SE = 11%; treatment effect, $P = 0.01$). Survival of *T. canescens* immediately following fire averaged 13% (SE = 9%) across all burn plots and did not differ by treatment ($P = 0.21$). One year following fire, basal sprouting of top-killed *T. canescens* averaged 59% and was very heterogeneous across burn plots (SE = 12%), with no difference between spring and fall treatments ($P = 0.12$). We saw only 3 incidences of resprouting *Chrysothamnus viscidiflorus* (green rabbitbrush; 9% of total topkilled individuals) following spring burns and one *P. tridentata* basal sprout following fall burns (4% of total topkilled individuals; Table 1).

Perennial grass cover declined from 17% cover before fire to 6% cover following spring burns and from 14% cover before fire to 10% following fall burns. Control plots averaged 9% cover in both sample years (treatment*time, $P = 0.07$; Fig. 2). Forb cover averaged 5% (SE = 3%) prior to fires. One year after fire, forbs increased to an average of 13% in spring burn plots, which was almost entirely due to a large response of the native annual *Phaecelia linearis*, with slight declines in forb cover in fall fire (3%) and control (3%) plots (treatment, $P = 0.06$; time, $P = 0.47$; treatment*time, $P = 0.02$). Invasive annual *B. tectorum* cover was low across all treatments and did not increase following fire, averaging 1% prefire (SE = 0.3%) and 0.6% postfire (SE = 0.1%; treatment, $P = 0.12$; time, $P = 0.24$; treatment*time, $P = 0.84$; Fig. 2).

Community analyses revealed a postfire difference between spring and fall burns and unburned controls (MRBP: $P < 0.01$, $A = 0.151$). Three early seral species were common only in the higher severity spring burn treatments following fire ($P < 0.05$): *Plagobothrys tenellus* (Indicator value = 85), *Epilobium minutum* (57), and *Phaecelia linearis* (78), and two species were unique to (unburned islands within) fall burn treatments: *Artemisia tridentata* (43) and *Tetradymia canescens* (62). One species was distinct to the control treatment both before and after treatments, *Stipa occidentalis* (45), which appeared to be due to a patchy distribution and not a treatment effect.

3.2. *B. tectorum* -invaded site (Gillems Camp)

Fires at the invasive grass-dominated Gillems Camp were of high intensity and severity, top-killing most vegetation, and leaving few unburned islands. Prior to treatment, mean shrub cover was only 3% (SE = 0.4%) and was predominantly *E. nauseosa*. Shrubs decreased following fire to <0.01% cover in spring burn treatments and to 0.12% cover fall burn treatments (treatment, $P = 0.13$; time, $P < 0.01$; treatment*time, $P = 0.01$; Fig. 2). Fires top-killed 82% of *E. nauseosa* individuals with no difference between spring and fall burns ($P = 0.11$). No *E. nauseosa* individuals sprouted following higher severity spring burns, and only 4.5% (5 out of 84) of topkilled individuals in fall burns sprouted ($P = 0.04$; Table 1).

Native perennial bunchgrass cover averaged 9% across fire and control plots prior to treatment, with declines in the second year to an average of 5% (SE = 0.8; time effect, $P = 0.02$) but no evidence of differences between treatments (treatment, $P = 0.87$; treatment*time, $P = 0.23$; Fig. 2). Total forb cover ranged from 1 to 3% cover, with no differences between treatments or years (treatment, $P = 0.67$; time, $P = 0.59$; treatment*time, $P = 0.27$; Fig. 2). *B. tectorum* cover was higher before treatment (mean, 38%; SE = 3) than after treatment (mean, 9%; SE = 1) but there was no evidence that this reduction was due to fires, as this reduction also occurred in control plots (treatment, $P = 0.22$; time, $P < 0.01$; treatment*time, $P = 0.57$; Fig. 2).

Community composition differed in the first post-fire year between burn and control plots (MRBP: $P < 0.01$, $A = 0.110$), but not between spring and fall burn seasons. Indicator species analysis

Table 1

Individual shrub sample size prefire, percent aboveground consumption immediately after fire, percent basal sprouting and total percent survival (aboveground survival plus sprouts) one year following spring and fall prescribed fires in *Artemisia tridentata* ssp. *vaseyana*-dominated ecosystems at Lava Beds National Monument, California, USA. Fleener Chimneys was dominated by native vegetation, Gillems Camp was dominated by *Bromus tectorum*, and Merrill Caves had large amounts of *Juniperus occidentalis*.

Fleener Chimneys	Spring				Fall			
	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)
<i>E. nauseosa</i>	9	78	14	36	9	100	0	0
<i>C. viscidiflorus</i>	15	80	25	40	23	96	0	4
<i>P. tridentata</i>	17	59	0	41	23	61	7	43
<i>T. canescens</i>	42	98	46	48	51	94	71	73
<i>A. tridentata</i>	405	62	0	38	511	39	0	61
Gillems Camp	Spring				Fall			
	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)
<i>E. nauseosa</i>	131	83	0	17	103	82	6	19
<i>C. viscidiflorus</i>	1	100	0	0	0	—	—	—
<i>P. tridentata</i>	0	—	—	—	1	100	0	100
<i>T. canescens</i>	2	100	0	0	0	—	—	—
<i>A. tridentata</i>	2	100	0	0	0	—	—	—
Merrill Caves	Spring				Fall			
	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)	Prefire sample size	Topkilled (%)	Resprout (%)	Total Survival (%)
<i>E. nauseosa</i>	3	—	—	—	8	38	33	75
<i>C. viscidiflorus</i>	8	—	—	—	0	—	—	—
<i>P. tridentata</i>	25	—	—	—	17	100	6	6
<i>T. canescens</i>	0	—	—	—	0	—	—	—
<i>A. tridentata</i>	244	—	—	—	242	58	0	42

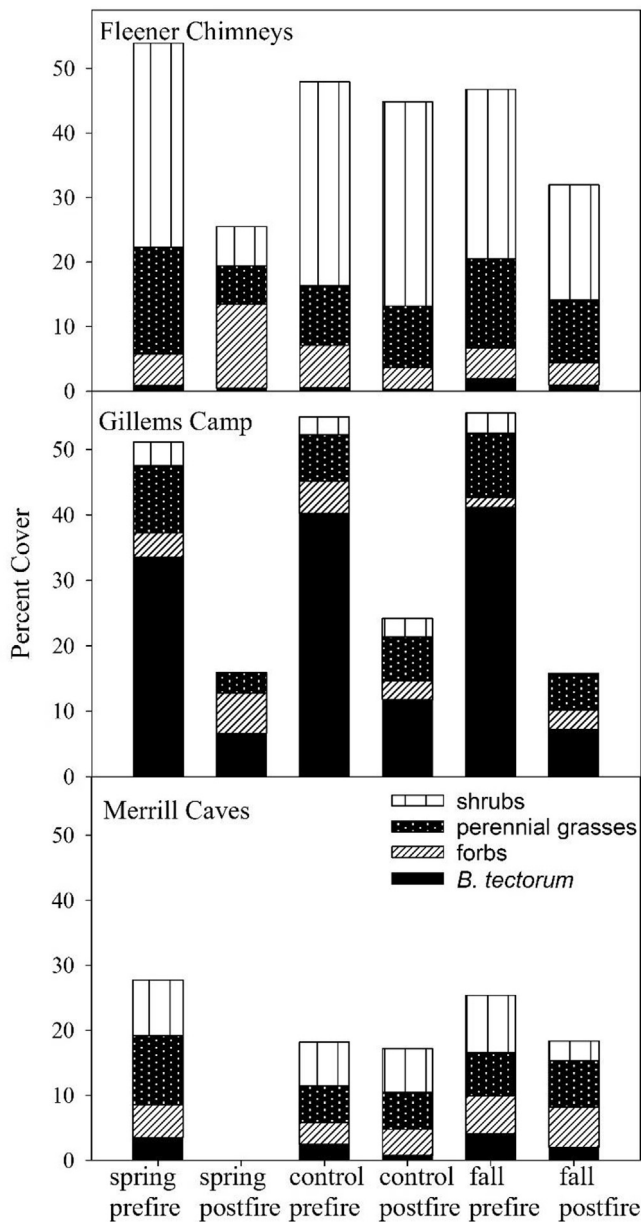


Fig. 2. Vegetation cover before (prefire) and after (postfire) spring and fall prescribed fires and unburned controls in *Artemisia tridentata* ssp. *vaseyana* ecosystems at Lava Beds National Monument, California, USA. Fleener Chimneys is in pristine, native-dominated condition; Gillems Camp is a *Bromus tectorum*-invaded site; Merrill Caves is characterized by dominance of *Juniperus occidentalis*.

revealed two early successional species that were common only following spring burns ($P < 0.05$), *Descurainia pinnata* (Indicator value = 69), and *Sisymbrium altissimum* (53), and two species which were indicator species in control plots, *Draba verna* (39), and *E. nauseosa* (87). No species were indicator species in fall burn plots.

3.3. Juniper dominated site (Merrill Caves)

Shrub cover at the juniper-dominated site, Merrill Caves, was primarily *A. tridentata* ssp. *vaseyana*, and averaged 8% (SE = 0.8) before burn treatments. Following fall burns, shrub cover was reduced to an average of 3.0% (SE = 0.9; treatment effect, $P = 0.05$). Mortality of the non-sprouting *A. tridentata* ssp. *vaseyana* averaged 58% across plots. Five *E. nauseosa* individuals (63% of total) survived

fall prescribed burns, with one additional individual sprouting after being topkilled. All *P. tridentata* individuals ($N = 17$) were topkilled in fall fires and only one of these individuals sprouted (Table 1). In spring burns, 44% of *J. occidentalis* were killed, and in fall burns, 46% were killed.

Fall prescribed fire had few immediate post-fire effects on the cover or composition of herbaceous vegetation at Merrill Caves. Perennial bunchgrass cover averaged 6% cover (SE = 0.8), with no treatment or year differences (treatment, $P = 0.45$; time, $P = 0.87$; treatment*time, $P = 0.92$; Fig. 2). Forb cover averaged 5% cover (SE = 1), with no differences between treatments or years (treatment, $P = 0.11$; time, $P = 0.80$; treatment*time, $P = 0.79$; Fig. 2). *B. tectorum* cover averaged 2% (SE = 1), and did not increase following fires at this site (treatment, $P = 0.33$; time, $P = 0.19$; treatment*time, $P = 0.92$; Fig. 2).

There was a difference in overall plant community composition between fall burns and control plots (MRBP: $P < 0.01$, $A = 0.090$). Indicator species analysis revealed two woody species which were common only in unburned control plots ($P < 0.05$), *P. tridentata* (Indicator value = 80), and *Leptodactylon pungens* (80). One annual early-seral forb species was distinct to the fall burn treatment, *Mentzelia albicaulis* (77).

4. Discussion

Across all burn plots, we quantified a disturbance-initiated shift in *Artemisia tridentata* ssp. *vaseyana* plant community composition from woody-dominance towards a dominance of herbaceous vegetation, which was consistent with expectations and with previous work (Seefeldt et al., 2007; Ziegenhagen and Miller, 2009). While fire behavior (flame lengths, rates of spread, etc.) was very similar for spring and fall seasons of burn (Ellsworth and Kauffman, 2010), the severity and small-scale heterogeneity of those fire effects differed by burn season and prefire condition. Lower severity fall season burns resulted in greater survival and reproductive effort in perennial, fire-adapted shrub and bunchgrass species (Ellsworth and Kauffman, 2010). Live plant tissues are generally more sensitive to heat early in the growing season, when growth points are active and moisture content is high (Wright and Klemmedson, 1965), likely contributing to higher mortality and reduced perennial plant cover following spring fires. Additionally, fall fires resulted in more heterogeneous burns, with many unburned islands inside the fire perimeters. These can serve as important seed sources for shrub recolonization of the post-fire environment (Condon and Weisberg, 2016). Spring fires, in contrast, favored post-fire colonization of early successional species that varied by prefire condition, with native forbs such as *P. linearis*, *Mentzelia albicaulis*, and *Crepis acuminata* germinating in native-dominated burn plots, and weedy species such as *B. tectorum*, *S. altissimum*, and *Lactuca serriola* in degraded plots (Ellsworth and Kauffman, 2013).

Community level post-fire response is a function of the adaptations that the individual species comprising the community have for resilience, resistance, and reestablishment following fire (Chambers et al., 2007; Ellsworth and Kauffman, 2010; Miller et al., 2013; Wroblewski and Kauffman, 2003). The dominant shrub species at this site was *A. tridentata* ssp. *vaseyana* which is often killed by fire and requires establishment by seed for shrub regeneration (Ziegenhagen and Miller, 2009). Seeds are typically only dispersed a short distance from parent plants, and remain viable only 4–6 years (Schlaepfer et al., 2014; Whisenant, 1990). *A. tridentata* ssp. *vaseyana* typically regains canopy coverage of 20–30% within 20–35 years (Miller and Heyerdahl, 2008; Ziegenhagen and Miller, 2009). Other shrub species of the sagebrush steppe range from weak to frequent sprouters following fire. For example, *T. canescens*,

a prolific resprouting species (Evans and Young, 1978; Pyle and Crawford, 1996) had resprouting rates between 46% after spring burns to 71% following fall burns in good condition sites (Table 1). The capacity of *E. nauseosa* and *P. tridentata* to sprout following fire is less clear (Young and Blank, 1995; Ziegenhagen and Miller, 2009). Havlina (1995) found that postfire mortality of *P. tridentata* was closely related to shrub age ($r^2 = 0.91$). Over 66% of shrubs <25 years sprouted following fire while only 20% of the shrubs older than 25 years sprouted. The survival and post-fire reproductive capacity (Ellsworth and Kauffman, 2010) of native bunchgrasses, and the seedbank of native plants (Ellsworth and Kauffman, 2013) at the native-dominated site provided a post-fire understory rich in native herbaceous diversity, with very little non-native grass.

Degraded sites are at higher risk for invasion following fire. Coupled with an increased fire return interval, these sites may become further dominated by invasives following disturbance (Chambers et al., 2007; D'Antonio and Vitousek, 1992). Previous studies conducted at Lava Beds National Monument showed that the high *B. tectorum* seed load inhibited the establishment of native bunchgrasses (Olson et al., 1980; Erhard, 1979). However, livestock exclusion has resulted in an increase in native flora in more recent years when compared to these older studies.

At the juniper-dominated Merrill Caves site, the increase in woody vegetation in the fire-free interval preceding the fires led to a decline in understory forbs, dense shrub cover, and an increasingly closed canopy. For example, prefire shrub cover at the native-dominated site was almost 4× greater than at the juniper-dominated site, indicating a suppression of native shrubs by the juniper overstory (Miller and Rose, 1999). About half of the juniper individuals and 63% of shrubs were killed by the burn treatments. This results in post-fire increases of available water, light, and nutrients to understory vegetation, and increased microsites for seed germination and seedling establishment (Bates et al., 2002; Roundy et al., 2014). We expect that earlier successional herbaceous species will continue to dominate the early post-fire period, providing a mosaic of herbaceous cover and unburned woody patches (Hanna and Fulgham, 2015).

We caution that the immediate post-fire effects, particularly those of invasive annual grasses, are not always indicative of longer term response to fire. In this study we saw no large post-fire dominance of *B. tectorum* in the first post-fire year. Other studies have found similar initial reductions in *B. tectorum*, due to consumption of litter and seeds, but by the second post-fire year there was an increase in *B. tectorum* cover, particularly on historically overgrazed or otherwise degraded areas (Miller et al., 2013; West and Hassan, 1985; Young and Evans, 1978). This suggests that it is likely that there will be increases in *B. tectorum* in the early post-fire successional period (~years 2–4) at the degraded Gillems Camp site. However, because there is ample seed source of native herbaceous vegetation, and a trajectory of recovery following cessation of grazing (Erhard, 1979), we expect continued co-dominance of native and invasive species.

Overall, our results suggest a resilience of the native vegetation to fire, as evidenced by survival and persistent cover of native woody and herbaceous species. As expected, the native dominated sites had more favorable post-fire plant community responses than the *B. tectorum*-dominated site. Lower severity fall fires tended to have higher incidences of native survival and regeneration as compared to higher severity spring fires. These results show that season of burn and associated differences in fire severity as well as pre-fire site condition are important considerations when evaluating appropriateness of fire management options in *A. tridentata* ssp. *vaseyana* ecosystems.

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THE ROLE OF FIRE IN STRUCTURING SAGEBRUSH HABITATS AND BIRD COMMUNITIES

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Abstract. Fire is a dominant and highly visible disturbance in sagebrush (*Artemisia* spp.) ecosystems. In lower elevation, xeric sagebrush communities, the role of fire has changed in recent decades from an infrequent disturbance maintaining a landscape mosaic and facilitating community processes to frequent events that alter sagebrush communities to exotic vegetation, from which restoration is unlikely. Because of cheatgrass invasion, fire-return intervals in these sagebrush ecosystems have decreased from an historical pattern (pre-European settlement) of 30 to >100 yr to 5–15 yr. In other sagebrush communities, primarily higher elevation ecosystems, the lack of fire has allowed transitions to greater dominance by sagebrush, loss of herbaceous understory, and expansion of juniper-pinyon woodlands. Response by birds living in sagebrush habitats to fire was related to the frequency, size, complexity (or patchiness), and severity of the burns. Small-scale fires that left patchy distributions of sagebrush did not influence bird populations. However, large-scale fires that resulted in large grassland expanses and isolated existing sagebrush patches reduced the probability of occupancy by sagebrush-obligate species. Populations of birds also declined in sagebrush ecosystems with increasing dominance by juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.) woodlands. Our understanding of the effects of fire on sagebrush habitats and birds in these systems is limited. Almost all studies of fire effects on birds have been opportunistic, correlative, and lacking controls. We recommend using the large number of prescribed burns to develop strong inferences about cause-and-effect relationships. Prescribed burning is complicated and highly contentious, particularly in low-elevation, xeric sagebrush communities. Therefore, we need to use the unique opportunities provided by planned burns to understand the spatial and temporal influence of fire on sagebrush landscapes and birds. In particular, we need to develop larger-scale and longer-term research to identify the underlying mechanisms that produce the patterns of bird responses to fire in sagebrush ecosystems.

Key Words: *Amphispiza belli*, *Centrocerus urophasianus*, *Bromus tectorum*, disturbance, exotic annual, fire regime, *Oreoscoptes montanus*, sagebrush ecosystems, *Spizella breweri*.

EL PAPEL DEL FUEGO EN LA ESTRUCTURA DE HABITATS DE ARTEMISIA Y COMUNIDADES DE AVES

Resumen. El fuego es una perturbación dominante y evidente en ecosistemas de artemisia (*Artemisia* spp.). En elevaciones bajas, en comunidades de artemisia xérica, el papel del fuego ha cambiado en las últimas décadas de una perturbación infrecuente que mantiene el mosaico del ecosistema y facilita los procesos de las comunidades, a eventos frecuentes que alternan las comunidades de artemisia a vegetación exótica, por lo cual la restauración no es muy prometedora. Debido a la invasión del zacate bromo, los intervalos de repetición de incendios en los ecosistemas de artemisia han disminuido de su patrón histórico (asentamiento pre-Europeo) de 30 a >100 años a 5–15. En otras comunidades de artemisia, principalmente en elevaciones más altas, la ausencia de fuego ha permitido transiciones tales como el incremento en dominancia de artemisia, la pérdida de la primera capa de vegetación de herbáceas y la expansión de bosques de juníperos-piñón. La respuesta al fuego de las aves que habitan en habitats de artemisia estaba relacionada a la frecuencia, tamaño, complejidad (o diversidad de parches), y a la severidad de los incendios. Incendios de pequeña escala que produjeron parches distribuidos de artemisia, no afectaron a las poblaciones de aves. Sin embargo, incendios de larga escala que resultaron en la expansión de largos pastizales y aislaron parches de artemisia existentes, redujeron la probabilidad de ser ocupadas por especies obligadas de artemisia. Las poblaciones de aves también disminuyeron en ecosistemas de artemisia, con el incremento en la dominancia de bosques de junípero (*Juniperus* spp.) y de piñón (*Pinus* spp.). Nuestro entendimiento de los efectos del fuego en habitats de artemisia y aves en este sistema es limitado. La mayoría de los estudios de los efectos del fuego en aves han sido oportunistas, correlativos y con falta de control. Recomendamos utilizar un gran número de quemas prescritas para desarrollar fuertes inferencias de las relaciones causa efecto. Las quemas prescritas son complicadas y altamente contenciosas, particularmente en comunidades de artemisia xérica de baja elevación. Es por esto que para entender la influencia espacial y temporal del fuego en paisajes y aves de artemisia, necesitamos utilizar la oportunidad única que nos dan los incendios planeados. En particular, necesitamos desarrollar investigación de amplia escala y de largo plazo, para identificar los mecanismos que producen los patrones de las respuestas de las aves hacia el fuego en ecosistemas de artemisia.

Fire is one of the dominant and most visible disturbances influencing sagebrush (*Artemisia* spp.) ecosystems in the Intermountain region of western North America. A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Pickett and White 1985:8). Fire is an important disturbance that maintains forb and grass components, facilitates nutrient cycling, and regulates other ecosystem processes within the sagebrush community. Because of variation in location, size, frequency, severity (level of biological and physical impact), and complexity of fires, the effects of fire on sagebrush habitats and bird communities are expressed at multiple scales in space from individual plants to landscapes and across time scales from immediately postfire to decades or longer.

Sagebrush habitats dominate >43,000,000 ha across western North America (Fig. 1) (McArthur 1994, McArthur 2000). Despite this wide distribution, sagebrush habitats are highly imperiled because of extensive degradation and loss across much of their distribution (Knick et al. 2003). Consequently, conservation of sagebrush habitats and birds is a primary management concern (Paige and Ritter 1999).

The historical fire regime and role of fire in sagebrush ecosystems has changed during the past century. Prior to the late 1800s, recurrent fires that varied in frequency and severity across a landscape resulted in a mosaic of sagebrush and interspersed grassland communities in different stages of community succession (Young et al. 1979). Landscapes now dominated by exotic annual grasses have drastically increased fire frequency in landscapes (Whisenant 1990, Billings 1994, Peters and Bunting 1994). In contrast, reduced fine fuel biomass because of livestock grazing or fire suppression has decreased fire frequencies in other regions (Miller and Wigand 1994, Miller and Rose 1999). In the interior Columbia Basin, the departure from pre-settlement patterns was greatest in sagebrush communities compared to other habitats (Hann et al. 1997, Hann et al. 2002).

In this review, we discuss the role of fire in influencing the composition and configuration of sagebrush systems and subsequent effects on birds living in these communities. We summarize information on the historical role of fire and the mechanisms by which land use and management practices have altered the fire regime. We then describe the effects of fire on bird communities caused by changes in the local vegetation and surrounding landscape. Because

more fire-related research has been conducted on Greater Sage-Grouse (*Centrocercus urophasianus*) than nongame species, we present findings separately. Finally, we identify the critical management needs and research issues.

HISTORICAL PATTERNS OF VEGETATION DYNAMICS AND BIRD COMMUNITIES

VEGETATION DYNAMICS

Sagebrush often is the dominant shrub on salt-free soils at elevations between 150 and 3,300 m where precipitation exceeds 178 cm (West 1983, Miller and Eddleman 2001). We distinguish, when possible, three subspecies of big sagebrush, which have different growth and foliage characteristics and occupy different ecological sites (Shumar and Anderson 1986, Jensen 1990). Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) vary along climate, elevation, and soil gradients. The landscapes occupied by each subspecies differ in their susceptibility to invasion by exotic plant species, the disturbance regime, and subsequent pattern of community succession and community response. Most studies of bird communities in sagebrush ecosystems have failed to recognize these differences (with the exception of recent research on Greater Sage-grouse). We also present ancillary information on dwarf sagebrush (low sagebrush [*Artemisia arbuscula*], black sagebrush [*A. nova*]), and salt desert shrub communities which often intergrade with big sagebrush communities.

Sagebrush is highly sensitive to fire; fire kills individual sagebrush shrubs and none of the primary species of *Artemisia* or subspecies can resprout from root crowns (West and Young 2000). Historically, native herbaceous species of annuals and perennials would increase in the absence of shrubs following fire. Recovery following burns to sagebrush-dominated landscapes is a function of shrub regeneration from existing seed sources. Seed production must come from remaining sagebrush plants that survive the fire or from pre-existing seed pools. Although sagebrush seeds present in the soils rarely germinate after 0.5–1 yr (Young and Evans 1978, Hassan and West 1986), recruitment of mountain big sagebrush following complete burns occurred from seeds produced 3 yr previously (R. F. Miller, personal observation). Seed dispersal is limited to the immediate area surrounding the mother plant (Young and

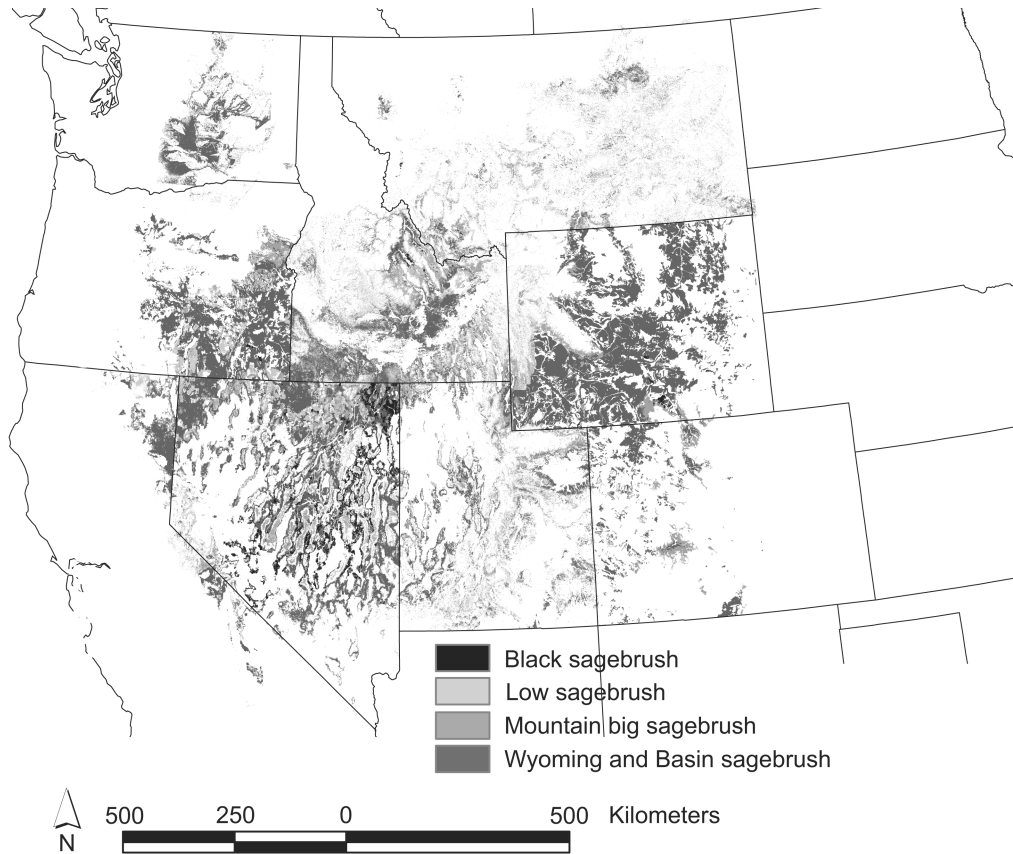


FIGURE 1. Sagebrush habitats cover approximately 43,000,000 ha in western North America. The map depicts the current distribution of the primary species of dwarf and tall sagebrush species (Comer et al. 2002). Sagebrush areas are not shown for states and provinces having limited geographic distribution of sagebrush or for which reliable maps were not available.

Evans 1989, Meyer 1994) and recovery of large expanses devoid of sagebrush following burns may require >100 yr (USDI 1996, Hemstrom et al. 2002). Therefore, completeness of the burn in destroying individual plants is the most important factor in determining the recovery dynamics of burned sagebrush landscapes.

Pre-settlement fire regimes have been described for a few communities of big and dwarf sagebrush systems bordering forested areas (summarized in Miller and Tausch 2001). However, the lack of large trees that bear fire history through scarring limits our ability to date pre-settlement fires and to determine return intervals for most sagebrush landscapes (Miller and Tausch 2001). Therefore, proxy information on geographic location and topography, plant life history and fire adaptations, fuel characteristics, and climate and weather patterns has been used to supplement the limited direct information.

Pre-settlement fire regimes in the sagebrush biome were highly variable both temporally and spatially. Severity and frequency of occurrence varied among different plant associations and site characteristics with mean fire-return intervals ranging from as little as 10 yr in higher elevation sites to greater than 200 yr in lower elevation, xeric regions (Fig. 2) (Miller and Tausch 2001). Severe fires that completely burned large areas likely were rare.

BASIN BIG SAGEBRUSH

Basin big sagebrush is the tallest form of big sagebrush (120–180 cm) and may reach 240 cm in height (Winward and Tisdale 1977). Basin big sagebrush occupies areas of deep, loamy soils in annual precipitation zones from 32–36 cm. Because these soils are highly fertile, most areas previously dominated by basin big sagebrush have been converted to

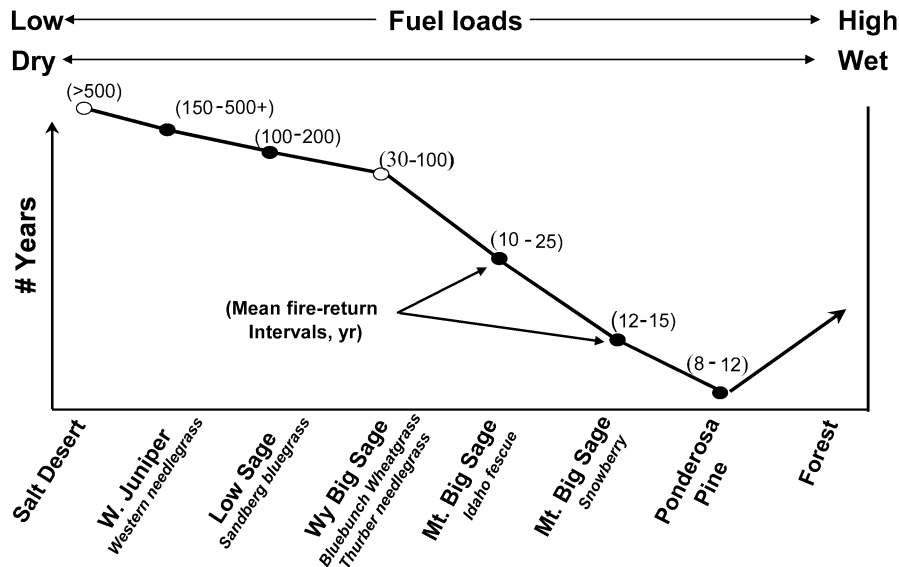


FIGURE 2. Presettlement mean fire-return intervals (MFRI) for salt desert, old growth western juniper-western needlegrass (*Stipa occidentalis*), low sagebrush (*Artemisia arbuscula* Nutt.)-Sandberg bluegrass (*Poa sandbergii* Vasey), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Welsh.)-bluebunch wheatgrass (*Agropyron spicatum* Pursh)-Thurber needlegrass (*Stipa thurberiana* Piper), mountain big sagebrush (*A. t.* ssp. *vaseyana* Rydb.)-Idaho fescue (*Festuca idahoensis* Elmer), mountain big sagebrush-snowberry (*Symphoricarpos* spp.), and ponderosa pine (*Pinus ponderosa* Laws.) communities. Solid circles are MFRI estimates supported by data, and open circles are estimates with little to no information (derived from Miller and Tausch 2001).

agriculture in Washington (Dobler et al. 1996) and an estimated 99% of lands once covered by basin big sagebrush now is absent from the Snake River Plains in Idaho (Noss et al. 1995). Basin big sagebrush is less resilient to disturbance than mountain big sagebrush but is more resilient than Wyoming big sagebrush. Historical fire-return intervals probably were >50 yr between fire events but fires may have been more frequent (10–20 yr) on productive sites containing greater amounts of basin wildrye grass (*Leymus cinereus*).

WYOMING BIG SAGEBRUSH

Wyoming big sagebrush is widely distributed through the Intermountain (McArthur 1994). Wyoming big sagebrush grows in shallower soils and more xeric conditions (20–30 cm/yr annual precipitation) compared to basin big sagebrush. The average size of Wyoming big sagebrush is 45–100 cm (Winward and Tisdale 1977). Very little direct information exists to document pre-settlement fire regimes in regions dominated by Wyoming big sagebrush; estimated fire-return intervals range from 50 to >100 yr (Wright and Bailey 1982). Fire occurrence,

severity, size, and complexity were probably highly variable in space and time. Due to limited fuels, most fires in the pre-settlement landscape probably were patchy, uneven burns that left islands of sagebrush within the burn that provided seed sources to initiate recovery to a shrubland landscape. However, occasional fires with limited spatial complexity probably occurred under severe weather conditions and in years following above average moisture resulting in the build up of fine fuels.

MOUNTAIN BIG SAGEBRUSH

Mountain big sagebrush grows at higher elevations (usually >1600 m) than basin or Wyoming big sagebrush. Mountain big sagebrush communities generally are more resilient to disturbance and recovers more rapidly than either basin or Wyoming big sagebrush because of greater precipitation (>30 cm/yr) and possibly longer seed viability. Mountain big sagebrush sites also are less susceptible to invasion by alien weeds than the other subspecies of big sagebrush. Historical fire-return intervals are thought to be relatively frequent (10–25 yr) in the more productive communities (Miller and Rose 1999, Miller

et al. 2000). However, drier sites with reduced fuel loadings may have had less frequent returns with moderate severity fires occurring between 30–70 yr. The fire regime for mountain big sagebrush associations in arid locations on pumice influenced soils was characterized by infrequent but high severity, stand replacement fires that occurred only under severe weather conditions and may have been >150 yr (Miller and Tausch 2001).

DWARF SAGEBRUSH

Dwarf sagebrush communities dominated by low sagebrush or black sagebrush often intergrade with big sagebrushes. Historic fire-return intervals of low sagebrush communities are perhaps more variable than big sagebrush species. The average fire-return interval in low sagebrush-bluebunch wheatgrass (*Pseudoroegneria spicata*) probably ranged between 20–50 yr. For low sagebrush-Sandberg's bluegrass, the average fire-return interval probably was >100 yr (Young and Evans 1981, Miller and Rose 1999).

Salt Desert Shrub

Salt desert shrublands, dominated by members of the Chenopodiaceae, cover approximately 16,000,000 ha of western North America (Blaisdell and Holmgren 1984). Individual shrubs are widely spaced and total vegetative cover often is sparse. Invasion by exotic annuals generally is not a problem except in localized regions and northern parts of the range. Historical fire returns may have been as long as 500 yr or greater in salt desert shrub communities. Fire disturbance in these communities generally was not a significant factor in community dynamics. However, fire frequency has increased in recent decades concurrent with increases in biomass and continuity of fine fuels and biomass as a consequence of invasion by exotic plants (West and Young 2000, Brooks and Pyke 2001).

BIRD COMMUNITIES IN SAGEBRUSH ECOSYSTEMS

Bird species whose distribution is closely tied to sagebrush habitats during at least part of the year are considered sagebrush obligates (Braun *et al.* 1976, Paige and Ritter 1999). These include Greater Sagegrouse, Gunnison Sage-Grouse (*Centrocercus minimus*), Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*), and Brewer's Sparrow (*Spizella breweri*) although these species also may use other shrubland habitats. Gray Flycatcher

(*Empidonax wrightii*) relies heavily, although not exclusively, on sagebrush habitats (Sterling 1999). The above species place their nests in or beneath big sagebrush shrubs and occur in a wide spectrum of structural conditions. Other widespread species that use sagebrush habitats include Lark Sparrow (*Chondestes grammacus*) and Black-throated Sparrow (*Amphispiza bilineata*). Green-tailed Towhee (*Pipilo chlorurus*) is common in mesic sagebrush communities and the Loggerhead Shrike (*Lanius ludovicianus*) occurs throughout most of the sagebrush biome, with the highest densities associated with the taller shrub communities (Yosef 1996). Species primarily associated with grasslands adjacent to sagebrush habitats include Burrowing Owl (*Athene cunicularia*), Western Meadowlark (*Sturnella neglecta*), Horned Lark (*Eremophila alpestris*), Vesper Sparrow (*Pooecetes gramineus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Long-billed Curlew (*Numenius americanus*) (Knick and Rotenberry 2002). Grasshopper and Vesper sparrows are associated with perennial bunchgrass cover (Janes 1983, Vander Haegen *et al.* 2000). Long-billed Curlews (*Numenius americanus*) and Burrowing Owls (*Athene cunicularia*) are generally associated with shorter stature grasslands in open habitats (Green and Anthony 1989, Pampush and Anthony 1993).

Patterns of distribution and bird diversity are dictated in part by structural and floristic characteristics of vegetation at a local scale (Rotenberry 1985) and sagebrush habitats generally support fewer bird species than other more diverse habitats (Rotenberry 1998). Species diversity increases when sagebrush habitats form a shrub-grassland mosaic. Avian diversity further increases when tree components, such as pinyon-juniper woodlands, form part of the mosaic (Medin *et al.* 2000). However, as dominance by trees increases, the shrub layer and often the herbaceous components decrease (Miller *et al.* 2000) and result in a decrease in avian abundance and diversity (Medin *et al.* 2000).

Bird assemblages in presettlement sagebrush-dominated sites near the end of a fire cycle likely were dominated by the sagebrush obligate species. Grassland species, such as Vesper and Grasshopper sparrows (*Ammodramus savannarum*), Western Meadowlarks (*Sturnella neglecta*), and Horned Larks (*Eremophila alpestris*) would increase following a fire as a function of shrub removal. Songbird species obligate to sagebrush habitats may not respond immediately to landscapes in which <50% of original shrub canopy cover is reduced (Petersen and Best 1987). However, larger, high severity burns

like those in Wyoming big sagebrush-bunchgrass communities in which shrub removal is more complete likely resulted in reductions in these birds that use sagebrush, and even rendered blocks of habitat unsuitable for years until shrubs reestablished. In relatively mesic plant communities in the mountain big sagebrush cover type where mean fire-return intervals were <20 yr, burns also probably were spatially complex due to their low severity. Increased fire occurrence in this cover type usually resulted in more but smaller fires (Miller and Rose 1999).

Recent large-scale conversion of shrublands to expanses of annual grasslands is contributing to a reduced structural complexity in the plant community and a corresponding decrease in bird community diversity. At the other extreme, high densities of sagebrush or pinyon and juniper and depleted herbaceous understories caused by livestock grazing and fire suppression have simplified these systems and do not provide suitable habitat for grassland species. Thus, the relatively low diversity in native shrubsteppe systems has been reduced and habitats and avian communities further homogenized.

DISRUPTIONS TO NATURAL FIRE REGIMES IN SAGEBRUSH COMMUNITIES

LIVESTOCK GRAZING

Livestock grazing over the past 140 yr is the single most important influence that has changed sagebrush habitats and influenced fire regimes throughout the Intermountain West (Robertson 1954, Bock et al. 1993, West and Young 2000). Livestock grazing can increase the frequency of fires by disturbing soils and reducing competition from native grasses to facilitate spread of the highly flammable cheatgrass (Shaw et al. 1999). In mesic sagebrush communities not favorable to cheatgrass, grazing by livestock on perennial grasses and forbs reduced the fine fuels available to spread fires across a landscape and increased the interval between fires (Miller and Rose 1999, Miller and Tausch 2001). Excessive grazing of herbaceous components in these systems increases shrub density and cover. In south central Oregon, the role of fire was greatly reduced after 1870, just after the introduction of large numbers of livestock, but 46 yr before organized fire suppression (Miller and Rose 1999). Active fire suppression (especially after the 1940s) and a reduction in human ignition furthered the reduction in fires (Miller and Rose 1999). Finally, management of sagebrush landscapes has been directed primarily toward increasing forage biomass and conditions for

livestock grazing. Prescribed fires have been used to eradicate sagebrush (Vale 1974, Braun et al. 1976) and large areas replanted to nonnative perennial grasses, such as crested wheatgrass (*Agropyron cristatum*) (Hull 1974, Evans and Young 1978, Young 1994). However, shrub eradication also may increase the susceptibility of the area to weed invasions and increased risk to subsequent fires.

ENCROACHMENT BY JUNIPER AND PINYON PINE WOODLANDS

Communities dominated by juniper (*Juniperus* sp.) and pinyon (*Pinus* sp.) woodlands further disrupt natural fire regimes because they become essentially fire-proofed and lengthen the time between fires (Miller and Tausch 2001). Sites that have transitioned from shrubsteppe to woodland may now burn only with severe weather conditions that create crown fires in tree-dominated communities. The consequences of burns also are much different than in historic times because those communities now may be converted to habitat sinks dominated by annual grasslands.

Juniper and pinyon species currently occupy over 30,000,000 ha in the Intermountain West. Prior to European settlement, pinyon-juniper woodlands were estimated to have occupied less than 30,000,000 ha (Gedney et al. 1999). While these woodlands have fluctuated historically in extent (Tausch 1999), the post-settlement expansion is unprecedented compared to those during the Holocene (Miller and Wigand 1994). The increase in juniper and pinyon woodlands are primarily a result of livestock grazing that reduced the grass and forb fuels coupled with a corresponding decrease in historical fire frequencies that killed fire-prone woodlands (Savage and Swetnam 1990, Miller and Rose 1999, Miller and Tausch 2001). Approximately 45 yr are required for a tree to reach 3 m in height; trees <3 m are easily killed by fires (Miller and Tausch 2001). Climate shifts also have played a role in the expansion of juniper and pinyon woodlands and increased atmospheric carbon dioxide may be accelerating rates of canopy expansion (Miller and Rose 1999, Miller and Tausch 2001).

NON-NATIVE PLANT INVASIONS

CHEATGRASS

The introduction of cheatgrass to the arid portions of the sagebrush biome has fundamentally and perhaps irreversibly altered the natural fire regime by increasing the frequency and severity of fires (West

1979). Consequently, wildfires have caused extreme rates of fragmentation and loss of shrublands and now maintain the vast expanses of exotic annual grasslands by short fire-return intervals (Young and Evans 1973, Peters and Bunting 1994). Fire frequencies reduced from 30 to >100 yr between fire events to as low as 5–15 yr in parts of the Snake River Plains (Whisenant 1990) have altered significantly not only current habitats but also the future dynamics of these systems (Knick and Rotenberry 1997, Knick 1999). Many Wyoming big sagebrush communities in more arid regions at low elevations now exist in an grassland state from which recovery to a shrubland landscape may not be possible (Westoby 1981, Laycock 1991, Allen-Diaz and Bartolome 1998, West and Young 2000).

Cheatgrass was well established throughout much of its current distribution in the Intermountain West by 1930 (Stewart and Hull 1949, Piemeisel 1951, Klemmedson and Smith 1964, Mack 1981). However, cheatgrass has rapidly increased its dominance in native plant communities in the past 30 yr (Monsen 1994). Although cheatgrass can colonize regions in the absence of fire (d'Antonio 2000), the combination of fire, livestock grazing, habitat management practices, other disturbances, and climate conditions have most rapidly facilitated the heavy dominance by cheatgrass in sagebrush systems (d'Antonio and Vitousek 1992, Young 1994). Cheatgrass now dominates the understory in many sagebrush ecosystems and an estimated 25% of the original sagebrush steppe has been converted to annual grasslands (West 2000).

Cheatgrass colonizes and dominates a system through a variety of mechanisms by which it outcompetes native plants for resources and promotes a self-sustaining fire disturbance (Pyke and Novak 1994, Pyke 2000). Cheatgrass outcompetes native plants by germinating in the autumn, remaining dormant through winter, and putting on new growth during early spring. The shallow rooting system is especially adapted to capture available soil water and nutrients. Cheatgrass sets abundant seed annually and senesces earlier than native grasses which advances the onset of the fire season. The dense, continuous cover of cheatgrass compared to intermittent fuels provided by native bunchgrasses promotes fire spread resulting in the increase in fire frequency and larger, more complete, and less complex fire patterns.

OTHER NON-NATIVE PLANT INVADERS

We have focused on cheatgrass in this review because of its ability to change the form and function

of entire landscapes. Other exotic plants that may invade independently of or subsequent to cheatgrass domination (Shaw *et al.* 1999) include medusahead wildrye (*Taeniatherum asperum*), yellow star-thistle (*Centaurea solstitialis*) and other species of the genus *Centaurea*, halogeton (*Halogeton glomeratus*), rush skeleton-weed (*Chondrilla juncea*), and barbwire Russian thistle (*Salsola paulsenii*). The unfortunate reality is that we may not yet be at the bottom of the ecological barrel in the succession of sagebrush landscapes. Removing or controlling cheatgrass, such as by use of herbicides (Ogg 1994, Shaw and Monsen 2000), may only open the landscape to an increasingly undesirable plant community that is incompatible with birds dependent on sagebrush ecosystems.

USE OF PRESCRIBED FIRE IN SAGEBRUSH ECOSYSTEMS

The use of prescribed fire to manipulate habitats is one of the most common yet most contentious issues in management of sagebrush ecosystems (Miller and Eddleman 2001, U.S. Department of Interior 2002, Wambolt *et al.* 2002). Total area of prescribed burning by the U.S. Bureau of Land Management increased from 56,000 ha in 1995 to 861,094 ha in 2001 (National Interagency Fire Center 2003). Cost to conduct prescribed burns increased from \$1,200,000 in 1996 to \$10,600,000 in 1999. Objectives for prescribed burning include (1) control of annual grasses, (2) reduction of cover density of sagebrush, (3) promotion of grass and forb growth, and (4) the control expansion of juniper and pinyon woodlands. Despite the increased amount of areas treated by prescribed fire, its use should be considered cautiously because subsequent restoration of sagebrush communities after burning is extremely difficult due to low and variable precipitation, competition for resources by exotic vegetation, disruption of nutrient cycles, and continued disturbance by grazing domestic livestock (Allen 1988, Meyer 1994, Roundy *et al.* 1995, McIver and Starr 2001). Therefore, use of prescribed burning to reduce density of sagebrush and promote grass and forb growth should be considered only in those sagebrush types, such as mountain big sagebrush landscapes, that have favorable precipitation and consequent resilience to disturbance. Although individual small burns (<10 ha) are recommended (USDI 2002), the high cost of conducting small projects may be prohibitive.

Prescribed burning may reduce cheatgrass on a short-term basis but original densities can return within 2 yr from seeds remaining in the seed bank

(Pyke 1994). Timing of prescribed burns to control cheatgrass is critical. Prescribed fires during the period of seed maturation can reduce the densities of cheatgrass. However, fires conducted after seed dispersal have little effect and may increase future dominance of exotic plants because of nitrogen released during the burn (Stubbs 2000, Brooks and Pyke 2001). Prescribed burning also may facilitate invasion by an additional suite of noxious weeds. We conclude that fires, including prescribed burns in more xeric landscapes dominated by Wyoming and basin big sagebrush, likely will have the unintended consequence of stimulating cheatgrass production and dominance (Bunting et al. 1987).

THE EFFECT OF FIRE ON BIRDS IN SAGEBRUSH HABITATS

Very little information has been published on bird response to fire in sagebrush environments. Our search of the primary literature revealed few published papers that examined direct effects of a particular fire event, although several additional papers evaluated the longer-term effect of fires at a landscape scale (Table 1). With few exceptions, studies of a particular fire event examined short-term responses in abundance, as opposed to the response of demographic parameters such as productivity and survival. Few studies used before and after treatment designs with controls (Petersen and Best 1999). Such studies examining short-term responses to fire have serious limitations (Rotenberry et al. 1995, Petersen and Best 1999). Chief among them is that shrubsteppe songbirds may respond slowly to environmental disturbances (Best 1972, Castrale 1982, Wiens and Rotenberry 1985, Wiens et al. 1986) and the observed short-term response may not accurately portray long-term effects (Petersen and Best 1999, Knick and Rotenberry 2000).

EFFECTS OF FIRE

Birds that use sagebrush as their primary habitat declined dramatically in landscapes where shrub removal was complete and at large scales (Bock and Bock 1987, Knick and Rotenberry 1995, Knick and Rotenberry 1999). Loggerhead Shrikes, which also rely on shrublands for nesting habitat, were reduced by approximately 50% following a large mosaic burn in a basin and Wyoming sagebrush community (Humble and Holmes, unpubl. data). Because extensive, high-severity fires are increasing in frequency in lower elevation xeric communities, substantial expanses of habitat unsuitable for shrub dependent

species are created until shrubs reinvade and establish appropriate cover. In unaltered systems this process can take decades (Hemstrom et al. 2002). When sagebrush re-establishment is precluded either by recurring wildfire or by lack of seed sources within the burned area, habitat loss for birds depending on sagebrush habitats may be permanent.

Numbers of songbird species obligate to sagebrush ecosystems were not greatly reduced over the short term with partial removal (<50%) of sagebrush (Best 1972, Petersen and Best 1987, Petersen and Best 1999). Although approximately 50% of the sagebrush cover was removed, a patchy distribution of sagebrush remained at a larger scale in the landscape and continued to provide the habitat structure and components used by nesting birds.

Numbers of Horned Larks and Vesper Sparrows increased or remained unchanged following fire (Table 1). Similar responses by these species (as well as decreases in one or more sagebrush obligate species) have resulted when shrubs were removed through mechanical clearing or herbicide (Best 1972, Schroeder and Sturges 1975, Wiens and Rotenberry 1985).

Abundance of Western Meadowlarks or Grasshopper Sparrows did not change in response to burns (Table 1), although their habitat associations suggest that they should benefit from increases in the cover of grasses. Western Meadowlarks had greater probabilities of occurrence in regions where landscape measures of shrub cover were lower because of frequent and recurring wildfires (Knick and Rotenberry 1999).

Burning could improve habitat for Long-billed Curlews by removing shrubs and creating a more open habitat (Pampush and Anthony 1993). In the year following a fall range fire, breeding density of Long-billed Curlews increased 30% at a site in western Idaho (Redmond and Jenni 1986). Burrowing Owls have colonized recently burned areas (Green and Anthony 1989), but this may have been due to combined changes in habitat structure and prey populations. Long-term population increases for Long-billed Curlews and Burrowing Owls, determined from Breeding Bird Surveys (Sauer et al. 2001), suggest populations of these species may be benefiting from conversion of sagebrush habitats to more open annual grasslands in the Columbia Plateau.

Only one study (Petersen and Best 1987) examined how fire influenced reproductive success of songbirds. Nestling growth or reproductive output for either Sage Sparrow or Brewer's Sparrow was unchanged in 3 yr following a fire that removed approximately 45% of the shrubs (Petersen and Best

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE OF BREEDING BIRDS TO FIRE IN SAGEBRUSH HABITATS OF NORTH AMERICA. LITERATURE ON THE RESPONSE OF GREATER SAGE-GROUSE IS SUMMARIZED IN TABLE 2. NP INDICATES THAT THE INFORMATION WAS NOT PROVIDED.

Species	State	Years after fire	Size (ha) and No. of fires ^a	Fire Type ^b	No. of replicate sites	Response ^c	Reference ^d	Comments
Long-billed Curlew (<i>Numenius americanus</i>)	ID	1	142	w	1	+	1	
Mourning Dove	OR, ID, UT, WY, MT	np	np	np	13	–	2	Occurred on 8% of burned transects; 69% of adjacent unburned transects.
Gray Flycatcher (<i>Zenaidura macroura</i>)	NV	1–2	15,000	w	12	–	3	
Horned Lark (<i>Eremophila alpestris</i>)	ID	1–3	np	p	4	+	4	About 45% burned in mosaic.
	UT	3–4	np	p	2	+	5	Compared one burned to one unburned seeding.
	NV	1–2	15,000	w	12	+	3	
	OR, ID, UT, WY, MT	np	np	np	13	0	2	Greater numbers of detections on burned transects; not statistically significant.
Sage Thrasher (<i>Oreoscoptes montanus</i>)	OR	<5	np	np	8	0	6	Higher density in unburned; not statistically significant.
	ID	1–7	np	p	4	+	4	Densities higher 2–7 yr post-fire; Significant in year 4; 45% of treatment plots burned. Compared one burned to one unburned seeding.
	UT	3–4	np	p	2	0	5	
	NV	1–2	15,000	w	12	–	3	
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Not detected on burned transects and 54% of adjacent unburned transects.
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	NV	1–2	15,000	w	12	0	3	
Brewer's Sparrow (<i>Spizella breweri</i>)	ID	1–7	np	p	4	m	4	Reduction in density 1–2 yr postfire; pre-fire densities in 3–7 yr; 45% of treatment plots burned.
	MT	2–3	220	w	2	–	7	One burned and one unburned site; 100% sagebrush mortality.
	UT	3–4	np	p	2	–	5	One burned and one unburned seeding.
	NV	1–2	15,000	w	12	–	3	
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Not detected on burned transects; occurred on 92% of adjacent unburned transects.
	OR	<5	np	np	8	–	6	Density 75% lower at burned sites.
	ID	>5	np	w	119	–	8	Probability of occurrence reduced in landscapes with shrub loss due to wildfire.
Vesper Sparrow (<i>Poocetes gramineus</i>)	ID	1–7	np	p	4	+	4	Colonized burned plots 3 yr post-fire; 45% of treatment plots burned.
	UT	3–4	np	p	2	0	5	One burned and one unburned seeding.

TABLE 1. CONTINUED.

Species	State	Years after fire	Size (ha) and No. of fires ^a	Fire Type ^b	No. of replicate sites	Response ^c	Reference ^d	Comments
Vesper Sparrow (<i>Poocetes gramineus</i>)	NV	1-2	15,000	w	12	+	3	
	OR, ID, UT, WY, MT	np	np	np	13	0	2	Greater numbers of detections in unburned; not statistically significant.
Lark Sparrow (<i>Chondestes grammacus</i>)	OR	<5	np	np	8	+	6	One burned and one unburned site;
	MT	2-3	220	w	2	-	7	100% sagebrush mortality
	OR, ID, UT, WY, MT	np	np	np	13	0	2	Not detected on burned transects; occurred on 15% of adjacent unburned transects.
Sage Sparrow (<i>Amphispiza belli</i>)	ID	1-7	np	p	4	0	4	45% of treatment plots burned.
	ID	3-21	np	w	164	-	8	Examined cumulative effect of multiple wildfires.
	NV	1-2	15,000	w	12	-	3	
	OR, ID, UT, WY, MT	np	np	np	13	-	2	Absent on burned transects; occurred on 85% of adjacent unburned transects.
Grasshopper Sparrow (<i>Ammodramus saviannarum</i>)	OR	<5	np	np	8	-	6	Density 90% lower in burns.
	MT	2-3	220	w	2	-	7	
Western Meadowlark (<i>Sturnella neglecta</i>)	MT	2-3	220	w	2	0	7	
	UT	3-4	np	p	2	0	5	One burned and one unburned seeding.
	NV	1-2	15,000	w	12	m	3	Difference observed only year one post-fire.
	ID	1-7	np	p	4	0	4	45% of treatment plots burned.
	OR	<5	np	np	8	+	6	
	ID	>5	np	w	119	+	8	Probability of occurrence greater in landscapes with less shrub cover due to recurring wildfire.
	OR, ID, UT, WY, MT	np	np	np	13	-	2	Mean number of detections on burned less than half that of unburned.

^anumber of fires reported for each study = 1.^b+ = increase; - = decrease; 0 = no effect or study inconclusive; m = mixed response.^cw = wildland fire; p = prescribed fire; np = type of fire not provided in source.^dreferences: 1 = Redmond and Jenni 1986; 2 = Welch 2002; 3 = McIntyre 2002; 4 = Petersen and Best 1987; 5 = Castrale 1982; 6 = Reinkensmeyer 2000; 7 = Bock and Bock 1987; 8 = Knick and Rotenberry 1999.

1987). The lack of measurable short-term responses in this and other studies of the effects of disturbance on shrubland birds may be in part attributable to time lags on individual and population responses stemming at least in part from site tenacity by breeding adults (Wiens *et al.* 1986, Knick and Rotenberry 2000).

EFFECTS OF FIRE SUPPRESSION

The expansion of juniper and pinyon woodlands in regions where fire has been suppressed has changed habitat structure and composition of associated bird assemblages. Woodland species, including Ash-throated Flycatcher (*Myiarchus cinerascens*), Pinyon Jay (*Gymnorhinus cyanocephalus*), American Robin (*Turdus migratorius*), Mountain Bluebird (*Sialia currucoides*), Juniper Titmouse (*Baeolophus ridgwayi*), and Western Kingbird (*Tyrannus verticalis*), among others, colonize shrubsteppe habitat once sufficient woodland structure is provided (Medin *et al.* 2000). Brown-headed cowbirds (*Molothrus ater*) also increased in communities having juniper woodlands (Rienkensmeyer 2000, Noson 2002). Shrub cover consistently declined in big sagebrush communities when juniper increased (Tausch and West 1995, Miller *et al.* 2000). Herbaceous vegetation also declined where restrictive soil layers were present (Miller *et al.* 2000). Loss of structural complexity in the shrub and herbaceous layers as a result of woodland development negatively affects many wildlife species. Shrub and ground nesting birds declined as a function of increasing western juniper density (Fig. 3). Brewer's Sparrows had lower nest survival in areas of increased tree density (Welstead 2002) and abundance decreased as a function of proximity to woodland edge (Sedgewick 1987). Thus, reduced use of habitat in or near woodlands may stem in part from avoidance of nest predators.

SAGE-GROUSE AND FIRE

Fire has been promoted widely as a tool to improve habitat quality for nesting and brood-rearing in sage-grouse (Wambolt *et al.* 2002). The primary management objective by using fire is to achieve or maintain a balance of shrubs, forbs, and grasses, at various scales throughout the landscape. In mountain big sagebrush, burns may be conducted to limit the expansion of fire-prone juniper and pinyon to reduce potential perches for raptors and to limit the conversion of shrub steppe habitats. The outcomes of fire on sage-grouse habitat may be a function of site potential, site condition, functional

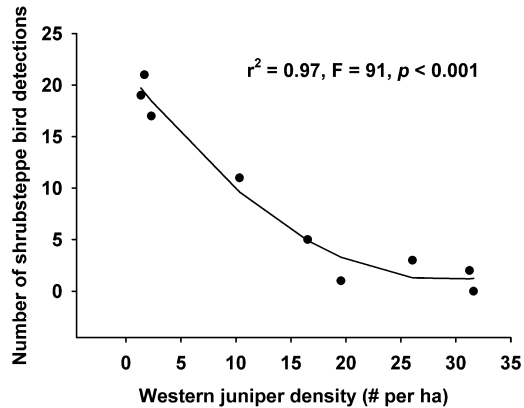


FIGURE 3. Abundance of ground and shrub nesting bird species in relation to density of western juniper trees >8 cm diameter at breast height in Lassen County, California 2002 (Point Reyes Bird Observatory, unpubl. data). Data points represent average values of four point count sampling stations within each study site. The abundance index is the mean number of detections per survey point within 100 m.

plant groups, and pattern and size of burn (Miller and Eddleman 2001).

Direct evidence that prescribed fires have benefited sage-grouse is virtually non-existent (Table 2). A short-term increase in forb production occurs after some fires (Harniss and Murray 1973; Martin 1990; Pyle and Crawford 1996) but not others (Fischer *et al.* 1996; Nelle *et al.* 2000). Forb response following a fire is a function not only of pre-burn site condition but also precipitation patterns. Because recovery of sagebrush canopy cover to pre-burn levels may require 20 yr or longer, short-term benefits of increased forb production may not balance the loss of sagebrush canopy requisite for nesting by sage-grouse (Fischer *et al.* 1996, Nelle *et al.* 2000).

Declines in lek attendance by Greater Sage-Grouse and rates of lek extinction during the 5 yr after a fire were greater in a Wyoming big sagebrush community where 57% of the habitat was affected by a prescribed fire compared to the surrounding regions (Connelly *et al.* 2000). Dramatic declines in populations of Greater Sage-Grouse were correlated with habitat losses from a 2,000% increase in fire incidence in Idaho and subsequent conversion of Wyoming big sagebrush communities to cheatgrass habitats (Crowley and Connelly 1996). Therefore, the usefulness of prescribed fire for sage-grouse in arid sagebrush communities probably is very limited.

Negative impacts from fire exist even in the more resilient mountain big sagebrush communities. For both nesting and brood rearing, Greater Sage-Grouse

TABLE 2. RESPONSE BY SAGE GROUSE AND IMPORTANT BROOD REARING HABITAT FEATURES TO FIRE IN SAGEBRUSH HABITATS.

Response variable	State	Dominant sagebrush type	Years post burn	Response ^a	Reference
Rate of lek loss	ID	Wyoming	1–5	–	Connelly et al. 2000
Lek attendance	ID	Wyoming	1–5	–	Connelly et al. 2000
Nesting use	ID	Wyoming	1–2	0	Martin 1990
	OR	Various	1–60	–	Byrne 2002
Brood rearing use	OR	Various	1–60	–	Byrne 2002
Movement patterns	ID	Wyoming	1–3	0	Fischer et al. 1997
Forb cover	ID	Wyoming	1–3	0	Fischer et al. 1996
	ID	Mountain	>10	0	Nelle et al. 2000
	ID	Mountain	1–2	+	Martin 1990
	OR	Mountain	1–2	+	Pyle and Crawford 1996
Insect abundance	OR	Mountain	1–2	0	Pyle and Crawford 1996
	ID	Wyoming	1–3	–	Fischer et al. 1996
	ID	Mountain	>10	0	Nelle et al. 2000

^a + = increase; – = decrease; 0 = no effect or study inconclusive

avoided burns that were <20 yr old and lacked sagebrush cover (Byrne 2002). In landscapes with a short fire-return interval, unburned areas played an important role in population maintenance.

Although sage-grouse evolved in an ecosystem where fire was an important disturbance factor, fire-return intervals have been lengthened in mountain big sagebrush and shortened in Wyoming sagebrush. Decisions to use or suppress fire for managing habitat for sage-grouse must be made with extreme caution and on a site-by-site basis.

CRITICAL MANAGEMENT QUESTIONS AND RESEARCH ISSUES

Successional dynamics in sagebrush ecosystems are described by state-and-transition models of alternative pathways and thresholds (Westoby 1981, Laycock 1991, Allen-Diaz and Bartolome 1998, West and Young 2000). We need to identify environmental factors, such as plant association, current condition, soil type, elevation, and climate that facilitate transition into undesirable states following fire disturbance. We then need to map those regions that have a high risk of displacement of sagebrush by cheatgrass or that are at risk of pinyon-juniper expansion. Identification of those environmental factors and corresponding maps of risk assessment would greatly assist land managers in understanding the potential effect of fire in sagebrush communities. This information could be used by agencies to prioritize areas for prescribed burning, fire suppression, and rehabilitation activities.

Sagebrush is one of the few habitats in which

large areas of planned burning occurs every year, thus presenting an opportunity to conduct experiments absent in most other areas of North America. Therefore, planned burns provide an opportunity to determine the influence of fire disturbance on sagebrush ecosystems. Study designs that include control sites can be used to identify pre- and post-fire dynamics and to determine causal relationships between birds and habitats. Although most prescribed fires are site-specific, larger-scale objectives also are possible because managers use multiple burns to manipulate landscapes at the large spatial extents used by birds such as sage-grouse (Hann and Bunnell 2001, Morgan et al. 2001). Because distribution and abundance of birds in sagebrush communities is based on a complex process of selection for habitat features (Wiens et al. 1987, Rotenberry and Knick 1999, Knick and Rotenberry 2002), we recommend large-scale (>100,000 ha) and long-term (>10 yr) designs to adequately understand the mechanisms by which birds respond to fire and plant community succession in sagebrush habitats.

We emphasize that demographic parameters such as productivity and survival are a critical component in elucidating the mechanisms by which populations respond to habitat changes due to fire. Except for measures of nest success, no studies have determined the effects of fire on productivity per unit area or age-structured survivorship of birds in sagebrush habitats. Development of demographic models (Caswell 2001) can provide the mechanisms of population response to habitat disturbance but requires the commitment of large-scale and long-term research and funding.

SUMMARY

Fire was a spatially and temporally complex disturbance in the sagebrush biome ranging from 10 to >200-yr return intervals with varying severities in communities dominated by sagebrush (*Artemisia* spp.) and may have been >500 yr in some salt-desert shrub communities. The frequency of fires that completely burn large areas has increased dramatically in some regions, particularly in Wyoming big sagebrush communities at low elevations containing a cheatgrass understory. In other regions, widespread reductions in fire frequency and extent followed the introduction of livestock to western rangelands and resulted in increased shrub cover, loss of herbaceous understory, and increasing rates of woodland encroachment. Populations of bird

species that use sagebrush as their primary habitat declined either from conversion of sagebrush landscapes to cheatgrass dominated grasslands or to increases in woodland cover. We expect that populations of grassland birds, including Long-billed Curlews, Horned Larks, and Burrowing Owls, will increase with greater proportions of grasslands in the landscape. Similarly, increases in pinyon and juniper should benefit populations of bird species associated woodlands.

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