Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes

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Abstract. Sagebrush landscapes provide habitat for Sage-Grouse and other sagebrush obligates, yet historical fire regimes and the structure of historical sagebrush landscapes are poorly known, hampering ecological restoration and management. To remedy this, General Land Office Survey (GLO) survey notes were used to reconstruct over two million hectares of historical vegetation for four sagebrush-dominated (Artemisia spp.) study areas in the western United States. Reconstructed vegetation was analyzed for fire indicators used to identify historical fires and reconstruct historical fire regimes. Historical fire-size distributions were inverse-J shaped, and one fire >100 000 ha was identified. Historical fire rotations were estimated at 171-342 years for Wyoming big sagebrush (A. tridentata ssp. wyomingensis) and 137–217 years for mountain big sagebrush (A. tridentata ssp. vaseyana). Historical fire and patch sizes were significantly larger in Wyoming big sagebrush than mountain big sagebrush, and historical fire rotations were significantly longer in Wyoming big sagebrush than mountain big sagebrush. Historical fire rotations in Wyoming were longer than those in other study areas. Fine-scale mosaics of burned and unburned area and larger unburned inclusions within fire perimeters were less common than in modern fires. Historical sagebrush landscapes were dominated by large, contiguous areas of sagebrush, though large grass-dominated areas and finer-scale mosaics of grass and sagebrush were also present in smaller amounts. Variation in sagebrush density was a common source of patchiness, and areas classified as "dense" made up 24.5% of total sagebrush area, compared to 16.3% for "scattered" sagebrush. Results suggest significant differences in historical and modern fire regimes. Modern fire rotations in Wyoming big sagebrush are shorter than historical fire rotations. Results also suggest that historical sagebrush landscapes would have fluctuated, because of infrequent episodes of large fires and long periods of recovery and maturity. Due to fragmentation of sagebrush landscapes, the large, contiguous expanses of sagebrush that dominated historically are most at risk and in need of conservation, including both dense and scattered sagebrush. Fire suppression in Wyoming big sagebrush may also be advisable, as modern fire rotations are shorter than their historical counterparts.

Key words: fire management; fire rotation; fire-size distribution; historical fire regime; land survey; sagebrush.

INTRODUCTION

Although sagebrush (*Artemisia* spp.) covers approximately 47 million ha of the western United States, historical fire regimes and landscape structure of sagebrush ecosystems are relatively unknown. It is generally thought that fire suppression and land-use change following Euro-American settlement have significantly altered the size, frequency, and severity of fire in sagebrush areas (Miller et al. 2011). For example, cheatgrass (*Bromus tectorum*) invasion has been linked to a cycle of increases in fire intensity and severity that promotes further invasion of cheatgrass and degrades remaining areas of sagebrush (Baker 2006). However, assessing changes to fire regimes and the resulting

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impacts on landscape structure is difficult, because of a lack of data relating to historical fires in sagebrush. For the purposes of this study, we define historical fires as those occurring prior to widespread Euro-American settlement in the late 1800s to early 1900s. Although we define modern fire regimes as post-Euro-American settlement, reliable fire data are only available after 1983 (Baker 2013).

Altered fire regimes may present a significant obstacle for the continued survival of increasingly isolated populations of sagebrush-obligate species. The amount of available suitable habitat, for example, is at least partially determined by the mosaic patterns of burned and unburned areas within a landscape. Small fires, which are often a part of prescribed-burning programs, leave small patches that may be unsuitable for Brewer's Sparrows (*Spizella breweri*) and Sage Thrashers (*Oreoscoptes montanus*; Castrale 1982, Kerley and Anderson 1995). Pedersen et al. (2003) found that small, frequent fires that leave large unburned areas may have positive effects on greater Sage-Grouse (*Centrocercus urophasia-nus*) habitat, but large, infrequent fires resulting in large contiguous burns may lead to the extirpation of local populations.

The effectiveness of fire management in sagebrush depends on a solid understanding of historical fire-size distribution, rotation, and patchiness, which are largely unknown. Previous understanding of fire rotation is largely derived from fire scars in adjoining woodlands rather than sagebrush (e.g., Miller et al. 2011), requiring corrections to estimate what fraction of the fires actually burned in the sagebrush (Baker 2006). For example, mean composite fire intervals (mean CFIs) are commonly cited, but are unstable, decreasing as the number of fire scars and the area sampled increase (Arno and Peterson 1983), and have other limitations (Baker 2011). Only paleo-estimates are derived directly from sagebrush landscapes, but few are available (Mensing et al. 2006, Jacobs and Whitlock 2008, Nelson and Pierce 2010). None of these sources provides information about fire sizes or patchiness.

The extent of unburned area inside historical fire perimeters is also poorly known. Fire intensity and the resulting mosaic of burned and unburned area are a function of available fuel, shrub density, moisture, winds, and other factors (Sapsis and Kauffman 1991, Wright and Pritchard 2006). Fine-fuel amounts and fuel continuity in modern sagebrush landscapes have often been elevated by cheatgrass invasion, but also often have been severely reduced by overgrazing, raising the possibility that historical fires may have had less unburned area (Baker 2006). Wrobleski and Kaufman (2003) suggested that large, unfragmented expanses of sagebrush and drier burning conditions may also have made historical fires less patchy than their modern counterparts. Baker (2013) found that modern sagebrush fires leave an average of 20% unburned area within fire perimeters, but historical unburned area is unknown.

It is likely, however, that fire regimes were not consistent across all sagebrush-dominated landscapes, in part because sagebrush taxa and fuels recover differently after fires. Although three-tip (A. tripartita) and silver sagebrush (A. cana) may be capable of resprouting (White and Currie 1983), fires in most western sagebrush are typically stand replacing (Baker 2006). Post-fire recovery in sagebrush occurs slowly due to low seed survival following fires, generally low seed viability (<1 year, Miller et al. 2011) and slow seed dispersal rates. Seed dispersal from surviving plants is limited to short distances near the fire perimeter or around unburned plants within the burned area (Mueggler 1956). Full recovery in mountain big sagebrush may take 75 or more years following a large fire, or may occur more rapidly (within 25-35 years) following a small fire (Baker 2011). For particularly large fires, seeds may take up to 70 years to reach the center of the burned area (Welch and Criddle 2003), increasing full recovery time in mountain big sagebrush to 75–100 years (Baker 2011). The time required for full recovery in Wyoming big sagebrush is unknown, but likely much longer (Baker 2011). Recovery periods have been used to estimate sagebrush fire rotations, but estimates are based on limited data (Baker 2011).

Fire regimes may also vary among floristic provinces. Using modern data, one study found that number of fires and area burned increased in all provinces except the Snake River Plain from 1980-2007 (Miller et al. 2011). Average fire size remained unchanged, except in the Southern Great Basin, where it increased. Fire location was strongly correlated with cheatgrass, particularly in the Snake River Plain and Great Basin. However, subsequent analysis with more complete data found no significant trend in area burned from 1984-2008 (Baker 2013). Estimated fire rotations by province differed, ranging from 92 years in the Snake River Plain to 1755 years on the Colorado Plateau. In contrast, fire rotations did not differ significantly among sagebrush taxa, suggesting that province-scale climate had more effect, than fuels and vegetation, on recent fire.

Lack of evidence about historical fire leaves unresolved competing ideas about the structure of historical sagebrush landscapes. One common view is that historical fire regimes in sagebrush left large, contiguous areas of sagebrush and restricted piñon-juniper (Pinus edulis or P. monophylla with Juniperus spp.) woodlands to fire-safe sites, such as rocky uplands (Davies et al. 2011, Miller et al. 2011). However, large historical fires could have instead resulted in large areas dominated by grasses or other early-successional vegetation. Alternatively, fire regimes consisting of many small fires may have left a finer-scale mosaic of sagebrush and grass (Klebenow 1972). In contrast, Vale (1975) found that the majority of sagebrush landscapes were covered by thick stands of sagebrush, with grasslands limited to wetter valley bottoms or canyons or, more rarely, to mountain slopes. More recent studies have attributed the presence of dense sagebrush to grazing and fire suppression (e.g., Miller et al. 1994). Patterning in sagebrush-woodland landscapes may also link to a combination of fire and environmental setting, including topography and soils (e.g., Miller and Heyerdahl 2008). Until historical fire regimes are better understood, historical landscape structure will also remain uncertain.

As shown above, estimates of historical fire regimes in sagebrush are handicapped by a lack of data derived directly from sagebrush areas. One promising and underutilized source, which we employ to reconstruct historical fire regimes and sagebrush landscapes, is the use of General Land Office (GLO) surveys conducted prior to, or near the time of, Euro-American settlement, typically from about AD 1860–1900. Surveyors recorded dominant plants in order of abundance, bearing-tree diameters and species, and boundaries between vegetation communities (Galatowitsch 1990). Researchers

Hypothesis	Description							
H_1	Historical (i.e., pre-Euro-American settlement) fire-size distributions were inverse J-shaped, consisting of many small fires and few large ones.							
H_2	Historical sagebrush fires were patchy, as are some modern fires, leaving an average of 20% or more of the area unburned within the fire perimeter.							
H_3	Historical fire rotations are within the ranges estimated by Baker (2011): low sagebrush, >200 yr; mountain big sagebrush, 150–300 yr; Wyoming big sagebrush, 200–350 yr.							
H_4	Historical fire rotations and size differed by sagebrush taxa, and fire rotations within sagebrush taxa were the same across floristic provinces.							
H_5	Historical landscapes were commonly dominated by large contiguous patches of sagebrush interrupted by piñon-juniper woodlands on rocky areas.							
H_6	Some historical landscapes were dominated by large contiguous patches of grassland or resprouting shrubs from large fires, with smaller inclusions of unburned sagebrush.							
H_7	Some historical landscapes had finer mosaics of sagebrush and grass, as a result of smaller fires that burned at lower intensity.							
H_8	Historical landscapes differed among areas dominated by different sagebrush taxa, but not among regions.							
H_9	Historical sagebrush landscapes were dominated by low or moderate density sagebrush.							

TABLE 1. Hypotheses to be tested.

have successfully used section-line descriptions to reconstruct historical vegetation and measure change in a few western non-forested areas (Buffington and Herbel 1965, Gibbens et al. 2005, Fritschle 2008 and 2009). By focusing on post-fire successional characteristics recorded within the surveys, it may be possible to reconstruct historical vegetation patterns and the disturbance regimes that helped create and maintain them in sagebrush landscapes.

This study tests nine hypotheses that address the incomplete understanding, reviewed above, about historical sagebrush fire regimes and historical landscapes (Table 1). First, we reconstruct and analyze multiple parameters of historical fire regimes, including fire-size distributions, patchiness, and fire rotations, in order to compare them across study areas and sagebrush types, as well as with modern fire regimes, to test four hypotheses (H_1 - H_4 in Table 1). Second, we examine historical landscape structure by identifying major landscape types and determining the relative amounts of dense and scattered sagebrush present historically $(H_5-H_9$ in Table 1). To do this, we use historical vegetation data, contained in the original GLO survey notes, to reconstruct historical vegetation and potential fires. We focus on Wyoming big sagebrush (A. tridentata ssp. wyomingensis) and mountain big sagebrush (A. tridentata ssp. vase yana), because these taxa are dominant throughout much of the western United States and are present in large amounts in all study areas. However, substantial amounts of low sagebrush (A. arbuscula), black sagebrush (A. nova), and dwarf sagebrush (A. arbuscula ssp. longicaulis, A. arbuscula ssp. longiloba, and A. nova) were also present in some study areas, and are included in the analysis where possible.

Methods

Study area selection

We selected four study areas totaling 351 townships, including one from each of the four major sagebrushdominated provinces in the western United States (Fig. 1). GLO vegetation data were available for 2.8 million ha of the total area, of which approximately 2.2 million hectares were sagebrush, associated grasslands, or sagebrush with other shrubs. We initially selected study areas based on (1) the presence of large contiguous areas of sagebrush today, (2) designation as key habitat area for Greater Sage-Grouse (Doherty et al. 2010) or other protected areas, and (3) the presence of a mixture of mountain big sagebrush and Wyoming big sagebrush.

We further refined study areas at the township level based on the date and quality of information in the original GLO surveys. Surveys conducted at or near the time of Euro-American settlement were preferred to limit the effects of settlement. For our study areas, earliest survey years varied from 1868 in Nevada to 1875 in Oregon, median survey years varied from 1881 in Wyoming to 1892 in Idaho, with third quartiles from 1881 in Wyoming to 1910 in Oregon. Surveyors were instructed to record houses, fields, livestock, and other evidence of settlement, but in only a few cases did surveys mention evidence of settlers. Also, although livestock grazing undoubtedly had begun in some sample areas, fires were detectable and reconstructed for periods of 35-80 years prior to the survey date (see Area of interest and fire identification), so the record in most areas extends before livestock introduction or before widespread grazing. Many survey lines were recorded as having "good grass" or "excellent grass," suggesting potential value for future grazing and little or no impact evident yet from livestock. Lines surveyed in later years generally were in rugged, mountainous terrain or land unfit for agriculture, among the last areas settled. The best surveyors distinguished areas of dense and scattered vegetation, sagebrush height, and specific species of grass and shrubs. Usable surveys specifically mentioned sagebrush, grass, and timbered areas. We excluded surveyors who consistently did not record vegetation along section lines or were ambiguous (e.g., only "good grazing") were excluded. We checked for survey fraud by comparing survey plat maps to

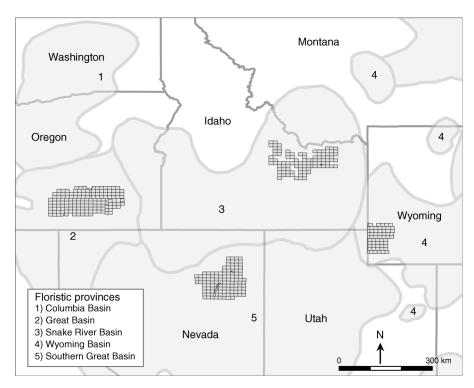


FIG. 1. Study area locations (townships) and floristic provinces (from Stiver et al. 2006) in the main part of the range of sagebrush in the western United States.

current topographical maps (Livermore 1991), but none was found.

Data entry and polygon creation

We entered section-line descriptions, including beginning-of-line information, end-of-line summaries and entry/exit points recorded along the line, into ArcGIS (ESRI, Redlands, California, USA) using a form to record the surveyor's descriptions verbatim and to classify vegetation according to vegetation type, vegetation density, understory, and understory density. We defined vegetation by the tallest layer of plants, and entered shorter layers as understory. Data entries were linked to a specific directional route in an ArcGIS database created from section/township line and polygon files from BLM's Geographic Coordinate Database (*available online*).² The data set contained 35 541 surveyor observations representing 41 653 km of section lines.

Once we completed the initial data entry, we reclassified line segments into broader categories to focus the analysis (Table 2). New codes preserved detail in areas dominated by sagebrush, grassland, grass-and-sagebrush mosaic, rabbitbrush (*Chrysothamnus* spp.), and areas where sagebrush was the first or second shrub listed (as surveyors were instructed to list plants in order of abundance). Where surveyors indicated small patches

of sagebrush mixed with grass, but did not give specific entry or exit points for sagebrush patches, we have interpreted fine-scale patchiness and used the term "grass-and-sagebrush mosaic." We use this term to distinguish these areas from areas described as "scattering sagebrush," which we have interpreted as nonpatchy, low-density sagebrush, or areas with larger sagebrush patches for which surveyors recorded entry and exit points.

Next, we converted reclassified lines to Thiessen polygons in ArcGIS to enable analysis of patches and landscape composition. Thiessen polygons are generated using a set of spatially distributed points, each of which becomes the seed for one Thiessen polygon. Each Thiessen polygon surrounds the area that is closer to its seed point than to any other seed point (Rhynsburger 1973). First, we removed line segments shorter than 160 m, because they create unnatural patchiness due to the pattern of the survey lines. We converted the remaining line segments to midpoints, which we then used to generate the Thiessen polygons. The polygon creation process automatically assigned spaces left by removing short segments to the adjacent vegetation types. We then dissolved adjacent polygons with the same reclassification to form single "patches" that we used to create patch-size distributions and calculate patch statistics. Our trials of the procedure using modern data showed that removing segments shorter than 160 m gave the most statistically accurate reconstruction of patch sizes and patch size distribution (Appendix A). These

² http://www.geocommunicator.gov

TABLE 2. Vegetation classification codes used in the study.

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CC)u	65

Codes	
Main†	
Black sagebrush Black sagebrush–sagebrush Burned Grassland Grass-and-sagebrush mosaic Rabbitbrush Sagebrush–bitterbrush Sagebrush–bitterbrush Sagebrush–greasewood Sagebrush–mountain shrubs‡ Sagebrush–shadscale Sagebrush–winterfat	
Other categories	
Shrub Bitterbrush dominant Greasewood dominant Mountain shrubland‡ Shadscale dominant Winterfat dominant	
Woodland	
Aspen Fir/pine/spruce Mahogany Piñon–juniper	
Other	
Dead timber No vegetation Not recorded Riparian vegetation Unidentified understory Unidentified woodland	

Notes: Species include bitterbrush (Purshia tridentata), black sagebrush (Artemisia nova), curlleaf mountain mahogany (Cercocarpus ledifolius), fir (Abies spp. or Pseudotsuga menziesii), greasewood (Sarcobatus vermiculatus), juniper (Juniperus spp.), pine (Pinus spp.), piñon pine (Pinus edulis or P. monophylla), quaking aspen (Populus tremuloides), rabbitbrush (Chrysothamnus ssp.), shadscale (Atriplex confertifolia), spruce (Picea spp.), and winterfat (Krascheninnikovia lanata).

[†]Where surveyors provided additional information, the following modifiers were used as appropriate: with trees, dense, dense with trees; scattered, scattered with trees. Modifiers are only used with the main codes. "With trees" is used when scattering timber is present with a main-code understory. These categories were not included in the area of interest (AOI).

[‡] Includes all shrubs not specifically mentioned elsewhere that occur at higher elevations. Common surveyor names include snowbrush (*Ceanothus velutinus*), chokecherry (*Prunus virginiana*), mountain brush (unknown), manzanita (*Arctostaphylos patula*), and chaparral (unknown).

segments represented only 0.25% of total line length for the main codes (Table 2), and their removal did not significantly affect results (Appendix A: Table A1), except that the smallest patches were excluded from analysis.

Area of interest selection and fire identification

We used the reconstructed vegetation map to select a final area of interest (AOI) for locating possible sagebrush fires for hypothesis testing. The AOI contained all polygons classified as sagebrush, grass-andsagebrush mosaic, rabbitbrush, or sagebrush with a codominant shrub (Table 2, main codes). However, we excluded grasslands that clearly corresponded to mapped wetlands, springs, or current riparian vegetation, because these areas were not likely successional to sagebrush. We did include burned areas identified by the surveyors if ReGAP data indicated current vegetation was sagebrush (data available online).³ We did not include "with trees" categories in the AOI for fire analysis, as they are not clearly historical sagebrush, and could represent post-fire recovery in woodlands, temporary invasion of sagebrush or grassland by trees, or natural transitions between sagebrush and forest. We identified excluded areas using topographic maps, current ReGAP vegetation data, and USFWS National Wetland Inventory data (data available online).⁴

We identified historical fires within the AOI using various fire indicators (Table 3). We primarily based identification on the presence of post-fire successional vegetation, such as areas dominated by grasses or resprouting shrubs or areas of scattered sagebrush, often combined with contextual evidence, particularly adjacent unburned vegetation. In some cases where grasslands were recorded by surveyors, fire presence was uncertain, because context and modern vegetation data were not persuasive for either including or excluding the patch as a potential fire. We marked these patches as ambiguous. Where surveyors recorded entire townships of "scattered sagebrush," these townships were also marked as ambiguous, unless part of a larger burned area with either (1) a clearly defined boundary between scattered and denser sagebrush in another township or (2) unburned patches of denser sagebrush or other vegetation in another part of the fire. In areas dominated by mountain big sagebrush, we did not include ambiguous patches of scattered sagebrush in fire-related calculations. We chose to do this because mountain big sagebrush often occurs in association with abundant amounts of grasses and shrubs (Welch and Criddle 2003), resulting in a grass-dominated appearance and potentially lower shrub densities. Finally, because township boundaries were generally surveyed separately from township interiors, we did not include patches that included only township boundaries, and did not match vegetation within the township interiors, as potential fires.

We grouped patches into fire events by adjacency and successional stages. We grouped patches if directly adjacent or connectable through the middle of a section, where Thiessen polygons are less definitive. We also grouped patches if separated by less than two sections of scattered sagebrush with trees, as the scattered sagebrush suggests the fire may have burned through these areas. For adjacent patches surveyed in different years, we grouped earlier post-fire successional stages (e.g.,

³ http://gapanalysis.usgs.gov

⁴ http://www.fws.gov/wetlands/index.html

TABLE 3. Fire indicators used in the study.

Indicator	Description
Recorded vegetation had post-fire characteristics	
Grasses dominant	For example, terms include grass, bunchgrass, grassland.
Resprouting shrubs common or dominant	For example, rabbitbrushes (<i>Chrysothamnus</i> spp., <i>Ericameria</i> spp.) or horsebrushes (<i>Tetradymia</i> spp.).
Scattered sagebrush dominant	Only if patches had clearly defined outer boundaries with denser sagebrush and/or other vegetation types or included internal areas of denser sagebrush; also, patches did not correspond to ReGAP patches of low density sagebrush types (e.g., low sagebrush).
Grasslands or resprouting shrubs were successional, not persistent vegetation	Grasslands did not correspond to present wetlands, rivers, major creeks, springs, or riparian vegetation, suggesting they were not persistent grasslands; grasslands or resprouting shrubs have shown "recovery" and are now dominated by sagebrush, suggesting they were successional.
Adjoining non-sagebrush vegetation had post-fire characteristics	Described as "burned" or "dead trees," suggesting fire also burned into these areas.
Potential fire areas were bounded relatively sharply by vegetation that does not appear to have burned recently, suggesting a fire boundary	Non-scattered or dense vegetation, including sagebrush, other shrubs, sagebrush with other shrubs, or woodlands dominant; resprouting shrubs were not common or dominant.

Note: Indicators are based on reviews of post-fire succession in sagebrush (Blaisdell 1953, Lesica et al. 2007, Baker 2009).

"grassland"), surveyed at earlier dates, with later successional states (e.g., "scattered sagebrush") that were surveyed later, if they were congruent with a single event. We assessed this using estimated post-fire recovery times for Wyoming and mountain big sagebrush (from Baker 2011). We assumed that historical and modern fire-recovery rates were similar, and that the time to reach 30% of pre-burn cover in mature, nonscattered stands of sagebrush following modern fires would be the same length of time surveyors would have described sagebrush as scattered following historical fires (Fig. 2). Thus, we grouped adjacent patches in areas that are currently Wyoming big sagebrush, if surveyed less than 80 years apart, and adjacent patches in areas currently mountain big sagebrush, if surveyed less than 35 years apart. We grouped adjacent patches now in low sagebrush at 80 years or less, and areas now with both mountain and Wyoming big sagebrush at 35 years or less. Although these periods may seem long, multiple studies have documented that sagebrush remains in a grassy or scattered condition for decades after fire (e.g., Blaisdell 1953, Lesica et al. 2007, Baker 2009; Fig. 2).

Hypothesis testing

We tested our hypotheses both including ambiguous fire patches and with ambiguous patches excluded, and have qualified our results accordingly. We assessed firesize distributions (H_1) by calculating the areas of individual patches and fire events and using these data to construct patch-size and fire-size distributions. We measured unburned area (H_2) by calculating the percentage of unburned area relative to the total area within all fire perimeters for fires with a burned area larger than 500 ha, the approximate minimum area within which GLO data can detect unburned area. We drew fire perimeters using the Feature to Polygon tool in ArcGIS. We included unburned areas that were within the fire perimeter but not part of the AOI if they could reasonably be assumed to be unburned (e.g., dense sagebrush with trees, woodlands, or dense non-sagebrush shrub-cover). We did not include areas of scattered sagebrush with trees, grassland with trees, or areas with no vegetation data in the unburned area, because of the same ambiguities that led us to exclude all "with trees" categories from the AOI. We interpreted areas where surveyors recorded grass-and-sagebrush mosaic or mixed-density sagebrush, but did not provide specific entry or exit points, as a fine-scale mosaic of burned and unburned area, which we assessed by calculating the percentage of these areas relative to total burned area.

We calculated fire rotations (H_3) for historical sagebrush areas that are presently sagebrush, and adjacent expanded areas that were sagebrush at the time of the surveys, but are presently grasslands, humanaltered vegetation (e.g., developed areas, croplands or pastures, introduced vegetation), or recently burned areas. We did not include GLO-surveyed sagebrush areas that are currently woodlands, as these could result from trees invading historical sagebrush or from postfire succession from sagebrush to woodland. Estimates using these expanded categories were not significantly different from those derived from ReGAP sagebrush alone (Appendix B: Tables B1 and B2). We considered estimated fire-rotation ranges to be within the expected ranges (Table 1) if (1) the entire estimated range was within the expected range or (2) either the lower or higher limit of the estimated range was outside of, but within 50 years of the expected range, but not both.

We calculated fire rotation by intersecting the AOI with ReGAP data, calculating the total area and burned area for each ReGap category, and dividing the period of observation by the percentage of each category's area that burned, a standard formula (Baker and Ehle 2001). We used 40–80 years as the period of observation in areas dominated by Wyoming big sagebrush or low

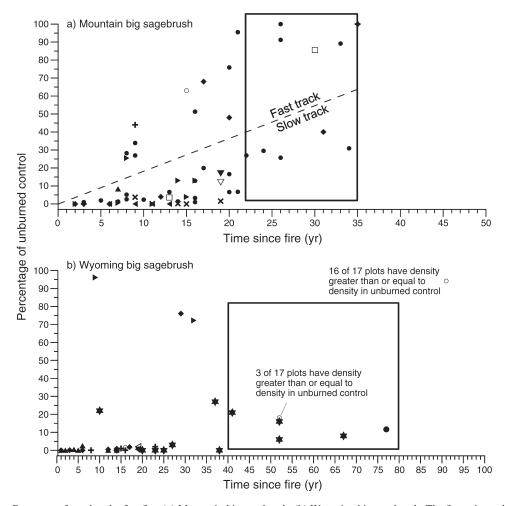


FIG. 2. Recovery of sagebrush after fire: (a) Mountain big sagebrush, (b) Wyoming big sagebrush. The figure is modified from Fig. 11.3 in Baker (2011), reprinted with permission of the University of California Press (© Cooper Ornithological Society). The boxed area represents the range of recovery values used in this study to calculate fire rotations. Each symbol represents a single sample plot from all known studies, indicated by different symbols, in the western United States, except that points from one study were omitted for data <20 years for which no recovery had occurred. The fast-track and slow-track line indicates a potential difference in recovery rates for mountain big sagebrush, but fast-track recovery is rarer. Stands used were mature, meaning that pre-burn cover was not scattered and showed only minor variations between studies.

sagebrush and 22–35 years for areas dominated by mountain big sagebrush. Ranges are based on Baker's (2011) graphs of post-fire recovery in sagebrush (Fig. 2). The lower limit represents the approximate time when all plots included in the study had greater than 0% sagebrush cover, and the upper limit is the approximate time to reach 30% cover relative to an unburned control (Baker 2011). Beyond 30% cover, it is doubtful that a surveyor would describe vegetation as "scattered."

Finally, we compared mean patch size and fire rotation between sagebrush categories (H_4) using t tests (Ott 1988). We compared mean patch size for Wyoming big sagebrush and mountain big sagebrush, the only two categories with sufficient sample area, using a standard two-sample t test of geometric mean patch size, with each study area serving as a replicate. We compared fire rotations for the two taxa using paired t tests to

minimize differences between individual study areas. For the paired t test, we used average fire rotations from each study area and the upper and lower limits of each estimated range. Since Wyoming's fire rotations were consistently longer than those in other study areas, we also performed the tests using the other three study areas alone. Because this study included only one estimated fire rotation per taxa for each province, we compared estimated fire rotations among study areas, but did not subject them to significance testing.

We analyzed overall landscape composition using the presence and proportion of specific landscape compositions (H_5-H_8) by study areas and by sagebrush taxa. Our factors of interest were: (1) dominant vegetation type, (2) presence or absence of other vegetation types interrupting the dominant vegetation type, and (3) relative patch size of the dominant and interrupting

			Patches			Fires				
Study area	Total area for AOI (ha)	Total burned area (ha)	Number	Minimum area (ha)	Maximum area (ha)	Geometric mean area (ha)	Number	Minimum area (ha)	Maximum area (ha)	Geometric mean area (ha)
Idaho	585 835	123 645	123	22	47 591	156	72	40	47 966	257
		(176 644)	(159)	(22)	(47 591)	(174)	(87)	(48)	(48 069)	(322)
Nevada	509 575	57 515	144	18	9 167	135	65	33	32 143	209
		(83 524)	(150)	(18)	(21 975)	(137)	(71)	(33)	(37 668)	(225)
Oregon	674 119	144 828	86	18	105 168	207	48	23	126 164	226
-		(184 716)	(110)	(18)	(131 633)	(210)	(57)	(23)	(156 434)	(231)
Wyoming	424 153	15 611	29	35	3 884	257	17	35	9 888	260
		(44 803)	(36)	(35)	(24 556)	(318)	(19)	(35)	(24 749)	(379)
Total	2 194 284	341 599	382	18	105 168	164	202	23	126 164	233
		(489 687)	(455)	(18)	(131 633)	(176)	(234)	(23)	(156 434)	(270)

TABLE 4. Sizes of identified historical (i.e., pre-Euro-American-settlement) fire patches and fires.

Notes: Table entries include results for non-ambiguous patches and, in parenthesis, for non-ambiguous plus ambiguous patches. Ambiguous patches either were grassland patches or were entire townships surveyed as "scattered sagebrush" both lacking in sufficient context to identify them clearly as fires. AOI stands for area of interest.

vegetation types. We included vegetation classes outside the AOI as interruptions, but did not use them as dominant vegetation types. For landscape types dominated by a single vegetation type, we did not consider patches as dominant unless their total area was about one township (9324 ha) or greater. Once we identified landscape types and associated taxa, we compared them between the two sagebrush taxa and across study areas by calculating the percentages of landscape types for each AOI. We also calculated total area classified as sagebrush with trees, or sagebrush and a codominant shrub with trees, for each study area. To test H_9 , we examined variation in sagebrush density by calculating the percentages of total sagebrush area that were scattered and dense and the number of patches belonging to each class.

RESULTS

We calculated results including and excluding ambiguous patches. To simplify, we have reported detailed results, calculated including ambiguous patches, in the text. Where results excluding ambiguous patches differed, we have also summarized or reported appropriate statistics in the text. Tables include both sets of results.

Estimated parameters of historical fire regimes

We identified a total of 455 potential fire patches, of which 73 were ambiguous (Table 4). Regarding H_1 , that historical fire-size distributions were inverse J-shaped, patch-size and fire-size distributions, pooled across all study areas, were indeed inverse-J shaped (Fig. 3a, b), so we did not reject H_1 . Distributions for individual study areas were also inverse-J shaped (Fig. 3c–i). We identified one fire >100 000 ha in Oregon, and maximum fire sizes ranged from 24 749 ha in Wyoming to 156 434 ha in Oregon. When ambiguous patches were excluded, maximum fire sizes were smaller, ranging from 9888 ha in Wyoming to 126 614 ha in Oregon (Table 4). Three of the largest fires had a clear southwest-tonortheast orientation (Fig. 4).

We rejected hypothesis H_2 , that historical sagebrush fires were patchy, leaving an average of 20% or more of the area unburned, as unburned area (e.g., Fig. 4) accounted for only 3.5% of total area within fire perimeters, for fires pooled across all study areas (Table 5). Unburned area ranged from 0.3% in Wyoming to 6.9% in Idaho. When we considered only fires with unburned area within the fire perimeter, unburned areas were 4.0% of the combined total area within fire perimeters. Wyoming had the least unburned area, 0.5%, and Idaho had the most, 8.0%. Surveyors recorded fine-scale mosaics of burned and unburned area in Idaho, Nevada, and Oregon, and these accounted for 3.5% of total burned area in these three study areas (Table 6). When we considered only fires with fine-scale mosaics, these areas made up 7.0% of total burned area. The amount of fine-scale mosaics showed greater variability than larger unburned areas, ranging from 0.5% in Oregon to 16.5% in Nevada.

We did not reject hypothesis H_3 for Wyoming big sagebrush, that historical fire rotations are within previously estimated ranges (Baker 2011), as the overall fire rotation was 171-342 years (Table 7). No study area had an estimated range that fell entirely within the expected range; however, estimated values for Idaho, excluding ambiguous patches, met the expected range with an estimated fire rotation of 169-338 years. We also did not reject hypothesis H_3 for mountain big sagebrush, which had an overall estimated fire rotation of 137-217 years (Table 7). Our estimated ranges for Idaho and Nevada also met the expected range, while estimates for Oregon and Wyoming were completely outside of it. Values for Oregon ranged from 48-77 years, and values for Wyoming ranged from 588-2139 years. Values for these study areas may have been affected by small sample sizes of mountain big sagebrush in Oregon (14966 ha) and identified fires in Wyoming (19, including ambiguous patches). We estimated fire rotations for low sagebrush, only available in Oregon, at 93-187 years, so we rejected H_3 for low sagebrush. No

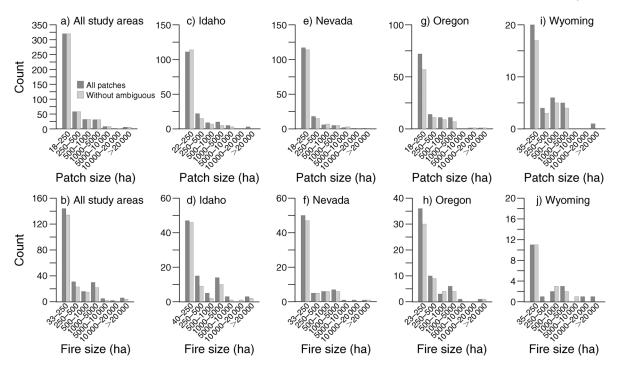


FIG. 3. Historical (i.e., pre-Euro-American settlement) patch-size and fire-size distributions: (a) combined patch-size distribution for all study areas, (b) combined fire-size distribution for all study areas, (c) patch-size distribution for Idaho, (d) fire-size distribution for Idaho, (e) patch-size distribution for Nevada, (f) fire-size distribution for Nevada, (g) patch-size distribution for Oregon, (h) fire-size distribution for Oregon, (i) patch-size distribution for Wyoming, and (j) fire-size distribution for Wyoming.

previous estimates were available for black or dwarf sagebrush for comparison, but both exceeded 1200 years. When we excluded ambiguous patches, estimated fire rotations were longer. However, our estimated fire rotation for all study areas was still within the expected range for mountain big sagebrush, but was longer than the expected range for Wyoming big sagebrush.

When we compared mountain big sagebrush and Wyoming big sagebrush, our two-sample *t* test showed significant differences in geometric mean patch- and firesize for $\alpha = 0.05$ (for patches t = 3.83, df = 549, P = 0.000; for fires t = 2.10, df = 158, P = 0.038). Both geometric mean patch and fire size were larger in Wyoming big sagebrush. Both patch and fire sizes remained significantly different between the two taxa ($\alpha = 0.05$) when ambiguous patches were excluded (Appendix B: Table B3). Therefore, we did not reject hypothesis H_4 , that historical fire size differed by sagebrush taxa, for both patch and fire size.

When we compared fire rotations for mountain big sagebrush and Wyoming big sagebrush, for data pooled across all four study areas, the only significant difference ($\alpha = 0.10$) was in the lower limit of estimated fire rotations, excluding ambiguous patches (t = 4.13, df = 3, P = 0.026). When we excluded Wyoming, differences were nearly significant ($\alpha = 0.10$) for the average fire rotation and the upper limit of estimated rotations (for average t = 0.125, df = 2, P = 0.125; for upper limit t = 2.83, df = 2, P = 0.106). We found significant differences $(\alpha = 0.10)$ when ambiguous patches were excluded, and when comparing the lower limits of estimated rotations (Appendix B: Table B3). We could not perform significance testing for differences in fire rotation among study areas. However, estimated fire rotations for mountain big sagebrush in Wyoming and Oregon did not overlap with estimated rotations for any of the other study areas. Additionally, when we excluded ambiguous patches, the estimated fire rotation for Wyoming big sagebrush in Wyoming also failed to overlap with estimated ranges from the other study areas. Some of these differences may be attributed to small sample sizes. Because of these differences in fire rotation between taxa and study areas, we did not reject the first part of hypothesis H_4 , that historical fire rotations differed by sagebrush taxa, but did reject the second part of H_4 , that historical fire rotations within sagebrush taxa were the same across floristic provinces.

Historical landscape composition

We did not reject hypotheses H_5 - H_7 , as we identified all three landscape compositions (Fig. 5) within at least one study area. Large contiguous expanses of sagebrush (the landscape type corresponding to $H_{5;}$ Fig. 5a) were the most dominant landscape type, common across wide, gentle sagebrush plains or valley bottoms dominated by Wyoming big sagebrush and slopes dominated by either Wyoming big sagebrush or mountain big sagebrush. These areas, typically covering multiple townships, were found in all study areas. This landscape type represented from 70% to 92% of the AOI in all study areas, with a pooled value of 82%. For individual study areas, 66-85% of this landscape type was associated with Wyoming big sagebrush, with a pooled value of 77%, and from 1% to 20% was associated with mountain big sagebrush, with a pooled value of 11%. Other sagebrush types were also present in Oregon, Nevada, and Wyoming. Though dominant, sagebrush was occasionally interrupted by piñon-juniper woodlands in rocky areas (as in H_5) or small patches of grass or other shrubs. Quaking aspen (Populus tremuloides) and curlleaf mountain mahogany (Cercocarpus ledifo*lius*) were also present in small amounts, often near areas of mountain big sagebrush. In these areas, forest tended to occur at the upper boundary of the sagebrush rather than as patches on rocky areas within the sagebrush.

However, unlike the typical idea of H_5 , we also identified a large amount of sagebrush with trees, or sagebrush and a codominant shrub with trees included in this landscape type. These areas were found in both sagebrush types; however, 75% was associated with Wyoming big sagebrush or other low-elevation sagebrush types, while only 25% was found in areas of mountain big sagebrush. Total area of sagebrush with trees, or sagebrush with a codominant shrub with trees, was 204 493 ha. Nearly 60% of this was in Nevada. Total area of these categories found in each study area ranged from 3.5% of the AOI in Idaho to 23.4% in Nevada. Oregon and Wyoming had similar amounts, 6.9% and 5.1%, respectively. Of these areas, 83.9% was found in large contiguous areas of sagebrush, the landscape type corresponding to H_5 . When we considered only areas of sagebrush with trees, not sagebrush and a codominant shrub with trees, 97.8% of the total 167 544 ha was associated with this landscape type. Areas of sagebrush with trees were found (1) as isolated patches within the larger sagebrush landscape, (2) in clusters of small- or medium-sized patches mixed with similarly sized patches of sagebrush, and (3) as patches near woodland edges.

We found large contiguous areas dominated by grass or resprouting shrubs resulting from fires, the landscape type corresponding to H_6 (Fig. 5b), in Idaho and Oregon, the study areas with the most total burned area (Table 4). Respectively, these areas covered approximately 1% and 21% of the AOI for the two study areas. We found only small grass-dominated areas in Nevada and Wyoming. In Oregon, ReGAP data indicated that these areas were primarily Wyoming big sagebrush, with a single area dominated by mountain big sagebrush along the southeastern edge. In Idaho, grassy areas included both Wyoming and mountain big sagebrush.

Nevada was the only study area with significant amounts of fine scale grass-and-sagebrush mosaic, the landscape type corresponding to H_7 (Fig. 5c), covering



FIG. 4. Part of a historical (i.e., pre-Euro-American settlement) fire in eastern Idaho showing a distinct southwest-to-northeast orientation. Large unburned areas of dense sagebrush are present within the fire perimeter.

roughly 6% of the AOI. This occurred at lower elevations dominated by Wyoming big sagebrush, and landscape composition in the area consisted of patches of mosaic intermixed with similarly sized patches of sagebrush or grassland.

We identified a fourth landscape type, consisting of small intermixed patches of sagebrush, woodlands, and other shrublands (Fig. 5d), in all four study areas, covering from 2-5% of the AOIs in individual study areas or 4% of the pooled AOI area. This landscape type was associated with mountain big sagebrush and showed greater variety in the types of woodlands, shrublands, and codominant shrubs present than the other landscape types. Woodlands included quaking aspen, curlleaf mountain mahogany, and a variety of conifers. Common shrublands included chaparral (unknown), montane shrublands (Arctostaphylos patula, Ceanothus velutinus, Prunus virginiana, and other unknown species), and bitterbrush (Purshia tridentata). We also saw patches of sagebrush with trees, or sagebrush and a codominant shrub with trees. Of the 28 668 ha classified as sagebrush and a codominant shrub with trees, 71.4%was associated with this landscape type, mostly (18 160 ha or 63.3%) in Nevada.

Study area		All	fires with burned a	area >500 ha	Fires with unburned area only			
	Unburned patches within fire perimeters (ha)	Number of fires	Total area within fire perimeters (ha)	Unburned area as a percentage of total area (%)	Number of fires	Total area within fire perimeter (ha)	Unburned area as a percentage of total area (%)	
Idaho	11 988	16	127 916	9.37	8	115 743	10.36	
	(12 310)	(25)	(178 926)	(6.88)	(9)	(154 583)	(7.96)	
Nevada	865	13	51 420	1.68	2	35 557	2.43	
	(1 959)	(16)	(81 856)	(2.39)	(4)	(64 199)	(3.05)	
Oregon	2 575	<u>)</u> 9	174 082	1.48	4	170 069	1.51	
e	(3 824)	(11)	(217 999)	(1.75)	(4)	(209 570)	(1.82)	
Wyoming	0	6	14 426	0.00) 0) Ó	0.00	
	(128)	(7)	(43 697)	(0.29)	(1)	(25 372)	(0.50)	
All	15 428	<u>4</u> 4	367 844	4.19	14	321 369	4.80	
	(18 221)	(59)	(522 478)	(3.49)	(18)	(453 724)	(4.02)	

TABLE 5. Unburned area within fire perimeters for identified historical (i.e., pre-Euro-American-settlement) fires with burned area greater than 500 ha.

Notes: Numbers in parenthesis include ambiguous patches in calculations. Ambiguous patches were either (1) grassland patches or (2) entire townships surveyed as "scattered sagebrush," both lacking in sufficient context to identify them clearly as fires.

Wyoming big sagebrush and mountain big sagebrush exhibited different landscape compositions, thus we did not reject the first part of H_8 , that historical landscapes differed among areas dominated by different sagebrush taxa. Large contiguous areas of sagebrush with small interruptions of piñon-juniper, the most common landscape type observed, were more common in Wyoming big sagebrush than mountain big sagebrush. Large grass-dominated areas were fewer, but occurred in both sagebrush types. We found fine-scale grass-andsagebrush mosaics in only one study area, and these mosaics were dominated by Wyoming big sagebrush. We identified intermixed sagebrush, woodland, and shrubland mosaics in mountain big sagebrush in every study area, but not in Wyoming big sagebrush. In contrast, we observed few differences among study areas; the minor differences were in landscape types most directly associated with post-fire recovery (i.e., presence of large grasslands and grass-and-sagebrush mosaics). Therefore, we also did not reject the second

part of hypothesis H_8 , that historical landscapes did not differ among regions.

Dense sagebrush was a significant part of historical landscapes, thus we rejected H_9 , that historical sagebrush landscapes were dominated by low or moderate density sagebrush. Of all areas identified as sagebrush or sagebrush with a codominant shrub, surveyors described 29.7% of patches as dense, and 28.3% as scattered. The remaining 42.0% of patches had no density description, suggesting they were moderate in density, neither scattered nor especially dense. Dense patches made up 24.5% of the pooled AOI for all study areas, and scattered patches covered 16.3% of total area. Dense patches were more common and included more total area than scattered patches in all states except Wyoming, where no patches were described as dense. Patch density was described least often in Nevada, with only 6.2% of total sagebrush area, or 34.6% of patches, described as scattered or dense. In contrast, 91.0% of sagebrush area or 74.2% of patches in Idaho had a density description. We observed variation in sagebrush

TABLE 6. Fine-scale mosaic pattern of identified historical (e.g., pre-Euro-American settlement) fires greater than 500 ha.

			All fires	>500 ha	Fires with fine-scale mosaics only			
Study area	Area showing fine-scale mosaic (ha)	Number of fires	Total burned area (ha)	Fine-scale mosaic as a percentage of total burned area (%)	Number of fires with fine-scale mosaic	Total burned area (ha)	Fine-scale mosaics as a percentage of burned area (%)	
Idaho	458	16	115 517	0.40	1	2 368	19.34	
	(770)	(25)	(166 392)	(0.46)	(3)	(5 2 9 0)	(14.56)	
Nevada	12 278	13	¥9 655	24.73	ÌÍ	32 143	37.88	
	(12 435)	(16)	(75 614)	(16.45)	(2)	(42 091)	(29.54)	
Oregon	806	<u>9</u>	138 252	0.58	3	128 164	0.62	
•	(806)	(11)	$(177\ 011)$	(0.46)	(3)	(159 819)	(0.50)	
Wyoming	0	6	14 286	0.00) O) O	0.00	
, 0	(0)	(7)	(43 106)	(0.00)	(0)	(0)	(0.00)	
All	13 542	44	316 116	4.26	4	162 675	8.32	
	(14 596)	(60)	(461 325)	(3.16)	(7)	$(207\ 200)$	(7.04)	
All but	13 542	38	303 424	4.46	4	162 675	8.32	
Wyoming	(14 596)	(52)	(419 017)	(3.48)	(7)	$(207\ 200)$	(7.04)	

Notes: Numbers in parenthesis include ambiguous patches in the calculation. A fine-scale mosaic was interpreted where surveyors indicated small patches of sagebrush mixed with grass but did not give specific entry or exit points for sagebrush patches.

Study area and parameter	Wyoming big sagebrush†	Mountain big sagebrush‡	Low sagebrush§	Black sagebrush¶	Dwarf sagebrush#
Idaho					
Sample area (ha) Burned (%)	463 035 23.67 (33.27)	105 671 18.37 (19.98)			
Fire rotation (yr)	(55.27) 169–338 (120–240)	(19.98) 120–191 (110–175)			
Nevada					
Sample area (ha) Burned (%)	326 576 12.13 (18.63)	48 016 15.70 (16.88)		40 196 2.88 (3.12)	
Fire rotation (yr)	330–660 (215–429)	(10.00) 140–223 (130–207)		(3.12) 1 389–2 778 (1 282–2 564)	
Oregon					
Sample area (ha) Burned (%)	457 343 17.41 (21.18)	14 966 44.82 (45.46)	120 738 27.55 (42.83)		
Fire rotation (yr)	230–460 (189–378)	49–78 (48–77)	145–290 (93–187)		
Wyoming					
Sample area (ha) Burned (%)	242 781 4.88 (15.02)	71 423 3.74 (3.74)			53 473 0.24% (1.98%)
Fire rotation (yr)	819–1639 (266–533)	588–2 139 (588–2 139)			16 667–33 333 (2 020–4 040)
All but Wyoming					
Sample area (ha) Burned (%)	1 246 954 18.35 (25.00)	168 653 19.96 (21.36)	120 738 27.55 (42.83)	40 196 2.88 (3.12)	
Fire rotation (yr)	218–436 (160–320)	110-175 (103-164)	145–290 (93–187)	1 389–2 778 (1 282–2 564)	
All					
Sample area (ha) Burned (%)	1 489 735 16.16 (23.38)	240 076 15.13 (16.11)	120 738 27.55 (42.83)	40 196 2.88 (3.12)	53 473 0.24% (1.98%)
Fire rotation (yr)	247–495 (171–342)	145–231 (137–217)	145–290 (93–187)	1 389–2 778 (1 282–2 564)	16 667–33 333 (2 020–4 040)
Previous CFI estimates (yr)††	<100	≤35			
Previous fire rotation estimates (yr)‡‡	200-350	150-300	>200		
Modern fire rotation (1984–2008)§§	156–212	215	227		196

TABLE 7. Historical (pre-Euro-American settlement) fire rotations for ReGAP categories plus adjacent expanded areas of ReGAP grassland, human-altered vegetation, and recently burned areas.

Notes: Table entries include results for non-ambiguous patches and, in parenthesis, for non-ambiguous plus ambiguous patches. Expanded area includes areas that were sagebrush at the time of the surveys but now are classified as various ReGAP categories: cultivated cropland, Colombia Plateau steppe and grassland, developed (low-, medium-, and high-intensity, and open space), intermountain basins semi-desert grassland, introduced upland vegetation annual grassland, introduced upland vegetation perennial grassland and forbland, Northern Rocky Mountain lower montane, foothill, and valley grassland, Northern Rocky Mountain subalpine-upper montane grassland, open water (fresh), pasture/hay, quarries, mines, gravel pits and oil wells, recently burned grassland, Rocky Mountain alpine-montane wet meadow, and Rocky Mountain subalpine-montane mesic meadow. CFI stands for composite fire interval. Empty cells mean that we did not calculate fire rotation or include sample size for those sagebrush/ study area combinations because the specified type of sagebrush was either not present in the study area or covered less than 1500 ha.

† Includes ReGAP inter-mountain basins big sagebrush shrubland and steppe (dominated by *A. tridentata* ssp. *wyomingensis*), plus categories listed in the notes.

‡ Includes ReGAP inter-mountain basins montane sagebrush steppe (dominated by *A. tridentata* ssp. *vaseyana*), plus categories listed in the notes.

§ Includes ReGAP Columbia Plateau low sagebrush steppe (dominated by A. arbuscula and A. longiloba), plus categories listed in the notes.

¶ Includes ReGAP Great Basins xeric mixed sagebrush shrubland (dominated by *A. nova* at mid and low elevations, *A. arbuscula* at higher elevations, and sometimes co-dominated by *A. tridentata* ssp. wyomingensis), plus categories listed in the notes. # Includes ReGAP Categories Wyoming basins dwarf sagebrush shrubland (dominated by *A. arbuscula* ssp. longicaulis, *A.*

arbuscula ssp. longiloba, and A. nova), plus categories listed in the notes.

†† From Miller et al. (2011).

‡‡ From Baker (2011).

§§ From Baker (2013; Table 3, perimeter estimates).

density in all landscape types with sagebrush, and in both Wyoming big sagebrush and mountain big sagebrush. However, variation in density was most prominent in landscapes dominated by large contiguous areas of sagebrush, the landscape type corresponding to H_5 , where differences in sagebrush density were more common than other types of interruptions (e.g.,

woodlands, small grasslands, patches of other shrubs). DISCUSSION

Fire and patch-size distributions

Our results showed that historical fire- and patch-size distributions were inverse-J shaped, consisting of many small fires and few large ones. As no other study reconstructed a historical size distribution for sagebrush, no comparison is available. However, inverse-J distributions are found for many ecosystems (Moritz et al. 2005), and our results are consistent with patch-size distributions for modern wildfires in sagebrush (Baker 2013). The consistency of both patch- and fire-size distributions across all study areas is similar to Baker's (2013) findings for modern sagebrush wildfires, adding support to the suggestion that fire regimes in sagebrush are primarily controlled by weather or climate, rather than local fuel conditions. Additional evidence for the role of weather and climate can be seen in the southwestto-northeast orientation of several of the largest fires. This orientation corresponds to the prevailing direction of strong winds, often associated with cold fronts, a pattern also observed in modern sagebrush wildfires (Baker 2013) and large fire events in other ecosystems (e.g., Rothermel et al. 1994).

Geometric mean patch and fire sizes across all study areas were significantly different between mountain big sagebrush and Wyoming big sagebrush, with larger patches and fires in Wyoming big sagebrush. This is likely because mountain big sagebrush more often occurs in small patches interrupted by woodlands or other shrub types, resulting in less uninterrupted area for fires to burn. We did not expect to see differences in geometric mean patch sizes by province, but they may be partially due to the small sample size or differences in the amount of each sagebrush taxon in individual study areas. For example, geometric mean fire size for Wyoming big sagebrush was larger in Idaho than Nevada. Idaho had over 100 000 ha more Wyoming big sagebrush than Nevada, and included three fires $>20\ 000$ ha compared to one in Idaho.

Estimated fire rotations

Comparison of our results with expected values (Table 7) suggests that historical fire rotations may have been longer in Wyoming big sagebrush, but similar or shorter in mountain big sagebrush and low sagebrush, than previous fire-rotation estimates (Baker 2011). Commonly cited mean-CFI estimates for Wyoming big sagebrush, generally <100 years and 35 years or less in mountain big sagebrush (Miller et al. 2011)

were far too short (Table 7). Differences in fire rotations between provinces may be the result of small sample sizes for mountain big sagebrush in Oregon and the small number of fires identified in Wyoming. However, modern wildfire rotations in Wyoming are also significantly longer than those in other provinces, for all sagebrush taxa (Baker 2013). This suggests that estimated fire rotations accurately describe differences in historical fire rotations between Wyoming and the other study areas and are not solely the result of sample size. No clear explanation of this is evident, but terrain, climate, or some other unchanging underlying factor, not modern alterations, is the likely cause.

We found that historical fire rotations in mountain big sagebrush were significantly shorter than those in Wyoming big sagebrush. Baker (2013) found no significant differences in wildfire rotation by taxa for modern fires. However, modern wildfire rotations in Wyoming big sagebrush are shorter than those in mountain big sagebrush in the Northern Great Basin, Snake River Plain, and Southern Great Basin, likely due to increases in fire in Wyoming big sagebrush caused by cheatgrass invasion (Baker 2013).

Our estimated historical fire rotations were longer than modern fire rotations in Wyoming big sagebrush (Table 7), also supporting the idea that fire has increased in Wyoming big sagebrush. In contrast, historical fire rotations in mountain big sagebrush were similar to, or perhaps slightly shorter than, modern fire rotations (Table 7). Modern fire rotations may be much shorter than historical rotations in low and dwarf sagebrushes, although our sample areas are small (Table 7). Miller et al. (2011) hypothesized that modern fire rotations have increased in mountain big sagebrush and decreased in Wyoming big sagebrush. Our results appear to support the idea of a decrease in Wyoming big sagebrush, but an increase in mountain big sagebrush is not evident, if ambiguous patches are omitted, or is at most small, if ambiguous patches are included (Table 7).

Unburned area and landscape composition

Historical fires appear to have had less unburned area than modern wildfires, which averaged about 20% unburned area (Baker 2013). This supports Wrobleski and Kauffman's (2003) suggestion that modern fires have more unburned area due to the effects of grazing on modern landscapes and the fragmentation of previously large, contiguous patches of sagebrush by roads and development. We identified two forms of historical unburned area: large inclusions of unburned sagebrush or other vegetation within the fire perimeter and a finer-scale mosaic pattern. Our results show that historical fire regimes encompassed a range of sizes and intensities, with larger, more intense fires resulting in larger unburned areas and smaller, less intense fires showing a finer scale mosaic. This is significant, as variation in modern fire size and intensity may be decreasing. Miller et al. (2011) found that within-year

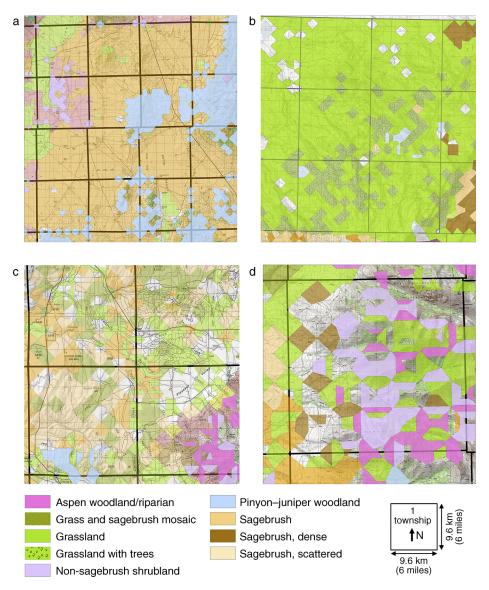


FIG. 5. Examples of historical (i.e., pre-Euro-American settlement) landscape types. Black boxes are township boundaries. (a) Large, contiguous areas of sagebrush interrupted by piñon-juniper woodlands in rocky areas, (b) large, contiguous area dominated by grass or resprouting shrubs, (c) finer scale grass-and-sagebrush mosaic, and (d) small patches of sagebrush mixed with woodland and non-sagebrush shrubland.

variation in fire size had decreased in all provinces between 1960 and 2007, and other studies (e.g., Brooks et al. 2004) have found increasing fire intensities due to cheatgrass. However, our results may underestimate historical unburned area, particularly at fine scales, due to the relatively coarse resolution of the GLO data.

Our results show that historical sagebrush landscapes included multiple sizes and configurations of patches. However, over 80% of sagebrush landscapes were dominated by large, contiguous areas of sagebrush with occasional small interruptions by woodlands, smaller burned areas, areas of sagebrush with trees, and other types of shrublands. In contrast, modern sagebrush landscapes are highly fragmented, and fragmentation is frequently cited as one of the biggest threats to sagebrush ecosystems (e.g., Knick et al. 2003).

Variation in sagebrush density caused by fires and the presence of multiple post-fire successional stages was the most significant historical source of variation within these areas. There is some debate in the literature as to whether dense sagebrush commonly occurred historically (Vale 1975, Welch and Criddle 2003) or is an undesirable result of human settlement and landscape alterations (e.g., Miller et al. 1994, Olson and Whitson 2002). However, the GLO data clearly show that dense sagebrush was a significant component of historical sagebrush landscapes, accounting for roughly 30% of sagebrush area, and sagebrush that was normal or dense



PLATE 1. Large expanses of sagebrush with trees, as shown here on the lower western slopes of Steens Mountain, southeastern Oregon, USA, occurred historically in sagebrush landscapes, likely representing natural postfire recovery in woodlands near sagebrush or naturally fluctuating tree invasion into sagebrush. Photo credit: W. L. Baker.

(i.e., not "scattered") was roughly 84% of sagebrush area. Although density was subjective, surveyor descriptions of "dense" sagebrush suggest these areas had sufficient cover and density to make surveying physically difficult. Numerous surveyors described both dense and scattered sagebrush, often adjacent to each other or in the same township. In other cases, patches of lowerdensity sagebrush types in the ReGAP data clearly correspond to patches of scattering sagebrush in the GLO data, suggesting that surveyors were well aware of "normal" sagebrush densities and were quite capable of identifying both dense and scattered sagebrush. Surveyors earned bonuses for surveying more difficult, dense vegetation (GLO 1902). However, this does not mean surveyors exaggerated sagebrush densities. Survey notes were checked and approved by the Surveyor General (GLO 1902), and modern studies have confirmed low rates of bias and error in survey notes (e.g., Bourdo 1956, Galatowitsch 1990, Williams and Baker 2010).

The commonly held view is that these large expanses of sagebrush were maintained by fires, which restricted piñon-juniper woodlands to fire-safe rocky areas (West 1984, Miller and Rose 1995, Davies et al. 2011). This landscape type was dominant (over 80% of combined AOIs), but fire rotations were generally too long for fire to be the primary or only factor preventing trees from encroaching into sagebrush. Moreover, our study shows that large areas of sagebrush with trees (Plate 1) were historically present, both on the fringes of woodland and as isolated patches on non-rocky areas surrounded entirely by sagebrush.

Historical trees in sagebrush could have been the result of post-fire recovery in burned woodlands, natural tree invasion into sagebrush, naturally occurring lowdensity woodlands, or a naturally occurring transition between ecosystems (Romme et al. 2009). Notably, comparison with ReGAP data did not show a consistent pattern of recovery to woodland in these areas, nor did these areas consistently remain stable, which would have suggested natural, low-density woodlands or transitions. Instead, scattered piñon-junipers in sagebrush, while expanding in some areas, have contracted or disappeared in others. In many cases, current vegetation is sagebrush, and trees have all but disappeared. This transition may be the result of subsequent fires, as fire rotations in these areas were long enough (Table 7) to allow the temporary expansion of trees into sagebrush (Baker 2011).

Recent piñon-juniper expansion is generally attributed to a variety of causes, including fire exclusion, the introduction of livestock, and favorable climate periods (Miller and Rose 1999, Miller et al. 2008). Conifer encroachment in sagebrush has been cited as a cause of ecosystem change, decreasing biodiversity, and increased fragmentation of sagebrush landscapes (Davies et al. 2011). Restoration of fire regimes is a frequently proposed solution to piñon-juniper expansion (e.g., Davies et al. 2011). However, our findings show that

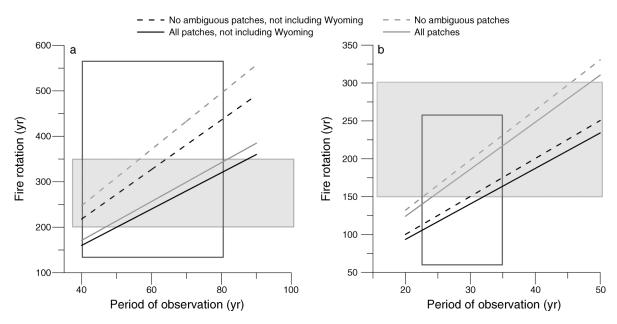


FIG. 6. Estimated historical (i.e., pre-Euro-American settlement) fire rotation sensitivity to period of observation for (a) Wyoming big sagebrush and (b) mountain big sagebrush. The shaded box represents the expected range of fire rotation values, and the unshaded box represents the range of values seen in this study.

restoration of fire regimes to a historical state would likely not eliminate piñon-juniper expansion, which appears to have been a natural, but fluctuating feature of these landscapes under historical fire regimes.

Ambiguity and uncertainty

Our results include some ambiguity and uncertainty that must be acknowledged (see Appendix C for an expanded discussion). First, information within the survey notes is sometimes ambiguous; however, this type of uncertainty is inescapable in working with GLO data. A second source of uncertainty comes from a limited understanding of post-fire recovery in sagebrush. Although post-fire successional stages are well documented, recovery time is poorly known, particularly for Wyoming big sagebrush, and appears to be highly variable (Baker 2011). Recovery rates directly affect the period of observation for fires, and our fire-rotation estimates were sensitive to the period of observation used (Fig. 6). Estimated fire rotations also varied depending on whether ambiguous patches were included. However, the amount of change depended on the size of the ambiguous patches and the fire sample size within individual study areas. Highly accurate estimates of fire rotations require a period of observation at least as long as the fire rotation (Baker 2009), a limitation of survey-based estimates. Nevertheless, the surveys provide one of the few available estimates of historical fire rotation based on data derived entirely from sagebrush. Additional research on post-fire recovery in sagebrush would lessen uncertainty relating to recovery rates and help narrow fire-rotation estimates.

Finally, there is some inherent uncertainty in understanding of historical sagebrush density that affects how fire-recovery indicators are perceived and interpreted. Although dense sagebrush was clearly common in historical landscapes, areas of low density can occur for reasons unrelated to fire. This study takes a compromise approach by classifying scattered sagebrush as a fire indicator when additional contextual evidence suggests a fire and as ambiguous when additional data are not present. It is unlikely that all areas of scattered sagebrush recorded by the surveyors represent post-fire recovery, but it is equally unlikely that they are all caused by environmental factors. Therefore, the true fire rotation likely lies somewhere in the middle of the two estimated ranges.

Changes in fire regimes

Our results show clear differences, and a few similarities, between historical and modern fire regimes. Modern fire rotations are shorter than historical fire rotations in Wyoming big sagebrush, low, and dwarf sagebrushes, but are no different from, or at most only slightly longer than historical fire rotations in mountain big sagebrush. Historically, fire rotations in Wyoming big sagebrush were significantly longer than those in mountain big sagebrush, but this difference is no longer present, likely because of increased wildfire in Wyoming big sagebrush (Baker 2013). Historical fires were less patchy, suggesting that land-use history significantly affects fire regimes. Livestock grazing and fragmentation have likely resulted in lower-intensity modern fires that even the combined influence of cheatgrass invasion and climate change have yet to overcome. The presence of large historical fires suggests that even the largest modern fires may individually be within the historical range of variability for fire size. However, shorter modern fire rotations in Wyoming big sagebrush likely mean that large wildfires are occurring more frequently because of cheatgrass invasion, human-set fires, and possibly climatic change (Miller et al. 2011, Baker 2013).

Managing fluctuating sagebrush landscapes

Inverse-J fire-size distributions suggest large infrequent fires were followed by periods with smaller fires (Baker 2011). Landscape composition and patch structure would have varied throughout fire rotations, depending on whether recent fires had been large or small. This can be seen in the presence of a few very large grass-dominated areas, larger expanses of unbroken sagebrush, and more limited fine-scale grass-andsagebrush mosaics. Sagebrush landscapes were not dominated by these mosaics of small patches (e.g., Klebenow 1972). Slow recovery after fire means that fire-related variation in sagebrush density remains apparent for decades across landscapes. Historically, long fire rotations allowed sagebrush to recover fully, reach maturity, and dominate large unbroken expanses with substantial areas of dense sagebrush for long periods, before being replaced by grasslands and/or resprouting shrubs after the next large fire.

Fluctuation would also have affected wildlife. Natural variation in fire sizes would have created areas of habitat suited to a diverse range of species within larger expanses of sagebrush. The size of these expanses would also have allowed local populations to survive large, infrequent fires, as suitable habitat would likely have been accessible elsewhere. Historically, patches created by fire would have been surrounded by a matrix of sagebrush and would not have permanently diminished sagebrush area, as burned areas would ultimately have returned to sagebrush after passing through post-fire successional stages.

In contrast, the total area of modern sagebrush has been drastically reduced, and what remains is often highly fragmented by roads or other human developments (Knick et al. 2003). As of 2000, 50-60% of native sagebrush steppe had an understory of exotic annual grasses or had been entirely converted to nonnative annual grasslands (West 2000). Current area affected is likely greater. Landscape conversion and fragmentation have isolated local populations of sagebrush obligates and left them vulnerable to habitat disturbances (Knick et al. 2003, Beck et al. 2012), as other areas of suitable habitat may not be nearby or easily accessible. This is especially problematic as large fires, which have been linked to extirpation of local populations of Sage-Grouse (Pedersen et al. 2003), may be occurring more frequently.

Due to the extensive fragmentation of modern sagebrush ecosystems (Knick et al. 2003), large expanses of sagebrush are most threatened. If the goal is restoration of sagebrush landscapes, a focus on preserving or restoring large, landscape-scale patches of sagebrush is most important, as is inclusion of areas of dense and scattered sagebrush, as both were significant components of historical landscapes. Large unfragmented expanses are also critical for continued survival of sagebrush-obligate species (Beck et al. 2012). Chaining, herbicide application, and other treatments designed to thin stands of dense sagebrush to restore "natural" levels (e.g., Vallentine 1989, Olson and Whitson 2002) are not needed. These treatments are generally detrimental to sagebrush-obligate species (Beck et al. 2012). Dense sagebrush historically dominated large areas, as shown earlier from historical accounts (Vale 1975), and fires continue to create successional sagebrush at rates similar to, or greater than historical rates.

We suggest that proposals to undertake control of piñon-juniper encroachment for ecological restoration are premature, if they assume that trees are generally unnatural in sagebrush because of fire exclusion (e.g., Davies et al. 2011). Our findings show this assumption is not supported, as trees naturally occurred in sagebrush landscapes, just as they do today (Plate 1). Moreover, modern fire rotations are shorter than, or similar to historical fire rotations; thus, fire exclusion cannot generally explain contemporary trees in sagebrush. Our findings and earlier syntheses (Romme et al. 2009) showed that removing trees in sagebrush would not be ecological restoration, if it delays natural recovery of former woodlands, removes natural low-density woodlands, or alters naturally fluctuating woodland-sagebrush boundaries. There may be reasons, other than ecological restoration, to remove trees from sagebrush, but unless (1) historical data show the specific area to have been sagebrush and (2) natural explanations of young trees can be excluded, so the cause is known to be a land use, tree removals would not represent ecological restoration of sagebrush. GLO data can provide the first step in this needed determination.

Intentional fire suppression, as suggested by Davies et al. (2011) and Baker (2011), may be necessary in Wyoming big sagebrush, because of shorter modern fire rotations and the need to minimize post-fire cheatgrass invasion. These trends also suggest that prescribed burning of Wyoming big sagebrush is unnecessary. The use of prescribed fire in mountain big sagebrush to control conifer encroachment (e.g., Davies et al. 2011) lacks a firm basis unless local analysis of modern and historical trees in mountain big sagebrush has been completed, as suggested here.

Overall, we find that historical sagebrush landscapes were complex, often dominated by large expanses of mature sagebrush that varied in density, but with finerscale sagebrush mosaics, recently burned areas, and significant areas of sagebrush with trees. These landscapes fluctuated over decades to centuries at both local and landscape scales, as infrequent episodes of large fires were followed by periods of recovery and extended dominance by mature sagebrush. If the goal is to use historical evidence to guide preservation or ecological restoration of sagebrush landscapes, effective plans will require detailed local analysis of these complex historical landscapes, which can be provided by GLO survey data.

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LITERATURE CITED

- Arno, S. F., and T. D. Peterson. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Research Paper INT-301. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Baker, W. L. 2002. Indians and fire in the Rocky Mountains: The wilderness hypothesis renewed. Pages 41–76 *in* T. R. Vale, editor. Fire, native peoples, and the natural landscape. Island Press, Washington, D.C., USA.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.
- Baker, W. L. 2009. Fire ecology in Rocky Mountain landscapes. Island Press, Washington, D.C., USA.
- Baker, W. L. 2011. Pre-EuroAmerican and recent fire in sagebrush ecosystems. Pages 185–201 in S. T. Knick and J. W. Connelly, editors. Ecology and conservation of Greater Sage-grouse: a landscape species and its habitats. Studies in Avian Biology, vol. 38. University of California Press, Berkeley, California, USA.
- Baker, W. L. 2013. Is wildland fire increasing in sagebrush landscapes of the western United States? Annals of the Association of American Geographers 103:5–19.
- Baker, W. L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Canadian Journal of Forest Research 31:1205–1226.
- Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444–455.
- Blaisdell, J. P. 1953. Ecological effects of planned burning of sagebrush-grass range on the upper Snake River plains. USDA Technical Bulletin 1075. U.S. Government Printing Office, Washington, D.C., USA.
- Bourdo, E. A. 1956. A review of the General Land Office survey and of its use in quantitative studies of former forests. Ecology 37:754–768.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.
- Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35:139–164.
- Castrale, J. S. 1982. Effects of two sagebrush control methods on nongame birds. Journal of Wildlife Management 46:945– 952.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush communities. Biological Conservation 144:2573–2584.

- Doherty, K. E., J. D. Tack, J. S. Evans, and D. E. Naugle. 2010. Mapping breeding densities of greater sage-grouse: A tool for range-wide conservation planning. Bureau of Land Management, Washington, D.C., USA.
- Fritschle, J. A. 2008. Reconstructing historic ecotones using the Public Land Survey: the lost prairies of Redwood National Park. Annals of the Association of American Geographers 98:24–39.
- Fritschle, J. A. 2009. Pre-EuroAmerican settlement forests in Redwood National Park, California, USA: a reconstruction using line summaries in historic land surveys. Landscape Ecology 24:833–847.
- Galatowitsch, S. M. 1990. Using the original land survey notes to reconstruct presettlement landscapes in the American West. Great Basin Naturalist 50:181–191.
- General Land Office (GLO). 1902. Manual of surveying instructions for the survey of the public lands of the United States and public land claims. U.S. Government Printing Office, Washington, D.C., USA.
- Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 6:651–668.
- Jacobs, K., and C. Whitlock. 2008. A 2000-year environmental history of Jackson Hole, Wyoming, inferred from lakesediment records. Western North American Naturalist 68:350–364.
- Kerley, L. L., and S. H. Anderson. 1995. Songbird responses to sagebrush removal in a high elevation sagebrush steppe ecosystem. Prairie Naturalist 27:129–146.
- Klebenow, D. A. 1972. The habitat requirements of sage grouse and the role of fire in management. Proceedings of the Tall Timbers Fire Ecology Conference 12:305–315.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.
- Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology and Management 60:261–269.
- Livermore, M. 1991. Fictitious surveys. P.O.B. Publishing Company, Canton, Michigan, USA.
- Mensing, S., S. Livingston, and P. Barker. 2006. Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. Western North American Naturalist 66:64–77.
- Miller, R. F., and E. K. Heyerdahl. 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. International Journal of Wildland Fire 17:245–254.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long term conservation. Pages 145–184 *in* S. T. Knick and J. W. Connelly, editors. Ecology and conservation of Greater Sage-grouse: a landscape species and its habitats. Studies in Avian Biology, Vol. 38. University of California Press, Berkeley, California, USA.
- Miller, R. F., and J. A. Rose. 1995. Historic expansion of Juniperus occidentalis (western juniper) in southeastern Oregon. Great Basin Naturalist 55:37–45.
- Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.
- Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the intermountain sagebrush region: plant composition. Pages 101–146 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.
- Miller, R. F., R. J. Tausch, E. D. McArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of

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piñon-juniper woodlands: a regional perspective in the Intermountain West. Research Paper RMRS-RP-69. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

- Moritz, M. A., M. E. Morais, L. A. Summerall, J. M. Carlson, and J. Doyle. 2005. Wildfires, complexity, and highly optimized tolerance. Proceedings of the National Academy of Sciences USA 102:17912–17917.
- Mueggler, W. F. 1956. Is sagebrush seed residual in the soil of burns, or is it wind borne? Research Note No. 35. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Nelson, N. A., and J. Pierce. 2010. Late-Holocene relationships among fire, climate and vegetation in a forest-sagebrush ecotone of southwestern Idaho, USA. Holocene 20:1179– 1194.
- Olson, R. A., and T. D. Whitson. 2002. Restoring structure in late-successional sagebrush communities by thinning with tebuthiuron. Restoration Ecology 10:146–155.
- Ott, L. 1988. An introduction to statistical methods and data analysis. Third edition. PWS-Kent Publishing Company, Boston, Massachusetts, USA.
- Pedersen, E. K., J. W. Connelly, J. R. Hendrickson, and W. E. Grand. 2003. Effect of sheep grazing and fire on sage grouse populations in southeastern Idaho. Ecological Modeling 165:23–47.
- Rhynsburger, D. 1973. Analytic definition of Thiessen polygons. Geographical Analysis 5:133–134.
- Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon– juniper vegetation of the western United States. Rangeland Ecology and Management 62:203–222.
- Rothermel, R. C., R. A. Hartford, and C. H. Chase. 1994. Fire growth maps for the 1988 Greater Yellowstone Area fires. General Technical Report INT-304. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Sapsis, D. B., and J. B. Kauffman. 1991. Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. Northwest Science 65:173–179.
- Stiver, S. J., A. D. Apa, S. E. Bohne, S. D. Bunnell, P. A. Deibert, S. C. Gardner, M. A. Hilliard, C. W. McCarthy, and M. A. Shroeder. 2006. Greater sage-grouse comprehensive

conservation strategy. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

- Vale, T. R. 1975. Presettlement vegetation of the sagebrushgrass area of the intermountain west. Journal of Range Management 28:32–36.
- Vallentine, J. F. 1989. Range developments and improvements. Third edition. Academic Press, San Diego, California, USA.
- Welch, B. L., and C. Criddle. 2003. Countering misinformation concerning big sagebrush. Research Paper RMRS-RP-40. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- West, N. E. 1984. Successional patterns and productivity potentials of piñon–juniper ecosystems. Pages 1301–1322 in Developing strategies for rangeland management. Natural Resource Council/National Academy of Science. Westview Press, Boulder, Colorado, USA.
- West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15–26 *in* P. G. Entwhistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhoff, editors. Proceedings: Sagebrush steppe ecosystems symposium. USDI Bureau of Land Management Publication, Boise, Idaho, USA.
- White, R. S., and P. O. Currie. 1983. The effects of prescribed burning on silver sagebrush. Journal of Range Management 36:611–613.
- Williams, M. A., and W. L. Baker. 2010. Bias and error in using survey records for ponderosa pine landscape restoration. Journal of Biogeography 37:707–721.
- Williams, M. A., and W. L. Baker. 2011. Testing the accuracy of new methods for reconstructing historical structure of forest landscape using GLO survey data. Ecological Monographs 81:63–88.
- Wright, C. S., and S. J. Pritchard. 2006. Biomass consumption during prescribed fires in big sagebrush ecosystems. Pages 489–500 in P. L. Andrews and B. W. Butler, editors. Fuels management: how to measure success. Conference proceedings, 28–30 March 2006, Portland, Oregon, USA. USDA Forest Service Proceedings RMRS-P-41. Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Wrobleski, D. W., and J. B. Kauffman. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. Restoration Ecology 11:82–90.

SUPPLEMENTAL MATERIAL

Appendix A

Minimum line and polygon trials (Ecological Archives A023-026-A1).

Appendix **B**

Additional tables on fire rotations and fire sizes (*Ecological Archives* A023-026-A2).

Appendix C

Ambiguity and uncertainty (Ecological Archives A023-026-A3).