

Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest

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Citation: Walker, R. B., J. D. Coop, S. A. Parks, and L. Trader. 2018. Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere* 9(4):e02182. 10.1002/ecs2.2182

Abstract. Extensive high-severity wildfires have driven major losses of ponderosa pine and mixed-conifer forests in the southwestern United States, in some settings catalyzing enduring conversions to non-forested vegetation types. Management interventions to reduce the probability of stand-replacing wildfire have included mechanical fuel treatments, prescribed fire, and wildfire managed for resource benefit. In 2011, the Las Conchas fire in northern New Mexico burned forested areas not exposed to fire for >100 yr, but also reburned numerous prescribed fire units and/or areas previously burned by wildfire. At some sites, the combination of recent prescribed fire and wildfire approximated known pre-settlement fire frequency, with two or three exposures to fire between 1977 and 2007. We analyzed gridded remotely sensed burn severity data (differenced normalized burn ratio), pre- and post-fire field vegetation samples, and pre- and post-fire measures of surface fuels to assess relationships and interactions between prescribed fire, prior wildfire, fuels, subsequent burn severity, and patterns of post-fire forest retention vs. conversion to non-forest. We found that Las Conchas burn severity was lowest, and tree survival was highest, in sites that had experienced both prescribed fire and prior wildfire. Sites that had experienced only prescribed or prior wildfire exhibited moderate burn severity and intermediate levels of forest retention. Sites lacking any recent prior fire burned at the highest severity and were overwhelmingly converted to non-forested vegetation including grassland, oak scrub, and weedy, herbaceous-dominated types. Burn severity in the Las Conchas fire was closely linked to surface woody fuel loads, which were reduced by prior wildfire and prescribed fire. Our results support the restoration of fire regimes via prescribed fire and resource benefit wildfire to promote the resiliency of forest types vulnerable to fire-mediated type conversion. The application of prescribed fire to reduce surface fuels following wildfire may reduce forest loss during subsequent fire under more extreme conditions. These findings are especially relevant given likely increases in vulnerability associated with climate change impacts to wildfire and forest dynamics.

Key words: ecological restoration; fuel treatment; *Pinus ponderosa*; reburning; resilience; resource objective wildfire; Rx fire; transformation; type conversion.

Received 21 December 2017; revised 1 March 2018; accepted 5 March 2018. Corresponding Editor: Franco Biondi.

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INTRODUCTION

Major losses of ponderosa pine and dry mixed-conifer forests across the western United States have been driven by recent wildfires of unprecedented intensity, severity, and scale

(Dennison et al. 2014, Stephens et al. 2014, Fornwalt et al. 2016), in many cases leading to apparent long-term vegetation conversion to non-forested types (Savage and Mast 2005, Abella and Fornwalt 2015, Coop et al. 2016, Lauvaux et al. 2016, Rother and Veblen 2016,

Minor et al. 2017, Tepley et al. 2017). Recent increases in high-severity fire in these systems, which were historically characterized primarily by low-severity fire with short return intervals (Touchan et al. 1996, Everett et al. 2000, Veblen et al. 2000), have been attributed primarily to direct and indirect human influences. Intense livestock grazing of grassy understories had largely eliminated surface fire by the turn of the 20th century and was followed by direct wildfire suppression (Savage and Swetnam 1990, Allen et al. 2002). These land use legacies led to forests with higher tree densities and greater vertical and horizontal fuel continuity than may have existed for millennia (Covington and Moore 1994, Swetnam et al. 1999). In addition to elevated fuel loads, warmer temperatures and increased aridity in the western United States have lengthened fire seasons and increased flammability (Dennison et al. 2014, Jolly et al. 2015, Abatzoglou and Williams 2016). Under future climate projections, these factors are expected to further influence fire frequency, seasonality, and severity (Flannigan et al. 2009, Littell et al. 2010, Westerling et al. 2011). Modern human ignitions have also expanded the duration of the fire season into periods when natural ignitions are rare (Balch et al. 2017), though human ignitions likely shaped pre-settlement fire regimes (Stephens et al. 2007).

Under altered fire regimes, ponderosa pine and dry mixed-conifer forests may be vulnerable to fire-driven conversion to non-forested vegetation. Several studies have documented sparse tree regeneration by obligate-seeding conifers of these forest types within recent wildfire interiors (Haire and McGarigal 2010, Ouzts et al. 2015, Chambers et al. 2016, Rother and Veblen 2016, Owen et al. 2017, Tepley et al. 2017). Factors that reduce post-fire tree regeneration include poor seed dispersal by wind-dispersed conifers into large, severely burned patches (Bonnet et al. 2005, Coop et al. 2010, Chambers et al. 2016, Rother and Veblen 2016, Owen et al. 2017). This constraint is amplified by episodic seed production and seedling establishment that may already be limited by inter-annual climate variation (Petrie et al. 2016). Strong positive feedbacks may also play significant roles in maintaining non-forested vegetation types as alternate

stable states. First, competition from highly fire-adapted, resprouting grasses and shrubs can severely constrain tree seedling establishment (Roccaforte et al. 2012). Second, vigorous regrowth of grasses and shrubs (combined with large dead and down woody fuels following severe wildfire) can contribute to high subsequent wildfire severity (Parks et al. 2014a), eliminating tree seedlings and young trees, and maintaining non-forested communities. As such, once established, non-forested vegetation types may exhibit remarkable persistence as alternate stable states (e.g., Gambel's oak scrub in the southwestern United States; Guiterman et al. 2017). Finally, warmer temperatures, increased drought, and longer and drier fire seasons associated with climate change are expected to further constrain tree regeneration and elevate the probability of additional wildfire (Westerling 2006, Johnstone et al. 2010, Williams et al. 2012, Harvey et al. 2016, Stevens-Rumann et al. 2018).

Ecological, economic, and social impacts of wildfire and fire-driven forest losses compel management interventions to increase forest resistance and resilience to fire and, where possible, restore pre-settlement stand structure and processes (Moore et al. 1999, Swetnam et al. 1999, Allen et al. 2002). While mechanical treatments may be useful to restore forest and fuel structure and elevate stand fire resistance, fire itself is essential to restoring ecological function (Agee et al. 2000, Pollet and Omi 2002, Martinson and Omi 2003, Fulé et al. 2012). Prescribed fire has been shown to reduce the potential for crown fire and tree mortality in fire-adapted landscapes (Harrington 1996, Fernandes and Botelho 2003, Strom and Fulé 2007, Ryan et al. 2013, van Mantgem et al. 2016). Numerous remote sensing-based studies have also shown that exposure to previous wildfires can moderate subsequent burn severity and reduce the probability of reburn (Collins et al. 2009, Parks et al. 2014a, Prichard and Kennedy 2014, Holsinger et al. 2016, Stevens-Rumann et al. 2016, Lydersen et al. 2017). Though their individual effects are commonly investigated, the additive effects of prescribed fire and prior wildfire on subsequent fire severity, tree mortality, and fuel loadings have not been examined. The combination of prescribed fire on top of earlier wildfire may allow managers to achieve fuel reduction and

stand structure objectives across larger areas more efficiently than through repeated prescribed fire alone (North et al. 2012, Houtman et al. 2013).

In 2011, the Las Conchas wildfire burned 63,370 ha in the Jemez Mountains of northern New Mexico, largely under extremely dry, hot, and windy conditions. Much of this fire burned very severely (with ~30% classified as high severity; MTBS 2013), leading to extensive losses of ponderosa pine and mixed-conifer forest types, especially where stands had not experienced any fire during the last century of fire suppression. However, the Las Conchas fire also overlapped 32 earlier prescribed fire units in Bandelier National Monument and the Santa Fe National Forest and reburned portions of several recent prior wildfires (four of these are shown in Fig. 1). At some sites, the combination of recent prescribed fire and wildfire approached known pre-settlement fire frequency, with two or three exposures to fire between 1977 and 2007 (Table 1). In an earlier study, Coop et al. (2016) found that Las Conchas burn severity was reduced where it overlapped prior fire, but large proportions of the vegetation within these prior wildfire perimeters had already been type-converted from forest to non-forested states. Such non-forested vegetation types, including resprouting woody shrublands and native and non-native herbaceous communities, were highly fire resistant and resilient in contrast to forests not recently exposed to fire. Whether forested areas that had persisted through prior wildfire and prescribed fire treatments showed decreased Las Conchas burn severity and reduced tree mortality remained an open question.

In this study, we examined the influence of prescribed fires, prior wildfires, and their additive effects on subsequent wildfire severity and impacts to forest stands during 2011 Las Conchas fire in northern New Mexico. Specifically, we sought to determine whether prior exposure to one or more fires increased tree retention during the Las Conchas fire. We employed three complementary approaches that utilized satellite imagery, pre- and post-fire measures of vegetation, and pre- and post-fire measures of surface fuels and forest structure to address the following questions:

1. Was Las Conchas burn severity (as inferred from remotely sensed reflectance, e.g., differenced normalized burn ratio [dNBR]) significantly reduced by prescribed fire, prior wildfire, or their combination?
2. In stands that were forested preceding Las Conchas, did prescribed fire, prior wildfire, or their interaction increase tree retention and hinder subsequent conversion to non-forested vegetation types?
3. Did management units with different recent fire histories, including prescribed fire and/or prior wildfire, display differences in pre- and post-Las Conchas fuel loads that could account for variation in burn severity and forest retention?

METHODS

Study area

The climate of the study region is semiarid and continental. In nearby Los Alamos (2243 m), mean (1981–2010 norm) annual precipitation is 47.7 cm, with 45% (21.3 cm) occurring during the summer monsoon period from July to September; mean annual temperature is 9.1°C. Elevations within the study area range from ~1750 to 3350 m. Our study focuses on stands with dominance (prior to the 2011 Las Conchas fire) by ponderosa pine (*Pinus ponderosa* var. *scopulorum*) and mixed-conifer forest types that included ponderosa pine, Douglas fir (*Pseudotsuga menziesii* var. *glauca*), southwestern white pine (*Pinus strobiformis*), and white fir (*Abies concolor*), sometimes intermixed with aspen (*Populus tremuloides*), as described in Muldavin et al. (2011) and Coop et al. (2016). Small-scale logging and extensive livestock grazing occurred historically within portions of the study area, but not for nearly a century within the boundaries of Bandelier National Monument.

Our study was conducted within a portion of the 2011 Las Conchas fire perimeter (63,370-ha) in Bandelier National Monument and the adjacent Santa Fe National Forest, located in northern New Mexico (Fig. 1). The historic fire regimes of this landscape are some of the most well characterized in the world (Allen et al. 1995, Touchan et al. 1996, Margolis and Malevich 2016). Throughout the ponderosa pine

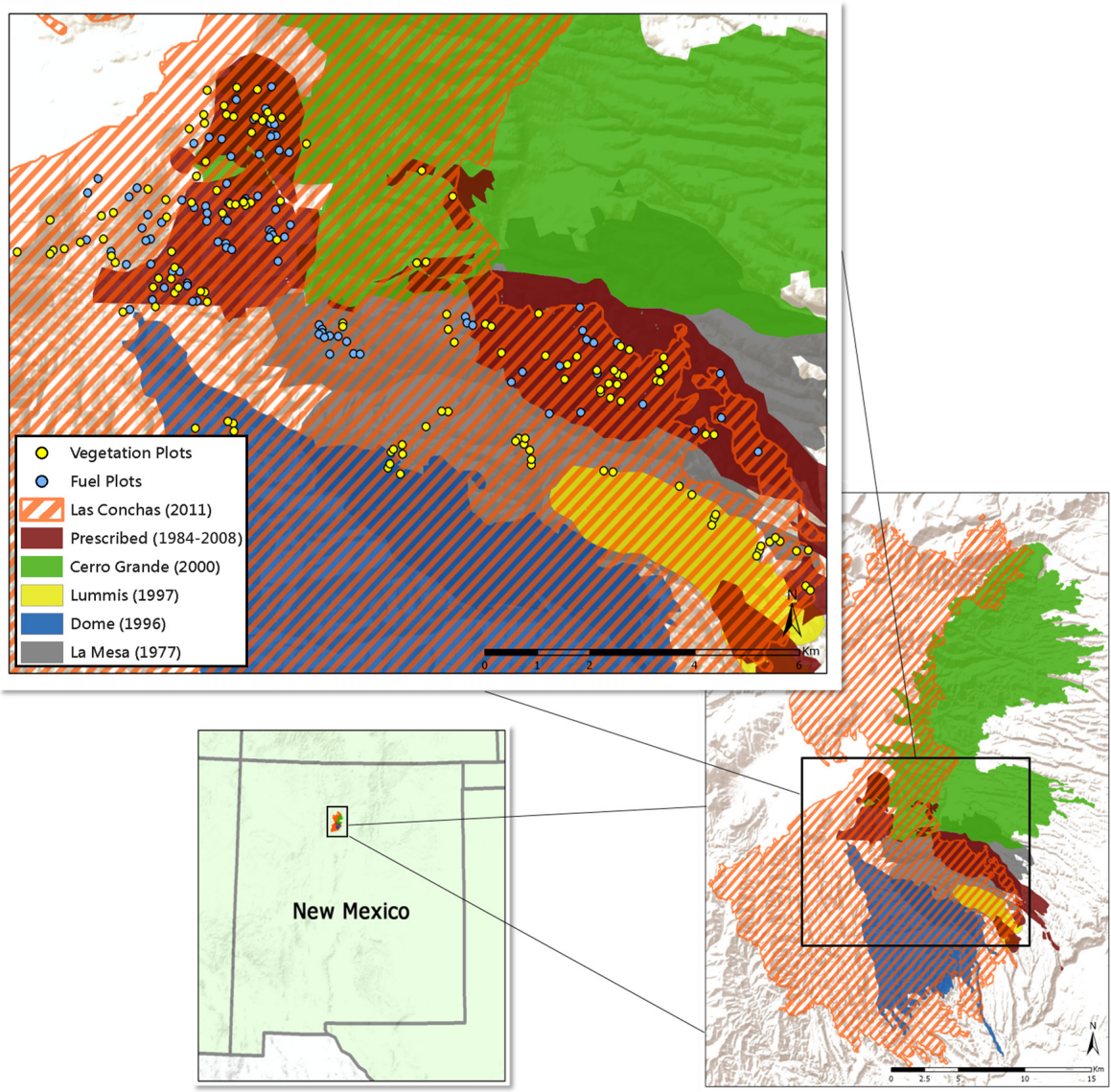


Fig. 1. Locations of the 2011 Las Conchas Fire, a series of prior prescribed fires, prior wildfires, and field sample plots in the Jemez Mountains of northern New Mexico.

and mixed-conifer stands that form the focus of this study, there is strong and abundant evidence of historic, low-severity fire with short (~5–18 yr) return intervals (Foxx and Potter 1978, *unpublished report on file with Bandelier National Monument*; Touchan et al. 1996, Margolis and Malevich 2016). Reductions in herbaceous vegetation due to heavy livestock grazing in the 1890s led to an abrupt end to frequent low-severity fire; the cessation of this

fire regime was reinforced by later direct fire suppression (Allen 1989, Touchan et al. 1996).

A series of large fires with extensive high-severity components began to impact the region in 1977 with the 6250-ha La Mesa Fire, followed by the 6684-ha Dome Fire in 1996, and the 19,425-ha Cerro Grande fire in 2000. Substantial portions of these earlier fires were reburned by the Las Conchas fire in 2011. Between 1984 and 2008, Bandelier National Monument's Fire

Table 1. Total number of fuel sample plots within each fire effects project area that conform to each fire history treatment.

Fire history treatment	Management unit 1 (<i>n</i> = 18)	Management unit 7 (<i>n</i> = 14)	Management unit 9 (<i>n</i> = 30)	Management unit 14 (<i>n</i> = 14)	Escobas mesa unit (<i>n</i> = 19)
No prior fire	2	14	–	–	–
Wildfire only	1	–	–	14	–
Rx only	–	–	27	–	–
Rx + wildfire	15	–	3	–	19z
Wildfire year	2000	–	2000	1977	1977
Rx fire year	1992	–	2007	–	1995, 1998, 1999

Note: Year of prescribed fire and prior wildfire events are included where applicable. Dash symbol indicates a non-applicable field.

Management Program and the Santa Fe National Forest also conducted 32 prescribed fires that were reburned during the Las Conchas fire. These treatments were applied across areas with a variety of fire histories including high-, moderate-, and low-severity prior wildfire, prior prescribed fire, and no prior fire and ranged in size from ~1.5 to 613 ha (K. Beeley, *unpublished data on file with Bandelier National Monument*). Where prescribed fires overlapped with earlier wildfires, recent pre-Las Conchas fire, return intervals at some sites resembled those recorded prior to the period of modern fire suppression (Table 1).

Our study focused on areas within the vicinity of previously prescribed fires for which we had pre-Las Conchas vegetation and fuel data. To define our study area, we buffered all prescribed burn units by 2.5 km and intersected this buffer with the portion of the Las Conchas fire that burned between 26 and 29 June 2011 (www.geo.mac.gov). We excluded portions of the Las Conchas fire that burned after 29 June to ensure sample sites burned under the extreme fire weather conditions when the fire made its largest runs and exclude areas known or thought to have burned due to management interventions (e.g., backing fires) under more moderate weather conditions.

Burn severity analysis

Las Conchas burn severity was measured as dNBR (Key and Benson 2005) that was produced for an earlier study (Coop et al. 2016) with Landsat Thematic Mapper satellite imagery (30-m resolution). From a 60 × 60 m lattice of points covering the study area (representing 25% of all 30-m pixels), we extracted dNBR and fire history treatment type (prescribed fire [Rx] and prior

wildfire). Because of potential direct and indirect influences of topography on Las Conchas burn severity (Haire et al. 2017), we also extracted values of elevation (m) and slope inclination (°) using a 30-m resolution digital elevation model. We characterized recent fire activity prior to Las Conchas as four distinct fire history treatments, as follows: (1) Rx + wildfire, (2) Rx only, (3) wildfire only, and (4) no prior fire.

We utilized simultaneous autoregressive (SAR) models, which incorporate a spatial term into the standard regression equation to account for spatial autocorrelation, to evaluate the influence of recent fire history on Las Conchas burn severity. Simultaneous autoregressive modeling was conducted using the *spdep* spatial analysis package (Wimberly et al. 2009, Bivand et al. 2013) in R (R Development Core Team 2016). Model selection followed the approaches of Kissling and Carl (2008), Wimberly et al. (2009), and Prichard and Kennedy (2014). First, to determine which predictors to include in the SAR, we used a stepwise selection procedure of a set of linear models that included all predictors of interest (including the four fire history treatments and normalized [0–1] elevation and slope terms). The best-fitting linear model was determined based on minimum Akaike information criterion (AIC). The residuals of this model were tested for spatial autocorrelation using Moran's *I* from 1000 Monte Carlo simulations. Subsequently, we used these predictors to develop SARs with incrementally increasing neighborhood sizes (increasing number of nearest neighbors for each point: 4, 8, 12). We then selected the SAR with the neighborhood size that (1) minimized AIC and (2) produced residuals that did not show spatial autocorrelation. The no prior fire category was

used as the baseline condition (intercept) against which the other fire history treatments were compared. We calculated the Nagelkerke likelihood-based pseudo- R^2 statistic (Nagelkerke 1991, Burnham and Anderson 2003) for the final model. We also conducted parallel analyses using the relativized burn ratio (RBR) metric of burn severity (Parks et al. 2014b).

Pre- to post-Las Conchas vegetation change

To characterize patterns of forest retention vs. conversion resulting from the Las Conchas fire across the four fire history treatments, we re-measured 129 pre-fire, field-sampled vegetation plots during July and August 2016, five years post-Las Conchas. We selected these plots from 510 vegetation plots occurring within the Las Conchas perimeter, first measured between June and September 2003–2006, 5–8 yr pre-Las Conchas, and 3–29 yr after earlier wildfires (Muldavin et al. 2011). To qualify for re-measurement, plots must have contained mature conifer trees when measured prior to the Las Conchas fire. Plots were re-located using a handheld GPS unit and pre-fire photographs. Re-measurement was conducted using the original sampling protocols, described fully in Muldavin et al. (2011). Briefly, within 20 × 20-m plots, a list of all live vascular plant species was compiled and ocular coverage estimates were made for each species, by stratum. The midpoints of nine coverage ranges were used to record coverage estimates as follows: 0.05% (trace, present on plot but <0.1%); 0.5% (<1%); 2.5% (1–4%); 7.5% (5–10%); 17.5% (10–25%); 29% (25–33%); 41.5% (33–50%); 62.5% (50–75%); and 87% (≥75%). Repeat plot photographs were also taken from the same locations as pre-Las Conchas photographs.

A previous study by Coop et al. (2016) utilized the same 510 pre-Las Conchas field-sampled vegetation plots to characterize relationships between pre-Las Conchas vegetation composition and previous wildfire and designated four broad vegetation types corresponding to quadrants of this ordination space, including (1) forested stands of ponderosa pine or mixed-conifer dominance that had not burned at high severity prior to Las Conchas, (2) oak scrub, associated with prior high-severity fire, (3) ruderal herb- and shrub-dominated communities

that often contained a substantial component of New Mexico locust (*Robinia neomexicana*), also generated by earlier high-severity fire, and (4) savanna/meadow communities dominated by native grasses but occasionally and infrequently including surviving trees, which had generally burned at low to moderate severity.

We utilized this nonmetric multidimensional scaling (NMS)-derived species space to examine pre-to-post-Las Conchas changes in forest vegetation associated with the four fire history treatments. Using R function `addpoints.nmfs` (Roberts 2014), NMS axis scores were calculated for the 129 post-Las Conchas vegetation plots. These new points were added to the original (Coop et al. 2016) NMS ordination space. To quantify and illustrate the direction and magnitude of compositional change, we tallied the numbers of points that moved to a new quadrant of ordination space following the Las Conchas fire, displayed vectors running from each pre-Las Conchas point location to its respective post-Las Conchas location, and calculated the mean extent and direction of change for each fire history treatment.

Pre- and post-Las Conchas fuel loads

To mechanistically explore causes of variation in Las Conchas burn severity and post-Las Conchas conifer retention, we utilized data collected on a series of permanent fire effects monitoring plots with different fire history treatments, sampled by Bandelier National Monument's Fire Ecology Program. Plots within each of five management units conformed to one of the four previously described treatments (Table 1). We utilized surface fuels and tree data from 95 of these plots measured prior to Las Conchas (2002–2010) and post-Las Conchas (2014–2016). Within each 50 × 20 m plot, surface fuel data were collected along four transects using the standard Brown's Line sampling method (Brown 1974). Each transect extended 15.2 m in a random azimuth from the centerline of the plot; 1-h (<0.64 cm) and 10-h (0.64–2.54 cm) fuels were measured along 1.8 m, 100-h (2.54–7.62 cm) fuels along 3.7 m, and 1000-h (>7.62 cm diameter) fuels were measured by decay class along 15.2 m. Litter and duff depths were recorded every 1.5 m (10 measurements per transect). All trees with a diameter at breast height (DBH)

greater than 2.5 cm were sampled; information collected included the following: genus, species, DBH, height, crown base height, crown ratio, and status (live or dead).

We again employed SAR models to examine the influence of pre-Las Conchas surface fuel loads, tree basal area, and tree density on burn severity, using the same model selection procedure described above. Predictors included per-plot totals of 1-, 10-, and 100-h fuels (hereafter, “fine woody debris”), 1000-h fuels (hereafter, “coarse woody debris”), litter + duff, and live, dead, and total tree basal area and density.

RESULTS

Burn severity

Lowest mean Las Conchas burn severity was observed in the Rx + wildfire treatment, whereas the no prior fire treatment exhibited the highest burn severity (Fig. 2). The two fire history treatments that included only one fire type showed intermediate levels of burn severity. The best-fitting SAR model (Table 2) included all fire history treatments, elevation, and slope as significant predictors of burn severity and utilized a neighborhood size of $k = 4$. This model confirmed a statistically strong reduction in burn severity imparted by fire history treatment. The

Rx + wildfire treatment drove the greatest reductions in burn severity with moderate reductions in the single fire-type treatments relative to the no prior fire condition (model intercept; Table 2). The inclusion of normalized elevation and slope inclination improved model fit; burn severity increased with increasing elevation but decreased with slope inclination. Model residuals did not show spatial autocorrelation. Model permutations of RBR with the same factor sets produced similar model coefficients and test statistics to those of the dNBR models (these results will not be discussed further).

Pre- to post-Las Conchas vegetation change

Patterns of pre- to post-Las Conchas vegetation change varied greatly between fire history treatments, with the extent of change inversely related to prior fire exposure (Fig. 3). Forest retention was greatest in the Rx + wildfire treatment, where overall vegetation composition and structure was largely unchanged by the Las Conchas fire. Though some sample sites within this treatment clearly burned severely and shifted in ordination space from forest toward non-forested states (increasing scores on either NMS 1 or 2; Fig. 3a), these changes were offset in part by opposing changes toward increased forest cover by other samples (decreasing scores on either

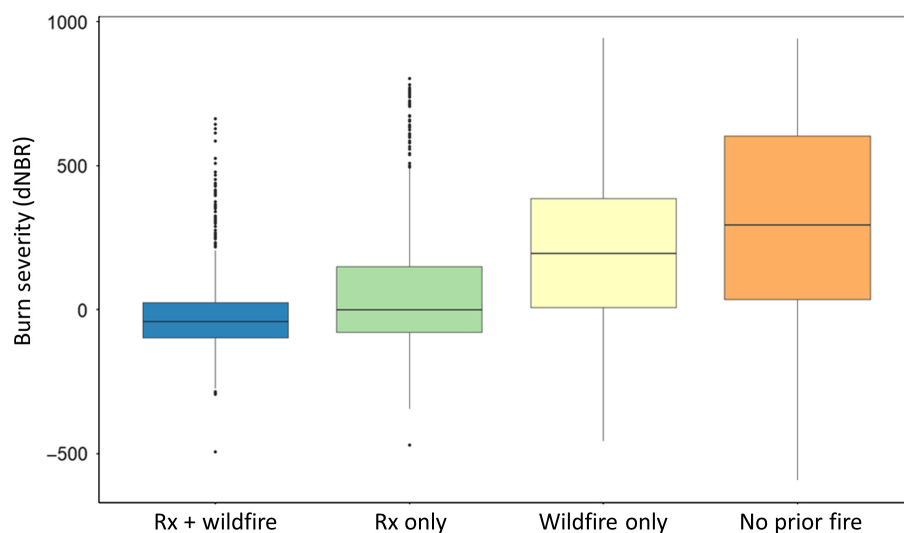


Fig. 2. Mean values of Las Conchas burn severity (differenced normalized burn ratio [dNBR]) by fire history treatment. The simultaneous autoregressive model of Las Conchas burn severity (Table 2) indicated that all fire history treatments were significantly different from the no prior fire treatment.

Table 2. Simultaneous autoregressive model of Las Conchas burn severity (differenced normalized burn ratio) with fire history treatment and topographic factors.

Factor	β	SE	<i>P</i>
Intercept	113.24	25.21	***
Wildfire only	−23.27	5.65	***
Rx only	−27.77	7.93	***
Rx + wildfire	−39.71	7.65	***
Elevation	211.41	43.94	***
Slope inclination	−17.26	7.83	*

Notes: SE, standard error. Model $n = 29926$; Akaike information criterion = 88370; $P < 0.001$; Nagelkerke pseudo- $R^2 = 0.87$; $\alpha = 0.05$.

* $P < 0.05$, *** $P < 0.001$.

axis; Fig. 3a) over the decade-long interval between initial and follow-up measurements. Sample units within the Rx-only and prior wildfire-only treatments showed substantially greater loss of forest cover and degree of change (Figs. 3b, c), with important distinctions associated with earlier fire type. Samples in the Rx-only treatment tended to have higher initial tree cover (low scores on NMS 1), and loss of forest cover at these sites was often associated with increased native herbaceous cover (increasing scores on NMS 2; Fig. 3b). Pre-Las Conchas samples in the wildfire-only treatment generally contained some component of resprouting woody shrubs (associated with score on NMS 1) that were elevated post-Las Conchas. Finally, samples in the no prior fire treatment showed the greatest magnitude of change (Fig. 3d). Before Las Conchas, these sites were the most densely forested (lowest mean scores on NMS 1 and 2); after Las Conchas, they were among the least forested (highest scores on NMS 2; Fig. 3d). Of 16 no prior fire samples located in the forest quadrant of ordination space prior to Las Conchas, only one (6%) remained forest post-Las Conchas, with most (12 samples, or 67%) transformed to herbaceous-dominated meadow or ruderal vegetation types.

Fuel loads and burn severity

Mean values of pre- and post-Las Conchas surface fuel loads, live and dead tree basal areas, and tree densities indicated that the fire effects plots exposed to Rx and prior wildfire had the lowest pre-Las Conchas surface fuel loads and

the smallest subsequent reduction in post-Las Conchas tree density and basal area (Table 3). Pre-Las Conchas surface fuels (litter + duff, fine woody debris, and coarse woody debris) and total tree density all showed positive correlations to burn severity (Fig. 4). The most parsimonious SAR model predicting dNBR from pre-Las Conchas fuels included fine woody debris, coarse woody debris, and tree density as positive predictors of burn severity (Table 4). This model also utilized a neighborhood size of $k = 4$, and model residuals did not show spatial autocorrelation.

DISCUSSION

Combined prescribed fire and prior wildfire mirroring pre-settlement fire regimes reduced subsequent burn severity and fire-driven forest losses (Figs. 2, 3), effects that were associated with reduced pre-fire fuel loads. These findings are consistent with a number of studies demonstrating that recent prescribed fire or wildfire reduced subsequent satellite-inferred burn severity (Finney et al. 2005, Arkle et al. 2012, Miller et al. 2012, Parks et al. 2014a, Stevens-Rumann et al. 2016). Building on these works, the results of our field- and remote sensing-based investigation demonstrate that while single fire types (wildfire vs. prescribed fire) independently showed reduced subsequent burn severity, their additive effects on both burn severity reduction and enhanced forest retention were considerably stronger (Figs. 2, 3).

We also observed differences between our single treatment types; burn severity was more strongly reduced within prescribed fire perimeters than those of wildfires. Wildfires occurring under more extreme conditions than prescribed fire would be expected to impart greater tree mortality, with increases in dead and live surface fuels as dead trees fell and more rapid regrowth occurred (Coppoletta et al. 2016, Harris and Taylor 2017). This expectation is borne out by greater shrub cover and litter loads in our wildfire-only vs. Rx-only treatments (Fig. 3, Table 4). These live and dead fuel loads would be expected to cause greater Las Conchas fire intensity than occurred within prescribed fire boundaries. However, we did not observe strong differences in pre-Las Conchas down woody fuels between

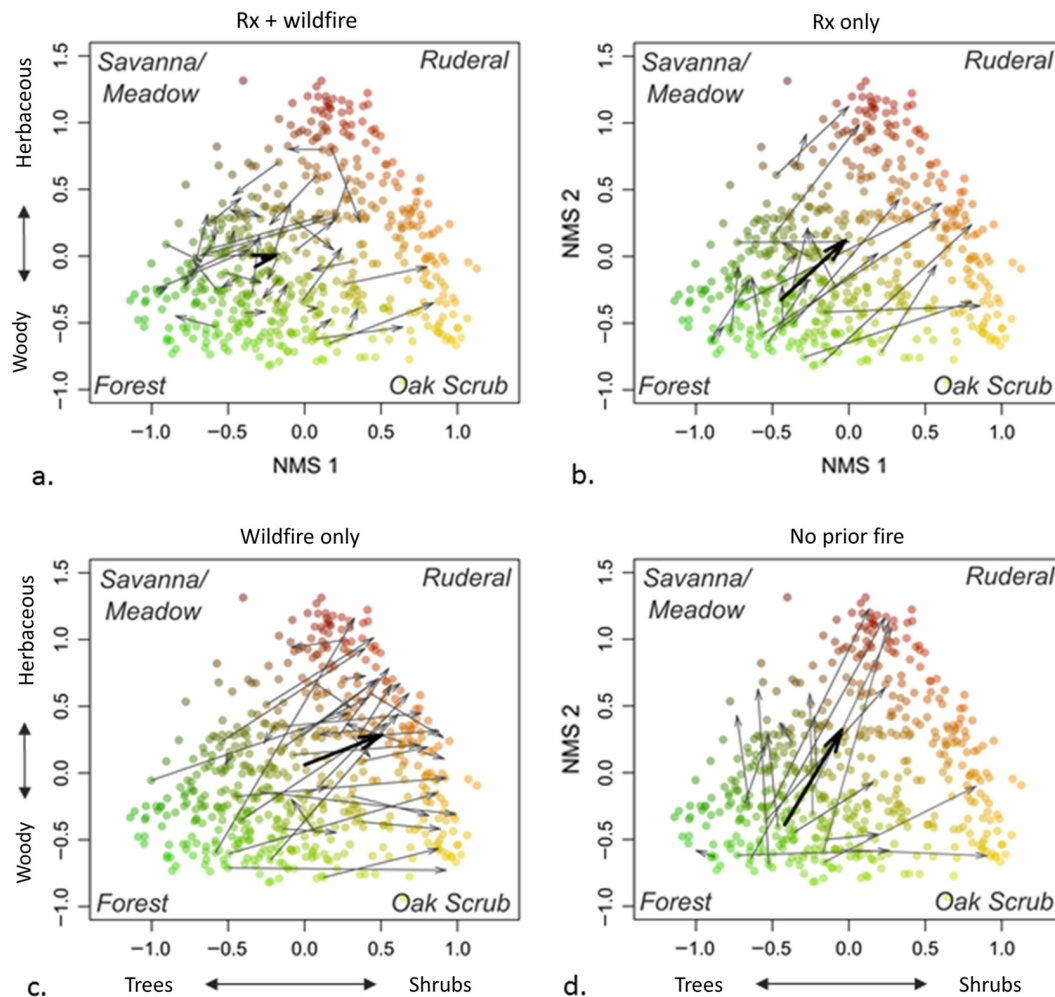


Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of 510 pre-Las Conchas vegetation samples. Increasing scores on NMS 1 (shift from green to yellow points) are correlated with a transition from tree to shrub dominance; increasing scores on NMS 2 (shift from green and yellow points to red points) are associated with the transition from woody to herbaceous plant dominance. Vector direction and length illustrate the magnitude of post-Las Conchas shifts in dominant vegetation type at 129 re-measured plots, with the bold vector indicating mean change for each fire history treatment.

single treatment types (Table 4). In some (but not all) areas, prescribed fire treatments occurred more recently than prior wildfires (Table 1), and several studies have demonstrated that reburn severity increases as a function of time between fires due to fuel accumulation (van Wagtenonk et al. 2012, Parks et al. 2014a). However, an important consideration is that fire had been excluded for over a century prior to prescribed fire application at the majority of our Rx-only plots, potentially limiting treatment effectiveness

due to challenges and risks associated with implementing prescribed fire in fuel-rich stands, such as unwanted fire behavior, spread, or severity (Ryan et al. 2013).

Field-measured patterns of pre- to post-fire compositional change associated with each fire history treatment type paralleled variation in satellite-inferred burn severity. Combined antecedent wildfire and prescribed fire yielded the highest forest retention following the Las Conchas fire, relative to plots with only a single prior

Table 3. Pre- and Post-Las Conchas surface fuel loads, tree density, and basal area by fire history treatment.

	Rx + wildfire (<i>n</i> = 37)		Rx only (<i>n</i> = 27)		Wildfire only (<i>n</i> = 15)		No prior fire (<i>n</i> = 16)	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Year of sample	2002, 2008	2014, 2016	2008	2016	2002, 2010	2014, 2016	2002, 2009	2014, 2015
Litter (Mg/ha)	4.4 ± 2.5	5.2 ± 3.7	4.5 ± 2.5	3.5 ± 1.2	8.2 ± 3.0	2.9 ± 2.0	6.4 ± 2.6	4.5 ± 3.4
Duff (Mg/ha)	7.6 ± 9.9	10.6 ± 11.5	14.9 ± 7.5	5.4 ± 3.5	20.0 ± 10.5	3.1 ± 3.5	22.4 ± 8.5	10.7 ± 9.8
Fine woody debris (Mg/ha)	3.3 ± 3.3	3.0 ± 3.1	8.5 ± 4.3	8.0 ± 3.2	9.3 ± 6.1	8.2 ± 3.2	7.0 ± 4.7	5.5 ± 3.8
Coarse woody debris (Mg/ha)	9.9 ± 14.7	10.9 ± 19.3	35.0 ± 30.0	27.4 ± 14.6	32.4 ± 23.5	44.9 ± 19.3	46.4 ± 34.3	25.2 ± 21.3
Live tree density (stems/ha)	414.6 ± 326.7	261.4 ± 237.7	886.7 ± 430.4	242.6 ± 170.5	809.3 ± 434.6	0.4 ± 1.6	590.6 ± 135.8	128.2 ± 124.8
Dead tree density (stems/ha)	142.9 ± 175.6	112.1 ± 146.1	218.5 ± 136.8	590.0 ± 342.6	226.0 ± 145.5	384.0 ± 252.5	186.3 ± 139.9	353.8 ± 188.0
Live basal area (m ² /ha)	21.2 ± 22.8	17.5 ± 19.4	36.5 ± 8.2	16.6 ± 12.3	20.7 ± 17.9	2.7 ± 10.3	36.9 ± 9.7	14.3 ± 12.4
Dead basal area (m ² /ha)	4.5 ± 7.8	5.6 ± 10.6	14.7 ± 10.4	27.8 ± 12.7	7.2 ± 8.6	20.8 ± 11.3	10.3 ± 6.5	24.5 ± 13.2

Notes: Fine woody debris refers to 1-, 10-, and 100-h fuels; coarse woody debris refers to 1000-h fuels. Values of mass, density, and area are mean ± one standard deviation.

fire type or no recent exposure to fire (Fig. 3). Though some plots within this fire history treatment did burn at high severity and were converted to non-forested vegetation under the extreme burning conditions of the Las Conchas fire, others showed increased tree cover over the 10-yr sampling interval, with the net compositional and structural change being almost zero (Fig. 3a). In contrast, single fire-type treatments showed substantially greater net shifts in ordination space (Fig. 3b, c). We also found marked differences in the responses of the single fire-type treatments. Many of the prior wildfire-only plots contained greater proportions of resprouting shrubs prior to Las Conchas and shifted farther toward shrub dominance (NMS axis 1; Fig. 3b) following reburning. Higher pre-Las Conchas shrub dominance in wildfire-only compared to Rx-only perimeters may have been imparted by greater severity of wildfire during drier and hotter conditions than are typical for prescribed fire. For example, nitrogen losses increase with fire severity (Belillas and Feller 1998), and one of the main shrub species more common in wildfire than prescribed fire units, New Mexico locust (*Robinia neomexicana*), is a nitrogen-fixer. Once established, resprouting woody species appear to benefit from subsequent wildfire (Coop et al. 2016, Guiterman et al. 2017). In contrast, pre-Las Conchas Rx-only plots generally exhibited more forest cover, and less shrub or herbaceous cover, than prior wildfire-only plots (Fig. 3c). However, these Rx-only plots showed shifts toward

decreased tree cover and increased herb and shrub cover upon reburning, shifting toward the same central portion of ordination space that was occupied by pre-Las Conchas prior wildfire plots.

The Las Conchas fire drove the maximum compositional change in forest stands with no prior exposure to fire (Fig. 3d), which were nearly uniformly converted from forest to non-forest. Early post-fire composition of these sites was largely herb-dominated, suggesting that the resprouting woody species common to wildfire-only treatments were less frequent in forests with no recent fire exposure, and had not yet become widely established five years after Las Conchas fire. Though the duration of these forest to non-forest conversions is not yet known, we anticipate limited propagule availability of obligate-seeding conifers in large openings (Ouzts et al. 2015, Chambers et al. 2016, Owen et al. 2017) and strong competition by graminoids and resprouting woody species (Roccaforte et al. 2012). Savage and Mast (2005) recorded fire-driven shifts from ponderosa pine to non-forested communities that had persisted at least three to six decades, including within the La Mesa fire in our study area. In the Hayman burn in Colorado, Chambers et al. (2016) determined that areas >50 m from a seed source were not recovering toward pre-fire ponderosa pine forest densities 15 yr post-fire, and suggested that recovery in these areas would take many additional decades to centuries, even assuming a favorable climate

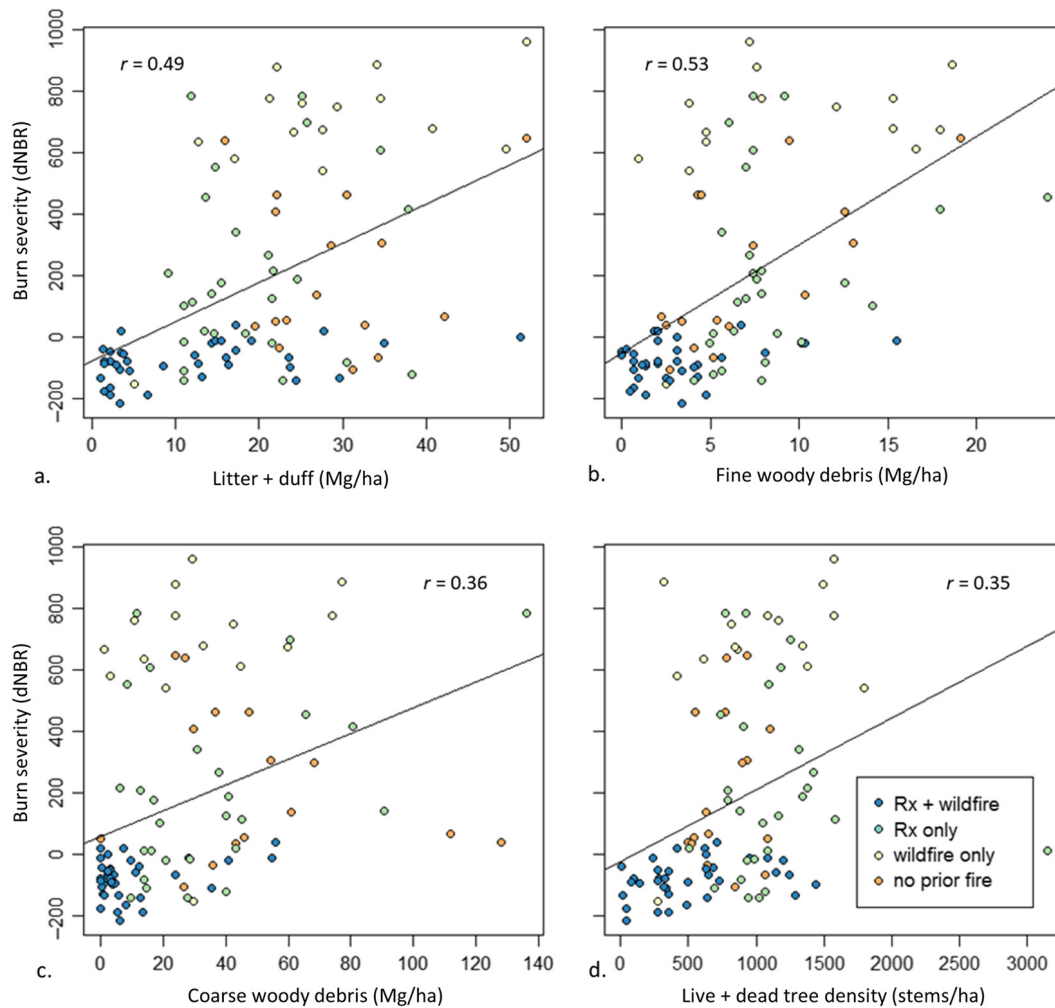


Fig. 4. Relationships (Pearson's r) between burn severity and four fuel measures: (a) litter + duff, (b) fine woody debris (1-, 10-, 100-h), (c) coarse woody debris (1000-h), and (d) tree density, measured at permanent fire effects sample plots, by fire history treatment.

Table 4. Parsimonious simultaneous autoregressive model of burn severity (differenced normalized burn ratio) predicted by pre-Las Conchas surface fuel loads and live tree density.

Factor	β	SE	P
Intercept	25.43	77.62	
Fine woody debris	11.85	3.73	***
Coarse woody debris	1.65	0.65	*
Tree density (live + dead)	0.07	0.04	0.088

Notes: SE, standard error. Fine woody debris refers to 1-, 10-, and 100-h fuels; coarse woody debris refers to 1000-h fuels. Model $n = 95$; Akaike information criterion = 1259; $P < 0.001$; Nagelkerke pseudo- $R^2 = 0.71$; $\alpha = 0.05$.

* $P < 0.05$, *** $P < 0.001$.

and no further disturbance. In comparison, within the Las Conchas fire perimeter, 32,251 ha (more than half of the total fire area) is >50 m from a surviving seed source and the mean distance from a non-forested site to a surviving tree seed source is 274 m (J. Coop, *unpublished data*). Additionally, climate across our study area appears to have been particularly limiting to ponderosa pine establishment: Most tree seedlings planted post-fire in a portion of the study area were killed by recent drought (J. Coop, *personal observation*), and no seedlings were recorded in any of our sample sites even proximal to surviving seed sources.

Satellite-inferred burn severity and fire-induced tree mortality were associated with surface fuel loads, but less so with measured attributes of stand structure (Fig. 4, Tables 3, 4). Forest persistence following the extreme Las Conchas fire event necessarily depended on conditions that (1) precluded active crown fire spread as fire moved into any given stand and (2) precluded transition from surface fire to crown fire as fire moved through the stand (Rothermel 1983, Scott and Reinhardt 2001). Prior wildfire resulting in patchy canopy openings (not examined here) would be expected to be most effective at inducing the former effect, and prescribed fire or wildfire that consumed mostly surface fuels, the latter. As such, the combination of wildfire and prescribed fire together should be most effective at increasing forest resistance to active crown fire. Pre-Las Conchas variation in surface fuels and tree density across the five management units was consistent with reductions associated with repeated exposure to fire (i.e., combined prior wildfire and prescribed fire; Fig. 4a–c, Table 3). Similarly, van Mantgem et al. (2016) found that repeated prescribed fires resulted in substantially greater surface fuel reductions than a single fire. Huffman et al. (2018) examined the influences of repeated resource objective wildfire (natural ignitions allowed to burn to accomplish ecological objectives) on surface and canopy fuels, also finding decreased fine surface fuel loads in repeat vs. single fire samples. They attributed this difference primarily to cleanup effects of the second fire removing fuels in places that were missed by the first (Huffman et al. 2018). Our best-fitting SAR model (Table 4) included two surface fuel terms as predictors of Las Conchas burn severity, fine woody debris, and coarse woody debris. Tree density was also retained in this model, though with a *P*-value of 0.09. Tree density was lowest in our Rx + wildfire samples; in addition to reductions in canopy density caused by early wildfire, it is likely that wildfire and subsequent prescribed fire killed tree seedlings that did not subsequently contribute to increased mature tree density.

Variation within each of the five management units and permanent plots used to sample pre- and post-Las Conchas fuels and stand structure provided insights into the mechanisms driving

patterns and variability of fire effects across the study area. However, concentrations of fuels within specific units may provide a limited representation relative to the more comprehensive coverage of the satellite-inferred burn severity and field vegetation samples. While fuel availability was identified as an important mechanism in determining burn severity and tree mortality, models also indicated that two topographic factors, elevation and slope, were associated with variation in burn severity across the study area (Table 2). The positive relationship between burn severity and elevation may be attributed to a combination of factors including the tendency for higher elevations to be more productive and fuel-rich due to increased moisture (Dillon et al. 2011, Parks et al. 2014a) and/or the non-uniform distribution of fire treatments across the study area (i.e., repeated prescribed fire exposure tended to occur at lower elevations). We note that despite the inclusion of these topographic factors in our models, fire treatments continued to stand out as strong and significant predictors of burn severity (Table 2), demonstrating the potential of repeated fire exposure as a management tool for restoring and enhancing forest landscape resilience.

Management implications and conclusions

Retention of ponderosa pine and dry mixed-conifer forests facing increasing wildfire activity compels the restoration of forest and fuel structures conducive to frequent, low-severity fire (Covington et al. 1997, Mast et al. 1999). Our results are consistent with numerous observational studies demonstrating that prescribed fire, resource objective wildfire, and especially sequential exposure to fire, can yield stand conditions aligned with fuel mitigation objectives and reduced burn severity of subsequent wildfire (Finney et al. 2005, Hunter et al. 2011, Larson et al. 2013, Stevens-Rumann et al. 2013, van Mantgem et al. 2016, Huffman et al. 2017, Lydersen et al. 2017). It has been suggested that the current pace and scale of fuel reduction treatments are not adequate in addressing the large expanses of forests lands in need of restoration (Ryan et al. 2013, North et al. 2012). Consequently, our results suggest that expanding area treated in terms of prescribed fire and allowing fire to burn for resource benefit (under suitable

weather conditions) will reduce the potential for fire-facilitated conversions to non-forest over larger landscapes.

Three primary factors are known to govern fire behavior: weather, topography, and fuels, of which only fuels can be directly controlled through management intervention (Agee 1996). While mechanical fuel reduction treatments can generate fire resistant stand structure, their repeated application over large areas is usually not practical due to cost, legal, or logistical constraints (Hartsough et al. 2008, North et al. 2015). Managers may be able to take advantage of resource objective wildfire and follow-up prescribed fire to reduce fuels across more extensive areas and sites not conducive to mechanical treatments (e.g., steep slopes, roadless areas), thereby promoting multiple short-interval fire entries. The use of repeated resource benefit and prescribed fire may also facilitate burning at low to moderate severity under mild weather conditions. In contrast, a fire, such as Las Conchas, which burned largely under extreme weather conditions, drove high forest mortality even in some areas that had been exposed to a single prior wildfire or prescribed fire (Table 3), and resultant dead and down fuel loads and shifts toward ruderal and shrubby vegetation types (Fig. 3) point to a major net loss in forest resilience.

In addition to providing general support for more use of fire to meet management objectives, our study also suggests that the benefits of fire may be optimized by its sequential application, particularly the use of prescribed fire following wildfire. As indicated by pre- and post-Las Conchas measures of surface fuel loads (Table 3), downed and dead woody materials may rapidly accumulate post-wildfire, sometimes exceeding pre-fire loads. Strategically applying prescribed fire after wildfire can consume these accumulated fuels, thereby reducing subsequent surface fire intensity that would occur under more extreme conditions and increasing the probability that residual live trees will survive subsequent fire events. However, we also caution that where fire-driven type conversions to non-forested states have already occurred, repeated burning can eliminate post-fire regeneration by obligate-seeding tree species, and may promote the maintenance of stable, non-forested alternate

states (Coop et al. 2016). Effects and interactions of repeated wildfires are complex (Prichard et al. 2017), and management of post-fire landscapes will require type- and location-specific nuance that may entail balancing sometimes competing objectives of residual forest resistance to reburning, forest recovery in non-forested burn interiors, and general landscape resilience.

In our study system, the additive effects of repeated exposure to fire reduced the likelihood of shifts toward successional trajectories conducive to enduring conversions to non-forested states (Savage and Mast 2005, Coop et al. 2016, Coppoletta et al. 2016). The rate and extent of such shifts is expected to increase in the future, driven by direct and fire-mediated effects of climate (Parks et al. 2017). By embracing sequential low- to moderate-severity fire in frequent-fire-adapted forest types, managers can utilize the ecological memory of these systems evident in their fire-adapted traits, thereby enhancing resilience in a future of volatile disturbance and decreasing the loss of the legacies necessary for recovery (Johnstone et al. 2016).

ACKNOWLEDGMENTS

This research was supported by an agreement between the Aldo Leopold Wilderness Research Institute and Western State Colorado University (15-CR-11221639-118). We thank the staff of Bandelier National Monument for facilitating access and field sampling and Esteban Muldavin, with the New Mexico Natural Heritage Program, for providing pre-Las Conchas field vegetation samples. Dave Roberts provided code for the `addpoints.nmms` R function. For assistance with field sampling, we thank Carissa Callison, Hanna Davis, Nicole Dotson, and Jessie Marlenee. We also thank two anonymous reviewers who provided feedback that substantially improved this manuscript.

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