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Influences of prior wildfires on vegetation response to subsequent fire in a reburned Southwestern landscape

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Abstract. Large and severe wildfires have raised concerns about the future of forested landscapes in the southwestern United States, especially under repeated burning. In 2011, under extreme weather and drought conditions, the Las Conchas fire burned over several previous burns as well as forests not recently exposed to fire. Our purpose was to examine the influences of prior wildfires on plant community composition and structure, subsequent burn severity, and vegetation response. To assess these relationships, we used satellite-derived measures of burn severity and a nonmetric multidimensional scaling of pre- and post- Las Conchas field samples. Earlier burns were associated with shifts from forested sites to open savannas and meadows, oak scrub, and ruderal communities. These non-forested vegetation types exhibited both resistance to subsequent fire, measured by reduced burn severity, and resilience to reburning, measured by vegetation recovery relative to forests not exposed to recent prior fire. Previous shifts toward non-forested states were strongly reinforced by reburning. Ongoing losses of forests and their ecological values confirm the need for restoration interventions. However, given future wildfire and climate projections, there may also be opportunities presented by transformations toward fire-resistant and resilient vegetation types within portions of the landscape.

Key words: Bandelier National Monument; New Mexico, USA; fire severity; general resilience; Jemez Mountains, New Mexico, USA; landscape memory; ponderosa pine (Pinus ponderosa)*; prescribed fire; relativized burn ratio.*

INTRODUCTION

Land use legacies and climate have altered fire regimes across montane forests of much of the southwestern U.S. (e.g., Allen et al. 2002), and many recent wildfires in this region have been uncharacteristically large and severe (Dennison et al. 2014, O'Connor et al. 2014). Large openings resulting from high-severity fire in former ponderosa pine (*Pinus ponderosa*) and mixed conifer forests may be persistent given tree seed source limitations, climatic constraints on reproduction and survival, and competition from herbaceous and shrubby vegetation (Bonnet et al. 2005, Haire and McGarigal 2010, Roccaforte et al. 2012). Additionally, positive feedbacks associated with subsequent reburning are predicted to reinforce vegetation changes originating from previous high-severity fire (Savage and Mast 2005). Consequently, there are growing concerns that contemporary fire regimes may exceed ecological thresholds for some conifer forest types, catalyzing long-term conversion to non-forested alternative stable states (Barton 2002, Savage and Mast 2005, Falk 2013).

Enhancing the resistance and resilience of ecosystems has been endorsed as an important management goal for a future of certain change (Millar et al. 2007). Resistance can be defined as "staying essentially unchanged despite the presence of disturbance," while resilience is "returning to the reference state (or dynamic) after a temporary disturbance" (Grimm and Wissel 1997). While the processes differ, the outcome of both properties is retention of the prior state. While high-severity wildfire can drive vegetation conversions from forests to alternative states, such post-fire states may exhibit increased resistance and resilience to future burning. Fuel reduction treatments intended to reduce burn severity represent a widely employed management approach for increasing resistance to wildfire (Agee and Skinner 2005), but reductions in fuels and subsequent burn severity

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may also be imparted by wildfire itself (e.g., Parks et al. 2014*a*). Resilience to wildfire comprises recovery to pre-fire conditions or trajectories, and may depend largely on species traits and patterns of community composition and structure (e.g., Halpern 1988, Larson et al. 2013). For example, in Mediterranean forests, resprouting oaks show higher resilience to wildfire than pines reproducing from seed (Díaz-Delgado et al. 2002, López-Poma et al. 2014). Likewise, in the southwestern U.S., while dense ponderosa pine forests do not exhibit resilience to high-severity fires, herbaceous and resprouting shrub communities generated by such fires (Savage and Mast 2005) would be expected to be highly resilient to burning due to species traits that promote survival and rapid regrowth.

Assessing patterns of conversion, resistance, and resilience can only be done following disturbance, and requires both pre- and post-disturbance measures of state variables. In 2011, the 63000-ha Las Conchas fire in New Mexico, USA reburned portions of several earlier burns, largely under extreme fire weather and drought conditions. Vegetation within these burns was sampled between 2002 and 2006 (Muldavin et al. 2011), providing an opportunity to assess change via re-measurement. The purpose of our research was to examine the correspondence between previous burning and pre-Las Conchas vegetation composition and structure, and the influences of both on subsequent burn pattern and post-Las Conchas vegetation responses. We hypothesized that prior exposure to fire led to the establishment and/or maintenance of vegetation types that would exhibit (1) greater resistance to subsequent wildfire via reduced burn severity, and (2) high resilience to reburning via rapid post-fire recovery relative to forests not exposed to recent prior fire. While we expected sharp differences between sites that had and had not previously burned, we were also interested in variation along gradients of fire severity and vegetation composition. Lastly, we hypothesized that (3) compositional and structural changes wrought by previous wildfires would be reinforced by reburning in the Las Conchas fire, particularly shifts toward non-forested, herbaceous, and resprouting woody vegetation (Savage and Mast 2005).

METHODS

This study was conducted within the perimeter of the Las Conchas fire in the eastern Jemez Mountains of New Mexico (Fig. 1). Climate is semiarid and continental. Mean annual temperature (1981–2010 norms) in nearby Los Alamos (2243 m) is 9.1°C; mean annual precipitation is 47.7 cm, with 45% (21.3 cm) arriving during the July–September summer monsoon period. Elevations range from 1750 to 3350 m. Pre-Las Conchas vegetation types (Muldavin et al. 2011), included piñon (*Pinus edulis*) and juniper (primarily *Juniperus monosperma*) woodlands at the lowest elevations, ponderosa pine (*Pinus ponderosa* var. *scopulorum*) at intermediate elevations, and aspen (*Populus tremuloides*), and mixed-conifer stands including ponderosa pine, Douglas fir (*Pseudotsuga menziesii* var. *glauca*), southwestern white

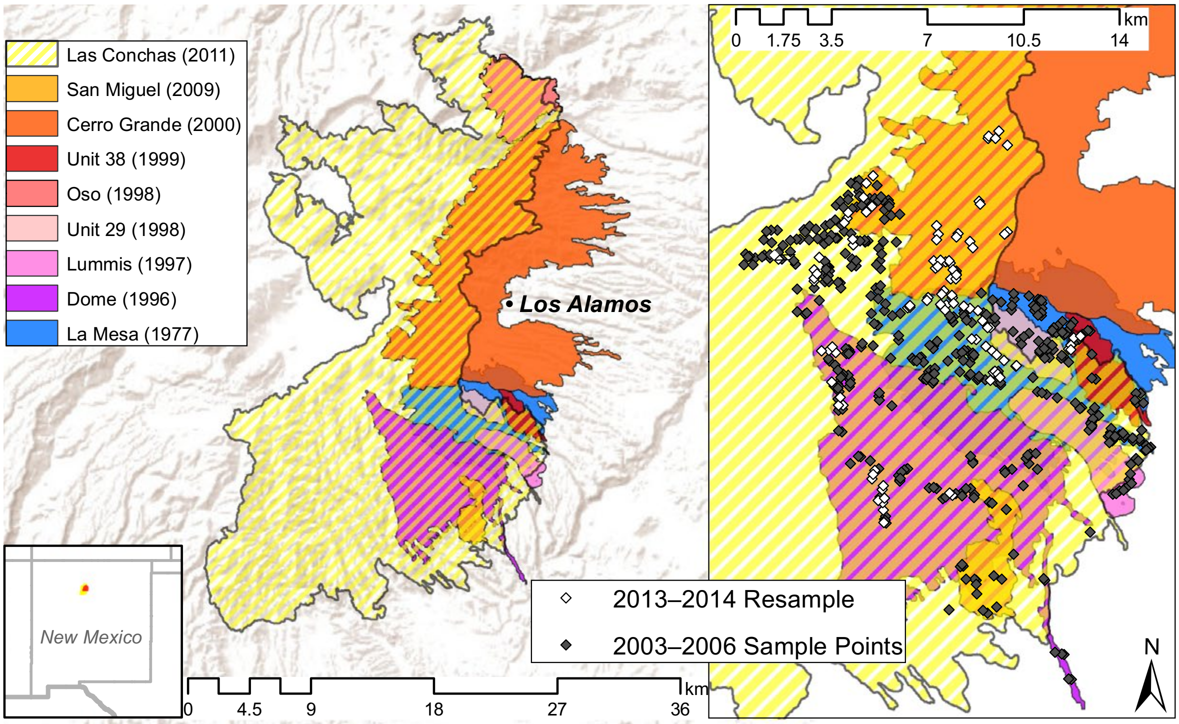

FIG. 1. Locations of burns and field sample plots in the Jemez Mountains, New Mexico, USA.

pine (*Pinus strobiformis*), white fir (*Abies concolor*), and Engelmann spruce (*Picea engelmanii*) at progressively higher elevations. Patches of aspen and shrublands dominated by New Mexico locust (*Robinia neomexicana*) and oaks (*Quercus* × *pauciloba* and *Q. gambelii*) were associated with historic and/or recent stand-replacing burns (Margolis et al. 2007, Muldavin et al. 2011).

Across gradients in topography and vegetation, presettlement fire regimes undoubtedly varied, but are widely accepted to have included a substantial component of low-severity fire with short return intervals, particularly in formerly widespread ponderosa pine and mixed conifer stands. From fire-scarred trees, Foxx and Potter (1978) found mean fire intervals of 5–18 yr; Touchan et al. (1996) reported mean fire intervals for all trees of 5.5–11.5 yr for ponderosa pine and 5.0–18.9 yr for mixed conifer stands. This fire regime ceased with the removal of fine fuels by heavy livestock grazing in the 1890s and later direct fire suppression. Foxx et al. (2013) present some evidence for infrequent, small (~5–50 ha) fires of variable severity through most of the 20th century, with two fires of ~500–1000 ha. In 1977, the 6250-ha La Mesa fire was the first of a series of much larger, higher-severity fires to impact the region (Fig. 1; Appendix S1), leading up to and including the 63370-ha Las Conchas fire in 2011.

To examine patterns of vegetation change resulting from the Las Conchas fire, we utilized 510 field-sampled vegetation plots measured prior to Las Conchas (June–September 2003–2006; Muldavin et al. 2011), occurring in upland habitats, with >20% vegetation cover, and within the Las Conchas perimeter. Of these, 102 were re-measured after the Las Conchas fire in 2013 or 2014. Plots were re-located using a hand-held GPS unit and pre-fire photographs. Original sampling protocols, described fully in Muldavin et al. (2011), were followed for re-measurement. Within 20 × 20-m plots, cover by all species and strata (tree, woody plants ≥5 m; shrub, woody plants <5 m, includes tree seedlings and saplings, graminoids, and forbs) was visually estimated. Coverage values were entered as the midpoint of nine cover ranges, as follows: 0.05% (trace, present on plot but <0.1%), 0.5% (0.1–1%), 1.5% (1–2%), 7.5% (5–10%), 17.5% (10–25%), 37.5% (25–50%), 62.5% (50–75%), 85% (75–95%), and 97.5% (≥95%). To ensure that re-sampled plots represented the full range of pre-Las Conchas compositional variation, we stratified re-sampling by four vegetation types delineated by the ordination axes of a nonmetric multidimensional scaling analysis (NMS).

Burn severity grids for five wildfires (Dome, Lummis, Oso, Cerro Grande, and San Miguel; Fig. 1) and two prescribed burns (Units 29 and 38; Fig. 1) that predated the Las Conchas fire were generated from Landsat Thematic Mapper (TM) imagery distributed by the Monitoring Trend in Burn Severity project (MTBS; Eidenshink et al. 2007). Because the Las Conchas MTBS imagery was affected by the Landsat 7 scan line corrector failure, we used pre- and post-fire Landsat 5 imagery obtained from USGS-EROS to generate the Las Conchas burn severity grids. We measured burn severity as the relativized burn ratio (RBR), a satellite-inferred measure of fire-induced ecosystem change that has high correspondence to field-based measures of burn severity (Parks et al. 2014*b*). The correlation between RBR and field data shows a modest improvement (3–6% increase in r^2) over other commonly used satellite-inferred metrics of severity (i.e., dNBR, RdNBR; Parks et al. 2014*b*). Additionally, use of a relativized measure, as opposed to an absolute measure such as dNBR, better facilitates comparisons between different fires and vegetation types and is less dependent on the amount of pre-fire vegetation (Miller and Thode 2007). The 1977 La Mesa fire predated TM imagery and it was not possible to directly calculate RBR; however, MSS imagery was available. As such, we predicted burn severity (RBR) for the La Mesa fire based on the robust relationship ($r^2 > 0.7$) between dNDVI and RBR from several fires in the Gila Wilderness, New Mexico (Appendix S2). All burn severity grids include the dNBR offset, which accounts for differences due to phenology or precipitation between pre- and post-fire images, further improving comparison among fires (Key and Benson 2006, Parks et al. 2014*b*).

To characterize relationships between pre-Las Conchas vegetation and burn severity, we conducted a nonmetric multidimensional scaling (NMS) using R package vegan (Oksanen et al. 2012). The NMS was based on a Sørensen (Bray-Curtis) distance matrix calculated from 510 samples of coverages of 433 species and four vegetation structural strata. We assessed correlations between NMS axis scores, previous burn severity, subsequent Las Conchas burn severity, and topographic variables. Scores on NMS axes 1 and 2 were strongly related to pre-Las Conchas vegetation structure and burn severity, and allowed us to differentiate between four vegetation groups (forest, savanna/meadow, oak scrub, and ruderal; described in Results) to stratify samples for re-measurement. To assess differences in vegetation response to the Las Conchas fire, we utilized ANOVA to test for differences between these four groups in previous burn severity, Las Conchas burn severity, and two metrics of resistance and resilience: pre- to post-Las Conchas changes in vegetation composition (Sørensen distance) and total vegetation cover change. To assess the directionality of compositional change within the context of our original NMS ordination, we calculated NMS axis scores for the 102 post-fire samples (Roberts 2014, function addpoints.nmds) in R (R Core Development Team 2014). Locations of re-measured plots in species-space were added to our original NMS to illustrate post-Las Conchas compositional shifts.

RESULTS

Nonmetric multidimensional scaling produced a three-dimensional solution with a stress of 0.15

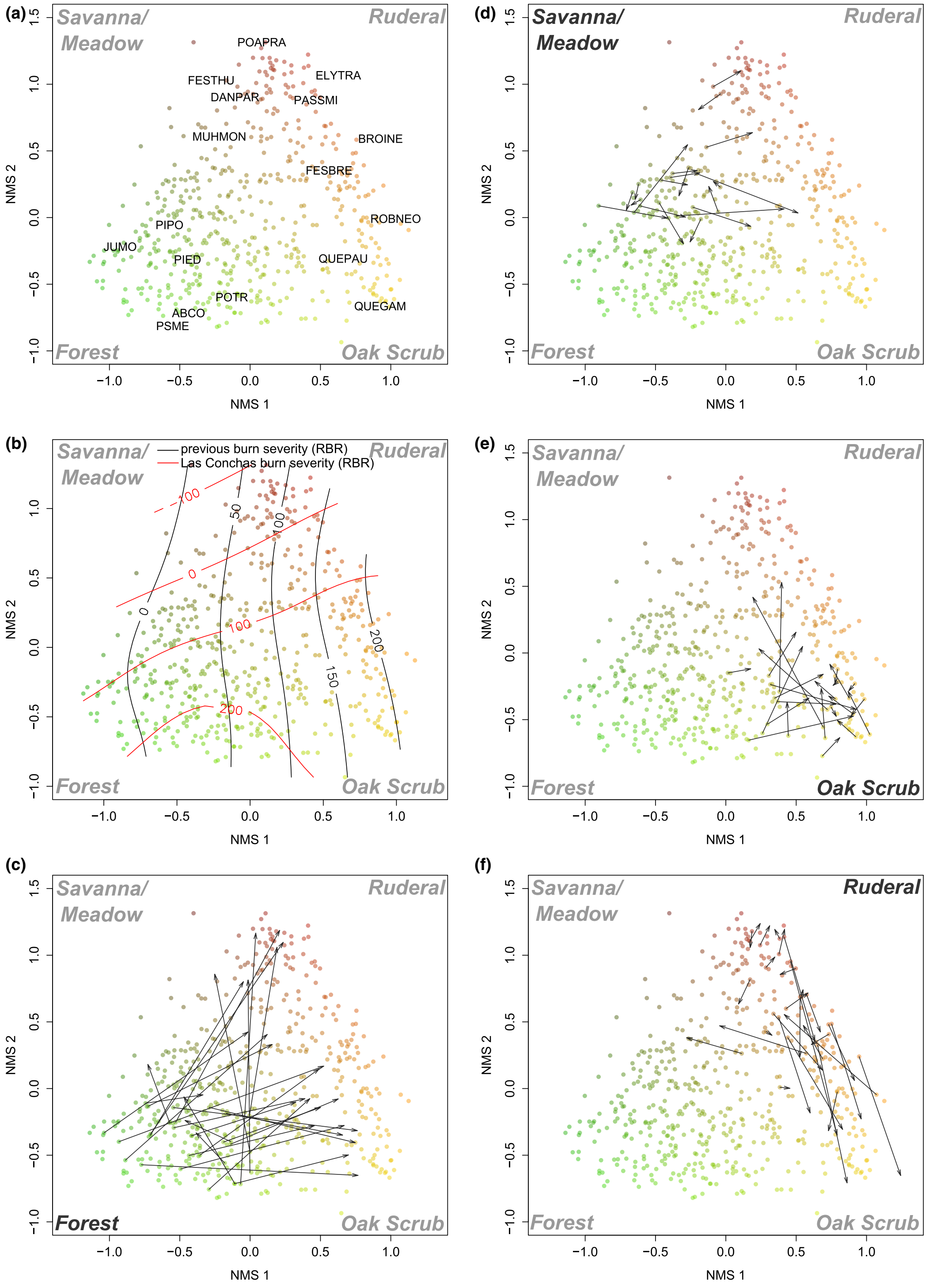

FIG. 2. Nonmetric multidimensional scaling (NMS) axes 1 and 2 of pre-Las Conchas vegetation, (a) vegetation types and locations of species codes representing the centers of their distributions in ordination space, as follows: *Abies concolor* (ABCO), *Juniperus monosperma* (JUMO), *Pinus edulis* (PIED), *P. ponderosa* (PIPO), *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), *Bromus inermis* (BROINE), *Danthonia parryi* (DANPAR), *Elymus trachycaulus* (ELYTRA), *Festuca brevipila* (FESBRE), *F. thurberi* (FESTHU), *Muhlenbergia montana* (MUHMON), *Pascopyrum smithii* (PASSMI), *Poa pratensis* (POAPRA), *Quercus gambelii* (QUEGAM), *Q. pauciloba* (QUEPAU), *Robinia neomexicana* (ROBNEO), (b) relationships to previous burn severity (black) and subsequent Las Conchas burn severity (red) and (c–f) changes in site scores following the Las Conchas fire with arrows representing the extent and direction of change in species-space for re-measured sites within each of four vegetation types: (c) forest, (d) savanna/meadow, (e) oak scrub, and (f) ruderal. Values of RBR <35 correspond with a burn severity classification of unchanged/very low, 35–129 were low, 130–297 were moderate, and >297 were high).

(Fig. 2a). The first axis, NMS 1, represented a gradient of burn severity (RBR) of the most recent previous fire (Fig. 2b; *r* = 0.52). Correspondingly, pre-Las Conchas tree canopy cover (including one-seed juniper, aspen, ponderosa pine, white fir, Douglas fir, and piñon pine) declined (*r* = −0.67) and non-tree woody cover (including Gambel's oak, wavyleaf oak, and New Mexico locust) increased (*r* = 0.68) along this axis. NMS 1 also illustrated a shift from three native understory and meadow bunchgrasses (mountain muhly, *Muhlenbergia montana*; Thurber's fescue, *Festuca thurberi*; and Parry's oatgrass, *Danthonia parryi*) to a suite of native and exotic species (including Kentucky bluegrass, *Poa pratensis*; western wheatgrass, *Pascopyrum smithii*; smooth brome, *Bromus inermis*; slender wheatgrass, *Elymus trachycaulis*; and hard fescue, *Festuca brevipila*), several of which are known to have colonized burns via post-fire seed mixtures (Foxx et al. 2013). NMS 2 represented a gradient of woodiness, from high cover by trees (*r* = −0.52) and shrubs (*r* = −0.44), to graminoids (*r* = 0.70) and forbs (*r* = 0.30; Fig. 2a). This axis was correlated with subsequent Las Conchas burn severity (Fig. 2b; *r* = 0.38). Neither NMS 1 nor 2 were correlated with time since fire or number of recorded fires. NMS 3 was correlated with elevation (*r* = 0.63) and will not be discussed further.

Site scores on NMS 1 and 2 were used to differentiate between four vegetation groups (Fig. 2a), as follows: (1) forests, with below median scores on both NMS 1 and 2 and high tree cover; (2) savanna/meadow sites below the median of NMS 1 but above that of NMS 2, with reduced or no tree canopy cover and high cover by native grasses; (3) oak scrub, above the NMS 1 median but below the NMS 2 median, with high shrub cover, mainly by resprouting oaks; and (4) ruderal communities above NMS 1 and 2 median values, with cover dominated by New Mexico locust and a wide range of herbs including many weedy and nonnative species.

Las Conchas burn severity was strongly reduced in previous burns; mean Las Conchas RBR was 194 in pixels not recently burned, and 118 in reburned pixels. Re-sampled sites showed strong differences in previous and subsequent burn severity between our four vegetation types (Table 1). Forest sites, which had not been strongly impacted by previous wildfire (occurring outside of burn perimeters or with low values of previous burn severity), burned at high severity during Las Conchas (RBR = 315; Table 1). Savanna/meadow sites, on average, previously burned at moderate severity (RBR = 79) but were unchanged by the Las Conchas fire (RBR = 8). Oak scrub sites, on average, burned at moderate severity in both previous fires (RBR = 226) and subsequent reburning (RBR = 199). Ruderal communities, on average, showed moderate burn severity in previous wildfires (RBR = 229) but reburned at much lower severity (RBR = 56; Table 1).

Each of the four vegetation types exhibited distinct pre- to post-Las Conchas changes in composition and cover (Table 1, Fig. 2c-f). Forested sites showed the greatest changes in composition and losses in cover (Table 1), and were overwhelmingly transformed by burning during Las Conchas (Fig. 2c). Only four re-measured sites (14%) remained in this quadrant of ordination space; six (21%) shifted to the savanna/meadow type, 11 (38%) shifted into oak scrub, and eight (28%) to the ruderal type. Savanna/meadow sites exhibited the smallest changes in composition and total cover (Table 1, Fig. 2d). Of the re-measured savanna/meadow samples, 12 (60%) were retained in this quadrant of ordination space, three (15%) shifted into the forest quadrant, indicating recent tree recruitment in spite of burning, one (5%) shifted into the oak scrub type, and four (20%) moved into the ruderal quadrant. Oak scrub samples showed the highest compositional fidelity following reburning with 19 re-measured samples (79%) retained in this quadrant (Fig. 2e). None of these samples shifted to forest or savanna/meadow types, though five (21%) moved into the ruderal group. Finally, 20 samples (69%) classified as ruderal were retained in this type, with seven (24%) transitioning to oak scrub and two (7%) to savanna/meadow (Fig. 2f).

Discussion

Extensive conversions from forested to non-forested vegetation types across the eastern Jemez Mountains were driven by a recent series of wildfires leading up to and including the Las Conchas fire. Historical photos and ecological data collected prior to the 1977 La Mesa fire (Foxx et al. 2013), and the abundance of snags in 1977–2000-era burns (e.g., Fig. 3) demonstrate this landscape was extensively forested preceding recent fires. Prior to the Las Conchas fire, earlier burns showed sharply reduced conifer canopy cover, expanded cover by resprouting shrubs and aspens, and increased cover by a suite of native and introduced forbs and graminoids (Fig. 2a). Shifts from forested to shrub- and ruderal-dominated states were strongly related to previous burn severity (Fig. 2b), but were unrelated to time since fire, indicative of the altered successional pathways and long-term nature of ecological transformations driven by prior high-severity wildfire in former frequent-fire ponderosa pine and mixed conifer landscapes (Savage and Mast 2005, Haire and McGarigal 2010, Foxx et al. 2013). In forested stands not exposed to recent previous fire, the Las Conchas fire drove similar patterns of change as preceding fires elsewhere (Table 1), with most sites converted from forested to non-forested vegetation types (Figs. 2c, 3a).

While earlier wildfires underlay major shifts away from forested conditions within our study landscape, resultant vegetation exhibited much greater resistance and resilience to subsequent burning, even under the extreme conditions of the Las Conchas fire. The net

(a) Forest—Plot 9360

(b) Savanna/Meadow—Plot 9298

(c) Oak Scrub—Plot 9656

(d) Ruderal—Plot 9622

FIG. 3. Representative photos of pre- (2006) and post-Las Conchas (2014) field samples illustrating changes in each of four vegetation types. All photos by J. Coop.

Table 1. Previous burn severity, Las Conchas burn severity, compositional dissimilarity, and change in cover by vegetation type for samples re-measured 2–3 yr after the Las Conchas fire, New Mexico, USA.

	Forests (n = 29)	Savanna/Meadow (n = 20)	Oak Scrub (n = 24)	Ruderal (n = 29)
Previous burn severity				
RBR	42 ± 65^{a}	79 ± 79^{a}	226 ± 107^{b}	269 ± 191^{b}
Las Conchas burn severity				
RBR	315 ± 169^{a}	8 ± 136^{b}	199 ± 123^{c}	56 ± 168^{b}
Vegetation response				
Pre- to post- Las Conchas compositional distance	0.77 ± 0.18^{a}	0.41 ± 0.19^{b}	0.46 ± 0.19^{b}	0.50 ± 0.2^{b}
Cover (%) change	−55 ± 39^{a}	−21 ± 24^{b}	−36 ± 34^{a,b}	−22 ± 35^{b}

Note: Values given are means ± standard deviation. Significant differences (Tukey's HSD <0.05) across vegetation types (rows) are indicated with different superscripted letters.

effect of both properties was close retention of pre-Las Conchas conditions, whether the site was essentially unaffected by reburning (resistance), or impacted but recovered (resilience). Most of our previously burned sites exhibited both properties, though with varying signal across gradients of severity and vegetation composition. Resistance to fire in reburns, demonstrated by decreased Las Conchas burn severity (RBR), is consistent with studies elsewhere (Miller et al. 2012, Parks et al. 2014*a*). Particularly in savanna/meadow (Figs. 2d, 3b) and ruderal communities (Figs. 2f, 3d), where previous fires appear to have reduced ground, understory, and/or canopy fuels, field measures also confirmed that the Las Conchas fire caused only minor changes in vegetation cover and composition. Increased resilience is especially evident in sites that burned at higher severities but quickly recovered. Communities dominated by resprouting woody species, including oaks, aspen, and New Mexico locust, rebounded rapidly (2–3 yr post-fire) toward pre-Las Conchas levels of cover with minimal compositional change (Figs. 2e, 3c). As predicted by Savage and Mast (2005), where the Las Conchas fire reburned community types generated by previous fires, the directionality of earlier shifts was largely reinforced (Fig. 2d–f). Areas of uncertainty include the future responses of these states to a third fire and long-term successional trajectories with or without fire. In any case, the potential for natural forest recovery is improbable within the near term.

These findings point toward risks, but also opportunities, for fire and fuels management. The divergent post-fire responses we observed in each of our four coarse vegetation types (forest, savanna/meadow, oak scrub, and ruderal communities) may help inform management prospects. Extensive fire-driven conversions from forests to alternative states, reinforced by reburning, inevitably entail unacceptable losses of biota, ecological communities, and ecosystem services (e.g., Hurteau and North 2008). These changes confirm the need for a suite of intervention strategies to maintain and recover ponderosa pine and mixed conifer stands on the landscape, including the restoration and maintenance of fire-resistant stand structure through mechanical treatments and prescribed fire (Covington et al. 1997, Allen et al. 2002). In large openings distant from seed sources, replanting will also be essential for the post-fire regeneration of conifers that depend on reproduction from seed. Low reburn severity in the ruderal communities we describe here suggest that tree seedlings planted in these vegetation types may have lower risks of being killed by subsequent fire, depending on fire-free intervals. Our findings reinforce the view that wildfire may sometimes act as a fuel treatment that reduces subsequent burn severity, and also support the strategic use of managed and prescribed fire to achieve these means, even when the severity of such burns may be higher than anticipated (Fulé et al. 2004). Las Conchas burn severity was reduced most strongly by two fires managed for resource benefit (Lummis and San Miguel) followed by two prescribed fires (Units 28 and 39). The duration of fire-driven fuel reductions in Southwestern, montane systems likely lasts for at least two decades (Parks et al. 2014*a*), but how such effects vary along environmental gradients and with vegetation composition and structure is not known. Further consumption of down and dead fuels during subsequent fire (e.g., the strong reductions visible in Fig. 3b–d) within this interval would be expected to create even longer-lasting effects, though this is also a subject that requires further research. The fire-driven expansion of sparsely-treed savannas and meadows in the study area may compensate for or even restore systems lost to conifer encroachment in the absence of fire (e.g., Coop and Givnish 2007). Reduced reburn severity in this vegetation type (Table 1, Fig. 3b) indicates that the restoration of frequent, low-severity fires consistent with historical parameters (e.g., Touchan et al. 1996) may be practicable.

It may also be useful to distinguish between specified and general resilience (Folke et al. 2010). The former term (specified) may be applied to the resilience of particular components of a system to specific disturbances, and is illustrated by the resilience of oak scrub and non-resilience of forested stands to high-severity fire within our study landscape. The latter term (general) concerns the resilience of the larger landscape to a broader range of potential future disturbances. In some cases, transformations at fine scales may impart resilience at a coarser scale (Folke et al. 2010). Is landscape resilience enhanced or diminished by conversions to fire-resistant and resilient savanna, meadow, oak scrub, and ruderal vegetation types within portions of that landscape? Given interactions between the trajectory of increasing wildfire activity in the southwestern U.S. (Dennison et al. 2014), accelerating drought- and heat-induced tree mortality (e.g., McDowell and Allen 2015), and the costs and constraints of management, this question, and its particulars, including appropriate proportions, patch size and configuration, and the role and capacity for management, is becoming increasingly relevant.

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