Received: 5 June 2018 | Revised: 25 July 2018 | Accepted: 2 October 2018

DOI: 10.1111/jvs.12690

RESEARCH ARTICLE

Journal of Vegetation Science IAVS

Montane valley grasslands are highly resistant to summer wildfire

Martina M. Suazo[1,2] | Scott L. Collins[2] | Robert R. Parmenter[1,2] | Esteban Muldavin[3]

[1]National Park Service, Valles Caldera National Preserve, Jemez Springs, New Mexico

[2]Department of Biology, University of New Mexico, Albuquerque, New Mexico

[3]Department of Biology, Natural Heritage New Mexico, University of New Mexico, Albuquerque, New Mexico

Correspondence
Martina M. Suazo, National Park Service, Valles Caldera National Preserve, Jemez Springs, NM.
Email: martina_suazo@nps.gov

Funding information
The National Park Service; The Southwest Jemez Mountains Collaborative Forest Landscape Restoration Program

Co-ordinating Editor: David Ward

Abstract

Aims: Understanding the ecological role of fire in shaping plant communities in fire-prone ecosystems is needed for ecosystem restoration, preservation and management. We investigated the effects of wildfire on plant community structure and the biotic and abiotic factors that are most influential in stabilizing and/or driving change before and after burning in high-elevation montane grasslands dominated by C_3 species receiving a mean annual precipitation of 545 mm.

Location: Valles Caldera National Preserve, Jemez Mountains, New Mexico, USA.

Methods: Long-term data (10 year pre-fire; 5 year post-fire) on plant community composition of nine burned and seven unburned grassland sites were used to determine the response of montane grasslands to a summer wildfire. We used multivariate and univariate analyses to determine changes in plant community composition and structure, pre- and post-wildfire on burned and unburned grasslands.

Results: The montane grassland community consisted of 155 plant taxa, including 44 perennial grasses, one annual grass, 92 perennial forbs and nine annual forbs. We found that these fire-adapted plant communities were highly resilient to fire; fire had no significant effects on composition or structure beyond the normal range of inter-annual variability. Instead, seasonal precipitation had the largest influence on plant community dynamics over time, with lower average plant canopy height and diversity during drought periods.

Conclusion: Our results show that fire has very limited effects on the composition and structure of these C_3-dominated montane grasslands. Our results support efforts by land managers to reintroduce fire on these historically burned landscapes.

KEYWORDS

C_3 grasses, community dynamics, montane valley grassland, resilience, wildfire

1 | INTRODUCTION

Changes in ecological communities are largely driven by disturbance events that take place across a variety of temporal and spatial scales (Pickett & White, 1985). These disturbances result in a mosaic of patch types that differ in age, thus creating a source of spatial and temporal heterogeneity. This is especially the case in grassland ecosystems where disturbed patches often support a species assemblage that is, for a period of time, different from that of pre-disturbed conditions (Collins & Smith, 2006). These patches vary in resource availability, species composition, vegetation structure and ecosystem processes within a region (Milchunas & Lauenroth, 1993; White & Jentsch, 2001).

Anthropogenic disturbances such as livestock grazing (VanAuken, 2009), development (York 2011) and fire suppression (Allen, 1989;

Nomenclature: USDA Plants Database (http://plants.usda.gov/java/; accessed 5 Mar 2018)

Coop & Givnish, 2007a; VanAuken, 2009) have all contributed to the decline of grassland ecosystems in western North America. Fire is an essential ecological component for maintaining the health and proper functioning of forests across the southwestern United States by maintaining community structure, ecosystem functioning and species diversity via fuel removal and the release of organically stored nutrients (Dewar, 2011). Because montane grasslands are interspersed throughout mountain ranges within forest stands there can be important fire regime interactions at a landscape scale that have implications for impacts in more localized habitats. For example, in montane grasslands of the Jemez Mountains in north-central New Mexico, frequent fires (fire return intervals of < 10 year) typically move along forest–grassland ecotones, killing seedling trees encroaching into grasslands (Conver, Falk, Yool, & Parmenter, 2018). Fire has been the single most important factor in preventing forest encroachment and maintaining the integrity of grassland communities; however, as a result of anthropogenic-induced fire suppression, nearly 18% of grassland in this area has been lost to tree encroachment between 1935 and 1996 (Coop & Givnish, 2007a).

Most grassland studies of fire impacts focus on warm-season, C_4-dominated systems at relatively lower elevation with lower average annual precipitation. Studies have found that fire favours C_4 grasses (Collins & Calabrese, 2012; Tix & Charvat, 2005) and that the expansion of C_4 grasses in the late Miocene was driven by frequent fire (Scheiter et al., 2012). Therefore, it is generally thought that C_4 species are better adapted to fire than cool-season C_3 species (Ripley, Donald, Osborne, Abraham, & Martin, 2010). Consequently, most studies on fire impacts to grasslands are conducted in C_4-dominated grasslands, thereby leaving the more mesic C_3 grassland response to fire less well documented. Also lacking have been the long-term studies of wildfire impacts that include knowledge of pre-fire conditions and post-fire succession beyond the first two or three growing seasons following fire. Furthermore, the effects of fire on species in mountain grasslands are often studied in forest understories rather than open grassland ecosystems.

In this context, we investigated the effects of an extensive summer wildfire on plant community structure in the primarily C_3-dominated montane valley grasslands of the Valles Caldera National Preserve, located in the centre of the Jemez Mountains in northern New Mexico, USA. Using an established, long-term, pre- and post-wildfire grassland sampling array we asked: (a) how did these montane grasslands respond in terms of plant species composition, abundance and spatial distribution before and after the wildfire, and (b) what biotic and abiotic factors are most influential in stabilizing and/or driving change before and after burning.

2 | METHODS

2.1 | Site description

The Valles Caldera National Preserve (Preserve) is located in the Jemez Mountains of north-central New Mexico, USA (Supporting Information Appendix S1), and consists of high-elevation forest and grassland systems that lie at the head of the Jemez River watershed which flows into the Rio Grande Valley. The 36,017 ha Preserve is centred on a volcanic caldera approximately 24 km in diameter that erupted 1.2 million years ago (Goff, 2009) and comprises large areas of low-lying mountain meadows and riparian vegetation with sloped mountain valley grasslands bordered by several forested lava domes ranging in elevation from 2,590 to 3,505 m. An estimated 10,522 ha of montane grassland occurs in the Preserve, dominated mostly by C_3 grasses that are typical of Southern Rocky Mountain Montane–Subalpine Grassland per the US National Classification (http://usnvc.org/). These include perennial bunch grasses such as *Festuca idahoensis*, *F. arizonica*, *F. thurberi*, *Danthonia parryi* and *Poa pratensis* along with a relatively cold-tolerant C_4 species, *Muhlenbergia montana*, which commonly occurs in sub-alpine grasslands across the southwestern US (Brown, 1994). The grasslands of the Preserve have formed on prehistoric lake beds that are between 70,000 and 500,000+ years old whose soils consist primarily of Mollisols that have developed from older quaternary alluvial fan (Qf) deposits from the surrounding domes (Muldavin, 2003).

Prior to 1900, fires occurred on average every 1.6 year somewhere on Preserve grasslands, with widespread fires occurring at decadal intervals and smaller low intensity fires, particularly in valley grasslands, occurring every 2.7–10.1 year (Dewar, 2011). In addition, the Preserve has undergone extensive livestock grazing during the 19th and 20th centuries but currently supports only a relatively small (<800 head) herd of cattle and a population of approximately 2,000 elk (*Cervus canadensis*) native to the region (cattle have grazed all study sites to a limited degree both pre- and post-fire). Mean annual precipitation derived from the 2004–2015 water years (Oct–Sept) is 545 mm; 60% of this precipitation is produced by monsoonal rainfall between the months of June and September and winter precipitation is primarily in the form of snowpack (data from Western Regional Climate Center, https://wrcc.dri.edu/vallescaldera/).

In summer 2011, the Las Conchas Wildfire burned through 63,131 ha of forest and grassland vegetation, and at the time, was the largest wildfire in recorded New Mexico history. Fire intensity varied from stand replacement in the forest to low-intensity ground fire in the open grasslands. The grassland sites in this study burned over the course of 5 days from 27 June to 1 July, with an average wind speed of 2 m/s and gusts with a maximum of 17.1 m/s. There was 36% average relative humidity with a 10.3% minimum and 89.2% maximum. Average air temperature for this time period was 18.0°C, 3.6°C minimum and 28.3°C maximum.

2.2 | Field data collection

A rangeland monitoring programme was established in the Preserve in 2001 consisting of 44 vegetation monitoring sites (Barnes, 2003). These sites were stratified by relatively homogenous repeating ecotypes, which were identified by soil type, land form, community composition, management history and future management potential. Three ecotypes occur across the Preserve: Mountain Meadow,

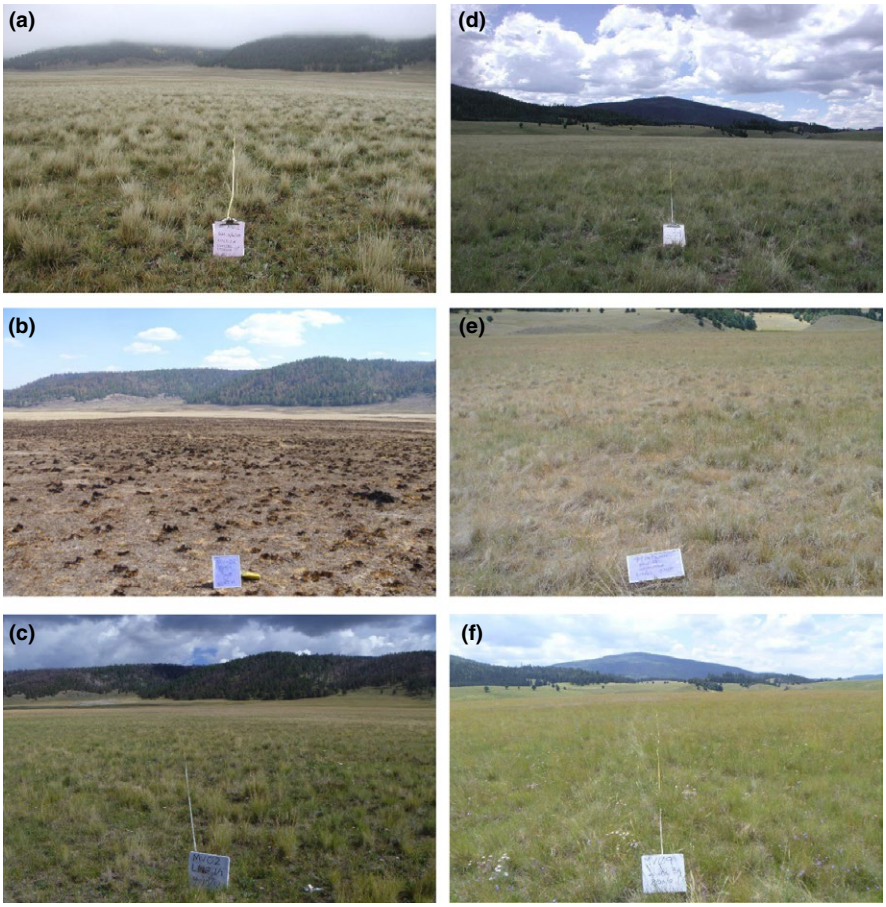

FIGURE 1 Time series photographs for paired burn and control sites. (a) 2005 pre-burn for burned site MV06. (b) 2011 immediate post-burn for burned site MV06. (c) 2012 post-burn for burned site MV06. (d) 2005 pre-burn for control site MV09. (e) 2011 immediate post-burn for control site MV09. (f) 2012 post-burn for control site MV09 [Colour figure can be viewed at wileyonlinelibrary.com]

Mountain Valley and Grazeable Woodland (Barnes, 2003). For our analysis of fire effects on montane grassland communities, we used 16 monitoring sites from the Mountain Valley (MV) ecotype that were representative of Southern Rocky Mountain Montane Grasslands with respect to species dominance and site conditions.

The MV ecotype is located on the upper slope margins of the valleys, which consists of open grasslands dominated by native bunch grasses, particularly the C_3 grasses *Festuca arizonica* and *Danthonia parryi* (Barnes, 2003). Downslope, the grasslands grade to wet meadows and herbaceous wetlands and upslope to mixed coniferous forests. The MV ecotype is composed of two different soil types: Tranquilar-Jarmillo complex (series 302) characterized by a surface horizon of silt clay loam/loam to 33 and 91 cm in depth, respectively; Cosey-Jarmillo association (series 304) with a silt loam to 38 cm (NCSS, 1987).

Of 16 available MV sites, nine were completely burned in 2011, 10 years after their establishment, and these serve as the treatment group. The other seven sites were not burned over the entire 15 years of record and serve as the reference or control group. Our on-site fire observations were that the 2011 fire was low intensity and moved rapidly and more or less uniformly across the surface of the sites (Figure 1).

Each monitoring site consisted of three, 100-m transect lines radiating outward from a central location at 0°, 120° and 240°. The line-point intercept sampling method was used to identify and measure plant species present at each meter for a total of 100 points per line and 300 points per site. Measurements were taken with the use of a thin steel rod or dowel, 1.2 m in length by 1 cm in diameter. The species of every live plant touching the rod, or intersecting the vertical line drawn by the rod from the top of the plant canopy down to the ground surface, was recorded to species level in most cases. The surface substrate touched by the base of the rod at ground level was also recorded and used to determine basal litter coverage. If one species occurred more than once at a particular point, only its highest appearance was recorded. Canopy height measurements, estimated to the nearest centimeter, were recorded as the height of the point at which the tallest plant intersected the sampling rod. Where there was no live canopy, the height was recorded as 0 cm. Two photos were taken of each transect line with the measuring tape present on the ground for a total of at least six photographs per site per year. Photo monitoring and data collection were conducted annually during the growing season (Jun–Sept). Long-term measurement of grassland species composition at these sites was conducted from 2001 until present, although not all sites were sampled in all years (Table 1). Raw data and a complete species list are presented in Supporting Information Appendices S2 and S3, respectively.

Annual peak standing crop biomass was measured by clipping all herbaceous vegetation at ground level at each sampling site using four replicate 0.25 m^2 rings randomly placed inside of ungulate

TABLE 1 Site characteristics for all monitoring plots

Site	Treatment	Total years grazed	Years grazed pre-fire	Years grazed post- fire	Years NOT sampled	Soil series[a]	Aspect (°)	Slope %	Elevation (m)	Dominant grass[b]
MV02	BURN	6	6	0	1	302	211	2	2,607	FESX1, MUMO, POPR
MV03	BURN	6	6	0	3	308	181	5	2,611	FESX1, MUMO, POPR
MV04	BURN	7	3	4	1	302	153	4	2,623	DAPA, POPR, FESX1
MV05	BURN	6	2	4	2	304	68	5	2,734	DAPA, POPR, FESX1
MV06	BURN	5	5	0	1	302	45	3	2,656	DAPA, FESX1
MV07	BURN	6	6	0	5	304	328	8	2,692	DAPA, FESX1
MV08	BURN	5	5	0	1	304	198	8	2,702	DAPA, FESX1
MV09	CONTROL	6	6	0	1	302	168	2	2,585	FESX1, MUMO
MV10	CONTROL	6	6	0	2	302	245	4	2,559	FESX1, MUMO
MV11	CONTROL	11	6	5	3	302	269	11	2,574	FESX1, POPR
MV12	CONTROL	11	6	5	2	304	62	6	2,685	DAPA, POPR, FESX1
MV13	CONTROL	11	6	5	3	304	27	4	2,662	DAPA, POPR, FESX1
MV15	BURN	12	7	5	4	304	67	8	2,650	DAPA, POPR, FESX1
MV17	CONTROL	13	8	5	2	302	123	3	2,608	POPR
MV18	BURN	12	7	5	5	302	50	7	2,670	DAPA, POPR, FESX1
MV20	CONTROL	11	6	5	4	304	36	5	2,614	DAPA, POPR

[a]Soil Series taken from USDA NRCS Soil Survey of Sandoval County Area, New Mexico. [b]Dominant plant species by abundance. DAPA, *Danthonia parryi*; FESX1, *Festuca arizonica* and *Festuca idahoensis* consolidated; MUMO, *Muhlenbergia montana*; POPR, *Poa pratensis*.

grazing exclosures approximately 2 × 2 m in size. Biomass was dried at 60°C for 48 hr and weighed to the nearest gram.

Some closely related species present at these sites have similar morphology and were identified inconsistently by different sampling teams over time. To address this problem the following species were combined at the genus level: *Antennaria parvifolia*, *Antennaria rosea*, *Antennaria rosulata*, *Festuca arizonica*, *Festuca idahoensis*, *Bromus anomalus*, *Bromus porteri* and multiple sedge species.

2.3 | Statistical analysis

Assessments within and between burn and control sites, 10 years before and 5 years after the 2011 fire, were used to determine spatial and temporal response of grassland communities to fire. Abundance data for all plant species encountered at each survey site for all years sampled were aggregated and transformed to the 4th root in order to achieve the highest level of normality possible. We used NMDS with a Bray-Curtis similarity index to display spatial variability in species composition among sites and treatments, post-burn trajectories for each site and distribution and abundance of the four most common grasses. We then ran PERMANOVA with a Bray-Curtis similarity index to make pair-wise comparisons between the following: pre-fire vs post-fire among burned sites, pre-fire vs post-fire among unburned sites and post-fire burned vs post-fire unburned sites. We used SIMPER to classify each monitoring site based on the top four most abundant species present across all sites and SIMPER was also used to identify which species contributed most to compositional differences temporally and spatially. The species with the largest contribution to compositional differences were determined to be those in the top 15% cumulative contribution range. All multivariate analyses were conducted using Primer 6 (PRIMER-E, Plymouth, UK).

Repeated measures ANOVA was used to test for differences in plant canopy height, species richness, species evenness and grass and forb abundance between the burn and control groups for all years sampled using the treatment and year interaction term. In order to reduce the influence of extraneous variation on the response, we used a randomized block design (RBD) with each site treated as a separate block and sampling years treated as replicates for two treatment types – *before* (2001–2010) and *after* (2011–2015) fire in order to identify temporal changes in plant canopy height, species richness, species evenness and grass and forb abundance. Lastly, resilience was measured using $ln(Biomass_{year}/Total\ Average\ Biomass_{2002\text{–}2010})$; Tilman & Downing, 1994) with significance testing using one sample *t*-test between each post-fire year and the 10-year (pre-fire) average in annual standing biomass.

To determine the influence of abiotic drivers on plant community structure, we used simple linear regression to correlate monsoon season precipitation accumulation over the months of June and July prior to the sampling with plant canopy height, species richness, species evenness, and abundance of grass and forb functional types for all sites combined. Precipitation data were acquired from four different meteorological stations located throughout the Preserve. Each site was paired with its nearest weather station to most accurately represent the local weather conditions. Furthermore, percentage ground covered by litter, a factor known to affect community structure of herbaceous communities (Facelli & Pickett, 1991), was correlated to species evenness over time for all sites combined using Spearman ranked correlation in order to identify the role of this biotic factor in community change after fire.

3 | RESULTS

We found a total of 155 plant taxa across all sites and years, with grasses accounting for 22% of total species richness (44 perennial, one annual) and half of the total canopy cover, while forbs account for 62% of species richness (92 perennial, nine annual) but only 27% of total

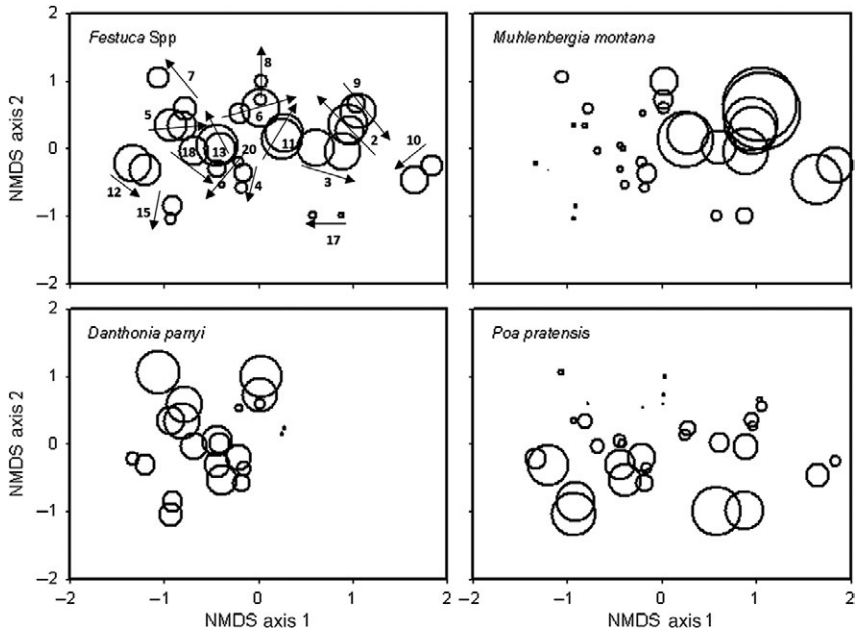

FIGURE 2 NMDS bubble plots show spatial distribution of the four most common species across all sites between the two time periods (before and after fire); arrows in the *Festuca* spp. illustrate direction of temporal trajectory for all four panels. Bubble size illustrates relative species abundance, therefore, scaling is not standardized across all four panels

TABLE 2 PERMANOVA and SIMPER results of pair-wise comparisons for plant community assemblages in burned and control treatment groups, before and after fire for 2010 and 2011 only

A. Community pair-wise comparisons

	PERMANOVA				PERDISP[a]		
Pre (2010)–Post (2011)	***n***	***t***	***p***	**Permutations**	***t***	***p***	**Permutations**
Pre-fire, Post-fire.BURN	16, 9	1.7	0.002*	999	0	0.9	999
Pre-fire, Post-fire.CONTROL	16, 7	1.3	0.1	996	0	0.7	999
Post-fire.BURN, Post-fire. CONTROL	9, 7	1.2	0.1	963	0	0.8	999

B. SIMPER (Significant contributors)

Pre-fire, post-fire. BURN species	Pre-fire Av.Abund	Post-fire.BURN Av.Abund	Av.Diss	Diss/*SD*	Contrib%	Cum.%
Danthonia parryi	2.36	2.59	1.47	1.09	4.23	4.23
Agrostis scabra	1.2	0	1.12	1.57	3.23	7.47
Trifolium repens	1.4	0.45	1.08	1.51	3.12	10.58
Poa fendleriana	1.57	0.85	1.08	1.33	3.11	13.7

p-value 0.05 = *
Abundance values are based on data transformation to the 4th root. Comparisons with significance are highlighted.
[a]PERDISP is a permutational dispersion test, i.e. test of variability or spatial spread between groups.

canopy cover (Supporting Information Appendix S3). Sites were dominated by six combinations of four abundant grass taxa: *Danthonia parryi*, *Festuca* spp., *Muhlenbergia montana* and *Poa pratensis* (Table 1). We found these species to be present at every site and also to be the most abundant overall; however, their abundance and distribution varied widely across sites (Figure 2). Based on PERMANOVA, this variation in abundance drives significance between site comparisons where species composition among all 16 sites was significantly different prior to the fire; therefore, these sites were not true replicates as initially assumed. Each site consists of the same suite of species but with frequencies that fluctuate enough to create a different community configuration and result in significant spatial difference prior to wildfire. Clustering of sites by species dominance occurs to some extent where sites to the right in the NMDS lack *D. parryi* but have high levels of *M. montana* and *Festuca*

TABLE 3 PERMANOVA and SIMPER results of pair-wise comparisons for plant community assemblages in burned and control treatment groups, before and after fire for years 2010 and 2012 only

A. Community pairwise comparisons

	PERMANOVA				PERDISP[a]		
Pre(2010)-Post(2012)	***n***	***t***	***p***	**Permutations**	***t***	***p***	**Permutations**
Pre-fire, Post-fire.BURN	16, 7	1.3	0.1	997	0.4	0.7	999
Pre-fire, Post-fire.CONTROL	16, 7	1.4	0.02*	996	1.1	0.3	999
Post-fire.BURN, Post-fire. CONTROL	7, 7	0.7	0.9	744	1.3	0.2	999

B. SIMPER (significant contributors)

Pre-fire, Post-fire. CONTROL species	Pre-fire Av.Abund	Post-fire. CONTROL Av.Abund	Av.Diss	Diss/*SD*	Contrib %	Cum.%
Danthonia parryi	2.36	1.83	1.62	1.27	4.59	4.59
Trifolium repens	1.4	0.29	1.17	1.54	3.32	7.91
Bouteloua gracilis	0.44	1.14	1.06	1.17	3.02	10.93
Agrostis scabra	1.2	0.34	1.02	1.41	2.89	13.82

p-value 0.05 = *
Abundance values are based on data transformation to the 4th root. Comparisons with significance are highlighted.
[a]PERDISP is a permutational dispersion test, i.e. test of variability or spatial spread between groups.

spp. (Figure 2). Sites to the upper left of the NMDS have low frequency of *P. pratensis* and abundant *D. parryi*, and are also geographically close together. Sites in the lower left of Figure 2 are all dominated by *D. parryi*, *P. pratensis* and *Festuca* spp. with similar relative abundances across sites; cattle have grazed all of these sites during the 5 year following fire (Table 1).

Immediate post-burn effects were tested by comparing community composition between years 2010 and 2011 using PERMANOVA. Significant differences occurred between pre-fire and the post-fire burn treatment group, but not for the unburned sites (Table 2A). Based on SIMPER, the differences between pre- and post-burn were driven by a small increase in *Danthonia parryi*, and declines in the abundance of *Agrostis scabra*, *Trifolium repens* and *Poa fendleriana* (Table 2B). Based on our comparisons for years 2010 and 2012, however, these differences were no longer significant due primarily to the recovery of *A. scabra*. We also found significant differences between the pre-fire and post-fire unburned control group, indicating an effect of factors other than fire (Table 3A). This dissimilarity was driven by most of the

TABLE 4 PERMANOVA and SIMPER results of pair-wise comparisons for plant community assemblages in burned and control treatment groups, before and after fire for 15-year study period (2001–2015)

A. Community pairwise comparisons

Pre(2001–2010)-Post(2011–2015)	PERMANOVA				PERDISP[a]		
	n	t	*p*	Permutations	t	*p*	Permutations
Pre-fire, Post-fire.BURN	132, 40	2.5	0.001*	998	0	0.8	999
Pre-fire, Post-fire.CONTROL	132, 28	1.8	0.005*	997	1	0.2	999
Post-fire.BURN, Post-fire. CONTROL	40, 28	1.6	0.01*	999	2	0.009	999

B. SIMPER (Significant contributors)

Pre-fire, Post-fire.BURN species	Pre-fire Av.Abund	Post-fire. BURN Av.Abund	Av.Diss	Diss/*SD*	Contrib %	Cum. %
Danthonia parryi	2.18	2.65	1.54	1.12	4.23	4.23
Elymus elymoidies	1.15	1.37	1.02	1.37	2.81	7.04
Poa fendleriana	1.43	0.92	0.99	1.28	2.72	9.76
Bryophyte species	1.25	0.8	0.97	1.28	2.66	12.42
Taraxacum officinale	1.27	1.55	0.93	1.22	2.57	14.99

SIMPER: Significany contributors

Pre-fire, Post-fire.CONTROL species	Pre-fire Av.Abund	Post-fire. CONTROL Av.Abund	Av.Diss	Diss/*SD*	Contrib %	Cum.%
Danthonia parryi	2.18	1.9	1.59	1.21	4.31	4.31
Bouteloua gracilis	0.47	1.01	1	1	2.7	7.01
Poa fendleriana	1.43	1.08	0.96	1.23	2.59	9.6
Bryophyte species	1.25	0.68	0.95	1.26	2.58	12.19
Elymus elymoidies	1.15	1.37	0.85	1.31	2.31	14.49

SIMPER: Significance contributors

Post-fire.BURN, Post-fire. CONTROL Species	Post-fire. BURN Av.Abund	Post-fire. CONTROL Av.Abund	Av.Diss	Diss/*SD*	Contrib %	Cum.%
Danthonia parryi	2.65	1.9	1.61	1.22	4.35	4.35
Elymus elymoidies	1.37	1.37	0.97	1.4	2.61	6.96
Bouteloua gracilis	0.03	1.01	0.9	0.91	2.44	9.41
Poa fendleriana	0.92	1.08	0.89	1.17	2.4	11.81
Symphyotricum ascendens	0.9	0.84	0.84	1.25	2.28	14.09

p-value 0.05 = *
Abundance values are based on data transformation to the 4th root. Comparisons with significance are highlighted.
[a]PERDISP is a permutational dispersion test, i.e. test of variability or spatial spread between groups.

same species that contributed to the difference between the pre-fire and post-fire burn groups. In general, there was a relatively large decline in the average abundance of *D. parryi*, *T. repens* and *A. scabra* in addition to an average increase in *Bouteloua gracilis* in 2012 compared to 2010 (Table 3B).

When all 16 sampling sites for the entire 15-year study period were grouped according to treatment, all pair-wise comparisons (pre-fire–post-fire, burned–unburned) were found to be significantly different (Table 4A). Based on SIMPER, the largest contributors to the difference between the pre-fire and post-fire burn groups were *D. parryi*, *Elymus elymoides*, and *Taraxacum officinale*, which all increased in abundance on average, along with declines in *Poa fendleriana* and non-vascular bryophyte species (Table 4B). The significance between pre-fire and the post-fire control group was explained by an average decrease in *D. parryi*, *P. fendleriana* and bryophytes as well as an average increase in *B. gracilis* and *E. elymoides*. Overall, temporal differences within sites were much smaller than the spatial differences among sites, but there was no consistent direction or degree of dispersion of samples in the NMDS after fire within the two treatment groups (Figure 3). Trends within each treatment group were not apparent and both treatment groups behaved similarly following the fire. Also, despite no clear clustering of control and burn groups either before or after fire, they were significantly different after fire (Table 4A).

In addition, pre- and post-fire comparisons were made over the entire 15-year study period for each site individually. Based on PERMANOVA, not all sites differed significantly between the two time periods. Eight of the 16 sites were significantly different post-fire and these consisted of five burn and three control sites. The other half was not significantly different post-fire and consisted of four burn and four control sites. In these temporal comparisons the only detectable change in composition from fire was the loss of *Symphyotrichum ascendens* and *Deschampsia caespitosa* at two sites (MV7 and MV18, respectively) in 2011, and they have not reappeared since the fire. These two species were relatively rare, with average cover values less than 2%. *S. ascendens* was present at all other sites but *Deschampsia* was not. Rare species (in terms of frequency) such as bryophytes, *A. scabra*, *P. fendleriana*, *Vicia americana* and *Symphyotrichum* contributed most to the differences seen post-fire for each site individually, but in general the species with the largest contribution to dissimilarity varied across sites and was not consistent within treatment group. Of the species that contributed to the top 15% cumulative abundance, some increased (*V. americana*) while others decreased (*A. scabra*, *P. fendleriana*, *S. ascendens*) after 2011 but, again, some of these declined in the control sites as well so a clear effect of fire was not detectable.

Annual standing crop biomass immediately after the fire in 2011 was significantly lower than the pre-fire average ($p = 0.0001$), yet biomass fully recovered to pre-fire levels by 2012. Standing biomass for each post-fire year, from 2012 to 2014, did not differ from the 10-year pre-fire average, however, biomass levels for 2015 were significantly ($p = 0.002$) higher than the pre-fire average (Figure 4). This temporal trend tracks average precipitation accumulation for the months of June and July as well as for the full water year (Supporting Information Appendix S4).

Based on repeated measures ANOVA, no significant differences occurred between the burn and control treatment groups in any year for plant canopy height, species richness, species evenness, grass and forb abundance (Table 5). The randomized block design (RBD) tests found that all variables other than species richness were significantly higher in both burned and unburned areas after the fire (Table 5).

All five community structure variables were positively correlated with summer monsoonal precipitation, but not winter or annual totals (Figure 5). This indicates that temporal patterns in plant community structure are strongly driven by climate overshadowing any effect of burning for all years, even after the fire. Litter, as a biotic influence on community trends, was negatively correlated with species evenness ($r^2 = -0.67$, $p < 0.001$).

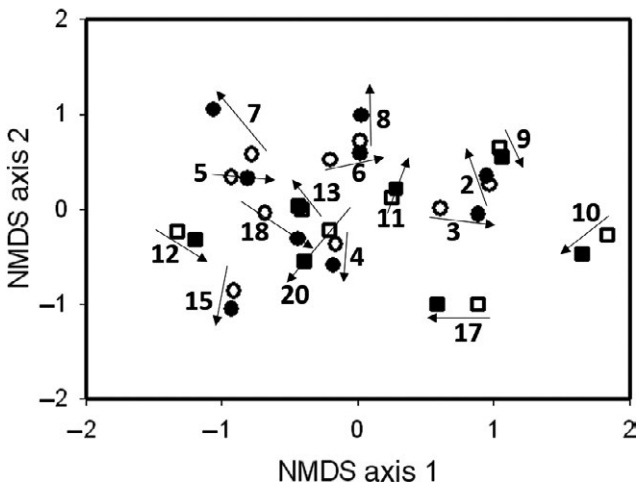

FIGURE 3 NMDS of the pre- and post-burn cluster centroids for all 16 sites, arrows illustrate direction of temporal trajectory. Circle = Burn, Square = Control; Open symbols = Pre-Fire, Filled symbols = Post-Fire

4 | DISCUSSION

Fire is a natural disturbance that can be used as a management tool for maintaining healthy ecosystems, particularly for those that have

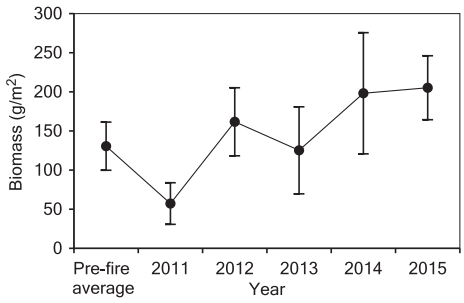

FIGURE 4 Average annual standing crop biomass in g/m^2 including long term pre-fire average (2001–2010) and all post-fire years

evolved with fire (Wright & Bailey, 1980). The potential negative impacts of fire include the loss of herbaceous cover, which leads to water run-off and erosion, consequently impacting water quality and watershed function (Dahm, Candelaria-Ley, Reale, Reale, & Van Horn, 2015).

TABLE 5 Results of repeated measures ANOVA and randomized block design for five plant community variables

	df	Sum Sq	*F*-value	*p*-value
Repeated measures ANOVA				
Treatment: Year				
Plant height	1	17	0.301	0.59
Richness	1	18	0.611	0.43
Evenness	1	10,376	0.435	0.51
Grass	1	133	0.018	0.89
Forb	1	4,025	0.819	0.37
Random block design				
Before/After fire				
Plant height	1	331.5	4.7563	0.03*
Richness	1	70.9	3.0605	0.08
Evenness	1	40,2486	14.6929	<0.05***
Grass	1	51,215	7.8948	<0.05**
Forb	1	50,697	9.4613	<0.05**

p-value 0.05 = *; 0.01 = **; 0.001 = ***

Fire may increase opportunities for invasion or colonization of undesired species (Hunter, Omi, Martinson, & Chong, 2006), and change plant community composition in a way that impacts habitat type and quality leading to altered trophic structure and dynamics (Ford & McPherson, 1996). However, despite the intensity and size of the Las Conchas wildfire, the burn had few impacts on the montane valley grasslands of the Valles Caldera National Preserve. There were no differences in plant canopy height, species richness, species evenness and grass and forb abundance between the burn and control groups for any year, including the year immediately after the fire. Pre-fire biomass conditions were reached by the second growing season after fire, and no new exotic species were detected; naturalized species, such as *P. pratensis*, followed the same post-fire temporal recovery trend in abundance as native species. These results lead us to suggest that this montane grassland system is highly resilient to wildfire.

We acknowledge the inherent variability in different wildfire events and note that our results are technically limited to a single wildfire event. Natural wildfires (unlike prescribed burns) are rarely replicated due to unknown fire-return probabilities. In our study, the Las Conchas fire burned for five consecutive days and we sampled multiple sites across the landscape that had burned on different days. Hence, the Las Conchas fire comprised a series of daily fire events (each one slightly different from the others) that could serve as replicated fire treatments. These circumstances have the advantage of controlling for site/habitat characteristics, while maintaining

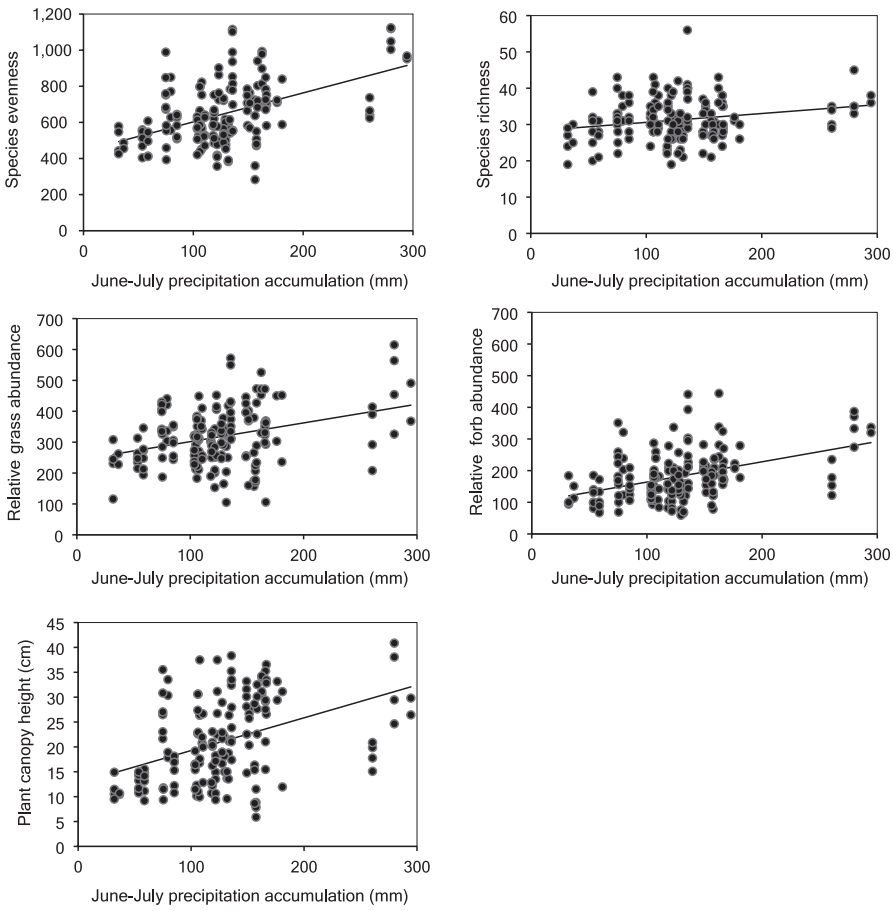

FIGURE 5 Relationship between cumulative seasonal precipitation (June plus July) and plant canopy height, species richness, species evenness, and grass and forb abundance

approximately the same weather conditions between each fire event. In general, fire studies are considered as single events, with site- and time-specificity, and the statistical "replication" for inference comes with multiple studies in similar habitats over many years and wildfire events. The Las Conchas fire burned on the Preserve during a period of near-record drought, representing an extreme fire event. As such, we consider our results of minimal fire impact on these montane grasslands to be indicative of the highly resilient nature of these grassland communities.

The Preserve's grasslands follow a common trend observed in other grassland systems where a small number of dominant species account for the majority of herbaceous cover while the majority of species are relatively rare (Collins & Glenn, 1991). The only detectable change in composition from fire was the loss of *S. ascendens* and *D. caespitosa* following the burn. Because the relative abundance of *S. ascendens* is low it may still be present in the community but simply has not been documented since 2011. *D. caespitosa* typically prefers moist habitats, such as wet meadows, and can tolerate all but the most severe fires (Debenedetti & Parsons, 1984). A decline in population may suggest a drying out of habitat resulting in conditions unsuitable for persistence. However, *D. caespitosa* decreases with cattle grazing, which may explain its relatively low abundance and subsequent inability to recover after fire under continued grazing pressure (Mueggler & Stewart, 1980).

All plant community analyses showed that the control group followed the same trends as the burn group after fire. Fluctuations in community structure were not driven by fire, nor were they due to post-fire succession, but rather, they responded to other abiotic and biotic factors. The species with the greatest contributions to significance between pre-fire and both post-fire treatment groups, for the full study period, were similar, suggesting that factors driving temporal change were consistent between the two treatments, therefore eliminating fire alone as a significant influence on community change. Similarly, a synthesis on fire effects in C_4-dominated North American semi-arid grasslands receiving <600 mm mean annual precipitation found a neutral to negative response in above-ground net primary productivity after fire, regardless of season of fire, grazing history and mean or actual precipitation (Scheintaub, Derner, Kelly, & Knapp, 2009). Furthermore, variability in above-ground net primary productivity (ANPP), which was similar to that of plant community composition, cover and diversity, was not attributed to any particular site or fire characteristic.

Significant positive correlations between precipitation and plant community characteristics showed that climatic variables had a greater influence on community structure in both treatment types than fire. Similarly, responses of ANPP in C_3-dominated semi-arid rangelands to precipitation in the northern mixed prairie of Montana were greater than those to fire, grazing or the interaction of fire and grazing (Vermeire, Crowder, & Wester, 2014). These findings highlight the influence of water availability on these grassland systems and its role in shaping these plant communities relative to fire.

In addition, species evenness showed a significant negative correlation with ground cover of dead plant material across all sites. Litter accumulation can suppress plant growth; therefore, removal of dead plant material can increase germination by making resources such as sunlight more readily available (Foster & Gross, 1998; Scheintaub et al., 2009; Xiong & Nilsson, 1999). However, control sites that did not undergo burning also exhibited this same response, which is likely due to litter reduction from cattle grazing given that five of the seven control sites were grazed in the 5 years following the 2011 fire. Overall, the burn sites in our study were not grazed by cattle to the same degree as the controls (Table 1). As a result, litter removal whether by fire or grazing coupled with precipitation trends resulted in similar post-fire responses across these grassland sites. A conceptual model of grazing, fire and climate in grasslands showed that annual fluctuations in ANPP increased as mean annual rainfall decreased and that 50% of inter-annual variability in biomass production resulted from deviation from mean precipitation in a given year (Oesterheld, Loreti, Semmartin, & Paruelo, 1999). Our findings here support this model where burning had little effect on composition; grazed and ungrazed sites were not consistently different post-fire and the main driver of change in community structure and composition was monsoon season precipitation.

Several studies have shown fire to favor expansion of C_4 species (Collins & Calabrese, 2012; Scheiter et al., 2012; Tix & Charvat, 2005) and have also found a C_4 subspecies to be better adapted to fire than its C_3 counterpart (Ripley et al., 2010). Still, uncertainty exists in determining if fire-adapted plant species are so as a result of their photosynthetic pathway or as a result of adaptations to a specific fire regime. Results from an experimental fire in the northern Chihuahuan Desert in New Mexico showed that plant demography was highly impacted by fire (Parmenter, 2008); of five abundant C_4 grass species, three were significantly negatively impacted by fire. Overall, in our study area we show that C_3 plant species from open grasslands are adapted to wildfire and document a relatively high level of resistance and resilience. There was no significant decline in average plant canopy height, species diversity or abundance by functional group; species evenness was actually shown to increase after burning indicating higher resilience to fire than in desert grasslands. It is unclear, however, if these grasslands are representative, in terms of resilience, of other high-elevation grasslands that evolved with fire or if the unique environmental conditions of the caldera formation create a relatively higher resistance to fire.

Fire management activities on the Preserve are focused on reducing the risk of landscape-level high-severity forest fires. Because the Preserve's landscape is a mosaic of forest stands and intervening valley grasslands (Figure 1), natural and managed fires tend to burn both forest and grassland habitats. Our results support land and fire management efforts to maintain the use of fire as a tool in ecological restoration and preservation by providing evidence that any risk of adverse or unwanted impacts on plant community composition and function for high-elevation fire-adapted grasslands is minimal. As in C_4 grasslands (Collins & Calabrese, 2012), burning in the Preserve sustained diversity. Furthermore, maintaining fire frequency or fire return interval is

crucial for maintaining ecosystem function because these grasslands are adapted to a particular fire regime (Dewar, 2011; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). In addition, timing of fire is a crucial factor influencing the subsequent recovery of a plant community. Cool season fires have minimal effects as herbaceous plants are dormant. For the Preserve, natural wildfires typically ignite during the driest part of the year (June) just prior to the start of the monsoon season (Dewar, 2011).

It is unknown if the potential for more frequent, high-intensity fire under climate warming will alter these low-intensity, fire-adapted ecosystems in terms of community composition and ecological function. Indeed, it is possible that as climate continues to warm we may see that future high-intensity forest fires may actually expand montane grasslands. What is not known is how these newly created grasslands will respond to continued burning and at what level of intensity future burning will reach given the amount of surface fuel remaining. However, in the context of this study, a significant impact to these plant communities from wildfire burning was not detected outside a normal range of variability, therefore demonstrating a relatively high level of resistance to fire. In conclusion, our results demonstrate that these primarily C_3-dominated montane grasslands are highly resistant to fire. Therefore, the use of fire as a management tool will help maintain the health and resilience of this landscape as well as reduce the loss of grassland to shrub and tree encroachment driven by fire suppression (Allen, 1989; Coop & Givnish, 2007a). In addition, natural systems that are extremely resistant to environmental extremes should be preserved and protected from anthropogenic development activities, as they may be able to naturally resist climate change better than other less resistant/resilient ecosystems.

ACKNOWLEDGEMENTS

We thank the Valles Caldera National Preserve, under both the United States Department of Agriculture's Valles Caldera Trust and the Department of Interior's National Park Service, for supporting the long-term grassland monitoring programme; botanist Will Barnes for the establishment of this monitoring programme as well as the numerous field botanists who have assisted with the data collection over the many years of this study. Financial support for the project was provided by the National Park Service and the Southwest Jemez Mountains Collaborative Forest Landscape Restoration Program. Additional field assistance for biomass sampling was provided by numerous citizen volunteers and the Sierra Club.

ORCID

Martina M. Suazo http://orcid.org/0000-0002-9312-2570

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Distribution of Mountain Valley grassland study sites in the Valles Caldera National Preserve, New Mexico with Las Conchas Fire burn area.

Appendix S2. Plant Species Abundance Data. All species averages per treatment group for each year, no transformation.

Appendix S3. Plant species characteristics.

Appendix S4. (A) Average precipitation accumulation for June and July averaged over four weather stations. (B) Precipitation accumulation by water year (Oct–Sept) averaged over four weather stations.

How to cite this article: Suazo MM, Collins SL, Parmenter RR, Muldavin E. Montane valley grasslands are highly resistant to summer wildfire. *J Veg Sci*. 2018;29:1017–1028. https://doi.org/10.1111/jvs.12690