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Research Article

Effects of Recent Wildfires in Piñon-Juniper Woodlands of Mesa Verde National Park, Colorado, USA

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ABSTRACT

Pinus edulis–Juniperus osteosperma (piñon-juniper) woodlands in the southwestern United States are of high conservation value and are threatened by changing climate and increasing frequency of large, severe fires. We followed vegetation development after three recent fires (1989, 1996, and 2000) in Mesa Verde National Park (MEVE). Two types of piñon-juniper vegetation are found in MEVE: *sprouting woodlands* (SPW), dominated by species that resprout after injury, and *obligate seeding woodlands* (OSW), dominated by non-sprouting species. SPW stands showed greater resilience than OSW in terms of recovery of pre-fire structure and species composition, and vulnerability to invasion by nonnative plant species. After all three fires, plant cover increased more rapidly in SPW stands; all major pre-fire species were present within 2 y, and fewer nonnative species became established. Plant cover developed more slowly in OSW stands; nonnative plant species proliferated, in places being more abundant than the newly germinating native species. No reestablishment of piñon or juniper trees has been observed. If current trends persist, some portions of the burned SPW may be converted to a persistent shrubland type, while much of the burned OSW may be converted to a persistent, novel herbaceous vegetation type with a large component of nonnative species. Similar changes after fire can be expected in piñon-juniper woodlands like those in MEVE, which are widely distributed throughout the region.

Index terms: Bromus tectorum; *Juniperus osteosperma*; nonnative plants; *Pinus edulis*; post-fire vegetation change

INTRODUCTION

Since the late 1980s, large and severe wildfires, severe droughts, and temperatures above historical norms have become increasingly prevalent throughout much of the world (Westerling et al. 2006; Allen et al. 2010), with substantial ecological changes being observed in many types of natural vegetation (Bradford et al. 2020). A vegetation type of particular concern in the southwestern United States is *Pinus edulis–Juniperus osteosperma* (piñon-juniper) woodlands, which cover millions of hectares across a broad region, including many national parks and other protected areas recognized for their significant natural habitats and characteristics (Romme et al. 2009). Climate conditions are projected to become marginal or unsuitable for piñon across much of its present range (Rondeau et al. 2011). And even where climate remains suitable for piñon, the woodland ecosystems of which it is a part are at risk of severe fires, insect outbreaks, and expansion of nonnative plant species (Mueller et al. 2005; Floyd et al. 2006; Board et al. 2018; Weisberg et al. 2018). However, we have inadequate information about the specific changes now occurring as a result of fire, climate change, and invasive species in southwestern piñon-juniper woodlands, and thus it is difficult to forecast the future of these ecosystems.

In the past, post-fire development of piñon-juniper woodlands did not garner a great deal of research attention, in part because much of the management focus was to reduce the "encroachment" of piñon and juniper trees into rangelands where forage production was a major objective, rather than on maintaining existing woodlands (Redmond et al. 2014; Weisberg et al. 2018). Recently, however, piñon-juniper has emerged as a vegetation type of conservation value and concern (e.g., Rondeau et al. 2011; Board et al. 2018). This change in perspective has developed both because many high-quality piñon-juniper woodlands have been recently lost or degraded, and because of the many ecosystem services provided by this woodland (e.g., the rich diversity of plants and animals that it supports; Floyd 2003). For example, some 25 obligate bird species are associated with piñon-juniper woodlands, and at least some are declining, notably the piñon jay (*Gymnorhinus cyanocephalus*), a sensitive species listed by the New Mexico Bureau of Land Management (Johnson et al. 2017; Boone et al. 2018), in part due to thinning treatments (Magee et al. 2019).

Our objective in this paper is to summarize the effects of recent fires and post-fire invasions of nonnative species in piñon-juniper woodlands of Mesa Verde National Park (MEVE), located in southwestern Colorado, USA. Observations and research since the early 1990s have provided longitudinal data (Johnson and Miyanishi 2008) on vegetation and climate history, woodland structure and composition, and effects of recent fires and nonnative plant species. Most of the Mesa Verde landform is encompassed by a national park, and as such is a protected area where natural vegetation processes have played out, and will continue to do so, with minimal human intervention. Piñon-juniper woodlands similar to those of Mesa

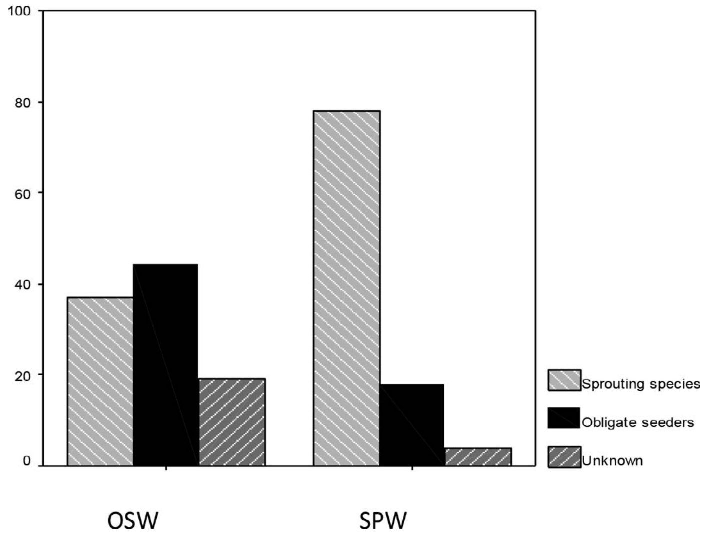

Figure 1.—Functional types of unburned piñon-juniper woodlands were defined by the relative percent of sprouting species and obligate seeding species, with obligate seeding woodlands composed of a mix of seeding and sprouting species, while SPW is strongly dominated by sprouting species.

Verde are also widespread across much of the Colorado Plateau. Some of our data have been published previously (Floyd et al. 2006, 2009, 2015); here we selectively integrate some of those previous data with new information to provide overall interpretations and syntheses.

Post-fire regeneration of the tree canopy in piñon-juniper woodlands is typically a very slow process, occurring over decades or centuries (Erdman 1970; Barney and Frischknect 1974; Koniak 1985; Huffman et al. 2012; Hartsell et al. 2020), and we have not observed new piñon or juniper trees becoming established in any of the places that burned within the past 30 y at Mesa Verde. But we have seen considerable variation in post-fire response of the understory, notably in relation to species composition and physiognomic structure. Variation in post-fire understory characteristics are important not only for their own roles in community structure and function, but because the understory can either facilitate or hinder the process of tree reestablishment; for example, shrubs can function as "nurse plants" that create locally favorable microclimatic conditions for new tree seedlings, whereas heavy grass cover often inhibits tree seedling establishment (Floyd 1982; Chambers et al. 1999; Redmond et al. 2018).

We distinguish two fundamental types of understory composition and structure in the piñon-juniper woodlands of Mesa Verde: (1) stands having a large proportion (~80%) of sprouting shrubs and herbs often resistant to drought (Winkler et al. 2020), which we call "sprouting woodlands" (SPW); and (2) stands in which many species (~40%) regenerate after fire via seed germination rather than vegetative sprouting, which we call "obligate seeding woodlands" (OSW) (Figure 1). Visual observations and previous studies suggest that early post-fire vegetation dynamics differ substantially between these two stand types. Here we elucidate and test the importance of these differences by evaluating two hypotheses:

H_1: SPW stands are more resilient than OSW stands, in the sense that SPW recovers pre-fire understory structure and species composition more quickly than does OSW.

H_2: OSW is more vulnerable to rapid and marked changes in species composition after fire than is SPW, especially as driven by invasion of nonnative species.

Study Area

Mesa Verde is a prominent south-dipping cuesta located in southwestern Colorado, USA. Our studies were conducted from 1990 through 2017 in MEVE, which occupies the northern portion of the cuesta, and Ute Mountain Ute tribal lands, which adjoin the park on the south. The 53,876 ha Mesa Verde cuesta is composed of high, gently sloping terrain cut by deep canyons spanning elevations between 1850 m and 2650 m. Mancos shale at the base is overlain by Point Lookout Sandstones and Menefee shales, which are capped by the resistant Cliffhouse Sandstone (Griffitts 1990). Due to the gentle southerly dip of these beds, the older Point Lookout sandstones are exposed at the highest elevations, while the younger Menefee and Cliffhouse formations form the deep canyons and spectacular alcoves, sites of Ancestral Puebloan cliff dwellings, in the lower reaches of the mesa.

Climate records have been kept at Park Headquarters, located near the center of the cuesta. Mean daily temperature (1924–2018) was 9.8 °C (49.7 °F); mean annual precipitation (1924–2018) was 45.5 cm (17.9 inches) with bimodal distribution, with peaks in winter and late summer. Since the mid-1990s, hotter and drier conditions have been common at Mesa Verde as in much of the Southwest; average daily temperatures were mostly above the long-term average from 2000 to 2018, with very high temperatures in 2012, 2017, and 2018. Extremely low precipitation was recorded in 2002, 2012, 2017, and 2018.

Piñon and juniper are the major tree species in both OSW and SPW. Understories of OSW typically include native perennial grasses *Poa fendleriana* (mutton grass), *Elymus elymoides* (squirreltail grass), and *Eriocoma hymenoides* (Indian rice grass), forbs *Pedicularis centranthera* (dwarf lousewort), *Lupinus ammophilus* (sand lupine), *Astragalus schmolliae* (Schmoll's milkvetch), and the shrub *Purshia tridentata* (antelope bitterbrush). Understories of SPW are dominated by the shrubs *Quercus gambelii* (Gambel's oak), *Amelanchier utahensis* (Utah serviceberry), *Fendlera rupicola* (fendlerbush), and *Artemisia nova* (black sagebrush), with forbs such as *Hackelia gracilenta* (Mesa Verde stickseed), *Lupinus caudatus* (tailcup lupine), and *Comandra umbellata* (bastard toadflax), and perennial grasses such as *Pascopyrum smithii* (western wheatgrass) in the open spaces between shrubs (Apppendix 1).

The legacy of human land use is critical to understanding the role of fire in dynamics of piñon-juniper woodlands. Large populations, with estimates of up to 197,000 Ancestral Puebloans, occupied Mesa Verde and the surrounding region for several centuries prior to the late 1200s, with five waves of immigration and two emigrations (Varien et al. 2007). Impacts on piñon-juniper woodlands—clearing of trees for crops, building materials, and fuelwood—were greatest during the first

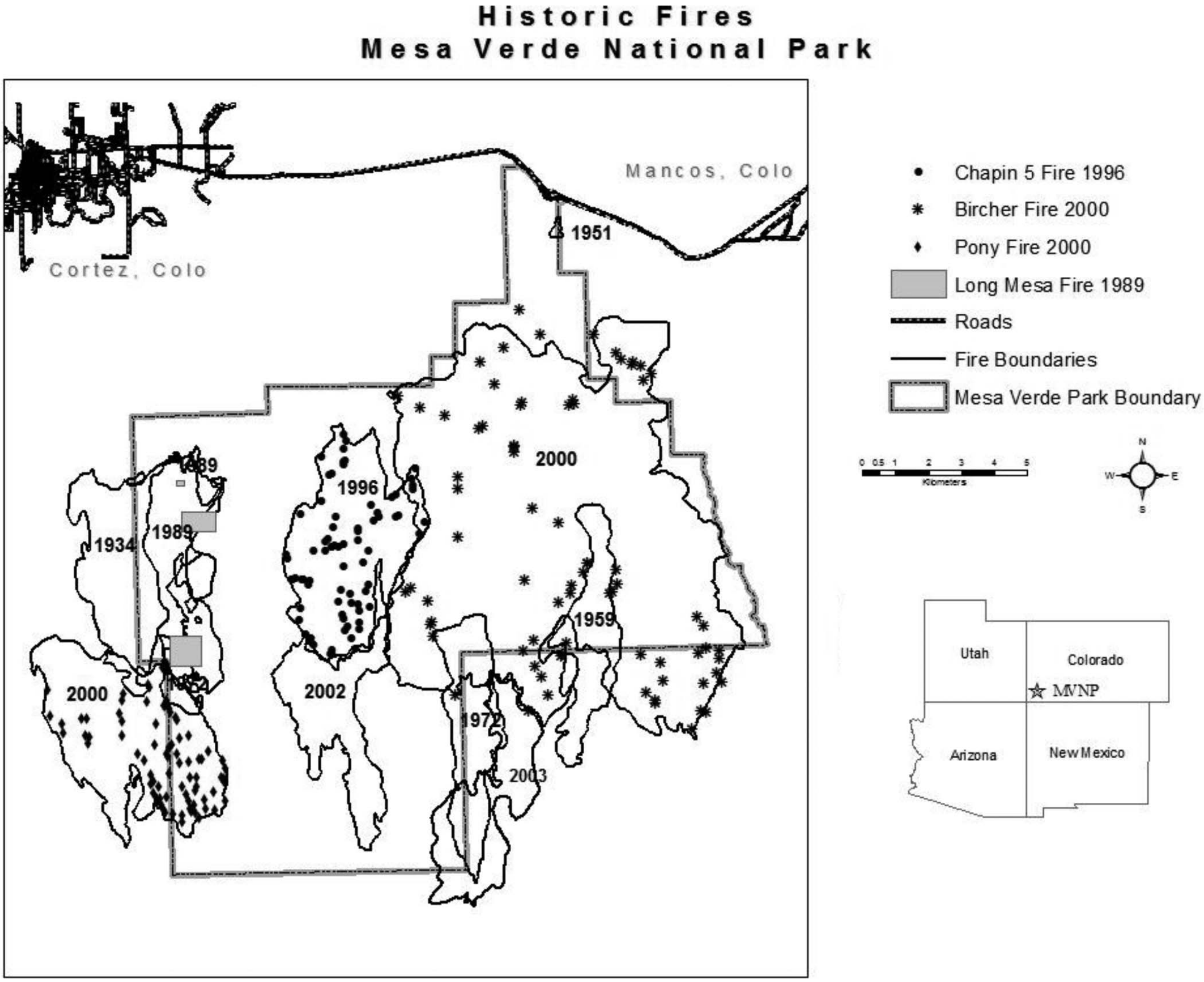

Figure 2.—Mesa Verde National Park boundary, recent fire perimeters, and sample point locations. Studies were initiated after a large wildfire in 1989, followed by one in 1996 and two in 2000. As can be seen in the figure, a very large proportion of the park has burned over the past 80 y. Sampling was accomplished using large systematic grids in 1989. Other fires were sampled at randomly selected locations.

waves of population increase around 600 AD, followed by lighter impacts in the latter part of the Ancestral Puebloan occupation. Human populations then were relatively low from about 1300 until the late 1800s, and woodland again grew to cover much of the cuesta and surrounding areas. Soil cores from the northern part of the Mesa Verde cuesta reveal that fires increased during the Ancestral Puebloan occupation, but decreased sharply during the 1300–1800 period (Herring et al. 2014); Floyd et al. (2004) estimated a fire rotation of ~400 y in Mesa Verde woodlands during that latter period. Park records show that few fires occurred in MEVE during the early to mid-1900s, but the fire regime changed abruptly in the late 1900s with large severe fires in 1989, 1996, 2000, and 2002, and smaller fires in 2003 and 2008. Notably, late 20th century fires deposited soil charcoal at the highest frequency recorded in the last 4000 y (Herring et al. 2014).

METHODS

Post-fire Vegetation Structure

Our work was based on opportunistic sampling after the 1989, 1996, and 2000 fires in MEVE (Figure 2). Results pertaining to invasive plant species were reported in Floyd et al. (2006), but here we reanalyze the original data in the context of the two structural types of piñon-juniper woodlands and confine our sampling to areas that had natural regeneration (excluding aerial seeding or other mitigations). All of the fires burned under similar weather conditions of low humidity, high temperatures, and high winds. However, post-fire climatic conditions were very different: the 1989 fire was followed by average to above-average precipitation and average to cool temperatures, the 1996 fire was followed by average temperatures and a mix of wet winters and very dry years, whereas the 2000 fire complex was followed by exceptionally hot and dry years.

Sampling methodology was similar after all three major fires, although details differed somewhat because of different sources and levels of funding after each fire. In the 1989 burn, 240 sampling locations were placed every 100 m in a systematic grid placed on a representative portion of the burned area and including both OSW and SPW woodland types. Data were collected June through August of 1991, 1992, and 1994 in the 1989 burn. Each location was sampled using a point-frame (Floyd and Anderson 1982, 1987) consisting of a 0.25 m^2 quadrat with horizontal and vertical lines intersecting at 25 points within the frame. The type of cover beneath each point—native and nonnative forbs, shrubs, grasses, litter, bare mineral soil, or rock—was recorded.

In the 1996 burn, 80 sampling locations were distributed among all affected plant communities using a stratified random sampling design; locations were sampled in 1997, 1998, and 1999. The 2000 fire complex was sampled in 2001 and 2002 at 120 sample locations, again distributed among all affected plant communities using a stratified random sampling design. At each location in the 1996 and 2000 burns, two 100 m transects were established at right angles to one another and the point frame was systematically placed every 10 m along each transect.

Percent cover under each point-frame was calculated and cover data from each burn and sampling date were transformed with an arcsin transformation. Analysis of Variance (ANOVA) was then used to test for differences in plant cover by life form in SPW and OSW.

Unburned areas were not included in the studies of the 1989 or 1996 burns due to budget limitations and managers' urgent need for information on the burned areas. In the 2000 burn, however, in addition to the samples in the burned area we were able to sample 128 locations in unburned SPW and 208 locations in unburned OSW vegetation. The unburned samples were taken either adjacent to the burn perimeter or in unburned islands within the overall burn perimeter. Unburned locations were sampled as above and data were analyzed as in the burned locations.

Plant Species Composition

At the terminus of each of the sampling transects described above, we placed two 15 m × 15 m releve plots in which all plant species were assigned a cover/abundance value (5 = >75% cover, 4 = 50–75% cover, 3 = 25–50% cover, 2 = 5–25% cover, 1 = <5% cover, + = <5% cover scattered abundance and r = < 5% cover, rare) (Mueller-Dombois and Ellenberg 2003). Data were collected in early summer and early fall of each year for 2 y after the 1989 fire, 3 y after the 1996 fire, and 2 y after the 2000 fire.

To determine the relative cover of native and invasive nonnative species, at each sample location in the 1996 fire we also set out circular plots (500 m^2) in which the cover of invasive plants was visually estimated. The circular plot was divided into quarter sections and the cover of *Bromus tectorum* (cheatgrass) and *Carduus nutans* (muskthistle) was estimated visually in 1997, 1998, and 1999.

Seed Bank Analysis: Bulk soils were collected from paired plots, burned and unburned, in OSW and SPW, in and adjacent to the 2000 burn; a total of 400 soil samples were collected at 10 cm depths. Samples were floated, bulk vegetative material was removed, and seeds were sieved. Seeds were sorted into species, genera, or in some cases plant family. Seed volumes were measured for each recognizable taxon (58% of the seeds) and extrapolated to number per liter. Seed viability was not tested.

Changes in Woodland Cover 1994–2009

Two vegetation mapping projects in which the authors participated were available for MEVE (Floyd et al. 1994; Thomas et al. 2009). The 1994 vegetation map included the 1989 fire but predated the 1996, 2000, and later fires. The 2009 map included all fires from 1989 to 2003. Cross-walking vegetation associations between the two maps identified the vegetation associations from each that represented the respective OSW and SPW types, as well as the areas of tree-dominated woodland vs. shrub- or herbaceous-dominated vegetation. For example, the 2009 map identified a "post-fire mixed herbaceous" class that had replaced previous woodland of both types. We overlaid these two maps to document changes in the extent and spatial distribution of OSW and SPW, and of tree-dominated stands, resulting from recent fires.

RESULTS

Post-fire Vegetation Structure

Comparisons of vegetation trends in the three recent burns for which we have longitudinal data must be made cautiously, because none of the fires overlapped, and—despite being on similar substrates and topographic positions—the local elevation, fire size, and post-fire climate conditions varied after the fires. Also, data were collected with different objectives and funding sources. Only in the 2000 fires were we able to establish a robust design where unburned patches were compared with nearby burned areas. Therefore, we highlight only the strong and consistent patterns that emerge in the data. Nevertheless, some strong consistent patterns were apparent (Figures 3–5).

In all three burns, shrub cover showed a relatively rapid and steady increase over time. Shrub cover also was consistently greater in SPW than in OSW, and this difference was significant (<0.05) in eight of the nine years in which plant cover was measured. Total biotic cover, the sum of grass, forb, and shrub, was greater in SPW, due largely to the contribution of the shrub component.

Comparing plant cover in the three burns at 2 y post-fire (1991, 1998, and 2002 for the 1989, 1996, and 2000 fires, respectively), total cover was greater in SPW than in OSW in all three burns (44% vs. 26% in the 1989 burn; 51% vs. 45% in the 1996 burn; and 25% vs. 9% in the 2000 burn).

We evaluated the relative degree of recovery of pre-fire vegetation structure in SPW and OSW by comparing percent cover of each plant life form (grass, forb, and shrub) in the burned vs. unburned samples collected in 2002. We divided the mean percent cover of the burned samples by the mean percent cover of the unburned samples, and multiplied by 100 to express the ratio of burned/unburned cover as a percentage (Figure 6). Grass cover in burned areas was very low compared with unburned areas in both OSW and SPW, indicating only limited recovery of pre-fire cover after 2 y. Shrub cover in burned areas

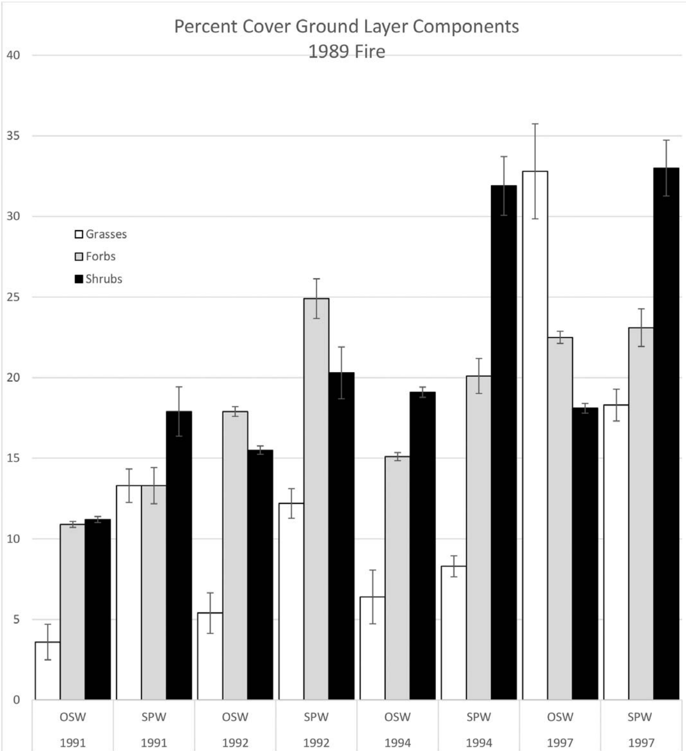

Figure 3.—Percent cover of ground layer components in obligate-seeding woodlands (OSW) and sprouting woodlands (SPW) following the 1989 Long Mesa fire, Mesa Verde National Park. Error bars represent 1 standard error. Significantly different values at $P < 0.05$ level occurred in 1991, 1992, and 1997 for grasses, in 1992 for forbs, and in 1991, 1994, and 1997 for shrubs. Sample sizes: OSW $n = 60$, SPW $n = 414$. All years were relatively wet and cool.

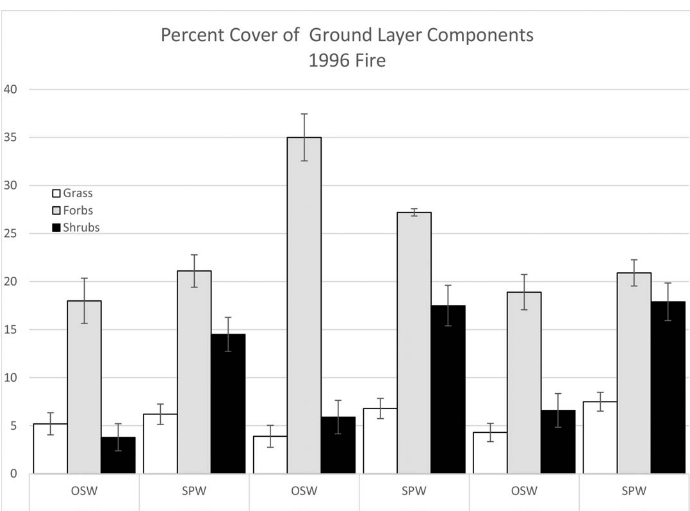

Figure 4.—Percent cover of ground layer components in obligate-seeding woodlands (OSW) and sprouting woodlands (SPW) following the 1996 Chapin 5 fire, Mesa Verde National Park. Error bars represent 1 standard error. Significantly different values at $P < 0.05$ level comparing OSW and SPW occurred in 1999 for grasses, in 1998 for forbs, and in all years for shrubs. Sample sizes: OSW $n = 112$, SPW $n = 216$. Years 1997 and 1998 were relatively wet and cool, while 1999 was very dry with average temperatures.

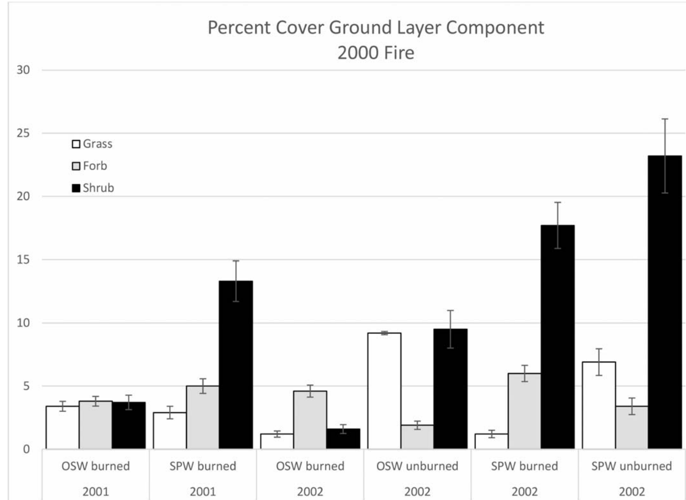

Figure 5.—Percent cover of ground layer components in burned and unburned obligate-seeding woodlands (OSW) and sprouting woodlands (SPW) following the 2000 Bircher and Pony Fires, Mesa Verde National Park. Data presented are average percent cover. Error bars represent 1 standard error. Significant differences ($P < 0.05$) were seen between burned and unburned samples in 2002 in grasses and forbs. All comparisons were significant ($P < 0.05$) for the shrub component. Sample sizes: OSW unburned $n = 208$, burned $n = 567$, SPW unburned $n = 128$, burned $n = 256$. Years 2001 and 2002 were very dry with average or high temperatures.

also was quite low in OSW, although shrub cover in burned SPW was 75% of the cover of unburned areas after 2 y. Forb cover in burned areas actually exceeded that in unburned, especially in OSW where forb cover in burned areas was more than double the cover in unburned areas.

Plant Species Composition

The mean number of species of grasses and forbs was significantly greater in burned releve plots (OSW and SPW plots

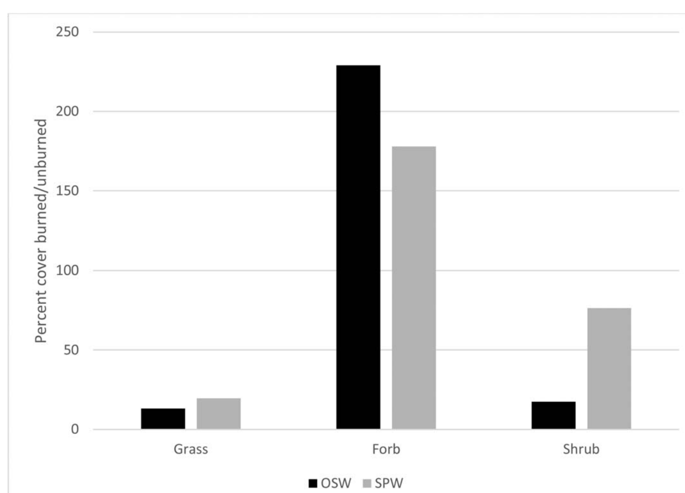

Figure 6.—Percent cover of forbs, grasses, and shrubs in burned and unburned OSW and SPW sample points expressed as a percent (burned/unburned), 2 y after the 2000 fire.

Table 1.—Species richness of shrubs, grasses, forbs, and invasive species in sample plots in the 2000 fires. Data were collected in 2002. Data are mean number of species per 1000 m^2 plot $\pm$ standard error, followed by significance of ANOVA tests.

Life form	Unburned ($n = 42$)	Burned ($n = 57$)	
Shrub	3.9 ± 0.34	2.7 ± 0.29	n.s.
Grass	1.7 ± 0.20	3.4 ± 0.25	$F = 14.5, P < 0.05$
Forb	7.2 ± 1.0	11.8 ± 0.86	$F = 7.2, P < 0.05$
Invasive species	1 ± 0.01	2.3 ± 0.13	$F = 3.2, P < 0.05$

combined) than in unburned plots in 2002, although the number of shrub species did not differ between burned and unburned plots (Table 1). Within the burned plots, overall species richness was greater in OSW than in SPW. We recorded a total of 142 plant species in sample plots within burned OSW, of which 17 (12%) were grasses, 105 (74%) were forbs, and 16 (11%) were shrubs. We recorded 82 species in plots of burned SPW, of which 16 (20%) were grasses, 48 (58%) were forbs, 16 (20%) were shrubs, and 2 (2%) were succulents.

Seed Bank Analysis: A greater diversity of seed taxa was found in soils of OSW: 33 types were present, 20 of which were identified to species or family, while 13 more were unique taxa but could not be identified, and 6 species were nonnative species (Table 2). In contrast, in SPW only 9 taxa were present; 8 were identified, of which 2 were nonnative species.

Table 2.—Density (#/liter soil) of each seed taxon identified in soils from burned obligate seeding woodlands (OSW) and sprouting woodlands (SPW) at Mesa Verde National Park in 2002.

Woodland type	Taxon	*N*	Mean density	Std. deviation
OSW	*Artemisia* sp.	3	118.3	84.19
OSW	Asteraceae	1	71.4	–
OSW	*Astragalus* sp.	1	14.3	–
OSW	Boraginaceae	1	50	–
OSW	Brassicaceae	7	398.6	510.45
OSW	*Carduus nutans*	3	70.6	105.4
OSW	*Chenopodium alba*	54	2288.1	4963.86
OSW	*Cordylanthus wrightii*	1	7.1	–
OSW	*Descurania* sp.	2	229.2	147.31
OSW	*Dracocephalum parviflorum*	2	86.1	12.95
OSW	*Helianthus* sp.	3	72.5	37.1
OSW	*Juniperus osteosperma*	5	106.2	116.08
OSW	*Lactuca serriola*	21	63.2	58.41
OSW	*Lappula redowski*	1	8	–
OSW	Malvaceae	2	21.5	13.67
OSW	*Nicotiana attenuata*	2	281.2	309.37
OSW	*Opuntia* sp.	1	31	–
OSW	Poaceae	21	122.4	236.43
OSW	*Polygonum sawachensis*	25	282.9	635.43
OSW	*Portulaca* sp.	4	702.1	671.45
OSW	Solanaceae	1	33.3	–
OSW	*Taraxacum officinale*	4	87.7	69.57
OSW	*Tragopogon* sp.	1	7.1	–
OSW	Unknown 25	1	6	–
OSW	Unknown 26	10	57.2	82.09
OSW	Unknown 27	1	24	–
OSW	Unknown 28	3	440.7	488.17
OSW	Unknown 29	3	1245.4	1845.62
OSW	Unknown 30	7	292	644.34
OSW	Unknown 31	1	23.8	–
OSW	Unknown 32	1	6	–
OSW	Unknown 33	1	8	–
OSW	Unknown 34	15	807.6	2137.33
SPW	*Chenopodium alba*	8	2218.8	3650.64
SPW	*Dracocephalum parviflorum*	2	316.1	314.45
SPW	*Juniperus osteosperma*	1	62.5	–
SPW	*Lactuca serriola*	1	100	–
SPW	*Nicotiana attenuata*	1	62.5	–
SPW	Poaceae	2	33.3	9.67
SPW	*Polygonum sawachensis*	1	140	–
SPW	*Salsola iberica*	1	120	–

Changes in Woodland Cover 1994–2009

A comparison of vegetation maps of MEVE created in 1994 and 2009 reveals that the extent of tree-dominated OSW was significantly reduced by large stand-replacing wildfires in 1996, 2000, and 2002, and by smaller wildfires in 2003 and 2008. Comparing the Floyd et al. (1994) map and the Thomas et al. (2009) map, we determined that there remained 3645 ha of OSW with mature trees within the park in 2009, a nearly 50% reduction in tree-dominated OSW compared with the extent in 1994 (Figure 7).

The extent of tree-dominated SPW also was reduced by fires between 1994 and 2009. Much of the SPW type in 1994 had only a sparse tree canopy, and was dominated by shrubs, the result of extensive fires in the late 1800s (Floyd et al. 2000, 2004). Some areas lacked trees altogether and were essentially shrublands, although they had the same environmental conditions (soils, elevation, and topographic position) as the nearby woodlands, and therefore had the potential to eventually develop into woodlands. Shrublands and sparse SPW woodlands covered 11,500 ha in 1994, but shrublands covered 14,272 ha in 2009, representing a 25% decrease in the portion of the SPW woodland type having a tree canopy.

DISCUSSION

Climate changes predicted for the southwestern United States are expected to cause major disruptions and reorganizations of biotic communities. In particular, Thorne et al. (2018) deemed piñon-juniper woodlands to have "moderately to critical vulnerability" depending on the global climate models used in their predictions. In addition to more frequent droughts and rising temperatures, more frequent fires are predicted, and fire will likely be a major process of transformation in piñon-juniper vegetation. We can see this process playing out already in MEVE, where severe fires in just the last 30 y have burned a substantial portion of the park, following more than a century of very little fire activity. Our studies of three of those major fires show that the two major structural types of piñon-juniper woodlands at MEVE respond differently to fire. These differences have important implications for the resilience and management of similar piñon-juniper vegetation throughout the region

Relative Resilience of SPW and OSW in Recovering Structure and Composition

Our data support our first hypothesis (H_1), that SPW stands are more resilient than OSW stands, in the sense that SPW

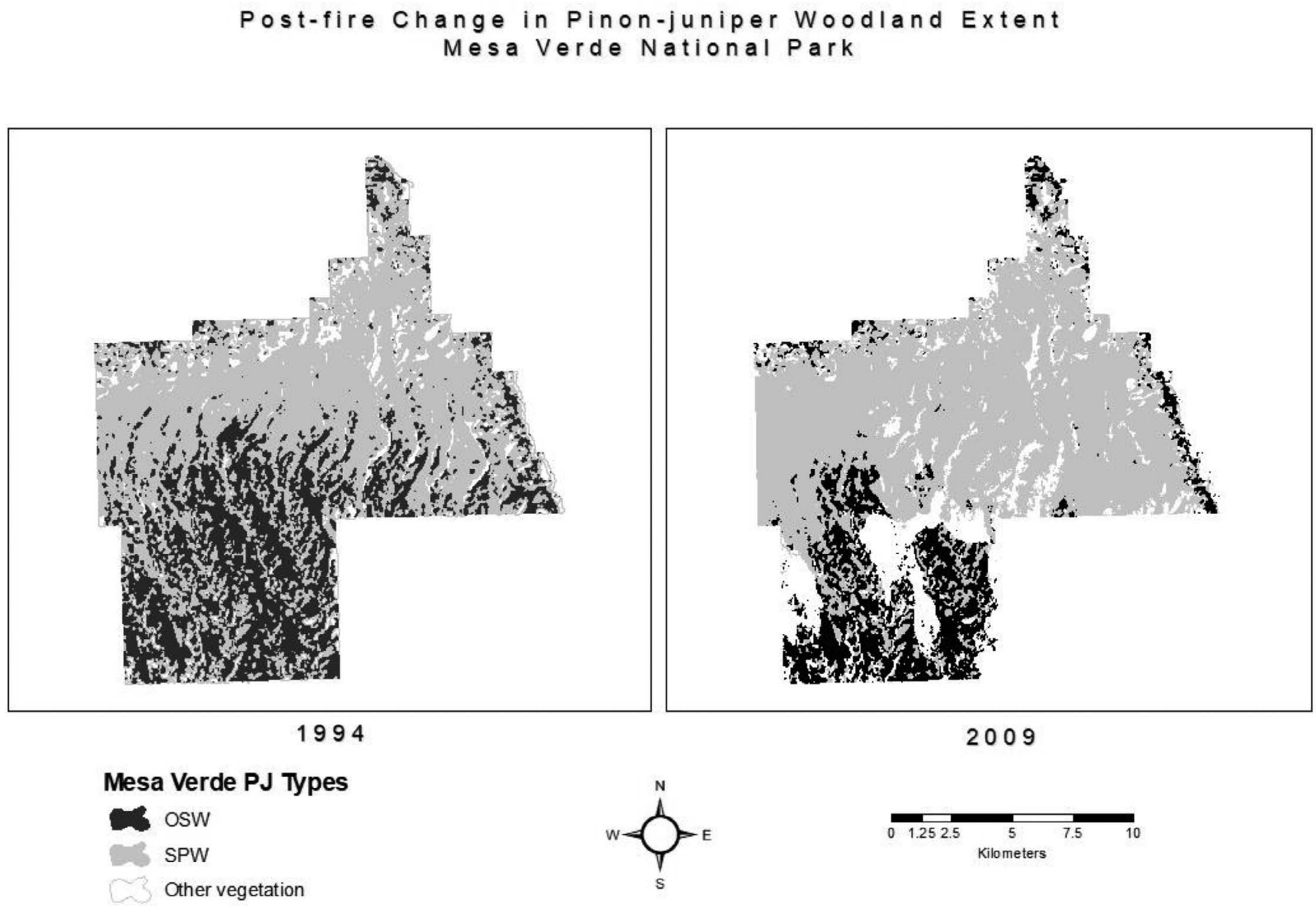

Figure 7.—The extent of tree-dominated piñon-juniper woodlands in Mesa Verde before and after recent wildfires. The tree-dominated area in the 1994 map was 7213 ha (Floyd et al. 1994) and in the 2009 map the area was reduced to 3645 ha (Thomas et al. 2009).

recovers pre-fire understory structure and species composition more quickly than does OSW. This is best seen following the 2000 fire, where we have data in 2002 from both burned and nearby unburned areas. The cover values for all plant life forms during the first 2 y after the 2000 fire were the lowest seen after any of the three fires that we documented (Figures 3–5), probably because of the hot, dry climate conditions of 2000–2002. Thus, vegetation responses to the 2000 fire are perhaps our best indicators of post-fire responses to be expected after future "global-change-type" droughts (Breshears et al. 2005).

If we sum the percent cover values of all three plant life forms (grasses, forbs, and shrubs) in each category (burned/unburned, OSW/SPW) from Figure 5, it is clear that total plant cover was greater in burned SPW than in burned OSW, primarily because of the high shrub cover. In fact, shrub cover in burned SPW was already 75% of shrub cover in unburned SPW (Figure 6). Grass cover was about the same in burned SPW and OSW (but lower than in unburned in both types), and forb cover was somewhat higher in burned SPW than in burned OSW (although higher than in unburned in both types). Note that even though shrub percent cover was approaching that of unburned stands, shrub heights and biomass were still considerably less in burned areas than in unburned.

We have observed that all of the shrub species characteristic of unburned SPW woodlands were well represented in burned SPW during the first few years after all of the fires of the last 30 y. This is not surprising, given the propensity of those species to resprout after injury to the aboveground parts and their known resilience to drought (Winkler et al. 2019). The major forbs and grasses of unburned SPW also were conspicuous again within one or a few years after fire. Although we do not have quantitative data on floristic composition pre- and post-fire, these observations indicate that SPW stands recover pre-fire species composition relatively quickly, and that SPW is thus relatively resilient to fire in terms of community composition as well as vegetation structure.

OSW appears less resilient than SPW in terms of composition as well as structure. Two of the important shrub species of OSW, antelope bitterbrush and big sagebrush, do not resprout, or resprout only weakly after fire, but must reestablish from seed. Thus, their recovery is slower than that of the very vigorously sprouting shrubs of SPW. Moreover, some 40% of the forb and grass species of OSW reestablish via seed germination (Figure 1);

Table 3.—Cover of nonnative plant species 2 and 3 y after the 1996 fire in OSW and SPW woodlands of Mesa Verde National Park. Values are mean ± standard error, analyzed by independent samples *t*-test; *P* values show difference between OSW and SPW.

Year	Woodland type	Cover of nonnative plants (percent)	Significance
1998	OSW	1.7 ± 0.53	$t = 1.91$, $P = 0.057$
1998	SPW	0.63 ± 0.23	
1999	OSW	21.4 ± 2.38	$t = 4.4$, $P < 0.001$
1999	SPW	9.8 ± 1.10	

we have observed these species in the burned areas, but they are redeveloping their pre-fire abundance more slowly than are the predominantly sprouting herbaceous species of SPW.

Vulnerability to Invasion of Nonnative Species

Our data also support our second hypothesis (H_2), that OSW is more vulnerable to rapid and marked changes in species composition after fire than is SPW, especially as driven by invasion of nonnative species. Plant species richness is greater in burned OSW stands (140 species recorded in our sample plots) than in burned SPW stands (81 species) (Appendix 1). Soil seed banks also appear to hold more taxa in OSW than in SPW (Table 2). The numbers alone suggest that reestablishing all of these species and their relative abundance after fire may be a slower process and more vulnerable to compositional change in OSW stands than in SPW stands, further supporting the idea that SPW is more resilient in terms of compositional recovery after fire. Many of the herbaceous species in both types are absent or rare in undisturbed vegetation (e.g., *Dracocephalum parviflorum* [American dragonhead] and *Chenopodium fremontii* [Fremont's goosefoot]), but flourish in burned or otherwise disturbed areas, apparently germinating from a large soil seed bank (Table 2).

But the biggest contributor to compositional vulnerability after fire, in OSW stands especially, is the striking proliferation of nonnative plant species in the burned areas. In 1991, 2 y after the 1989 fire, we began to observe a proliferation of muskthistle and a very low (<1%) cover of cheatgrass in burned OSW. Neither of these nonnative species had been conspicuous in MEVE prior to 1989. However, within 2 y following the 1996 fire, both species had invaded the burned landscape prolifically. Here, we make a new analysis of data previously published (Floyd et al. 2006), comparing nonnative cover (primarily muskthistle and cheatgrass) in burned OSW vs. SPW stands 2 and 3 y after the 1996 fire. In 1998, there was still a low cover of nonnatives (~1%), with no statistical difference between OSW and SPW ($t = 1.3$, $P = 0.057$). After the wet winter of 1998/1999, however, cheatgrass expanded greatly, with mean 21% cover in OSW and 10% in SPW (Table 3). Floyd et al. (2006) concluded that a major reason for the greater expansion of nonnative plant species in OSW than in SPW was the slower recovery of native plant cover in OSW and the resultant greater availability of bare soil where nonnative seeds could germinate and establish.

Since 1999, we have observed cheatgrass to expand into almost all of the burned areas in the park, with especially high cover in burned OSW. Many other nonnative forb species also have spread into burned areas, with especially high numbers and cover values in OSW. To date, we have documented 20 nonnative species in burned OSW stands, and 12 nonnatives in burned SPW (Appendix 1). Extensive nonnative plant invasion has also been documented following fires in other piñon-juniper woodlands throughout the region (Shinneman and Baker 2009; Sherrill and Romme 2012; Balch et al. 2013; Urza et al. 2019).

What is the Future of Piñon-Juniper Woodlands in Mesa Verde National Park?

We have not observed piñon or juniper recolonizing either the OSW or SPW in MEVE following fires of the past 30 y. Lack of tree regeneration this soon after fire is not necessarily of immediate concern, because even under the best of conditions it can take many decades for piñon and juniper to recolonize (Erdman 1970; Barney and Frischknect 1974; Koniak 1985; Huffman et al. 2012; Hartsell et al. 2020). However, there is evidence that piñon establishment in particular is declining even in undisturbed woodlands throughout the region relative to historical patterns (Redmond et al. 2012; Redmond and Barger 2013; Floyd et al. 2015). Therefore, it is important to monitor vegetation characteristics such as available nurse plants (Chambers et al. 1999), seed-dispersing animals such as piñon jay (Balda and Bateman 1972; Ligon 1978; Johnson et al. 2017), and climate conditions (moisture, moderate temperatures) that are needed for eventual tree reestablishment in burned areas, and to follow developments in the understory that will influence the rate and probability of tree reestablishment in the future.

If tree reestablishment should fail to occur in MEVE woodlands that have burned in recent (and future) fires, or if tree reestablishment were to be even slower than usual, we anticipate different trajectories for OSW and SPW vegetation. We further anticipate that the differences in structure and composition would become much greater than the historical differences in these two woodland types.

Much of the burned SPW might be converted into a shrubland vegetation type, as has occurred in some ponderosa pine (*Pinus ponderosa*) and dry mixed-conifer forests in northern New Mexico, southern Colorado, and central Arizona (Guiterman et al. 2018; Huffman et al. 2020). Shrublands dominated by Gambel's oak and other resprouting species are resilient to recurring fire and can be long-persisting even in the absence of fire. Even if much of the SPW becomes converted to shrubland, however, it probably will retain most of its non-arboreal native species diversity and most of its ecological function (e.g., productivity, nutrient cycling, soil stabilization), and will remain resilient to future fires.

The future of burned OSW is more worrisome than the future of SPW from a conservation and management standpoint. The tree canopy in most of MEVE's burned OSW woodland has been replaced by what Thomas et al. (2009) describe as a "post-fire mixed herbaceous" community of variable composition, including many native forbs and grasses but also many nonnative species. Prominent nonnative species include cheatgrass, muskthistle, *Bromus inermis* (smooth brome), and *Salsola tragus* (Russian thistle) (Thomas et al. 2009). Although it is conceivable that the native species might eventually displace and eliminate the nonnatives, we see no evidence that this is occurring now.

Moreover, the novel post-fire community that now exists is highly flammable, due in particular to the influx of nonnative cheatgrass and smooth brome, along with the native grasses and other herbaceous species (e.g., Byers et al. 2001; Brooks et al. 2004; Keeley 2006; Balch et al. 2013; Keeley et al. 2019). The historical fire regime in MEVE was characterized by fires at long intervals (many decades or centuries). But this novel abundance and continuity of fine fuels is unprecedented and could result a switch to far more frequent, recurring fires. Recurring fires would inhibit tree reestablishment and facilitate continuing invasion and dominance by nonnative grasses and forbs.

Such a radical transformation of OSW woodlands in Mesa Verde National Park, and in similar piñon-juniper woodlands elsewhere in the region, would be a most unfortunate loss for conservation of biodiversity and ecological function. The intact old-growth OSW woodlands that still remain in MEVE support piñon trees of a range of ages, with some more than 500 y old and junipers that are even older (Floyd et al. 2004, 2015). This demographic span is important because piñon exhibit age-specific sensitivity to climate pattern (Ogle et al. 2000; Hanna et al. 2018) and thus at least some age classes may persist into the drier and hotter future. They provide rich habitat for declining piñon jays and other birds (Johnson et al. 2017; Boone et al. 2018; Magee et al. 2019) and thousands of plant and animal species (Floyd 2003) such as piñon mice (*Peromyscus truei*; Aimee et al. 2018) and soil arthropods (Higgins et al. 2014). In addition to fire, Mesa Verde's old-growth woodlands are threatened by climate change and insect outbreaks. Extensive mortality of the oldest piñon trees occurred during the early 2000s when drought and above-average temperatures killed millions of piñons across the region, either directly (Breshears et al. 2005) or through outbreaks of *Ips confusus* (bark beetles). Major structural changes resulted, shifting tree composition to greater dominance by juniper (Negron and Wilson 2003; Mueller et al. 2005; Clifford et al. 2011, 2013; Redmond et al. 2014, 2018; Floyd et al. 2015). Hence the conclusion (e.g., Rondeau et al. 2011; Board et al. 2018) that southwestern piñon-juniper woodlands are of tremendous conservation value and are threatened by current and projected future trends in climate, fire, and invasive species.

CONCLUSIONS

Natural areas like MEVE, where ecological processes can play out with minimal human interference, provide excellent opportunities for study and understanding of vegetation dynamics (Turner et al. 2015). A vegetation type of particular concern in the southwestern United States is piñon-juniper woodlands, which appear to be especially vulnerable to undesirable ecological changes associated with projected increases in the frequency of severe droughts and fires. Longitudinal data collected after recent large severe fires in MEVE document the changes that have occurred to date, and provide insights into potential future trajectories of similar woodlands throughout the region.

Nearly one-half of the piñon-juniper vegetation in MEVE has burned in the past 30 y, and in much of this burned landscape, invasive cheatgrass and other nonnative species have proliferated (see Figures S1 and S2 in online supplemental material). Woodlands composed of a large proportion of resprouting species (SPW), especially shrubs, appear more resilient to fire than woodlands composed mostly of obligate seeding species (OSW). SPW stands in MEVE recovered vegetative cover and species composition more quickly after fire than did OSW stands. OSW stands also were particularly vulnerable to invasion by nonnative species; most of the native understory species are still present in those areas, but the community composition today is profoundly changed from what it was before the fires.

Piñon and juniper trees have not yet reestablished in any of the areas burned in the last 30 y in MEVE. Although slow tree recovery after fire is typical of this vegetation type, changes in the understory resulting from nonnative species invasion may inhibit tree establishment for an indefinite time. Notably, the flammable, nonnative grasses like cheatgrass could potentially fuel more frequent burning than was characteristic of the period prior to the late 20th century, inhibiting development of the native flora and facilitating continued dominance by nonnative species.

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