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ARTICLE

Postfire futures in southwestern forests: Climate and landscape influences on trajectories of recovery and conversion

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Abstract

Southwestern ponderosa pine forests are vulnerable to fire-driven conversion in a warming and drying climate, yet little is known about what kinds of ecological communities may replace them. To characterize postfire vegetation trajectories and their environmental determinants, plant assemblages (361 sample plots including 229 vascular plant species, surveyed in 2017) were sampled within eight burns that occurred between 2000 and 2003. I used nonmetric multidimensional scaling, *k*-means clustering, principal component analysis, and random forest models to assess relationships between vegetation pattern, topographic and landscape factors, and gridded climate data. I describe seven postfire community types, including regenerating forests of ponderosa pine, aspen, and mixed conifers, shrub-dominated communities of Gambel oak and mixed species, and herb-dominated communities of native bunchgrasses and mixtures of ruderal, native, and nonnative species. Forest recovery was generally associated with cooler, mesic sites in proximity to forested refugia; shifts toward scrub and grassland types were most common in warmer, dryer locations distant from forested refugia. Under future climate scenarios, models project decreases in postfire forest recovery and increases in nonforest vegetation. However, forest to nonforest conversion was partially offset under a scenario of reduced burn severity and increased retention of forested refugia, highlighting important management opportunities. Burning trends in the southwestern United States suggest that postfire vegetation will occupy a growing landscape fraction, compelling renewed management focus on these areas and paradigm shifts that accommodate ecological change. I illustrate how management decisions around resisting, accepting, or directing change could be informed by an understanding of processes and patterns of postfire community variation and likely future trajectories.

KEYWORDS
climate change, high-severity fire, ponderosa pine, RAD, resilience, resist–accept–direct, succession, vegetation type conversion

INTRODUCTION

Changing disturbance regimes and climate are poised to reshape many of Earth's forested ecosystems; however, the short- and long-term ecological outcomes of this reorganization are highly uncertain (Overpeck et al., 1990; Seidl et al., 2017). Because forests are composed of large and long-lived trees with strong microclimate buffering (Davis et al., 2018), they can exhibit substantial inertia in responding to external climate forcing. Severe disturbance can surmount lags in climate-related tree mortality and diminishing regeneration, catalyzing rapid ecological reorganization favored by climate change (e.g., Crausbay et al., 2017). Fundamentally, disturbances provide opportunities for ecological reorganization by removing portions of the extant community and allowing their replacement by alternate species, resulting in modified species assemblages. The proportion of the predisturbance community that is replaced, what replaces it, and the duration of replacement varies as a function of disturbance type, severity, extent, and post-disturbance conditions (Batllori et al., 2020). In forests dominated by few tree species, severe disturbance coupled with a changing climate can drive persistent conversion toward alternate and nonforested communities (Batllori et al., 2020; Davis et al., 2020; Johnstone et al., 2016; Whitman et al., 2019), yet in many cases the characteristics and controls of these replacing communities remain poorly understood.

In southwestern North America, a growing body of work has highlighted the potential for the combined effects of increasing wildfire activity and climate change to drive lasting forest conversion via elevated tree mortality and reduced regeneration (e.g., Haffey et al., 2018; Remy et al., 2021; Savage & Mast, 2005). Increasing forest fire activity (Dennison et al., 2014; Westerling et al., 2006), including increasing area burned at high severity (Parks & Abatzoglou, 2020; Singleton et al., 2019), is attributed largely to warmer and drier conditions associated with anthropogenic climate change (Abatzoglou & Williams, 2016; Westerling et al., 2006). Although ponderosa pine (*Pinus ponderosa*) and dry mixed-conifer forest types in this region were adapted to a historical fire regime characterized by low-severity fire with short return intervals, they are highly vulnerable to uncharacteristically severe fire (Fornwalt et al., 2016; Hagmann et al., 2021; Savage & Mast, 2005). Tree mortality during fire events may also be enhanced by warmer and drier conditions (van Mantgem et al., 2013). Consequently, recent severe fires have produced very large treeless patches (i.e., 100–10,000 ha; Singleton, Thode, Sánchez Meador, Iniguez, & Stevens, 2021).

Postfire forest recovery processes in southwestern forests are also impeded by increasing wildfire activity and climate. Following severe fire, reestablishment of ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), and other wind-dispersed, obligate-seeding conifer species are dependent on nearby live tree seed sources (Chambers et al., 2016; Haffey et al., 2018; Kemp et al., 2016; Owen et al., 2017) found at the burn perimeter or in forest refugia within the burn matrix. Within exceptionally large and homogeneous high-severity patches, natural reforestation is strongly constrained (Chambers et al., 2016). These constraints can be reinforced by reburning that kills tree seedlings (Prichard et al., 2017). Further, climate change can prevent tree regeneration where the physiological tolerances of tree seedlings are exceeded. Regeneration failure in response to warmer temperatures and increasing drought stress has been observed in many locations (Davis et al., 2019; Stevens-Rumann et al., 2018) and is projected to worsen for ponderosa pine and mixed-conifer forests in the southwestern United States (Rodman et al., 2020).

Although substantial recent work provides evidence and predictions of forest loss associated with changing fire regimes and climate, the ecological outcomes of their losses—the plant communities that will fill in behind them—are poorly understood. Descriptive studies in this region, mostly from one or a few burns, suggest that following high-severity fire, woody communities may be dominated by genera of resprouting broadleaf shrubs such as oak (*Quercus*) and ceanothus (*Ceanothus*), and herbaceous communities can be composed of a wide range of native and nonnative species (Abella & Fornwalt, 2015; Barton & Poulos, 2018; Coop et al., 2016; Haffey et al., 2018; Savage & Mast, 2005; Stevens et al., 2015). The extent and nature of replacing vegetation types has important implications for biological diversity, ecosystem function, and management. For example, shifts from conifers toward broadleaf trees, shrubs, or grasslands (which themselves may consist of invasive annuals or native perennials) may result in very different fuel characteristics and thus future fire probability and effects (Landesmann et al., 2020), altered ecohydrology (LaMalfa & Ryle, 2008), and changes in carbon fluxes and albedo (Mack et al., 2021).

Postfire forest futures under changing climate may be shaped by burn severity and spatial pattern, topography, and geography. Burn severity can regulate site insolation, temperature, and moisture availability via canopy cover and soils (Davis et al., 2018), promoting or inhibiting the growth of tree seedlings and competing vegetation (Stevens-Rumann et al., 2018). Burn spatial pattern can determine propagule availability, for example, in the size of high-severity patches (Singleton, Thode, Sánchez Meador, Iniguez, & Stevens, 2021) and the abundance and configuration of forest refugia (Coop et al., 2019; Downing et al., 2019). These patterns interact with terrain to shape the likelihood of forest recovery (Peeler & Smithwick, 2020). Topography exerts important controls on thermal conditions and moisture availability, enhancing or reducing postfire regeneration but also determining the composition of replacing plant communities (Littlefield, 2019; Singleton, Thode, Sánchez Meador, & Iniguez, 2021). Finally, the location of any given site within the fine- and broad-scale climate gradients that control species' elevational and geographic ranges (e.g., trailing vs. leading edge) may correspond with the likelihood of postfire forest conversion (Parks et al., 2019).

Increasing forest change associated with changing fire and climate compels new approaches to management. Over the last several decades, interventions in dry southwestern forests have focused largely on thinning and prescribed burning to restore and retain historical ponderosa pine and mixed-conifer forest structure and composition (Allen et al., 2002). However, the long-term effectiveness of such interventions, intended to increase forest ecosystem resistance to disturbance, may be challenged by continued warming and expansion of wildfire activity (Loehman et al., 2018). Postfire forest recovery efforts such as planting tree seedlings also face a wide range of challenges (Fargione et al., 2021). Fundamentally, in portions of tree species' ranges where future climatic conditions exceed their physiological tolerances, efforts to maintain them may be futile. Recent studies project substantial, climatically determined losses of dry southwestern forest types by the end of the 21st century (Parks et al., 2019; Rodman et al., 2020). An improving understanding of forest resilience mechanisms (Falk et al., 2022) further highlights expanding vulnerabilities and may also facilitate more accurate projections around the extent and rate of anticipated change. Although the ultimate duration of fire-driven forest conversion cannot be known with certainty, many such changes can be expected to persist over timescales exceeding management planning horizons and human lifespans (Coop et al., 2020). Consequently, management paradigms may need to shift to accommodate increasing ecosystem vulnerability and change (e.g., Hessburg et al., 2021; Schuurman et al., 2022).

One emerging paradigm, the RAD framework (Aplet & Cole, 2010; Schuurman et al., 2020), recognizes three fundamentally distinct strategies, which include resisting, accepting, or directing change. In the context of postfire management, a resist strategy would encompass any efforts to return a system to a prefire forest type (e.g., by supporting natural or artificial tree regeneration of prefire dominant species), an accept strategy would allow for fire-catalyzed conversion to alternative vegetation types, and a direct strategy might involve planting new combinations of tree species suited for future climate and disturbance (Stevens et al., 2021). Decisions as to whether to resist, accept, or direct change can be informed by the likely success or failure of resistance strategies, but also the nature of change in the absence of intervention. For example, the decision to accept fire-driven forest conversion might be contingent on the nature of the replacing vegetation type and the ecosystem services it provides: replacement by an alternate forest type may be more acceptable than replacement by nonforest vegetation, but replacement by a nonforest vegetation type dominated by native perennials might be preferred over one dominated by nonnative annuals. Thus, the development of plausible postfire ecological futures is a key research direction needed to support decision-making around wildfire-driven forest conversion in a future of continued climate change and increasing wildfire activity (Crausbay et al., 2022).

A rapidly growing body of literature is demonstrating the increasing vulnerability of southwestern forests to rapid, fire-catalyzed change, yet the ecological outcomes of these changes remain poorly understood. The purpose of this research was to characterize vegetation patterns and their relationships to environmental variation following high-severity fire in southwestern ponderosa pine forests and shed light on contemporary ecological outcomes and future trajectories in these systems. Specifically, the objectives of this study were to (1) characterize and contrast different patterns of postfire vegetation composition, in particular those expected to lead to forest recovery versus conversion to nonforest types, (2) assess relationships between postfire vegetation and a suite of climate and landscape variables, and (3) model postfire trajectories of forest recovery versus conversion to nonforest under different projected climate change and fire-severity scenarios. This understanding can then be used to inform decision-making under management frameworks such as RAD.

METHODS

Study area

The study area comprised eight wildfires that occurred between 2000 and 2003 (Table 1; Appendix S1: Figure S1) in the southwestern United States. These wildfires were

TABLE 1 Study site attributes.

Burn	Year	Area (ha)	Proportion moderate + high severity	MAT (C)	MAP (mm)	No. samples	
						Within refugia	High-severity openings
Cerro Grande	2000	17,919	0.51	8.9	537	17	33
Hayman	2002	52,353	0.65	6.7	503	26	73
Missionary Ridge	2002	27,891	0.53	5.2	734	12	38
Outlet	2000	5801	0.44	8.0	589	12	37
Ponil Complex	2002	36,051	0.51	7.8	492	12	38
Poplar	2003	6845	0.30	7.5	597	14	36
Pumpkin	2000	6510	0.38	6.6	610	13	37
Rodeo-Chediski	2002	186,873	0.68	10.6	551	24	76

Note: Study site attributes include area and proportion of moderate + high severity from the monitoring trends in burn severity (Eidenshink et al., 2007) and 30-year (1981–2010) mean annual temperature (MAT) and precipitation (MAP) from WorldClim (Hijmans et al., 2005).

selected based on (a) prefire forest type (ponderosa pine or dry mixed conifer), (b) a substantial component of stand-replacing fire within the burn perimeter, and (c) occurrence over a comparable period that allowed successional trajectories to be characterized (sampled in 2017, vegetation data represent conditions 14–17 years postfire).

Burns occurred across a broad range of topographic and climatic conditions (Table 1) within two ecoregions, the Arizona/New Mexico Mountains and the Southern Rockies. Within the Arizona/New Mexico Mountains Ecoregion, the Poplar and Outlet burns both sit at relatively high elevations on flat landscapes of the Kaibab Plateau north of the Grand Canyon. The Rodeo-Chediski burn straddles the plateaus and canyons of Mogollon Rim; only the northern portion of the burn above the rim was sampled in this study. The Pumpkin burn occupies an isolated volcanic mountain. Generally, these burns are located in relatively warm and dry conditions, with the mean annual temperature (MAT) between 6.6 and 10.6°C and mean annual precipitation (MAP) between 551 and 601 cm (Table 1). Within the Southern Rockies Ecoregion, the Cerro Grande, Missionary Ridge, and Ponil Complex occur upon a mix of relatively flat terrain on moderate-elevation mesas and steep-sided canyons; the landscape of Hayman is rolling with steep hills. These sites are generally cooler and see a broader range of precipitation, with MAT ranging from 5.2 to 8.9°C and MAP between 492 and 734 mm (Table 1).

Sample stratification

Sample stratification relied on 1-m-resolution maps of postfire tree cover (here, termed forested refugia), which were developed from National Agriculture Imagery Program (NAIP) imagery. Mapping methods are described in Walker et al. (2019). Within each burn, samples were stratified one-third in forested refugia and two-thirds in severely burned, nonforested openings. Within these classes, samples were further stratified by a metric accounting for both proximity to and abundance of forest refugia patches, intended to represent propagule availability for dominant, wind-dispersed, nonserotinous tree species. This metric is called the distance-weighted refugia density (DWD) and defined as

$$\mathrm{DWD} = \sum_{i=1}^{N} 1/(d_i + 1),$$

where i represents forested refugia pixels, and d is distance from the focal cell (Coop et al., 2019; Downing et al., 2019). The DWD values were calculated using a 150-m-radius moving window and binned into four quartiles each for refugia and nonforest pixels. Equal numbers of points were generated randomly within each quartile and sampled proportionally within each burn. Thus, samples within forested refugia and nonforested openings represent a broad range of seed source availability (i.e., from very small and isolated refugia to the centers of large forested patches, and from the centers of large, severely burned patches to very small openings surrounded by intact forest). Satellite-derived burn severity, the differential normalized burn ratio (dNBR) (Key & Benson, 2005), generally exhibited low values (ca. −400 to 200) in forested refugia, indicating they burned at low-moderate severity or not at all. Within the nonforest class, areas with a dNBR < 400 were excluded to ensure sample locations were forested prefire (excluding, e.g., meadows and barren rock). Thus, all nonforest samples represent areas where forest canopy was entirely removed by fire, though these areas still exhibited some variation in burn severity at the higher (400–1300 dNBR) end of the spectrum. Sampling did not take place in areas subject to postfire reforestation, salvage logging, or subsequent wildfire. Sampled points were required to have a separation of at least 150 m, and points within 150 m of the burn perimeter were excluded from sampling.

Field data collection

Vegetation data were collected in 5.64-m-radius (100-m^2) circular plots. The spatial coordinates (Universal Transverse Mercator North American Datum 83) of each plot center were recorded, and photos were taken along the N–S axis of each plot. Within each sample, a list of all live vascular plant species with canopy cover at least 0.25 m^2, or 0.25% of the 100-m^2 plot, was compiled. Ocular coverage estimates were made for each species, by stratum. The midpoints of nine coverage ranges were used to record coverage estimates as follows: 0.5 (0.25%–1%), 2.5 (1%–5%), 7.5 (5%–10%), 17.5 (10%–25%), 29 (25%–33%), 41.5 (33%–50%), 62.5 (50%–75%), and 87.5 (>75%). Strata were as follows: 1 (canopy tree, >5 m), 2 (subcanopy tree or very tall shrub, 2–5 m), 3 (tall shrub/seedling, 0.5–2 m), 4 (short shrub/tree seedling, 0–0.5 m), and 5 (herbaceous). Individuals of all tree species were assigned to one of three categories: (1) residual (establishment predated the wildfire), (2) postfire regeneration (establishment occurred after the fire), or (3) unknown. For all trees (defined as ≥1.37 m in height) species identity and diameter at breast height (DBH) were recorded. For seedlings (<1.37 m) all individuals were tallied by species. The vast majority of vegetation cover was by common, widely distributed, and easily field-identified plant species. Collections were made for all unknown plant species; these were subsequently identified using published flora, herbarium collections, and digital resources (e.g., SEINet; https://swbiodiversity.org/seinet/).

Climate variables, topography, burn severity, and landscape context

For each sample location, annual climate means were downloaded as scale-free point estimates from downscaled historical data layers (ClimateNA; Wang et al., 2016). Although annual means do not fully capture all of the relevant climate variation that could potentially influence the abundance of each of the many plant species encountered in our samples, they are highly representative of the regional gradients that are well known to correspond to broader shifts in species ranges, vegetation composition, structure, and physiognomy (e.g., O'Donnell & Ignizio, 2012; Stephenson, 1990). The objective of this analysis was not to test for the effects of particular climate extremes on specific patterns or processes (e.g., effects of recent atmospheric drought on tree regeneration) but rather to explore generally how gradients in postfire climate correspond to variation in postfire vegetation types; thus, spatially interpolated means provided the most suitable starting point. Climate data represented the postfire period and two future scenarios. To represent postfire conditions, for each study burn I averaged each full year between the fire and the year of sampling (e.g., for Cerro Grande, which occurred in 2000, climate represents the average over the period 2001–2016). I also downloaded climate means for each sample site for two Representative Concentration Pathway (RCP) 4.5 scenarios for the year 2055, one representing warm and arid conditions (2055 dry; HadGEM2 ES) and one representing warm and more mesic conditions (2055 wet; Geophysical Fluid Dynamics Laboratory Coupled Model 3).

A principal component analysis (PCA) on climate variables was used to identify major axes of climate variation and reduce collinearity of predictor variables in subsequent analyses, following the methods of Whitman et al. (2015). Annual means for 13 variables were included in the PCA (Table 2); these included six temperature variables (growing degree days >5°C [DD5] MAT, mean temperature of the coldest month [MTCM], mean temperature of the warmest month [MWMT], number of frost-free days [NFFD], and temperature difference between the warmest and coldest month [TD]), three precipitation variables (MAP, mean summer precipitation [MSP], and mean winter precipitation [MWP]), and four synthetic measures of water balance (annual heat moisture [AHM], climate moisture deficit [CMD], Hargreaves reference evaporation [Eref], and summer heat moisture [SHM]). Variable selection for the PCA followed Hamann et al. (2015), but with the inclusion of two additional heat-moisture variables. The PCA was first conducted using means from the postfire period and then applied to the two future projections.

Site scores on the first three PCA axes (representing warmth, winter aridity, and summer aridity, described in further detail in the *Results* section) were employed as predictor variables in subsequent analyses. Additionally, I examined correlations between vegetation and four topographic and landscape factors. Percentage slope and aspect were extracted for each sample plot location from a 30-m digital elevation model (DEM); aspect was transformed to a southwest (SW) aspect index (running from 1 for SW to −1 for northeast). The relativized differential normalized burn ratio (RdNBR) (Miller & Thode, 2007) was extracted from burn severity maps

TABLE 2 Principal component analysis (PCA) axis loadings.

Climate variable	Abbreviation	PC1 (55%)	PC2 (26%)	PC3 (9%)
Annual heat-moisture index (MAT+10)/(MAP/1000)	AHM	0.25	0.37	0.24
Hargreaves climatic moisture deficit (mm)	CMD	0.32	−0.11	0.14
Growing degree-days above 5°C	DD5	0.37	0.06	−0.15
Hargreaves reference evaporation (mm)	Eref	0.34	−0.06	−0.13
Mean annual precipitation (mm)	MAP	−0.12	−0.44	−0.42
Mean annual temperature (°C)	MAT	0.37	−0.00	−0.10
Mean coldest month temperature (°C)	MCMT	0.34	−0.05	0.16
Mean annual summer (May–September) precipitation (mm)	MSP	−0.10	0.45	−0.38
Mean warmest month temperature (°C)	MWMT	0.37	0.00	−0.15
Mean annual winter (October–April) precipitation (mm)	MWP	−0.05	−0.53	−0.19
Number of frost-free days	NFFD	0.32	−0.03	−0.10
Summer heat-moisture index ([MWMT]/[MSP/1000])	SHM	0.20	−0.40	0.32
Temperature difference between MWMT and MCMT (°C)	TD	0.18	0.09	−0.58

acquired from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink, 2007). Finally, as a measure of potential propagule availability for obligate-seeding trees, DWD was calculated for a 600 × 600-m window around each sample site, based on the optimal window size found by Coop et al. (2019) and Downing et al. (2019). Seven severely burned plots were located too close to the burn edge (<300 m) to permit this calculation; these plots were excluded from subsequent analysis.

Plant community analysis

Vegetation data from samples occurring in stand-replacing patches ($N = 361$) were used to explore multivariate patterns of plant community composition following high-severity fire using gradient analysis and cluster analysis. First, Sørensen compositional dissimilarity between all sample pairs was calculated from cover values of 229 species. This distance matrix was then used to generate a three-dimensional (3D) nonmetric multidimensional scaling (NMS), which arranges samples such that rank pairwise compositional dissimilarity is related monotonically to pairwise Euclidean distance in a low-dimensional ordination space. The optimal number of NMS dimensions (in this case, three) was determined by plotting ordination stress against number of dimensions.

To classify assemblages into "community types" representing divergent postfire successional assemblages, I employed a *k*-means clustering of sample scores on each NMS axis. *K*-means partitions observations into *k* clusters based on Euclidean distance (in this case, in 3D NMS species space) from the nearest mean. The advantages of this approach include the minimization of within-cluster variance in species space and clear correspondence between the NMS ordination and the classification. The optimal number of community types was determined by assessing the proportion of additional variance reduced by the inclusion of each additional class and selecting the number of classes beyond which variance reductions were considered insubstantial. All community analyses were conducted in R (R Core Team, 2020). The NMS ordination employed the vegan package (Oksanen et al., 2019); cluster analysis relied on the cluster package (Maechler et al., 2019).

I examined Pearson correlations between NMS axis scores and the climate, topographic, and landscape context variables described earlier; relationships between key variables were also visualized using the *ordisurf* function of the vegan package (Oksanen et al., 2019) to map isoclines onto ordination diagrams. For each community type I also calculated the mean and standard deviation for variables of interest, including coverages by dominant plant species and life form.

I also sought to address the question of how different community types of high-severity patches were from communities within nearby forested refugia that were unburned or experienced lower-severity surface fire. Because prefire data on forest community composition were lacking, I developed a measure of the relative difference between each of the community types and forest refugia vegetation. I calculated the average Sørensen compositional dissimilarity between each sample site and the closest three samples from nearby forest refugia patches. This analysis utilized the full set of samples from both forested refugia and severely burned patches

($N = 498$; Table 1). Dissimilarity was averaged across each community type. I contrasted this mean dissimilarity between any given community type and neighboring forests with dissimilarity within those forests, measured identically (mean dissimilarity of any given forest sample with the closest three neighboring forest samples).

Random forest predictions

To further explore vegetation–environment relationships and how vegetation might shift under future climate, I employed a random forest analysis. In particular, I contrasted how trajectories leading toward forest versus nonforest vegetation types might differ under different future climate and burn-severity scenarios. Accordingly, I aggregated samples from the seven community types identified by cluster analysis (described in detail in the results) into two broad groupings: a trajectory of forest recovery ($n = 189$) and one representing nonforest vegetation types ($n = 172$).

A random forest model was developed using the randomForest package (Liaw & Wiener, 2002). Predictor variables included the three climate indices (PCA axis scores), slope, SW aspect, RdNBR, and DWD. I first predicted forest versus nonforest trajectories using recent postfire climate variables. To determine which predictor variables to include in each random forest model, I examined Gini statistics. Reducing the number of predictor variables by excluding those with the lowest Gini statistic reduced model accuracy, so the full suite of predictors was retained for each model. To determine model fit, I first examined confusion matrices of classification accuracy and the out-of-the-bag (OOB) error rate as estimated in the randomForest package (Liaw & Wiener, 2002). I then contrasted OOB error with a separate cross-validation utilizing the package rfUtilities (Evans & Murphy, 2018).

I subsequently applied the model to the two different 2055 climate projections under three different burn-severity scenarios, as follows. First, for each climate scenario (2055 dry and 2055 wet), burn severity and all landscape context variables were modeled as they were measured in field samples. I next considered a less-severe burn scenario (moderate) in which burn severity (RdNBR) was reduced by 20% and DWD was increased by 20% for each sample. I then developed a scenario representing elevated burn severity (severe), in which RdNBR increased by 20% and refugia abundance and proximity decreased by 20%. From each model output, the percentage increase or decrease in representation by forest or nonforest vegetation was quantified.

RESULTS

Climate variation across sample sites

Three PCA axes accounted for 90% of the variation in postfire climate means across sample locations. The first principal component (PC1, accounting for 55% of variation) was strongly positively associated with thermal variables, including growing degree-days, MAT, and MWMT (Figure 1, Table 2); henceforth, this axis is referred to as the warmth index. The second principal component (PC2, accounting for 26% of variation) was negatively related to MAP and MWP but positively related to MSP (Figure 1, Table 2) and is henceforth referred to as the winter aridity index. The third principal component (PC3, accounting for 9% of variation) was negatively related to MAP and MSP (Table 2) and is hereafter referred to as the "summer aridity index". This axis was also negatively correlated with seasonal temperature differences.

Plant community compositional variation and relationships to environment

The NMS ordination produced a 3D solution with a final stress of 0.179. Each axis showed relationships to shifts in plant species composition, structure, and abiotic factors (Figure 2). The first axis, NMS 1, was strongly negatively correlated to cover by tree species (Pearson's $r = -0.61$; Figure 2a), unrelated to shrub cover (Figure 2b), and weakly linked to declining forb cover ($r = -0.14$) and increases in graminoids ($r = 0.12$; Figure 2c). Site score on NMS 1 was positively associated with the warmth index ($r = 0.55$; Figure 2d) and winter aridity ($r = 0.51$; Figure 2e). NMS 1 was also weakly related to topographic variables, including slope ($r = -0.19$) and SW aspect ($r = -0.14$), and burn severity ($r = -0.13$). NMS 2 represented increasing shrub cover ($r = 0.40$; Figure 2b) and, to a lesser extent, decreasing tree cover ($r = -0.18$; Figure 2a). This axis was associated with increasing winter aridity ($r = 0.26$; Figure 2d), decreasing summer aridity ($r = -0.19$; Figure 2e), and decreasing proximity to and abundance of patches of intact forest (DWD, $r = -0.14$, Figure 2f). NMS 3 (not illustrated) represented decreasing cover by shrubs and forbs ($r = -0.38$ and -0.23, respectively) and was linked to decreasing warmth ($r = -0.26$) and increasing winter and summer aridity ($r = 0.41$ and 0.14, respectively).

Seven k-means-derived clusters (henceforth referred to as postfire community types) optimally partitioned variation in plant community composition, accounting

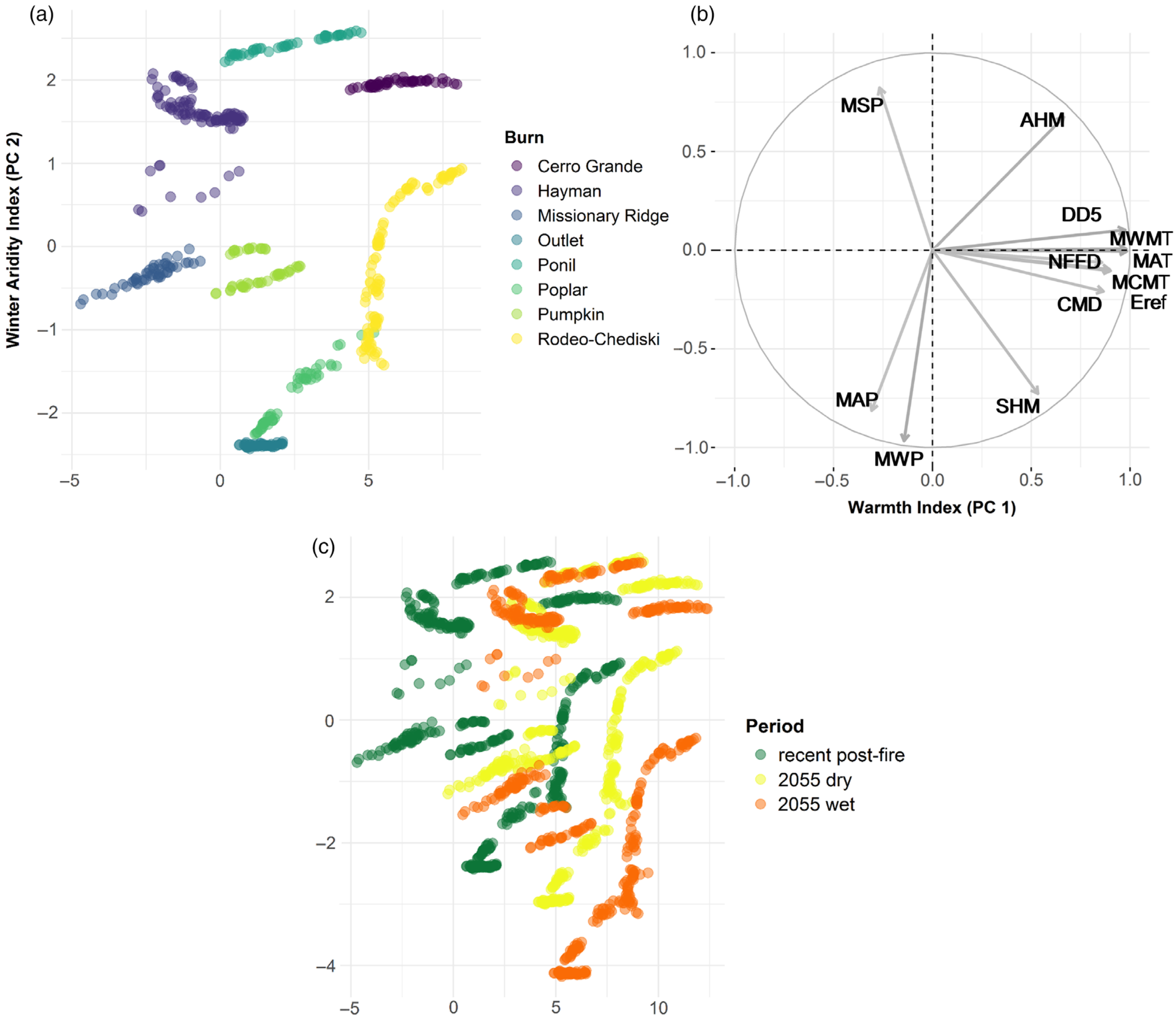

FIGURE 1 (a) Locations of sample sites, by burn, on the first and second principal component analysis (PCA) axes of climate variation; (b) first and second PCA loadings for 13 mean monthly climate variables (2001–2016; abbreviations given in Table 2) extracted from interpolated climate grids (Wang et al., 2016) for each sample location; (c) sample site locations in current (postfire) climate space and two Representative Concentration Pathway (RCP) 4.5 scenarios for the year 2055, one representing warm and arid conditions (2055 dry, HadGEM2 ES) and one representing warm and wetter conditions (2055 wet, Geophysical Fluid Dynamics Laboratory [GFDL] Coupled Model 3 [CM3]). AHM, annual heat-moisture; CMD, Hargreaves climatic moisture deficit; DD5, growing degree-days above 5°C; MAP, mean annual precipitation; MAT, mean annual temperature; MCMT, mean coldest month temperature; MSP, mean annual summer (May–September) precipitation; MWMT, mean warmest month temperature; MWP, mean winter (October–April) precipitation; NFFD, number of frost-free days.

for 75% of the total variance in ordination space. Most community types occupied distinct portions of ordination space (Figure 3). Community types also exhibited clear differences in cover by plant life forms and species (Table 3). Community types were named based on dominant species or mixtures of species within a dominant lifeform. Two types, the aspen and ponderosa pine community types, included substantial cover by regeneration of those tree species (34.6% and 16.7%; Figure 3, Table 3). Aspen communities also included moderate cover by a range of shrubs, forbs, and graminoids (Table 3), in particular *Carex siccata* (5.8%). The mixed-conifer community type displayed much sparser tree regeneration (and sparse plant cover generally) that included some ponderosa pine (1.9%), Douglas fir (1.4%), and aspen (2.0%). However, the most abundant species in this type was a prostrate shrub

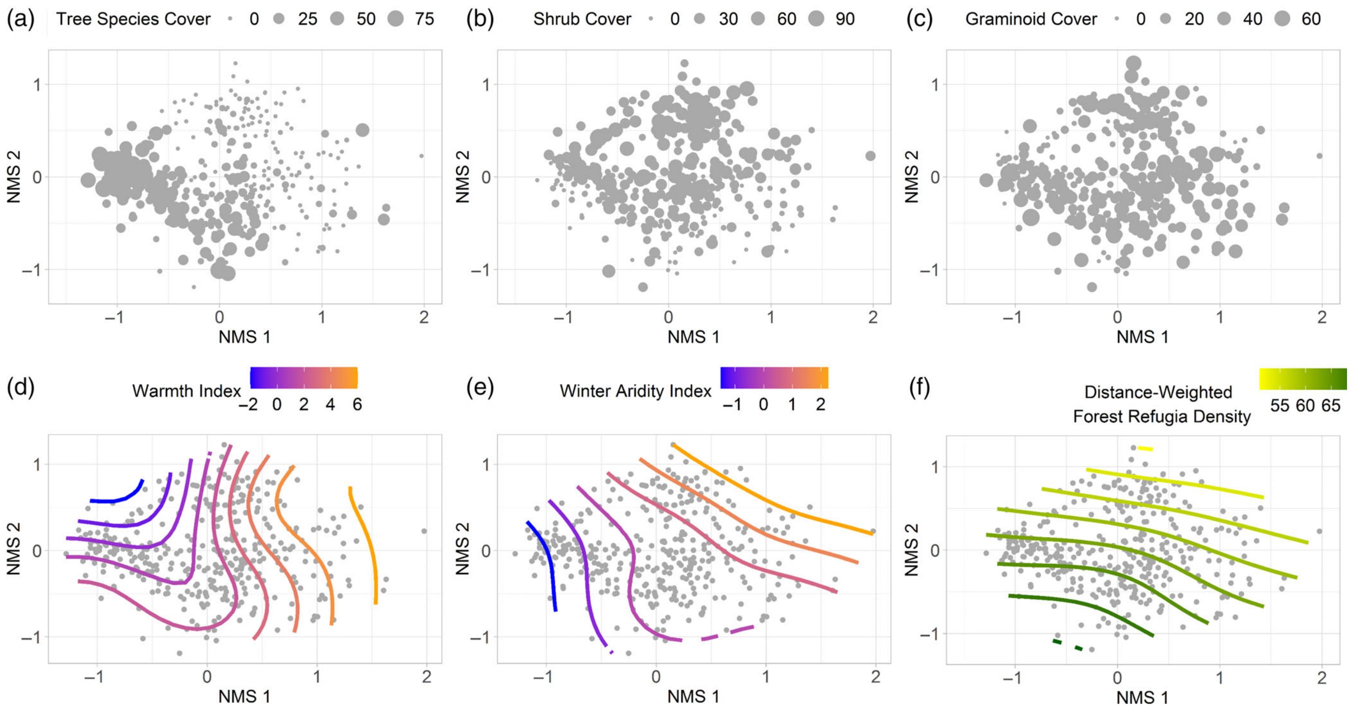

FIGURE 2 Nonmetric multidimensional scaling (NMS) of 361 vegetation samples from areas of stand-replacing fire in eight southwestern burns. Only the first two NMS axes (NMS 1 and 2) are illustrated. Changes in cover by different lifeforms within species space is illustrated the size of the dots representing (a) tree species, (b) shrubs, and (c) graminoids in the top row. Relationships between NMS axes and three environmental variables, (d) warmth (PC1), (e) winter aridity (PC2), and (f) proximity and abundance of forest refugia (DWD), are illustrated in the contour plots in the bottom row.

with high leaf area, *Arctostaphylos uva-ursi*, albeit also occurring with relatively low cover (5.5%).

The remaining community types in the classification were dominated by shrubs, grasses, and forbs. This classification revealed two community types composed primarily of shrubs (Figure 3, Table 3). These included an oak scrub type, dominated by *Quercus gambelii* (18.5%) but with high cover by graminoids including *Bromus inermis* (5.8%), and a mixed-shrub community with variable species dominance, most notably by *Robinia neomexicana* (19.6%). Another important species occurring frequently in this community was the nonnative grass *Bromus tectorum* (6.0%). Two communities were dominated by graminoids (Figure 3, Table 3). The first was a bunchgrass type, with high cover by native bunchgrasses including *Muhlenbergia montana* (6.1%). The second, here referred to as the ruderal grass type, was variably dominated by a range of weedy or nonnative grasses and forbs, including *Bromus tectorum* (9.7%), *Artemisia dracunculus* (5.3%), and *Verbascum thapsus* (2.6%).

Community types showed clear relationships with underlying variation in environmental factors (Figures 2 and 3, Table 4), including spatial climate means, topography, and postfire landscape context (RdNBR and DWD). Aspen was associated with cooler and more mesic climate (low warmth and winter aridity indices) and relatively high burn severity (RdNBR) (Table 4). The ponderosa pine and mixed-conifer types were found where proximity to and abundance of intact forest patches were highest (high DWD), but within different climatic spaces: ponderosa pine occurred at intermediate values of climate indices, mixed conifer at cooler sites but with drier winters (Table 4). Mixed-conifer communities also burned the most severely (mean RdNBR 903). Mixed-shrub communities occurred in areas with wetter winters and summers and on relatively steep slopes. Oak scrub tended to occur at slightly warmer and drier sites than the other woody-plant-dominated communities described earlier, and also at very low values of DWD (Table 4). Finally, both of the grass-dominated communities occurred in the warmest climate settings and on shallow slopes (Table 4). Whereas the bunchgrass community exhibited a burn severity that was lower than the other communities, ruderal grass showed higher burn severity and the lowest values of DWD.

How distinct are postfire communities from adjacent forests?

Samples from postfire communities within high-severity patches were compositionally divergent from samples

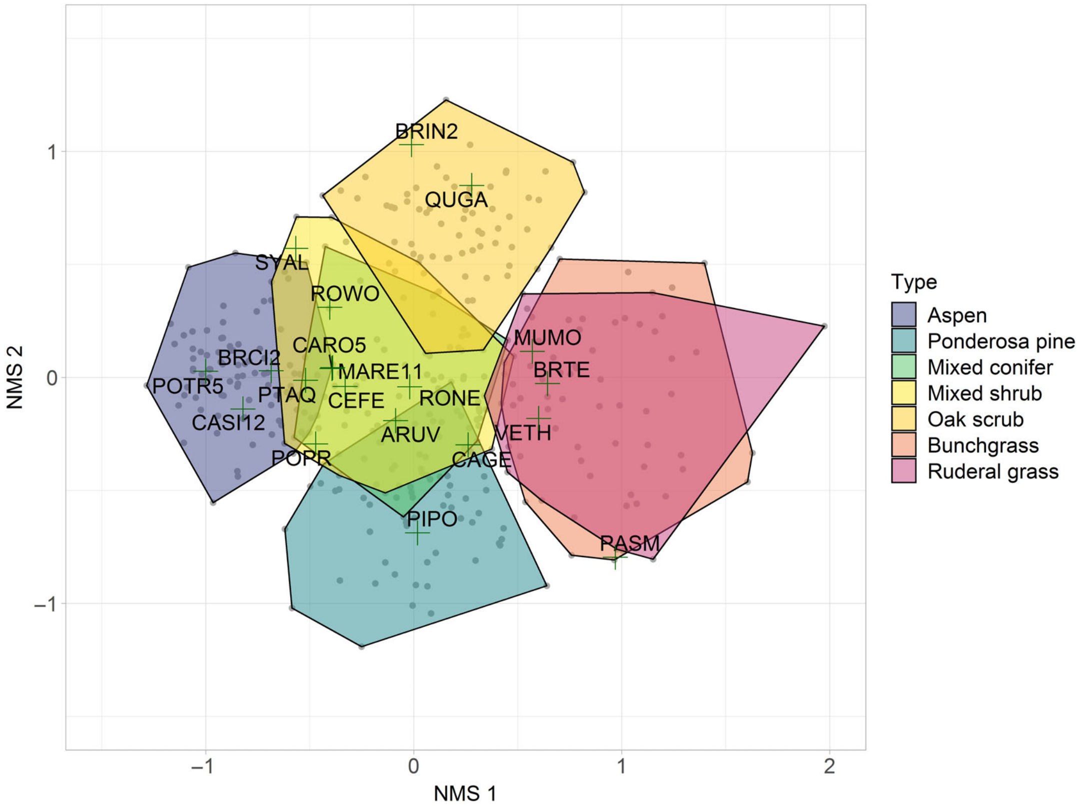

FIGURE 3 Vegetation types (clusters) and species centroids of the most abundant 20 vascular plant species within the first two nonmetric multidimensional scaling (NMS) axes. The mixed shrub type appears superimposed on the mixed-conifer type, and the ruderal grass type is superimposed on the bunchgrass type; these are separated on NMS 3 (not shown). Species codes are as follows: ARUV, *Arctostaphylos uva-ursi*; BRCI2, *Bromus ciliatus*; BRIN2, *Bromus inermis*; BRTE, *Bromus tectorum*; CAGE, *Carex geyeri*; CARO5, *Carex rossii*; CASI12, *Carex siccata*; CEFE, *Ceonothus fendleri*; MARE11, *Mahonia repens*; MUMO, *Muhlenbergia montana*; PASM, *Pascopyrum smithii*; PIPO, *Pinus ponderosa*; POPR, *Poa pratensis*; POTR5, *Populus tremuloides*; PTAQ, *Pteridium aquilinum*; QUGA, *Quercus gambelii*; RONE, *Robinia neomexicana*; ROWO, *Rosa woodsii*; SYAL, *Symphoricarpos albus*; VETH, *Verabascum thapsus*.

TABLE 3 Cover by life form and dominant species within each community type.

Community type	*N*	Cover by tree species (%)	Cover by shrubs (%)	Cover by forbs (%)	Cover by graminoids (%)	Dominant species (percentage cover)
Aspen	89	36.7	12.7	10.1	11.2	*Populus tremuloides* (34.6%)
Ponderosa pine	56	19.2	10.7	8.0	12.4	*Pinus ponderosa* (16.7%)
Mixed conifer	44	5.3	12.1	5.2	13.0	*Arctostaphylos uva-ursi* (5.5%)
Mixed shrub	37	1.8	39.2	11.4	15.8	*Robinia neomexicana* (19.6%)
Oak scrub	66	1.1	31.5	7.6	18.8	*Quercus gambelii* (18.5%)
Bunchgrass	36	3.9	10.3	4.6	18.1	*Muhlenbergia montana* (6.1%)
Ruderal grass	33	0.6	17.3	9.8	21.3	*Bromus tectorum* (9.7%)

from nearby forests, though they exhibited a range of dissimilarity (Figure 4). As a baseline for these comparisons, within-forest sample Sørensen dissimilarity averaged 0.75. Ponderosa pine communities, dominated by tree regeneration, were only marginally compositionally distinct, with a mean dissimilarity from these forests of 0.77. The bunchgrass and oak scrub communities were the next most compositionally similar to intact forests, with mean dissimilarities of 0.82 and 0.84, respectively. The mixed-conifer type exhibited a slightly greater difference of 0.85. The remaining three communities, aspen, mixed shrub, and ruderal grass, all showed the greatest dissimilarities from intact, adjacent forests: 0.89, 0.91, and 0.92, respectively.

TABLE 4 Mean values of key abiotic variables for each community type.

Community type	*N*	Warmth index (PC1)	Winter aridity index (PC2)	Summer aridity index (PC3)	Slope (%)	SW aspect	Burn severity (RdNBR)	DWD
Aspen	89	0.29	−1.11	0.21	12.0	−0.06	881	63.0
Ponderosa pine	56	2.55	−0.20	0.03	10.5	−0.03	791	68.3
Mixed conifer	44	−0.38	1.44	0.11	13.4	−0.38	903	69.2
Mixed shrub	37	2.33	−0.68	−0.70	15.6	−0.44	818	66.6
Oak scrub	66	3.03	1.28	−0.19	13.6	−0.39	811	54.0
Bunchgrass	36	4.37	0.92	0.40	8.6	−0.23	802	65.6
Ruderal grass	33	4.27	1.02	0.22	9.7	−0.41	843	51.1

Abbreviations: DWD, distance-weighted refugia density; RdNBR, relativized differential normalized burn ratio; SW, southwest.

Postfire futures under projected climate change

Random forest models were developed for two distinct postfire futures; these were a *forest* trajectory ($n = 189$) that included the aspen, mixed-conifer, and ponderosa pine communities, and a *nonforest* trajectory ($n = 104$), which included the oak scrub, mixed shrub, bunchgrass, and ruderal grass types. Out-of-the-bag (OOB) estimates of classification errors was 20.5%. An independent 10-fold cross-validation yielded nearly identical estimates of error (20.5%), with a kappa value of 0.58. Producer's and user's accuracy were approximately balanced for predictions (a confusion matrix presented in Appendix S1: Table S1).

The first two synthetic climate indices (warmth and winter aridity) were the most influential variables in the random forest model, as determined by the Gini statistic (Appendix S1: Figure S2). Decreases in the Gini statistic associated with the warmth and winter aridity index were 51 and 46, respectively; all other variables resulted in reductions of between 14 and 20.

The random forest model applied to future climate projections predicted substantial shifts in future representation by trajectories of forest recovery versus conversion to nonforest vegetation relative to recent conditions. Holding burn severity constant, under the 2055 dry scenario, the proportion of postfire sites predicted a 34% in forest recovery; under the 2055 wet scenario the decrease was 7%. Conversely, proportional representation of nonforest vegetation increased by 37% and 8% under the dry and wet 2055 climate scenarios, respectively. Projected changes were also subject to the influence of burn severity and the abundance and proximity of refugia (Figure 5). Shifts toward nonforest vegetation were offset under the moderate burn severity scenario, in which forest recovery declined by 23% but increased by 1% under dry versus wet conditions. Changes were amplified by increased burn severity under dry future conditions, in which forest recovery dropped by 39%; more severe fire did not alter outcomes under wetter climatic conditions.

DISCUSSION

Southwestern ponderosa pine forest landscapes that burned in high-severity fire at the turn of the 21st century are currently occupied by a diverse suite of forest and nonforest plant communities representing divergent successional trajectories. These range from rapid recovery to prefire forest to more enduring conversions to nonforest vegetation dominated by resprouting shrubs and mixtures of native and nonnative grasses. Postfire vegetation composition was most strongly associated with temperature and winter aridity but also shaped by landscape factors, including burn severity, proximity to and abundance of forested refugia, and topography. In particular, shifts toward shrubby and herbaceous vegetation were associated with warmer and more arid postfire climate locations, and models highlight the potential for the expansion of these nonforest vegetation types under future climates. Although the duration of these shifts cannot be known with certainty, they align with longer-term observations and projections of limited postfire tree regeneration and persistent nonforest vegetation across this region (Davis et al., 2019; Rodman et al., 2020; Savage & Mast, 2005). However, models also predicted that the extent of such shifts could be ameliorated by reduced burn severity and increased abundance of forested refugia within burn perimeters, highlighting a role for forest and fire management in mitigating the pace of forest transformation in upcoming decades.

Postfire community composition

Postfire plant assemblages across study burns, drawing from 361 samples of 229 species, exhibited extremely

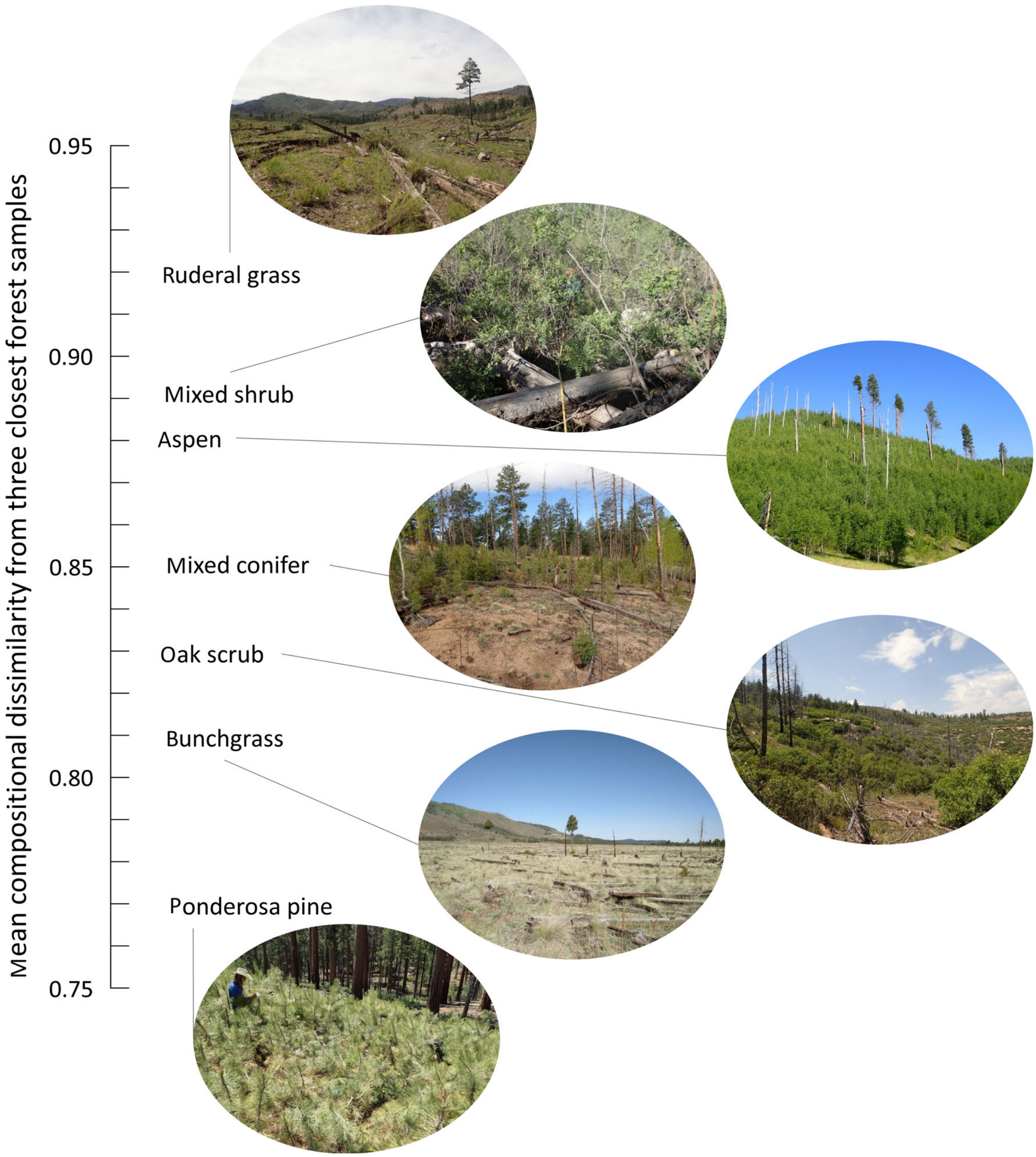

FIGURE 4 Differences between postfire community types and nearby forests, as measured by Sørensen compositional dissimilarity, and photos illustrating each community type.

broad compositional variation, ranging from sites nearly entirely dominated by regeneration of the presumed prefire dominant tree species, ponderosa pine, to diverse and novel assemblages of native and nonnative species of shrubs and herbs. Nonmetric multidimensional scaling (NMS) and *k*-means cluster analysis distinguished seven relatively distinct groupings, which were in turn each associated with underlying environmental variation. Three community types, ponderosa pine, aspen, and mixed conifer, represent recovery by one or more tree species toward a forested condition. These types were generally associated with cooler and more mesic conditions and moderate slopes. Both the ponderosa pine and mixed-conifer types were also associated with landscape locations with relatively high proximity to and abundance of forested refugia (as measured by the DWD metric), highlighting the importance of these postfire landscape components in promoting postfire regeneration by obligate-seeding plant species lacking reproductive adaptations to severe fire (Coop et al., 2019; Downing et al., 2019; Landesmann & Morales, 2018). The ponderosa pine community type occurred at 16% (56/361) of sample sites and was the most similar to adjacent forested refugia, with high cover by seedlings of the

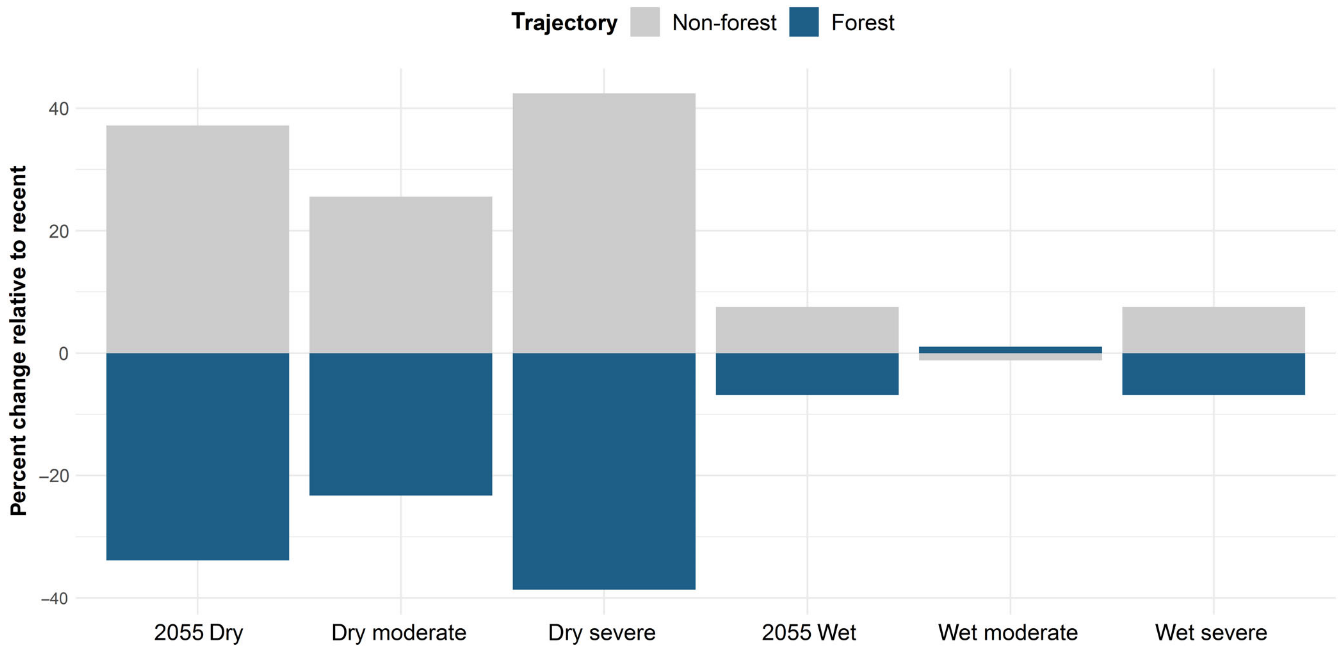

FIGURE 5 Random forest predictions of percentage change relative to recent sampled patterns in forest versus nonforest postfire trajectories under two climate and three burn-severity scenarios, as follows. 2055 dry and 2055 wet represent observed burn-severity patterns under drier and wetter future climates. For each climate scenario, relative to observed burn-severity and refugia pattern, moderate represents a 20% reduction in burn severity and a 20% increase in distance-weighted refugia density (DWD), and severe represents a 20% increase in burn severity and a 20% decrease in DWD.

dominant forest tree species, but also a suite of characteristic understory shrubs and grasses (e.g., *Ceonothus fendleri*, *Mahonia repens*, *Rosa woodsii*, *Muhlenbergia montana*, *Pascopyrum smithii*, and *Poa fendleriana*). In addition to promoting ponderosa pine regeneration, proximity to refugia may have facilitated postfire colonization by forest understory plant species. It is also notable that these samples burned at lower severity than other vegetation types, which may have allowed increased survival of forest understory species. Proximity to refugia and reduced burn severity could also facilitate more rapid recovery of a suite of prefire plant species via increased retention and colonization of fungal mycorrhizal associates (Dove & Hart, 2017).

Mixed-conifer and aspen community types comprised 12% and 25% of the sample (44 and 89 sites, respectively) and occurred where the postfire climate was coolest. Samples from these community types were relatively distinct from intact ponderosa pine forest communities of nearby forested refugia. These community types diverged importantly, however, in proximity to refugia and winter aridity. In mixed-conifer communities, plant cover was generally sparse (averaging only 36%), including cover by regenerating trees (5%, consisting of a mix of ponderosa pine, aspen, and Douglas fir). Despite the high proximity to refugia expected to facilitate conifer regeneration, these samples represented a slower trajectory of forest recovery, likely imparted by moisture-limited germination and establishment associated with high winter aridity (Hankin et al., 2019). In contrast, aspen communities exhibited nearly twice as much total plant cover (70%), with plentiful aspen regeneration (35%) and herbaceous cover, and occurred where postfire winter aridity was lowest and not associated with refugia. Where postfire climate is favorable, the rapid expansion of aspen in the interiors of burns is consistent with regeneration via resprouting in locations that were occupied by stands prior to fire. With small, wind-dispersed seeds that are easily dispersed long distances, aspen can also colonize new sites following fire (Romme et al., 2005), and severe disturbance may catalyze range shifts expected under a warming climate (Nigro et al., 2022). Long term, samples dominated by aspen regeneration may succeed toward conifers or persist as "stable" aspen stands, depending on subsequent disturbance, climate, and other factors (Morris et al., 2019; Mueggler, 1976; Rogers et al., 2014). Though aspen-dominated samples represent a rapid return to forested conditions, there are important functional distinctions between these deciduous broadleaf forest types and the conifer forests they are replacing (e.g., Betts & Ball, 1997; LaMalfa & Ryle, 2008).

Cluster analysis identified four vegetation types indicative of successional trajectories away from forested conditions, referred to here as oak-scrub, mixed-shrub, bunchgrass, and ruderal-grass communities. Severe fire-driven conversion from conifer forest to resprouting shrublands is an emerging phenomenon across a range of temperate forest systems globally (e.g., Airey Lauvaux et al., 2016; Barton & Poulos, 2018; Martín-Alcón & Coll, 2016). These transitions may also be associated with positive fire-vegetation feedback that increases the likelihood or severity of subsequent fire (Landesmann et al., 2020; Tepley et al., 2017) and may thus represent persistent alternate stable states (Falk, 2017) or "landscape traps" (Lindenmayer et al., 2011). In the Jemez Mountains in northern New Mexico, a series of severe fires between 1977 and 2000 generated extensive shrub fields dominated by Gambel oak, which then reburned at high severity in 2011, reinforcing the initial conversion from forest to nonforest (Coop et al., 2016). Older oak patches within this same landscape likely originated prehistorically during severe fires (Guiterman et al., 2018; Roos & Guiterman, 2021). Strong competition by Gambel oak scrub may further constrain tree seedling establishment (Singleton, Thode, Sánchez Meador, & Iniguez, 2021, but see Owen et al., 2017). Once established, it is clear that Gambel oak shrub fields can exhibit remarkable persistence; in fact, the conditions under which ponderosa pine forests might come to reoccupy these settings is largely unknown.

Similarly, little is known about mixed-shrub communities, frequently dominated by New Mexico locust, *Robinia neomexicana*. In contrast to Gambel oak–dominated communities, which are widespread across the southwestern United States, extensive patches of New Mexico locust are not common features on these landscapes. They have historically been considered to represent a multidecadal successional stage in mixed-conifer forests (Hanks & Dick-Peddie, 1974). Understanding their likely duration and dynamics under contemporary and future conditions that constrain succession toward forest communities is an important research direction in this region (Krofcheck et al., 2019).

Two distinct nonwoody postfire vegetation types include bunchgrass communities dominated largely by native perennial graminoids and forbs and ruderal grass communities containing a much larger component of weedy annuals and short-lived perennials, including nonnatives such as cheatgrass. The bunchgrass vegetation type described herein broadly overlaps with a range of native grassland vegetation types common to the plateaus and mountains of the southwestern United States, particularly those including a component of mountain muhly (e.g., Brown, 1994; Dick-Peddie, 1993). In many areas, these communities have been encroached by trees and other woody plants over the last century, which is largely ascribed to the loss of surface fire but may also be associated with climate, land use, and other factors (Coop & Givnish, 2007). Thus, in some cases, fire-driven conversion of ponderosa pine forests with a grassy understory toward bunchgrass communities can represent the restoration of historical conditions and could be a desirable outcome for land management (Hessburg et al., 2015). In contrast, shifts toward weedy and nonnative ruderal grass vegetation may be indicative of a growing threat to native biological diversity and ecosystem functions in dry forest communities (Peeler & Smithwick, 2018).

Patterns of compositional dissimilarity between adjacent forests and the communities described herein illustrate relationships that might not otherwise be apparent. Not surprisingly, regenerating ponderosa pine communities showed the strongest compositional affinity to nearby forests. However, bunchgrass and oak-scrub communities, though lacking tree regeneration, also showed relatively close affinities to forest vegetation—though physiognomically distinct, they harbor many of the same plant species, essentially representing forest communities without trees. Burn severity in these communities was clearly high enough to remove the forest canopy but apparently not enough to overcome the resilience of these fire-adapted understory species assemblages (Downing et al., 2020). In contrast, mixed-shrub and ruderal-grass communities appear to represent more opportunistic assemblages, dominated by off-site, postfire colonizers, including nonnative species. These communities burned at higher severity, which likely eliminated much of the prefire understory at these sites, demonstrating the importance of burn severity in shaping patterns of compositional change beyond thresholds for forest canopy loss (Strand et al., 2019). Similar ruderal vegetation types with abundant New Mexico locust and nonnative grasses, described by Coop et al. (2016), underwent substantial compositional shifts when they burned again during a subsequent wildfire, whereas native oak and grassland communities, once established, showed little change when exposed to fire again. This suggests that these novel communities, comprising new assemblages of native and nonnative species, may be relatively fluid and subject to further change over time.

Influence of climate and landscape context

Measures of postfire climate were closely associated with patterns of community composition, with landscape context and topographic factors showing less influence. Climate exerts a controlling influence on vegetation (Holdridge, 1967), particularly physiognomy (e.g., forest vs. nonforest; Brovkin et al., 1997). Temperature (PC1) was closely linked to shifts in species space, in particular from forested to nonforest communities, highlighting the vulnerability of postfire forest regeneration in this region to increasing temperatures (Davis et al., 2019; Parks et al., 2019; Rodman et al., 2020; Stevens-Rumann et al., 2018).

Winter aridity (PC2) was also strongly correlated with variation in postfire plant community composition across the study area, with high cover by tree regeneration generally occurring where winter precipitation was highest, transitioning to herb-dominated grasslands where winters were more arid. Winter aridity was also a strong predictor of forest recovery versus conversion to nonforest vegetation in random forest models, second only to temperature. In the southwestern United States, winter precipitation is strongly regulated by two atmospheric teleconnections, the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO). Above-average precipitation occurs during the positive, or warm, El Niño phase of ENSO, and below-average precipitation occurs during the negative, or cool, La Niña phase (Ropelewski & Halpert, 1987). These precipitation patterns are generally amplified when ENSO is in the same phase as the PDO (Mantua & Hare, 2002; Newman et al., 2016). During the interval between fire events (2000–2003) and field sampling (2017), ENSO was approximately balanced between positive and negative phases. However, PDO was generally negative, and several years (e.g., 2002, 2006, 2011–2013) were marked by negative phases of both ENSO and PDO (https://www.ncdc.noaa.gov/) and particularly strong regional droughts. Vegetation patterns, in particular the proportional abundance of trajectories of forest recovery versus conversion toward nonforest states, were likely shaped in part by such events. Ponderosa pine regeneration in western North America has been shown to track a climate dipole associated with ENSO, with recent declines brought about by growing aridity across both phases (Littlefield et al., 2020). Increases in the frequency of extreme and protracted ENSO events over the last century (Gergis & Fowler, 2009) attest to the potential for severe and protracted ENSO-modulated swings in precipitation patterns and plant–water balance under climate change in the southwestern United States.

Findings also highlight landscape context and topographic variation as important fine-scale controls on postfire ecosystem trajectories. Tree seed source pattern can control subsequent patterns of postfire tree regeneration (Haire & McGarigal, 2010), and metrics of refugia forest abundance and proximity can be useful predictors of forest recovery (Coop et al., 2019; Downing et al., 2019; Landesmann & Morales, 2018). Refugia configuration may also interact with topography (Peeler & Smithwick, 2020), which can control the ability of key resources such as soil moisture in systems where they are limited. These influences were not just associated with differences between forest and nonforest but also within these classes. Shifts from steeper to gentler slopes were associated with shifts from woody to nonwoody postfire vegetation types, suggestive of root functional trait variation in response to soil texture and depth (Schwinning & Ehleringer, 2001). Compositional variation was also tied to shifts in aspect, and each of the postfire communities described here tended to occur more commonly on NE-facing than SW-facing slopes (which were less likely to burn severely and more likely to serve as refugia that retained forest cover).

Forest recovery versus conversion under future climate and burning scenarios

Random forest models projected decreases in forest recovery and increases in the proportion of postfire landscapes occupied by nonforest communities under future climate (Figure 5). These findings parallel predicted reductions in postfire forest recovery across a range of western North American forest types (Davis et al., 2020; Flatley & Fulé, 2016; Liang et al., 2017; Parks et al., 2019; Rodman et al., 2020; Stralberg et al., 2018). Holding burn severity and refugia patterns constant, as measured across sample sites, postfire forest recovery decreased from current rates by 7% and 34% under two near-future (2055) climate scenarios. These findings appear to be somewhat more conservative than those of other recent studies, though different modeling approaches make direct comparisons difficult. Over a similar time frame, Rodman et al. (2020) projected a decline in the climate suitability of the montane zone from 50% to 12%–19% for ponderosa pine and from 38% to 14%–18% for Douglas fir in the Southern Rocky Mountains. Similarly, between the late 20th and late 21st centuries, Davis et al. (2020) projected shifts in climate suitability from 79% to 39% for ponderosa pine and from 85% to 66% for Douglas fir across the interior western United States.

Area burned at high severity in the southwestern United States has increased markedly in recent decades (Parks & Abatzoglou, 2020; Singleton et al., 2019), and further increases will set the stage for major expansions of nonforest vegetation through both increasing rates of forest loss and decreasing rates of forest recovery. It is important to note that the models presented herein only consider the latter process. Though postfire climate came out as by far the most important determinant of vegetation trajectories across a suite of analyses, random forest models also identified an influence of burn severity and DWD on postfire vegetation trajectories of forest versus nonforest. Even under warmer postfire climates, variation in burn severity and refugia proximity and abundance will still influence ecological outcomes. When burn severity was reduced and the abundance and proximity of refugia elevated, the proportion of nonforest vegetation declined under both dry and wet climate projections. In fact, under a wetter, warmer climate, reduced burn severity led to predictions of slightly greater forest recovery than was actually observed under recent conditions at field sites. These findings point to a role for land management to ameliorate projected declines via interventions that reduce burn severity and sustain refugia through fire events (Allen et al., 2002; Hessburg et al., 2015, 2021; Stevens et al., 2021). Higher burn severity and less refugia led to more shifts toward nonforested states, but only under the dry climate scenario. This implies that dry forest landscapes in the southwestern United States may be particularly vulnerable to compounding effects of increased burn severity and drought (Savage et al., 2013).

Management applications

Variation in postfire plant communities such as described here could inform new and different management strategies and tactics that supplement ongoing efforts to reduce uncharacteristically extreme wildfire behavior and effects. Trends of growing area burned severely in southwestern forests compel renewed focus on postfire landscape management. Increasing rates of ecological change associated with changing disturbance regimes and climate may require a shift in management paradigms, and altered postfire landscapes can provide opportunities for novel approaches that accommodate a changing environment. Ecologically informed postfire landscape management recognizes a fundamental distinction between areas retaining forest cover versus areas where forest cover was removed by fire, which call for distinct approaches (Stevens et al., 2021).

Differences in vegetation trajectories within high-severity patches could inform the management under the RAD framework, as decisions around resisting, accepting, or directing change will necessarily depend in part on the nature of change (Crausbay et al., 2022). An example decision framework illustrating how variation in postfire community composition might lead to different management objectives is presented in Table 5. Resisting change includes promoting recovery toward predisturbance forest conditions and will in many cases be highly desirable and most effectively achieved where postfire regeneration by prefire dominant tree species is abundant. In these settings, management interventions might focus on reducing the risk of severe reburning brought about by heavy fuels via targeted fuels reductions or prescribed burning under favorable conditions (Stevens et al., 2021). Accepting change allows for disturbance-catalyzed ecological shifts to continue to unfold and persist. Where shifts from ponderosa pine toward alternate forest types will still support a subset of key ecological and social values, they may therefore be acceptable to managers and society. Conversion from conifer to aspen forest might even be desirable where it results in a mosaic of patches of reduced landscape flammability (Stralberg et al., 2018), and increased albedo could compensate for changes in ecosystem carbon balance (Mack et al., 2021). Conversion from forest to native grassland or oak scrub might also be appropriate in some areas—these systems are expected to be highly resilient to reburning and support important ecosystem functions and services, for example, big-game habitat. Directing change implies management interventions where recovery to predisturbance conditions is not expected (e.g., due to warming conditions and lost seed sources), and the system can be actively pushed toward particular alternate outcomes at the expense of others. The mixed-shrub and ruderal-grass communities described here, including substantial components of nonnative and weedy species, might provide opportunities to direct change, for example, by promoting ecosystem transitions toward alternate tree species favored under future climate (e.g., assisted migration of low-elevation species or genotypes), though decisions such as these should be made within strong collaborative governance, particularly on public lands.

For southwestern ponderosa pine and dry mixed-conifer forests vulnerable to high-severity fire, a more fundamental resistance strategy within the RAD framework would include limiting the extent of severe fire. Findings suggest that reducing burn severity and increasing the proportion of forested refugia persisting in postfire landscapes will be useful in mitigating projected increases in fire-driven conversion from forest to nonforest conditions under future climates. A strong scientific foundation supports a suite of management interventions to accomplish these objectives, including mechanical fuels reductions treatments, but also the use of prescribed fire and managed fire occurring under moderate burning conditions (Agee & Skinner, 2005; Allen et al., 2002; Prichard et al., 2021; Singleton, Thode, Sánchez Meador, Iniguez, & Stevens, 2021). Such treatments might be designed to generate fine-scale landscape heterogeneity that enhances both resistance and resilience to subsequent fire (Churchill et al., 2013; Hessburg et al., 2015; Stephens et al., 2021) or with an eye toward future refugia formation when the next fire burns. Treatments should facilitate the restoration of fire regimes that best promote forest persistence (Walker et al., 2018), for example, by incorporating

TABLE 5 Example postfire decision-making framework based on differences in community types.

Community type	Strategy	Tactic	Rationale
Aspen	Accept	No management	Leave to increase mosaics of stands with reduced flammability, add diversity, and increase albedo.
Ponderosa pine	Resis	Fuel reduction, Rx fire	Sustain recovery, lower reburning risk by reducing heavy fuels, ladder fuels; thin dense patches.
Mixed conifer	Resist/direct	Augment with PIPO plantings	Increase resilience by increasing tree species diversity, adding more drought-/heat-tolerant species.
Mixed shrub	Resist/direct	Reforest with PIPO	Cool, mesic settings might support future PIPO, shrub cover may facilitate tree seedling establishment.
Oak scrub	Accept	No management	Allow transition to resilient native vegetation type.
Bunchgrass	Accept	Rx fire	Support transition to native vegetation type adapted to fire, drought.
Ruderal grass	Direct	Reforest with lower elevation tree genotypes, species	Promote recovery of forest/woodland values, shift dominance toward native species adapted to warm, dry climate.

Note: The strategic decision to resist, accept, or direct change might be informed by compositional variation, with different intervention tactics applied based on social-ecological values and opportunities presented within an alreadyaltered landscape.
Abbreviations: PIPO, *Pinus ponderosa*; Rx, prescribed.

newly developed principles of pyrosilviculture (North et al., 2021). However, the long-term effectiveness of such treatments under future climate change is not well understood. Indeed, assessing the durability of resistance tactics represents a pressing scientific need across a wide range of systems vulnerable to rapid ecological transformation (Crausbay et al., 2022). Where future climate exceeds species' bioclimate niches, substantial investment to sustain forests at increasingly marginal low-elevation sites may be doomed to fail. Instead, restoration efforts could be prioritized for cooler and wetter sites, where future climate is most likely to continue to support key species.

Conclusions and future research directions

The combination of increasing area burned severely in the southwestern United States and climate warming is expected to drive major changes in forested ecosystems, compelling new lines of scientific inquiry and shifts in management paradigms. Here, I describe postfire vegetation types from a broad sample of 14- to 17-year-old burns in this region, assess their relationships to underlying environmental variation, and explore how they might inform management interventions. The characterization presented herein is still relatively limited, and the development of a more intensive and extensive network of both pre- and postfire samples would facilitate the growth in our understanding of these systems that will be needed to match the scale of upcoming challenges. As an alternative to developing new long-term plot networks, data collection from already existing, extensive, and spatially representative samples, such as the US Forest Inventory and Analysis (FIA) plot network, might be enhanced and made more broadly accessible to researchers (Woolman et al., 2022). Repeated sampling will be necessary to gain a more complete picture of the dynamics of different postfire community types, particularly under future disturbances and climate change. Although the ultimate duration of fire-induced vegetation changes under a changing climate cannot be known, multiple lines of evidence suggest that the postfire community types described here may persist for long periods. To return to an earlier example, fire-generated Gambel oak patches have been shown to have persisted for centuries despite wide variation in fire regimes during that period (Roos & Guiterman, 2021). Thus, under contemporary burning regimes, we may anticipate that such community types will come to occupy a far greater proportion of the landscape than what has been observed historically.

Management of postfire landscapes would benefit from a stronger scientific foundation, necessitating working within a strong research-management coproduction framework (Meadow et al., 2015). For example, postfire management interventions might be replicated at different sites and along environmental gradients in order to gain insight into likely effectiveness under ongoing climate change. New management approaches, particularly those intended to direct change, will also require broad stakeholder participation beyond the research and management community. A growing body of observations, evidence, and models all indicate that retaining and recovering vulnerable southwestern forests—or accepting or directing shifts toward alternate vegetation types—will require experimentation and the social license for management activities to sometimes fail but in the process improve our understanding of valued ecosystems in an era of rapid change.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Miller et al., 2021) are available from the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2021-0003.

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SUPPORTING INFORMATION

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

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