Repeated Fire and Extended Drought Influence Forest Resilience in Arizona Sky Islands

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Abstract

Background

Wildfire size, severity, and frequency have been increasing in the southwestern US since the mid-1980s as a direct result of anthropogenic climate change and land management practices. Significantly, high severity burn area in Arizona and New Mexico has been increasing at a rate of about 1,000 ha per year since 1985. More frequent, higher severity wildfire, combined with two decades of drought, threatens the persistence, regeneration, and resilience of conifer trees in the dry pine forests of Southern Arizona's sky islands. Failure of conifers to recover may result in ecosystem reorganization as forested areas are replaced by oak or shrub woodlands. Here we report on radial tree growth, conifer regeneration, and community composition in the Santa Catalina Mountains following a series of wildfires in 2002, 2003 and 2020.

Results

In our tree growth analysis, we found a striking resilience to both drought and wildfire in three dominant conifers. Ponderosa pines (*Pinus ponderosa*) and Southwestern white pines (*Pinus strobiformis*) that survived both high and low severity fire showed non-significant positive growth trajectories following wildfire exposure in 2003. Douglas-fir (*Pseudotsuga menziesii*) growth was more climate-dependent and less fire-dependent than Pine growth. For areas that burned only in the earlier fires, conifer regeneration over the 17–18-year interval was found in the majority of burned plots, although density varied greatly. Community composition analysis in these areas indicated some loss of conifer overstory dominance in areas burned at high severity; in general, these were replaced mainly by Aspen (*Populus tremuloides*) in higher elevation stands, not deciduous or evergreen oaks.

Conclusions

Early post fire vegetation responses following the 2020 fire event were highly variable, in contrast to longer-term successional processes seen 17–18 years after the initial fire events. This wide variability one-year post-fire may be seen as a starting point for future trajectories of change in Southwestern forests under the influence of changing climate and fire regimes.

Background

Wildfire size, severity, and frequency have increased in the western U.S. since 1980, with area burned nearly doubling since 1984 (Westerling et al 2006, NIFC 2023). In Arizona and New Mexico between 1984 and 2015, total area burned increased at a rate of 6,360 ha per year, while area burned at high severity increased at a rate of 1,009 ha per year (Singleton et al 2019). This increase is correlated highly with decreasing precipitation, increasing temperatures, and increasing vapor pressure deficit, which in turn are

direct expressions of anthropogenic climate change (Littell et al 2009, Abatzoglou & Williams 2016, Meuller et al 2020, IPCC 2021). Currently, the southwestern US is experiencing the deepest and most persistent drought conditions in the past 1,200 years, as human-caused climate change has exacerbated drought conditions (Williams et al 2020).

As fire severity increases, areas that historically supported low-mixed severity fire regimes are now experiencing fires with a higher proportion of fire area burning at high severity (Abatzoglou et al 2017, Singleton et al 2021, Remy et al 2021). In the Southwest, pine-oak and dry conifer forests are adapted to low severity fire regimes, with relatively short return intervals (5 to 10 years) and evolutionary strategies such as thick bark and self-pruning limbs that prioritize survival over reproduction (Baisan et al 1996, Agee 1998, Stoddard et al 2021, Keeley & Pausas 2022). As high severity fire comprises an increasing proportion of burned areas, the natural fire resilience of conifers is tested (Haffey et al 2018). In addition, growing wildfire size increases the likelihood of overlapping burn scars from successive fires, leading to a higher probability of an area re-burning at uncharacteristically high frequency or severity in a relatively short time period (Thompson et al 2007, Holden et al 2010, Coop et al 2016). High severity reburns can overcome the natural resilience of even fire-adapted species, and result in recovery failure between fires (Enright et al 2015, Stevens-Remann et al 2016, Fairman et al 2019, Falk et al 2022, Seidl & Turner 2022).

Recovery from high severity fire proceeds differently for species with varying reproductive or adaptive traits (Keeley & Pausas 2022). For species that resprout basally, such as oaks, some individuals can survive topkill and resprout with their original root system intact, often by deploying non-structural carbohydrates (Hammett et al 2017). In most conifers of southern Arizona, reproduction is usually by seed (Williams 2009), a recovery strategy more dependent on post fire climate and ecosystem conditions. Regeneration failure may be due to large patches of high severity areas where there are no nearby seed sources (Boag et al 2020), unfavorable post fire climate conditions caused either by climate change or the fire itself (Dodson & Root 2013, Davis et al 2019, Stevens-Rumman & Morgan 2019, Stewart et al 2021), changes to soil organic matter (Certini et al 2011, Dove et al 2020), or competition from faster-growing species, especially shrubs (Tepley et al 2017). Recovery failure may lead to ecosystem reorganization (Fig. 1), in which forested areas convert to shrub communities or oak woodlands (Guiterman et al 2018, Poulos et al 2021). Depending on fire severity and other factors such as drought, reburning may reinforce and accelerate these conversions (Coop et al 2016, van Mantgem et al 2018), or alternatively maintain dynamic stability in the existing community (Peterson et al 1994, Thomas & Waring 2015).

These processes of resistance to disturbance, recovery, and reorganization following recovery failure are unified in an ecological process model of forest resilience (Falk et al. 2022, Seidl & Turner 2022). We apply this model to evaluate observed ecological responses to fire, and to provide structure for understanding the inherent noise in the early stages of post-fire recovery. Resistance refers to outcomes in which individual trees survive disturbance; in areas where this is a prevailing response, overall conifer mortality following fire was low, and both short- and long-term species composition will be similar to pre-fire conditions (although resistance can also be expressed as survivorship of individual trees within an

area of higher mortality). Recovery is a population-level recruitment response where post fire conifer mortality is high; in these areas, short-term species composition may diverge from the pre-fire community (e.g., shrub or resprouting oak dominance in areas with pre-fire conifer dominance). Over post-fire successional time however, conifer regeneration is sufficient to re-establish pre-fire species composition. Reorganization occurs if both resistance and recovery fail and represents a community-level shift in species or plant functional group composition (for example, from conifers to a community dominated by oaks, shrubs, or grasses). Such community reorganization may be either persistent (type conversion), or transient (Falk et al. 2022), such as post-fire successional dominance by trembling aspen (*Populus tremuloides* Michx.), New Mexican locust (*Robinia neomexicana* A. Gray), or bracken fern (*Pteridium aquilinum* (L.) Kuhn).

We use two sets of fires in the Santa Catalina mountains (SCM) and Rincon mountains (RM) in the Sky Islands bioregion in southeastern Arizona as a case study to examine these ideas. In the SCM, the Bullock Fire burned in 2002 (Fig. 2) and was at the time the largest documented wildfire in SCM history at 12,368 ha, followed in 2003 by the even larger Aspen Fire, which covered 34,297 ha. In 2020, the Bighorn Fire burned a total area of 48,557 ha, larger than the areas of the Bullock and Aspen Fires combined. Because the Bullock and Aspen Fires burned in successive years and had minimal spatial overlap, for this analysis we treat them as a single fire event (Bullock-Aspen). In the RM, the

Helen's 2 Fire burned 1,456 ha in 2003, followed by the 400-ha Deer Head Fire in 2014. We sampled plots in both mountain ranges in the summer of 2021 to address the following questions: 1) For conifer trees that survived Bullock-Aspen in the SCM, how did fire severity and drought influence annual tree growth rates over the ensuing 17–18 years? This question focuses on the persistence portion of the resilience model. 2) Is conifer (obligate seeder) regeneration occurring in the mixed conifer and ponderosa pine evergreen oak ecosystem types following Bullock-Aspen in the SCM, and Helen's 2-Deer Head in the RM and to what extent? How does fire severity and extended drought impact the recovery we see? This question focuses on the recovery portion of the model. 3) How have vegetation communities shifted in both the SCM and the RM since Bullock-Aspen and Helen's 2-Deer Head, and is there evidence of persistent ecosystem conversion? And 4) How did the Bighorn Fire influence initial post-fire ecological trajectories in the SCM? Can we use our first-year post-fire vegetation data as a starting point to examine future possible vegetation trajectories?

This last question set creates an opportunity to look at the data as a chronosequence, or a space for time substitution. By recording vegetation health and mortality one year after the Bighorn Fire we can reconstruct what the forest may have looked like immediately following the earlier Bullock-Aspen Fires in the SCM. This perspective allows us to infer a potential starting point for post-Bullock-Aspen recovery, and highlights the importance of long-term monitoring to fully capture ecological recovery. This study focuses primarily on the SCM, where we sampled the majority of our plots. Additional plots in the adjacent RM were used to fill in gaps in fire severity and ecosystem type combinations lacking in the SCM.

Methods

Study Area

Our study sites were located in the Santa Catalina Mountains (SCM) (32.4387° N, 110.7598° W) and the adjacent Rincon Mountains (RM) (32.2198° N, 110.5434° W) in southeastern Arizona, USA, 50 kilometers north and east of the city of Tucson respectively. Both mountain ranges are part of the Madrean Archipelago ("Sky Islands") bioregion between the Sierra Madre in northern Mexico to the Colorado Plateau in the southwestern United States (Brusca et al 2013). Vegetation in the Sky Island ranges is controlled strongly by elevation, aspect, and topographic complexity, creating unusually high alpha and beta diversity over relatively short horizontal distances, which have made them a model system for biogeography and climate change ecology. Both the SCM and RM extend from Sonoran Desert at the base (~ 700 m AMSL) to mixed conifer forests above 2500 m (Whittaker & Niering 1965, Whittaker & Niering 1975, DeBano et al 1995, Brusca et al 2013).

Our study sites were distributed across two different ecosystem types (ecosystem response units (ERU[1])): Ponderosa Pine Evergreen Oak (PPEO), and Mixed Conifer (MC). The PPEO ecosystem ranges from about 2000 m to 2500 m depending on aspect and is dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson[2]), Arizona Pine (*Pinus arizonica* Engelm.), Southwestern white pine (*Pinus strobiformis* Engelm.), emory oak (*Quercus emoryi* Torr.), and silverleaf oak (*Quercus hypoleucoides* A. Camus). The MC ecosystem ranges from about 2500 m to 2700 m and is dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), Southwestern white pine, gambel oak (*Quercus gambelii* Nutt.), and ponderosa pine. Following wildfire, New Mexico locust, Fendler's ceanothus (*Ceanothus fendleri* A. Gray), and bracken fern may be abundant in both ecosystems. In the MC, aspen may be abundant following high severity wildfire. For the purposes of this paper, we treat ponderosa pine and its subspecies Arizona pine as one ecospecies, henceforth ponderosa pine (Kral 1836).

The fire regime in the PPEO is historically low and mixed severity with typical return intervals of 5–10 years (Baisan et al 1996, Iniguez et al 2008, Farris et al 2013). This regime historically regulated conifer growth in both the SCM and the RM, with episodes of tree recruitment in longer fire intervals and population thinning in shorter intervals (Munier et al 2014, Iniguez et al 2015). Ponderosa pine, the dominant conifer in PPEO, is highly fire adapted with very thick bark and self-pruning lower limbs (Keeley 2012, Pausas 2015). In the MC, Douglas-fir and white fir are fire-vulnerable as seedlings, but then develop to become adequately fire adapted as adults, with thick bark and a moderate ability to self-prune lower limbs (Stevens et al 2020). All oak species (*Quercus* spp.) in our study area can resprout basally following fire (Barton 2002). Resprouting is also seen following wildfire in Fendler's ceanothus (Huffman & Moore 2004) and aspen (Alexander et al 1989).

The SCM have experienced three large fires since 2000 (Fig. 2). The Bullock Fire was ignited by lightning on 12 May 2002, and was contained 10 June, burning 12,368 ha[3] (Fig. 2A). Within the fire perimeter, 49%

burned at low, 38% burned at moderate, and 11% burned at high severity. The following year, the Aspen Fire burned 34,297 ha. It was ignited by lightning on 17 June 2003, and was contained 15 July; 33% of the Aspen fire burned at low severity, while 40% and 27% burned at moderate and high severity respectively (Fig. 2A). In 2020, the Bighorn Fire was ignited by lightning on 5 June and was contained on 23 July. The Bighorn burned 48,557 ha, of which 53%, 39%, and 8% burned at low, moderate, and high severity respectively (Fig. 2B).

Modern fuel loads in the SCM are influenced heavily by the historic federal policy of strict fire exclusion (Pyne 1997). Beginning in 1900, the previously widespread wildfire occurrence in the SCM declined dramatically and the time between fires lengthened, a stark contrast with the frequent, widespread fires of the previous centuries (Baisan et al 1996). By the time the Bullock Fire ignited, it had been 75 years since the last moderately widespread fire in the high elevations of the SCM.

The RM, a large portion of which is managed by the US National Park Service, has been managed more for wildland fire use with less complete suppression. As a consequence, fire exclusion in the RM was less severe than the SCM, although wildfires in the 20th century were nonetheless reduced in size and frequency compared to previous centuries; just two fires between 1943 and 1988 accounted for over 90% (4,782 ha) of burned area in the RM during this period (Parker 2006, Farris et al 2010). However, unlike in the SCM, fire activity increased before 2000 with the Rincon Fire burning 5,360 ha in 1994, less than a decade before our first fire of interest (Helen's 2, 2003). However, only two of seven of our plots sampled in 2021 overlap with the 1994 Rincon Fire [4]. In June 2003, the Helen's 2 Fire burned 1,456 ha; 18% burned at high severity, 42% burned at moderate severity, and 46% burned at low severity. In July 2014, the Deer Head Fire burned roughly 400 ha, almost exclusively at low severity (Fig. 2D).

Henceforth, we refer to the fires in two distinct groups: initial fire event and second fire event. In the SCM, the initial fire group includes the Bullock (2002) and Aspen (2003) Fires, treated as a single event for analytical purposes; the second fire was the Bighorn (2020). In the RM, the initial fire group includes the Helen's 2 (2003) and Deer Head (2014) Fire; in our study plots there is no fire in the second set in the RM. We included the Deer Head in the initial fire event because it had seven years of recovery time prior to sampling.

Plot Selection

To evaluate forest responses to a sequence of fires, we compiled an inventory of over 1000 prior study plots in the SCM where ecological data had been recorded by other researchers. From these, we prioritized plots in our target ERUs[5] where data comparable to our study design were most robust, including seven plots with recent extensive ecohydrological data (Youberg et al 2021). To maintain plot dispersion, we selected plots that were at least 200 m from the nearest adjacent plot. In the RM, our plots had not been sampled previously. We stratified our final plot selection to include representation of the two target ERUs (PPEO, and MC) across the range of fire severity from the two fire events (Bullock-Aspen and Bighorn Fires in SCM, and Helen's 2-Deer Head in the RM). To balance our sampling matrix for each ERU across

severity classes, we supplemented existing plots with randomly selected locations within ERU-fire severity combinations.

Fire severity history for each plot in the SCM and RM was calculated using Soil Burn Severity (SBS) derived from dNBR layers[6]. Because the Aspen and Bullock Fires have almost no overlap in their burn scars and burned in successive years, we treat them as a single fire event for the purposes of medium-term (decadal) post-fire response. For each fire burn severity layer in the SCM (Bullock-Aspen and Bighorn) we calculated mean fire severity using the zonal statistics tool that assigned the average soil burn severity of the surrounding 3x3 ([90 m]^2) neighborhood to each 30-m pixel for each fire event. This was done to represent fire severity more accurately at the plot scale, and to limit the inherent errors in pixel-scale burn severity mapping (Farris et al 2010). In the RM, we choose plots located in homogeneous burn severity areas, so that the average severity of the surrounding 3x3 pixel neighborhood was the same as the pixel of interest.

In both the SCM and the RM, we created categorical values for our plot stratification matrix using these averaged SBS values. In a typical SBS classification, a 0 value indicates the pixel was outside the burn perimeter, 1 is inside the perimeter but unburned, 2 is low severity, 3 is moderate, and 4 is high. Since we were using a 9-point average, we classified soil burn severity values under 1.5 as unburned, 1.6 to 3.0 as low, and ≥ 3.1 as high. We coded each plot by the sequence of fire severity exposure in initial fire and second fire events.

Field Methods

From May to September 2021, we sampled a total of 43 vegetation plots in the SCM and six in the RM (Fig. 2C, Supplemental Table S-1). Each plot measured 50 m by 20 m (0.1 ha) and was oriented perpendicularly to the local slope. In the SCM, the bottom left and right corners were marked with tagged rebars, and 1–3 living trees or intact stumps were tagged within the plot. In the RM, no permanent tagging was done at the request of the National Park Service. If the plot did not align with the mapped ERU, it was corrected according to US Forest Service Version 5 ERU Key for the SCM[7]. A significant number of the plots were mapped incorrectly and were corrected in the field, which resulted in unequal sample sizes between the ERUs; ERU and fire severity were reclassified in the field if significant discrepancies were observed (for example, stands classified as high severity in 2003 but dominated in 2021 by large old living trees). We recorded percent slope using a handheld clinometer, and aspect in degrees true.

In all plots, seedlings (defined here as trees under 1m tall) were counted and identified to species within three 2-meter belt transects. All live and dead trees over 1 m tall and ≥ 5 cm at diameter at breast height (dbh) were recorded, along with their species and diameter. We calculated total live and dead basal area (m^2) for each plot (Supplemental Table S-2). We measured the total height and canopy base height of all live trees to the nearest 0.1 m using a laser hypsometer. Woody shrubs, trees under 5 cm dbh but over 1 m tall, resprouting oaks, perennial forbs, and succulents (*Agave* spp., *Yucca* spp., *Opuntia* spp.) were counted as understory. We measured the canopy dimension of understory plants and shrub patches

across their major and minor axis to the nearest cm from above; overlapping canopies of a species were combined into one measurement (Minor et al 2017). Three plots were sampled in smaller plots (25 x 10 m) due to extreme plot steepness or impassable vegetation conditions; the resulting data were rescaled to be consistent with other plot measurements.

To quantify tree growth following fire exposure, we collected increment cores from 59 living trees in or adjacent to 19 of the SCM plots. We focused our sampling on ponderosa pine, Douglas-fir, and Southwestern white pine, and collected cores from each species in plots that were unburned in the 2020 Bighorn Fire for each fire severity class in the 2003 Aspen Fire (unburned, low, and high), using 5.15 mm increment borers to collect the cores between 40 and 60 cm above the ground surface.

Laboratory and Data Analysis

We mounted and sanded the increment cores according to standard dendrochronological methods (Speer 2010). We measured individual growth rings using a Velmex sliding electromechanical stage accurate to 0.01 mm. Ring widths were crossdated against the Palmer Drought Severity Index[8] (PDSI) for the SCM (Fig. 3A) and recorded in Tellervo software[9]. PDSI incorporates multiple climate variables that influence plant growth, including average and maximum monthly temperatures, vapor pressure deficit, and precipitation (Cook et al 2004). We confirmed our crossdating using the *corr.rwl.seg* function in the *dplR* package in R (Bunn et al 2023). Inside bark diameter (cm) was calculated for each tree (Laughlin et al 2011), and raw ring width values (mm) were subtracted from this using *bai.out* function in the *dplR* package in R to calculate annual radial growth in mm^2.

To assess controls on post-drought and fire tree growth, we used the *lmer* function in the *lme4* package (Bates et al 2015) in R to model mean annual basal area increment (BAI, mm^2) for 1960–2020 as a function of the following fixed effects: PDSI, fire severity, and time since fire, with year as a random effect to account for year-to-year variation in climate. Individual trees were modeled as a random effect, with each tree allowed to have a varying intercept.

Fire severity for each tree in the model was extracted from an RBR (relativized burn ratio) burn severity layer (Parks et al 2014). To avoid rank deficiency in the model, and to take into consideration residual fire effects on growth from previous fires, we modeled fire severity as a hyperbolically decaying variable, with fire severity discounted by time since the previous event. For the $(i,j)th$ pixel, the time-discounted fire severity is:

$$(S_f / T_f)_{ij}$$

where S_f is the RBR for the fth fire, and T_f is time in years since that fire. As there were no widespread wildfires in the high elevations of the SCM since at least 1927, the T_f for all trees starts at 33 years in 1960 as a conservative measure.

We considered temporal autocorrelation by creating a second model using the *lme* function in R package *nlme* (Pinheiro et al 2023), using the same fixed effects and no random effects, but allowing each tree to have a varying slope with respect to time (Fule et al 2022). In the above *lmer* model, the slopes of each tree must be the same, which assumes that the relationship between the effect and the explanatory variables are the same between groups (groups in this case being individual trees). If the slope is allowed to vary, as in the *lme* model, then this relationship is also allowed to vary between groups, thereby accounting for autocorrelation. We then compared these models using difference in Akaike Information Criterion (AIC) (Johnson & Omland 2004). The resulting models were similar overall, with only the ponderosa pine model showing improved performance of the *lmer* model based on AIC results. As a result, we chose the *lmer* model, which includes random effects but no specific autocorrelation term.

We calculated marginal R^2, which quantifies the amount of variation explained by fixed effects, and conditional R^2, which calculates the variation explained by fixed and random effects (Nakagawa & Schielzeth 2012), in R version 4.2.2 using the *rsquarredGLMM* function in the *MuMIn* package (Barton 2023). We also calculated cumulative growth for an 18-year pre-fire (1983–2001) and post-fire (2002–2020) period by severity class for each species by summing annual average BAI over the given time periods.

To determine overall conifer recovery that had occurred following the initial fire event but prior to the second fire event we calculated an inferred conifer recruitment variable, C_{rec}, from vegetation data in the SCM and RM. C_{rec} was calculated at the plot level as a sum of conifer seedlings, understory conifers, and conifer trees. C_{rec} is an inferred variable because it includes both living and dead trees under 15 cm dbh (inferred to have regenerated post initial fire event, or only shortly before), as well as young trees over 15 cm dbh in areas where initial fire event mortality was 100%. Each tree was multiplied by the natural log of its height, in order to conservatively weight taller, more established trees.

We fit a linear model to C_{rec} to evaluate the influence of slope, distance to a seed source, burn severity, and bracken fern dominance. We tested for significant differences between C_{rec} values for SCM and RM plots of the same ERU and severity class to determine if there was difference in recovery between the mountain ranges and found none. Specifying ERU as a random effect did not significantly improve model fit based on difference in AIC, so all C_{rec} data were modeled together, regardless of ERU and mountain range.

To assess community-level change, we calculated an importance value (IV) for each species in each plot. For overstory trees, this was the sum of relative density, relative height, and relative basal area, for a total possible score of 300. For understory plants, we summed relative cover and relative height for a total possible score of 200. From these importance values, we created chord diagrams using the *circlize* package in R (Gu 2014). Chord diagrams are often used to show transitions from one state to another; in this case we used chord diagrams to visualize the contributions to overall importance values from each severity class (Guiterman et al 2022). Understory and overstory importance values were aggregated by plant functional group. These functional groups for the overstory importance values are obligate seeder

conifers (labeled as Conifers), resprouting trees (all oaks, and alligator juniper *(Juniperus deppeana* Steud.), labelled as Oaks) and non-oak angiosperms (aspen, all maples*)*. For the understory, functional groups were obligate seeder conifers, resprouting trees, bracken ferns, woody shrubs, and New Mexico locust. From plots in the SCM, only plots that were unburned in the Bighorn Fire were included, to indicate community transitions from a single fire. To examine general forest dynamics following successive wildfires, we averaged stand density, basal area, percent dead density, and percent dead basal area for all plots in the SCM and RM (Supplement Table 4).

Results

Our results record individual persistence and mortality, population recovery, and community reorganization following two successive fires in the SCM and RM. Data for tree growth responses were only from the SCM; data for conifer recruitment and community reorganization results comes from both mountain ranges. Additional results can be found in the Supplemental Information.

Individual tree growth response and persistence

Growth variation (mean annual basal area increment in mm^2, BAI) in Southwestern white pine (Fig. 3b) and Douglas-fire (Fig. 3d) did not vary initially among severity classes until two successive drought episodes in 2006 and 2011, after which severity classes diverged. In ponderosa pine (Fig. 3c), separation among severity classes occurred later, in 2015. Following the respective divergence points, growth in both pine species in burned plots exceeded growth in unburned plots; post-divergence growth in Douglas-fire was lowest in low-severity plots.

Our modeling results show that annual growth in Southwestern white pine during the overall modeling period (1960–2020) was negatively affected by fire severity and time since fire (Table 1). However, fixed effects alone explained little of the overall variation (marginal R^2 = 0.02, conditional R^2 = 0.23). Ponderosa pine growth was not explained by fire severity, time since fire, or PDSI in our model. Douglas-fir growth was strongly and significantly positively correlated with PDSI (the strongest relationship of any species in the study), and to a lesser extent by time since fire, with no effect of fire severity. A low marginal R^2 (0.03) indicates Douglas-fir BAI is not highly explained by fixed effects in the model (conditional R^2 = 0.50).

Cumulative growth varied by species and severity class (Table 2). Burned Southwestern white pine growth increased post-fire compared to the pre-fire period, despite greater overall drought conditions; growth increased most in areas that experienced fire in 2002-3 compared to unburned areas. Similarly, Ponderosa pine growth increased most in low severity areas, although growth in high severity areas declined. For Douglas-fir, growth in burned areas declined in high and low severity areas, while growth in unburned areas increased.

Conifer Recruitment

Following the initial fire event, post-fire recruitment was present in 70% of high severity plots, 66% of low severity plots and 100% of unburned plots. However, recruitment density varied from only a few seedlings to dense stands of young trees. Mean C_{rec} was 91% higher in unburned PPEO areas than in MC, and 225% higher in high severity PPEO areas over MC; recruitment was similar between ERUs in low severity areas (Fig. 4a), although none of these differences were statistically significant due to high variability and low sample size ($p = 0.64$, 0.87, & 0.13 for unburned, low, and high severity ERU differences respectively). Median C_{rec} was often substantially lower than mean $C_{rec,}$ indicating large positive outliers in recruitment in low and unburned areas.

In the PPEO, conifer recruitment consisted entirely of ponderosa pine and Southwestern white pine, with the majority being ponderosa pine; at most, Southwestern white pine constituted 12% of recruitment at a single plot (Fig. 4b). In the MC, nearly all recruitment in high severity plots was ponderosa pine, whereas in low-severity and unburned plots recruitment was balanced among ponderosa pine, Douglas-fir and white fir (Fig. 4c). In our model, C_{rec} was affected negatively by slope ($F = 4.66_{1, 39,} p = 0.05$); neither fire severity in the initial fire event nor distance to a seed source were statistically significant (Supplemental Table S-4).

Almost all measured recruitment following the initial fire event experienced complete mortality in areas that burned in high severity in the second fire event, with some exceptions in the PPEO (Fig. 4d). Mean survivorship in areas that burned at low severity in the second fire was 29% in MC, and 31% in PPEO although these differences were not statistically significant. ($p = 0.21$). All recruits survived in areas that were unburned in the second event. We did not find first-year seedlings in any of plots during our 2021 field work, most likely due to the failure of the summer monsoon in 2020 (see Discussion).

Community Reorganization

In the Ponderosa Pine-Evergreen Oak (PPEO) ERU, high severity plots had slightly less dominance of overstory conifers than unburned or low severity plots, which were roughly equal (Fig. 5a). Low severity plots had higher proportions of overstory oaks and angiosperms, although overstory angiosperms comprised only a small proportion of total overstory importance values. High severity plots had greater shrub dominance than low or unburned plots; locust was dominant only in high severity areas. Most understory conifers were found in low severity sites. Understory oaks were more dominant in unburned areas. Ferns were approximately even between low and unburned plots; understory angiosperms were similar in low and high severity plots.

In the Mixed Conifer (MC) ERU, conifers constituted 83–91% of overstory importance values in low and unburned plots, but only 60% in high severity plots (Fig. 5b). Overstory oaks were not dominant in any severity class in MC; other overstory angiosperms (mostly aspen) accounted for 38% of the importance values in high severity plots (Table 3). Shrub dominance was split evenly among severity classes. High severity plots had a higher proportion of understory oaks, whereas low severity plots had higher proportions of ferns. Locust was dominant only in high severity plots and absent from low severity areas.

Vegetation Response to Sequential Fires

Stand density and basal area of all tree species varied following the second fire event (Supplemental Table S-2). In PPEO, density (33 stems/ha) and basal area (0.7 m^2/ha) were lowest in areas that burned at high severity in both fires (HH). For areas that burned at high severity only in the earlier event (HL or HU), stand density (mean = 84 stems/ha) and basal area (mean = 7.2 m^2/ha) were slightly higher, indicating recovery. In areas that were unburned on both events (UU), or burned at low severity in one or both fires (UL, LU, LL), stand density (mean = 252 stems/ha) and basal area (mean = 24.0 m^2/ha) were higher than other severity sequences.

Forest responses were slightly different in the MC. Stand density was lowest in areas that burned at high severity in the second fire event (UH, LH, HH: mean = 38 stems/ha), and also in areas that burned at high severity in the first fire but low in the second (HL, 40 stems/ha). Stand density was similar and substantially higher (mean = 410 stems/ha) in all other fire exposure combinations (LL, UL, HU, LU, UU). Live basal area followed similar patterns, lowest (mean = 9.2 m^2/ha) in areas burned at high severity in the more recent fire (HH, LH, UH), and also in areas with high severity in the initial fire and then lower in the subsequent event (HL, HU; mean = 6.6 m^2/ha). Basal area was highest (mean = 38.5 m^2/ha) in low and unburned severity sequences (LL, UL, LU, UU).

Discussion

Concerns over the loss of conifer forests due to shifting fire regimes and long-term drought have prompted significant research into forest resiliency and ecosystem conversion (Savage & Mast 2005, Coop et al 2020, Keyser et al 2020). Given the already dry conditions of Southwestern forests, a shift towards more frequent and high severity fire regimes may test the future resiliency of conifer forests to fire and drought. The extended and continuing multi-decadal drought in the southwestern region has been notable for multiple years of large wildfire events in 2002, 2003, and 2020 in the SCM, and 2003 and 2014 in the RM. To evaluate forest responses to these stressors, we applied a resilience framework (Falk et a. 2022) that examines mechanisms of persistence, recovery, and reorganization respectively. In response to the interacting stressors of repeated fire and extended drought, we hypothesized limited resilience (post-fire growth) in surviving trees, as well as reduced recovery by conifers compared to fire- and drought-tolerant shrubs and oaks, potentially leading to incipient ecosystem reorganization. We further predicted that these varying responses would be manifested differently in the two vegetation types that are the focus of this study (Fig. 6) (Savage et al 2013).

Growth responses

Studying tree growth responses in the SCM following the 2002-3 Bullock-Aspen fires and then unburned in the later Bighorn Fire allowed us to assess how fire exposure and drought affected the medium-term growth of surviving trees (Fig. 3). In general, we found substantial resilience to drought and fire exposure among surviving trees of all three species (Fig. 6, top row).

Growth in the three species in our study responded differently to drought and fire exposure. Basal area growth of ponderosa pine appears to be more affected by fire exposure than by drought, even though model results showed no significant effects. Trees exposed to high severity fire reflected an initial period of low growth for three years post fire, followed by a sustained positive growth trend until 2020. Trees in plots that burned at low severity showed fairly constant growth from 2003–2020, while tree growth in unburned plots declined beginning in 2015. Ponderosa pine growth was the least affected by severe drought years of the three species, with some classes not indicating reduced mean growth even in post-fire drought years (2006, 2012, 2018). This response contrasts with other work showing an increase in sensitivity to PDSI in ponderosa pine in Oregon, in which interannual variability explained by drought doubled in the last decades (Voelker et al 2018). These post-fire radial growth measurements indicate a high degree of adaptive resilience to drought and fire among ponderosa pine individuals who survived the initial exposure, perhaps facilitated by reduced stand density and competition.

Post-fire growth of both pine species in this study appear to have been affected by overcrowding resulting from the long and uncharacteristic period of fire suppression. Prior to 2002, almost all high elevation areas in SCM had not burned in at least 75 years, which is a significant departure from the historical mean fire regime (Safford & Van de Water 2014); under the historical fire regime, approximately 7–14 fires would have occurred during this period (Iniguez et al 2008). Although we did not have direct access to pre-Bullock/Aspen stand density for all plots, the low severity and unburned areas within our study indicate relatively high prevailing stand density (mean LL, LU, UL, UU = 252 stems/ha; basal area = 24.1 m^2/ha) resulting from fire exclusion over the past century. Both Southwestern white pine and ponderosa pine trees that burned at low severity had greater cumulative basal area growth in the drier post fire period (2002–2020) than the wetter pre-fire period (1983–2001). Southwestern white pine growth was also highly negatively affected by time since fire in our model, a variable that can be interpreted as a proxy for stand density. Combined, this indicates a stronger influence of tree density on basal area growth than PDSI. Although research specifically into Southwestern white pine is limited, one review of stand dynamics and disturbance ecology of the species suggests that reintroducing low-mixed severity burns would likely be beneficial for increasing overall resilience (Looney & Waring 2013). Additionally, Voelker et al (2018) found that long term fire suppression increased drought sensitivity in dry mixed conifer forests in Oregon by increasing stand basal area. Likewise, increased stand density resulting from fire exclusion has been associated strongly with inter-tree competition (Allen et al 2002, Marshall et al 2019).

Douglas-fir growth was the most affected by climate, and the least affected by fire severity of the three species. Growth in all severity classes declined from 1990 to 2002, and there are noticeable growth declines in each drought year since 2002 for all severity classes. All three severity classes were similar in growth until the 2011 drought year, after which tree growth in unburned and high severity plots growth rebounded to pre-fire/drought conditions, while low severity BAI stagnated. Cumulative growth results, combined with our modeling results, may suggest some influence of fire, however. Cumulative growth in Douglas-fir burned trees plummeted from the wetter pre-fire to drier post-fire period, whereas unburned tree growth increased. This may be a direct influence of wildfire, or it may be related to microclimate

variables, in which places that did not burn in 2003 were located in naturally wetter areas than sites that did burn (Sommers & Flannigan 2022). Additionally, locations that do burn may be even hotter and drier post-fire than refugia sites due to a lack of canopy and understory vegetation which may reduce runoff (Wolf et al 2021).

One consideration for the interpretation of these tree growth results is our relatively small sample size (Supplemental Table S-3), particularly when tallied by both species and severity class. Due to an uneven occurrence of ponderosa pine, Southwestern white pine, and Douglas-fir, as well as difficulty finding trees that survived a high severity burn, sample sizes across factorial groups varied between 4 and 8 cores. When possible, we cored trees within or adjacent to our established vegetation plots. Because there were frequently no surviving trees in the high severity burn areas, we sampled most of the trees in this class in a single high severity area that had more survivors; this site did have the highest RBR (burn severity) values of any area we sampled, but wider interpretation of individual species responses would benefit from a more comprehensive sampling design, particularly when comparing results among severity classes. Despite this limitation, our findings highlight the ecological importance of wildfire, especially among pine species where trees in low severity burned plots had greater average radial growth than unburned trees 17 years post-fire, possibly indicating the effects of overcrowding. For Douglas-fir, climate variation was more influential on radial growth than fire severity. Given climate predictions for increased drought stress in the Southwest, Douglas-fir growth may decline more markedly in the coming decades.

Post-fire Recruitment and Recovery

We recorded post-fire conifer recovery in a majority of burned plots (Fig. 6, middle row). Unburned plots in PPEO had the greatest mean recruitment, although this was affected in part by an outlier plot recording over 300 seedlings. High C_{rec} values in high severity plots, especially in the PPEO, may reflect the presence of recruitment that had already grown to be small overstory trees instead of seedlings or understory trees which were more common in low or unburned plots. Because C_{rec} is log weighted, taller trees influence the statistic more than seedlings or understory conifers. In MC plots, tree recruitment was highest in plots unburned in 2002-3, and declined progressively as burn severity increased.

Tree recruitment was related negatively to topographic slope in our model (Supplemental Table S-4). Slope has a negative relationship with water infiltration rates and a positive relationship with runoff (Nassif & Wilson 1975, Fox et al 1997). In combination, decreased infiltration and increased runoff leads to increased erosion rates and decreased available water for seedlings. A lack of plant cover following high severity wildfire may compound soil water limitation and further accentuate erosion (Benavides-Solario & MacDonald 2001, Robichaud et al., 2016). Plant cover decreases erosion by intercepting rain drops and limiting their ability to detach soil particles (Gabet and Dunne 2003). As a result, burned plots with steep slopes are more likely to experience extreme runoff and erosion responses that could limit subsequent recruitment.

Conifer recruitment was unaffected by distance to a seed source in our model, a variable found to be linked to conifer regeneration in other studies (Donnato et al 2009, Shive et al 2018, Boag et al 2020). Within the area sampled in this study, the 2002-3 fires left a complex landscape mosaic of fire severities and post-fire refugia, enhanced by the steep and complex Sky Island topography (Fig. 7); this landscape pattern has been found to be associated with increased levels of post-fire recruitment, in contrast to large homogeneous areas of tree mortality (Steel et al 2018, Coop et al 2019, Krawchuk et al 2020). A long history of fire exclusion in the Catalinas may have also helped establish a large conifer seed bank (Goubitz et al 2004).

One study modeling ponderosa pine regeneration following high severity wildfire found that fire-induced microclimate changes reduced the amount of water available to pine seedlings in the summer and fall after germination, partially by drying out the soil (Fedemma et al 2013). In this same study, winter frosts were highly negatively correlated with seedling survivorship; the SCM and RM experienced an extensive frost event in the winter of 2011, which was also a deep drought year. These authors also found strong correlations between germination and wetter conditions that same fall, which they speculate created resistance for seedlings to survive the winter. Moisture conditions (reflected in PDSI, Fig. 3A) have been below average in the SCM and the Rincons since 2002, and below average in 89% of years since 1994, with 2020 being the driest year on record[10].

Although the relationship was not significant in our model, several areas where we recorded no regeneration were in large patches of high severity burn with substantial bracken fern cover (Fig. 7). Prior research has suggested that bracken ferns inhibit germination and growth of conifers, possibly by outcompeting for resources (Ferguson & Boyd 1988). These authors and other have also described the existence of phytotoxins released by other ferns of the same genus that kill the conifer and other tree seedlings when absorbed by prohibiting root growth (Jatoba et al 2016). Bracken ferns are aggressive post-fire colonizers and have sustained large homogenous stands in the SCM and RM for up to 19 years post-fire (J. Malusa, University of Arizona, personal communication). Research regarding favorable growth conditions for Southwestern white pine seedlings also found decreased growth in areas with significant litter and duff cover (Goodrich & Waring 2016). Bracken ferns are annual plants and their aggressive growth can lead to large amounts of litter build up in a short time.

Community reorganization

Following wildfire, vegetation communities may remain similar to their pre-fire composition, or they may reorganize, either transiently or persistently (Fig. 6, bottom row). In the Southwest, this transition is driven primarily by high severity fire, and conversion is typically from forested areas to native shrublands and can be highly persistent (Guiterman et al 2022, Woolman et al 2022). In one case study, conversion from pine-oak forests to oak woodlands is well underway in the Chiricahua mountains in southeastern Arizona following high severity fire (Barton & Poulos 2018). This conversion has been linked to oaks' ability to resprout and tolerate increasing aridity (Poulos et al 2021). A shift to more drought and fire tolerant

species is an expected response when ecosystem stress increases (Young et al 2019, O'Connor et al 2020, Falk et al. 2022).

Fire suppression in both the SCM and the RM has greatly influenced community dynamics. Many of our study plots have burned only once in the past 75 years, whereas historically (pre-fire suppression) they likely would have burned at mixed severity seven to fourteen times in this period for PPEO and three to nine times in MC (Iniguez et al 2008, Farris et al 2013). In the MC, dominance by aspen is a common post-fire transient reorganization. In the PPEO, fire exclusion has resulted in an increase in conifer stand density at the expense of overstory oaks and understory shrubs. While we are interested in conifer recovery due to its climate dependent regeneration strategy, healthy PPEO stands include moderate oak and shrub dominance, particularly following wildfire (Wahlberg et al 2014, Huffman et al 2020). Oaks, shrubs, and other post-fire dominant species add to the overall diversity of these ecosystems, and their exclusion due to fire suppression does not mean these forests are healthier (Cocking et al 2014).

In our study area, post-fire vegetation dynamics over the 17 years following the Bullock/Aspen fires in the SCM and the Helen's 2 and Dear Head fire in the Rincons were influenced differently by fire severity in the two communities we studied. In mixed conifer areas, unburned and low severity plots were dominated almost entirely by conifers in the overstory. In high severity areas, aspen accounted for roughly 40% of overstory tree dominance, although this pattern was mostly clustered in two plots rather than spread evenly throughout. This is attributable to aspen's clonal resprouting ability, which tends to result in clustered regrowth (Schier et al 1985). Aspen dominance following high severity fire is a natural post-fire successional path, and we would expect that eventually conifers would return to these areas. However, oaks were not recovering to be more dominant than conifers in MC stands, and there was no strong overall trend toward post-fire oak reorganization (Fig. 5a).

In PPEO communities, conifers were less dominant in high severity areas compared to low or unburned ones, including in several plots that had no overstory recovery at all. These high severity plots also had higher proportions of understory oaks and shrubs. The overstory in unburned PPEO plots was dominated almost entirely by conifers, whereas low and high severity plots were more mixed among plant functional groups. As in MC, locust was dominant only in high severity areas (Fig. 5b).

In both ERUs, overstory oak dominance may be affected by our method for measuring resprouting oaks; conventional measures (such as DBH) suitable for single-stemmed plants with arboreal growth form can be problematic with post-fire oaks, which often resprout with many shoots at once, meaning that often no individual trunk is substantially larger in diameter than the others (Minor et al 2017). Because we categorized a tree as overstory only if it was greater than 5 cm in diameter, many of these recovering oaks were classified as understory. These post-fire recovering oaks may play a larger ecological role over time (Guiterman et al 2018, Huffman et al 2020).

Conclusion

The 2020 Bighorn fire left a complex post-fire mosaic over nearly the entire upper elevation of the SCM. While some areas (approximately 8% of area within the burn perimeter) burned at high severity, the majority (92%) of land within the fire perimeter was a mosaic of moderate and low burn severities and unburned areas. The largest contiguous patch of high-severity occurred in the northern portion of the range (Fig. 2b), reburning many areas that had also burned at high severity 17 years prior (Fig. 2a). Elsewhere, patches of low and moderate severity fire left scorched needles and bare soil within the complex SCM topography, which includes large areas of rock outcrops and other non-burnable areas. One year later, recovery was already underway: understory growth had initiated, with woody shrubs, oaks, and bracken ferns the first perennial plants to send up new growth. However, recruitment of conifers in burned areas was largely absent, possibly the result of the failed monsoon rains in the summer of 2020. In the short run, following two decades of severe drought, as well as the three largest, most severe wildfires in SCM history in only an 18-year span, the prospect of future healthy conifer forests in the high elevations seemed unlikely.

The summer of 2021 provided a climatic whiplash, delivering the third wettest monsoon in recorded history, as well as the singular wettest August ever[11]. That summer also provided a different perspective on the processes and pace of post-fire recovery. In our 43 field plots in the SCM, we found substantial conifer recruitment in areas unburned in the Bighorn across a range of burn severities and ecosystem types from the previous fires (Bullock and Aspen, 2002-3). In some plots, areas that had burned at high severity two decades previously were already dominated by young conifer trees that had regenerated post Bullock/Aspen. In others, especially areas that had burned at high severity twice, stands of bracken ferns or *Ceanothus* formed dense mats. In most areas, we did not see signs of irrevocable conversion to shrub or oak domination that has become common following wildfire in the Western US (Guiterman et al 2022). Instead, we saw an ecosystem in the very early stages of recovery processes that will play out over years and decades.

Management Implications

From a management perspective, our results suggest the merits of patience. Many conifer species are slow-growing and dependent on specific climate windows for successful seedling establishment, which may not occur immediately post fire. Although climate is shifting in generally predictable ways in the long-term (i.e., increasing temperatures and decreasing precipitation in the Southwestern US), it remains variable on shorter time scales, and long-term shifts in vegetation may be dependent on annual or decadal climate trends (Jackson 2021). As barren as severely burned areas may seem immediately post fire, our observations from 1 to 18 years post-fire are a reminder that forest recovery simply takes time. We observed many areas with transient shifts in species composition, where a temporary rearrangement of species dominance may fade into a more predicted successional trajectory given time. Our results also point to the benefits of reintroducing low-mixed severity fire back to forests with a history of fire exclusion when possible. These include lowering stand density and tree competition and reducing heterogeneity (Peterson et al 1994, Larson et al 2013, Zhang et al 2019).

Our observations and analyses suggest that managers may need to embrace change and heterogeneity of landscapes. While some shifts in species and trait dominance may appear undesirable, especially because they are partially occurring as a result of human-caused climate change, patches of oak or shrub dominated area in the Southwest are not inherently negative outcomes. They are native species that are often more drought and fire tolerant than the species they are replacing and can provide other ecological benefits such as habitat or food resources (Barton & Poulos 2018, Guiterman et al 2018). On landscape scales, and in mountain topography as steep and complex as the SCM and RM, widespread human intervention to prevent these transitions is likely not feasible in the long term if climate continues to change. We must trust in the resilience of ecosystems to regenerate and regulate themselves and accept that some transitions to different communities reflect ongoing long-term processes of ecosystem resilience.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors Contributions:

MF collected and analyzed the data and wrote the manuscript. DF contributed to experimental design, planning the study, and writing the manuscript.

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Tables

Table 1. Tree Ring Model Results. Model results for mean annual post-fire basal area increment (BAI) as a function of drought, time since fire, and fire severity. 95% confidence intervals in parentheses below parameter estimates for PIST (Southwestern white pine), PIPO (ponderosa pine) and PSME (Douglas-fir). Regression modeling sample size was *n*: ponderosa pine = 21, Southwestern white pine = 18, Douglas-fir = 21).

	Dependent variable:		
	BAI		
Fixed Effects	(*PIST*)	(*PIPO*)	(*PSME*)
Constant	**1,866.84**	**1,750.64**	**2,865.76**
	(1,581.52, 2,152.1)	(1,411.05, 2,090.23)	(2,104.89, 3,626.63)
PDSI	24.31	9.43	**175.57**
	(-16.30, 64.91)	(-36.52, 55.39)	(87.22, 263.92)
Time Since Fire	**-6.45**	0.71	**9.08**
	(-9.57, -3.34)	(-2.23, 3.64)	(3.58, 14.59)
Fire Severity	**-3.71**	-1.38	-2.64
	(-6.09, -1.33)	(-3.47, 0.71)	(-5.72, 0.45)
Note:	***p* < 0.05**		

Table 2. Mean cumulative growth (BAI, in mm^2) for Southwestern white pine, ponderosa pine, and Douglas-fir in two 18-year periods, 1983-2001 and 2002-2020.

Southwestern white pine	1983-2001	2002-2020	Change
Unburned	23,699	24,179	-19.6%
Low	30,572	38,653	+26.4%
High	36,843	29,617	+2.0%

Ponderosa pine	1983-2001	2002-2020	Change
Unburned	27,012	29,301	+8.47%
Low	33,090	41,661	+25.9%
High	39,332	34,359	-12.6%

Douglas-fir	1983-2001	2002-2020	Change
Unburned	55,472	60,435	+8.9%
Low	59,186	38,222	-35.4%
High	79,900	58,757	-26.4%

Table 3. Mean importance values (%) of overstory and understory vegetation for Mixed Conifer (above) and Ponderosa Pine-Evergreen Oak (below). Plot severity indicates soil burn severity in 2002-3 Bullock/Aspen Fires for SCM, and the Helens 2 fires for Rincon plots. All data shown are from plots unburned since 2014. Acronym definitions: NOA: non oak angiosperms, U Conifer: understory conifer, U Oak: understory oak, U NOA: understory non oak angiosperms.

MC	Conifer	Oak	NOA	Shrub	U Conifer	Locust	U Oak	Fern
High	59%	2%	38%	52%	3%	28%	11%	6%
Low	91%	8%	1%	48%	32%	0%	4%	17%
Unburned	82%	12%	4%	40%	47%	7%	6%	1%

PPEO	Conifer	Oak	NOA	Shrub	U Conifer	Locust	U Oak	Fern	U NOA
High	58%	2%	0%	27%	7%	7%	42%	13%	4%
Low	78%	18%	4%	3%	41%	0%	15%	34%	8%
Unburned	97%	3%	0%	13%	11%	0%	53%	23%	0%

Figures

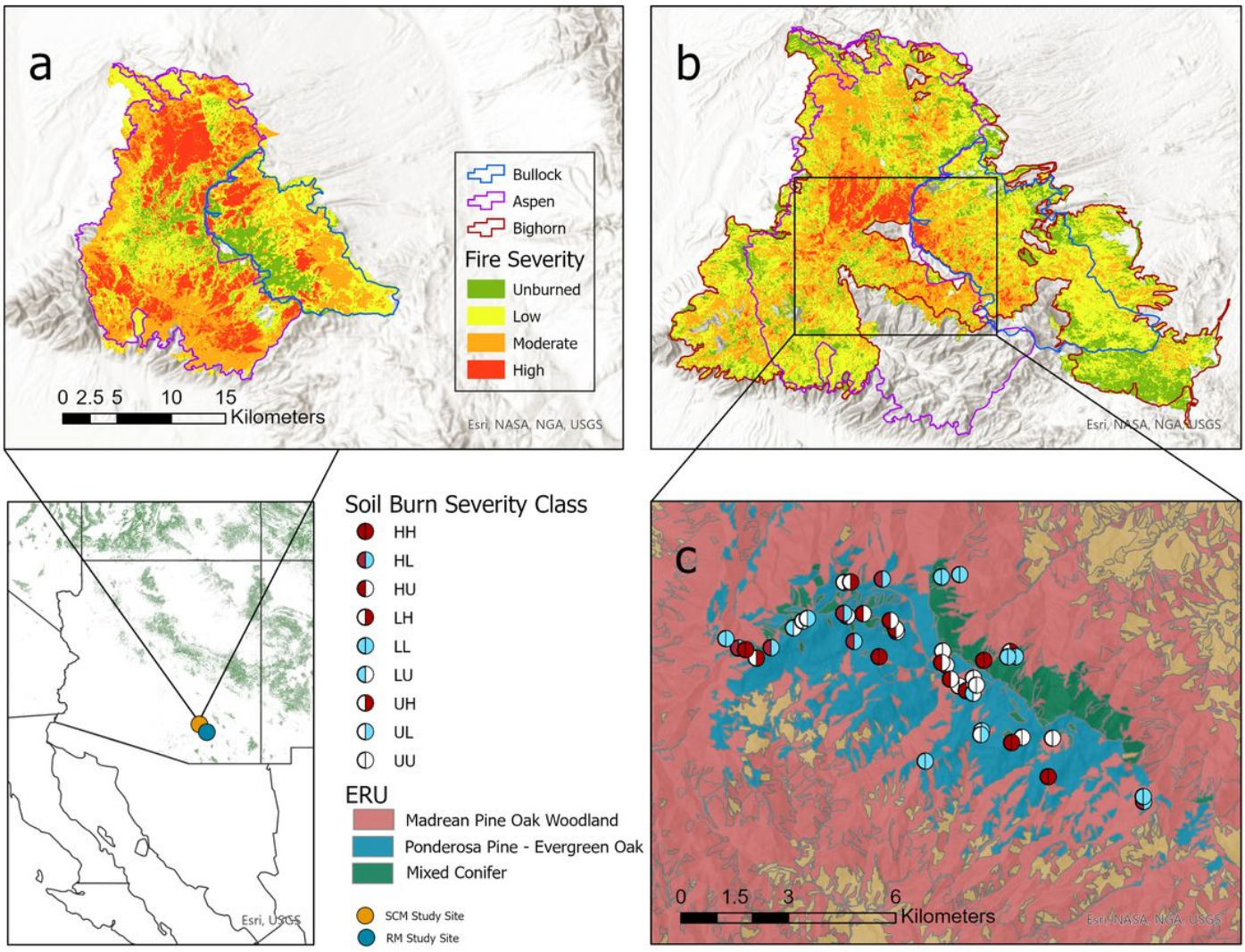

Figure 1

A conceptual diagram of resilience (resistance, recovery, and reorganization) following mixed severity wildfire**.** Time flows from left to right, and elevation increases from bottom to top of the figure. In the Mixed Conifer ecosystem (highest elevations), pre-fire forest stands are dense, with pines, firs, and aspen (a). Following high severity fire, locust (b) may dominate, or conifer seedlings may indicate recovery (c). Shade intolerant aspen (d) may resprout following fire, and in our study, we documented two-decade long dominance by bracken ferns (e). In the lower elevation Ponderosa Pine Evergreen Oak ecosystem, pre-fire stands (f) are dominated by pines but also contain larger oaks and shrub patches. Post fire, conversion to oak domination (g) may occur if oaks resprout but pines are not able to establish. If pine regeneration does occur, conversion to oak domination may be temporary (h) as the system reverts to a mixed community.

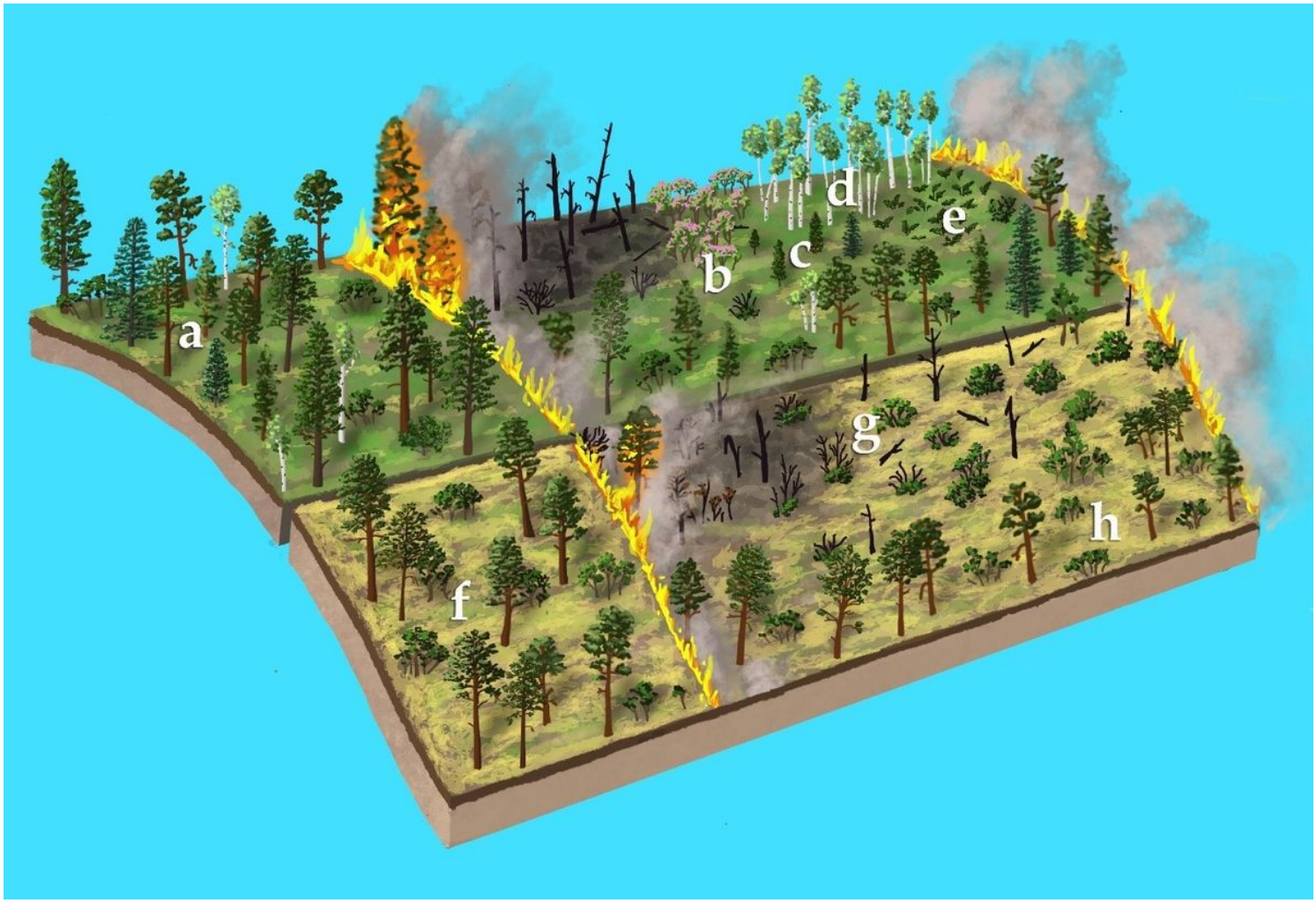

Figure 2

Fire severity maps and plot locations**.** Soil burn severity (SBS) for (A) Bullock and Aspen fires and (B) Bighorn fire. (C) Plot locations in SCM coded by severity class. (D) SBS for Helen's 2 (top) and Deer Head (bottom) fires in RM, as well as plot locations coded by severity class. Green land cover on the inset map represents forest cover. Codes for severity classes indicate fire severity in first set of fires followed by severity in second set of fires. HH (High High), HL (High Low), HU (High Unburned), LH (Low High), LL (Low Low), LU (Low Unburned), UH (Unburned High), UL (Unburned Low), UU (Unburned Unburned).

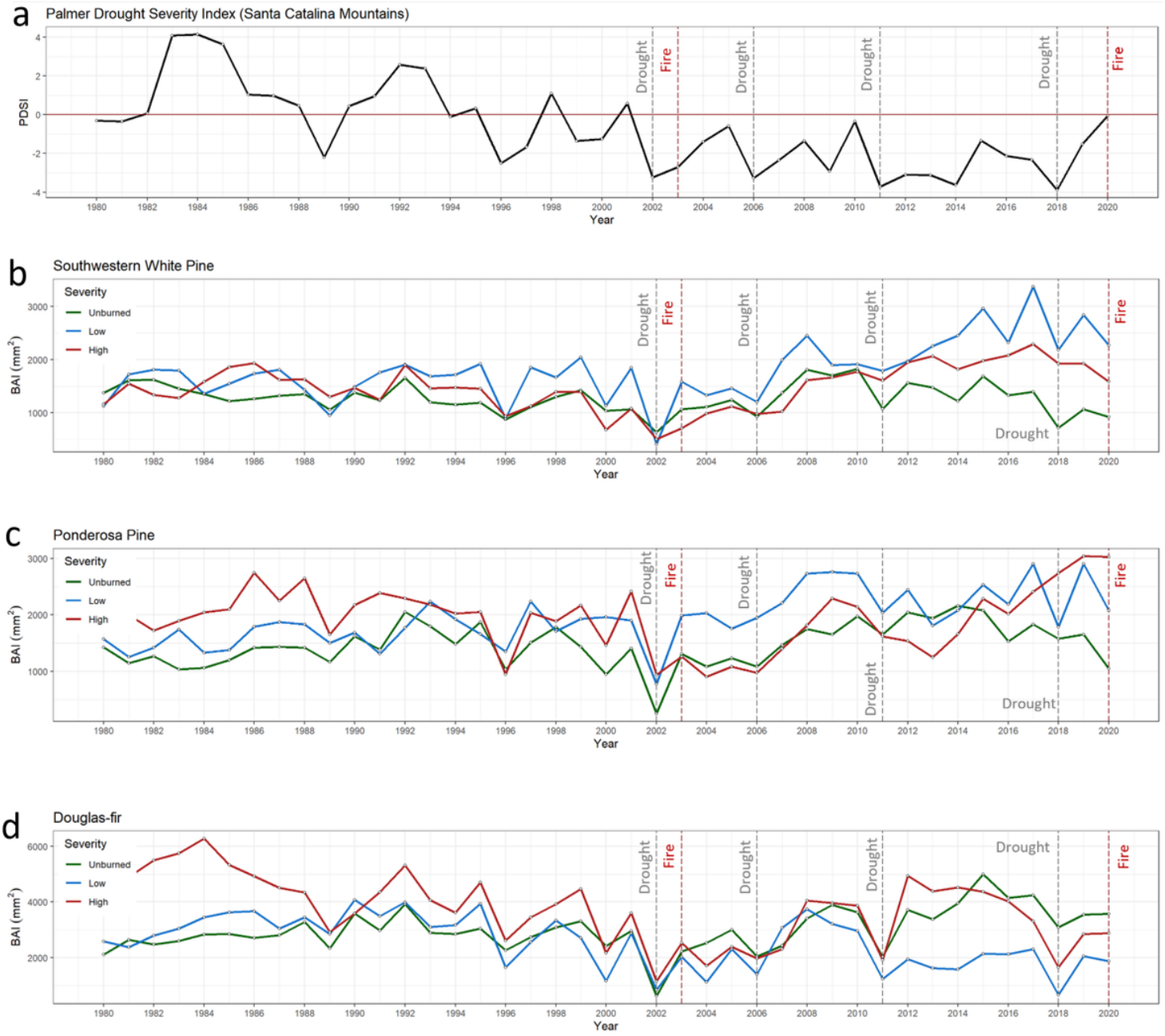

Figure 3

PDSI and mean annual tree growth 1960-2020. (A) Palmer Drought Severity Index in the SCM from 1980-2020. No PDSI value from 2002-2020 exceeds 0, the historic mean. Mean basal area increment (BAI, in mm2) from 1980 to 2020 in (b) Southwestern white pine, (c) ponderosa pine, and (d) Douglas-fir. Within species, mean BAI is plotted for all trees within severity classes (unburned, low- and high-severity) in the 2003 Aspen fire. Sample size for severity class within species is between 4 and 8 samples (Supplemental Table S-3).

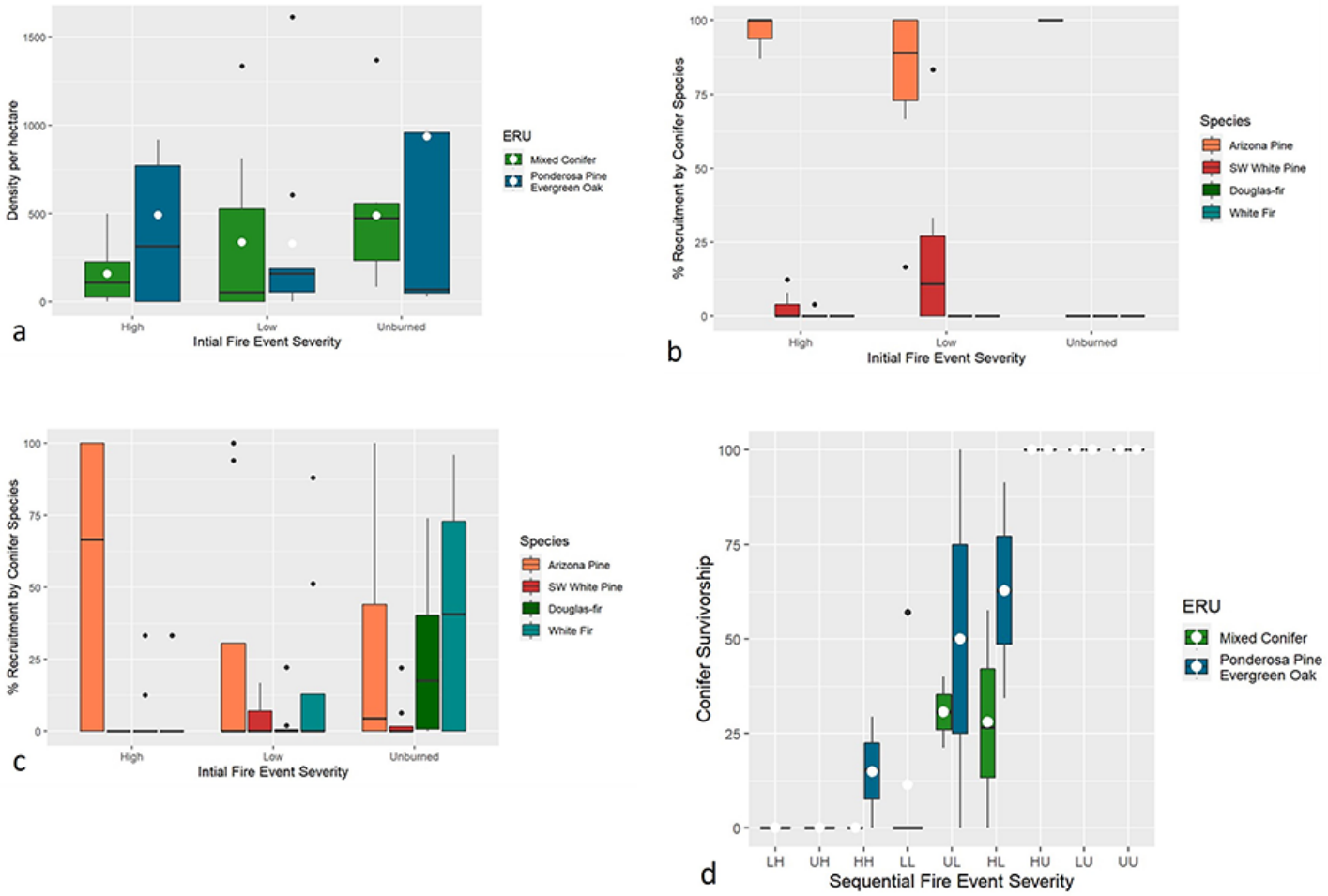

Figure 4

Post-fire conifer recruitment. (A) Conifer recruitment (Crec) since the initial fire event in SCM and RM, by severity class. Percent of post-initial fire event recruitment by species in PPEO (B) and MC (C) ERUs. (D) Survivorship (Crec) by sequential fire severity combinations following the second fire event. In all plots, black lines indicate the median; boxes contain the 25th to 75th percentiles, and whiskers indicate 10th and 90th percentiles; black dots indicate outlier values. White dots in A and D indicate group means. In unburned PPEO (panel A), an outlier with a value of 3580 stems/ha is included in analysis but not shown. In panel D, fire severity abbreviations refer to the fire severity in the initial fire event and second fire event sequentially; see Figure 1 for definitions. Also in panel D, there was no recorded recruitment in MC LL; only PPEO LL is shown.

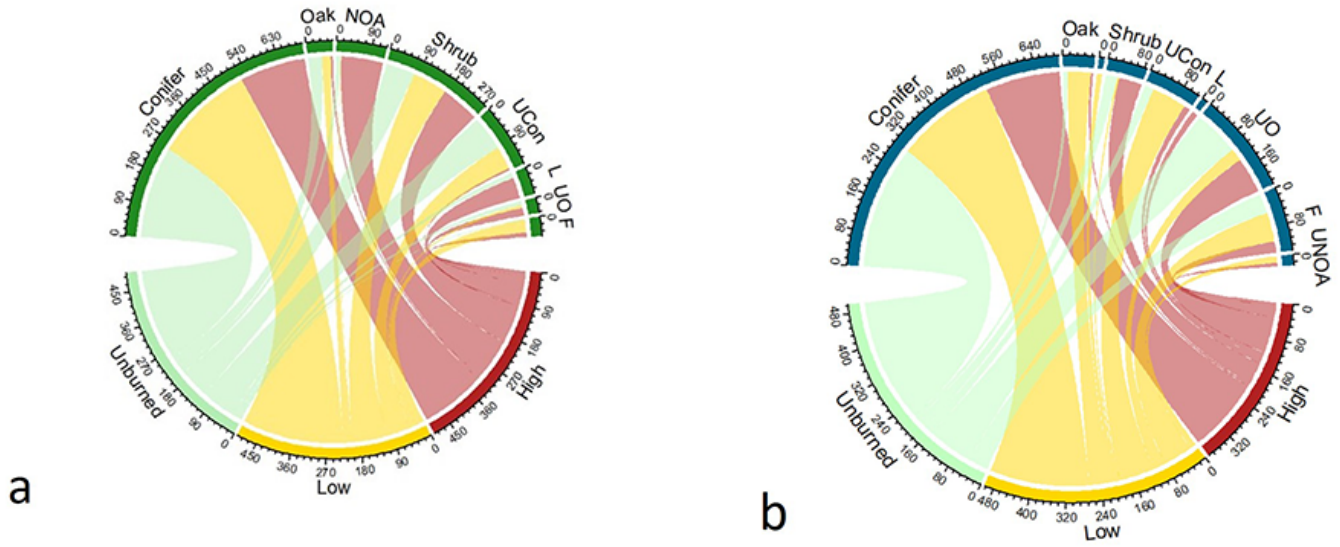

Figure 5

Chord diagrams of vegetation importance values for MC (a) and PPEO (b) ERUs**.** Variables on the upper segment refer to plant functional groups: Conifer, Oak (overstory), NOA (non-oak angiosperms, mostly aspen), Shrubs, UCon (understory conifers), L (Locust), UO (understory oaks), UNOA (understory non-oak angiosperms), and F (Ferns). In panel b, the unlabeled top section between Oak and Shrub is NOA. Bottom variables on diagrams indicate plot fire severity in the initial fire event; color band indicate the distribution of plant functional groups in each fire severity class as measured in 2021. Only plots unburned in the second fire event are included. Importance values for each severity class sum to 500. The width of the functional type on the top portion of the diagram (the *node*) signifies the contribution of that plant functional group to the total importance value. The width of each individual chord signifies the relative contribution from each severity class; the wider the chord, the greater the contribution to the post-fire community relative to other severity classes.

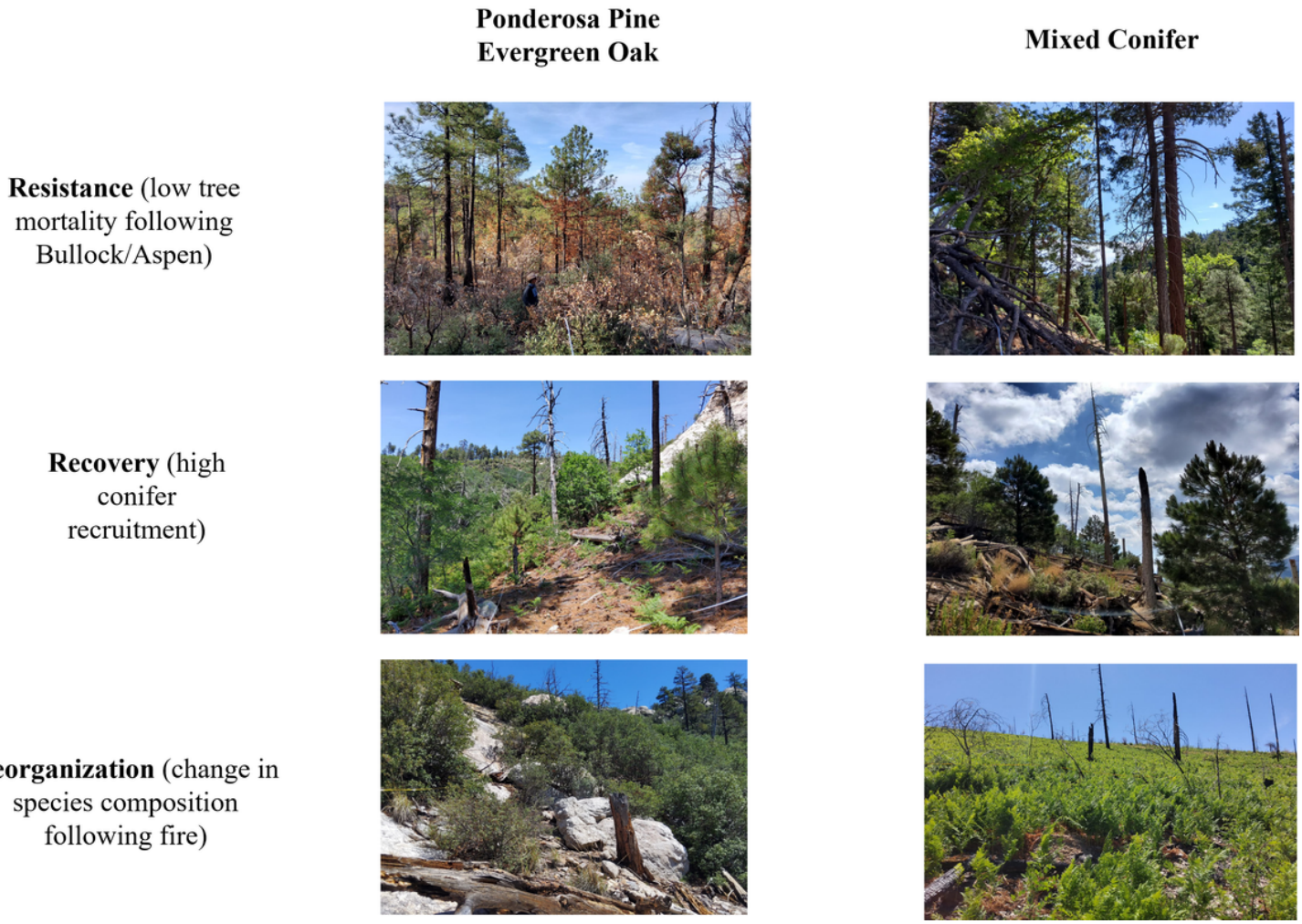

Figure 6

Observed forest response following Bullock & Aspen fires in 2002-3, as photographed in 2020. Photographer credit: Miles Fule.

Figure 7

View from SCM showing mosaic landscape following multiple fire events at various severities. Photographer credit: Miles Fule.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalInformation.docx