



ORIGINAL RESEARCH

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Repeated fire and extended drought influence forest resilience in Arizona Sky Islands

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Abstract

Background Wildfire size and severity have been increasing in the southwestern US since the mid-1980s as a direct result of anthropogenic climate change and land management practices. Large, high severity wildfire, including reburns, combined with two decades of drought, may result in ecosystem reorganization, as some areas dominated by conifer forest are no longer able to recover, and are replaced or outcompeted by oaks or shrubs. We apply a unifying resilience framework distinguishing post-fire processes of persistence, recovery, and reorganization of mixed conifer and pine-oak forests in two southern Arizona Sky Island mountain ranges. The Santa Catalina and Rincon Mountains experienced multiple wildfires in the early 2000s, followed by a large reburn in the Santa Catalina Mountains in 2020. We evaluated conifer radial tree growth as a measure of individual tree persistence, seedling recruitment as a measure of conifer and oak population recovery, and differences in species importance values in burned and unburned areas, to detect potential ecosystem reorganization, including changes in dominant plant trait groups.

Results In our tree growth analysis, we found resilience to both drought and wildfire in three dominant conifer species. 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 adversely affected by fire exposure. In areas that burned only once, post-fire conifer recruitment was found in the majority of burned plots that were sampled 18–19 years after fire, although density varied greatly. We found evidence of incipient community reorganization reflecting plant traits (e.g., resprouting species) especially in mixed-conifer communities. Composition analysis indicated some loss of conifer overstory dominance in areas burned at high severity in higher elevations; in general, these were replaced mainly by aspen (*Populus tremuloides*).

Conclusions The study landscapes showed evidence of all three post-fire processes of persistence, recovery, and reorganization in the 18–19 years after the initial fire events. The complex mosaic of fire severity and topography promoted landscape-scale recovery, while some high severity areas show evidence of incipient or transient reorganization. Early (1 year) post-fire vegetation responses following the 2020 reburn were highly variable and dependent on sequences of fire severity and plant traits; these constitute initial conditions for future trajectories of change in southwestern forests under the influence of changing climate and fire regimes.

Keywords Reburn, Alternative successional pathways, Ecosystem conversion, Ponderosa pine, Douglas-fir, Southwestern white pine, Mixed-conifer forest, Pine-oak forest, Persistence, Recovery, Reorganization

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Resumen

Antecedentes El tamaño y la severidad de los incendios de vegetación se han incrementado en el suroeste de los EEUU desde mediados de los 80's, como resultado directo del cambio climático de origen antropogénico y las prácticas de manejo de tierras. Incendios grandes, severos, y que incluyen el requemado de la vegetación, combinados con dos décadas de sequías, pueden resultar en la reorganización de los ecosistemas, como ocurre con algunas áreas dominadas por coníferas que no están en condiciones de recuperarse, y son reemplazadas o desplazadas competitivamente por robles o arbustos. Aplicamos un modelo conceptual unificado de resiliencia, que distingue los procesos post fuego de persistencia, recuperación, y reorganización, de un bosque mixto de coníferas y de pino-roble en dos áreas ubicadas en las llamadas "Islas de ecosistemas de altas montañas de Arizona" (*Arizona Sky Island mountain ranges*). En ellas, la vegetación de las montañas de Santa Catalina y de Rincón experimentó varios incendios a comienzos de los 2000's, seguidos de una re-quema en la montaña de Santa Catalina en 2020. Evaluamos el crecimiento radial de las coníferas como medida de la persistencia individual de árboles, el reclutamiento de plántulas como medida de la recuperación de coníferas y robles, y las diferencias en los valores de importancia de las especies en áreas quemadas y no quemadas, para detectar la reorganización potencial del ecosistema, incluyendo los cambios en las características de los grupos de especies dominantes.

Resultados En nuestro análisis del crecimiento de árboles, encontramos resiliencia tanto a la sequía como al fuego en tres especies dominantes de coníferas. El Pino ponderosa (*Pinus ponderosa*) y pinos blancos del suroeste (*Pinus strobiformis*) que sobrevivieron tanto a altas como a bajas severidades, mostraron trayectorias de crecimiento positivas no significativas luego de la exposición al fuego en 2003. El crecimiento del Pino oregón (*Pseudotsuga menziesii*), fue más clima-dependiente, y afectado adversamente por la exposición al fuego. En áreas que se quemaron sólo una vez, el reclutamiento de plántulas post fuego fue encontrado en la mayoría de las parcelas quemadas que fueron muestreadas 18–19 años luego del incendio, aunque su densidad varió grandemente. Encontramos evidencia de una reorganización incipiente de la comunidad que reflejaba las características de las plantas (i. e. especies rebrotantes), especialmente en comunidades de coníferas mixtas. Los análisis de composición indicaron alguna pérdida en la dominancia de los doseles de coníferas en áreas quemadas a alta severidad en elevaciones altas; en general, esas fueron reemplazadas por el álamo temblón (*Populus tremuloides*).

Conclusiones Este estudio de paisajes muestra evidencia de los tres procesos post fuego: persistencia, recuperación, y reorganización en los 18–19 años posteriores al evento de fuego inicial. El complejo mosaico de severidades y topografías diferentes promovieron la recuperación a escala de paisaje, mientras que algunas áreas quemadas a alta severidad muestran evidencias de una reorganización incipiente o transitoria. Inmediatamente (un año después) de una requema en el 2020, la respuesta de la vegetación fue altamente variable y dependiente de la secuencia de la severidad y de las características de las plantas; éstas constituyen las condiciones iniciales para las futuras trayectorias de cambios en los bosques del suroeste bajo la influencia de cambios en el clima y en los regímenes de fuegos.

Background

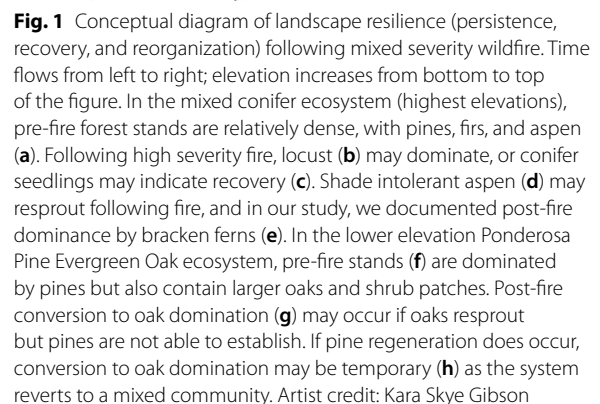
Wildfire size and severity have increased in the western US since 1980, with annual area burned nearly doubling since 1984 (Westerling et al. 2006, NIFC 2023). In Arizona and New Mexico between 1984 and 2015, area burned at high severity increased at a rate of 1009 ha per year (Singleton et al 2019). This increase is correlated highly with decreasing precipitation, increasing temperatures, and increasing vapor pressure deficit, all direct expressions of anthropogenic climate change (Abatzoglou & Williams 2016; Mueller et al 2020). Currently, the southwestern US is experiencing the deepest and most persistent drought conditions in the past 1200 years, exacerbated by anthropogenic climate change (Williams et al 2020).

Many areas in dry Southwest conifer forests that historically supported low to moderate severity fire

regimes are now experiencing fires with a higher proportion of area burning at high severity (Singleton et al 2021; Remy et al 2021). Regional pine-oak and dry conifer forests are adapted to low-moderate severity fire regimes, with relatively short return intervals (5 to 10 years) and evolutionary strategies such as resprouting, or thick bark and self-pruning limbs that prioritize survival over reproduction (Rodman et al 2021; Keeley & Pausas 2022). Recurring historical wildfires regulated stand density, primarily by thinning the high numbers of seedlings and saplings of conifer obligate seeders, while opening space for shrubs and oaks (Barton and Poulos 2018; Malone et al 2018). In contemporary forests, reburn dynamics have shifted, resulting in high severity fire comprising an increasing proportion of burned areas, due to denser forests with higher fuel loads with vertical and horizontal connectivity,

These various post-fire outcomes are reflected in conceptual models of forest resilience, based on mechanisms that determine multiple pathways in forested ecosystems driven by the legacies of disturbance and changing climate (Johnstone et al. 2016; Falk et al. 2022; Seidl & Turner 2022). A salient feature of these models is the operation of mechanisms at different levels of biological organization; where these mechanisms fail, the system

Reorganization occurs when both persistence and recovery fail and reflects a community-level shift in species or plant functional group composition or structure (Fig. 2, bottom row) (Laughlin et al 2012; Seidl and Turner 2022). For example, replacement species may be facultative sprouters, which confers several benefits over seed-dependent conifers, including the ability to resprout quickly from the root crown and take advantage of post fire nutrient flushes and newly opened space (Pausas & Keeley 2014). Community reorganization may be 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),



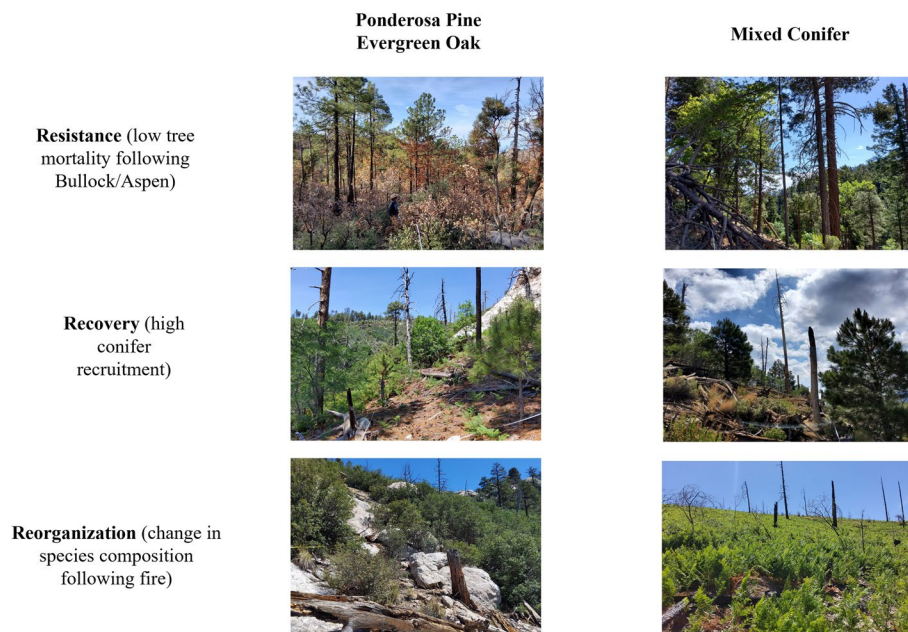


Fig. 2 Observed forest responses by community type following Bullock and Aspen fires in 2002–3, photographed in 2020. Photographer credit: Miles Fule

any of which may retransition back to conifer forests or reorganize further into oak and shrub communities. Community reorganization can also be persistent, reflecting a vegetation trajectory that “locks in” to an alternative state through the effects of competition, disturbance, and changing climate (Pausas & Keeley 2014; Falk et al. 2022). These three processes (persistence, recovery, and reorganization) are not mutually exclusive and may co-occur simultaneously or sequentially in any given location and across landscapes (Seidl and Turner 2022). We employed this framework to evaluate hypotheses regarding post-fire ecological change in the study ecosystem.

We studied landscapes in the Santa Catalina mountains and Rincon mountains in the Sky Islands bioregion of southeastern Arizona, USA, as a case study to examine post-fire resilience responses. These areas experienced multiple fires of varying size and sequences of severity from 2002 to 2020, across a range of plant community types (see the “Methods” section for details). We sampled plots in both mountain ranges in the summer of 2021 to address a series of questions and associated hypotheses based on the resilience framework:

- 1) *Persistence and growth*: For trees that survived fires in 2002–3 in the Santa Catalina Mountains, how did fire severity and drought influence annual tree growth rates over the ensuing 18–19 years? We hypothesized that drought, in combination with fire, would have a deleterious effect on annual tree growth rates across

all three species, and that forest structure (tree density and basal area) would reflect the legacy of both the initial fire and the reburn.

- 2) *Recovery*: How was conifer (obligate seeder) recruitment influenced by sequences of fire severity and extended drought? Given persistent drought conditions, we hypothesized that conifer regeneration would be limited, particularly in areas that burned twice at high severity, in plots more distant from an intact seed source, and in plots with high levels of competition from post-fire colonizing species.
- 3) *Reorganization*: How have forest structure and the relative importance of differing plant functional groups in the Santa Catalina and Rincon Mountains been influenced by sequences of fire severity? We theorized that resprouting plants such as oaks and shrubs would outnumber conifers in the post-fire period, potentially leading to a shift in dominant plant types away from obligate seeders. We further hypothesized that forest structure (density and basal area) would reflect combinations of severity of the initial fire and the reburn 18–19 years later, with lower density and BA in areas of high severity in one or both fires, higher in less severely burned areas.

Methods

Study area

Our study areas were the Santa Catalina Mountains (32.4387° N, 110.7598° W) and the adjacent Rincon

Mountains (32.2198° N, 110.5434° W) in southeastern Arizona, USA, 50 km north and east of the city of Tucson respectively. Both ranges are part of the Madrean Archipelago (“Sky Islands”) bioregion between the Sierra Madre in northern Mexico and 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 Santa Catalina and Rincon Mountains extend from Sonoran Desert at the base (~700 m AMSL) to mixed conifer forests above 2500 m (Whittaker & Niering 1965, 1975; Brusca et al 2013).

Study sites within these areas were located in two different community types (ecosystem response units (ERU¹)): Ponderosa Pine Evergreen Oak (“ponderosa-oak”), and Mixed Conifer. The ponderosa-oak ecosystem ranges in elevation from about 2000 to 2500 m depending on aspect, and is dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson²), Arizona Pine (*Pinus arizonica* Engelm.), southwestern white pine (*Pinus strobiformis* Engelm.), emory oak (*Quercus emoryi* Torr.), and silverleaf oak (*Quercus hypoleucoides* A. Camus). The mixed conifer ecosystem ranges from about 2500 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 mixed conifer community, 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).

Vegetation in both the ponderosa-oak and mixed conifer zones is adapted to the respective historical fire regimes, which were generally low and mixed severity with typical return intervals of 5–10 years in ponderosa-oak, 10–25 years in mixed conifer (Baisan et al 1998; Iniguez et al 2008; Farris et al 2013). Ponderosa pine, the dominant conifer in the ponderosa-oak community types, is highly fire-adapted with thick bark and self-pruning lower limbs (Keeley 2012; Pausas 2015). Douglas-fir and white fir are fire-vulnerable as seedlings, but become more fire resistant 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, indicative of an evolutionary adaptation to fire exposure (Barton 2002; Pausas & Keeley 2017; Keeley & Pausas 2022). Resprouting is also seen following wildfire in Fendler’s ceanothus (Huffman & Moore 2004) and aspen (Alexander et al 1989).

The Santa Catalina Mountains have experienced three large fires since 2000 (Fig. 3). The Bullock Fire was ignited by lightning on 12 May 2002 and was contained 10 June, burning 12,368 ha, 49% at low, 38% moderate, and 11% high severity (Fig. 3a).³ The following year, the Aspen Fire ignited by lightning on 17 June 2003 and was contained 15 July; this fire covered 34,297 ha, 33%, 40%, and 27% at low, moderate, and high severity respectively. 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 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, most of which was a reburn of the Aspen Fire (Fig. 3b).

The severity of the Bullock and Aspen fires was influenced heavily by a history of fire exclusion that began with the arrival of Euro-American colonists in the mid to late 1800s. The introduction of grazing, the forced cessation of Indigenous burning, and a strict Federal policy of near-complete fire suppression beginning in the early 1900s led to a dramatic decline in the number of wildfires and area burned across Western forests, and greatly lengthened the time between fires (Covington and Moore 1994; Pyne 1997). By the time the Bullock Fire ignited, more than 75 years had passed since the last moderately widespread fire in the high elevations of the Santa Catalina Mountains (Baisan et al 1998). Such long absences of fire across the west have resulted in significant alterations in forest composition and structure (O’Connor et al 2017; Hagmann et al 2021), resulting in abnormally heavy fuel loads. All the fires in this study occurred during an extended multi-decadal drought period (Williams et al. 2020).

The Rincon Mountains, a large portion of which is under jurisdiction of the US National Park Service, has been managed more for wildland fire use, and most of the range is roadless (Hunter et al 2014). As a result, fire exclusion in the Rincon Mountains has been less complete than the Santa Catalina Mountains, although wildfires in the twentieth century were still reduced in size

¹ Ecological Response Units of the Southwestern United States, https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd609789.pdf, accessed 11/18/22.

² USDA Plants Database, <https://plants.usda.gov/home>, accessed 11/18/22.

³ All fire data collected from National Interagency Fire Center (NIFC), <https://www.nifc.gov/fire-information/statistics>

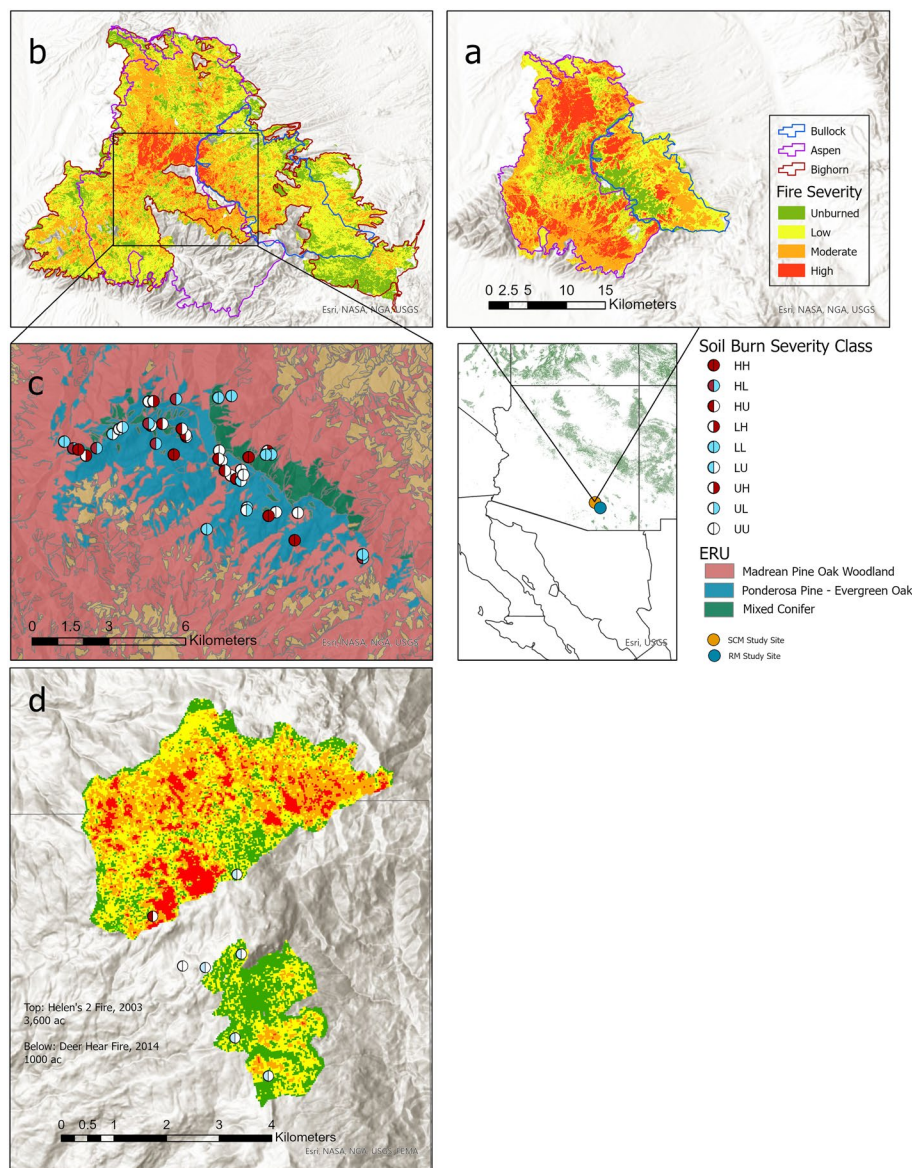


Fig. 3 Fire severity maps and plot locations. Counter clockwise from upper right: soil burn severity (SBS) for (a) 2002–3 Bullock and Aspen fires and (b) 2020 Bighorn fire in the Santa Catalina Mountains (SCM). (c) Plot locations in the Santa Catalina Mountains symbolized by reburn severity class. (d) SBS for 2003 Helen's 2 (top) and 2014 Deer Head (bottom) fires in the Rincon Mountains (RM); plot locations are symbolized by severity class. Symbols for severity classes indicate fire severity in first set of fires followed by severity in the reburn: 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. Green land cover on the inset map indicates forest cover. Scale is consistent in 3a and 3b

and frequency compared to previous centuries; just two fires between 1943 and 1988 accounted for over 90% (4782 ha) of burned area in the Rincon Mountains during this period (Parker 2006; Farris et al 2010). This more active fire history in the Rincon Mountains, particularly in the northern portion of the range, has left it less vulnerable to the large recent fires that have occurred in the Santa Catalina Mountains (Baisan and Swetnam 1990;

Iniguez et al 2009). In the Rincon Mountains, the Helen's 2 Fire burned 1456 ha in June 2003; 46%, 42%, and 18% burned at low, moderate, and high severity respectively. In July 2014, the Deer Head Fire burned roughly 400 ha, almost entirely at low severity and with no overlap with the Helen's 2 fire (Fig. 3d).

Henceforth, we refer to the fires in each range as the initial fire event and second fire event. In the Santa

Catalina Mountains, 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 Rincon Mountains, the initial fire group includes the Helen's 2 (2003) and Deer Head (2014) Fire; in our study plots, there is no second fire in the Rincon Mountains. We include the Deer Head in the initial fire event because there was 7 years of recovery prior to sampling. The majority of our plots sampled in this study were in the Santa Catalina Mountains, the primary study area; additional plots in the adjacent Rincon Mountains were used to fill gaps in fire severity and ecosystem-type stratification.

Plot selection

To evaluate forest responses to fire exposure, we established a network of study plots in the target two ecosystem types. We stratified our plot selection to include representation of the two target community types (ponderosa-oak and mixed conifer) across the range of fire severities from multiple events. To maintain plot dispersion, we selected plots that were at least 200 m from the nearest adjacent plot. We sampled some plot locations from prior studies (Iniguez et al 2008; Maghran 2014), and seven plots with recent extensive hydrological data collected by collaborating researchers (Youberg et al. 2021; Barra et al. 2025).

Fire severity history for each plot in the Santa Catalina and Rincon Mountains was calculated using Soil Burn Severity (SBS) derived from dNBR.⁴ We calculated mean fire severity using the zonal statistics tool in ArcGIS Pro (ESRI, Redlands, CA), which assigns the average soil burn severity of the surrounding 3×3 pixel neighborhood (0.8 ha) to each 30-m pixel for each fire event. This procedure was followed 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 Rincon Mountains, we choose plots located in homogeneous burn severity areas, so the average severity of the surrounding 3×3 pixel neighborhood was the same as the pixel of interest.

In both the Santa Catalina and Rincon Mountains, we created categorical values for our plot stratification matrix using these averaged SBS values. In a typical SBS classification, a 0 value indicates that 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. We classified soil burn severity values for the 9-pixel average 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 the initial and subsequent fires.

Field methods

From May to September 2021, we sampled a total of 49 vegetation plots, 43 in the Santa Catalina Mountains and six in the Rincon Mountains (Fig. 3c; Table S-1). Each plot measured 50 by 20 m (0.1 ha), oriented perpendicularly to the local slope. In the Santa Catalina Mountains, 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 Rincon Mountains, no permanent tagging was done at the request of the National Park Service. If the plot vegetation did not correspond to the mapped community type, it was corrected according to US Forest Service Version 5 ERU Key for the Santa Catalina Mountains,⁵ which resulted in unequal sample sizes between ERU. Fire severity was 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 as trees < 10 cm height) and saplings (10 cm to 1 m height) were counted and identified to species within three 2 by 50 m belt transects; we tallied cones in the same belt transects to quantify seed dispersal into the plot. All live and dead trees > 1 m tall and ≥ 5 cm at diameter at breast height (dbh) were recorded, along with species and diameter. We calculated total live and dead basal area (m^2) for each plot (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. We measured distance to the nearest seed source (defined as any living mature conifer tree in any direction from plot center) using the laser hypsometer. The hypsometer was accurate to a range of 500 m, so one seed source farther than this distance was recorded as 500 m. Woody shrubs, trees < 5 cm dbh but > 1 m tall, resprouting oaks, perennial forbs, and succulents (*Agave* spp., *Opuntia* spp., *Yucca* 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 (25×10 m) due to extreme plot steepness or impassable vegetation conditions; the resulting data were rescaled to be consistent with other plot measurements.

⁴ Monitoring Trends in Burn Severity, <https://www.mtbs.gov/direct-download>, accessed 11/18/20.

⁵ Ecological Response Units of the Southwestern United States. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd609789.pdf

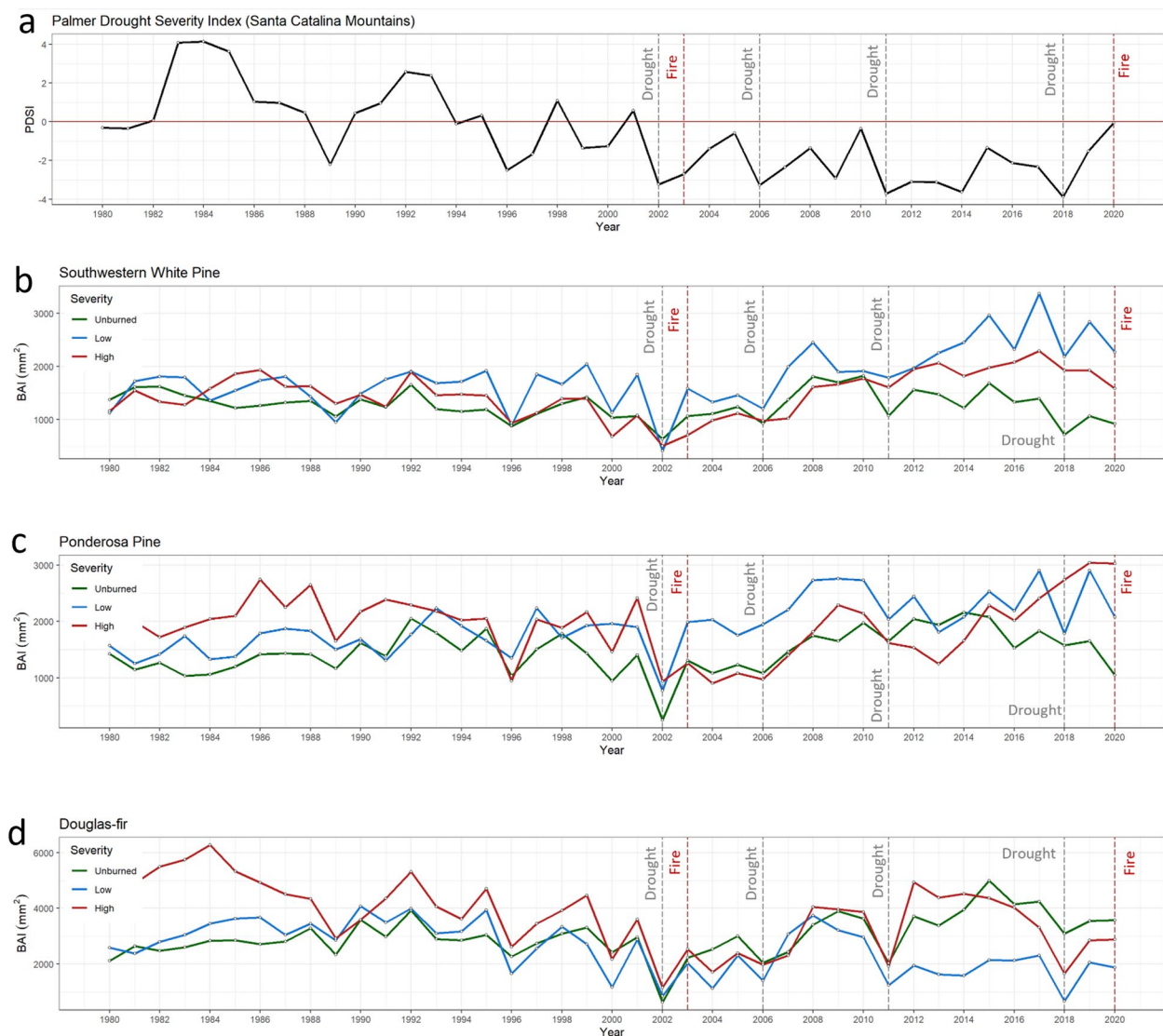


Fig. 4 PDSI and mean annual tree growth 1960–2020. **(a)** Palmer Drought Severity Index in the Santa Catalina Mountains from 1980 to 2020. No PDSI value from 2002 to 2020 exceeds 0, indicating drought conditions every year. PDSI is shown from 1960 to 2020 to show full extent of measurements used in regression modeling of BAI values. Mean basal area increment (BAI, in mm^2) is shown 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 details for severity class within species are provided in Table S-3

Persistence To quantify tree growth following fire exposure, we collected increment cores from 59 living trees in or adjacent to 19 of the Santa Catalina Mountains plots in 2021 (we did not collect increment cores from the Rincon Mountains). We sampled cores using 5.15 mm increment borers 40–60 cm above the ground surface from ponderosa pine, Douglas-fir, and southwestern white pine in plots that were unburned in the 2020 Bighorn Fire for each fire severity class in the 2003 Aspen Fire (unburned, low, and high).

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 Index⁶ (PDSI) for the study area (Fig. 4a) and recorded in Tellervo software.⁷ PDSI incorporates multiple climate variables that influence plant growth, including average and maximum monthly

⁶ WestWide Drought Tracker, wrcc.dri.edu, accessed 2/24/22.

⁷ Tellervo, <http://www.tellervo.org/>, accessed 9/1/21.

Table 1 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. Bold values indicate $p < 0.05$

Fixed effects	BAI (Dependent variable)		
	(PIST)	(PIPO)	(PSME)
Constant	1866.84 (1581.52, 2152.1)	1750.64 (1411.05, 2090.23)	2865.76 (2104.89, 3626.63)
PDSI	24.31 (− 16.30, 64.91)	9.43 (− 36.52, 55.39)	175.57 (87.22, 263.92)
Time Since Fire	− 6.45 (− 9.57, − 3.34)	0.71 (− 2.23, 3.64)	9.08 (3.58, 14.59)
Fire severity	− 3.71 (− 6.09, − 1.33)	− 1.38 (− 3.47, 0.71)	− 2.64 (− 5.72, 0.45)

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 v.4.0.2 (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 (or basal area increment, BAI) in mm^2 . BAI is a useful measure of annual tree growth as it minimizes age and size-related growth trends and requires no standardization for analysis (Fuchs et al 2019, Stern et al. 2023).

To assess controls on post-fire tree growth, we used the *lmer* function in the *lme4* package (Bates et al 2015) in R v.4.0.2 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 (Table 1). Individual trees were modeled as a random effect, with each tree allowed to have a varying intercept. The modeling period was 20 years longer than the periods of analysis or interpretation (1960–2020 for the modeling period compared to 1980–2020 for interpretation) to allow for a longer record of pre-fire climate and tree growth.

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 f th fire, and T_f is time in years since that fire. As there were no widespread wildfires in the high elevations of the Santa Catalina Mountains since at least 1927, the T_f for all trees starts at 33 years in 1960 as a conservative measure.

To determine potential effects of temporal autocorrelation, we compared two model types, one that accounts only for random effects, and one that includes a specific term for autocorrelation. In the *lmer* model, the slope of the relationship between the independent and dependent variables of each block must be the same (in both models, blocks are individual trees). In the second model, which was made using the *lme* function in R v.4.0.2 package *nlme* (Pinheiro et al. 2023), the slope of the relationship between the effect and explanatory variable is allowed to vary between blocks, thereby accounting for autocorrelation (Fule et al. 2022). The *lme* model used the same fixed effects and no random effects. We compared these models using difference in Akaike information criterion (AIC) (Johnson & Omeland 2004). The resulting models were similar overall; only the ponderosa pine model showing improved performance of the *lmer* model based on AIC results. Consequently, 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 jointly by fixed and random effects (Nakagawa & Schielzeth 2013), in R version 4.2.2 using the *rsquaredGLMM* function in the *MuMIn* package (Barton 2023). We calculated cumulative growth for 18-year pre-fire (1983–2001) and post-fire (2002–2020) periods by severity class for each species by summing annual average BAI over the given time periods.

Recovery To determine conifer recovery that occurred following the initial fire, we calculated an inferred conifer recruitment variable, C_{rec} , from plots in the Santa Catalina and Rincon Mountains that did not reburn after the initial fire event (all LU ponderosa-oak plots were from the Rincon Mountains; although LU mixed conifer plots in the Rincon Mountains burned more recently than those in the Santa Catalina Mountains, we found no systematic difference in recruitment patterns). C_{rec} was calculated at the plot level as the sum of conifer seedlings, understory conifers, and conifer trees. C_{rec} is an inferred variable because it includes both living and dead trees < 15 cm dbh (inferred to have regenerated following

the initial fire event, or only shortly before), as well as young trees > 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 evaluate the influence on C_{rec} of slope, distance to a seed source, burn severity (expressed by RBR), and bracken fern dominance. 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 (C_{rec} was modeled only in the Santa Catalina Mountains, as RBR values were not available for the Rincon Mountains).

Reorganization To assess community-level change, we calculated an importance value (IV) for each species in each plot in the Santa Catalina and Rincon Mountains. For overstory species, this was the sum of relative density, relative height, and relative basal area, for a total possible score of 300. For understory species, we summed relative cover and relative height for a total possible score of 200. The sum of these values for each functional group in each plot is a potential IV of 500; we averaged these plot-level functional group IVs to obtain an aggregate study area response by fire severity in 2002–3. Using these aggregate importance values, we created chord diagrams using the *circlize* package in R (Gu et al. 2014). Chord diagrams are often used in ecology to show transitions from one state to another; here, we used chord diagrams to visualize the outcomes by plant functional groups in each severity class from the earlier fire event (Spinger et al. 2018, Guiterman et al. 2022). The functional groups and terms used for overstory importance values are obligate seeder conifers (“Conifers”), resprouting trees (all oaks, and including for this purpose alligator juniper (*Juniperus deppeana* Steud.) (“Oaks”), and non-oak angiosperms (aspen, all maples, “NOA”). For the understory, functional groups were obligate seeder conifers, resprouting trees, bracken ferns, woody shrubs, and New Mexico locust. Only plots that were unburned since the initial fire event were included, to capture ongoing community transitions. We inferred incipient or transient reorganization where the relative proportions of plant functional groups varied among plots with differing fire severity in 2002–3, including unburned plots from those fires. To examine forest structural change following successive wildfires, we calculated stand density (stems/ha) and basal area (m^2/ha) and computed mean values for all combinations of severity in the initial fire and reburn.

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

	1983–2001	2002–2020	Change
Southwestern white pine			
Unburned	23,699	24,179	+ 2.0%
Low	30,572	38,653	+ 26.4%
High	36,843	29,617	+ 2.0%
Ponderosa pine			
Unburned	27,012	29,301	+ 8.4%
Low	33,090	41,661	+ 25.9%
High	39,332	34,359	– 12.6%
Douglas-fir			
Unburned	55,472	60,435	+ 8.9%
Low	59,186	38,222	– 35.4%
High	79,900	58,757	– 26.4%

Results

Our results record individual persistence and mortality, population recovery, and community reorganization following successive fires in the Santa Catalina and Rincon Mountains. Data for tree growth responses were only from the Santa Catalina Mountains; data for conifer recruitment and community reorganization results come from both mountain ranges.

Individual tree growth response and persistence

Growth (mean annual basal area increment in mm^2 , BAI) in southwestern white pine (Fig. 4b) and Douglas-fir (Fig. 4d) did not vary initially among severity classes until two successive drought episodes in 2006 and 2011, after which growth in different severity classes diverged. In ponderosa pine (Fig. 4c), 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-fir was lowest in low severity plots.

Modeling results indicate that annual growth in southwestern white pine during the overall modeling period (1960–2020) was affected negatively 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 variation 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), as well as by time since fire, with no effect of fire severity. A low marginal R^2 (0.03) indicates that Douglas-fir BAI was

not explained strongly by fixed effects in the model (conditional $R^2=0.50$).

Cumulative radial growth varied by species and severity class (Table 2). Radial growth in ponderosa and southwestern white pine in low severity plots was higher by 25–26% post-fire compared to the pre-fire period, despite greater overall drought conditions; growth in unburned plots of both species increased by smaller amounts (2–9%). Ponderosa pine growth decreased 12% in high severity areas, whereas southwestern white pine growth increased 2% in high severity areas. Douglas-fir growth increased in unburned plots but decreased in high and low severity burned areas.

Conifer recruitment

In plots that had not reburned since the initial fire event, recruitment was present in 70% of high severity plots, 66% of low severity plots, and 100% of unburned plots. Recruitment density varied from only a few seedlings to dense stands of young trees. Mean C_{rec} was 91% higher in unburned ponderosa-oak areas than in mixed conifer, and 225% higher in high severity ponderosa-oak areas over mixed conifer; recruitment was similar between the community types in low severity areas (Fig. 5a), although none of these differences was 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 ponderosa-oak communities, conifer recruitment consisted entirely of ponderosa pine and southwestern white pine, with the majority being ponderosa pine; southwestern white pine constituted at most 12% of recruitment at a single plot (Fig. 5b). In the mixed conifer, 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. 5c). LU plots in Rincon Mountain mixed conifer plots burned more recently (2014) than those in the Santa Catalina Mountains, but we found no systematic difference in recruitment values. In our model, C_{rec} was affected negatively by topographic slope ($F=4.66_{1, 39}$, $p=0.05$); neither fire severity in the initial fire event nor distance to a seed source was statistically significant (Table S-4). Average distance to a live conifer seed source was $26.7 \text{ m} \pm 63.3 \text{ m s.d.}$ (max 277 m) in ponderosa-oak plots, and $25.9 \text{ m} \pm 98 \text{ m s.d.}$ (max 500 m) in mixed conifer plots, and many plots had seed sources immediately adjacent. Cones were present in nearly all plots except those that burned at high severity in the earlier fire ($n_{U,L^*}=35$, mean = 13.75 cones/plot + 19.37 s.d.; $n_{H^*}=28$, mean = 0.71 cones/plot + 1.38 s.d.; $p < 0.0003$),

indicating seed dispersal from surviving trees (no significant differences existed between pine-oak and mixed-conifer plots).

No surviving recruitment was found in areas that reburned at high severity in the 2020 fire, with some exceptions in the ponderosa-oak community type (Fig. 6). Mean survivorship in areas that burned at low severity in the second fire was 29% in mixed conifer and 31% in ponderosa-oak although these differences were not statistically significant ($p=0.21$). We did not find second-year seedlings in any of plots during our 2021 field work, most likely due to the failure of the summer monsoon in 2020 (see the “Discussion” section).

Community reorganization

In the ponderosa pine-oak community type, unburned and plots that burned at high severity in 2002–3 had the most dominance of overstory conifers (Fig. 7a; Table 3). Low severity plots had higher importance values of overstory oaks and angiosperms, although overstory angiosperms comprised only a small proportion of this total. High severity burned 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 mixed conifer communities, conifers constituted 83–91% of overstory importance values in low and unburned plots, but only 59% in high severity plots (Fig. 7b, Table 3). Overstory oaks were not dominant in any severity class in mixed conifer; 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 co-dominant only in high severity plots and absent from low severity areas.

Discussion

In response to the interacting stressors of repeated fire and extended drought, we hypothesized limited persistence (expressed as reduced post-fire growth) in surviving trees, and reduced recovery by conifers in severely burned plots compared to fire- and drought-tolerant shrubs and oaks, potentially leading to incipient or transient ecosystem reorganization. We further hypothesized that these responses would manifest differently in the two vegetation types that are the focus of this study (Savage et al 2013).

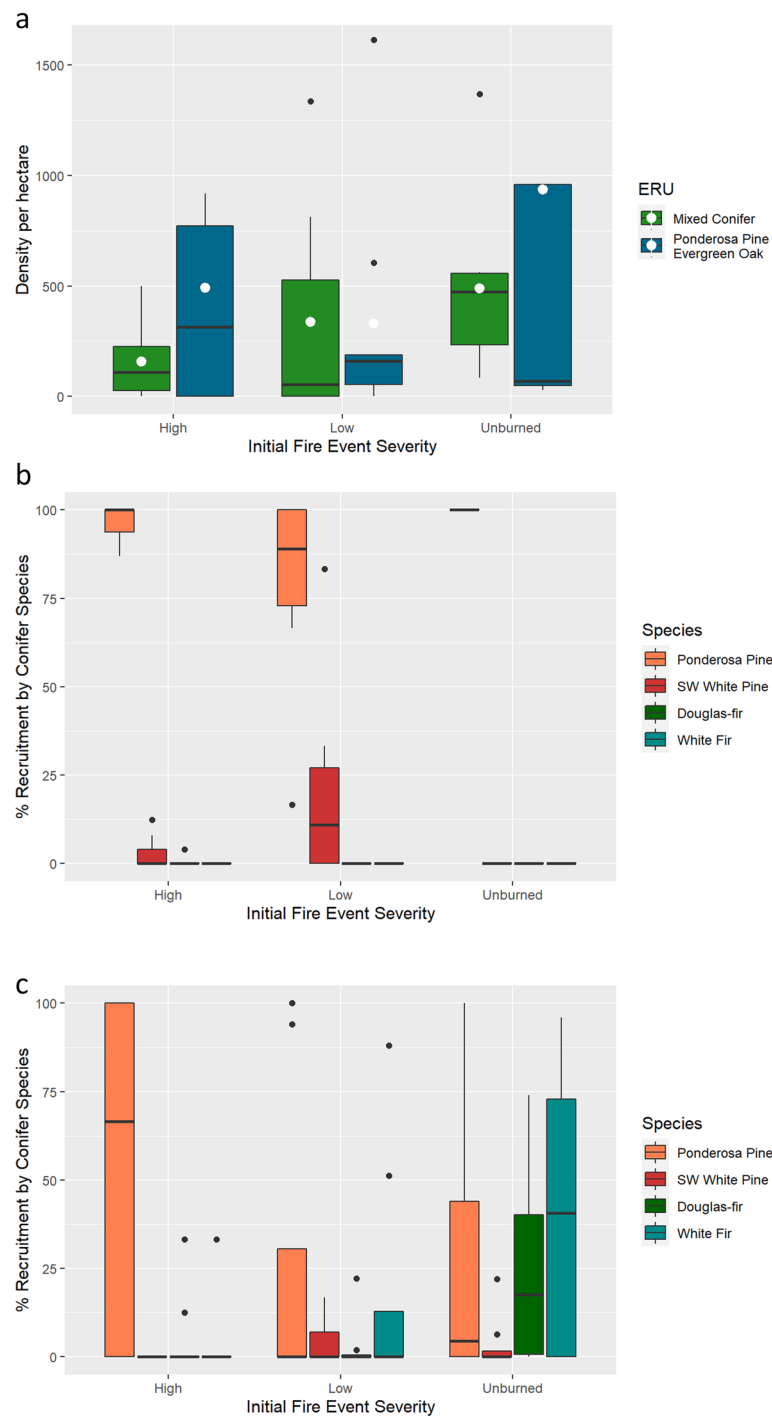


Fig. 5 Post-fire conifer recruitment in plots unburned since the initial fire. **a** Conifer recruitment (C_{rec}) in plots that were unburned since the initial fire event in the Santa Catalina and Rincon Mountains, by severity class. Percent of post-initial fire event recruitment by species in **(b)** ponderosa-oak and **(c)** mixed conifer communities. 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 indicate group means. In unburned ponderosa-oak **(a)**, an outlier with a value of 3580 stems/ha is included in analysis but not shown

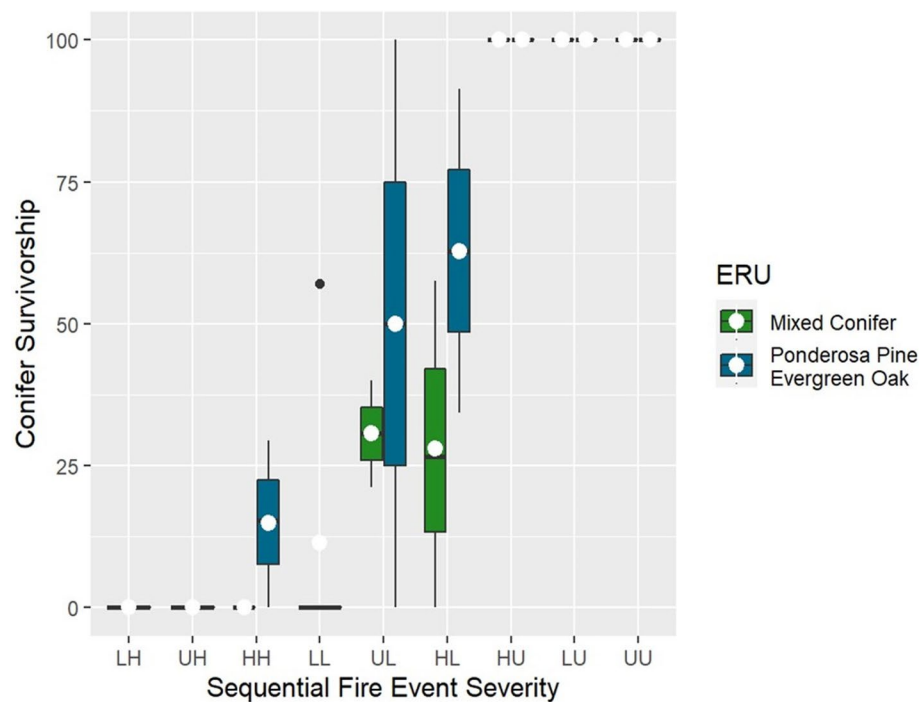


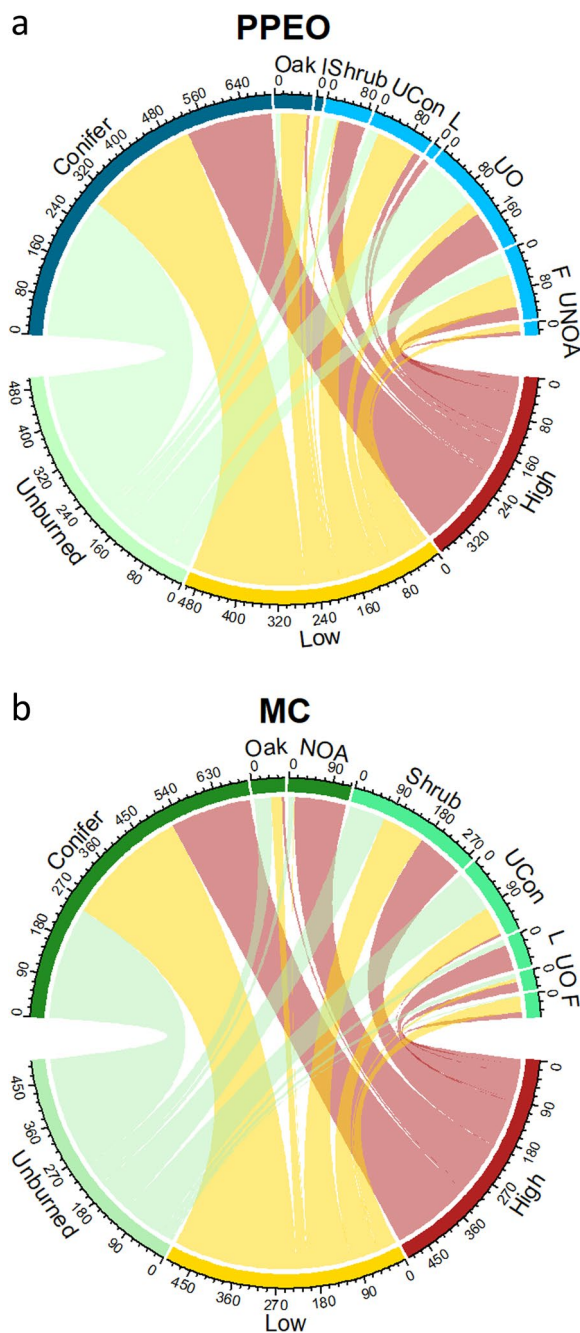
Fig. 6 Survivorship by sequential fire severity combinations in reburned plots in the 2020 Bighorn Fire. Black lines indicate the median; boxes contain the 25th to 75th percentiles, and whiskers indicate 10th and 90th percentiles; black dots indicate outlier values. White dots indicate group means. Fire severity abbreviations refer to the fire severity in the initial fire event and second fire event sequentially; see Fig. 3 caption for definitions. No recruitment was recorded in mixed conifer LL; in ponderosa-pine-oak, only LL is shown

Persistence: post-fire conifer growth

Growth in the three species in our study responded differently to drought and fire exposure. Basal area growth of ponderosa pine was affected more by fire exposure than by drought, although model results indicated non-significant effects (Table 1). 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). 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, suggesting persistence and growth recovery from damage at the individual level despite fire exposure. Ponderosa pine growth was the least affected by severe drought years of the three species, with some classes not manifesting reduced mean growth even in post-fire drought years (2006, 2012, 2018). Although this response contrasts with other work showing an increase in sensitivity to PDSI in ponderosa pine (Voelker et al 2019), these post-fire radial growth measurements indicate a degree of adaptive resistance to drought and fire among ponderosa and southwestern white pine individuals that survived the initial fire exposure.

The post-fire growth of both pine species in this study suggests possible release from overcrowding in the elevated forest densities characteristic of the period of fire suppression. Prior to 2002, almost all high elevation areas in the Santa Catalina Mountains had not burned in at least 75 years, 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 lacked pre-Bullock-Aspen plot-level stand density data, the low severity and unburned plots within our study contain relatively high stand density (mean LL, LU, UL, UU = 252 stems/ha; basal area = 24.1 m²/ha), a likely consequence of fire exclusion over the past century (Cocke et al 2005; Holden et al 2007) (*Supplemental Information: Post-fire vegetation structure response to reburning*).

Increased stand density resulting from fire exclusion has been associated strongly with inter-tree competition (Allen et al 2002; Marshall et al. 2019). Voelker et al. (2019) found that long-term fire suppression increased drought sensitivity in dry mixed conifer forests in OR, USA, by increasing stand basal area. Although research specifically into southwestern white pine is limited, studies of stand dynamics and disturbance ecology of the



◀ **Fig. 7** Chord diagrams of observed vegetation importance values 18–19 years post-fire in the Santa Catalina and Rincon Mountains in ponderosa pine-oak (**a**) and mixed conifer (**b**) communities. 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 segment between Oak and Shrub is NOA. Bottom variables in both panels indicate the plot fire severity (unburned, low, high) in the initial fire event: IV sum to 500 for each severity class (see text and Table 3, where these are expressed as percentages). Colored bands on the top of the panel indicate the post-fire proportions of plant functional groups in each fire severity class as measured in 2021: overstory functional groups in darker color, understory functional groups in lighter color. Only plots unburned since the initial fire are included

drought year since 2002 for all severity classes. All three severity classes were similar in growth until the 2011 drought year; by 2020, tree growth in unburned plots rebounded to pre-fire/drought conditions, higher than average growth in burned plots (Fig. 4). Cumulative growth in Douglas-fir trees in burned plots declined from the wetter pre-fire to drier post-fire period, whereas unburned tree growth increased. Model output and cumulative growth results suggest a negative influence of fire exposure in this species (Tables 1, 2). These conclusions are consistent with predictions of Douglas-fir responses to predictions increased drought stress in the Southwest (Welch et al. 2016; Rodman et al. 2020).

One consideration for interpretation of these tree growth results is our relatively small sample size (Table S-3) when stratified 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 were 4–8 trees. When possible, we cored trees within or adjacent to our established vegetation plots. A more comprehensive sampling design would support wider interpretation of individual species responses among severity classes. Despite this limitation, our findings highlight species differences in sensitivity to drought and wildfire exposure.

Post-fire recruitment and recovery

We recorded post-fire conifer recovery, as indicated by tree recruitment, in a majority of burned plots. Unburned plots in ponderosa pine-oak had the greatest mean recruitment, although this may be affected by an outlier plot recording over 300 seedlings. High C_{rec} values in high severity plots unburned in the Bighorn fire may reflect the presence of recruits that had already grown to be small overstory trees, instead of seedlings or understory trees that were more common in low or unburned

species suggest that thinning and low-moderate severity burns are beneficial for increasing overall resilience (Feeney et al 1998; Looney & Waring 2013; Knapp et al 2021). Southwestern white pine growth was affected negatively by time since fire in our model, which could indicate a trend of increasing stand density.

Douglas-fir growth was most affected by climate variation. Growth in all severity classes declined from 1990 to 2002; there were noticeable growth declines in each

Table 3 Mean importance values (%) of overstory and understory vegetation for mixed conifer (above) and ponderosa pine-evergreen oak (below), measured in 2021. Plot severity indicates soil burn severity (SBS) in 2002–3 Bullock/Aspen Fires for the Santa Catalina Mountains, and the 2003 Helens 2 fires for Rincon plots. Acronym definitions: *NOA* non-oak angiosperms, *U Conifer* understory conifer, *U Oak* understory oak, *U NOA* understory non-oak angiosperms (see Fig. 7a and b). Overstory and understory importance values each add to 100% respectively, summing to a total of 200% for each severity class. Totals may not add to 100% due to rounding

	Overstory			Understory					
	Conifer	Oak	NOA	Shrub	U Conifer	Locust	U Oak	Fern	U NOA
MC									
High	59%	2%	38%	52%	3%	28%	11%	6%	0%
Low	91%	8%	1%	48%	32%	0%	4%	17%	0%
Unburned	82%	12%	4%	40%	47%	7%	6%	1%	0%
PPEO									
High	96%	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%

plots. Because C_{rec} is log weighted, taller trees influence the statistic more than seedlings or understory conifers. In mixed conifer 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 (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); decreased infiltration and increased runoff lead to increased surface erosion and decreased available water for seedlings. A lack of plant cover following high severity wildfire may compound soil water limitation and further accentuate erosion (Robichaud et al. 2016; Neary and Leonard 2021). 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 and cone density were largely unaffected by distance to a seed source in our model, a variable found to be linked to conifer regeneration in many other studies (Haire & McGarigal 2008; Haffey et al 2018). 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, with multiple stages of recovery and reorganization often in a single location (Fig. 8). 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; Peeler and Smithwick 2020). Mean distance to a seed source was 26–27 m; all but three plots were within 100 m of a seed



Fig. 8 Post-fire landscape mosaic in the Santa Catalina Mountains showing the legacies of multiple fires, reflecting multiple phases of resilience. Photographer credit: Miles Fule

source. We measured distance to seed source regardless of slope position, so upslope and downslope seed (cone) dispersal were analyzed together; this procedure may have diluted the effect of dispersal distance, if only seed sources uphill from the measurement location were contributing seeds to plots in steep terrain. Conifer species in this study area do not form persistent soil seed banks; most seeds remain viable in the soil for less than 1 year and are thus only transient influences on subsequent recruitment compared to seed dispersal (Burns et al 1990; Korb et al 2019).

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. 8). Bracken ferns are aggressive post-fire colonizers and have sustained large homogenous stands in the Santa Catalina and Rincon

Mountains, and elsewhere in the Sky Island bioregion, for up to 19 years post-fire (JR Malusa, University of Arizona, personal communication; DA Falk, unpublished data). Prior research has suggested that bracken ferns inhibit germination and growth of conifers, possibly by outcompeting for resources (Ferguson & Boyd 1988), or from phytotoxins that kill conifer and other tree seedlings when absorbed, inhibiting root growth (Jatoba et al 2016). Research regarding favorable growth conditions for southwestern white pine seedlings also found decreased growth in areas with significant litter and duff cover (Goodrich & Waring 2017); bracken ferns are herbaceous perennial plants, and their aggressive growth can lead to large amounts of litter accumulation (Aira et al 2021; Gil da Costa et al 2024).

Community reorganization

We used a retrospective approach to assess post-fire vegetation change over the 18–19 years following the Bullock-Aspen and the Helen's 2 fires (7 years post-Deer Head fire in the Rincon Mountains). These changes were influenced differently by fire severity in the two communities we studied. In mixed conifer areas, unburned and low severity plots were dominated by conifers in both the overstory and understory (Table 3). In high severity areas, aspen accounted for roughly 40% of overstory tree co-dominance with conifers, although this pattern was largely concentrated in two plots, likely attributable to aspen's clonal resprouting habit, 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 most studies predict that conifers would eventually return to these areas. Overstory oaks were most important in low and moderate severity plots, and least in high severity plots. Understory oaks, locust, and shrubs had the highest importance values in high severity plots (Fig. 7b).

In ponderosa-oak communities, conifers were dominant in the overstory in all plot types but were mostly absent in high severity and unburned plots in the understory. Overstory oaks were most prevalent in low severity plots, as were understory conifers and ferns, while the highest importance values for shrubs were in high severity plots. Understory oaks were common across severity classes, but especially in low- and high severity plots (Fig. 7a).

In both community types, our estimates of overstory oak dominance may have been 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 as multi-stemmed plants,

often with no individual trunk substantially larger in diameter than the others (Minor et al 2017). Because we categorized a tree as overstory only if it was >5 cm in diameter, many of these recovering oaks were classified as understory. It is also possible that oaks were less common in the low severity Rincon Mountain plots compared to the Santa Catalina Mountains due to shorter time since fire (7 vs 18 years), although we found no community-level statistical differences between the two mountain ranges.

More time will be needed to evaluate whether these changes are transient successional trajectories or persistent alternative pathways (Falk et al. 2022; Seidl and Turner 2022). A growing body of ecological theory predicts the influence of plant functional traits on post-disturbance vegetation change (Noble and Slatyer 1980; Keeley and Pausas 2019; Marshall and Falk 2020). In the mixed conifer, dominance by aspen is a common transient reorganization following severe fire. In ponderosa-oak communities, fire exclusion has resulted in an increase in conifer stand density at the expense of overstory oaks and understory shrubs in long-unburned areas. While we are interested in conifer recovery due to its climate-dependent regeneration strategy, healthy stands also include areas of oak and shrub dominance (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 that these forests are healthier (Cocking et al 2014).

Post-fire recovering oaks may play a larger ecological role over time (Guiterman et al 2018; Huffman et al 2020). Barton and Poulos (2018) found persistent conversion from pine-oak forests to oak woodlands in the Chiricahua mountains in southeastern Arizona following high severity fire, linked in part to oaks' ability to resprout and tolerate increasing aridity (Poulos et al 2021a). 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).

Management implications

As wildfires become larger and potentially more severe, the ability of ecosystems to persist in their present form is increasingly challenged. Drought stress on trees increases their sensitivity to fire exposure and reduces the capacity for persistence, leading to elevated effective fire severity (van Mantgem et al. 2013, 2018). Growing exposure to high severity fire area raises the probability of large areas of ecosystem reorganization, which in many cases may become irreversible as climate continues to warm (Coop et al. 2020; O'Connor et al. 2020; Guiterman et al. 2022). These issues raise profound questions for land

managers attempting to maintain ecosystem integrity and sustainability.

In this study, we examined evidence for the main expressions of post-fire resilience, and the mechanisms that might contribute to them: persistence, recovery, and reorganization. Sampling across two ecosystem types 18–19 years post-fire, supplemented by sampling of first-year conditions following a 2020 fire in the Santa Catalina Mountains, we found extensive expressions of all three processes occurring simultaneously. Fire severity was a primary driver of the form of resilience manifested, although our observations indicated considerable complexity in the post-fire response.

Managers must always contend with the unpredictability of reburns and climate variation. In 2020, the Bighorn fire left a complex post-fire mosaic over nearly the entire upper elevation of the Santa Catalina Mountains, including most of our study area. While the fire left some large contiguous high severity patches, 92% of the area 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, reburning many areas that had burned at high severity 18 years prior. Extensive patches of low and moderate severity fire left scorched needles and bare soil within the complex Santa Catalina topography, which includes large areas of rock outcrops and other non-burnable areas. We stratified our sampling design to capture the short-term effects of this reburn mosaic on tree recruitment and forest structure.

In the spring and foresummer of the following year, recovery was underway in many areas: understory growth had initiated, with woody shrubs, oaks, and bracken ferns the first perennial plants to send up new growth. Recruitment of conifers in burned areas was largely absent, possibly as a result of 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 the Santa Catalina Mountains 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 wettest August on record.⁸ That summer also provided a different perspective on the processes and pace of post-fire recovery. In our 43 field plots in the Santa Catalina Mountains, we found substantial conifer recruitment in areas unburned in the Bighorn Fire (Fig. 6). In some plots, areas that had burned at high severity two decades previously were already dominated

by young conifer trees that had regenerated post Bullcock-Aspen. In others, especially areas that had burned at high severity twice, stands of bracken ferns or *Ceanothus* formed dense stands. In most areas, we found an ecosystem in the early stages of complex recovery processes that will play out over years and decades.

Our results confirm the importance to managers of reintroducing low-moderate severity fire to forests with a history of fire exclusion (Kolb et al 2007). Areas with low severity fire had high survivorship (persistence) and moderated stand density, reducing competition and favoring overstory tree vigor as well as development of the species-rich understory (Laughlin & Fule 2008; Korb et al 2020). Conifer seedlings had high survivorship in all combinations of reburn severity except for high severity areas the previous year (Fig. 6). Recruitment success also depends on yearly climate variation: young trees are vulnerable to extended droughts and elevated temperatures, conditions that are likely to become more common as climate continues to change (Lalor et al 2023; Crockett & Hurteau 2024). Nonetheless, our observations suggest that natural recovery may be sufficient in many areas, although the pace of recovery may vary with fire severity.

In terms of landscape management, our results indicate the merits of spatially and temporally heterogeneous fire treatments with persistence, recovery, and reorganization all present and contributing to ecosystem function (Fig. 8). While some shifts in species and trait dominance may appear undesirable, especially because they are occurring in part as a result of human-caused climate change, patches of oak or shrub dominated area in the Southwest are not inherently negative outcomes; these native species 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 and cultural value (Barton & Poulos 2018; Guiterman et al 2018). On landscape scales and in mountain topography as steep and complex as the Santa Catalina and Rincon Mountains, widespread human intervention to prevent these transitions is likely not feasible in the long term if climate continues to change. Managers can help guide the ability of ecosystems to regenerate and regulate themselves, with the understanding that some transitions to different communities may reflect ongoing long-term expressions of ecosystem resilience.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00419-7>.

Supplementary Material 1:

Table S-1A. Santa Catalina Mountain ponderosa-oak plots with associated fire and topographic characteristics.

⁸ Data from National Weather Service, <https://www.weather.gov/twc/TucsonClimateReports>

Table S-1B. Santa Catalina Mountain mixed conifer plots with associated fire and topographic characteristics.

Table S-1C. Rincon Mountain ponderosa-oak plots with associated fire and topographic characteristics.

Table S-1D. Rincon Mountain mixed conifer plots with associated fire and topographic characteristics.

Table S-2. Tree density, mortality, and basal area by community type (ERU), and the sequence of fire severity in successive fire exposures from plots from the Santa Catalina and Rincon Mountain study areas. Within ERUs, plots are listed in order of the severity of the more recent fire.

Table S-3. Sample size and average DBH (cm) of trees increment cored in the Santa Catalina Mountains, by species and burn severity.

Table S-4. C_{rec} modeling results.

Supplementary Material 2: Supplemental information: Post-fire vegetation structure response to reburning.

Acknowledgements

The authors thank Luke McGuire, Katherine Predick, Ann Youberg, Rebecca Beers, Craig Rasumussen, and Margaret Evans for their help and guidance with planning the study and analyzing and interpreting the data. Additional thanks to Lyra Rahner, Jo Martinez, Eamonn Mazur, and Camille McCollum for their excellent work in field data collection. The authors also thank anonymous reviewers for insightful and helpful comments, which contributed to improvement of the original manuscript.

Authors' contributions

MF and DF co-conceived and designed the study. MF led field data collection and data analysis and wrote the manuscript. DF contributed to study planning and design, data interpretation, and manuscript development and revisions.

Funding

Funding was provided by the Arizona Institute for Resilience, the USDA Coronado National Forest, Pima County Regional Flood Control, University of Arizona College of Science, and the University of Arizona Laboratory for Tree Ring Research.

Data availability

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

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 10 February 2025 Accepted: 23 September 2025

Published online: 06 November 2025

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