

Mexican mixed-species forest shows resilience to high-intensity fire

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Abstract

In the aftermath of a high-intensity wildfire in La Michilía Biosphere Reserve, Mexico, an initial study suggested a shift from an oak-pine forest to a grass-savanna ecosystem. We conducted repeated measurements on 60 permanent plots 1, 5, 10, and 20 years after the original wildfire at paired burned and unburned study sites to capture spatial and temporal dynamics in forest composition and structure. We found that the burned site regained most pre-wildfire characteristics two decades after the wildfire. The ongoing regeneration in the burned site suggests that despite the remaining differences, the site is approaching a complete recovery, with forest characteristics analogous to the unburned site. Our findings indicate that the combination of seeders' wildfire resistance and resprouters' post-wildfire sprouting strategies in mixed-species forests provides high resilience to high-intensity wildfire. Moreover, protecting La Michilía as a biosphere reserve and heightened public awareness of the natural environment likely played an indispensable role in facilitating the recovery of the post-wildfire ecosystem.

Key words: sprouting, seeding, climate, oak-pine forest, repeated measures

Introduction

Post-wildfire recovery is a complex process involving regrowth and re-establishment of plant communities in fireprone ecosystems. Resilience, in this context, refers to the ability of a plant community to recover and return to its original state following a disturbance such as fire (Angeler et al. 2019; Falk et al. 2022). Plants in fire-prone ecosystems have evolved mechanisms or adaptations to fire, such as protecting the cambium or the new shoots with thick bark and long needles (Keely et al. 2011; Keeley 2012; Pausas 2014; Falk et al. 2022) or avoiding torching by providing discontinuity between surface fuels and the tree canopy with self-pruning of lower branches (Falk et al. 2022). Obligate seeders (OS) rely on seed germination to colonize a burn area, producing large numbers of seeds stored in seed beds in mineral soil or branches and requiring a signal to stimulate post-fire germination (Keeley and Pausas 2022). In some cases, the signal comes from chemical compounds in the smoke (Pausas and Lamont 2022), for others with serotinous cones, the high-fire temperatures are needed to melt the resin that seals the pinecone scales to release the seeds (Johnson and Gutsell 1993; Moya et al. 2008). In contrast, resprouting species are characterized by a multistem habit and the ability to quickly regrow from surviving buds above- or below ground after being damaged or killed above ground (Fernandes et al. 2008; Bond and Midgley 2001; Clarke et al. 2013). Broadly, fire-adaptive traits that allow a species to withstand fire foster low-intensity surface

fires (He et al. 2012), while traits such as serotinous cones or high flammability (heat release) foster stand-replacing fires (Pausas and Lamont 2022). Resprouters are abundant in ecosystems characterized by moderate to high intensity and frequent fires (Lloret et al. 2005; Rodríguez-Trejo and Myers 2010; Keeley et al. 2011; Pausas and Keeley 2014). In oak-pine forests, dominant woody species have contrasting fire strategies: resistance-persisting after fire by survival or from propagules-or resilience-enduring after fire by sprouting from the top-killed stem (Barton 1999). Changes in the fire regime, such as increased frequency and intensity, tend to favor resprouters over seeders (Lamont et al. 2011; Baudena et al. 2019), although too short fire intervals can deplete the resprouters' stored reserves, reducing their ability to recover (Díaz-Delgado et al. 2002; Fairman et al. 2019). Climate change can significantly impact the ability of resprouters and seeders to recover from a fire. The increased frequency and intensity of fires associated with a warming climate may result in conditions less conducive to the survival of biological legacies (Johnstone and Chapin 2006; Falk et al. 2022; Harvey and Enright 2022; Ooi et al. 2022; Taber and Mitchell 2023). These legacies can influence the structure and composition of post-fire vegetation communities by affecting seed availability, soil properties, and the persistence of vegetation (Drever et al. 2006; Seidl et al. 2014; Johnstone et al. 2016). Additionally, higher temperatures and altered precipitation patterns may impact the ability of resprouters to regrow from underground structures and the germination and establishment of seeders, leading to diversity loss, landscape heterogeneity, and even transition to alternate stable community states (Johnstone et al. 2016; Barton and Poulos 2018; Coop et al. 2020; Villareal et al. 2020; Poulos et al. 2021; Falk et al. 2022; Harvey and Enright 2022; Tangney et al. 2022). The effects of climate change are particularly pronounced in ecosystems that are already under stress from other human activities (Loehman et al. 2020; Halofsky et al. 2020) and those with high fuel loads (Fulé et al. 2005). In these systems, it is even more critical to understand how fire, plants, and climate interact since uncharacteristic trends can trigger changes in fire regimes, for example, amplifying extreme fire behavior (Halofsky et al. 2020). The presence of resprouters and seeders in an ecosystem may be vital to adapting to the challenges posed by fire and climate change (Bond and Keeley 2005; Pardos et al. 2021) since the diversity of regeneration strategies can increase the overall resilience of the ecosystem. However, Barton and Poulos (2018) and Poulos et al. (2021) reported a transition of pine-oak ecosystems to oak shrublands in the Madrean Sky Islands of Arizona after recent moderate to high-severity fires. In contrast, severely burned pine forests in Jalisco, Mexico, rapidly recovered to dense stands (Quintero-Gradilla et al. 2019). Thus, understanding the complex interactions between fire, vegetation, and climate is crucial for developing effective management strategies to mitigate their impacts and conserve biodiversity.

Repeated measurements are valuable for understanding long-term vegetation dynamics and ecosystem thresholds, as this method accurately assesses changes in vegetation composition, structure, and function over time. The short-term effects of a high-intensity wildfire in the buffer zone of the Michilía Biosphere Reserve (MBR) in April 1996 indicated a possible transition from oak-pine forest to grass-savanna (Fulé et al. 2000). The forest was previously characterized by relatively frequent surface fires (mean fire interval \sim 5 years) prior to \sim 1930 when a change in land management led to extended fire exclusion (Fulé and Covington 1999). Fulé et al. (2000) established a study site to investigate its effects 1 month after the wildfire by sampling two nearby 30 ha study sites in the oak-pine forests in 1996 and repeated in 1997, one burned and an adjacent one unburned with similar prewildfire conditions. The 1996 wildfire appeared more severe than the historical fire regime, with the majority of plots experiencing top-kill and some experiencing complete tree mortality. However, the soil seemed only partially disturbed. Numerous living trees still stood after the wildfire, with many resprouting from the crown or the root collar 1-year postwildfire (Fulé et al. 2000). Considering that forested ecosystems' composition, structure, and functions typically recover over mid-to-long timeframes, Fulé et al. (2000) theorized that the burned area would eventually return to a stage similar to the pre-wildfire conditions because of the survival and recovery of the vegetation. Using the same plots established in 1996 by Fulé et al. (2000), we remeasured forest patterns 5-, 10-, and 20-year post-wildfire. We aimed to (1) assess the trajectory of the overstory structure and composition, (2) evaluate if there were changes in the overstory dominance two decades after the fire, and (3) determine the extent to which, 20 years after the wildfire, the burned site has regained its pre-wildfire characteristics. By tracking these variables, the study seeks to provide a more comprehensive understanding of how ecosystems recover from intense wildfires in oak-pine forests found in Madrean ecosystems on both sides of the US-Mexico border. Many prior studies examining the effects of intense wildfires in oak-pine forests are focused on the US. There is a notable scarcity of evidence concerning wildfire effects in the Mexico site, as indicated by the limited research conducted by Fulé et al. (2000), Rodríguez-Trejo and Fulé (2003), Martínez-Hernández and Rodríguez-Trejo (2008), Rodríguez-Trejo and Myers (2010), and Alanís-Rodríguez et al. (2012). Remarkably, it is particularly understudied over extended periods; to our knowledge, only two published studies exist evaluating post-fire effects. One of these studies is an 18-year post-fire examination of an endangered pine species conducted in Cerro El Potosí, Nuevo León (Arévalo et al. 2017). The other is a 9-year post-fire study carried out in a pineoak forest at Chipinque Ecological Park, Nuevo León (Alanís-Rodríguez et al. 2010; Alanís-Rodríguez et al. 2012), although neither of these studies involved repeated measurements. Long-term information is crucial for resource managers, as it can help them make informed decisions about post-fire management for conservation and adaptation strategies on these ecosystems.

Materials and methods

Study area

The World Network of Biosphere Reserves of the MAB P rogramme consists of 738 designated areas, 41 in Mexico. The MBR is located in the Sierra de Michis, on the eastern slope of the Sierra Madre Occidental, Durango State, Mexico, along the border of Durango and Zacatecas, and was established in 1977 to sustainably use resources in the buffer zone while preserving the core area of Cerro Blanco. As reported on the UNESCO website, the MBR consists of a 9423 ha core area managed for biological conservation and property of the state of Durango, a 26 510 ha of "buffer zone" managed under private or communal ownership (ejido), and approximately 97 149 ha of "transition zone" managed under private ownership (UNESCO 2018).

The Madrean oak-pine forests of Mexico are a global center of diversity due to a combination of pronounced climatic zonation and the overlapping location between temperate and tropical regions (Felger and Wilson 1994). The MBR spans an elevation range of 1734 to 2950 m and has a variable climate that ranges from semi-arid temperate in the northern buffer zone to subhumid temperate in the rest of the reserve. Annual precipitation also varies with elevation and ranges from 600 to 860 mm, with higher rainfall at higher elevations (Gonzalez-Elizondo and Gonzalez-Elizondo 1993). A wet season occurs between June and September (Fig. 1), followed by a light rainy season with occasional snowfall at higher elevations from October to January. The dry season occurs from February to May and November to December (Fig. 1). Vegetation is organized from lower-elevation oak savannas and grasslands, through mid-elevation oak-pine forests,



Fig. 1. Monthly temperature (a) and precipitation (b) from 1970 to 2015 from the Súchil weather station (elevation 2265 m). Error bars represent the standard deviation. Average temperature declined from 1970 to 1997 but returned to 1970s temperatures by the late 2000s. Average precipitation is highly variable, showing a slight decrease in the 1990s with a 31% average precipitation increase by the 2010s with respect to the 1970s. The 1970–2015 climograph (c) shows a dry season from February to May and October to December. Data source: CONAGUA National Network.



to higher-elevation pine–oak forests (Gonzalez-Elizondo and Gonzalez-Elizondo 1993).

The MBR oak-pine forest overstory was mainly composed of oaks, pines, cypresses, and heaths, with diverse grasses and sedges in the understory. Two oaks *Quercus eduardii* Trel. and Quercus hartwegii Benth. (=Q. obtusata Bonpl.), five pines Pinus arizonica Engelm. (=P. ponderosa), Pinus cembroides Zucc., Pinus engelmannii Carr., Pinus leiophylla Schltdl. & Cham. (=P.chihuahuana Engelm.), and Pinus teocote Schltdl. & Cham., a cypress Juniperus deppeana Steud., and a heath Arbutus arizonica (Gray) Sarg. were the most abundant. Their post-fire strategies are summarized in Table 1. Frequent, with a mean fire interval ranging from 6.33 to 9.94 years, and low-to-moderate intensity wildland fires were prevalent in the MBR from dry lightning strikes and traditional use of fire until it was excluded approximately in the early 1930s (Fulé and Covington 1999). Despite Mexico's endorsement of a wildfire suppression strategy, challenges related to economic and social factors have hindered the aggressive enforcement of this policy. Prior to the 1996 wildfire, the last recorded fire occurred in 1965 and in 1950 in the unburned and the burned site, respectively (Fulé and Covington 1999).

Field sampling

We re-sampled 60 permanent plots in the buffer zone of the MBR at approximately 2245 m elevation in the burned and unburned study sites 5 (2001), 10 (2006), and 20 years (2017) after the wildfire (Fig. 2). The 2017 measurement was conducted in early March, ahead of the 2017 growing season, so we considered it to represent the 2016 growth. Center plots were established in 1996 and remeasured in 1997 on a 100 x 100 m grid spacing (Fig. 3). For each 200 m² circular fixedarea plot, we re-measured live tree overstory characteristics (species, condition class, diameter at breast height, and total tree height) and cut trees by species, and their diameter at stump height. We also measured dead woody biomass, litter (distinguishable plant parts like bark and twigs scattered on the forest floor), and duff (partially decomposed organic matter found between the litter layer and the A1 soil horizon, with minimal similarities to the original plant structure), along a planar transect from the center plot in the direction established in 1996. Additionally, we tallied tree species regeneration across height classes (less than 40 cm, between 40.1 and 80 cm, and between 80.1 and 130 cm) over a nested 40 m² circular plot. For the complete procedures of field sampling methods, please refer to the Field Sampling section in Fulé et al. (2000).

Statistical analysis

We classified species according to their post-fire strategies *sensu* Pausas and Keeley (2014) framework, which categorizes plants into three groups: obligate resprouters (OR), plants that resprout as the primary mean of regeneration; facultative seeders (FS), plants that can regenerate through multiple mechanisms; or OS, plants that rely on seeding for population regeneration (Pausas and Keeley 2014) (Table 1).

We calculated descriptive statistics for key forest metrics to assess the forest changes after the wildfire. Metrics for live trees included tree density (TPA, number of trees ha^{-1}), regeneration density (number of young trees ha^{-1}), basal area (BA, $m^2 \cdot ha^{-1}$), each species' ecological importance value (EIV) determined by an equal combination of each tree species' relative density and relative basal area (Curtis and McIntosh

Table 1. Tree species in the study sites.

Species	Code	Tree taxa	Fire strategy	Sources	
A.arizonica	ARAR	Heath	Obligate resprouter	Barton (2005)	
J. deppeana	JUDE	Cypress	Facultative seeder	Rodríguez-Trejo et al. (2019)	
P. arizonica	PIAR	Pine	Obligate seeder	Rodríguez-Trejo and Fulé (2003)	
P. cembroides	PICE	Pine	Obligate seeder	Rodríguez-Trejo and Fulé (2003)	
P. engelmannii	PIEN	Pine	Obligate seeder	Ávila-Flores et al. (2016)	
P. leiophylla	PILE	Pine	Facultative seeder	Rodríguez-Trejo and Fulé (2003)	
P. teocote	PITE	Pine	Obligate seeder	Juárez Bravo et al. (2012)	
Q. eduardii	QUED	Oak	Obligate resprouter	Rodríguez-Trejo and Myers (2010)	
Q. hartwegii	QUHA	Oak	Obligate resprouter	Rodríguez-Trejo and Myers (2010)	

Fig. 2. We captured repeated photographs of each plot to document changes in the physical environment over time. In 1996, we took the first shot from 7.98 m to the north of each plot, facing toward the plot center. Subsequently, we took repeated photographs using a printed copy of the previous photograph as a reference for framing the shots. Images source: Peter Z. Fulé.



1951), the proportion of strategies and the ratio of seeders to resprouters (Lloret et al. 2005), and the Gini-Simpson index of tree species (GSI, Gini 1912; Simpson 1949). To reconstruct the conditions prior to the wildfire for the burned area, we followed the methods outlined in Fulé et al. (2000), summing live plus recently killed tree condition classes in the 1996 inventory to estimate forest characteristics prior to the 11 April 1996 wildfire. Metrics for regeneration included density per hectare and species by height class. Metrics for dead woody material included tree stump density, calculated by subtracting the previous inventory stump density per hectare (in cases where stump density per hectare was higher in the previous inventory, the stump density for the inventory was estimated as zero to reflect no new stumps), the dead woody biomass (Mg·ha⁻¹) for each fuel class, calculated using the approach of Sánchez and Zerecero (1983), and litter and duff. We quantified the means and variability (sem: standard error of the mean) of all forest metrics by inventory year and site.

We used R statistical software to assess changes between pre-wildfire and 20 years after the wildfire species EIV. We performed mixed-effects models, widely used to analyze repeated measures, with the "lme" function in R ("nmle" package version 3.1–162). The response variable in our models was "EIV," whereas the explanatory variables consisted of "Species," "Condition," and "Time." In addition, we treated "Plot" as random effects nested in "Site" (~1|Site/Plot). We used the corARMA class function in R ("nmle" package version 3.1–162) to account for autocorrelation between inventory years. We built simple models with only one explanatory term and more complex multivariable models with and without interactions. The models were built according to biological, spatial, and temporal hypotheses (Table S1). Then, we compared the goodness of fit between models and identified **Fig. 3.** Study area in La Michilía Biosphere Reserve (MBR), where **Fulé et al. (2000)** established 30 plots in each burned and unburned study site. Figs was created using ArcGIS Pro version 3.2.0 and assembled from the following sources: <u>ESRI World</u> <u>Countries Generalized</u> and <u>Mexico National Institute of Statistics and Geography (INEGI)</u> census data. Base map contours created from 1 arc sec 30 m resolution DEM courtesy of USGS 3 D Elevation Program.



the best model by examining whether there was a significant drop in AIC (Table S1). Finally, we used Tukey's Honest Significant Difference (HSD; $\alpha = 0.05$) post hoc test to evaluate the differences in species' family dominance means between sites and time since fire.

We used a non-metric multidimensional scaling (NMDS) ordination analysis followed by a non-parametric statistical test to determine whether the burned site had recovered its pre-wildfire characteristics. This approach allowed us to identify patterns in differences between pre- and post-wildfire forest characteristics. We conducted our analysis using the "metaMDS" function in R ("vegan" package version 2.6-4; Oksanen et al. 2022). Our dataset consisted of 19 forest structural variables by site, plot (n = 60), and inventory year. These variables included live tree density (trees ha⁻¹), live tree basal area $(m^2 \cdot ha^{-1})$, fine woody debris—woody debris with a diameter between 0.01 and 7.62 cm (FWD, Mg·ha⁻¹), coarse woody debris-down logs with at least 7.62 cm in diameter (CWD, Mg·ha⁻¹), litter depth (cm), duff depth (cm), EIV for nine tree species, and the proportion of OS, OR, and FS, and GSI. Since the variables have different units, we standardized our data by calculating relative values using the "decostand" function in R ("vegan" package version 2.6-4; Oksanen et al. 2022). Next, we used Euclidian dissimilarity to calculate the distance matrix and performed a two-dimensional NMDS. To verify significant differences between sites and inventory years, we analyzed similarity using the "anosim" function, a non-parametrical statistical test performed in R with 999 random permutations, randomly assigning samples to groups and indicating the percentage of simulated values greater than the observed "R-value" ("vegan" package version 2.6–4; Oksanen et al. 2022). The "anosim" statistic R compares the similarity between and within groups using ranks; when the null hypothesis is true, R is close to zero, and as the departure from the null hypothesis increases, R has a larger positive value when samples within groups are more similar to each other than to samples in other groups ("vegan" package version 2.6–4; Somerfield et al. 2021). Finally, we use pairwise permutation MANOVAS ($\alpha = 0.05$) post hoc test ("pairwise.perm.manova" function in "RVAideMemoire" package version 0.9–83) to evaluate the differences within "Site" and inventory years "Year."

Results

Trajectory of the forest structure and composition

The impact of the 1996 wildfire on the forest was most evident in the overstory, as illustrated by repeated photographs (Fig. 2). In the burned area, there was a significant decrease in tree density and basal area a year following the wildfire, with reductions of 88.9% and 67.4%, respectively. However, tree density and basal area increased rapidly 5 years after the wildfire. After a decade, the tree density reached 1625 trees ha⁻¹ (\pm 265.2) and the tree basal area increased to 6.9

Fig. 4. Basal area, tree density, EIV by tree species family, inventory year, and site (burned; unburned). Tree density and basal area of live trees in the burned site were reconstructed following the methods outlined in Fulé et al. (2000). The vertical dashed red line represents the fire event.



 $m^2 \cdot ha^{-1}$ (±0.8). Two decades after the wildfire, tree density stabilized at 1268.3 trees ha^{-1} (±265.2) while the tree basal area continued to increase to 7.8 m² \cdot ha⁻¹ (±0.9), representing 65% of the pre-wildfire basal area. In contrast, the unburned site experienced a gradual decline in tree density from 840 trees ha⁻¹ (\pm 100.7) in 1996 to 640 trees ha⁻¹ (\pm 85.6) in 2017 (Fig. 4a; Fig. S1), while the tree basal area remained relatively constant over time (Fig. 4b). Both sites remained predominantly dominated by oak species. The order of dominance in both sites was followed by pines, cypress, and heath. In the unburned site, cypress gained dominance over pines in the last two decades (Fig. 4c). It is worth noting that P. teocote was only found in the burned site while P. arizonica and P. cembroides were only found in the unburned site; however, these species represented a small fraction of the overstory and remained unchanged throughout the study. The proportion of OS (Table 1) was consistently higher in the burned site compared to the unburned site. Post-wildfire, the proportion of OR decreased from 80% to 58.5% in the burned site but quickly rebounded to 83%, 91%, and 85% at 5-, 10-, and 20-year

post-wildfire, respectively. The unburned site experienced a slight decrease in OR from 56% in 1996 to 48% in 2017 and an increase in FS from 39% to 49% over the same period (Fig. 5). The ratio of seeders to resprouters remained low in both sites, increasing in the burned site immediately post-fire but returning to a similar ratio two decades later (Table 2). The diversity of tree species in the overstory declined in the burned site immediately after the wildfire GSI = 0.22 (\pm 0.06) but fully recovered to pre-wildfire levels 20 years later, GSI = 0.59 (\pm 0.04). In contrast, the unburned site's species diversity remained relatively stable, with GSI = 0.68 (\pm 0.03) by 2017 (Fig. 6).

Pines and oaks were the most harvested. Cut tree diameters at stump height ranged from as little as 0.4 and 0.7 to as much as 46 and 55 cm for pines and oaks, respectively. Prior to the wildfire and up to 5 years post-wildfire, the burned site experienced higher tree harvesting than the unburned site, up to 32.9 (\pm 9.7) and 21.6 (\pm 9.2) trees ha⁻¹ in 2001, respectively. However, a decade after the fire, tree harvesting became higher in the unburned site compared to the burned **Fig. 5.** Proportion of species by strategy by site (burned; unburned) and inventory year. Tree density of live trees in the burned site pre-wildfire reconstructed following the methods outlined in **Fulé et al.** (2000). Tree taxa were classified according to their postfire strategies *sensu* **Pausas and Keeley** (2014) into three post-fire groups: obligate resprouters (OR), facultative seeders (FS), or obligate seeders (OS). The vertical dashed red line represents the fire event. The proportion of OS was consistently higher in the burned site compared to the unburned site. After the wildfire, the proportion of ORs initially decreased in the burned site but rebounded quickly. In contrast, the unburned site experienced a slight decrease in ORs and an increase in facultative seeders over the study period.



 Table 2. Seeders to resprouters ratio by site and inventory year

Site	1996	1997	2001	2006	2017
Burned	8	27	6	4	5
Unburned	24	23	25	23	26

Fig. 6. Gini Simpson diversity index (GSI) for tree species by site (burned; unburned) and pre-wildfire (PB), one (1), five (5), ten (10) and twenty (20) years post-wildfire. Tree density of live trees in the burned site pre-wildfire was reconstructed following the methods outlined in Fulé et al. (2000). The vertical dashed red line represents the fire event. The diversity of tree species in the overstory declined in the burned site immediately after the wildfire but fully recovered to pre-wildfire levels 20 years later. The unburned site remained relatively stable.



site, with 42.9 (\pm 9.9) and 34.9 (\pm 9.7) trees ha⁻¹, respectively. Harvesting decreased to 5.9 (\pm 2.1) and 11.7 (\pm 3.1) trees ha⁻¹ in the burned and unburned sites two decades after the wild-fire (Fig. S2).

Species regeneration occurred steadily, with oaks dominating both burned and unburned sites (Fig. 7). Regeneration of oaks was generally less in the burned site. A year postwildfire, oaks regenerated massively immediately after fire; however, many young trees died a decade after the wildfire before reaching the sapling stage. Two decades after the wildfire, the burned site had 550 young trees ha⁻¹ in the lowest two height classes and 58.3 young trees ha⁻¹ in the higher height class. In contrast, the unburned site had 1525.9 young trees ha⁻¹ in the lowest two height classes and 51.7 young trees ha⁻¹ in the higher height class. Cypresses regeneration was higher in all inventory years in the unburned site, reaching an average of 25.3 young trees ha⁻¹ in the two lowest height classes and 8.3 young trees ha⁻¹ in the higher height class, and 155.2 young trees ha⁻¹ in the two lowest height class and 60.3 young trees ha⁻¹ in the higher height class, respectively. The highest pine regeneration occurred 5 years post-fire, with an average recruitment of 375 in the two lowest height classes and 16.7 in the higher height class in the burned site compared to only 8.6 in the two lowest height classes in the unburned site. Additionally, there was a notable post-wildfire germination of manzanita (Arctostaphylos pungens Hbk.) immediately post-wildfire. This OS shrub (Márquez Linares et al. 2005) persisted over time, with an average of 1425 stems ha⁻¹ in the burned site two decades post-wildfire, contrasting with 341.7 average stems ha⁻¹ in the unburned site.

Forest floor fuel loads and depth were relatively low and similar between sites and inventory years (Fig. S3). Fine woody debris was mainly composed of 100 h dead fuel class (2.5 to 7.6 cm diameter) in both sites. The CWD was predominantly sound in the unburned site and absent in the burned site until 5 years post-wildfire. Rotten CWD started accumulating in the burned site 10 years post-wildfire. Two decades post-wildfire, total loads, mostly FWD, were higher in the burned site with 9.1 Mg·ha⁻¹ (\pm 3.3) compared to 6.1 Mg·ha⁻¹ (\pm 2.1) in the unburned site. Litter and duff depths were higher in the unburned site for each inventory year, reaching similar amounts by the last inventory. Litter depth was lowest the year after the wildfire, averaging 0.39 cm (\pm 0.05) in the burned site compared to

Fig. 7. Tree species regeneration density by height class (less than 40 cm, between 40.1 and 80 cm, and between 80.1 and 130 cm), family, site (burned; unburned), and inventory year. Tree taxa are identified by regeneration strategy as obligate resprouters (OR), facultative seeders (FS), or obligate seeders (OS). Species regeneration occurred steadily, with oaks dominating both burned and unburned sites.



2.49 cm (± 0.31) in the unburned site and reaching similar depths in 2017 [burned: 0.75 cm (± 0.08); unburned 0.73 cm (± 0.1)]. Duff depth was three times lower in the burned site 1-year post-wildfire [burned: 0.23 cm (± 0.03); unburned 0.69 cm (± 0.11)] and reached similar depths in 2017 [burned: 0.79 cm (± 0.09); unburned 0.64 cm (± 0.11)] (Fig. S3).

Species dominance

Following the wildfire, several species experienced a significant change in their ecological importance value, but all recovered their EIV two decades later. To assess the impact of various variables, we compared several simple models, each including "Species," "Time," or "Condition" as the explanatory variable. The model incorporating the interaction of "Time" with "Species" had the best fit (lowest AIC) among the seven mixed effects models examined (Table S1). Our statistical analysis revealed highly significant differences for both the factor "Species" (p value < 0.0001) and the interaction effect between "Species" and "Time" (p value < 0.0001), indicating their high strength as explanatory variables. Further analysis using Tukey's HSD showed significant differences in the ecological importance value of Q.eduardii and Q.hartwegii. Their dominance experienced a significant reduction after the fire but regained it 5 years post fire. We did not observe significant differences in the EIVs of A.arizonica, J.deppeana, P.engelmannii, or P.leiophylla a year after the wildfire. In fact, there were no significant differences in any of those four species' EIVs pre- and post-1996 wildfire (Fig. S4).

Has the burned site recovered its pre-wildfire characteristics?

Our analysis of NMDS revealed relatively little separation in ordination space between inventory years (Fig. 8). The NMDS ordination exhibited a good fit, as indicated by the 0.10 stress value. It showed a clear positive linear relationship between observed dissimilarity and ordination distances (non-metric and linear fit at 0.989 and 0.978, respectively). NMDS1 had a very strong negative correlation with plot tree density and positive correlations with FWD, and Litter, while NMDS2 had a strong positive correlation with Q.eduardii EIV (Table S2). The anosim test used to compare the dissimilarities between "Site" and "Year" based on Euclidean dissimilarity showed a small level of dissimilarity between burned and unburned sites and inventory years (R = 0.15; significance = 0.001) (Fig. S5). Further pairwise permanova analysis (Permutational Multivariate Analysis of Variance) with the Bonferroni adjustment method and 999 permutations revealed no differences between the burned and unburned sites pre-wildfire or between pre- and post-wildfire conditions in the unburned site. In contrast, the post hoc analysis found small but significant differences between pre-wildfire conditions and conditions 1, 5, and 20-year post-wildfire in the burned site. No significant differences existed between prewildfire conditions and conditions 10-year post-wildfire (Table S3).

Discussion

Fire has long been recognized as a critical ecological process regulating biological diversity (McLauchlan et al. 2020). **Fig. 8.** Two-dimensional non-metric multidimensional scaling (NMDS) plots for the 20 forest variables by site (burned; unburned) and inventory years in a reduced two-dimensional space (stress value = 0.10). The ellipses represent 95% confidence intervals. Black ellipses and red centroids represent the burned site, whereas dashed ellipses and green centroids represent the unburned site. Our analysis revealed a limited degree of differentiation in the ordination space across sites and inventory years, the conditions following the fire exhibited the most pronounced differences.



Under the historical frequent fire regime, pine–oak forests of western North America quickly recovered their pre-wildfire function and composition (O'Connor et al. 2017; Hagmann et al. 2021). This high fire resilience results from fire-adaptive traits (Keeley et al. 2011; Johnstone et al. 2016; Keeley et al. 2019). However, when subject to altered fire regimes, such as higher frequency, intensity, and/or size, wildfires may cause unpredictable and profound changes in plant communities, undermining ecosystem resilience (Coop et al. 2020; Cerano-Paredes et al. 2022; Diaz-Toribio and Martorell 2022).

After a high-intensity wildfire in MBR, Fulé et al. (2000) suspected that there could be a transition from oak-pine forest to grass-savanna due to what seemed to be high mortality 1-month post-wildfire. This observation appeared consistent with an atypically long exclusion of the frequent surface fire regime for about six decades (Fulé and Covington 1999); the long fire-free period could have contributed to fuel accumulation that supported uncharacteristically severe burning (Fulé et al. 2000; Cerano-Paredes et al. 2022). Returning 1-year postwildfire in 1997, they observed substantial survival of trees that appeared to have died and high resprouting of many topkilled trees (Fulé et al. 2000). These attributes correspond to the mechanisms of persistence and recovery, two critical elements of resilience (Falk et al. 2022), leading Fulé et al. (2000) to conclude that recovery was possible even after the severe 1996 wildfire.

We found notable changes in the first two decades after the 1996 wildfire. The decline of tree density of nearly 90% and basal area of nearly 70% in the burned area at La Michilía was similar to the high mortality observed in burned Madrean pine–oak forest of southern Arizona by Barton and Poulos (2018) and a burned forest of *Pinus douglasiana* Martínez in the Biosphere Reserve Sierra de Manantlán in Jalisco, Mexico by Quintero-Gradilla et al. (2019). Overstory dominance, our second study objective, remained relatively stable in the La Michilía site. This finding is similar to the forest recovery reported by Quintero-Gradilla et al. (2019) but contrasts with a long-term conversion of the Arizona forest to an oak shrubland (Barton and Poulos 2018; Poulos et al. 2021). Finally, for our third study objective, assessing the degree to which the burned La Michilía forest has regained pre-fire conditions in the 20 years since the burn, we found that individual as well as multivariate comparisons of structure, composition, and forest floor variables showed a convergence between the burned and unburned sites. The growing similarity supports the conclusion that the burned forest is recovering pre-fire characteristics, despite the uncharacteristically long period of fire exclusion from 1932 to 1996 (Fulé et al. 2000). There are nuances to this conclusion, as the burned and unburned sites are relatively more similar in structure than composition. Twenty years after the fire, resprouting oaks in the burned sites have greater dominance than pines as compared to the pre-fire condition or the unburned site.

There are several possible reasons for the difference between the relatively rapid recovery observed at La Michilía in this study as opposed to the vegetation type conversion that Barton and Poulos (2018) reported in the Chiricahua Mountains of Arizona. The fire regime may have been less affected at La Michilía, with a shorter period of fire exclusion, 64 years, as compared to the 94–111 years (1900–1994, 1900– 2011) in the Chiricahua Mountains (Seklecki et al. 1996). Human use of firewood at La Michilía may also have kept surface fuels low. As a result, the fire may have been less severe in La Michilía than in the Chiricahuas. In general, fires have been

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of reduced size and severity on the Mexican side of the US-Mexico border in recent decades, likely due to different landuse patterns (Villareal et al. 2019). It is also worth considering, as Villarreal and Yool (2008) pointed out, that while the US and Mexico share a common fire suppression policy, various economic and social factors have impeded its stringent enforcement in Mexico. As a result, the Madrean oak-pine forests in Mexico have sustained a greater degree of openness compared to their US counterparts, primarily due to ongoing wildfires, wood-cutting activities, and light grazing practices on ejido lands. Another contributing factor could be the presence in the Chiricahua Mountains, but not at La Michilía, of Quercus hypoleucoides A. Camus or silverleaf oak. This species was shown by Poulos et al. (2021) to dominate evapotranspiration in the burned Chiricahua forests at the expense of other species, such as pines. Finally, severe "megadrought" prevailed in the southwestern US during most of the post-1996 period (Williams et al. 2022) likely affecting pine regeneration (Barton et al. 2023). While the weather records near La Michilía show interannual variability, the drying trend observed by Williams et al. (2022) in the western US since 2000 was not evident in southern Durango.

Limitations of the present study include constraints on our ability to track all the trees accurately. We discovered errors in some of the repeated measures, likely due to shifts in personnel over different field visits as well as the lack of permanent tags on the trees. Keeping track of cut trees was sometimes uncertain, as noted above. It would be beneficial to add complementary research to expand the scope of the study to consider ecophysiological, hydrological, wildlife, and social implications of fire. However, despite these limitations, the long-term study at La Michilía is useful in the context of the relatively small body of research on post-fire changes in Mexico. Our findings highlight the importance of functional trait diversity and complementarity of seeders' fire resistance and resprouters' post-fire sprouting strategies and suggest that mixed-species forests have higher resilience to fire than expected.

While it is outside of the scope of this study, we believe that the Man and the Biosphere program of UNESCO also played a role in the ecosystem recovery. Within our 20-year monitoring, we noted less wood cutting, possibly due to its incorporation in 1977 into the World Network of Biosphere Reserves and in 1999 to the National Commission of Natural Protected Areas Mexico (La Comisión Nacional de Áreas Naturales Protegidas, CONANP) managed federally to facilitate and promote the holistic development process by ensuring the preservation, restoration, and enhancement of the environment's quality, along with the conservation and sustainable utilization of natural resources and ensuring legal compliance with the legislation (CONANP). Thus, many rural communities had to modify their practices to conform to the newly imposed regulations. Effective conservation of natural resources in protected areas requires understanding the interests and perspectives of local residents and their engagement in collaborative forest protection (Martínez-Torres et al. 2018). Without social cohesion around conservation goals, fire serves as a tool for degrading ecosystem integrity and facilitating landuse change elsewhere in central Mexico (Olivares-Martinez et al. 2023). Despite the high resilience of mixed-species forests, managers need to exercise caution under climate change, as increases in disturbance frequency and severity can significantly alter recovery trajectories and the structure, composition, and functioning of oak-pine forests. Considering the mounting environmental and social pressures on forest ecosystems, it is increasingly vital to maintain and foster their resilience and adaptive capacity. There is a growing recognition within society of the significance of protected natural areas as highly effective means for preventing biodiversity loss and potentially mitigating the impacts of climate change (Olmos Martínez et al. 2022).

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Data availability

Data generated and used for the analysis during this study are available in the DRYAD repository [DOI, https://doi.org/10 .5061/dryad.dncjsxm5r]

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2023-0185.

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