

POST-FIRE REGENERATION OF OAK-PINE FOREST ACROSS A CHRONOSEQUENCE IN WESTERN MEXICO: KEY SPECIES FOR FOREST RESTORATION

 EDEL JOSHUA ATONDO-BUENO¹,  SUSANA ZULOAGA-AGUILAR^{2*},  MIGUEL ÁNGEL MUÑOZ-CASTRO¹,
 RAMÓN CUEVAS-GUZMÁN²,  FABIOLA LÓPEZ-BARRERA³,  EDUARDO ALANÍS-RODRÍGUEZ⁴

¹ Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México.

² Departamento de Ecología y Recursos Naturales, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Autlán de Navarro, Jalisco, México.

³ Red de Ecología Funcional, Instituto de Ecología A.C., El Haya, Xalapa, Veracruz, México.

⁴ Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, Linares, Nuevo León, México.

*Author for correspondence: martha.zuloaga@academicos.udg.mx

Abstract:

Background: High-severity fires are serious anthropogenic threats to forests, as they can cause forest degradation on unrecoverable scales. Therefore, understanding the patterns and drivers of post-fire regeneration is essential to designing restoration proposals.

Hypotheses: After a high-severity fire, we expected greater species richness and abundance of individuals in flat sites than in hillside sites since seeds, nutrients, and organic matter accumulate in flat landforms. Compared to some *Pinus* species, *Quercus* species are more drought-tolerant after a forest fire and, therefore, they are expected to dominate post-fire chronosequences.

Study site: The study was conducted in the “La Primavera” Flora and Fauna Protection Area.

Methods: We sampled vegetation and microenvironmental variables from 2021 to 2022 at 18 sites located on flat and hillside areas, at 3, 9, and ≥ 20 years since the last high-severity forest fires (TSF).

Results: The richness of woody and herbaceous species was higher at 3 TSF and 9 TSF. The topographic condition did not significantly drive the richness and abundance of woody species, but richness and abundance of herbaceous species were significantly greater in flat sites. The oak tree *Quercus resinosa* Liebm. was the dominant species throughout the chronosequence.

Conclusions: *Quercus resinosa* represents a foundational species for recovering forest structure and composition. Flat sites may act as regeneration nuclei, but hillside sites require greater restoration efforts.

Keywords: Passive restoration, *Pinus oocarpa*, *Quercus resinosa*, species composition, vegetation structure, vegetation succession.

Resumen:

Antecedentes: Los incendios de alta severidad representan graves amenazas antropogénicas para los bosques, ya que pueden causar la degradación forestal a escalas irreversibles. Por lo tanto, comprender los patrones y los impulsores de la regeneración post-incendio es esencial para diseñar propuestas de restauración.

Hipótesis: Después de un incendio de alta severidad, esperamos una mayor riqueza de especies y abundancia de individuos en sitios planos que en sitios de ladera, ya que las semillas, los nutrientes y la materia orgánica se acumulan en zonas planas. En comparación con algunas especies de *Pinus*, las especies de *Quercus* son más tolerantes a la sequía post-incendio forestal y, por lo tanto, se espera que dominen en las cronosecuencias post-incendio.

Sitio de estudio: El estudio se realizó en el Área de Protección de Flora y Fauna “La Primavera”.

Métodos: Muestreamos la vegetación y variables microambientales de 2021 a 2022 en 18 sitios planos y de ladera, a los 3, 9 y ≥ 20 años desde el último incendio forestal de alta severidad (TDF).

Resultados: La riqueza de especies leñosas y herbáceas fue mayor a 3 TDF y 9 TDF. La condición topográfica no determinó significativamente la riqueza y abundancia de especies leñosas, pero la riqueza y abundancia de especies herbáceas fueron significativamente mayores en sitios planos. El encino *Quercus resinosa* Liebm. fue la especie más dominante a lo largo de la cronosecuencia.

Conclusiones: *Quercus resinosa* representa una especie fundacional para la recuperación de la estructura y composición del bosque. Los sitios planos pueden actuar como núcleos de regeneración, pero los sitios de ladera requieren mayores esfuerzos de restauración.

Palabras clave: Composición de especies, estructura de la vegetación, *Pinus oocarpa*, *Quercus resinosa*, restauración pasiva, sucesión de la vegetación.

This is an open access article distributed under the terms of the Creative Commons Attribution License CCBY-NC (4.0) international.

<https://creativecommons.org/licenses/by-nc/4.0/>



Forest fires are a natural part of the dynamics of most temperate and boreal forests because many of their species depend on fire to persist in these ecosystems (Frelich 2002, Rodríguez-Trejo 2014, Pausas & Keeley 2019). Therefore, species inhabiting these fire-prone ecosystems (or fire-dependent/influenced ecosystems, Hardesty *et al.* 2005) have developed mechanisms that allow them to complete their biological cycles and persist under natural fire regimes (*e.g.*, frequency, intensity, and extent; Bond *et al.* 2005, Bond & Keeley 2005, Keeley *et al.* 2011, Pausas & Keeley 2014, 2019). However, natural or historical fire regimes are altered by different anthropogenic activities (*e.g.*, agriculture, livestock, construction, fire exclusion or suppression policies, and cultural behavior) (Jiménez & Alanís-Rodríguez 2011, Bilbao *et al.* 2020, Ponce-Calderón *et al.* 2021) and climate change (*e.g.*, alterations in temperature and precipitation patterns), thereby increasing the probability of high-severity fires and the degradation and loss of forests on unrecoverable scales (Westerling *et al.* 2006, Abatzoglou & Williams 2016, Liu & Wimberly 2016, Montoya *et al.* 2023).

Fire severity is the response of ecosystems to fire intensity (*i.e.*, the amount of heat released in a given area and time) (DeBano *et al.* 1998, Keeley 2009, Rodríguez-Trejo 2014). High-intensity fires, resulting from increased fuel accumulation (organic matter in the soil, leaf litter, and fallen trunks) and extreme dry environmental conditions, favor the occurrence of high-severity fires (Bilbao *et al.* 2020, Ponce-Calderón *et al.* 2021). Consequently, these types of fires promote drier soil conditions, trigger soil erosion processes (Certini 2005, Rodríguez-Trejo 2014, Agbeshie *et al.* 2022), and even significantly affect the survival capability of fire-adapted species. This alteration often disrupts species composition (Johnstone & Chapin 2006, Crotteau *et al.* 2013, Gärtner *et al.* 2014, González-De Vega *et al.* 2018, Boucher *et al.* 2020, Etechells *et al.* 2020, Cadena-Zamudio *et al.* 2022) and the expected successional trajectory of communities (Connell & Slatyer 1977, Pulsford *et al.* 2016). In this sense, fire severity estimations are based on the degree of change in biotic and abiotic components, and the resilience of the vegetation to a given fire regime (Rodríguez-Trejo 2014). For instance, in the field, severity can be estimated as the proportion of dead plants and burning of vegetation, the loss of surface organic matter (*e.g.*, leaf litter, duff, fine roots, fallen trunks), and the level of soil degradation (Parsons *et al.* 2010, Silva-Cardoza *et al.* 2021).

In fire-prone ecosystems, the natural regeneration patterns of plants are mainly defined by attributes related to their persistence capacity (pre-existing seed bank, regrowth capacity, time and type of dispersal), their resistance or their tolerance to the passage of a fire (thick bark, seeds with thick testa), and the post-fire microenvironmental conditions that influence their germination and establishment (Noble & Slatyer 1980, Keeley *et al.* 2011, Chapin *et al.* 2014, Rodríguez-Trejo 2014, Pausas 2015, Boucher *et al.* 2020). Typically, post-fire natural regeneration of oak-pine forests (OPF) begins with the establishment of fast-growing, short-lived, heliophilous pioneer species that can tolerate and prosper in these conditions (Rodríguez-Trejo & Fulé 2003, Almazán-Núñez *et al.* 2016). The early stages of OPF succession often show the dominance of *Pinus* spp. seedlings due to their ability to germinate, tolerate, and grow under direct solar radiation but, in Mexico, the succession tendency is generally toward the dominance of *Quercus* species over time (González-Espinosa *et al.* 1991, Almazán-Núñez *et al.* 2016). In a post-fire chronosequence within a mixed pine-oak forest in NE Mexico, González-Tagle *et al.* (2008) observed that oak species dominated young and intermediate stands due to their resprouting ability. Contrarily, pine species tended to co-dominate with oaks in mature stands. Similarly, Barton & Poulos (2018) showed a transition of mixed pine-oak forest to oak shrublands after high-severity fires in Arizona. This transition is due to the limited recruitment of pines and the resprout of oaks, persisting even up to 14 years post-fire. These tendencies are consistent with the findings in similar ecosystems (Alanís-Rodríguez *et al.* 2012, An *et al.* 2019). While many of these studies prioritize describing the woody stratum, understanding the condition of the herbaceous stratum is equally crucial for proposing strategies addressed to facilitate soil recovery and accelerate regeneration of fire-affected areas. In warmer temperate forests, post-fire regeneration is dominated by oaks rather than by pines (Alfaro-Reyna *et al.* 2019) because of differential recruitment patterns between these groups, growth limitations, and their respective capacities to resprout in response to post-fire environmental challenges such as drought and temperature (Carnicer *et al.* 2014, Torres *et al.* 2016, Barton & Poulos 2018).

Successional changes in species composition and vegetation structure in post-fire OPF are influenced not only by fire severity and the rate of recovery dependent on time since fire (Flores-Rodríguez *et al.* 2021, Cadena-Zamudio *et*

al. 2022), but also by climatic and topographic conditions, edaphic characteristics, land use history, proximity to seed source, stochastic events, and microenvironmental conditions before and after the fire (González-Tagle *et al.* 2008, Rodríguez-Trejo 2014, An *et al.* 2019, Rago *et al.* 2023). On the other hand, local variations in resource availability (*e.g.*, seeds, nutrients, organic matter, moisture, microbiota) due to topographic conditions (*e.g.*, slope, elevation, and exposure) can determine species richness and abundance, as well as the composition and structure of vegetation over time (Alanís-Rodríguez *et al.* 2012, Chapin *et al.* 2014, Kane *et al.* 2015, Bassett *et al.* 2017, An *et al.* 2019). These factors lead to high heterogeneity in forest regeneration and resilience responses, posing a challenge when formulating effective restoration proposals (González-Tagle *et al.* 2008, An *et al.* 2019). Understanding the biological and physical processes of post-disturbance succession is the theoretical basis for restoration actions (active or passive). In this context, the description of successional stages is important, as it enables the identification of key species, or groups of species, that can facilitate or accelerate the regeneration process (Balaguer *et al.* 2014, Souza-Alonso *et al.* 2022, Rago *et al.* 2023).

Temperate forests in Mexico comprise ecosystems critically affected by human activity and forest fires (Zúñiga-Vásquez & Pompa-García 2019, Montoya *et al.* 2023). Historically, these forests have faced land-use changes, illegal logging, and anthropogenic fires (Challenger *et al.* 2009). It is estimated that 37 % of the total forest cover in this ecosystem is secondary vegetation (CONAFOR 2019), where most Mexican OPF remain in various successional stages (Challenger *et al.* 2009). In this context, successional studies based on a chronosequence approach (*i.e.*, sites with different post-disturbance times) offer the advantage of evaluating time-dependent ecological processes without long-term monitoring, despite the difficulty in meeting basic assumptions (*e.g.*, finding sites that vary only in age and controlling microenvironmental variables) and theoretical limitations (*e.g.*, lack of predictability due to stochastic events), which challenge its use and ecological interpretation (Johnson & Miyanishi 2008, Walker *et al.* 2010). “La Primavera” Flora and Fauna Protection Area (APFFLP in Spanish), located in western Mexico, allows the study of successional changes in species composition and vegetation structure along a chronosequence using sites with different recovery times after high-severity fires. Studying plant succession through chronosequences will allow to explore natural regeneration patterns in OPF and their relationship with microenvironmental conditions.

Our hypothesis proposes that the deposition of seeds, nutrients, and organic matter tends to accumulate mostly in the flat landforms. Hence, these sites are expected to exhibit greater species richness and abundance of individuals as compared to hillside sites. In contrast to some *Pinus* species, some Neotropical *Quercus* species are more tolerant to drier conditions after forest fires and climate change (Alfaro-Reyna *et al.* 2019). Therefore, *Quercus* will have a higher importance value index (IVI) throughout the post-fire chronosequence. This study aims to (1) describe post-fire differences in species composition, species richness, and structure of mixed OPF based on the recovery time since the last high-severity fire and two topographic conditions (flat *vs.* hillside sites), (2) determine microenvironmental variables associated with post-fire plant communities, and (3) identify key species for active restoration of the OPF after high-severity fires. Thus, this study would contribute to the knowledge of the natural regeneration trends in areas affected by severe fires in OPF as a reference framework for designing restoration proposals.

Materials and methods

Study site. “La Primavera” Flora and Fauna Protection Area (APFFLP; 30,500 ha) is located in Sierra Madre Occidental, western Mexico (20° 32' 36.33" - 20° 43' 33.36" N; 103° 27' 16.51" - 103° 41' 12.65" W, [Figure 1](#)) (SEMARNAT 2000). The APFFLP spans an elevation range of 1,400 to 2,200 m and features rugged landscape topography, regosol soil (92 %, characterized by low organic matter content), and high vulnerability to water erosion due to its recent geological history (Dye 2012). The prevailing climate is temperate subhumid, marked by distinct seasonality, summer rains and seven-month dry seasons. Precipitation ranges from 800 mm to 1,000 mm annually, with mean annual temperature of 18.7 °C (min and max values: 5 and 32 °C, CONABIO 2017), classifying the OPF as a dry ecosystem (IPCC 2003). The canopy cover of the OPF is dominated by *Quercus castanea* Née, *Q. laeta* Liebm., *Q. resinosa* Liebm., *Q. viminea* Trel., *Q. magnoliifolia* Née (Fagaceae), *Pinus oocarpa* Schiede ex Schltdl., *P. douglasiana* Martínez (Pinaceae), and *Clethra rosei* Britton (Clethraceae) (SEMARNAT 2000).

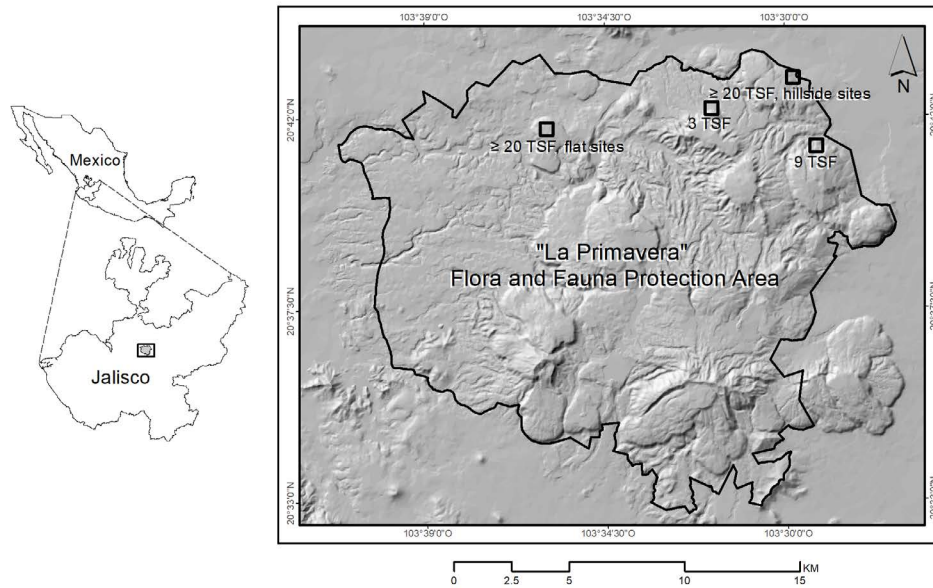


Figure 1. Location of sampling sites with 3, 9, and more than 20 years since the last high-severity fire (3 TSF, 9 TSF, and ≥ 20 TSF) in “La Primavera” Flora and Fauna Protection Area, western Mexico. Black outlined box symbols encompass sampling groups of 3 or 6 sites by post-fire time ($N = 3$), and topographic condition ($N = 2$). The 3 TSF and 9 TSF box with 3 flat sites and 3 hillside sites each; ≥ 20 TSF box with 3 sites each.

The historical fire regime of some mixed temperate forests in the Sierra Madre Occidental is characterized as superficial, with low intensity (burning at ground level and understory), and a return interval of 4-6 years (Fulé & Covington 1997, 1998, Rodríguez-Trejo 2008). This fire regime maintains a certain level of forest openness, regulates biomass accumulation, recycles nutrients, and promotes herbaceous species diversity (Fulé & Covington 1997). However, this regime has changed in recent decades due to fire suppression during certain periods, increasing local fuel loads (Jiménez & Alanís-Rodríguez 2011). Historically, APFFLP has faced various anthropogenic threats, including land-use changes for agriculture, extensive uncontrolled livestock grazing, forest resource exploitation, periodic use of fire for sugar harvest, recreational activities and, more recently, urban expansion (Huerta-Martínez & Ibarra-Montoya 2014). These factors increase the susceptibility of forest to fires, particularly during extreme conditions associated with climate change, given that most forest fires have an anthropogenic origin (Ibarra-Montoya & Huerta-Martínez 2016, Bassaber-Zuñiga *et al.* 2024). Consequently, forest fires have affected over 90 % of APFFLP, with a rising trend in frequency (approximately every seven years) and severity (Gallegos-Rodríguez *et al.* 2014, Huerta-Martínez & Ibarra-Montoya 2014). These fires impact on the carbon sequestration potential of forest and contribute to create heterogeneous landscape characterized by different successional stages (Balderas-Torres *et al.* 2013). However, there is no specific fire management plan implemented in the APFFLP.

Site selection. The Forest Fire Hazard Prediction System in Mexico (Vega-Nieva *et al.* 2020) allowed us to identify burned areas over the last 10 years. The severity of burned areas for each year was verified using the difference in Normalized Burn Ratio ($dNBR = \text{pre-fire NBR} - \text{post-fire NBR}$) (Key & Benson 2006). These indices were derived from the near-infrared (NIR) and short-wave infrared (SWIR) wavelengths of Landsat satellite images (Escuin *et al.* 2008). For the NBR spectral index, satellite images were selected for each year (earthexplorer.usgs.gov), followed by field verification. In 2021, two polygons were identified, where high-severity fires occurred ($dNBR > 380$) based on the methodology for temperate forests described by Silva-Cardoza *et al.* (2021). One had three years and the other had nine years since the last high-severity fire (referred to as time since the last fire, 3 TSF, and 9 TSF, respectively). High severity was confirmed at each site through a visual assessment of the burned or scorched crown extent (identified by brown or desiccated leaves and needles). More than 70 % of the tree canopy at each location showed signs

of burning or complete absence (Silva-Cardoza *et al.* 2021). As a reference area, a polygon without records of forest fires over more than 20 years (hereafter ≥ 20 TSF) was selected to describe the composition and structure of the vegetation in absence of recent fires. The ≥ 20 TSF estimation was obtained through informal interviews with current APFFLP managers (M. Carrillo, pers. comm.). In each polygon (3 TSF, 9 TSF, and ≥ 20 TSF, [Figure 2](#)), six sites were selected (a total of 18 sites) and half of them corresponded to each topographic condition (TC: flat and hillside sites), with a separation of at least 100 m each other. All hillside sites were located in NE aspects. Although there is criticism about using chronosequences for analyzing plant community succession due to the theoretical limitations of this approach (*e.g.*, predictability of successional replacement) (Johnson & Miyanishi 2008, Walker *et al.* 2010, Freestone *et al.* 2015), we consider that our study area meets the basic assumptions: sites differing only in age, within a sufficiently homogeneous landscape with similar climate and low number of tree species to describe (Walker *et al.* 2010, Freestone *et al.* 2015), and with clues about species-abundance-microclimate associations in relation to post-fire time.

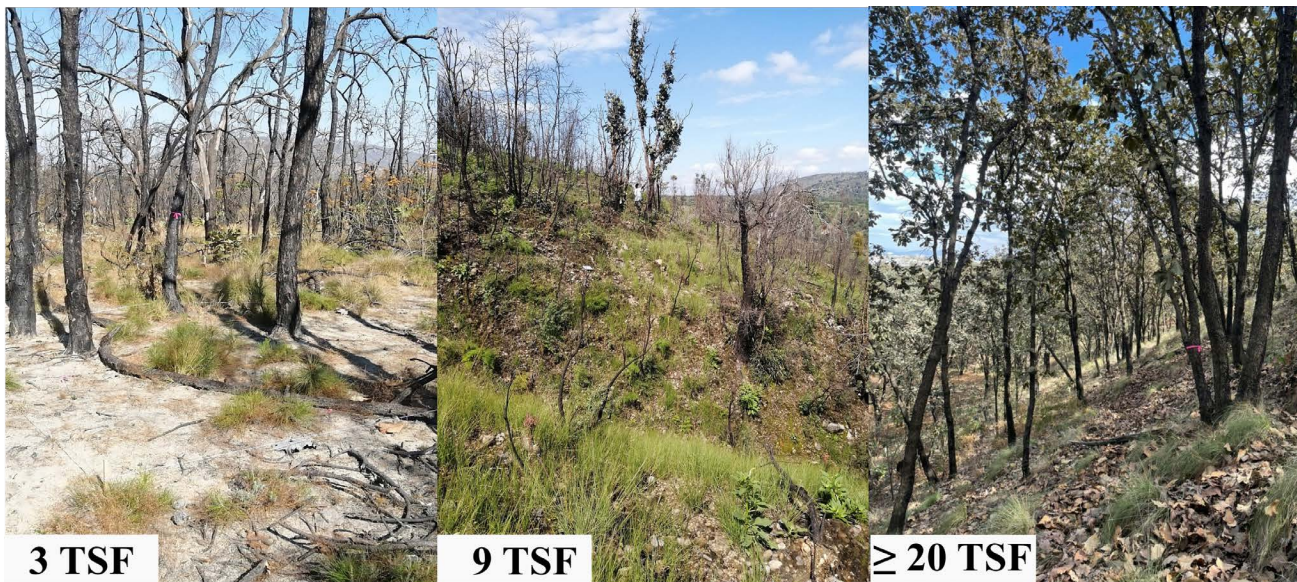


Figure 2. Photos of some sampling sites with 3, 9, and more than 20 years since the last high-severity fire (3 TSF, 9 TSF, and ≥ 20 TSF) in “La Primavera” Flora and Fauna Protection Area, western Mexico.

Sampling design. In recently burned sites at 3 TSF and 9 TSF, vegetation measurements were conducted between September and October 2021, while sites with ≥ 20 TSF were surveyed in January 2022. In the field, a 60×48 m grid was established at each burned site and TC using a stratified random design (with modifications; Vázquez-García & Givnish 1998). Within each grid, a subdivision was made at 12 m intervals, resulting in 20 subdivisions, with 10 squares randomly selected. In the center of each selected square, a circular plot ($r = 5.64$ m, 100 m^2) was established, with a total sampling area of $1,000 \text{ m}^2$ (0.1 ha) per site.

Field measurements. In each circular plot, the following data was collected for the woody stratum: number of tree individuals per species and total height (m) per individual/species, while diameter at breast height (DBH ≥ 2.5 cm) per individual/species was also registered to estimate basal area (m^2). Additionally, the number of resprouting individuals per tree species, originating from existing structures (stumps, root sprouts, etc.), was recorded. In the herbaceous stratum, four squares of 1×1 m were systematically established within each circular plot, where the number of individuals, average height (cm), and average cover (%) per species were registered. Species that could not be identified in the field were collected for herbarium preservation and later identification at the IBUG herbarium.

To characterize the plant communities, absolute and relative abundances (ABUN), frequency (FREQ), dominance (DOM, basal area), and cover (COV, only for herbaceous species) were calculated (%) for each species. Additionally, to identify key species associated with TSF, the species' importance value index (IVI) was calculated according to Curtis & McIntosh (1951) (Alanís-Rodríguez *et al.* 2020).

Microenvironmental variables were directly measured within the sites (3 sites \times 3 TSF \times 2 TC). Soil sampling was conducted in March 2022, where five independent samples were obtained from a depth of 30 cm at each site. These five samples were subsequently mixed in a single composite sample per site, resulting in 18 mixed samples. Then, the following soil determinations were conducted at the Soil Laboratory of Centro Universitario de Ciencias Biológicas y Agropecuarias of the Universidad de Guadalajara: pH (using a HI 2211 potentiometer, Hanna instruments), electrical conductivity ($\mu\text{mho}/\text{cm}$; with a YSI model 35 conductance meter), texture (using a Bouyoucos hydrometer), organic matter (%; Walkley & Black 1934), bulk density (g cm^{-3} , Blake & Hartge 1986), and cations (mg/L), including K, Na, Ca, and Mg, following the methods recommended in NOM-021-SEMARNAT-2000 (SEMARNAT 2002). In November 2022, within each site, microenvironmental variables were directly measured at five random locations at midday (3 sites \times 3 TSF \times 2 TC, 90 measurements per variable). Photosynthetically active radiation available for plants (PAR, $\mu\text{mol m}^{-2}\text{s}^{-1}$) was measured with a photoradiometer (Apogee, Instruments USA). The quality of light (red/far red ratio) was determined with an SKR 100/116 sensor (Skye Instruments Ltd., Powys, UK). Soil moisture content (SMC, %) and soil temperature (ST, $^{\circ}\text{C}$) were recorded using an SM 100 Waterscout sensor (Spectrum. Technologies, inc.). At each circular plot, we also recorded elevation (m asl), slope (%), percentage of woody cover, herbaceous cover, leaf litter cover, and rock and bare soil cover. All recorded variables are available in [Appendix 1](#).

Data analysis. To evaluate the effectiveness of our sampling efforts, we calculated the average of four non-parametric estimators to determine the proportion of species captured un samplings in relation to the total expected species richness. This approach facilitated the determination of the general trend of the expected species that we aimed to record during samplings. The estimators used were Chao 1 and ACE, which are based on species abundance, and Chao 2 and Jackknife 2, which are based on presence-absence data (Gotelli & Chao 2013). All these estimates were conducted using EstimateS version 9.1.0 (Colwell 2013).

To graphically visualize the similarity in species composition between sites as a function of TSF and TC, a main matrix was integrated with all species having $\geq 5\%$ in abundance in one or more circular plots (Gauch 1982). The species matrix was standardized and subjected to a double square root transformation (Clarke *et al.* 2014). This matrix was then used for ordination via non-metric multidimensional scaling (NMDS), a technique suitable for non-normally distributed data primarily used to visually represent groups or differences within large complex data (McCune & Grace 2002). Subsequently, a one-way analysis of similarity (ANOSIM, based on Bray-Curtis's distance) (999 permutations) was performed to evaluate differences in species composition and abundance as a function of TSF \times TC.

We employed a two-way Generalized Linear Mixed Model (GLMM) using the “lme” function on the “lme4” package (Bates *et al.* 2015) to explore the interactive effects of time since fire (3 TSF, 9 TSF, and ≥ 20 TSF) and topographic conditions (TC; flat and hillside sites) on woody vegetation structure (richness, number of individuals, basal area, and total height). In these models, TSF and TC served as fixed factors, while circular plots ($N = 10$) were nested within sites and sampling dates and treated as random factors. Variation in basal area and height of woody species was specifically assessed for individuals ≥ 4 m in height. Due to the lack of normal distribution of the residuals for a GLMM, the DBH variation between TSF-TC categories (3 TSF - flat, 3 TSF - hillside, 9 TSF - flat, 9 TSF - hillside, ≥ 20 TSF - flat, ≥ 20 TSF - hillside $N = 6$) was evaluated with a Kruskal-Wallis test. Additionally, to assess whether the number of resprouting individuals varied between the three most important tree species (with the highest IVI value, $N = 3$) and TSF-TC categories (3 TSF - flat, 3 TSF - hillside, 9 TSF - flat, 9 TSF - hillside, $N = 4$), a two-way GLMM was conducted with sites as a random factor. Also, a two-way GLMM was used to evaluate the effect of TSF and TC on the richness, number of individuals, average cover, and average height of the herbaceous stratum (*i.e.*, four subplots nested within each circular plot = 40 subplots per site).

To evaluate variation in soil attributes (pH, EC, OM, BD, K, Na, Ca, Mg) and microenvironmental variables (PAR, SMC, ST) in relation to TSF and TC, a two-way GLMM was performed, treating the site as a random factor. When necessary, response variables were transformed (*e.g.*, log and square root) to satisfy assumptions of models. Each model was validated by graphically checking the fit of residuals using the “plot” function, and the significance of the “t-values” of the model was evaluated with the “ANOVA” function. Post-hoc analyses were performed using the “emmeans” function (package “emmeans”; Russell *et al.* 2021). These analyses were carried out using R Studio v. 2022.02.2 (R Studio Team 2022).

To identify microenvironmental variables associated with species composition and abundance in post-fire plant communities, a matrix of variables was generated, excluding those with collinearity (Soil pH, soil texture, OM, K, Na, Mg, red/far red ratio, SMC, ST, elevation, slope, leaf litter cover, rock, and bare soil cover). The final matrix included time since the last fire (TSF), topographic condition (TC), electrical conductivity (EC), soil bulk density (BD), calcium (Ca), photosynthetically active radiation (PAR), average herbaceous species cover (Cher), and average canopy cover (CC). Qualitative TSF and TC variables were converted into auxiliary (or dummy) variables and treated as quantitative. Detrended Correspondence Analysis (DCA) was conducted using the species matrix to estimate gradient amplitudes, extracting a total inertia < 2. A direct linear ordination technique was used because scatter plots between species and microenvironmental variables did not exhibit unimodal relationships (McCune & Grace 2002). Canonical redundancy analysis (RDA) was also performed because, unlike other techniques, they represent the interactions between the species matrix and the microenvironmental variables matrix (predictor) (Legendre & Andersson 1999), in addition to identify species associated with each post-fire site. NMDS and ANOSIM analyses were performed using the Primer v. 7 (Clarke & Gorley 2015), as well as RDA using the PC-ORD v. 7.0 (McCune & Mefford 2016).

Results

Post-fire differences in floristic composition. Our sampling effort yielded the presence of 82 % of the expected species in the study area. In the woody stratum, 19 species across 16 genera and 12 families were recorded ([Appendix 2](#)). The families with the highest species richness were Asteraceae (4), followed by Fabaceae (3), Ericaceae (2), and Fagaceae (2) (58 %). The remaining families were represented by a single species (42 %). Regardless of topographic condition (TC) and time since the last fire (TSF), the most frequently occurring woody species along the chronosequence included *Quercus resinosa* (21 %), *Pinus oocarpa* (20 %), *Verbesina fastigiata* B.L. Rob. & Greenm. (16 %), *Quercus viminea* (1 %), and *Agarista mexicana* (Hemsl.) Judd (8 %), which showed resprouting structures ([Table 1A](#)). In the herbaceous stratum, 154 species from 108 genera and 40 families were recorded ([Appendix 2](#)). In addition, 11 morphospecies were identified at the family level, six Poaceae and five Asteraceae. The families with the highest species richness were Asteraceae (38), Poaceae (32), and Fabaceae (19) (57 %), while the others had < 8 species (43 %). The genera with the highest number of individuals were *Paspalum* (2,303 ind.), *Sporobolus* (2,120 ind.), and *Bulbostylis* (1,795 ind.) ([Table 1B](#)). The most frequently encountered herbaceous species between the post-fire sites included *Trachypogon spicatus* (L. f.) Kuntze, *Paspalum conjugatum* P.J. Bergius (5 %), *Eriosema grandiflorum* (Schltdl. & Cham.) G. Don, *Ageratina oligocephala* (DC.) R.M.King & H.Rob., and *Pteridium caudatum* (L.) Maxon (3 %) ([Table 1B](#)).

The NMDS ordination was adjusted to a two-dimensional solution, with a final stress of 0.06 (Supplementary material, [Figure S1](#)). In general, there was a marked differentiation between sites with ≥ 20 TSF from 3 TSF and 9 TSF. These differences were further stratified by TC. The ANOSIM test results confirmed significant dissimilarity in species composition and abundance, as influenced by TSF and TC (Global test $R = 0.998$, $P < 0.001$).

Regardless of TC, the importance value index (IVI) of *Q. resinosa* was 2.4 and 2.2 times higher at sites with ≥ 20 TSF, as compared to sites with 3 TSF and 9 TSF, respectively ([Table 1A](#)). Similarly, the IVI for *P. oocarpa* was 2.3 and 1.2 times higher at sites with ≥ 20 TSF, as compared to sites with 3 TSF and 9 TSF, respectively. In contrast, the IVI of *Q. viminea* was 6.6 and 2.9 times higher at sites with 3 TSF and 9 TSF, as compared to sites with ≥ 20 TSF,

respectively. *Agarista mexicana* and *V. fastigiata* were not recorded at sites with ≥ 20 TSF (Table 1B). For the herbaceous stratum, the IVI of *T. spicatus* was 9.32 and 18 times higher at sites with ≥ 20 , TSF compared to sites with 3 TSF and 9 TSF, respectively. *Eriosema grandiflorum* was 5.9 and 7.7 times greater at ≥ 20 TSF, as compared to sites with 3 TSF and 9 TSF, respectively. *Ageratina oligocephala*, *Aristida ternipes*, and *Paspalum conjugatum* were not recorded at sites with ≥ 20 TSF (Table 1B).

Table 1. Number of individuals (Num. Ind.), relative abundances (ABUN), frequency (FREQ), dominance (DOM), coverage (COV) and the importance value index (IVI) for the seven most frequent species in the woody (A) and the herbaceous (B) stratum of sites with 3, 9, and more than 20 years since the last high-severity fire (3 TSF, 9 TSF, and ≥ 20 TSF) in “La Primavera” Flora and Fauna Protection Area, western Mexico. Species are arranged in descending order based on IVI regarding ≥ 20 TSF. Species marked with an asterisk (*) were observed in the field with capacity of resprouting.

Species	3 TSF					9 TSF					≥ 20 TSF				
	Num. Ind.	ABUN (%)	FREQ (%)	DOM (%)	IVI (%)	Num. Ind.	ABUN (%)	FREQ (%)	DOM (%)	IVI (%)	Num. Ind.	ABUN (%)	FREQ (%)	DOM (%)	IVI (%)
A) Woody stratum															
<i>Quercus resinosa</i> *	108	28.65	21.66	33.06	27.79	92	20.77	20.13	52.48	31.13	379	68.04	68.04	65.38	67.15
<i>Pinus oocarpa</i> *	34	9.02	13.38	15.82	12.74	175	39.50	24.03	11.46	25.00	155	27.83	27.83	30.75	28.80
<i>Quercus viminea</i> *	54	14.32	14.65	43.96	24.31	29	6.55	5.84	19.87	10.75	20	3.59	3.59	3.84	3.67
<i>Agarista mexicana</i> *	58	15.38	11.46	5.10	10.65	15	3.39	3.90	9.26	5.51	0	0.00	0.00	0.00	0.00
<i>Clethra rosei</i> *	10	2.65	3.18	0.37	2.07	15	3.39	5.84	4.46	4.56	1	0.18	0.18	0.03	0.13
<i>Vachellia pennatula</i> *	2	0.53	0.64	0.01	0.39	2	0.45	0.65	0.01	0.37	2	0.36	0.36	0.01	0.24
<i>Verbesina fastigiata</i> *	77	20.42	19.75	1.37	13.85	71	16.03	23.38	1.77	13.72	0	0.00	0.00	0.00	0.00
B) Herbaceous stratum															
<i>Trachypogon spicatus</i> *	169	1.37	2.99	6.88	3.75	150	1.43	1.53	2.86	1.94	315	24.78	31.86	48.21	34.95
<i>Eriosema grandiflorum</i> *	171	1.39	2.18	2.22	1.93	121	1.15	1.81	1.48	1.48	195	15.34	12.19	6.48	11.34
<i>Pteridium caudatum</i>	218	1.77	3.05	4.45	3.09	278	2.65	2.58	5.57	3.60	88	6.92	4.99	1.64	4.52
<i>Ageratina oligocephala</i>	1228	9.96	5.97	7.32	7.75	22	0.21	0.56	0.40	0.39	0	0.00	0.00	0.00	0.00
<i>Aristida ternipes</i> *	101	0.82	1.62	3.09	1.84	274	2.61	3.55	7.77	4.65	0	0.00	0.00	0.00	0.00
<i>Paspalum conjugatum</i> *	1327	10.76	5.16	4.90	6.94	946	9.00	4.88	6.91	6.93	0	0.00	0.00	0.00	0.00
<i>Sporobolus macrospermus</i>	1770	14.35	4.29	4.53	7.72	348	3.31	1.95	1.95	2.40	2	0.16	0.28	0.07	0.17

Post-fire differences in plant community structure. Woody stratum characteristics exhibited significant variations as a function of TSF and TC interactions (Table 2A). The richness of woody species was not affected by TC, and there was no interaction between this factor and TSF. However, species richness was 1.7 and 1.5 times higher at sites with 3 TSF and 9 TSF, respectively, as compared to sites with ≥ 20 TSF (Table 2a and Table 3A). Sites with ≥ 20 TSF harbored 1.3 and 1.5 times more individuals established in hillside sites, as compared to sites with 3 TSF and 9

Table 2. Deviance table for Generalized Linear Mixed Models that evaluate differences in the characteristics of the woody (A) and herbaceous (B) stratum in sites with 3, 9, and more than 20 years since the last high-severity fire (TSF), situated in two topographic conditions (TC: flat and hillside sites) in “La Primavera” Flora and Fauna Protection Area, western Mexico. Numerator degrees of freedom = DF num.; Denominator degrees of freedom = DF den.; Number of individuals = Num. Ind.

Response variables	DF num.	DF den.	F	P
A) Woody stratum				
a) Richness				
TSF	2	128	15.94	< 0.0001
TC	1	128	1.71	0.193
TSF:TC	2	128	2.98	0.054
b) Num. Ind.				
TSF	2	128	4.98	0.008
TC	1	128	3.80	0.053
TSF:TC	2	128	8.06	0.0005
c) Basal area				
TSF	2	116	45.35	< 0.0001
TC	1	116	4.07	0.046
TSF:TC	2	116	1.94	0.148
d) Height				
TSF	2	116	96.03	< 0.0001
TC	1	116	12.83	0.0005
TSF:TC	2	116	6.40	0.002
B) Herbaceous stratum				
e) Richness				
TSF	2	140	234.94	< 0.0001
TC	1	140	4.36	0.038
TSF:TC	2	140	14.47	< 0.0001
f) Num. Ind.				
TSF	2	140	191.80	< 0.0001
TC	1	140	4.70	0.032
TSF:TC	2	140	22.22	< 0.0001
g) Coverage				
TSF	2	140	51.89	< 0.0001
TC	1	140	1.46	0.228
TSF:TC	2	140	5.24	0.006
h) Height				
TSF	2	140	89.93	< 0.0001
TC	1	140	23.88	< 0.0001
TSF:TC	2	140	32.88	< 0.0001

TSF within the same TC, respectively (Table 2b and Table 3A). No statistically significant interaction was found between TSF and TC concerning the basal area of established trees (Table 2c and Table 3A). Nevertheless, sites with ≥ 20 TSF recorded tree individuals with the largest basal area (Table 3A). Tree height was 2.7 and 3.1 times greater in flat sites with ≥ 20 TSF than in the same TC of sites with 3 TSF and 9 TSF (Table 2d and Table 3A). Similar results were observed for DBH of trees established on hillside sites ($\chi^2 = 64.4$, $df = 5$, $P < 0.001$, Table 3A). The diameter distribution of woody species showed an inverted *J*-trend in the recently burned sites (3 TSF and 9 TSF) (Figure 3). In these sites, the woody stratum was mostly composed by individuals < 11 cm DBH, whereas individuals in the woody stratum at sites with ≥ 20 TSF had 2.5-35 cm DBH. Notably, recently burned sites exhibited a heightened frequency of seedlings and juvenile individuals (< 5 cm DBH, including resprouting) of *Q. resinosa*, as compared to *P. oocarpa* (Figure 3). Additionally, a greater establishment of *P. oocarpa* seedlings (1 cm DBH) was found in sites with 9 TSF, in contrast to those with 3 TSF and ≥ 20 TSF. Furthermore, *Q. resinosa* juveniles were established more frequently on sites with ≥ 20 TSF (Figure 3). The number of resprouting individuals varied significantly between species in interaction with TSF-TC ($F_{6,22} = 2.8$, $P = 0.03$). On average, the number of resprouting individuals of *P. oocarpa* was 7 and 13 times higher in sites with 9 TSF from flat and hillside sites, respectively, as compared to the *Quercus* species and sites with 3 TSF (Appendix 3). In sites with 3 TSF, *Q. resinosa* was the species with the highest number of resprouting individuals in the hillside sites (27.33 ± 5.81 ind.). No resprouting individuals were recorded at sites with ≥ 20 TSF (Appendix 3).

The herbaceous stratum differed significantly as a function of TSF and TC interactions (Table 2B). In general, the highest number of herbaceous species was found on sites with 3 TSF and 9 TSF relative to sites with ≥ 20 TSF (Table 3B). Specifically, this diversity was 1.5 times higher at flat sites with 9 TSF, and hillside sites at 3 TSF (Table 3B).

Table 3. Characteristics of the woody (A) and the herbaceous (B) stratum in sites with 3, 9, and more than 20 years since last high-severity fire in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. Time since last fire = TSF; Topographic condition (flat and hillside sites) = TC; Number of individuals = Num. Ind.; Diameter at breast height = DBH. Mean \pm Standard error per site (0.1 ha). Different letters indicate statistically significant differences.

A) Woody stratum						
TSF	TC	Richness	Num. Ind.	Basal area (m ²)	Height (m)	DBH (cm)
3 yrs	Flat	2.51 \pm 0.37	5.37 \pm 0.71 ^c	0.017 \pm 0.03	5.29 \pm 0.90 ^c	9.77 \pm 2.11
	Hillside	3.33 \pm 0.30	8.43 \pm 0.95 ^c	0.019 \pm 0.04	5.22 \pm 1.33 ^c	10.97 \pm 3.84
9 yrs	Flat	2.80 \pm 0.41	9.60 \pm 1.64 ^b	0.018 \pm 0.04	4.64 \pm 0.53 ^c	9.10 \pm 1.34
	Hillside	2.72 \pm 0.12	7.14 \pm 1.30 ^{bc}	0.015 \pm 0.03	3.41 \pm 0.12 ^b	8.68 \pm 1.92
≥ 20 yrs	Flat	1.86 \pm 0.07	7.89 \pm 1.08 ^{abc}	0.053 \pm 0.05	14.60 \pm 1.43 ^a	25.33 \pm 2.14
	Hillside	1.87 \pm 0.15	10.93 \pm 0.76 ^a	0.028 \pm 0.03	9.92 \pm 0.43 ^d	16.72 \pm 1.10
B) Herbaceous stratum						
TSF	TC	Richness	Num. Ind.	Coverage (%)	Height (cm)	
3 yrs	Flat	4.95 \pm 0.29 ^b	8.28 \pm 0.84 ^a	11.68 \pm 0.92	19.46 \pm 0.90 ^d	
	Hillside	7.11 \pm 0.61 ^{ab}	7.06 \pm 0.49 ^b	11.56 \pm 1.18	28.20 \pm 3.08 ^c	
9 yrs	Flat	7.59 \pm 0.95 ^a	8.98 \pm 0.65 ^a	10.98 \pm 1.89	19.74 \pm 1.26 ^d	
	Hillside	6.16 \pm 1.40 ^{ab}	5.48 \pm 0.17 ^c	14.72 \pm 2.03	37.23 \pm 4.26 ^c	
≥ 20 yrs	Flat	1.78 \pm 0.34 ^c	3.55 \pm 0.22 ^d	23.95 \pm 2.79	56.72 \pm 5.42 ^a	
	Hillside	2.12 \pm 0.08 ^c	3.81 \pm 0.26 ^d	21.32 \pm 0.55	43.80 \pm 0.94 ^b	

The highest number of herbaceous individuals was recorded in flat sites at 3 TSF and 9 TSF, while sites with ≥ 20 TSF showed a similar number of individuals across TC (Table 3B). Regardless of TC, herbaceous cover was 3 and 2.7 times higher at sites with ≥ 20 TSF relative to sites with 3 TSF and 9 TSF (Table 3B). Regarding plant height, hillside sites presented taller plants at 3 TSF and 9 TSF conditions, whereas plant height at ≥ 20 TSF was greater in flat sites (Table 3B).

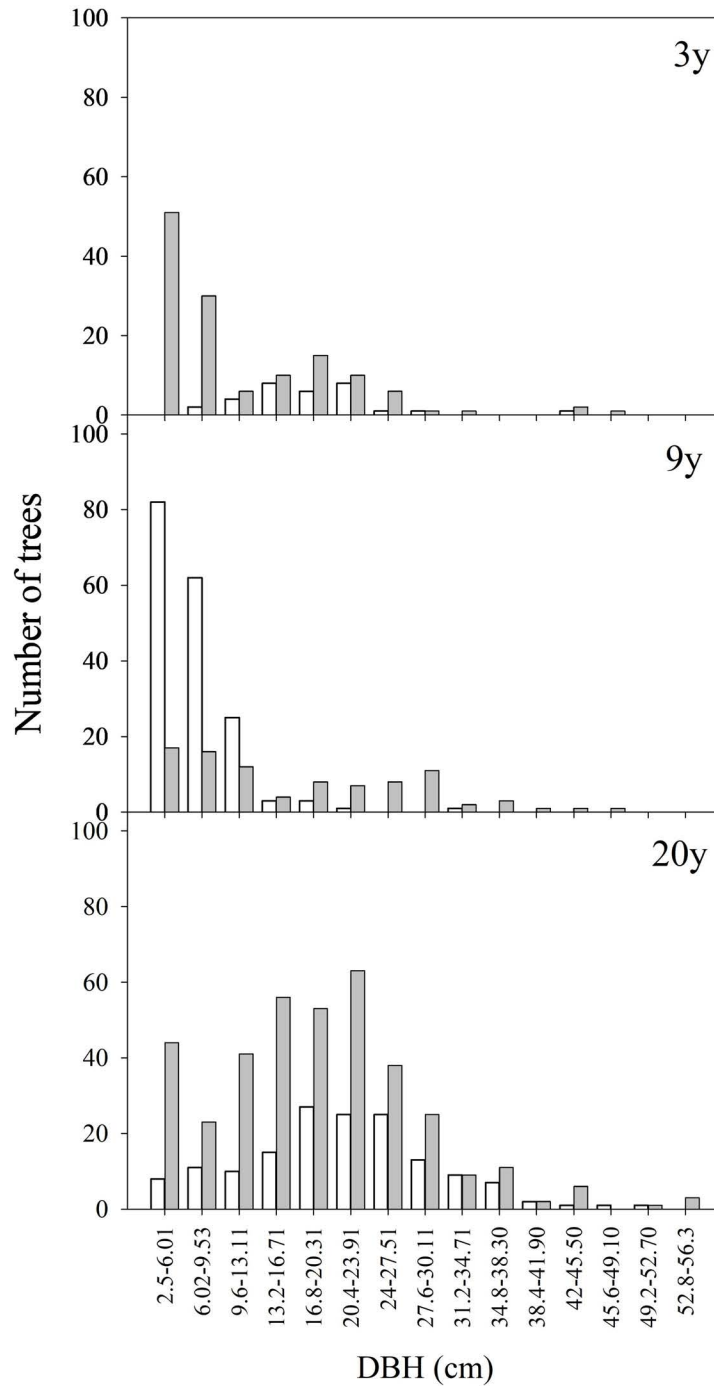


Figure 3. Number of individuals by diametric distribution of *Pinus oocarpa* (unfilled bars) and *Quercus resinosa* (gray bars) in sites with 3, 9, and more than 20 years since the last high-severity fire in “La Primavera” Flora and Fauna Protection Area, western Mexico.

Microenvironmental variables associated with post-fire plant communities. Most soil attributes varied significantly as a function of TSF and TC (Appendix 4). The OM, BD, and Na levels reached highest values at sites with ≥ 20 TSF (Appendix 5). Conversely, recently burned sites (3 TSF and 9 TSF) recorded higher K, Ca, and Mg values. Similarly, sites with different TSF varied concerning microenvironmental variables (Appendix 6). In contrast to sites with ≥ 20 TSF, recently burned sites (3 TSF and 9 TSF) had light values (PAR) 5 times higher, SMC up to 2 times lower, and higher ST (Appendix 7).

The RDA analysis extracted 77 % of the total variance explained in the first three axes. The first axis extracted 40 %, the second axis 25 %, and the third axis 12 % (Figure 4). The first axis revealed that canopy cover (CC) and soil bulk density (BD) were distinctive characteristics of sites with ≥ 20 TSF. In contrast, light (PAR) and herbaceous cover (Cher) dominate recently burned sites (Figure 4). In these latter environments, hillside sites had higher calcium (Ca) and electrical conductivity (EC) levels (Figure 4). On Axis 2, a gradient strongly marked by TC was reflected in sites that experienced recent fires (3 TSF and 9 TSF, 25 % variance explained).

Species associated with ≥ 20 TSF sites were *Q. resinosa*, *Bouteloua polymorpha*, *Chloris* sp., *Mimosa minutifolia*, and *T. spicatus* (Figure 4). In recently burned areas, the species associated with hillside sites were *Calliandra houstoniana* (Kunth) Barneby, *C. hirsuta* (G. Don) Benth., *Hemionitis angustifolia* (Kunth) Christenh., *Chromolaena odorata* (L.) R.M. King & H. Rob., *P. caudatum*, and *A. oligocephala* (Figure 4), while the species associated with flat sites were *P. conjugatum*, *Spermacoce verticillata* L., *Crotalaria sagittalis* L., *Zornia reticulata* Sm., *Tagetes filifolia* Lag., and *T. micrantha* Cav. These latter species seem to be associated with higher light levels (Figure 4). In both flat and hillside sites, woody species, such as *Q. resinosa*, *P. oocarpa*, and the herbaceous species *T. spicatus*, had higher abundances in sites with ≥ 20 TSF.

Discussion

Post-fire regeneration in a seasonally dry oak-pine forest. The seasonally dry oak-pine forest (OPF) affected by high-severity fires shows a successional tendency toward communities with lower floristic richness, mainly of herbaceous species. This decline in the number of individuals and species richness across all life forms during the recovery of forest communities is a typical trend observed in various fire-prone ecosystems (Capitaniao & Carcaillet 2008, Freestone *et al.* 2015, Heydari *et al.* 2020). The herbaceous stratum composition along the post-fire chronosequence is mainly represented by species from the families Asteraceae, Poaceae and Fabaceae, which are recognized as widely distributed species in Mexico (Villaseñor & Espinosa-García 2004, Villaseñor 2016, 2018).

Our first hypothesis is partially fulfilled for the herbaceous stratum. Although abundance and richness are influenced by soil and microenvironmental characteristics associated with the TC, they vary as a function of TSF. Recently burned environments in flat sites in (3 TSF and 9 TSF), with lower canopy cover and higher levels of K, Na, and OM, may favor greater richness and larger numbers of individuals in the herbaceous stratum individuals within the OPF. However, no clear trends are observed between TC along the different TSF. Previously, in the APF-FLP was reported that exchangeable cations (K, Na, Ca, Mg) undergo changes depending on the intensity of the fire, differentially affecting natural regeneration (Cadena-Zamudio *et al.* 2020). Under such conditions, the presence of perennial grass species, such as *Paspalum conjugatum*, *Sporobolus macrospermus*, and *Schizachyrium sanguineum*, which exhibit resprouting tendencies and tolerance to fire (*e.g.*, Everson *et al.* 2021), becomes more pronounced. In recently burned areas of the OPF, pioneer species such as those of the family Asteraceae, characterized by their prolific production of small and wind-dispersed seeds, facilitate the establishment of various plant species, which could be associated with a broad tolerance to open canopy conditions (*e.g.*, Heydari *et al.* 2016, 2020).

We identified TSF, not TC, as an essential driver of post-fire natural regeneration of woody plants of the OPF. The general pattern of succession after high-severity fires in the OPF implies an increase in the IVI of the woody stratum in detriment of the herbaceous stratum. The woody species more representative of Mexican OPF include the families Asteraceae, Ericaceae, Fabaceae, Fagaceae, and Pinaceae (Tellez *et al.* 2020). These families are key structural components of OPF landscape after fires (Alanís-Rodríguez *et al.* 2012, 2020). However, the low woody

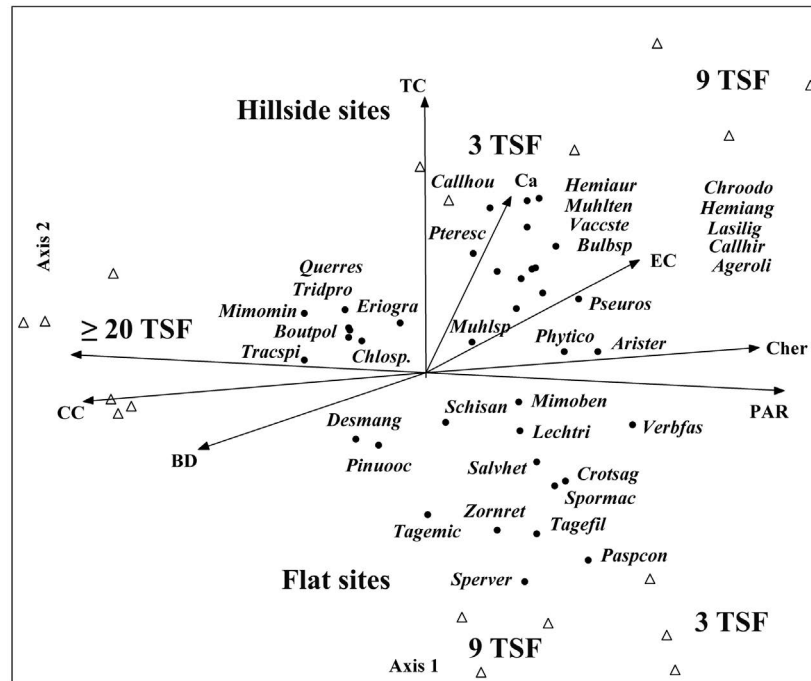


Figure 4. RDA ordination displays species scores from 18 sites with 3, 9, and more than 20 years since the last high-severity fire (3 TSF, 9 TSF, and ≥ 20 TSF) in two topographic conditions: flat and hillside sites, plotted relative to the significant explanatory variables, with fitted vectors indicating variable direction and strength. TC = topographic condition; EC = electrical conductivity; BD = soil bulk density; Ca = calcium; PAR = photosynthetically active radiation available to the plants; Cher = average herbaceous cover; CC = average canopy cover. Triangles represent sites. Black dots represent species. Species are encoded using their scientific name, comprising the initial four letters of the genus and the final three letters of the specific epithet.

species richness in sites with higher TSF of the OPF contrasts with that reported in similar secondary mixed pine-oak forests (González-Espinosa *et al.* 1991, Almazán-Núñez *et al.* 2016). This variation may be attributed to the higher moisture content and lower latitude characteristics of the OPF in Chiapas and Sierra Madre del Sur, as compared to our study site.

Our second hypothesis was fulfilled, as *Q. resinosa* establishment is favored, while *P. oocarpa* regeneration decreases, on sites with major time elapsed since the last fire, a trend observed in studies of competition between *Quercus* and *Pinus* (Retana *et al.* 2002, Torres *et al.* 2016, Barton & Poulos 2018). Environmental filters associated with site conditions, resprouting capacity, seed banks, and dispersal mechanisms are probably the most influential factors in the success of establishment and regeneration of oaks and pines (González-Espinosa *et al.* 1991, Rodríguez-Trejo & Fulé 2003, Rodríguez-Trejo & Myers 2010, Alfaro-Reyna *et al.* 2019). Although *P. oocarpa* shows higher number of resprouts than *Quercus* on recently burned sites (3 TSF and 9 TSF), it appears that most of these resprouts fail in persisting through time (Fulé & Covington 1998). This response could be related to the ability of *Q. resinosa* to tolerate water stress (*e.g.*, Carnicer *et al.* 2014, del Castillo *et al.* 2016, Torres *et al.* 2016, Arenas-Navarro *et al.* 2023). As other authors have pointed out, drier and warmer conditions would favor the regeneration and persistence of some oak species over pines (del Castillo *et al.* 2016, Alfaro-Reyna *et al.* 2019, Arenas-Navarro *et al.* 2023). The canopy type and competition for light are other factors associated with the success of the regeneration of oaks and pines (Retana *et al.* 2002, Alfaro-Reyna *et al.* 2019). Canopy openness and, consequently, higher light availability can favor the survival and growth of *Quercus* (González-Espinosa *et al.* 1991, Quintana-Ascencio *et al.* 1992, González-Tagle *et al.* 2008), excluding the regeneration of pines. The pioneer tree species, especially pines, play a critical role in ecosystems, as their heliophilous character and a great capacity for seed dispersal allows them to establish in open sites at a regional scale (Fulé & Covington 1998, Almazán-Núñez *et al.* 2016, Naudiyal & Schmerbeck 2017). However, *P. oocarpa* loses importance in sites with long periods since fire, which could be related to the lack of seed disper-

sal (it has serotinous cones) and the fact that the canopy cover of *Quercus* prevents its establishment and growth (Rodríguez-Trejo & Fulé 2003, Torres *et al.* 2016, Rodríguez-Trejo *et al.* 2019).

Additionally, the succession model based on the “initial floristic composition” (Egler 1954) could explain the natural regeneration pattern of the OPF. In this case, the species from advanced successional stages persist due to legacies associated with their ability to resprout, as was observed in *Pinus oocarpa*, *Q. resinosa*, and *Q. viminea*. Therefore, the capacity to resprout in species of *Pinus* and *Quercus* greatly favors the persistence of these species (Rodríguez-Trejo & Fulé 2003, Rodríguez-Trejo & Myers 2010, Alanís-Rodríguez *et al.* 2012, Gómez-Mendoza & Rodríguez-Trejo 2021) and the resilience of this ecosystem to fires.

Key species for forest restoration. Restoration strategies must be grounded in a prior evaluation of stressors (biological and physical) that limit the natural regeneration of an ecosystem (An *et al.* 2019, Paz *et al.* 2022, Souza-Alonso *et al.* 2022). Our data show that herbaceous species, which produce large amounts of small wind-dispersed seeds, dominate recently-burned sites. These sites also allow regrowth, germination, and establishment of seedlings, as well as the growth of juvenile individuals, of dominant tree species belonging to advanced stages of plant succession. Therefore, if the biological threshold has not been exceeded, actions such as passive restoration and fire protection (Holl & Aide 2011, Souza-Alonso *et al.* 2022) can favor the natural regeneration of areas affected by high-severity fires.

Understanding plant succession (species turnover over time) allows us to identify species that may favor and accelerate ecosystem regeneration (Balaguer *et al.* 2014) to propose strategies to accelerate this process and restore degraded areas (Prach & Walker 2011, Souza-Alonso *et al.* 2022). The successful regeneration of the dominant tree species, *Q. resinosa* and *P. oocarpa*, in the early stages of succession favors the fire-resilient character of this ecosystem. Therefore, if the objective is to accelerate the regeneration in recently burned sites, an effective restoration strategy could be planting juvenile individuals of *Q. resinosa* and *P. oocarpa* in open sites (without tree cover), together with nitrogen-fixing species.

Like other species, *Q. resinosa* and *P. oocarpa* present adaptations that allow them to resist fires (Rodríguez-Trejo & Fulé 2003, González-Tagle *et al.* 2008, Rodríguez-Trejo & Myers 2010). In the case of *Quercus*, the ability to regenerate vegetatively from dormant buds of stems is elevated, even from their early life-cycle stages (Gracia *et al.* 2002, Moreira *et al.* 2012, Clarke *et al.* 2013). Although both species are post-fire resprouters, *P. oocarpa* is also characterized by thick bark and serotinous cones (Rodríguez-Trejo & Fulé 2003, Rodríguez-Trejo 2008, Rodríguez-Trejo *et al.* 2019). Therefore, including these species in restoration programs would favor the resilience of the OPF to high-severity fires. Despite the adaptability of most species to post-fire environments, successful seed germination and establishment of new seedlings, including resprouting stems, rely on favorable climatic conditions after fires. Without these conducive conditions, the development of recruited and resprouting species becomes unattainable following a fire (Chapin *et al.* 2014, Rodríguez-Trejo 2014, Boucher *et al.* 2020). It is important to mention that, after high-intensity fires, the success of establishing and growing tree seedlings is negatively affected by the absence of mycorrhizae (Chapin *et al.* 2014), so the prior evaluation of the conditions of the microbiota and soil nutrients is an essential part of the restoration program.

Our data demonstrates that legumes are frequent species in less fertile sites with higher TSF. Since legumes are nitrogen-fixing species that play a key role as nurse plants (Callaway 2007, Löff *et al.* 2014), in burned sites they could act as nuclei to accelerate natural regeneration (Goergen & Chambers 2009). In the plant succession within the OPF, the presence of Fabaceae may be linked to an increase in the IVI of tree species on sites with higher TSF. Therefore, mixed planting of woody species, such as *Calliandra hirsuta* and *Mimosa minutifolia*, and herbaceous species, such as *Crotalaria sagittalis*, *Desmodium angustifolium*, and *Eriosema grandiflorum*, could favor the growth and survival of *Q. resinosa* and *P. oocarpa* individuals, particularly on hillside sites.

The abundance and IVI of the species comprising the post-fire chronosequence allow the identification of key species for the restoration of areas affected by high-severity fires in OPF. Based on abundance and IVI, we can conclude that *Q. resinosa* may represent a foundational species for recovering the structure and composition of OPF after high-severity fires. Our findings also indicate that flat sites are potential regeneration cores with greater

richness and numbers of individuals of herbaceous species, while hillside sites, which display lesser regeneration, require prioritized restoration efforts, possibly involving the introduction of oak species with greater resilience to high-severity fires. However, because of the current regime of high fire incidence and livestock activity within the APFFLP (Huerta-Martínez & Ibarra-Montoya 2014, CONAFOR 2022), establishing successful restoration strategies could be challenging and costly. In this context, the committed participation of government institutions, communal owners (such as Ejidos), scientists and the society, in general, is imperative to achieve feasible goals for restoring and preserving of this type of ecosystem. Despite the value of the APFFLP, information on post-fire regeneration patterns is scarce. The current work fills this gap contributing to the understanding of plant succession in areas affected by high-severity fires, and providing essential information for the design of restoration techniques.

Our findings allow us to propose potential restoration techniques for managing ecosystems facing similar disturbances. The proposed recommendations for ecological restoration in areas impacted by high-intensity fires involve identifying key species across various successional stages and understanding the microenvironmental conditions linked with the presence of these species, abundance and Importance Value Index (IVI). This information could facilitate the utilization of these species in diverse restoration techniques, including seed or seedling clusters, as well as larger-scale plantations.

Acknowledgments

We thank the three anonymous reviewers whose invaluable contributions significantly improved the quality of this manuscript. We extend our sincere gratitude to team of the Organismo Publico Descentralizado Bosque La Primavera for their invaluable assistance and support in carrying out this study. Specially thanks are extended to M. Carrillo, J. Alvarado, and S. Quintero. We also express our appreciation to J. Padilla, C. Jacobo, S. Cristobal, and D. Valladolid for their diligent efforts in the field, during data collection, and in species identification. Furthermore, we acknowledge the support of J. Alcocer and I. Pedroza for their contributions to soil analysis. E. Atondo (CVU 547478) has been granted a scholarship by Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) to pursue studies at BEMARENA (CUCBA, Universidad de Guadalajara).

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3440>

Literature cited

- Abatzoglou JT, Williams AP. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America* **113**: 11770-11775. DOI: <https://doi.org/10.1073/pnas.1607171113>
- Agbeshie AA, Abugre S, Atta-Darkwa T, Awuah R. 2022. A review of the effects of forest fire on soil properties. *Journal of Forestry Research* **33**: 1419-1441. DOI: <https://doi.org/10.1007/s11676-022-01475-4>
- Alanís-Rodríguez E, Jiménez-Pérez J, Valdecantos-Dema A, González-Tagle MA, Aguirre-Calderón ÓA, Treviño-Garza EJ. 2012. Composición y diversidad de la regeneración natural en comunidades de *Pinus-Quercus* sometidas a una alta recurrencia de incendios en el noreste de México. *Revista Mexicana de Biodiversidad* **83**: 1208-1214. DOI: <https://doi.org/10.22201/ib.20078706e.2012.4.1013>
- Alanís-Rodríguez E, Sánchez-Castillo L, Méndez-Osorio C, Canizales-Velázquez PA, Mora-Olivo A, Rubio-Camacho E. 2020. Structure and diversity of trees on post-fire regenerated areas in Sierra de Guerrero, Mexico. *Botanical Sciences* **98**: 210-218. DOI: <https://doi.org/10.17129/botsci.2220>
- Alfaro-Reyna T, Martínez-Vilalta J, Retana J. 2019. Regeneration patterns in Mexican pine-oak forests. *Forest Ecosystems* **6**: 50. DOI: <https://doi.org/10.1186/s40663-019-0209-8>

- Almazán-Núñez RC, Corcuera P, Parra-Juárez L, Jiménez-Hernández J, Charre GM. 2016. Changes in structure and diversity of woody plants in a secondary mixed Pine-Oak forest in the Sierra Madre del Sur of Mexico. *Forests* 7: 90. DOI: <https://doi.org/10.3390/f7040090>
- An JH, Lim CH, Cho YC, Lee CS. 2019. Early recovery process and restoration planning of burned pine forests in central eastern Korea. *Journal of Forestry Research* 30: 243-255. DOI: <https://doi.org/10.1007/s11676-018-0638-1>
- Arenas-Navarro M, Oyama K, García-Oliva F, Torres-Miranda A, Terrazas T. 2023. Seasonal temperature and precipitation regimes drive variation in the wood of oak species (*Quercus*) along a climatic gradient in western Mexico. *IAWA Journal* 11: 1-16. DOI: <https://doi.org/10.1163/22941932-bja10110>
- Balaguer L, Escudero A, Martín-Duque JF, Mola I, Aronson J. 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. *Biological Conservation* 176: 12-20. DOI: <https://doi.org/10.1016/j.biocon.2014.05.007>
- Balderas-Torres A, Ontiveros-Enríquez R, Skutsch M, Lovett J. 2013. Potential for climate change mitigation in degraded forests: a study from La Primavera, Mexico. *Forests* 4: 1032-1054. DOI: <https://doi.org/10.3390/f4041032>
- Barton AM, Poulos HM. 2018. Pine vs. oaks revisited: Conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. *Forest Ecology and Management* 414: 28-40. DOI: <https://doi.org/10.1016/j.foreco.2018.02.011>
- Bassaber-Zuñiga AI, Villegas MMM, Curiel-Guevara S, Rojas-Arias ML, Valdez-Rosas JS. 2024. Revisión de causas, consecuencias y medidas de respuesta frente a los incendios forestales: un enfoque en el estado de Jalisco. *e-CUCBA* 21: 100-114.
- Bassett M, Leonard SW, Chia EK, Clarke MF, Bennett AF. 2017. Interacting effects of fire severity, time since fire and topography on vegetation structure after wildfire. *Forest Ecology and Management* 396: 26-34. DOI: <https://doi.org/10.1016/j.foreco.2017.04.006>
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models Using lme4. *Journal of Statistical Software* 67: 1-48. DOI: <https://doi.org/10.18637/jss.v067.i01>
- Bilbao B, Steil L, Urbieta IR, Anderson L, Pinto C, Gonzalez MC, Millán A, Falleiro RM, Morici E, Ibarnegaray V, Perez-Salicrup DR, Pereira JM, Moreno JM. 2020. Incendios forestales. In: Moreno JM, Laguna-Defior C, Barros V, Calvo EB, Marengo JA, Oswald US, eds. *Adaptación frente a los riesgos del cambio climático en los países iberoamericanos – Informe RIOCCADAPT*. Madrid, España: McGraw Hill, pp. 435-496. ISBN: 9788448621643
- Blake GR, Hartge KH. 1986. Bulk Density. In: Klute A, ed. *Methods of Soil Analysis. Part 1-Physical and Mineralogical Methods*. United States: American Society of Agronomy, Inc., pp. 363-375. ISBN: 9780891188643. DOI: <https://doi.org/10.2136/sssabookser5.1.2ed.c13>
- Bond WJ, Keeley JE. 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20: 387-94. DOI: <https://doi.org/10.1016/j.tree.2005.04.025>
- Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *The New Phytologist* 165: 525-37. DOI: <https://doi.org/10.1111/j.1469-8137.2004.01252.x>
- Boucher D, Gauthier S, Thiffault N, Marchand W, Girardin M, Urli M. 2020. How climate change might affect tree regeneration following fire at northern latitudes: a review. *New Forests* 51: 543-571. DOI: <https://doi.org/10.1007/s11056-019-09745-6>
- Cadena-Zamudio DA, Flores-Garnica JG, Flores-Rodríguez AG, Lomelí-Zavala ME. 2020. Effect of fires on understory vegetation and chemical properties of temperate forest soil. *Agroproductividad* 13: 65-72. DOI: <https://doi.org/10.32854/agrop.vi.1684>
- Cadena-Zamudio DA, Flores-Garnica JG, Lomelí-Zavala ME, Flores-Rodríguez AG. 2022. Does the severity of a forest fire modify the composition, diversity and structure of temperate forests in Jalisco? *Revista Chapingo Serie Ciencias Forestales y del Ambiente* 28: 3-20. DOI: <https://doi.org/10.5154/r.rchsefa.2020.12.076>
- Callaway RM. 2007. Direct mechanisms for facilitation. In: *Positive Interactions and Interdependence in Plant Com-*

- munities*. Dordrecht, Netherlands: Springer, pp. 15-116. ISBN: 9781402062230. DOI: <https://doi.org/10.1007/978-1-4020-6224-7>
- Capitanio R, Carcaillet C. 2008. Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. *Forest Ecology and Management* **255**: 431-439. DOI: <https://doi.org/10.1016/j.foreco.2007.09.010>
- Carnicer J, Coll M, Pons X, Ninyerola M, Vayreda J, Peñuelas J. 2014. Large-scale recruitment limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as key regional drivers. *Global Ecology and Biogeography* **23**: 371-384. DOI: <https://doi.org/10.1111/geb.12111>
- Certini G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* **143**: 1-10. DOI: <https://doi.org/10.1007/s00442-004-1788-8>
- Clarke KR, Gorley RN. 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E Plymouth. <https://www.primer-e.com/> (Accessed November 24, 2022).
- Clarke KR, Gorley RN, Somerfield PJ, Warwick RM. 2014. *Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition*. Albany, New Zealand: PRIMER-E: Plymouth. ISBN: 1855311402, 9781855311404.
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* **197**: 19-35. DOI: <https://doi.org/10.1111/nph.12001>
- Challenger A, Dirzo R, López JC, Mendoza E, Lira-Noriega A, Cruz I. 2009. Factores de cambio y estado de la biodiversidad. In: *Capital natural de México, Vol. II: Estado de Conservación y Tendencias de Cambio*. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, pp. 37-73. ISBN: 978-607-7607-08-3
- Chapin III FS, Hollingsworth TN, Hewitt RE. 2014. Fire effects on seedling establishment success across treeline: implications for future tree migration and flammability in a changing climate. *JFSP Research Project Reports* **82**. <http://digitalcommons.unl.edu/jfspresearch/82>
- Colwell RK. 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9.0. <https://www.robertkcolwell.org/pages/estimates> (Accessed November 28, 2021).
- CONABIO [Comisión Nacional para el Conocimiento y Uso de la Biodiversidad]. 2017. *La Biodiversidad en Jalisco: Estudio de Estado, Vol. II*. Ciudad de México, México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. IBSN: 978-607-8328-94-9.
- CONAFOR [Comisión Nacional Forestal]. 2019. *El Sector Forestal Mexicano en cifras 2019 Bosques para el Bienestar Social y Climático*. <https://www.gob.mx/conafor/documentos/el-sector-forestal-mexicano-en-cifras-2019> (Accessed October 5, 2020).
- CONAFOR [Comisión Nacional Forestal]. 2022. Reporte de incendios. Cierre estadístico de 2022. <https://www.gob.mx/conafor/documentos/reporte-semanal-de-incendios> (Accessed May 18, 2023).
- Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**: 1119-1144. DOI: <https://doi.org/10.1086/283241>
- Crotteau JS, Morgan Varner III J, Ritchie MW. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management* **287**: 103-112. DOI: <https://doi.org/10.1016/j.foreco.2012.09.022>
- Curtis JT, McIntosh RP. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* **32**: 476-496. DOI: <https://doi.org/10.2307/1931725>
- DeBano LF, Neary DG, Ffolliott PF. 1998. Fuel and fire behavior. In: *Fire effects on ecosystems*. United States: John Wiley & Sons, pp. 49-70. ISBN: 9780471163565.
- del Castillo J, Comas C, Voltas J, Ferrio JP. 2016. Dynamics of competition over water in a mixed oak-pine Mediterranean forest: Spatio-temporal and physiological components. *Forest Ecology and Management* **382**: 214-224. DOI: <https://doi.org/10.1016/j.foreco.2016.10.025>
- Dye B. 2012. *La apasionante geología del Área de Protección de Flora y Fauna La Primavera. Bosque La Primavera*

- era, *Bosque para siempre*. Guadalajara, México: Área de Protección de Flora y Fauna La Primavera. <http://www.saudicaves.com/mx/geobook/primgeobk.pdf> (Accessed September 30, 2022).
- Egler FE. 1954. Vegetation science concepts I. Initial floristic composition. A factor in old-field vegetation development. *Vegetation* **4**: 412-417. DOI: <https://doi.org/10.1007/BF00275587>
- Escuin S, Navarro R, Fernández P. 2008. Fire severity assessment by using NBR (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) derived from LANDSAT TM/ETM images. *International Journal of Remote Sensing* **29**: 1053-1073. DOI: <https://doi.org/10.1080/01431160701281072>
- Etchells H, O'Donnell AJ, McCaw WL, Grierson PF. 2020. Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of southwest Australia. *Forest Ecology and Management* **459**: 117850. DOI: <https://doi.org/10.1016/j.foreco.2019.117850>
- Everson CS, Everson TM, Morris CD. 2021. The population dynamics of four grass species in relation to burning in the KwaZulu-Natal Drakensberg. *African Journal of Range & Forage Science* **38**: 23-38. DOI: <https://doi.org/10.2989/10220119.2020.1841292>
- Flores-Rodríguez AG, Flores-Garnica JG, González-Eguiarte DR, Gallegos-Rodríguez A, Zarazúa-Villaseñor P, Mena-Munguía S, Lomelí-Zavala ME, Ruíz-Guzmán E. 2021. Regeneración natural de pino y encino bajo diferentes niveles de perturbación por incendios forestales. *Revista Mexicana de Ciencias Forestales* **12**: 3-25. DOI: <https://doi.org/10.29298/rmcf.v12i65.776>
- Freestone M, Wills TJ, Read J. 2015. Post-fire succession during the long-term absence of fire in coastal heathland and a test of the chronosequence survey method. *Australian Journal of Botany* **63**: 572-580. DOI: <https://doi.org/10.1071/BT14345>
- Frelich LE. 2002. *Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests*. New York, United States: Cambridge University Press. ISBN: 9780521052474. DOI: <https://doi.org/10.1017/CBO9780511542046>
- Fulé PZ, Covington WW. 1997. Fire regimes and forest structure in the Sierra Madre Occidental, Durango, Mexico. *Acta Botánica Mexicana* **41**: 43-79. DOI <https://doi.org/10.21829/abm41.1997.791>
- Fulé PZ, Covington WW. 1998. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecology* **134**: 197-209. DOI: <https://doi.org/10.1023/A:1009789018557>
- Gallegos-Rodríguez A, González-Cueva GA, Cabrera-Orozco RG, Marcelli-Sánchez C, Hernández-Álvarez E. 2014. Efecto de la recurrencia de incendios forestales en la diversidad arbórea. *Revista Mexicana de Ciencias Forestales* **5**: 110-125.
- Gärtner SM, Bokalo M, Macdonald SE, Stadt K. 2014. Variation in post-wildfire regeneration of boreal mixed wood forests: underlying factors and implications for natural disturbance-based management. *New Forests* **45**: 215-234. DOI: <https://doi.org/10.1007/s11056-013-9404-6>
- Gauch HG. 1982. *Multivariate Analysis in Community Ecology*. New York, United States: Cambridge University Press. ISBN: 9780511623332. DOI: <https://doi.org/10.1017/CBO9780511623332>
- Goergen EM, Chambers JC. 2009. Influence of a native legume on soil N and plant response following prescribed fire in sagebrush steppe. *International Journal of Wildland Fire* **18**: 665-675. DOI: <https://doi.org/10.1071/WF08067>
- Gómez-Mendoza FF, Rodríguez-Trejo DA. 2021. Fire, mortality and resprouting in forest species at Sierra Norte de Puebla. *Madera y Bosques* **27**. DOI: <https://doi.org/10.21829/myb.2021.2732148>
- González-De Vega S, de las Heras J, Moya D. 2018. Post-fire regeneration and diversity response to burn severity in *Pinus halepensis* Mill. Forests. *Forests* **9**: 299. DOI: <https://doi.org/10.3390/f9060299>
- González-Espinosa M, Quintana-Ascencio PF, Ramírez-Marcial N, Gaytán-Guzmán P. 1991. Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. *Journal of Vegetation Science* **2**: 351-360. DOI: <https://doi.org/10.2307/3235927>
- González-Tagle MA, Schwendenmann L, Pérez JJ, Schulz R. 2008. Forest structure and woody plant species com-

- position along a fire chronosequence in mixed pine-oak forest in the Sierra Madre Oriental, Northeast Mexico. *Forest Ecology and Management* **256**: 161-167. DOI: <https://doi.org/10.1016/j.foreco.2008.04.021>
- Gotelli NJ, Chao A. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin SA, ed. *Encyclopedia of Biodiversity*. Waltham, United States: Academic Press, pp. 195-211. DOI: <http://dx.doi.org/10.1016/B978-0-12-384719-5.00424-X>
- Gracia M, Retana J, Roig P. 2002. Mid-term successional patterns after fire of mixed pine-oak forests in NE Spain. *Acta Oecologica* **23**: 405-411. DOI: [https://doi.org/10.1016/S1146-609X\(02\)01169-4](https://doi.org/10.1016/S1146-609X(02)01169-4)
- Hardesty J, Myers R, Fulks W. 2005. Fire, ecosystems and people: a preliminary assessment of fire as a global conservation issue. *Fire Management* **22**: 78-87.
- Heydari M, Faramarzi M, Pothier D. 2016. Post-fire recovery of herbaceous species composition and diversity, and soil quality indicators one year after wildfire in a semi-arid oak woodland. *Ecological Engineering* **94**: 688-697. DOI: <https://doi.org/10.1016/j.ecoleng.2016.05.032>
- Heydari M, Moradzadeh H, Omidipour R, Mezbani A, Pothier D. 2020. Spatio-temporal changes in the understory heterogeneity, diversity, and composition after fires of different severities in a semiarid oak (*Quercus brantii* Lindl.) forest. *Land Degradation & Development* **31**: 1039-1049. DOI: <https://doi.org/10.1002/ldr.3518>
- Holl KD, Aide TM. 2011. When and where to actively restore ecosystems? *Forest Ecology and Management* **261**: 1558-1563. DOI: <https://doi.org/10.1016/j.foreco.2010.07.004>
- Huerta-Martínez FM, Ibarra-Montoya JL. 2014. Incendios en el Bosque La Primavera (Jalisco, México): un acercamiento a sus posibles causas y consecuencias. *Ciencia UAT* **9**: 5-9.
- Ibarra-Montoya JL, Huerta-Martínez FM. 2016. Cambio climático y predicción de incendios al 2050 en el Bosque La Primavera, Jalisco. *Revista Mexicana de Ciencias Forestales* **7**: 39-50.
- IPCC [Intergovernmental Panel on Climate Change]. 2003. Good practice guidance for land use, land-use change and forestry. In: Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, Buendia L, Miwa K, Ngara T, Tanabe K, Wagner F, eds. *Good practice guidance for land use, land-use change and forestry*. Kanagawa, Japan. ISBN: 4887880030.
- Jiménez J, Alanís-Rodríguez E. 2011. Análisis de la frecuencia de los incendios forestales en la Sierra Madre Oriental y Occidental del norte de México y sur de Estados Unidos de América. *Ciencia UANL* **14**: 255-263.
- Johnson EA, Miyanishi K. 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* **11**: 419-431. DOI: <https://doi.org/10.1111/j.1461-0248.2008.01173.x>
- Johnstone JF, Chapin FS. 2006. Fire interval effects on successional trajectory in boreal forests of Northwest Canada. *Ecosystems* **9**: 268-277. DOI: <https://doi.org/10.1007/s10021-005-0061-2>
- Kane VR, Lutz JA, Cansler CA, Povak NA, Churchill D, Smith DF, Kane JT, North MP. 2015. Water balance and topography predict fire and forest structure patterns. *Forest Ecology and Management* **338**: 1-13. DOI: <https://doi.org/10.1016/j.foreco.2014.10.038>
- Keeley JE. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* **18**: 116. DOI: <https://doi.org/10.1071/WF07049>
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406-411. DOI: <https://doi.org/10.1016/j.tplants.2011.04.002>
- Key CH, Benson NC. 2006. Landscape Assessment. In: Lutes DC, Keane RE, Caratti JF, Key CH, Benson NC, Sutherland S, Gangi LJ, eds. FIREMON: Fire effects monitoring and inventory system. General Technical Report RMRS-GTR-164-CD. Fort Collins, United States: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 1-51.
- Legendre P, Andersson MJ. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**: 1-24. DOI: [https://doi.org/10.1890/0012-9615\(1999\)069\[0001:DBRATM\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2)
- Liu Z, Wimberly MC. 2016. Direct and indirect effects of climate change on projected future fire regimes in

- the western United States. *Science of The Total Environment* **542**: 65-75. DOI: <https://doi.org/10.1016/j.scitotenv.2015.10.093>
- Löf M, Bolte A, Jacobs DF, Jensen AM. 2014. Nurse trees as a forest restoration tool for mixed plantations: effects on competing vegetation and performance in target tree species. *Restoration Ecology* **22**: 758-765. DOI: <https://doi.org/10.1111/rec.12136>
- McCune B, Grace JB. 2002. *Analysis of ecological communities*. Glendened Beach, United States: MJM Software Design. ISBN: 0972129006.
- McCune B, Mefford MJ. 2016. PC-ORD. Multivariate Analysis of Ecological Data. Version 7.0. Corvallis, Oregon, United States: MJM Software Design. <https://www.wildblueberrymedia.net/pcord> (Accessed February 27, 2023).
- Montoya LE, Corona-Núñez RO, Campo JE. 2023. Fires and their key drivers in Mexico. *International Journal of Wildland Fire* **32**: 651-664. DOI: <https://doi.org/10.1071/WF22154>
- Moreira B, Tormo J, Pausas JG. 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. *Oikos* **121**: 1577-1584. DOI: <https://doi.org/10.1111/j.1600-0706.2011.20258.x>
- Naudiyal N, Schmerbeck J. 2017. The changing Himalayan landscape: pine-oak forest dynamics and the supply of ecosystem services. *Journal of Forestry Research* **28**: 431-443. DOI: <https://doi.org/10.1007/s11676-016-0338-7>
- Noble IR, Slatyer RO. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**: 5-21. DOI: <https://doi.org/10.1007/BF00121013>
- Parsons A, Robichaud PR, Lewis SA, Napper C, Clark JT. 2010. *Field guide for mapping post-fire soil burn severity*. General Technical Report RMRS-GTR-243. Fort Collins, United States: Department of Agriculture, Forest Service, Rocky Mountain Research Station. DOI: <https://doi.org/10.2737/RMRS-GTR-243>
- Pausas JG. 2015. Bark thickness and fire regime. *Functional Ecology* **29**: 315-327. DOI: <https://doi.org/10.1111/1365-2435.12372>
- Pausas JG, Keeley JE. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* **204**: 55-65. DOI: <https://doi.org/10.1111/nph.12921>
- Pausas JG, Keeley JE. 2019. Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment* **17**: 289-295. DOI: <https://doi.org/10.1002/fee.2044>
- Paz H, Ortiz-Alcaraz A, Del-Val E. 2022. The effects of the aggressive species *Pteridium caudatum* on the vegetation of Socorro Island: Restoration challenges and opportunities. *Journal for Nature Conservation* **67**: 126-160. DOI: <https://doi.org/10.1016/j.jnc.2022.126160>
- Ponce-Calderón LP, Rodríguez-Trejo DA, Villanueva-Díaz J, Bilbao BA, Álvarez-Gordillo GDC, Vera-Cortés G. 2021. Historical fire ecology and its effect on vegetation dynamics of the Lagunas de Montebello National Park, Chiapas, Mexico. *iForest* **14**: 548-559. DOI: <https://doi.org/10.3832/ifer3682-014>
- Prach K, Walker LR. 2011. Four opportunities for studies of ecological succession. *Trends in Ecology & Evolution* **26**: 119-123. DOI: <https://doi.org/10.1016/j.tree.2010.12.007>
- Pulsford SA, Lindenmayer DB, Driscoll DA. 2016. A succession of theories: purging redundancy from disturbance theory. *Biological Reviews* **91**: 148-167. DOI: <https://doi.org/10.1111/brv.12163>
- Quintana-Ascencio PF, González-Espinosa M, Ramírez-Marcial N. 1992. Acorn removal, seedling survivorship, and seedlings growth of *Quercus crispipilis* in successional forests of the highlands of Chiapas, Mexico. *Bulletin of the Torrey Botanical Club* **119**: 6. DOI: <https://doi.org/10.2307/2996914>
- RStudioTeam. 2022. RStudio: Integrated Development for R. Boston, United States. <http://www.rstudio.com/> (Accessed November 14, 2022).
- Rago MM, Urretavizcaya MF, Morelli P, Mohr-Bell D, Guzmán M. 2023. Early vegetation recovery following a mid to high-severity fire in the Andean-Patagonian forests. *Austral Ecology* **49**. DOI: <https://doi.org/10.1111/aec.13319>
- Retana J, Espelta JM, Habrouk A, Ordoñez JL, de Solà-Morales F. 2002. Regeneration patterns of three Mediterra-

- nean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience* **9**: 89-97. DOI: <https://doi.org/10.1080/11956860.2002.11682694>
- Rodríguez-Trejo DA. 2008. Fire regimes, fire Ecology, and fire management in Mexico. *AMBIO: a Journal of the Human Environment* **37**: 548-556. DOI: <https://doi.org/10.1579/0044-7447-37.7.548>
- Rodríguez-Trejo DA. 2014. Incendios de vegetación, su ecología, manejo e historia. México: Biblioteca Básica de Agricultura. ISBN: 9-786077-152378.
- Rodríguez-Trejo DA, Fulé PZ. 2003. Fire ecology of Mexican pines and a fire management proposal. *International Journal of Wildland Fire* **12**: 23. DOI: <https://doi.org/10.1071/WF02040>
- Rodríguez-Trejo DA, Myers RL. 2010. Using characteristics of oaks as guides to restoring fire regimes in Mexican pine-oak and oak forests. *Ecological Restoration* **28**: 304-323. DOI: <https://doi.org/10.3368/er.28.3.304>
- Rodríguez-Trejo DA, Muñoz PM, Lara PJM. 2019. Efectos del fuego en el arbolado de un bosque tropical de pino y en el de una selva baja caducifolia en Villaflores, Chiapas, México. *Ciencia Florestal* **29**: 1033-1048. DOI: <https://doi.org/10.5902/1980509833952>
- Russell A, Buerkner P, Herve M, Love J, Singmann H. 2021. Package ‘emmeans.’ R package version, 1(4). <https://github.com/rvlenth/emmeans> (Accessed November 14, 2022).
- SEMARNAT [Secretaría del Medio Ambiente y Recursos Naturales]. 2000. Programa de Manejo Área de Protección de Flora y Fauna La Primavera. México: SEMARNAT, Comisión Nacional de Áreas Protegidas. https://www.conanp.gob.mx/que_hacemos/pdf/programas_manejo/primavera.pdf (Accessed April 4, 2020).
- SEMARNAT [Secretaría del Medio Ambiente y Recursos Naturales]. 2002. Norma Oficial Mexicana NOM-021-RECNAT-2000, Especificaciones de Fertilidad, Salinidad y Clasificación de Suelos, Estudio, Muestreo y Análisis. Diario Oficial de la Federación. 2da Sección. <http://www.ordenjuridico.gob.mx/Documentos/Federal/wo69255.pdf> (Accessed May 5, 2022).
- Silva-Cardoza AI, Vega-Nieva DJ, López-Serrano PM, Corral-Rivas JJ, Briseño-Reyes J, Briones-Herrera CI, Loera-Medina JC, Parra-Aguirre E, Rodríguez-Trejo DA, Jardel-Peláez E. 2021. Metodología para la evaluación de la severidad de incendios forestales en campo, en ecosistemas de bosque templado de México. México: Fondo Sectorial para la Investigación, el Desarrollo y la Innovación Tecnológica y Forestal CONAFOR-CONACYT, proyecto CONAFOR-CONACYT-2018-C02-B-S131553. http://forestales.ujed.mx/incendios2/php/publicaciones_documentos/7_3_Silva%20et%20al%2020211201_Metodologia_severidad_v1.pdf (Accessed October 2021).
- Souza-Alonso P, Saiz G, García RA, Pauchard A, Ferreira A, Merino A. 2022. Post-fire ecological restoration in Latin American forest ecosystems: insights and lessons from the last two decades. *Forest Ecology and Management* **509**: 120083. DOI: <https://doi.org/10.1016/j.foreco.2022.120083>
- Tellez O, Mattana E, Diazgranados M, Kühn N, Castillo-Lorenzo E, Lira R, Montes-Leyva L, Rodriguez I, Flores-Ortiz CM, Way M, Dávila P, Ulian T. 2020. Native trees of Mexico: Diversity, distribution, uses and conservation. *PeerJ* **8**: 1-26. DOI: <https://doi.org/10.7717/peerj.9898>
- Torres I, Pérez B, Quesada J, Viedma O, Moreno JM. 2016. Forest shifts induced by fire and management legacies in a *Pinus pinaster* woodland. *Forest Ecology and Management* **361**: 309-317. DOI: <https://doi.org/10.1016/j.foreco.2015.11.027>
- Vázquez-García JA, Givnish TJ. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* **86**: 999-1020. DOI: <https://doi.org/10.1046/j.1365-2745.1998.00325.x>
- Vega-Nieva DJ, Briseño-Reyes J, Briones-Herrera C. 2020. Manual de usuario del Sistema de Predicción de Peligro de Incendios Forestales (SPPIF) de México. <http://forestales.ujed.mx/incendios2> (Accessed October 10, 2020).
- Villaseñor JL. 2016. Checklist of the native vascular plants of Mexico. *Revista Mexicana de Biodiversidad* **87**: 559-902. DOI: <https://doi.org/10.1016/j.rmb.2016.06.017>
- Villaseñor JL. 2018. Diversidad y distribución de la familia Asteraceae en México. *Botanical Sciences* **96**: 332-358. DOI: <https://doi.org/10.17129/botsci.1872>

- Villaseñor JL, Espinosa-García FJ. 2004. The alien flowering plants of Mexico. *Diversity and distributions* **10**: 113-123. DOI: <https://doi.org/10.1111/j.1366-9516.2004.00059.x>
- Walker LR, Wardle DA, Bardgett RD, Clarkson BD. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* **98**: 725-736. DOI: <https://doi.org/10.1111/j.1365-2745.2010.01664.x>
- Walkley A, Black IA. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science* **37**: 29-38. DOI: <https://doi.org/10.1097/00010694-193401000-00003>
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**: 940-3. DOI: <https://doi.org/10.1126/science.1128834>
- Zúñiga-Vásquez JM, Pompa-García M. 2019. The occurrence of forest fires in Mexico presents an altitudinal tendency: a geospatial analysis. *Natural Hazards* **96**: 213-224. DOI: <https://doi.org/10.1007/s11069-018-3537-z>

Associate editor: Ernesto Badano

Author contributions: EJAB, conceptualization, investigation, methodology, field sampling, data curation, formal analysis, writing - original draft and editing; MSZA, investigation, methodology, data curation, formal analysis, writing - review and editing; MAMC, conceptualization, investigation, methodology, writing - review and editing; RCG, investigation, data curation, formal analysis, writing - review and editing; FLB, conceptualization, investigation, methodology, writing - review and editing; EAR, investigation, writing - review and editing.

Supporting Agencies: Consejo Nacional de Humanidades, Ciencias y Tecnologías and Universidad de Guadalajara.

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.

Appendix 1. Response variables linked to their respective objectives, sampling units, and statistical analysis.

Objective	Registered variables/units	Sampling units	Statistical analysis
1 Describe post-fire differences in species composition, species richness and structure of mixed OPF based on recovery time since the last high-severity fire and two topographic conditions (flat vs. hillside sites).	Species composition: Abundance of species.		NMDS, ANOSIM. Also used for DCA and RDA.
	Structure of woody stratum: Number of species (Richness).	In ten circular plot ($r = 5.64$ m, 100 m ²) per site.	Two-way GLMM.
	Number of individuals per species.		Two-way GLMM.
	Height (m) per individual/species.		Two-way GLMM.
	Diameter at breast height (DBH, cm) per individual/species.		Kruskal-Wallis test.
	Basal area (m ²).		Two-way GLMM.
	Number of resprouting individuals per species.		Two-way GLMM.
	Structure of herbaceous stratum: Number of species (Richness).	In four squares of 1 × 1 m within each circular plot per site.	Two-way GLMM.
	Number of individuals per species.		
	Average height (cm) per species.		
Average cover (%) per species.			
2 Determine microenvironmental variables associated with post-fire plant communities.	Soil pH, Electrical Conductivity (EC, $\mu\text{mho/cm}$), Soil texture, Organic matter (OM, %), Bulk density (BD, g cm^{-3}), K (mg/L), Na (mg/L), Ca (mg/L), Mg (mg/L).	One composite soil sample per site was collected.	Two-way GLMM. DCA and RDA.
	Radiation available to the plants (PAR, $\mu\text{mol m}^{-2}\text{s}^{-1}$), quality of light (red/far red ratio), Soil moisture content (SMC, %), Soil temperature (ST, °C).	At each site, directly measured at five random locations.	
	Elevation (m asl), Slope (%), Woody cover (%), Herbaceous cover (%), Leaf litter cover (%), Rocks cover (%), Bare soil (%).	In ten circular plot ($r = 5.64$ m, 100 m ²) per site.	DCA and RDA.
3 Identify key species for the active restoration of the OPF after a high-severity fire.	Woody stratum: Abundance and Importance value index (IVI) (%), sum of abundance, frequency, and dominance).	Per time since the last fire (TSF).	
	Herbaceous stratum: Abundance and Importance value index (IVI) (%), sum of abundance, frequency, and coverage).		

Plant succession pattern and forest restoration

Appendix 2. Species registered in sites with 3, 9, and more than 20 years since the last high-severity fire (3 TSF, 9 TSF, and ≥ 20 TSF) in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. H = herbaceous; S = shrub; T = tree. Marked with an x the presence of each species in each TSF.

Family	Species	Author	Growth form	3	9	≥ 20
				TSF		
Acanthaceae	<i>Elytraria imbricata</i>	(Vahl) Pers.	H		x	
Apiaceae	<i>Eryngium beecheyanum</i>	Hook. & Arn.	H	x		
	<i>Eryngium heterophyllum</i>	Engelm.	H		x	
	<i>Eryngium mexiae</i>	Constance	H		x	
Apocynaceae	<i>Asclepias jaliscana</i>	B.L. Rob.	H		x	
	<i>Mandevilla hypoleuca</i>	(Benth.) Pichon	H		x	
	<i>Plumeria rubra</i>	L.	T	x		
Asparagaceae	<i>Agave bulliana</i>	(Baker) Thiede & Eggli	H	x	x	
	<i>Agave guadalajarana</i>	Trel.	S	x	x	
	<i>Agave jaliscana</i>	(Rose) A. Berger	S		x	
	<i>Bessera elegans</i>	Schult.f.	H	x	x	
	<i>Echeandia flexuosa</i>	Greenm.	H	x	x	
Asteraceae	<i>Ageratina oligocephala</i>	(DC.) R.M. King & H. Rob.	S	x	x	
	<i>Ageratum corymbosum</i>	Zuccagni.	S		x	
	<i>Baccharis pteronioides</i>	DC.	S		x	
	<i>Barkleyanthus salicifolius</i>	(Kunth) H. Rob. & Brettell	S	x	x	
	<i>Bidens pilosa</i>	L.	H	x	x	
	<i>Brickellia cuspidata</i>	S.Watson	S	x		
	<i>Chromolaena odorata</i>	(L.) R.M. King & H. Rob.	S	x	x	
	<i>Chromolaena ovaliflora</i>	(Hook. & Arn.) R.M. King & H. Rob.	S	x	x	
	<i>Coreopsis petrophila</i>	A. Gray	S		x	
	<i>Cosmos bipinnatus</i>	Cav.	H	x	x	
	<i>Cosmos crithmifolius</i>	Kunth	H	x	x	
	<i>Cosmos landii</i>	Sherff	H	x		
	<i>Dyssodia tagetiflora</i>	Lag.	H	x		
	<i>Eremosis foliosa</i>	(Benth.) Gleason	S	x	x	x
	<i>Erigeron canadensis</i>	L.	H	x	x	
	<i>Galinsoga parviflora</i>	Cav.	H	x	x	
	<i>Heterotheca inuloides</i>	Cass.	H	x		
	<i>Iostephane heterophylla</i>	(Cav.) Benth.	H	x	x	
	<i>Jaegeria hirta</i>	(Lag.) Less.	H	x		

Family	Species	Author	Growth	3	9	≥ 20
				form	TSF	
	<i>Perymenium bupthalmoides</i>	DC.	H	x	x	
	<i>Psacalium poculiferum</i>	(S. Watson) Rydb.	H	x	x	
	<i>Pseudognaphalium canescens</i>	(DC.) Anderb.	H	x		
	<i>Pseudognaphalium roseum</i>	(Kunth) Anderb.	H	x	x	
	<i>Sonchus oleraceus</i>	L.	H	x	x	
	<i>Stevia ovata</i>	Willd.	H	x	x	
	<i>Stevia viscida</i>	Kunth	H	x		
	<i>Tagetes filifolia</i>	Lag.	H	x	x	
	<i>Tagetes micrantha</i>	Cav.	H	x	x	x
	<i>Tridax procumbens</i>	L.	S	x	x	x
	<i>Verbena carolina</i>	L.	H		x	
	<i>Verbesina fastigiata</i>	B.L. Rob. & Greenm.	S	x	x	
	<i>Verbesina alternifolia</i>	(L.) Britton ex Kearney	S	x	x	
	<i>Verbesina sphaerocephala</i>	A. Gray	S	x	x	
	<i>Zinnia angustifolia</i>	Kunth	H	x	x	
Begoniaceae	<i>Begonia tapatia</i>	Burt-Utley & McVaugh	H	x	x	
Bignoniaceae	<i>Tecoma stans</i>	(L.) Kunth	T		x	
Boraginaceae	<i>Wigandia urens</i>	(Ruiz & Pav.) Kunth	S	x	x	
Cactaceae	<i>Mammillaria jaliscana</i>	(Britton & Rose) Boed.	S			x
Campanulaceae	<i>Diastatea tenera</i>	(A. Gray) McVaugh	H	x	x	
	<i>Lobelia fenestralis</i>	Cav.	H	x		
Caryophyllaceae	<i>Drymaria gracilis</i>	Cham. & Schldl.	H	x	x	
Cistaceae	<i>Crocanthemum glomeratum</i>	(Lag.) Janch.	S	x	x	
	<i>Lechea tripetala</i>	(Moc. & Sessé ex Dunal) Britton	H	x	x	
Clethraceae	<i>Clethra rosei</i>	Britton	T	x	x	x
Commelinaceae	<i>Commelina dianthifolia</i>	Redouté	H	x	x	
Convolvulaceae	<i>Ipomoea capillacea</i>	G. Don	H	x	x	
Cyperaceae	<i>Bulbostylis capillaris</i>	(L.) Kunth ex C.B. Clarke	H	x	x	
	<i>Bulbostylis juncooides</i>	(Vahl) Kük. ex Osten	H	x		
	<i>Bulbostylis</i> sp.	-	H	x	x	
	<i>Cyperus brevifolius</i>	Endl. ex Hassk.	H	x		
	<i>Cyperus manimae</i>	Kunth	H	x	x	
	<i>Cyperus seslerioides</i>	Kunth.	H		x	

Plant succession pattern and forest restoration

Family	Species	Author	Growth	3	9	≥ 20
				form	TSF	
	<i>Cyperus sesquiflorus</i>	(Torr.) Mattf. & Kük.	H	x	x	
	<i>Cyperus</i> sp.	-	H	x	x	
Dennstaedtiaceae	<i>Pteridium caudatum</i>	(L.) Maxon	S	x	x	x
Ericaceae	<i>Agarista mexicana</i>	(Hemsl.) Judd	T	x	x	
	<i>Vaccinium stenophyllum</i>	Steud.	S	x	x	
Euphorbiaceae	<i>Euphorbia guadalajarana</i>	S. Watson	H	x	x	
	<i>Euphorbia</i> sp.	-	H	x	x	
	<i>Euphorbia succedanea</i>	L.C. Wheeler	H		x	
Fabaceae	<i>Calliandra hirsuta</i>	(G. Don) Benth.	S	x	x	
	<i>Calliandra houstoniana</i> (Mill.) Standl. var. <i>anomala</i>	(Kunth) Barneby	S	x	x	x
	<i>Chamaecrista rotundifolia</i>	(Pers.) Greene	H	x	x	
	<i>Crotalaria pumila</i>	Ortega	H		x	
	<i>Crotalaria sagittalis</i>	L.	H	x	x	
	<i>Dalea leporina</i>	(Aiton) Bullock	H	x		
	<i>Dalea pectinata</i>	Kunth	S	x		
	<i>Dalea</i> sp.	-	S	x	x	
	<i>Desmodium angustifolium</i>	(Kunth) DC.	S	x	x	x
	<i>Desmodium orbiculare</i>	Schltl.	S	x	x	
	<i>Desmodium polystachyum</i>	Schltl.	H		x	
	<i>Desmodium</i> sp.	-	H	x		
	<i>Eriosema diffusum</i>	(Kunth) G. Don	H	x		
	<i>Eriosema grandiflorum</i>	(Schltl. & Cham.) G. Don	S	x	x	x
	<i>Indigofera densiflora</i>	M. Martens & Galeotti	S	x	x	
	<i>Lysiloma</i> sp.	-	T	x	x	
	<i>Marina nutans</i>	(Cav.) Barneby	S	x		
	<i>Mimosa benthamii</i>	J.F. Macbr.	T	x	x	
	<i>Mimosa minutifolia</i>	Robinson & Greenm.	S			x
	<i>Vachellia pennatula</i>	(Schltl. & Cham.) Seigler & Ebinger	T	x	x	x
	<i>Zornia reticulata</i>	Sm.	H	x	x	
Fagaceae	<i>Quercus resinosa</i>	Liebmann	T	x	x	x
	<i>Quercus viminea</i>	Trel.	T	x	x	x
Gentianaceae	<i>Chironia</i> sp.	-	H	x		
Hypericaceae	<i>Hypericum philonotis</i>	Schltl. & Cham.	H	x		
Iridaceae	<i>Sisyrinchium</i> sp.	-	H	x		

Family	Species	Author	Growth	3	9	≥ 20
				form	TSF	
Lamiaceae	<i>Hyptis oblongifolia</i>	Benth.	S		x	
	<i>Hyptis</i> sp.	-	S		x	
	<i>Salvia firma</i>	Fernald	S	x	x	
	<i>Salvia heterotricha</i>	Fernald	S	x	x	x
Lentibulariaceae	<i>Pinguicula parvifolia</i>	B.L. Rob.	H		x	
Lythraceae	<i>Cuphea llavea</i>	Lex.	S	x		
Malpighiaceae	<i>Aspicarpa brevipes</i>	(DC.) W.R. Anderson	S	x		
Malvaceae	<i>Heliocarpus terebinthinaceus</i>	(DC.) Hochr.	S		x	
	<i>Sida</i> sp.	-	H	x		
	<i>Waltheria indica</i>	L.	S	x		
Melastomataceae	<i>Heterocentron subtriplinervium</i>	A. Braun & Bouche.	S	x	x	
Olacaceae	<i>Fraxinus uhdei</i>	(Wenz.) Lingelsh.	T		x	
	<i>Ximenia parviflora</i>	Benth.	S	x	x	
Orchidaceae	<i>Bletia neglecta</i>	Sosa	H	x	x	
	<i>Bletia roezlii</i>	Rchb.f.	H		x	
	<i>Habenaria jaliscana</i>	S. Watson	H	x	x	
Orobanchaceae	<i>Castilleja nervata</i>	Eastw.	H	x		
Oxalidaceae	<i>Oxalis decaphylla</i>	Kunth	H	x	x	
Phytolaccaceae	<i>Phytolacca icosandra</i>	L.	H	x	x	
Pinaceae	<i>Pinus oocarpa</i>	Schiede ex Schltdl.	T	x	x	x
Poaceae	<i>Aristida laxa</i>	Cav.	H		x	
	<i>Aristida ternipes</i>	Cav.	H	x	x	
	<i>Bouteloua hirsuta</i>	Lag.	H	x		
	<i>Bouteloua polymorpha</i>	(E. Fourn.) Columbus	H			x
	<i>Chloris</i> sp.	-	H			x
	<i>Cynodon dactylon</i>	(L.) Pers.	S		x	
	<i>Digitaria filiformis</i>	(L.) Koeler	H	x		
	<i>Digitaria ternata</i>	(A. Rich.) Stapf	H		x	
	<i>Eragrostis curtipedicellata</i>	Buckley	H	x		
	<i>Eragrostis mexicana</i>	(Hornem.) Link	H	x	x	
	<i>Heteropogon</i> sp.	-	S	x		
	<i>Lasiacis ligulata</i>	Hitchc. & Chase	H	x	x	x
	<i>Melinis repens</i>	(Willd.) Zizka	H	x	x	x
	<i>Muhlenbergia capillaris</i>	Trin.	H	x		

Plant succession pattern and forest restoration

Family	Species	Author	Growth	3	9	≥ 20
				form	TSF	
	<i>Muhlenbergia longiligula</i>	Hitchc.	H	x		
	<i>Muhlenbergia macroura</i>	Hitchc.	H	x		
	<i>Muhlenbergia</i> sp.	-	H	x	x	
	<i>Muhlenbergia tenella</i>	Trin.	H	x	x	
	<i>Oplismenus burmannii</i>	(Retz.) P. Beauv.	H		x	
	<i>Paspalum conjugatum</i>	P.J. Bergius	H	x	x	
	<i>Paspalum notatum</i>	Flüggé	H	x		
	<i>Paspalum tenellum</i>	Willd.	H	x		
	<i>Schizachyrium sanguineum</i>	(Retz.) Alston	H	x	x	x
	<i>Setaria parviflora</i>	(Poir.) Kerguélen	H	x		
	<i>Sporobolus macrospermus</i>	Scribn. ex Beal	H	x	x	x
	<i>Trachypogon spicatus</i>	(L. f.) Kuntze	H	x	x	x
Polygalaceae	<i>Polygala berlandieri</i>	S. Watson	H	x	x	
Pteridaceae	<i>Hemionitis angustifolia</i>	(Kunth) Christenh.	S	x	x	x
	<i>Hemionitis aurantiaca</i>	(Cav.) Christenh.	S	x	x	
	<i>Hemionitis hirsuta</i>	(Link) Christenh.	S	x	x	
Rubiaceae	<i>Bouvardia ternifolia</i>	Schltld.	S	x	x	x
	<i>Crusea longiflora</i>	(Willd. ex Roem. & Schult.) W.R. Anderson	H	x		
	<i>Crusea</i> sp.	-	H	x		
	<i>Hexasepalum</i> sp.	-	H	x		
	<i>Hexasepalum teres</i>	(Walter) J.H. Kirkbr.	H	x	x	
	<i>Mitracarpus hirtus</i>	DC.	H	x	x	
	<i>Richardia scabra</i>	L.	H		x	
	<i>Spermacoce verticillata</i>	L.	H	x	x	
Saxifragaceae	<i>Heuchera longipetala</i> Moc. ex Ser. var. <i>orizabensis</i>	(Hemsl.) R.A. Folk	H		x	
Solanaceae	<i>Physalis nicandroides</i>	Schltld.	H		x	
	<i>Physalis</i> sp.	-	H	x	x	
	<i>Solanum americanum</i>	Mill.	H	x		
	<i>Solanum ferrugineum</i>	Jacq.	S	x		
	<i>Solanum nigrum</i>	Acerbi ex Dunal	S	x	x	
	<i>Solanum</i> sp.	-	S	x		
	<i>Solanum torvum</i>	Sw.	S	x		
Passifloraceae	<i>Turnera callosa</i>	Urb.	H	x		
Urticaceae	<i>Urtica</i> sp.	-	S		x	
Verbenaceae	<i>Lippia umbellata</i>	Cav.	S	x		

Appendix 3. Average number of tree individuals that exhibit resprouting for the three dominant species contributing to canopy cover in sites with 3, 9, and more than 20 years since the last high-severity fire (TSF) in two topographic conditions (TC: flat and hillside sites) in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. Mean \pm Standard error.

TSF	TC	<i>P. oocarpa</i>		<i>Q. resinosa</i>		<i>Q. viminea</i>	
3 yrs	Flat	26.67 \pm	7.75	14.67 \pm	7.69	09.00 \pm	5.57
3 yrs	Hillside	06.00 \pm	0.00	27.33 \pm	5.81	15.33 \pm	5.93
9 yrs	Flat	408.67 \pm	139.14	55.33 \pm	33.29	22.00 \pm	19.55
9 yrs	Hillside	267.67 \pm	205.61	20.00 \pm	11.59	17.33 \pm	6.36
\geq 20 yrs	Flat	0.00 \pm	0.00	0.00 \pm	0.00	0.00 \pm	0.00
\geq 20 yrs	Hillside	0.00 \pm	0.00	0.00 \pm	0.00	0.00 \pm	0.00

Plant succession pattern and forest restoration

Appendix 4. Deviance table for Generalized Linear Mixed Models that evaluate the differences in soil attributes registered in sites with 3, 9, and more than 20 years since the last high-severity fire in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. TSF = time since the last high-severity fire; TC = topographic condition (flat and hillside sites); EC = electrical conductivity; K = potassium; Na = sodium; Ca = calcium; Mg = magnesium; OM = organic matter; BD = bulk density of the soil.

Factor	DF num.	DF den.	F	P
a) EC				
TSF	2	10	16.8	0.006
TC	1	10	5.0	0.049
TSF:TC	2	10	0.8	0.476
b) Soil pH				
TSF	2	10	0.01	0.980
TC	1	10	2.53	0.140
TSF:TC	2	10	2.0	0.180
c) K				
TSF	2	10	4.36	0.433
TC	1	10	0.14	0.709
TSF:TC	2	10	0.27	0.764
d) Na				
TSF	2	10	7.64	0.009
TC	1	10	0.48	0.505
TSF:TC	2	10	1.64	0.241
e) Ca				
TSF	2	10	12.7	0.008
TC	1	10	21.2	0.001
TSF:TC	2	10	18.1	< 0.001
f) Mg				
TSF	2	10	9.69	0.004
TC	1	10	0.20	0.658
TSF:TC	2	10	2.51	0.130
g) OM				
TSF	2	10	7.96	0.008
TC	1	10	10.9	0.008
TSF:TC	2	10	4.16	0.048
h) BD				
TSF	2	10	31.6	< 0.001
TC	1	10	6.26	0.033
TSF:TC	2	10	1.11	0.366

Appendix 5. Soil attributes registered in sites with 3, 9, and more than 20 years since the last high-severity fire in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. TSF = time since last high-severity fire; TC = topographic condition (flat and hillside sites); EC = electrical conductivity; K = potassium; Na = sodium; Ca = calcium; Mg = magnesium, OM = organic matter; BD = bulk density of the soil. Mean ± Standard error. Different letters indicate statistical differences only between TSF.

TSF	TC	EC ($\mu\text{mho}/\text{cm}$)	Soil pH	K (mg/L)	Na (mg/L)	Ca (mg/L)	Mg (mg/L)	OM (%)	BD (g cm^{-3})							
3	Flat	0.03 ± 0.00	b	6.48 ± 0.13	516.40 ± 29.84	ab	397.70 ± 79.39	ab	127.87 ± 05.05	b	132.37 ± 04.10	a	0.39 ± 0.09	b	1.28 ± 0.01	a
3	Hillside	0.03 ± 0.00		6.56 ± 0.13	445.63 ± 35.68		244.50 ± 20.33		364.63 ± 46.58	a	167.40 ± 18.66		1.57 ± 0.83		1.26 ± 0.05	
9	Flat	0.04 ± 0.00	a	6.59 ± 0.22	623.30 ± 135.04	a	190.43 ± 41.23	b	156.00 ± 05.78	b	123.43 ± 35.96	ab	2.24 ± 1.51	a	1.12 ± 0.03	b
9	Hillside	0.05 ± 0.01		6.43 ± 0.05	594.70 ± 25.61		199.13 ± 60.16		237.03 ± 52.41	b	113.60 ± 05.40		1.70 ± 0.75		1.02 ± 0.01	
≥ 20	Flat	0.03 ± 0.00	b	6.74 ± 0.11	386.43 ± 87.14	b	399.70 ± 88.08	a	197.50 ± 56.39	b	098.27 ± 11.99	b	1.33 ± 0.13	a	1.35 ± 0.04	a
≥ 20	Hillside	0.03 ± 0.00		6.32 ± 0.01	419.63 ± 32.40		445.40 ± 62.41		129.23 ± 22.21	b	062.13 ± 03.63		1.53 ± 0.49		1.26 ± 0.03	

Plant succession pattern and forest restoration

Appendix 6. Deviance table for Generalized Linear Mixed Models that evaluate the differences in the microenvironment variables in sites with 3, 9, and more than 20 years since the last high-severity fire in an oak-pine forest in “La Primavera” Flora and Fauna Protection Area, western Mexico. TSF = time since last high-severity fire; TC = topographic condition (flat and hillside sites); PAR = photosynthetically active radiation available to the plants; SMC = soil moisture content; ST = soil temperature.

Factor	DF num.	DF den.	F	P
a) PAR				
TSF	2	10	92.7	< 0.001
TC	1	10	0.25	0.62
TSF:TC	2	10	2.09	0.17
b) SMC				
TSF	2	10	20.3	0.003
TC	1	10	2.1	0.173
TSF:TC	2	10	6.7	0.014
c) ST				
TSF	2	10	19.2	< 0.001
TC	1	10	1.09	0.319
TSF:TC	2	10	7.5	0.010

Appendix 7. Microenvironmental variables registered in sites with 3, 9, and more than 20 years since the last high-severity fire in an oak-pine forest in La Primavera Flora and Fauna Protection Area, western Mexico. TSF = time since last high-severity fire; TC = topographic condition (flat and hillside sites); PAR = photosynthetically active radiation available to the plants; SMC = soil moisture content; ST = soil temperature. Mean \pm Standard error. Different letters indicate statistical differences only between TSF.

TSF	TC	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		SMC (%)		ST ($^{\circ}\text{C}$)	
3 yrs	Flat	1549.87 \pm 097.29	a	12.71 \pm 0.18	b	48.00 \pm 0.12	b
3 yrs	Hillside	1314.47 \pm 162.05		16.51 \pm 2.11		46.67 \pm 0.64	
9 yrs	Flat	1364.53 \pm 065.01	a	18.96 \pm 2.50	a	45.07 \pm 0.27	a
9 yrs	Hillside	1545.47 \pm 118.01		26.30 \pm 1.94		42.20 \pm 1.22	
\geq 20 yrs	Flat	271.27 \pm 96.49	b	27.62 \pm 0.43	a	42.33 \pm 0.79	a
\geq 20 yrs	Hillside	200.95 \pm 38.95		22.68 \pm 1.79		44.73 \pm 0.58	