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Contemporary Fire Regimes Provide a Critical Perspective on Restoration Needs in the Mexico-United States Borderlands

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ABSTRACT: The relationship between people and wildfire has always been paradoxical: fire is an essential ecological process and management tool, but can also be detrimental to life and property. Consequently, fire regimes have been modified throughout history through both intentional burning to promote benefits and active suppression to reduce risks. Reintroducing fire and its benefits back into the Sky Island mountains of the United States-Mexico borderlands has the potential to reduce adverse effects of altered fire regimes and build resilient ecosystems and human communities. To help guide regional fire restoration, we describe the frequency and severity of recent fires over a 32-year period (1985-2017) across a vast binational region in the United States-Mexico borderlands and assess variation in fire frequency and severity across climate gradients and in relation to vegetation and land tenure classes. We synthesize relevant literature on historical fire regimes within 9 major vegetation types and assess how observed contemporary fire characteristics vary from expectations based on historical patterns. Less than 28% of the study area burned during the observation period, excluding vegetation types in warmer climates that are not adapted to fire (eg, Desertscrub and Thornscrub). Average severity of recent fires was low despite some extreme outliers in cooler, wetter environments. Midway along regional temperature and precipitation gradients, approximately 64% of Pine-Oak Forests burned at least once, with fire frequencies that mainly corresponded to historical expectations on private lands in Mexico but less so on communal lands, suggesting the influence of land management. Fire frequency was higher than historical expectations in extremely cool and wet environments that support forest types such as Spruce-Fir, indicating threats to these systems possibly attributable to drought and other factors. In contrast, fires were absent or infrequent across large areas of Woodlands (~73% unburned) and Grasslands (~88% unburned) due possibly to overgrazing, which reduces abundance and continuity of fine fuels needed to carry fire. Our findings provide a new depiction of fire regimes in the Sky Islands that can help inform fire management, restoration, and regional conservation planning, fostered by local and traditional knowledge and collaboration among landowners and managers.

RESUMEN: La relación entre la gente y los incendios forestales siempre ha sido paradójica: el fuego es esencial como proceso ecológico y herramienta de gestión, pero también puede ser perjudicial para la vida y la propiedad. En consecuencia, los regímenes de incendios se han modificado a lo largo de la historia, mediante quemas intencionales para promover sus beneficios o mediante la supresión activa para reducir sus riesgos. La reintroducción del fuego y sus beneficios a las montañas de las Islas del Cielo, en la frontera entre Estados Unidos y México, tiene el potencial de reducir los impactos adversos de los regímenes de fuego alterados y construir ecosistemas y comunidades humanas resilientes. Para fortalecer la restauración de incendios en la región, describimos la frecuencia y severidad de los incendios recientes en un período de 32 años (1985-2017) en una vasta región binacional de la frontera entre Estados Unidos y México, evaluamos la variación en la frecuencia y severidad de los incendios a lo largo de gradientes climáticos y en relación con la vegetación y la tenencia de la tierra. Sintetizamos bibliografía relevante sobre los regímenes históricos de incendios en nueve tipos de vegetación principales y analizamos si las características observadas de los incendios contemporáneos varían con respecto a expectativas basadas en patrones históricos. Menos del 28% del área de estudio se quemó durante el período de observación, excluyendo los tipos de vegetación en climas más cálidos que no están adaptados al fuego (por ejemplo, los Matorrales Desértico y Espinoso). La severidad media de los incendios recientes fue baja a pesar de algunos valores extremos en entornos más fríos y húmedos. En un punto intermedio en los gradientes regionales de temperatura y precipitación, aproximadamente el 64% de los Bosques de Pino-Encino se quemaron por lo menos una vez durante el periodo de estudio. Las frecuencias de incendios tuvieron correspondencia general con las expectativas históricas para las tierras privadas en México, aunque de menor forma en tierras comunales, lo que sugiere que el manejo ejerce influencia sobre los regímenes de incendios. En los entornos extremadamente frescos y húmedos que albergan tipos de bosques como los de Picea-Abies la frecuencia de los incendios excedió las expectativas históricas, lo que indica que las amenazas a estos sistemas pueden atribuirse a las sequías y otros factores. En cambio, los incendios fueron inexistentes o poco frecuentes en grandes zonas de Bosques Abiertos (~73% sin quemar) y Pastizales (~88% sin quemar) debido posiblemente al sobrepastoreo, que reduce la abundancia y continuidad de los combustibles finos necesarios para el transporte del fuego. Nuestros resultados proporcionan una nueva descripción de los regímenes de incendios en las Islas del Cielo que puede contribuir al manejo del fuego, la restauración y la planificación de la conservación regional, fomentada por el conocimiento local y tradicional y la colaboración entre propietarios y responsables del manejo.
Palabras clave: incendio forestal, Islas del Cielo, severidad del fuego, tratamientos de combustibles, condiciones de referencia, Landsat, clima

KEYWORDS: Wildfire, Sky Islands, fire severity, fuels treatments, reference conditions, Landsat, climate

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Background

Fire shapes ecosystems across the globe through direct and indirect effects on many processes including biogeochemical cycles and the distribution of vegetation communities.[1,2] Fire is also a major evolutionary force that has shaped adaptations of plant species, composition of vegetation communities, and the ecology and distributions of animal and human populations.[3,4] Hence, in systems where natural fire regimes have been altered by reducing or augmenting fire frequency or severity, the sustainability of ecosystem structure and function may be threatened.[5,6] Changes in fuel structure and ignition patterns can alter the size and severity of fires, and affect biodiversity and landscape heterogeneity, property values, and human health.[7,8] Increased fire frequency due to warmer, drier climates can be detrimental in fire-prone shrublands, woodlands, and forests, where shortened fire-free intervals limit plant recruitment, particularly by species that rely on seeds for postfire regeneration.[9] Depending on ecological context, adverse impacts of altered fire regimes may be reduced by implementing restoration strategies, such as prescribed burning and managed wildfires that are based on information about historical fire regimes.[10]

In the Sky Islands region of the United States-Mexico borderlands, innovative restoration projects initiated by grassroots organizations illustrate how local communities can engage directly with their environments to build resilient ecosystems and human communities.[11] Restoration of fire-adapted landscapes, where frequent low-severity fire was common, has the potential to contribute to multiple restoration goals including protecting water resources, enhancing habitats for wildlife species, and creating and maintaining the flow and connectivity of ecosystem services across landscapes.[5] Within the context of restoration, information on timing and spatial patterns of fire and its effects on plants and animals can be integrated with conservation.[3] Importantly, the considerable knowledge and experience of traditional practitioners in the region could contribute significantly to meeting the challenges of designing and conducting vegetation treatments, prescribed burns, or managed wildfire necessary for restoration.[12-14]

Restoring natural fire regimes at landscape scales in the United States-Mexico borderlands, however, is complicated by several factors. Various local-scale fuels reduction treatments have been applied in parts of the borderlands region over the past 3 decades, but have shown mixed success in mitigating future wildfire risk and improving ecosystem resilience.[15] Lack of funding for large-scale fuels management and regulatory issues complicate implementation of landscape-scale, multi-jurisdictional fuels treatments in both Mexico and the United States.[16,17] The region has complex land ownership and land tenure patterns with varying land uses, management objectives, and human population densities.[18] In the United States, most land is publicly owned and managed by federal, state, and tribal organizations with top-down fire management plans. In Mexico, large-scale fire suppression and management activities were rare historically and most lands are privately or communally owned, with few scattered protected areas overlaid on these lands. Identifying restoration needs and tailoring restoration activities across such a diverse landscape requires recognizing how legacies of management and human activities may have shaped historical and contemporary fire patterns.

Like other parts of western North America where fire suppression was prevalent, this region has seen a general trend toward more and larger fires over the past 3 decades, particularly in the United States.[19,20] Understanding the natural variability of fire activity in relation to both climate and human activities is critical to evaluating shifts in fire regimes.[21] Historically, an abundance of ignition sources from both lightning and humans, and a consistent period of dry weather during late spring and early summer fostered wildfire in the Madrean Sky Island region, except at lower elevations in Desertscrub and subtropical Thornscrub, which lacked fuel continuity.[22,23] Wildfires spread unimpeded and burned extensive areas across the southwestern United States prior to European settlement. On the US side of the border, livestock grazing and active fire suppression essentially eliminated large fires from the late 19th century to the 1980s,[24,25] whereas in Mexico, fire suppression was highly variable, and frequent fires continued in some areas, based on information from the few remote sites that have been studied.[26,27]

Evaluating the characteristics of contemporary fires and their relationship to both climate conditions and human activities in the Sky Islands is now possible due to recently developed data sets. Satellite data from the past 32 years shows that large fires were common during this period in both the United States and Mexico, with the largest fires (>25 000 ha) observed primarily in the United States during recent droughts.[19] Identifying climate conditions where recent fires burned, the severity and frequency of fire, and the influence of land management can provide information that is critical and complementary to historical perspectives, and inform fuels treatments and restoration planning, given the uncertainty around how fires and vegetation communities will respond to future climate change.[28]

The goal of this study is to describe and analyze patterns of recent wildfires to help guide long-term restoration and fire management in the Sky Islands region of the United States and Mexico. We addressed the following questions:

1. How do recent patterns of fire severity and fire frequency vary across the region?
2. How do recent fires differ across vegetation types, land tenure, and climatic gradients?
3. Where and how do contemporary fire characteristics compare to expected patterns based on known historical fire regimes? What are the climatic, biotic, and land-use characteristics that support these fires?

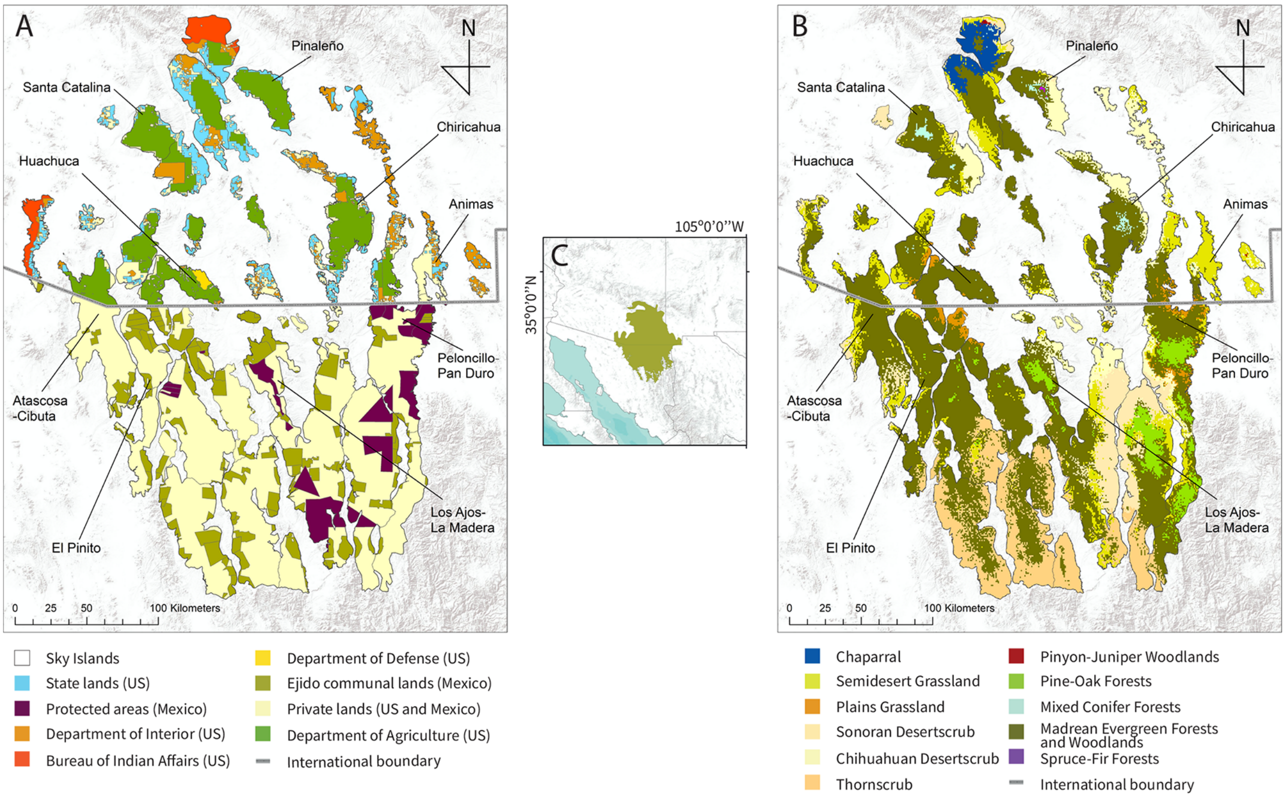

Figure 1. Maps depicting the distribution of land tenure parcels (A) and the distribution of vegetation communities (B) of the Sky island mountain ranges of the United States and Mexico, and the general location of the Madrean Archipelago ecoregion (C). Land ownership/tenure data were obtained and compiled from multiple databases.[32-36]

Methods

Study area

The 74 788 km^2 Madrean Archipelago Ecoregion of the United States and Mexico is a global biodiversity hotspot situated in a broad transition zone between the Nearctic and Neotropical biotic realms.[29,30] Biogeographical and historical complexity of the region is driven by the influences of the Sierra Madre Occidental and lowland Neotropics to the south, the Rocky Mountains to the north, and the Chihuahuan and Sonoran deserts to the east and west.[31]

Our study area consists of 39 Sky Island mountain complexes within the Madrean ecoregion (22 in the United States and 17 in Mexico), with a surface area of approximately 39 000 km^2 (Figure 1). These complexes were delineated based largely on physiographic criteria;[37] upper elevations range from a minimum of ~1600 m in the west to above 3300 m, with generally larger ranges that reach higher elevations in the north and east. The region is characterized by bimodal precipitation with summer (June to September) monsoon storms from the east, and winter (November to March) storms of Pacific origin that produce snow at higher elevations.[38]

The Sky Islands are generally rugged and remote with limited road access or human populations, especially in Mexico.[39] Valleys at the base of the mountains and foothills support a variety of land uses and human settlements that are probable sources of fire ignition and fuels management. The upper-elevation forests and woodlands of the Sky Islands in the United States are primarily managed by the US Forest Service (USFS), Department of Interior (DOI), and Bureau of Indian Affairs (BIA), with state and private lands in foothills and lower elevations (Figure 1A). In Mexico, most upper-elevation forests and woodlands are privately owned and include some scattered protected areas (Figure 1A). The foothills and lower elevations are a mosaic of *ejido* (communal) and private lands with fewer protected areas, which impose management restrictions but do not affect land tenure (Figure 1A). Although ejidos are sometimes thought to be more intensively managed than private lands, the influence of land tenure on vegetation and land use is complex and varies spatially and with environmental and social factors.[40,41]

Conceptual models of vegetation–fire relationships in the Sky Islands

The Sky Islands of our study region contains 11 vegetation types originally mapped by Brown et al in 1998[42] and updated by Rehfeldt et al in 2012[43] (Table 1, Figure 1B). We merged these types into 9 groups based on shared historical characteristics of fire regimes (fire frequency and severity) and vegetation responses to fire. The resulting groups included 4 broad vegetation formations (Semidesert and Plains Grasslands, Sonoran and Chihuahuan Desertscrub, Chaparral, Foothills Thornscrub) and 5 woodland and forest communities

Table 1. Vegetation types[43] found within the study region summarizing dominant species, species traits, and fire-regime characteristics. We grouped the original communities into 4 broad vegetation formations and 5 woodland and forest types for analyses. Fire-regime descriptions represent our conceptual model of expectations for each type, based on the literature.

VEGETATION TYPE	COMMON SPECIES	TRAITS OF DOMINANT PLANT SPECIES	FIRE FREQUENCY (INTERVAL RANGE IN YEARS)	HIGH-SEVERITY % AVERAGE (RANGE)	HIGH-SEVERITY PATCH SIZE (HA)	POSTFIRE VEGETATION RECOVERY (YEARS)	CITATIONS
Spruce-Fir Forests (41[a])	*Picea engelmannii* *Abies concolor* *Pinus ponderosa* *P. strobiformis* *Pseudotsuga menziesii* *Populus tremuloides* *Quercus gambelii*	Early seral resprouters and late seral seed established	Infrequent (30-100)	20 (5-80)	⩽1000	Slow (50-150)	O'Conner et al;[44] Margolis et al[45]
Mixed conifer forests (43)	*Abies concolor* *P. ponderosa* *Pseudotsuga menziesii* *Populus tremuloides* *Q. gambelii*	Thick barked conifers survive fires; some have high dispersal abilities Deciduous species resprout	Frequent (5-20)	5 (3-10)	Minimal, ⩽100	Slow (50-200)	O'Conner et al;[44] Swetnam and Baisan[46]
Pine-oak forests (10)	*Pinus arizonica* *P. strobiformis* *P. engelmannii* *P. leiophylla* *P. ponderosa* *Q. hypoleucoides* *Q. gambelii*	Thick barked conifers survive fires; some resprout; serotiny also present Deciduous species resprout	Frequent (5-15)	5 (3-10)	Minimal, ⩽100	Moderate (10-100)	Barton;[47] Iniguez et al;[48] Kaib et al;[49] Swetnam and Baisan;[46] Swetnam et al[25]
Madrean evergreen forests and woodlands (33)	*P. engelmannii* *P. leiophylla* *Q. arizonica* *Q. emoryi* *Q. hypoleucoides* *Q. oblongifolia*	Thick barked pines survive fires; some resprout; grass-stage seedlings Oak species resprout	Frequent (3-10)	Unknown	Unknown	Very fast (3-20)	Danzer et al;[50] Kaib et al;[49] Swetnam and Baisan[46]
Grasslands (40, 47)	*Andropogon* spp. *Bouteloua* spp. *Aristida* spp. *Muhlenbergia* spp. *Schizachyrium* spp. *Sporobolus* spp. *Yucca elata*	Grasses resprout postfire	Frequent (2-10)	90 (80-95)	⩽200	Very fast (1-5)	Bahre;[24] Kaib et al;[49] McPherson;[51] Wright and Bailey[52]

(continued)

Table 1. (Continued)

VEGETATION TYPE	COMMON SPECIES	TRAITS OF DOMINANT PLANT SPECIES	FIRE FREQUENCY (INTERVAL RANGE IN YEARS)	HIGH-SEVERITY % AVERAGE (RANGE)	HIGH-SEVERITY PATCH SIZE (HA)	POSTFIRE VEGETATION RECOVERY (YEARS)	CITATIONS
Pinyon-juniper woodlands (8)	*Juniperus depeanna* *J. scopulorum* *P. edulis* *P. discolor*	Mainly species with large seeds dispersed by animals	Infrequent (100-400)	10 (3-40)	Minimal, ⩽200	Very slow (100-300)	Baker and Shinneman;[53] Floyd et al;[54] Huffman et al;[55] Romme et al[56]
Chaparral (6)	*Arctostaphhylos pungens* *Berberis fremontii* *Ceanothus greggii* *Q. turbinella*	Obligate seeders and resprouters reestablish quickly	Infrequent (30-100)	80% avg (70-95%)	⩽200	Slow (30-150)	Cable;[57] Brooks et al[58]
Desertscrub (35, 39)	*Agave* spp. *Cylindropuntia* spp. *Dasylirion* spp. *Fouquieria splendens* *Larrea tridentata* *Opuntia* spp. *Parkinsonia* spp. *Prosopis* spp. *Senegalia* *Yucca* spp.	Few species adapted to fire	Very infrequent (likely >250-year intervals)	NA	NA	NA	Bahre;[24] Thomas;[59] Van Devender et al[23]
Thornscrub (34)	*Bursera* spp. *Ceiba acuminata* *Fouquieria macdougalii* *Ipomoea arborescens* *Lysiloma* spp. *Parkinsonia praecox* *Prosopis* spp. *Stenocereus thurberi* *Vachellia campechiana*	Few species adapted to fire	Very infrequent (likely >200-year intervals)	NA	NA	NA	Van Devender et al[23]

[a]Numbers correspond to vegetation types of Rehfeldt et al[43] within each category.

(eg, Spruce-Fir Forest, Madrean Evergreen Forests and Woodlands, etc.). The predominant vegetation type is Madrean Evergreen Forests and Woodlands (~20 000 km^2) at moderate to high elevations, followed by Desertscrub (6500 km^2) and Thornscrub (~5000 km^2) at low elevations in the south, and Grasslands (~4000 km^2) at low elevations in the north and central portion of the study area. Pine-Oak (~1500 km^2), Mixed Conifer (~200 km^2), and Spruce-Fir (~7 km^2) forests are restricted to the highest elevations (Figure 1). Chaparral (~900 km^2) and Pinyon-Juniper Woodlands (~18 km^2) are mapped only in the 2 northernmost Sky Islands, but similar vegetation occurs in northern Sonora. Information on dominant species in each vegetation type and fire adaptation and reproduction and regime traits are summarized in Table 1, and more detailed descriptions are provided in the Supplemental Materials.

Characteristics of historical fire regimes (ie, fire severity, fire frequency, and high-severity patch size) prior to European settlement were identified from various sources including regional dendrochronology and ecology studies and historical accounts (Table 1; see details in Supplemental materials). Fire in forested vegetation communities ranged from infrequent stand-replacing fires (spruce-fir forests; 100-400 years[45,44]) to frequent mixed-severity (mixed conifer; 10-20 years[44,46]) and low-severity (pine-oak forests; 5-10 years[25,46-49]) (Table 1). Fire regimes in woodland vegetation types ranged from frequent (evergreen forest and woodlands; 3-10 years) to infrequent (pinyon-juniper; 100-400 years;[53-56] chaparral 30-100 years[57,58]). Fire frequency in low-elevation types is driven by fuel availability and moisture, with high frequency in grasslands (2-10 years[24,49,51,52]) and low frequency in thornscrub (>200 years[23]) and desertscrub (>250 years[23,24,59]) (Table 1).

Fire identification and fire severity mapping

In the United States, federal agencies maintain a comprehensive spatial database of large (>400 ha) wildfires mapped from satellite imagery (1984-present) through the monitoring trends in burn severity (MTBS) program.[59] Since an equivalent database does not exist for lands in Mexico, we developed a comparable database of fire perimeters and burn severity products for the Sky Islands in Mexico.[19,60,61] Fire perimeter[62] and severity[63] data sets are available from USGS ScienceBase and links are provided in the Supplemental Materials section.

We used Landsat-derived differenced normalized burn ratio (dNBR) images from 335 fires identified across the region from 1984 to 2017 to quantify spatial patterns of high-severity fire, which is an important indicator of potential for vegetation recovery.[10] Before classification, we used the aggregate function[64] to resample the dNBR images; the maximum dNBR value was assigned to ~1 km cells. Determining a threshold value for high severity is a subjective process without prefire and postfire field data to guide the classification.[65] In the absence of field data for the 335 fires, we classified the dNBR images into binary maps of high severity (1) or not (0) using multiple thresholds; high severity was classified using a single value from 450 to 650 in increments of 10 (ie, total of 21 classified maps). The percent high severity for each fire was calculated for each classified map by summing the raster cells with value = 1 and dividing by the total number of raster cells in the dNBR image.

Characterizing the regional climatic environment

Our goal in characterizing the environment was to better understand how fire regimes vary across broad regional gradients and with human influence.[66,67] To describe the regional climatic environment, we transformed 20 bioclimatic variables (Table 2) into 2 orthogonal axes using principal components analysis (PCA) in *R*[68] (prcomp function). The PCA was conducted using all raster cells from the bioclimatic variables so results could be mapped and sampled for further analysis. The first 2 principal components were retained; these axes described most of the variability (PC1 = 0.62; PC2 = 0.28). PC1 represented a general temperature gradient expressed as a latitudinal and altitudinal energy and phenology gradient, with highest positive loadings including Beginning of the frost-free period (0.27) and Degree-days < 0°C (0.25) (Table 2). PC2 represented a heat-moisture and precipitation gradient which varied with longitude (ie, Continentality) and elevation; highest positive loadings included Summer heat moisture index (SHM) (0.39), Annual heat moisture index (AHM) (0.38), and Mean annual precipitation (MAP) (Table 2). We selected 2 of the variables with the highest loadings to aid in interpretation of results (ie, MAT and bFFP for PC1 and MAP and AHM for PC2). Maps of PC1 and PC2 can be found in the Supplemental Materials.

Statistical analyses

To assess regional variation in recent fires (eg, question 1), we summarized observed fire severity and frequency from mapped data and computed descriptive statistics. To assess environmental variation in recent fire severity (eg, question 2), we developed generalized additive models (GAMs)[70] using high-severity composition as the response and mean PC1 and PC2 values within each fire perimeter as predictors. Data for fires in each country were modeled separately (n = 203 fires times 21 thresholds = 4263 data points for United States; n = 132 fires times 21 thresholds = 2772 data points for Mexico). As high-severity composition was measured using multiple thresholds, model fit reflected both variability due to threshold and trends in high severity across PC1 and PC2. Confidence intervals (95%) were developed using 1000 points generated across the climate gradients as a way to evaluate model fit.[71] We displayed the GAM smooth plots in panels to examine differences in relationships across PC1 and PC2, facilitating visualization of

Table 2. Climate data (1981-2010 climate normals; AdaptWest Project[69]) used to derive the principal components (PC) for the study region. Loadings for the first 2 principal components (PC1 and PC2) are listed, and variables selected to provide a general interpretation of results are shown in bold.

ACRONYM	VARIABLE DEFINITION	PC1	PC2
AHM	**Annual heat moisture index, (MAT + 10)/(MAP/1000)**	−0.10	**0.38**
bFFP	**Julian date on which the frost-free period begins**	**0.27**	0.04
CMD	Hargreave's climatic moisture index	−0.22	0.22
DD_0	Degree-days < 0°C (chilling degree days)	0.25	−0.05
DD5	Degree-days above 5°C (growing degree days)	−0.28	0.02
eFFP	Julian date on which the frost-free period ends	−0.27	−0.07
EMT	Extreme minimum temperature over 30 years	−0.27	−0.07
Eref	Hargreave's reference evaporation	−0.26	0.04
MAP	**Mean annual precipitation (mm)**	−0.01	**−0.41**
MAT	**Mean annual temperature (°C)**	**−0.28**	0.02
MCMT	Mean temperature of the coldest month (°C)	−0.28	−0.05
MSP	Mean summer precipitation (mm) (May to September)	−0.11	−0.37
MWMT	Mean temperature of the warmest month (°C)	−0.26	0.13
NFFD	Number of frost-free days	−0.27	−0.02
PPT_sm	Summer precipitation (mm) (June to August)	−0.12	−0.36
PPT_wt	Winter precipitation (mm) (December to February)	0.13	−0.26
SHM	Summer heat moisture index, MWMT/(MSP/1000)	0.01	0.39
Tave_sm	Summer mean temperature (°C) (June to August)	−0.27	0.11
Tave_wt	Winter mean temperature (°C) (December to February)	−0.28	−0.04
TD	Continentality (°C), expressed by MCMT-MWMT	0.14	0.33

high-severity composition across climate, vegetation types, and land management (eg, question 3).

We calculated 2 fire-regime metrics in addition to high severity (%) described above: (1) number of times burned and (2) mean fire return interval (eg, question 1). Metrics were examined across the PC climate gradients and compared observations to expectations for each vegetation type (eg, question 2 and 3; Table 1). To quantify the number of times burned, we used the fire perimeter data to map the total number of fires within 100-m resolution grid cell. The mean fire return interval within the study period was calculated by generating annual raster maps of each fire year in which grid cell value was set to year if burned or zero if unburned. The annual raster layers were sampled at random locations ($n = 5000$) to generate a matrix of random locations (rows) and year of burning (columns). The observed mean fire return interval for each random point location was calculated as

$$\frac{\sum_{i=1}^{n-1}\left(fireyear_{i+1} - fireyear_{i}\right)}{n-1}$$

where the sum of the lag differences in fire years is divided by the number of intervals (ie, number of fire years n minus 1). Finally, a data set of the values for times burned and mean fire return interval was combined with values for PC1 and PC2, vegetation types, management, and country at the random point locations. Using the sample data, we identified what range of climatic, biotic and land-use characteristics support contemporary fires that differ in each of the 3 fire-regime metrics (eg, questions 2 and 3). Data and code used for the analysis can be found on Github: https://github.com/HaireLab/Fuego-en-la-Frontera.

Results

Regional patterns of burned area, fire frequency, and fire severity (Question 1)

Approximately 8675 km^2 of the 39 698 km^2 study area (21.8%) burned between 1985 and 2017 (10 480 km^2 total area when including areas that reburned), with much of that occurring in Madrean evergreen forests and woodlands and pine-oak forests (Table 3). As a percentage of total area, 64% of pine-oak forests

Table 3. Total area occupied by each vegetation type,[43] area burned by vegetation type, and percentage of total area burned. Totals at bottom include total area of all vegetation types, total area burned across all vegetation types, and percentage of total area burned.

VEGETATION TYPE	AREA (KM^2)	AREA BURNED	
		(KM^2)	(%)
spruce-fir forests	7	6	90
mixed conifer forests	203	175	87
pine-oak forests	1478	949	64
evergreen forests and woodlands	20598	5639	27
Grasslands	5087	924	18
pinyon-juniper woodlands	18	0	0
chaparral	882	84	10
desertscrub	6462	748	12
thornscrub	4963	150	3
Total	39698	8675	22

and 27% of Madrean evergreen forests and woodlands burned. Similarly, nearly all spruce-fir and mixed conifer forests burned, and most spruce-fir forest burned twice. Fires in chaparral, pinyon-juniper woodlands, desertscrub, and thornscrub were limited, but a moderate proportion (12-18%) of burned area was observed in desertscrub and grassland relative to total area (Table 3).

Over 25% of areas that burned experienced more than one fire across time, with areas that reburned scattered across mountain ranges (Figure 2A). Some locations burned up to 4 (3500 ha) or rarely 5 times (80 ha) (Figure 2A). Higher incidences of reburning were observed near the United States-Mexico border including in mountains just south of the Mexico border.

Some larger mountain ranges in Mexico had only a few small fires and minimal reburning, especially in thornscrub in the south and southwestern portions of the study region. In the United States, there were instances where very large portions of some ranges burned in a single fire, with scattered reburning by subsequent smaller fires (eg, Santa Catalina, Rincon, and Chiricahua).

Geographic distribution of dNBR values varied among mountain ranges and across latitude, in both the mean and range of values (Figure 2B). The dNBR values were fairly low overall, but ranges extended to $\geqslant$900 in 4 ranges: Pinaleño (max = 986), Chiricahua (max = 951), Santa Catalina (max = 933), and Los Ajos (max = 927).

Sky Islands in the central part of the region near the international border in Mexico had greater heterogeneity in fire effects. For example, Atascosa-Cibuta (M = 33; SD = 185; max = 721) and El Pinito (M = 45; SD = 142; max = 632) had among the highest variation, whereas borderland ranges in the United States tended to exhibit less variation with distributions often skewed toward higher values (eg, Huachuca (M = 77; SD = 88; max = 809) and Animas (M = 54; SD = 102; max = 743; Figure 2B).

Vegetation, land management, and fire severity across climate gradients (Question 2)

The PC1 gradient represented a transition from earlier spring onset and higher temperatures typical of lowlands to later spring onset and cooler temperatures that characterize montane environments. In general, PC1 values were lower in Mexico corresponding to generally lower maximum elevations of mountain ranges to the south (Figure 3A and B). Grassland, Desertscrub, and Thornscrub (found only in Mexico) had much lower values along this gradient. In contrast, values were higher for mesic forests and woodland types that tend to occur at higher elevations and latitudes, especially mixed conifer and spruce-fir forests, which occur mostly or completely in the United States (Figure 3A). True chaparral, which only occurs in the United States, had moderate values along the gradient.

Along the PC2 gradient, vegetation types mirrored PC1 density distributions, with some distinctions in location and interpretation of heat moisture and precipitation (Figure 3C and D). In the United States, spruce-fir forests occur in environments with lower heat moisture and more precipitation, transitioning to dry forests where conditions are somewhat higher in heat moisture but lower in precipitation. In Mexico, thornscrub occurs midway on the PC2 heat moisture/precipitation gradient; while grasslands and desertscrub in both countries, as well as chaparral in the United States, have relatively higher heat moisture and lower precipitation.

Land tenure classes in the United States were unevenly distributed along PC1, with BIA, DOI, and state lands predominant at the lower to middle portions of the PC1 gradient

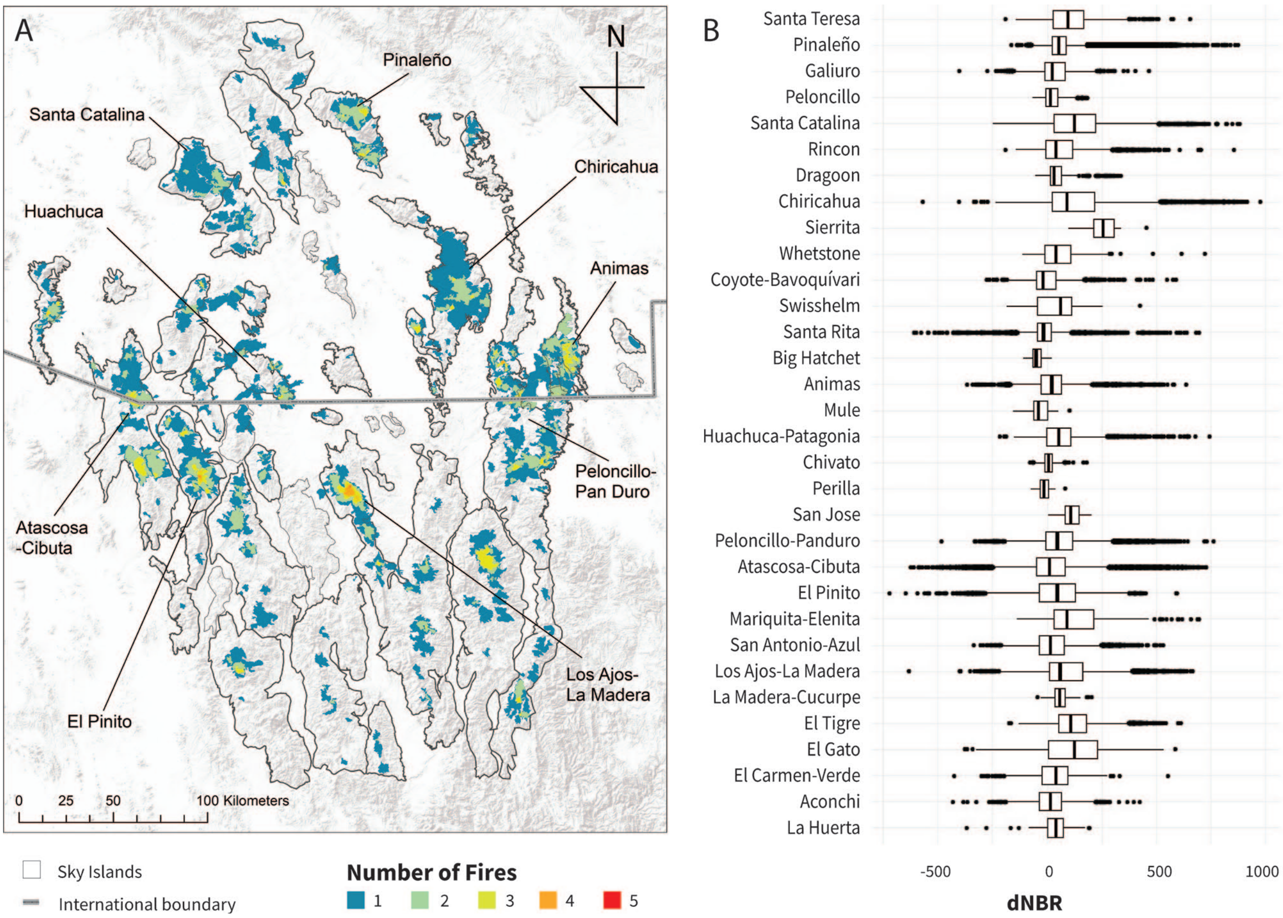

Figure 2. Number of fires during the period from 1985 to 2017 (A), and dNBR values for each mountain range, ordered from north to south (B).

(Figure 3E and F). As the gradient shifts to later spring onset and cooler temperatures, these tenure classes are less common and Department of Defense (DOD) and USFS classes become more common. The USFS is the only tenure class at the upper end of the gradient where cooler temperatures and later spring are common. In Mexico, ejidos, private, and protected areas are present across the lower to middle range of this environmental gradient (Figure 3F). Values for ejido lands were lower in areas with relatively later spring and lower mean annual temperature, whereas protected areas were more common in those conditions, indicating distributions at low and high elevations and latitudes, respectively.

Along the second gradient (PC2), USFS and DOD lands were common at the lower to mid-range, where heat moisture is relatively low and annual precipitation is relatively high (Figure 3G and H). A diversity of land tenure classes occupies the middle to upper range of PC2; DOI and state lands were present at the upper end of the gradient in the United States (ie, higher heat moisture and lower annual precipitation). In Mexico, land tenure classes overlap across the range of environments present from the middle to upper range of the gradient (Figure 3H).

High-severity patterns (ie, sites with remarkable prefire to postfire changes) were closely related to environmental gradients along PC1, based on model statistics for both nations (34.7% and 43.6% deviance explained for Mexico and United States respectively; Figure 4A and B). High-severity patches were sparse or absent in places with early growing seasons and warmer annual temperatures. Midway along the PC1 gradient, patterns became more variable, especially for fires in Mexico, but trends indicated low overall amounts of high severity. In general, high severity increased along PC1 gradient; however, the steep upward slope in Mexico was driven by a single outlier at the high end of PC1. High severity in several US fires at the upper end of PC1 (cooler temperatures, later spring) resulted in a steep upward trend. The range in high severity was greater for different threshold values for most fires in Mexico versus the United States (Figure 4A and B) consistent with the heterogeneity of dNBR values noted in section "Regional patterns of burned area, fire frequency, and fire severity." Mexico fires exhibiting variability in severity composition with different threshold classifications were located within the middle portions of PC1 and PC2.

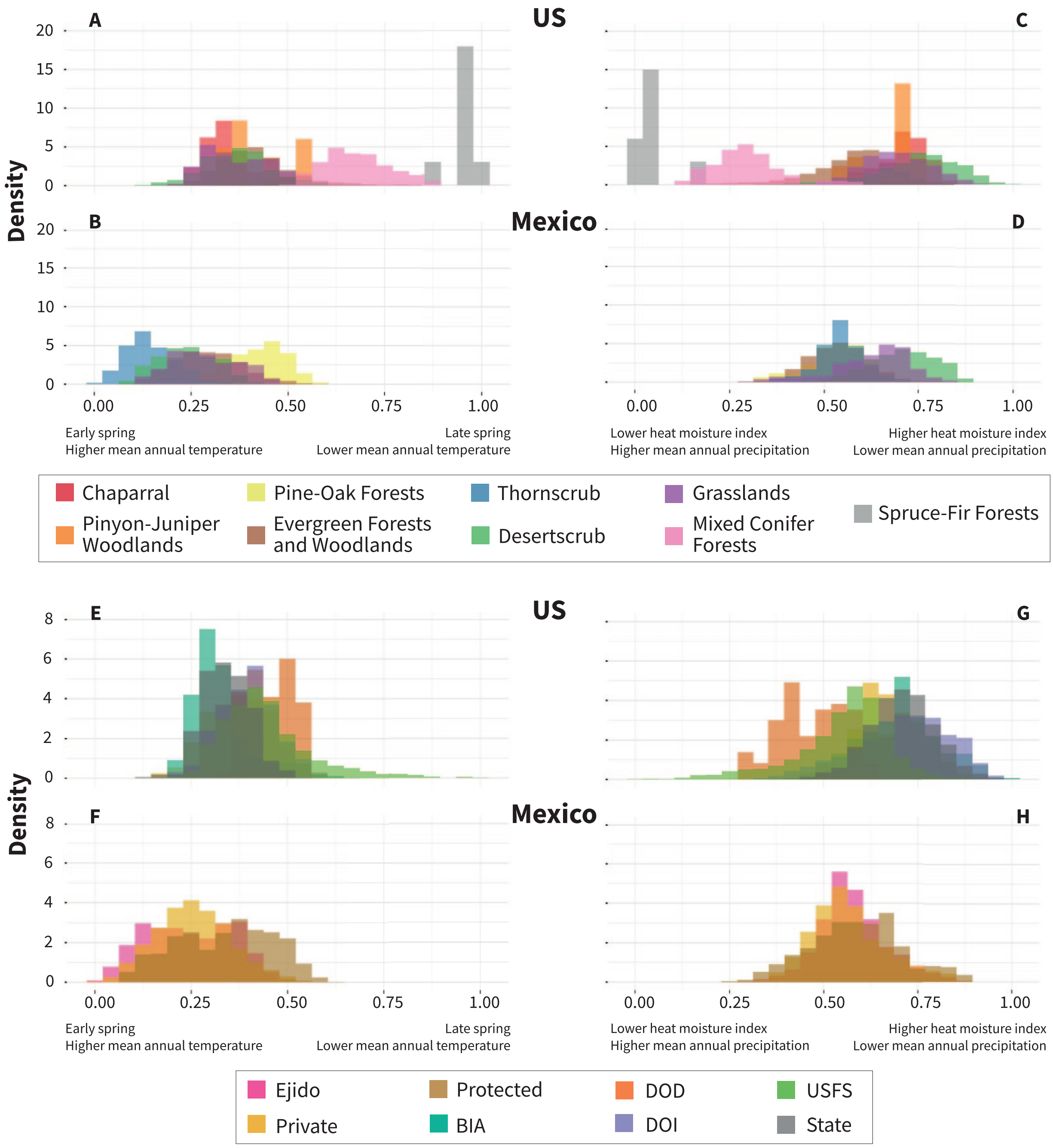

Figure 3. Histogram density plots of vegetation types (A, B, C, and D) and land tenure classes (E, F, G, and H) across PC1 (A, B, E, and F) and PC2 (C, D, G, and H) climate gradients. Data were plotted separately for the United States (A, C, E, and G) and Mexico (B, D, F, and H) to illustrate the difference in distributions and where unique vegetation types occur.

The heat moisture-annual precipitation gradient (PC2) was a good predictor of high-severity fires in the United States (deviance explained = 53.9%) (Figure 4C). A steady downward trend was observed as climate environments moved from lower to higher heat moisture and from higher to lower precipitation. In Mexico, however, high severity had a significant but weaker relationship with PC2 (deviance explained = 5.09%). Overall, high-severity composition of fires in Mexico was low along this gradient, based on the model fit line (Figure 4D).

Of areas that burned, those that burned only once were most common and occurred across a broad range of PC gradients (Figure 5A to D). Areas with late spring and lower temperature (PC1) and heat moisture and higher precipitation (PC2) burned twice during the study period. Vegetation types at these locations were mixed conifer and spruce-fir forests (Figure 3A; Table 4), and tenure was primarily USFS with some BIA and private land (Figure 5A; Table 4). Areas that burned twice were located in more central portions of the PC gradients in several vegetation types, under a variety

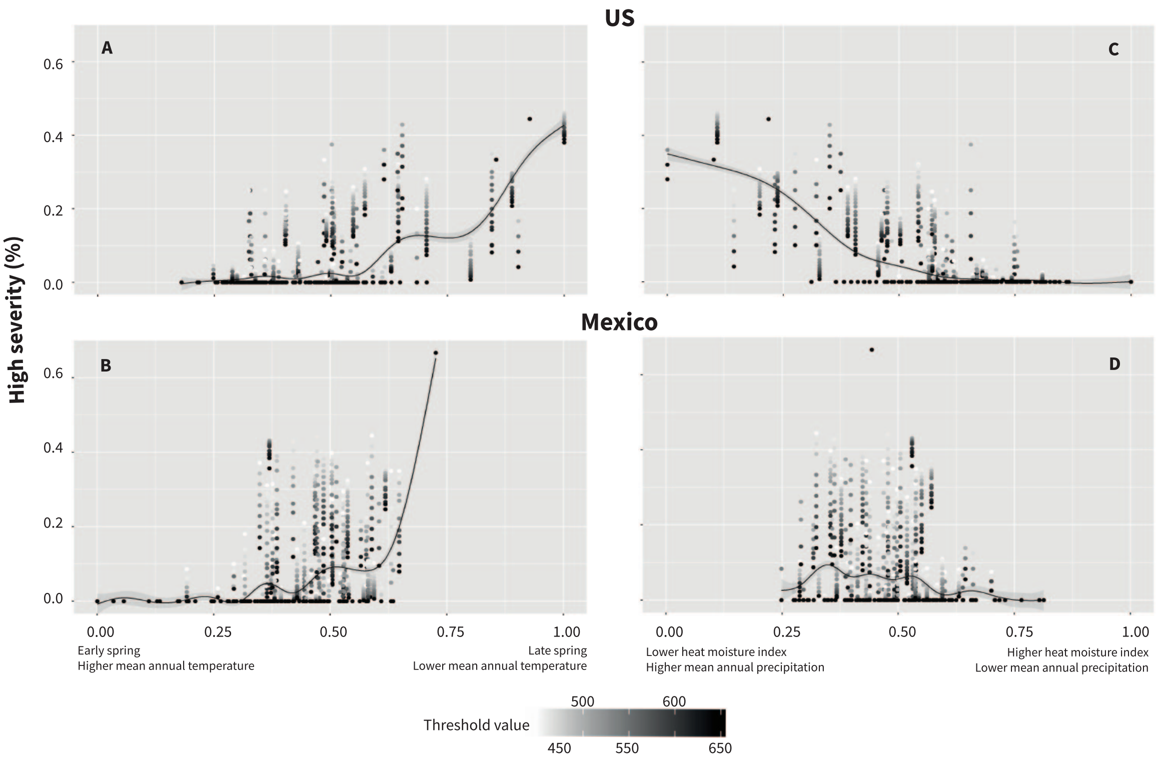

Figure 4. Scatterplots of high severity (%) for all fires in the United States and Mexico across PC1 (A, B) and PC2 (C, D). Threshold values were used to create gradients for the points, illustrating variability in composition with different classification schemes. Generalized additive model (GAM) smooth lines were added to examine local changes in composition across PC1 and PC2. Plots for the United States (A, C) and Mexico (B,D) illustrate where the climate space for fire overlaps in the 2 countries; some environments were unique.

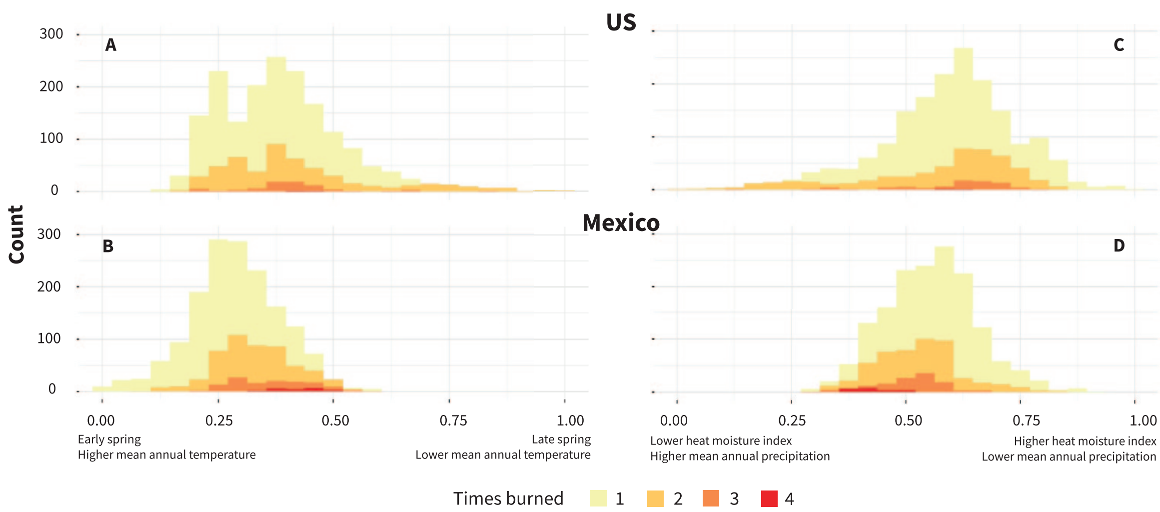

Figure 5. Histogram of times burned within the study period (1985-2017) across climate for all fires in the United States and Mexico across PC1 (A, B) and PC2 (C, D), based on a random sample of the mapped number of fires shown in Figure 2. Data were plotted separately for the United States (upper) and Mexico (lower) to help identify unique patterns.

of tenures (Figure 3; Table 4). Highest fire frequency (mean ⩾ 2.4) was observed in grasslands under state or DOI management and in pine-oak forests in protected areas in Mexico (Table 4).

The shortest fire return intervals were rare, but places that burned at intervals of 5.5 to 10 years occurred in warmer, drier environments in both the United States and Mexico (Figure 6). In the United States, longer fire return intervals generally occurred in areas with higher PC1 and lower PC2 values (Figure 6A and C, Table 4). In Mexico, longer fire return intervals (mean 16-20 years) were observed in pine-oak forests; maximum intervals of 21 to 25 years occurred in Madrean evergreen forests and woodlands and pine-oak forests on both ejido and private lands (Figure 6; Table 4). Intervals of 26 to 28 years were also rare but did occur in scattered locations across climate, vegetation, and tenure.

Table 4. Number of times burned, mean fire return interval, and mean principal component values for vegetation types under various land tenure classes. Statistics are based on a random sample of point locations that burned more than once during the study period (1985-2017).

LAND TENURE CLASS[a]	TIMES BURNED			MEAN FIRE RETURN INTERVAL				CLIMATE GRADIENT	
	MEAN	MAX	SD	MEAN	MIN	MAX	SD	PC1 (MEAN)	PC2 (MEAN)
Spruce-fir forests									
USFS	2.0	2.0	0.0	13.0	13.0	13.0	0.0	0.9	0.1
Mixed conifer forests									
BIA	2.0	2.0	NA	3.0	3.0	3.0	NA	0.5	0.6
Private	2.0	2.0	0.0	17.0	17.0	17.0	0.0	0.6	0.4
USFS	2.0	2.0	0.0	15.1	1.0	21.0	4.8	0.7	0.3
Pine-oak forests									
Ejido	2.0	2.0	0.0	18.6	6.0	24.0	8.0	0.5	0.4
Private	2.3	4.0	0.5	12.2	4.0	24.0	3.7	0.4	0.5
Protected	2.9	4.0	0.8	13.5	7.0	26.0	6.1	0.4	0.4
Evergreen forests and woodlands									
BIA	2.0	2.0	NA	7.0	7.0	7.0	NA	0.2	0.6
DOD	2.0	2.0	0.0	24.0	24.0	24.0	0.0	0.3	0.6
DOI	2.3	3.0	0.4	14.7	5.0	28.0	6.5	0.4	0.6
Ejido	2.1	3.0	0.3	13.6	5.0	25.0	8.2	0.4	0.5
Private	2.2	4.0	0.4	10.4	1.0	28.0	5.7	0.3	0.5
Protected	2.2	3.0	0.4	14.6	2.0	27.0	6.5	0.4	0.5
State	2.2	3.0	0.4	10.6	5.0	28.0	6.7	0.3	0.6
USFS	2.1	4.0	0.3	10.5	1.0	27.0	6.0	0.4	0.5
Grasslands									
DOI	2.5	4.0	0.6	9.7	4.5	15.0	3.3	0.4	0.7
Private	2.2	3.0	0.4	12.0	4.5	17.0	4.7	0.4	0.7
Protected	2.1	3.0	0.3	11.0	3.0	23.0	5.2	0.3	0.7
State	2.4	3.0	0.5	8.1	6.0	15.0	2.6	0.4	0.7
USFS	2.0	2.0	0.0	9.1	3.0	15.0	4.1	0.3	0.6
Thornscrub									
Private	2.0	2.0	0.0	13.4	10.0	14.0	1.5	0.2	0.4
Desertscrub									
DOI	2.0	2.0	0.0	4.0	4.0	4.0	0.0	0.4	0.8
Private	2.0	3.0	0.2	13.9	5.0	18.0	3.9	0.4	0.6
State	2.0	2.0	0.0	23.3	9.0	28.0	9.5	0.3	0.8
USFS	2.1	3.0	0.3	11.9	3.0	28.0	5.0	0.4	0.6

[a]Land tenure classes: BIA, Bureau of Indian Affairs; DOD, Department of Defense; DOI, U.S. Department of the Interior, Private, Protected (Protected Areas in Mexico), State; USFS, United States Forest Service.

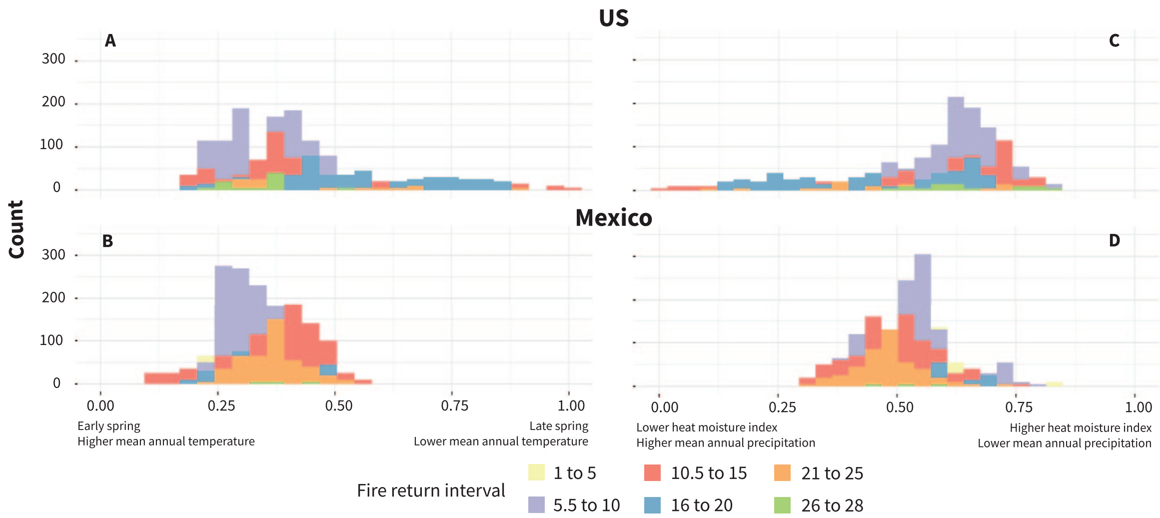

Figure 6. Fire return intervals (mean) for all fires in the United States and Mexico across PC1 (A, B) and PC2 (C, D), based on a random sample of locations across maps of fire years. Data shown in the plots include only locations that burned more than once in the United States (upper facet) and Mexico (lower facet).

Discussion

Our analyses across this vast, culturally and ecologically diverse region illuminates important contemporary patterns of fire occurrence and fire effects and how they have varied from those experienced historically. Results of this study, in combination with recent work on traits and spatiotemporal distribution of recent fires in this large region of high conservation value[18,19] are especially significant in Mexico, where past studies in the Sky Islands region were limited to only a few small areas.[25,27,72] Understanding fire regimes across climate gradients that underpin plant community composition and structure can aid in evaluating the potential impacts of human activities on fire.[21] In the middle zone of the climate gradient, the Nearctic-Neotropical transition encompasses forest and shrub communities that are more amenable to fuel management (or restoration activities). In contrast, forests and desert communities in extreme climates are subject to increased fire frequency from human activities, invasive species, and climate change that can result in dramatic shifts in vegetation communities. Differences observed between recent fire characteristics and expectations based on historical information highlights the many ways past human-ecosystem interactions, land tenure, and bioclimatic settings can interact to influence fire regimes. Addressing interactions between land use, climate, and fire is critical for fostering dialog among diverse stakeholders and guiding restoration and land management objectives, especially in areas at risk of high-severity fire.

Regional overview

Recent fires influence landscape pattern and process across the Sky Islands region. Numerous fires occurred during the study period and burned >10 000 km^2 of land, with over 25% of areas experiencing more than one fire during the period. Average fire severity was low during the study period across the region, with a few notable exceptions. That is, except for a few fires in cold/wet sites that occur exclusively in the United States, most other fires average less than 10% high severity within the fire perimeter (Figure 4). In all, less than 28% of the study area burned across a period of 27 years, excluding vegetation types in warmer climates that are not adapted to fire such as desertscrub and thornscrub. Fires in grasslands were much less frequent than expected, suggesting an overall fire deficit (ie, lack of fire) and the need to promote fire in these warm, dry environments at lower elevations. In contrast, fire was more common in some cooler mesic environments that historically burned very infrequently, suggesting a fire surplus. The occurrence of fires across wide ranging environments and diverse ownership, tenure and land use make interpretation of the fire-regime complex.

Sky Islands adjacent to the United States-Mexico border displayed some novel contemporary fire-regime characteristics. Mountain ranges along the border had the greatest number of fires and mix of severities (Figure 2), with previous research showing high variation of fire size and shape,[19] and ignition dates[73] outside the normal fire season. Such contemporary fire-regime characteristics may be attributed, in part, to human activities. This includes a highly heterogeneous mix of land uses along the border, high population densities in border towns, and immigration policies that funnel movements of immigrants who use fire for cooking and warmth, which provides ignition sources, into remote areas.[74] Fire effects skewed toward higher severity in the Sky Islands just north of the United States border, which are focal areas for immigrants, and mixed and lower severities in Mexico, where immigrant traffic is presumably lower. Apart from anthropogenic ignition sources, the differences in observed fire severity between United States and Mexico are related to differences in historical legacies of land management, fire use, fire suppression, and fuel accumulation. Communities living near borderland ranges are likely most impacted by alteration of ecosystem services,[75] including those influenced by wildfire. Information on current fuel conditions and fire history can help guide fuel-reduction treatments and manage wildfires in areas near human communities that are at greatest risk of hazardous fire, and foster continued burning in areas of Mexico that benefit from frequent, low-severity fires.

One of the primary ways that people influence ecosystems is by altering the location and timing of fire.[76] A focus on anthropogenic alterations to fire regimes in the Madrean Sky Islands has added benefits toward restoration because of the potential to highlight the relevance of traditional knowledge systems and practices. Sustained use of fire for active management of forests and woodlands was practiced historically by native peoples of the American Southwest for propagation of wild plants and crop cultivation,[77,78] and such management supported a continuous frequent fire regime in some locations throughout the 19th and 20th centuries.[79,80] Recent efforts in Mexico seek to reconcile more recently adopted fire-fighting efforts with the ecological use of fire and community fire management.[13] Systems based on traditional knowledge have evolved to work in concert with social and ecological conditions,[14] and thus it is possible that traditional knowledge and practice may provide management alternatives that restore ecosystems as climatic conditions change.

Restoring natural fire regimes to the Madrean region has important implications for wildlife conservation. Wildlife in these systems have evolved in the presence of frequent fire, which helps foster habitats for many species and promotes landscape heterogeneity.[81,82] Landscape heterogeneity from varying fire severities, frequencies, and sizes can lead to increased biodiversity,[83,84] but responses to burn severity can differ based on historical fire regimes,[85] times since fire,[86] and prefire conditions linked to timber harvest.[87] Fire is important for nutrient cycling[88] and invigorating vegetation growth in ways that foster low shrubby, herbaceous, and grassy vegetation, which provides important food and cover for a multitude of wildlife species,[89,90] including breeding birds.[91,92] Hence, ensuring land management practices that promote (restore) and maintain natural fire regimes, combined with other active restoration measures are complementary and essential for long-term maintenance of biodiversity and ecosystem services.

Implementation of landscape-scale restoration planning and subsequent actions in the study area, with a focus on fire, requires binational cooperation and coordination between land management agencies, tribes, and private and communal landowners. Moving forward, it is critical to continue to engage a wide range of stakeholders in the United States and Mexico, including First Nations and local communities. Two recent examples from both sides of the international border showcase efforts to implement multistakeholder fire treatments with participation of local communities in the Sky Islands of Sonora[93] and in the FireScape program in Arizona (azfirescape.org).

Climate, land use, and vegetation conditions where fire characteristics diverge from historical regimes

Mesic high elevation forests. Fires with the greatest proportion of high-severity areas occurred predominantly in Mixed Conifer and Spruce-Fir forests in cooler, wetter climates of the United States. In these settings, such fire characteristics largely match historic expectations for severity;[45,44] however, our analyses found that >85% spruce-fir and mixed conifer forests in the Sky Islands burned during the study period and that fires in spruce-fir forests were much more frequent than they were historically.[44]

Although high-severity fires are part of the historical fire regime within these vegetation types, the size, and frequency of these fires could have deleterious effects on persistence of these forests, which have high conservation value.[94] While it is difficult to correlate the impact of land management and historical fire suppression on high-severity fire events, increased fire frequency combined with recent drought events suggest climate forcing as a likely mechanism.[95-97] Spruce-fir and mixed conifer systems evolved with high-severity fire and are able to slowly regenerate and recover during fire-free periods, which can last decades to centuries. Extreme drought required to foster fire in mesic spruce-fir forests were historically rare[98] but are becoming more common, particularly in southwestern North America[99] where they augment risk of type conversion into forest communities that are adapted to more frequent fire and drought.[10]

Frequent fire patterns observed within spruce-fir forests will likely continue unless management actions may reduce some of the factors that increase risk. Reducing future fire activity in remaining stands could be accomplished by reducing fuels in adjacent mixed conifer and pine forests to prevent fire spread into upper elevations. While forest restoration in mixed conifer forests has also been proposed to reduce high-severity fire risk for Mexican spotted owl habitat, uncertainty remains with the short-term impacts versus potential long-term benefits of these treatments on this species[100] and effectiveness of treatments in mitigating fire behavior.[101]

Madrean Evergreen Forests and Woodlands. Madrean evergreen forests and woodlands are the dominant vegetation type across the region and in the adjacent Sierra Madre Occidental, and contribute significantly to regional biodiversity.[102,103] More than half the total area burned in the study region occurred within this vegetation type which is supported by warm to moderate temperatures and relatively early onset of the growing season (Figure 3). However, overall area burned included only 27% of total coverage of this vegetation type, indicating an overall fire deficit. Areas that burned multiple times had slightly less-frequent fire than historical intervals of 3 to

10 years. While approximately 50% of this vegetation type in the region is privately owned, only approximately 22% of private lands burned during the study period, which contrasts sharply with 49% that burned on USFS lands and frequent fire observed on DOI lands (5-28 years; Table 4). Fires were even less common on ejido lands in Mexico, with only 15% burned and high variability in high-severity fire. These contrasts suggest that variation in land management practices on private versus ejido lands may have driven these fire patterns, with important implications for restoration.

The fire deficit on ejido and private lands suggests activities such as grazing may have altered the abundance and spatial continuity of fine fuels, thereby precluding fire spread. Such drivers had major impacts on fire regimes in southern Arizona after the 1890s,[24,46] and approximately 40 years later in a northern Sky Island in Mexico.[27] Observed differences between private and ejido lands in Mexico may be due to more intensive management of communal lands, lower elevation settings and thus greater aridity, or closer to human population centers, which is associated with more intensive land uses. Given limited understanding of the ecology and fire histories of Madrean evergreen forests and woodlands, high relative abundance of this vegetation type in the study area, and resilience to fire (shown, for instance, through resprouting), they present a unique opportunity for land managers to experiment with different restoration strategies to achieve desired future conditions.[104,105]

Grasslands. Historically, frequent low-intensity fires were relatively common in the warm, dry environments that support grasslands in the region (Figure 3), but livestock grazing since the late 19th century effectively reduced fine fuels that foster fire spread, interrupted the fire cycle, and ultimately contributed to changes in species composition and structure.[106,107] In the past, grassland fires were important ignition sources for fires in higher elevation Madrean woodlands and forests.[49] We found that only a small percentage of Grasslands experienced fire within the study period, and those that did burn in the United States showed fire frequencies within the historical range ($\bar{x} = 8.1 - 9.7$ years) with slightly longer intervals in Mexico ($\bar{x} = 11 - 12$ years). Restoration of grassland fire regimes is a management priority in some US landscapes where private landowners and federal agencies often collaborate on managed burns in an effort to reduce woody vegetation cover, increase native grass cover, and reduce stream channel erosion.[108-110] However, elsewhere in the region livestock grazing may be contributing to the observed fire exclusion, particularly in Mexico and within state lands in the United States, where fire exclusion is likely a key factor in reduced fire frequency in the adjacent uplands.

Vegetation types where fire characteristics are similar to historical regimes

Fire regimes observed in some pine-oak forests, prevalent in wetter and cooler environments in the upper elevations of Mexico, appeared to be within the range of historical variability. In fact, 64% of these forests burned at least once during the study period, and the greatest number of reburns was observed in protected areas like the Área de Protección de Flora y Fauna Ajos-Bavispe in Mexico. On private lands in Mexico, fire frequency roughly corresponded with historic fire-return intervals but was less frequent than that found historically on ejido lands (18.6 years), which suggests land management has limited fire in some areas. Frequent fires observed in pine-oak forests in Mexico, suggest a need to restore frequent fire in other vegetation communities across the region and maintain fire regimes in areas with mixed land tenures. Therefore, it is critical to understand the environmental conditions that set the stage for these fires, as well as how private and communal landowners engage with fire when they occur, to design a robust regional fire strategy that can be implemented in other areas.

The mix of high- and low-severity fires in pine-oak forests suggest that these communities may still be at risk of conversion from high-severity fire. Recent high-severity fires may limit pine regeneration and drive conversion of mixed pine-oak stands to oak woodlands in some places.[111] Pine regeneration requires significant fire-free intervals,[112] and thus reburning high-severity patches may be detrimental to regeneration. However, managing for continued burning within areas that burned at lower severities can help to reduce tree densities and accumulated fuels.

Conclusions

Until recently, our understanding of contemporary fire regimes in the Madrean Sky Islands was derived from data and research conducted primarily in the southwestern United States. We investigated wildfire regimes in both Mexico and the United States and across a range of land tenure types, resulting in new findings and a more complete picture of regional fire regimes that can help inform fire management, restoration, and regional conservation planning.

We identified areas in upper-elevation pine-oak forests of Mexico with characteristics similar to estimated historical fire regimes, while high-elevation spruce-fir and mixed conifer forests in the United States appear to be burning more frequently than historically, which represents a potential threat to these regionally rare vegetation types. Our results suggest that while fire remains an active natural disturbance in some parts of the Madrean Sky Islands, human land uses and the legacies of fire suppression continue to shift fire regimes away from historical patterns. Woodlands and grasslands experienced an overall fire deficit compared to historical, suggesting a need to implement large- and local-scale fire treatments in these vegetation types. Sky Islands on the United States-Mexico border exhibited the greatest fire-regime variability corresponding to human activities; communities along the border may be especially vulnerable to wildfire risks, and cross-boundary, multijurisdictional fire management may be necessary to counter the potentially deleterious effects of possible high-severity fire in remaining unburned areas.

Restoring wildlife habitats and landscape connectivity, protecting water sources, and sustaining cultural and economic values associated with traditional livelihoods can benefit from restoration programs that include fire. Regional conservation partnerships like Sky Islands Research Collaborative, Malpai Borderlands Group, and Wildlands Network Mexico, are important for fostering regional and international relationships and collaborations necessary to achieve these goals. Promoting connections across landscapes and people in the borderlands through restoration, collaborative conservation, and communication is essential for sustaining these landscapes into the future.

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Author Contributions

MLV, SLH, JMI and CCM conceived the study. MLV and CRC developed remote sensing fire products. SLH and MLV analyzed the data. JMI, ADF, CCM, JSS and MLV developed the conceptual models of historical fire regimes. SLH, MLV and CCM developed visualizations and maps. All authors contributed to writing the paper. CCM translated the manuscript to Spanish.

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Supplemental material

Supplemental material for this article is available online.

REFERENCES

1. Bond WJ, Woodward FI, Midgley GF. The global distribution of ecosystems in a world without fire. *New Phytol*. 2005;165:525-538.
2. Bowman DM, O'Brien JA, Goldammer JG. Pyrogeography and the global quest for sustainable fire management. *Annu Rev Environ Resour*. 2013;38:57-80.
3. Kelly LT, Brotons L, Giljohann KM, McCarthy MA, Pausas JG, Smith AL. Bridging the divide: integrating animal and plant paradigms to secure the future of biodiversity in fire-prone ecosystems. *Fire*. 2018;1:29.
4. Pausas JG, Keeley JE. A burning story: the role of fire in the history of life. *Bioscience*. 2009;59:593-601.
5. Pausas JG, Keeley JE. Wildfires as an ecosystem service. *Front Ecol Environ*. 2019;17:289-295. doi:10.1002/fee.2044.
6. Keeley JE, Pausas JG. Distinguishing disturbance from perturbations in fire-prone ecosystems. *Int J Wildland Fire*. 2019;28:282-287.
7. Cameron PA, Mitra B, Fitzgerald M, et al. Black Saturday: the immediate impact of the February 2009 bushfires in Victoria, Australia. *Med J Aust*. 2009;191:11-16.
8. Bowman DM, Balch J, Artaxo P, et al. The human dimension of fire regimes on Earth. *J Biogeogr*. 2011;38:2223-2236.
9. Enright NJ, Fontaine JB, Bowman DM, Bradstock RA, Williams RJ. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front Ecol Environ*. 2015;13:265-272.
10. Stephens SL, Agee JK, Fulé PZ, et al. Managing forests and fire in changing climates. *Science*. 2013;342:41-42. doi:10.1126/science.1240294.
11. Norman LM. Editorial: combining the science and practice of restoration ecology; a case study of partnership in the Madrean Archipelago Ecoregion. *Special Collection for "Air, Soil and Water Research" on the Sky Island Restoration Collaborative*. https://journals.sagepub.com/page/asw/collections/special-collections/binational-sky-island-restoration-collaborative. Updated 2020.
12. Raish C, González-Cabán A, Condie CJ. The importance of traditional fire use and management practices for contemporary land managers in the American Southwest. *Environ Hazards*. 2005;6:115-122. doi:10.1016/j.hazards.2005.10.004.
13. Rodríguez-Trejo DA, Martínez-Hernández PA, Ortiz-Contla H, Chavarría-Sánchez MR, Hernández-Santiago F. The present status of fire ecology, traditional use of fire, and fire management in Mexico and Central America. *Fire Ecol*. 2011;7:40-56. doi:10.4996/fireecology.0701040.
14. Martínez-Torres HL, Castillo A, Ramírez MI, Pérez-Salicrup DR. The importance of the traditional fire knowledge system in a subtropical montane socio-ecosystem in a protected natural area. *Int J Wildland Fire*. 2016;25:911-921. doi:10.1071/WF15181.
15. Laushman K, Munson S, Villarreal M. Wildfire risk and hazardous fuel reduction treatments along the United States of America-Mexico border: a review of the science (1986 – 2019). *Air Soil Water Res*. 2020:13;1-7.
16. USOPA (US Office of Policy Analysis). *Wildland Fire Management Program Benefit-Cost Analysis: A Review of Relevant Literature*. Washington, DC: Department of the Interior, Office of Policy Analysis. https://www.doi.gov/sites/doi.gov/files/migrated/ppa/upload/Wildland_fire_literature_review_060812FINAL.pdf. Updated 2012.
17. Council WFE. The national strategy: the final phase in the development of the National Cohesive Wildland Fire Management Strategy. https://www.forestsandrangelands.gov/documents/strategy/strategy/CSPhaseIIINationalStrategyApr2014.pdf. Updated 2014. Accessed 11 December 2015.
18. Villarreal ML, Haire SL, Bravo JC, Norman LM. A Mosaic of land tenure and ownership creates challenges and opportunities for transboundary conservation in the US-Mexico borderlands. *Case Stud Environ*. 2019;3:1-10. doi:10.1525/cse.2019.002113.
19. Villarreal ML, Haire SL, Iniguez JM, Montaño CC, Poitras TB. Distant neighbors: recent wildfire patterns of the Madrean Sky Islands of southwestern United States and northwestern Mexico. *Fire Ecol*. 2019;15:2.
20. Singleton MP, Thode AE, Sánchez Meador AJ, Iniguez JM. Increasing trends in high-severity fire in the southwestern USA from1984 to 2015. *For Ecol Manag*. 2019;433:709-719. doi:10.1016/j.foreco.2018.11.039.
21. McWethy DB, Higuera PE, Whitlock C, et al. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Glob Ecol Biogeogr*. 2013;22:900-912. doi:10.1111/geb.12038.
22. Baisan CH, Swetnam TW. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Can J For Res*. 1990;20:1559-1569.
23. Van Devender TR, Felger RS, Búrquez A. Exotic plants in the Sonoran Desert region, Arizona and Sonora. *California Exotic Pest Plant*. 1997;3:1-6.
24. Bahre CJ. Wildfire in southeastern Arizona between 1859 and 1890. *Desert Plants*. 1985;7:190-194.
25. Swetnam TW, Baisan CH, Kaib J. *Forest Fire Histories of the Sky Islands of La Frontera: Changing Plant Life of La Frontera*. Albuquerque, NM: University of New Mexico Press; 2001:95-119.
26. Cortés Montaño C, Fulé PZ, Falk DA, Villanueva-Díaz J, Yocom LL. Linking old-growth forest composition, structure, fire history, climate and land-use in the mountains of northern México. *Ecosphere*. 2012;3:1-16. doi:10.1890/ES12-00161.1.
27. Meunier J, Romme WH, Brown PM. Climate and land-use effects on wildfire in northern Mexico, 1650–2010. *For Ecol Manag*. 2014;325:49-59. doi:10.1016/j.foreco.2014.03.048.
28. Flatley WT, Fulé PZ. Are historical fire regimes compatible with future climate? Implications for forest restoration. *Ecosphere*. 2016;7:e01471. doi:10.1002/ecs2.1471.

29. Felger. *Northern Sierra Madre Occidental and its Apachian Outliers: A Neglected Center of Biodiversity*. Wild Sonora. http://wildsonora.com/reports-papers-journal-articles/northern-sierra-madre-occidental-and-its-apachian-outliers. Updated 1995. Accessed 25 February 2020.
30. Mittermeier R, Gil P, Hoffman M, et al. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. San Pedro Garza García, Mexico: Cemex; 2004 Published online.
31. Warshall P. *The Madrean Sky Island Archipelago: A Planetary Overview: Biodiversity and Management of the Madrean Archipelago. The Sky Islands of Southwestern United States and Northwestern Mexico*. Washington, DC: U. S. Department of Agriculture, Forest Service; 1995:6-18.
32. Arizona State Land Department, Arizona Land Resources Information System. Arizona land ownership. https://land.az.gov/maps-gis-0. Updated 2010.
33. Bureau of Land Management. Bureau of land management surface land ownership. https://www.blm.gov/services/geospatial. Updated 2012.
34. Data Basin. Ajos-Bavispe 2010. https://databasin.org/datasets/a937245d8de7468f9db11fbde5ca0903. Updated 2010.
35. INEGI Reforma Agraria. Ejidos of Mexico. https://databasin.org/datasets/a5e789aa10fb4efbbd8b7b5a1cf8d423. Updated 2017.
36. Commission for Environmental Cooperation (CEC). Protected areas of Mexico. https://databasin.org/maps/fdd3836a52b5469a98627abf4aa6a46b. Updated 2008.
37. Deyo NS, Devender TRV, Smith A, Gilbert E. Documenting the biodiversity of the Madrean Archipelago: an analysis of a virtual flora and fauna. In: Gottfried GJ, Ffolliott PF, Gebow BS, Eskew LG, Collins LC, eds. *Merging Science and Management in a Rapidly Changing World: Biodiversity and Management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts, 2012 May 1-5; Tucson AZ* (Proceedings RMRS-P-67). Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; 2013:292-299.
38. Sheppard PR, Comrie AC, Packin GD, Angersbach K, Hughes MK. The climate of the US Southwest. *Clim Res*. 2002;21:219-238. doi:10.3354/cr021219.
39. Flesch AD. Patterns and drivers of long-term changes in breeding bird communities in a global biodiversity hotspot in Mexico. *Divers Distrib*. 2019;25:499-513. doi:10.1111/ddi.12862.
40. Bonilla-Moheno M, Aide TM, Clark ML. The influence of socioeconomic, environmental, and demographic factors on municipality-scale land-cover change in Mexico. *Reg Environ Change*. 2012;12:543-557. doi:10.1007/s10113-011-0268-z.
41. Bonilla-Moheno M, Redo DJ, Aide TM, Clark ML, Grau HR. Vegetation change and land tenure in Mexico: a country-wide analysis. *Land Use Policy*. 2013;30:355-364. doi:10.1016/j.landusepol.2012.04.002.
42. Brown DE, Reichenbacher F, Franson SE. *Classification of North American Biotic Communities*. Salt Lake City, UT: University of Utah Press; 1998.
43. Rehfeldt GE, Crookston NL, Sáenz-Romero C, Campbell EM. North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. *Ecol Appl*. 2012;22:119-141. doi:10.1890/11-0495.1.
44. O'Connor CD, Falk DA, Lynch AM, Swetnam TW. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleño Mountains, Arizona, USA. *For Ecol Manag*. 2014;329:264-278.
45. Margolis EQ, Swetnam TW, Allen CD. Historical stand-replacing fire in upper montane forests of the Madrean Sky Islands and Mogollon Plateau, southwestern USA. *Fire Ecol*. 2011;7:88-107.
46. Swetnam TW, Baisan CH. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen CD, ed. *Fire Effects in Southwestern Forest: Proceedings of the 2nd La Mesa Fire Symposium*. Washington, DC: USDA Forest Service, Rocky Mountain Research Station; 1996:11-32.
47. Barton AM. Pines versus oaks: effects of fire on the composition of Madrean forests in Arizona. *For Ecol Manag*. 1999;120:143-156.
48. Iniguez JM, Swetnam TW, Baisan CH. Spatially and temporally variable fire regime on Rincon Peak, Arizona, USA. *Fire Ecol*. 2009;5:3-21. doi:10.4996/fireecology.0501003.
49. Kaib M, Baisan CH, Grissino-Mayer HD, Swetnam TW. *Fire History in the Gallery Pine-Oak Forests and Adjacent Grasslands of the Chiricahua Mountains of Arizona*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station; 1996:253-264.
50. Danzer SR, Baisan CH, Swetnam TW. The influence of fire and land-use history on stand dynamics in the Huachua Mountains of Southeastern Arizona. In: Ffolliott PF, DeBano LF, Baker MB, et al., eds. *Effects of Fire on Madrean Province Ecosystems: A Symposium Proceedings*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station; 1996:265-270.
51. McPherson GR. The role of fire in the desert grasslands. In: McClaran MP, Van Devender TR, eds. *The Desert Grassland*. Tucson, AZ: University of Arizona Press; 1995:130-151.
52. Wright HA, Bailey AW. *Fire Ecology: United States and Southern Canada*. New York: John Wiley & Sons; 1982.
53. Baker WL, Shinneman DJ. Fire and restoration of piñon–juniper woodlands in the western United States: a review. *For Ecol Manag*. 2004;189:1-21. doi:10.1016/j.foreco.2003.09.006.
54. Floyd ML, Romme WH, Hanna DD. Fire history and vegetation pattern in Mesa Verde national Park, Colorado, USA. *Ecol Appl*. 2000;10:1666-1680.
55. Huffman DW, Fule PZ, Pearson KM, Crouse JE. Fire history of pinyon–juniper woodlands at upper ecotones with ponderosa pine forests in Arizona and New Mexico. *Can J For Res*. 2008;38:2097-2108.
56. Romme WH, Allen CD, Bailey JD, et al. Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinon–juniper vegetation of the western United States. *Rangel Ecol Manag*. 2009;62:203-222.
57. Cable DR. *Range Management in the Chaparral Type and Its Ecological Basis: The Status of Our Knowledge*. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1975.
58. Brooks ML, Esque TC, Duck T. Creosotebush, blackbrush, and interior chaparral shrublands [Chapter 6]. In: Hood SM, Mill M, eds. *Fire Ecology and Management of the Major Ecosystems of Southern Utah*. Fort Collins CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; 2007: 97-110.
59. Thomas PA. Response of succulents to fire: a review. *Int J Wildland Fire*. 1991;1:11-22. doi:10.1071/wf9910011.
60. Villarreal ML, Poitras TB. *Mapped Fire Perimeters from the Sky Island Mountains of US and Mexico: 1985-2011*. Reston, VA: U.S. Geological Survey; 2018. doi:10.5066/F76Q1WJ1.
61. Villarreal ML, Poitras TB. *Differenced Normalized Burn Ratio (dNBR) data of wildfires in the Sky Island Mountains of the southwestern US and Northern Mexico from 1985-2011*. Reston, VA: U.S. Geological Survey; 2018. doi:10.5066/P9P3NIXR.
62. Villarreal ML, Poitras TB, Conrad CR. *Mapped Fire Perimeters from the Sky Island Mountains of US and Mexico:1985-2017*. Reston, VA: U.S. Geological Survey; 2020. doi:10.5066/P9BB5TIO.
63. Villarreal ML, Conrad CR. *Differenced Normalized Burn Ratio (dNBR) Data of Wildfires in the Sky Island Mountains of the Southwestern US and Northern Mexico from 2011-2017*. Reston, VA: U.S. Geological Survey; 2020. doi:10.5066/P99S0I9W.
64. Hijmans RJ, van Etten J. raster: geographic data analysis and modeling. *R Package Version 2*. http://CRAN.R-project.org/package=raster. Updated 2016.
65. Kolden CA, Smith AM, Abatzoglou JT. Limitations and utilisation of monitoring trends in burn severity products for assessing wildfire severity in the USA. *Int J Wildland Fire*. 2015;24:1023-1028.
66. Batllori E, Miller C, Parisien M-A, Parks SA, Moritz MA. Is US climatic diversity well represented within the existing federal protection network? *Ecol Appl*. 2014;24:1898-1907.
67. Whitman E, Batllori E, Parisien M-A, et al. The climate space of fire regimes in north-western North America. *J Biogeogr*. 2015;42:1736-1749. doi:10.1111/jbi.12533.
68. R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing; 2019. https://www.R-project.org/
69. AdaptWest Project. Gridded current and projected climate data for North America at 1 km resolution, interpolated using the ClimateNA v5. 10 Software. https://adaptwest.databasin.org/pages/adaptwest-climatena. Updated 2015.
70. Wood SN. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Ser B Stat Methodol*. 2011;73:3-36.
71. Simpson GL. Modelling palaeoecological time series using generalised additive models. *Front Ecol Evol*. 2018;6:149.
72. Yocom Kent LL, Fulé PZ, Brown PM, et al. Climate drives fire synchrony but local factors control fire regime change in northern Mexico. *Ecosphere*. 2017;8:e01709.
73. Villarreal ML, Haire SL, Poitras TB, Iniguez JM, Cortés Montaño C. Contemporary fire regimes of the Madrean Sky Islands of US and Mexico. Biodiversity and Management of the Madrean Archipelago Conference: collaboration Now for the Future: biodiversity and Management of the Madrean Archipelago IV; May 14-18, 2018; Tucson, AZ.
74. United States Government Accountability Office. *Arizona Border Region: Federal Agencies Could Better Utilize Law Enforcement Resources in Support of Wildland Fire Management Activities*. https://www.gao.gov/assets/590/586139.pdf. Updated 2011.
75. Norman LM, Villarreal ML, Lara-Valencia F, et al. Mapping socio-environmentally vulnerable populations access and exposure to ecosystem services at the U.S.–Mexico borderlands. *Appl Geogr*. 2012;34:413-424. doi:10.1016/j.apgeog.2012.01.006.
76. Ellis EC, Ramankutty N. Putting people in the map: anthropogenic biomes of the world. *Front Ecol Environ*. 2008;6:439-447.
77. Liebmann MJ, Farella J, Roos CI, Stack A, Martini S, Swetnam TW. Native American depopulation, reforestation, and fire regimes in the Southwest United States, 1492–1900 CE. *Proc Natl Acad Sci USA*. 2016;113:E696-E704.

78. Sullivan AP, Forste KM. Fire-reliant subsistence economies and anthropogenic coniferous ecosystems in the Pre-Columbian northern American Southwest. *Veg Hist Archaeobotany*. 2014;23:135-151.
79. Fule PZ, Ramos-Gómez M, Cortés-Montaño C, Miller AM. Fire regime in a Mexican forest under indigenous resource management. *Ecol Appl*. 2011;21: 764-775.
80. Petrakis RE, Villarreal ML, Wu Z, Hetzler R, Middleton BR, Norman LM. Evaluating and monitoring forest fuel treatments using remote sensing applications in Arizona, USA. *For Ecol Manag*. 2018;413:48-61.
81. Ffolliott PF. *Effects of Fire on Madrean Province Ecosystems: A Symposium Proceedings*. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1996.
82. Villarreal ML, Gass L, Norman L, et al. Examining wildlife responses to phenology and wildfire using a landscape-scale camera trap network. In: Gottfried GJ, Ffolliott PF, Gebow BS, Eskew LG, Collins LC, eds. *Merging Science and Management in a Rapidly Changing World: Biodiversity and Management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts, 2012 May 1-5; Tucson AZ*. Fort Collins, CO: Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 2013:503-505.
83. Sanderlin JS, Block WM, Strohmeyer BE. Long-term post-wildfire correlates with avian community dynamics in ponderosa pine forests [Chapter J]. In: Ralston BE, ed. *Proceedings of the 12th Biennial Conference of Research on the Colorado River Plateau.* Reston, VA: U.S. Geological Survey.2016: 89-101.
84. Tingley MW, Ruiz-Gutiérrez V, Wilkerson RL, Howell CA, Siegel RB. Pyrodiversity promotes avian diversity over the decade following forest fire. *Proc R Soc B Biol Sci*. 2016;283:20161703.
85. Latif QS, Sanderlin JS, Saab VA, Block WM, Dudley JG. Avian relationships with wildfire at two dry forest locations with different historical fire regimes. *Ecosphere*. 2016;7:e01346. doi:10.1002/ecs2.1346.
86. Hutto RL, Patterson DA. Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire. *Int J Wildland Fire*. 2016;25:1074-1085.
87. Hutto RL, Hutto RR, Hutto PL. Patterns of bird species occurrence in relation to anthropogenic and wildfire disturbance: management implications. *For Ecol Manag*. 2020;461:117942.
88. Callegary JB, Norman LM, Eastoe CJ, Sankey JB, Youberg A. Post-Wildfire Potential for Carbon and Nitrogen Sequestration in the Southwestern United States in Restored Ephemeral and Intermittent Stream Channels. Air, Soil and Water Research; Special Collection, "Case Studies of a Grassroots Binational Restoration Collaborative in the Madrean Archipelago Ecoregion (2014- 2019)." https://ui.adsabs.harvard.edu/abs/2016AGUFMEP22B..01C/abstract. Updated 2020.
89. Bock CE, Block WM. Fire and birds in the southwestern United States. In: Saab V, Powell H, eds. *Fire and Avian Ecology in North America*. Camarillo, CA: Cooper Ornithological Society; 2005:14-32. https://www.fs.usda.gov/treesearch/pubs/24000. Accessed 25 February 2020.
90. Fontaine JB, Kennedy PL. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecol Appl Publ Ecol Soc Am*. 2012;22:1547-1561. doi:10.1890/12-0009.1.
91. Kirkpatrick C, Conway CJ, Jones PB. Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. *J Wildl Manag*. 2006;70:1005-1012. doi:10.2193/0022-541X(2006)70[1005:DARAOF]2.0.CO;2.
92. Flesch AD, Sánchez CG, Amarillas JV. Abundance and habitat relationships of breeding birds in the Sky Islands and adjacent Sierra Madre Occidental of northwest Mexico. *J Field Ornithol*. 2016;87:176-195. doi:10.1111/jofo.12151.
93. Pérez-Salicrup DR, Ortíz Mendoza R, Garduño Mendoza E, et al. Coordinación institucional para la realización de quemas prescritas y quemas controladas en México. *Rev Mex Cienc For*. 2018;9:252-270.
94. Koprowski JL, Alanen MI, Lynch AM. Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol Conserv*. 2005;126:491-498. doi:10.1016/j.biocon.2005.06.028.
95. Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. Warming and Earlier Spring Increase Western U.S. Forest Wildfire activity. *Science*. 2006;313:940-943. doi:10.1126/science.1128834.
96. Seager R, Ting M, Held I, et al. Model projections of an imminent transition to a more Arid climate in Southwestern North America. *Science*. 2007;316:1181-1184.
97. Littell JS, McKenzie D, Peterson DL, Westerling AL. Climate and wildfire area burned in western U.S. *Ecol Appl*. 2009;19:1003-1021. doi:10.1890/07-1183.1.
98. Cook ER, Seager R, Cane MA, Stahle DW. North American drought: reconstructions, causes, and consequences. *Earth-Sci Rev*. 2007;81:93-134. doi:10.1016/j.earscirev.2006.12.002.
99. Woodhouse CA, Meko DM, MacDonald GM, Stahle DW, Cook ER. A 1200-year perspective of 21st century drought in southwestern North America. *Proc Natl Acad Sci USA*. 2010;107:21283-21288.
100. Ganey JL, Wan HY, Cushman SA, Vojta CD. Conflicting perspectives on spotted owls, wildfire, and forest restoration. *Fire Ecol*. 2017;13:146-165. doi:10.4996/fireecology.130318020.
101. Prichard SJ, Peterson DL, Jacobson K. Fuel treatments reduce the severity of wildfire effects in dry mixed conifer forest, Washington, USA. *Can J For Res*. 2010;40:1615-1626. doi:10.1139/X10-109.
102. González-Elizondo MS, González-Elizondo MS, Tena-Flores JA, Ruacho-González L, López-Enríquez IL. Vegetación de la Sierra Madre Occidental, México: una síntesis. *Acta Botanica Mexicana*. 2012;100:351-403. doi:10.21829/abm100.2012.40.
103. Kobelkowsky-Vidrio T, Ríos-Muñoz CA, Navarro-Sigüenza AG. Biodiversity and biogeography of the avifauna of the Sierra Madre Occidental, Mexico. *Biodivers Conserv*. 2014;23:2087-2105. doi:10.1007/s10531-014-0706-6.
104. Roccaforte JP, Fulé PZ, Covington WW. Monitoring landscape-scale ponderosa pine restoration treatment implementation and effectiveness. *Restor Ecol*. 2010;18:820-833. doi:10.1111/j.1526-100X.2008.00508.x.
105. Waltz AEM, Stoddard MT, Kalies EL, Springer JD, Huffman DW, Meador AS. Effectiveness of fuel reduction treatments: assessing metrics of forest resiliency and wildfire severity after the Wallow Fire, AZ. *For Ecol Manag*. 2014;334:43-52. doi:10.1016/j.foreco.2014.08.026.
106. Bahre CJ. *A Legacy of Change: Historic Human Impact on Vegetation in the Arizona Borderlands*. Tucson, AZ: University of Arizona Press; 1991.
107. McPherson GR. *Ecology and Management of North American Savannas*. Tucson, AZ: University of Arizona Press; 1997.
108. Gottfried GJ, Allen LS. A plan for landscape fire restoration in the Southwestern Borderlands. *Ecol Restor*. 2009;27:129-131.
109. Sayre NF. A history of working landscapes: the Altar Valley, Arizona, USA. *Rangelands*. 2007;29:41-45.
110. Villarreal ML, Norman LM, Buckley S, Wallace CSA, Coe MA. Multi-index time series monitoring of drought and fire effects on desert grasslands. *Remote Sens Environ*. 2016;183:186-197. doi:10.1016/j.rse.2016.05.026.
111. Barton AM, Poulos HM., Pine vs. oaks revisited: conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. *For Ecol Manag*. 2018;414:28-40. doi:10.1016/j.foreco.2018.02.011.
112. Iniguez JM, Swetnam TW, Baisan CH. Fire history and moisture influences on historical forest age structure in the sky islands of southern Arizona, USA. *J Biogeogr*. 2016;43:85-95. doi:10.1111/jbi.12626.