



ORIGINAL RESEARCH

Open Access



Long-term recovery of Mexican spotted owl nesting habitat after fire in the Lincoln National Forest, New Mexico

Tara D. Durboraw^{1*} , Clint W. Boal², Mary S. Fleck³ and Nathan S. Gill¹

Abstract

Background: Dry mixed-conifer forests of the southwestern United States are experiencing rapid, anthropogenically driven fire regime change. Prior to the Euro-American settlement, most of these forests experienced frequent surface fires but are now vulnerable to uncharacteristically large, high-severity fires. Fire directly influences the structure and composition of these forests and, in turn, the wildlife that inhabit them. Changing fire regimes result in a certain decline of some species and uncertain consequences for others. The Mexican spotted owl (*Strix occidentalis lucida*) is a federally listed threatened species of particular note in southwestern mixed-conifer forests. High-severity fire is cited as the owl's primary threat in the revised species recovery plan, but uncertainties surround the impacts of high-severity fire on the habitat of the threatened owl, particularly across a timeframe longer than a few years. Our objective was to explore the *long-term* (100-year) effects of fire severity on elements of forest structure vital for Mexican spotted owl nesting. We quantified structural attributes for nest/roost habitat across mixed-conifer forests that burned at varying severity levels and time periods in the last century. We then examined the drivers of structural attributes by detecting statistical differences between severity classes and time periods through permutational multivariate analysis of variance.

Results: High-severity fire has the strongest deleterious impact on elements of forest structure (total basal area, percent medium tree basal area, percent large tree basal area, large tree density, and canopy cover) vital to Mexican spotted owl nesting, and although the structural differences between severity classes diminish with time, it took ≥ 80 –100 years to reach the structural conditions desired for Mexican spotted owl nesting after stand-replacing fires. The most important attribute measured, canopy cover, required 90–100 years after high-severity fires to reach levels most suitable for Mexican spotted owls in the Lincoln National Forest.

Conclusions: As fires increase in frequency, severity, and size compared to the last century, the Lincoln National Forest is projected to face an overall decrease in the structural conditions needed for Mexican spotted owl nesting habitat in this region. Short intervals between uncharacteristically high-severity fires in particular pose an imminent threat to nesting habitat.

Keywords: Burn severity, Fire severity, Mexican spotted owl, Mixed-conifer, Post-fire habitat, Sacramento Mountains, *Strix occidentalis lucida*, Succession, Time since fire

*Correspondence: tara.durboraw@gmail.com

¹ Department of Natural Resources Management, Texas Tech University, Goddard Building Box 42125, Lubbock, TX 79409, USA
Full list of author information is available at the end of the article

Resumen

Antecedentes: Los bosques de coníferas mixtos-xéricos del sudoeste de los EEUU están experimentando un rápido cambio, de origen antropogénico, en sus regímenes de fuego. Antes de la colonización euroamericana, la mayoría de esos bosques tenía un régimen de fuegos superficiales, pero ahora son vulnerables a grandes incendios, atípicos y de alta severidad. El fuego influencia directamente la estructura y composición de esos bosques y, en consecuencia, sobre la fauna que los habita. Los cambios en los regímenes de fuego resultan en cierta declinación de algunas especies, y tiene consecuencias inciertas sobre otras. El búho manchado mexicano (*Strix occidentalis lucida*), es una especie listada como amenazada por el gobierno federal y de notoria importancia en los bosques mixtos de coníferas del suroeste de los de EEUU. Los incendios de alta severidad han sido citados como la principal amenaza hacia este búho en la revisión de planes de recuperación de especies, aunque cierta incertidumbre rodea los impactos de incendios de alta severidad en el hábitat de subespecies amenazadas, particularmente en un período de tiempo de varios años. Nuestro objetivo fue estudiar los efectos a largo plazo (100 años) de fuegos de alta severidad sobre algunos elementos de la estructura del bosque, y que son vitales para el anidamiento del búho manchado mexicano. Cuantificamos luego los atributos estructurales del hábitat para el anidamiento y/o percheo de este búho a través de bosques mixtos de coníferas quemados a distintas severidades y tiempos durante la última centuria. Examinamos luego los elementos que motivaron los cambios en los atributos estructurales mediante la detección de diferencias estadísticas entre clases de severidad y períodos de tiempo usando PERMANOVA.

Resultados: Los fuegos de alta severidad tienen el impacto deletéreo más grande en los elementos de la estructura del bosque (área basal total, porcentaje medio del área basal, el porcentaje de área basal de grandes árboles, densidad de árboles grandes, y cobertura del dosel), y que resultan vitales para el anidamiento del búho manchado mexicano, y aunque las diferencias estructurales entre clases de severidad disminuye con el tiempo, tardan entre ≥ 80 y 100 años en recuperar las condiciones deseables para el anidamiento del búho manchado mexicano luego de incendios que reemplazaron todo el rodal. El principal atributo medido (cobertura del dosel) requirió entre 90 y 100 años luego de un incendio de alta severidad para alcanzar hábitats aceptables para el búho moteado mexicano en el bosque Nacional Lincoln.

Conclusiones: En la medida que los fuegos se incrementen en frecuencia, severidad y tamaño, comparados con la centuria pasada, se proyecta que el bosque Nacional Lincoln va a enfrentar un decremento en las condiciones estructurales necesarias para el hábitat de anidamiento del búho manchado mexicano en esta región. Intervalos de tiempo cortos entre fuegos no característicos y de alta severidad en particular, supone una amenaza inminente para el hábitat de anidamiento de este búho.

Background

Patterns of wildfire in the southwestern United States have been dramatically altered in the last 150 years. Many southwestern mixed-conifer forests have been shaped by low-severity, high-frequency fire regime with a minimum fire return interval of 4–6 years and maximum fire return interval of 18–32 years, only rarely burning at higher severity. In addition to natural ignitions from lightning strikes, indigenous use of fire shaped patterns of burning at high frequency over thousands of years (Allen 2002). These fire regimes were interrupted around the 1850s with the Euro-American settlement (Allen et al. 2002; Brown et al. 2001; Coop et al. 2019; Swetnam and Baisan 1994). Post-settlement anthropogenic forces, namely climate change, fire suppression, and land-use practices, have shifted the historic fire regimes of these semi-arid forest systems towards uncharacteristic fire severity and frequency (Fulé et al. 2009; Singleton et al. 2019).

Due to anthropogenic fire regime alteration, many southwestern mixed-conifer forests are now vulnerable to uncharacteristically large, high-severity fires, leading to altered forest structure and a risk of conversion in vegetation community composition, including possible shifts to non-forest composition (Coop et al. 2019; Fornwalt et al. 2016). Fire size, severity, and frequency have increased throughout southwestern mixed-conifer forests in response to suppression-induced structural change (increased density and fuel accumulation; Fulé et al. 2009) and climate change (hotter, drier conditions; Westerling et al. 2006). Suitable conditions for fire in these forests are expected to continue increasing with climate change (Hurteau et al. 2014; Singleton et al. 2019) and have already led to return intervals as short as 3–14 years, including some high-severity reburns (Holden et al. 2010). Such changes have uncertain consequences for vegetation dynamics and wildlife habitat,

having already led to the possible decline of many native vertebrates (Allen et al. 2002).

A species of particular concern in light of this fire regime change is the Mexican spotted owl (*Strix occidentalis lucida*), a recognized subspecies of the spotted owl, which commonly uses dense canopies in mature mixed-conifer forests within the Southwest (U.S. Fish and Wildlife Service 2012; 1995). This subspecies was listed as federally threatened under the Endangered Species Act in 1993 (58 Federal Register 14248) due to the threat of historic and continued habitat alteration from timber harvest practices (U.S. Fish and Wildlife Service 1995). Due to its protected status and overall population decline observed in its westerly distributed subspecies, the California spotted owl (Gutiérrez et al. 2017), the spotted owl has been the center of much controversy (Jones et al. 2020), initially raising conflict between timber harvest activities (a job-creating and economically profitable activity) and the conservation of old-growth forest valuable for the owl species (Simberloff 1987). The controversy has since shifted to conflicting views on the impacts of both high-severity fire and severe fire-mitigating activities (e.g., fuel reduction treatments) on all three subspecies (Ganey et al. 2017; Peery et al. 2019).

Since its initial listing, protective restrictions on timber harvesting near nest/roost locations and an increase of larger, more severe wildfires within the Mexican spotted owl's range have shifted the recognized primary threat to this protected owl. Now, rather than habitat loss from timber harvest, the primary threat is identified as the increased risk of stand-replacing fires throughout the geographic distribution of the owl (U.S. Fish and Wildlife Service 1995; 2012; Wan et al. 2018). A stand-replacing fire is one that kills all or most of the living overstory trees in a forest stand, potentially initiating a pulse of regeneration. As the occurrence of larger, more severe fires continues to increase in southwestern mixed-conifer forests (Fulé et al. 2009; Hurteau et al. 2014; Singleton et al. 2019; Westerling et al. 2006), the effects on Mexican spotted owl habitat remain in question.

Despite the fact that stand-replacing wildfire is recognized as the primary threat to the Mexican spotted owl, and the fact that the area burned in its range is projected to increase by 13-fold in the next six decades (U.S. Fish and Wildlife Service 2012; Wan et al. 2019), uncertainties still surround the impacts of both high-severity fire and fire-mitigating activities (i.e., fuel reduction treatments) on the owl (Ganey et al. 2017; Peery et al. 2019). In comparison to other spotted owl subspecies, fewer studies have investigated the relationship between the Mexican spotted owl and fire (Ganey et al. 2017; U.S. Fish and Wildlife Service 2012), and of those limited studies, results focus on short-term effects and typically fail

to account for fire severity, making it somewhat difficult to reconcile findings (Wan et al. 2018). One to four years after fire, Bond et al. (2002) found little impact of fire on owl survival, reproduction, and mate/site fidelity while Jenness et al. (2004) found occupancy/reproduction in burned areas was slightly lower than in unburned areas, but different severities across burned areas did not have a significant effect. Ganey et al. (2014a) found that owls foraged disproportionately in burned areas during winter, favoring post-fire habitat in their ecosystem. These three studies examined short-term (≤ 6 years) data after fire, and only limited analyses of the impact of severity were considered. Lommler (2019) observed that Mexican spotted owl occupancy within the perimeter of the Rodeo-Chediski fire, a fire that burned 187,000 ha in east-central Arizona in 2002, was lower than occupancy outside of the perimeter more than a decade after the fire. Mexican spotted owls avoided nesting/roosting in areas with $\geq 33\%$ fire-killed canopy (moderate- to high-severity fire) 13–15 years following the fire, and a negative relationship between owl occupancy and salvage logging was also found, suggesting that such practices degrade owl habitat (Lommler 2019). Wan et al. (2020) found differences in the effects of fire severity on the Mexican spotted owl habitat; high-severity fire reduced nesting habitat suitability at broad scales more than lower severity fire when habitat suitability was modeled in the first 3 years after fire. Furthermore, Wan et al. (2019) found that stand-replacing fire is expected to increase dramatically within the range of the Mexican spotted owl over the long term (by 2080s), highlighting the need to understand the long-lasting effects of high-severity fire on forest structure.

We designed the current study to address the long-term (100-year timeframe) effects of fires of different severities on elements of mixed-conifer forest structure

Table 1 Minimum desired conditions, outlined in the first revision of the Mexican spotted owl recovery plan, for the management of Mexican spotted owl forested recovery nesting and roosting habitat in mixed-conifer forests of the Basin and Range East EMU, in which the study area falls (Tables C.2 and C.3 in U.S. Fish and Wildlife Service 2012)

Structural attribute	Size class of trees included (cm dbh)	Minimum desired condition
Total basal area	> 2.54	$\geq 33.3 \text{ m}^2/\text{ha}$
Percent medium tree basal area	30–46	> 30%
Percent large tree basal area	> 46	> 30%
Large tree density	> 46	$\geq 37 \text{ trees/ha}$
Canopy cover	-	$\geq 60\%$

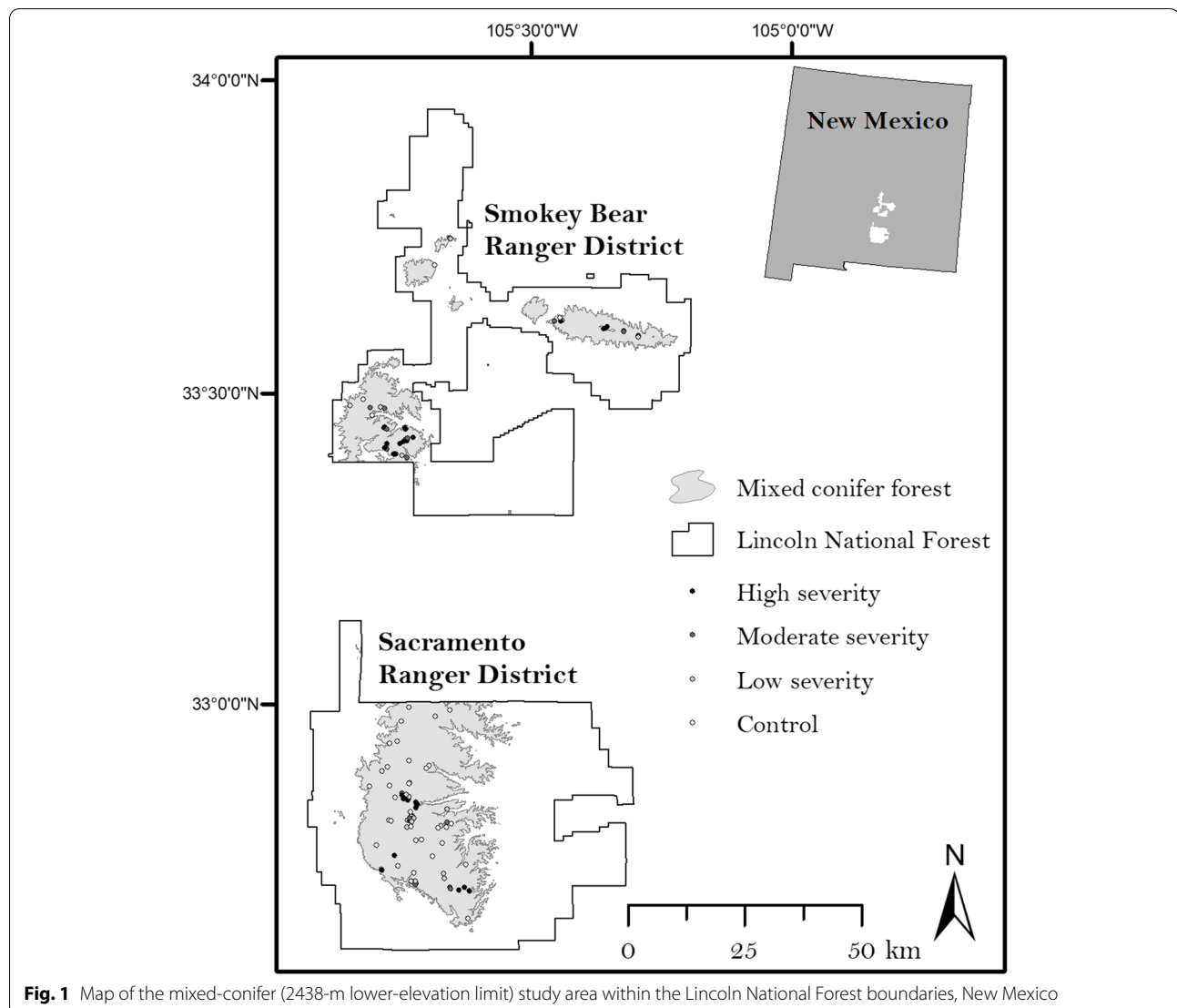
important for Mexican spotted owl nesting habitat—canopy cover, basal area, large/medium tree basal area, and large tree density (detailed in Table 1). This approach is based on nesting habitat being the assumed limiting factor for Mexican spotted owl populations (U.S. Fish and Wildlife Service 2012; Wan et al. 2020). We did this by quantifying whether forest structure met those conditions desired for nest/roost habitat (Table 1) at randomly placed points within the mixed-conifer forest that did not burn (control) and burned between 1921 and 2020 in the Lincoln National Forest, New Mexico.

Methods

Study area

Our observational study was conducted in the Sacramento (222,117 ha) and Smokey Bear (171,350 ha) Ranger Districts of the Lincoln National Forest in the

Sacramento Mountains of south-central New Mexico. The study area is contained within the Basin and Range East Ecological Management Unit (EMU), one of the five EMUs within the US range of the Mexican spotted owl (U.S. Fish and Wildlife Service 2012). Mexican spotted owls occur in high-elevation forested “sky islands” (isolated mountain ranges capped with forests and surrounded by low-elevation desert and grasslands) and deep, intertwined canyons within this EMU (U.S. Fish and Wildlife Service 2012). In the Lincoln National Forest, Mexican spotted owls primarily nest in the mixed-conifer forest (92% of nests; Ganey et al. 2013), so we restricted the study area to this forest type (Fig. 1) and above 2438 m (Ronco et al. 1983). Average precipitation was 76 cm/year at Cloudcroft, New Mexico (2640 m elevation), within the Sacramento Ranger District (from 1981 to 2010 30-year normal; Western



Regional Climate Center 2021); 60–70% of precipitation comes during summer (July–September) monsoons, and the remainder is largely snowfall (Brown et al. 2001; Kauffman et al. 1998).

Mixed-conifer forests in the study area are dominated by white fir (*Abies concolor*) and/or Douglas fir (*Pseudotsuga menziesii*) with a common occurrence of southwestern white pine (*Pinus strobiformis*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*; Brown et al. 2001; Ganey and Vojta 2011; Kauffman et al. 1998). Gambel's oak (*Quercus gambelii*) is prevalent in much of the midstory, and the most frequently occurring shrub is mountain spray (*Holodiscus dumosus*). Mixed-conifer forest within the defined elevation range comprises 26% (132930 ha) of the Lincoln National Forest, and for comparison, roughly 8.5% of the Lincoln National Forest is designated as Mexican spotted owl protected activity centers (PACs; Ganey et al. 2014b). PACs are established to protect areas used by resident Mexican spotted owl(s) and represent a minimum of 243 protected hectares delineated around known nests/roosts—a 40-ha core area centered on a nest tree and an additional ≥ 203 ha potentially being used for foraging (U.S. Fish and Wildlife Service 2012).

The primary disturbances that historically shaped diversity in the mixed-conifer forests of the Lincoln National Forest included fire (Brown et al. 2001), but following the Euro-American settlement of the region in the mid-1800s, forest structure was expansively homogenized through activities such as logging, grazing, agriculture, and fire suppression (Ganey et al. 2013; Kauffman et al. 1998), similar to much of the mixed-conifer forest of the region. Prevalent commodity-oriented logging from the 1880s to the 1940s removed much of the heterogeneous, old-growth mixed-conifer forest on this landscape, and logging, although not at the same magnitude, still occurs throughout the study area with the intent of reducing fire danger levels (Kauffman et al. 1998; Ganey et al. 2013; USDA Forest Service). The percent of vegetation treatments that timber sales comprised on the Smokey Bear and Sacramento districts was 31% from 1980 to 1999 and reduced to just 6% from 2000 to 2010 (U.S.D.A. Forest Service n.d.). As a result, while 10–26% of mixed-conifer stands were estimated to be in the old-growth condition in 1880 prior to the Euro-American settlement, less than 5% of old-growth mixed-conifer stands in the Sacramento Mountains remained as of the late twentieth century (Kauffman et al. 1998). More recently, the Lincoln National Forest, along with six other southwestern national forests, underwent an approximately 1-year injunction that suspended timber harvesting due to the deleterious effects of such practices, namely even-aged silviculture, on Mexican spotted owl

habitat (WildEarth Guardians v. United States Fish and Wildlife Service n.d.) until its dismissal in October of 2020 (U.S.D.A. Forest Service 2020).

Plot placement/stratification

Spatial information and severity data for fires within our study area dating from 1984 to the present (hereafter “recent fires”) were obtained from the Monitoring Trends in Burn Severity (MTBS) project (MTBS 2019), and spatial information for fires within our study area dating from 1921 to 1983 (hereafter “older fires”) was obtained from the National Wildfire Coordinating Group (NWCG 2020). It is important to note that historical reconstructions like the NWCG spatial information may underestimate the area burned on a landscape (Syphard and Keeley 2016). However, in an effort to ensure plots were defined by the correct disturbance category, we looked for visual evidence of historic fire (or lack thereof for the control plots) such as fire scars and char. To ensure that we captured variability in habitat that burned at different severities, we initially stratified plots in the recent fires by differenced normalized burn ratio (dNBR; MTBS 2019); however, final fire severity classes for analysis were not determined until after data collection from the field to improve classification accuracy (see the “Defining fire severity” section). Using Geographic Information Systems (GIS; ArcGIS version 10.7), we randomly generated 125 survey plots stratified by time of fire (2010s, 1990s–2000s, 1950s–1960s, 1920s, or control—no fire in the last > 100 years) in the 100-year timeframe and, for recent fires, by fire severity (high, medium, low). Additionally, all plots were above 2438-m elevation, were within 500 m of a trail or road, and fell outside of Lincoln National Forest's documented logged areas and areas defoliated by insects within the last 21 years (temporal extent of data). No sites were located in areas that burned more than once in the last 100 years, and all plots were separated by > 100 m from other plots of the same age-severity class. Plots were located in distinct patches of burned forest and were not spatially autocorrelated with other plots of the same category of fire severity and decade (Figure S1; Table S1). Occasionally, plots that had initially been selected failed to meet these conditions due to deficiencies in the reference data used. In these cases, in-field adjustments were made to relocate plots away from disqualifying characteristics, or alternate random plots were generated in their place if necessary. Following data collection, 12 plots were permanently removed from the study for various discrepancies (e.g., error in sampling methods, or fire severity could not be determined—see the “Defining fire severity” section), resulting in further analysis of 113 total burned and control plots.

Sampling design

We conducted forest structure surveys during the summer of 2020. At the 113 plots, data were collected in a 0.1-ha circular plot centered on the nearest tree or snag of sufficient diameter at breast height (dbh) to approximate the minimum sized tree for Mexican spotted owl nesting (27 cm dbh; Seamans and Gutierrez 1995). This protocol maintained realistic potential nesting habitat condition by avoiding small trees and treeless areas (Ganey et al. 2013). If the plot had no tree or snag ≥ 25 cm, we centered the plot on the largest tree—this happened only once at a plot that burned moderately in the 1950s; this plot was centered on a tree 24 cm in dbh. Within the 0.1-ha circular plot, we established three bisecting 36-m transects for measuring canopy cover. We also established a nested 0.03-ha circular plot for measuring other elements of forest structure (see below). We modeled our plots after the sampling design of Ganey et al. (2013; Fig. 2).

At the plot center, we recorded the aspect, slope, elevation, and Universal Transverse Mercator (UTM) coordinate pair. Aspect was defined as the cardinal direction of downhill, and the slope was measured using a Laster Technology, Inc. TruPulse 200 hypsometer. Elevation and geographic coordinates were recorded using a DeLorme Earthmate PN-60w. In the entire 0.1-ha plot, we counted, documented the status [alive, fire-killed, dead before fire, or dead-unknown; determined based on tree/snag characteristics described by Harvey et al. (2014)], and measured the dbh of all trees and snags ≥ 25 cm in dbh. Within a predetermined 0.067-ha section of the 0.1-ha plot (see Fig. 2) at older fire plots ($n=45$), we used an increment borer to take tree core samples from as close to the tree base as possible from all live conifers ≥ 25 cm in dbh. If fewer than 10 trees occurred within this area, every live conifer ≥ 25 cm dbh in the entire 0.1-ha plot was sampled to assure sufficient sample depth. In the 0.03-ha circular

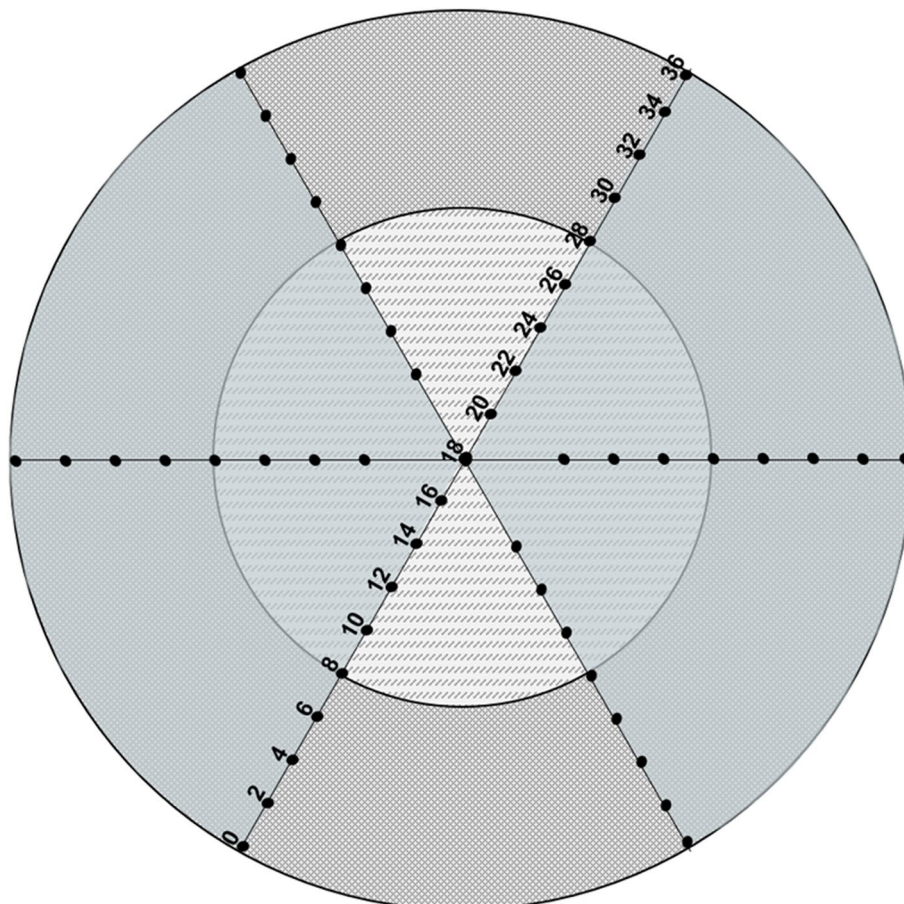


Fig. 2 Schematic diagram of the study's sampling design. The 0.1-ha circular plot contains a nested 0.03-ha circular plot centered on a tree or snag ≥ 25 cm in diameter at breast height. The density and status of trees, shrubs, and snags of different size classes were measured in these plots. The canopy cover was measured at each point every 2 m along the three transects that bisect the plot. The area shaded in darker blue-gray indicates the predetermined 0.067-ha portion from which tree-ring samples were taken to estimate fire severity at plots that burned > 50 years ago

nested plot, we counted, documented the status (fire-killed, dead before fire, dead after fire, established after fire, survived fire), and measured the dbh of small trees/shrubs (standing woody growth > 1.4 m tall and < 25 cm in dbh) and stumps/log bases at the older fire plots. The three 36-m transects bisecting the plot were randomly oriented and spaced evenly by 60°. We classified canopy cover as “open” or “closed” using a moosehorn densiometer along these transects at 2-m intervals, skipping the middle 4 m on the second and third transect to avoid oversampling at the plot center (total $n=50$ two-measurements per plot).

Defining fire severity

Two different approaches had to be taken to define fire severity using field measurements based on the longevity of fire evidence over time—one approach for recent (later than 1984) fires and another, more time-intensive approach for older (before 1984) fires (Fig. 3). The recent fires were initially stratified by dNBR-derived severity classes, but these classes (yielding only one severity value per 900 m²) proved inconsistent with field observations at the spatial scale relevant to spotted owl nesting habitat (Figure S2). Thus, we recategorized the plot severity by percent fire-killed basal area of dominant trees (≥ 25 cm

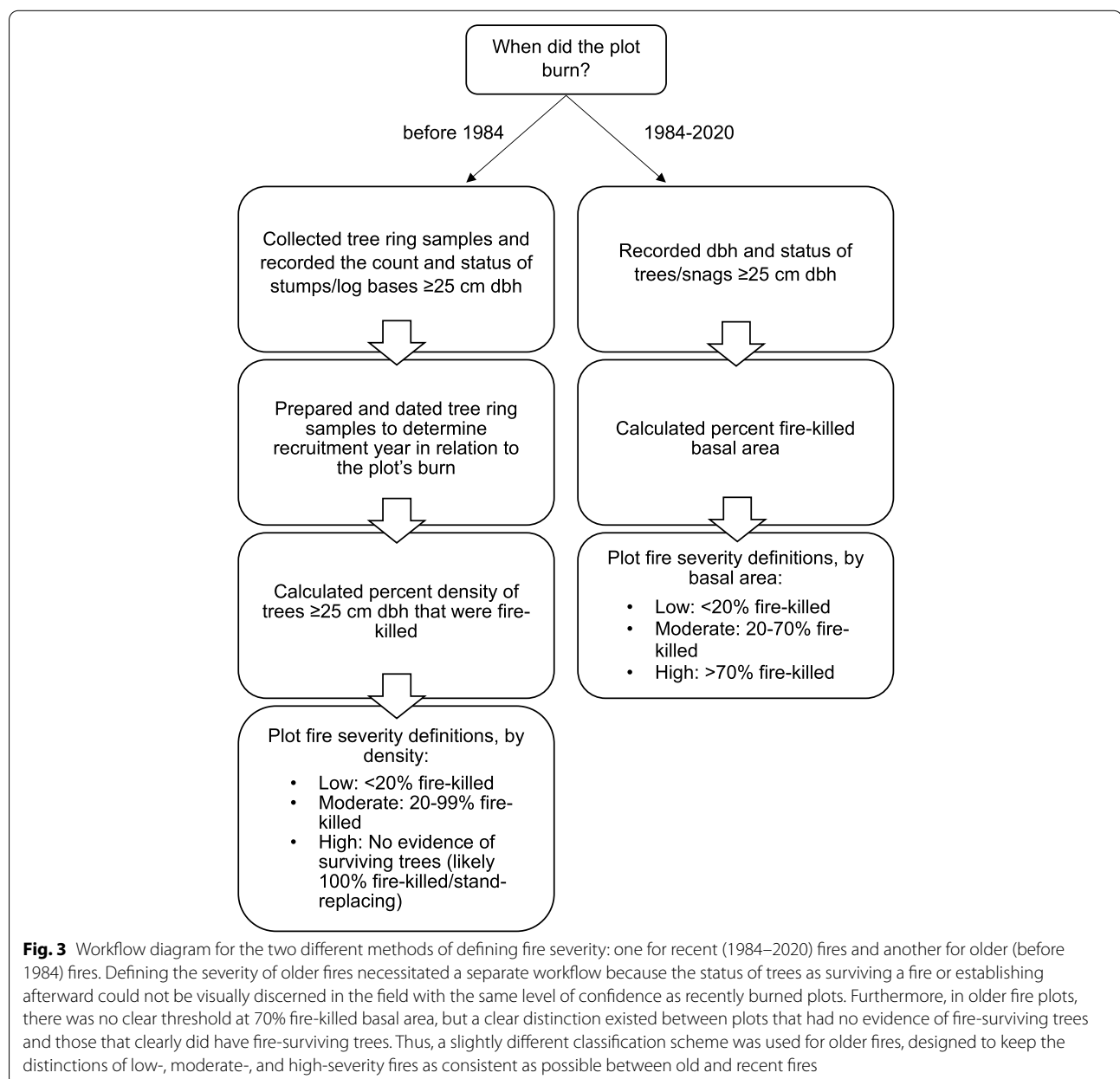


Table 2 Plots ($n = 113$) were categorized by disturbance history, including the decade of the fire and severity. The time period 2010s consisted of fires in 2012; the time period 1990s–2000s consisted of fires in 2004 and 1994; the time period 1950s–1960s consisted of fires in 1967, 1956, 1953, and 1951; and the time period 1920s consisted of fires in 1927 and 1921

Time period	Fire severity	N
2010s "recent fires"	High	12
	Moderate	8
	Low	3
1990s–2000s "recent fires"	High	6
	Moderate	4
	Low	8
1950s–1960s "older fires"	High	5
	Moderate	3
	Low	5
1920s "older fires"	High	8
	Moderate	3
	Low	10
Control (no evidence of fire over > 100 years)	-	38
Total	-	113

dbh) within 0.1-ha plots. Thresholds for the three severity classes were set at <20% fire-killed dominant tree basal area (low severity) and >70% fire-killed dominant tree basal area (high severity). These thresholds coincided with natural breaks in the distribution of the data (Figure S2) and severity classes defined in other studies (Agee 1996; Hessburg et al. 2016; Odion et al. 2014). Due to uncertainty in timing and agent of mortality, 4.7% of recently burned plots could not be classified into a severity class and were excluded from further analysis (Figure S3). Forty-one recently burned plots remained in the dataset after these exclusions (Table 2).

The older burn plots required additional steps to define severity in order to avoid misclassification into higher-than-actual severity classes due to loss of evidence over time. Tree core samples enabled us to determine the tree establishment year and relate it to the plot burn year. We prepared and dated tree-ring samples according to standard dendrochronological methods outlined by Stokes and Smiley (1968) to determine individual recruitment years and, ultimately, inform if a tree was established before or after the fire. Along with the status of trees/snags ≥ 25 cm in dbh, we used observations of density and status (fire-killed, established after the fire, etc.) of stumps and log bases ≥ 25 cm in basal diameter that occurred within the sampling plot to determine each plot's dominant tree density at the time of the fire. We determined severity classes from the percent density of trees ≥ 25 cm in dbh

(dominant trees) that were fire-killed. Because this definition of severity class differs from our definition used for recent fire data, the high-severity class threshold differed also—only plots that may have had stand replacement (i.e., the highest extreme was 100% mortality) were considered high severity (Figure S4). This decreased our chance of misclassification of these plots where evidence of less-than-stand-replacing fire has deteriorated over many decades, while still allowing for three distinct classes of severity. Data from older fire plots exhibited more error in severity classification than plots from more recent fires. Due to this uncertainty, 12.8% of older burn plots could not be classified into a severity class and were excluded from further analysis (Figure S4). Thirty-four older fire plots remained in the dataset after these exclusions. Following stratification of the in situ measurements of severity, we had 113 total plots representing 13 different age-severity classes of fire history (Table 1).

Statistical analysis

After collecting forest structure data, we compared our measurements with the minimum desired conditions outlined in the first revision of the Mexican spotted owl recovery plan (Table 1; Ganey et al. 2016; U.S. Fish and Wildlife Service 2012) and then evaluated differences between stands of different severities and time since fire. All data processing, statistical analysis, and figure generation were performed in R statistical software (R Core Team 2020).

To detect structural differences between forest stands of different fire severity classes, we conducted a permutational multivariate analysis of variance (PERMANOVA) on the structural attributes. PERMANOVA tests and pairwise post hoc tests were conducted in the *vegan* and the *pairwiseAdonis* packages, respectively (Martinez Arbizu 2017; Oksanen et al. 2020).

To address how the effects of severity changed with time since fire, we performed three separate rounds of

Table 3 Distribution of the plots meeting all criteria simultaneously across their disturbance history categories (total basal area ≥ 33.3 m²/ha, percent medium tree basal area > 30%, percent large tree basal area > 30%, large tree density ≥ 37 trees/ha, and canopy cover $\geq 60\%$). Categories not listed (plots that burned at medium or high severity in any year) had 0% of plots that met all criteria)

Disturbance agent and decade	Severity	Percentage of plots meeting all criteria
Control	N/A	13.2
Fire (1990s–2000s)	Low	25.0
Fire (1950s–1960s)	Low	20.0
Fire (1920s)	Low	10.0
Total		7.96

PERMANOVA, comparing control plots that had not burned in the last century ($n=38$) with three different subsets of the data: (1) all burned plots ($n=75$) regardless of time since fire, (2) only more recent fire plots that burned later than 1984 ($n=41$), and (3) only older fire plots that burned earlier than 1984 ($n=34$).

To further explore the effects of time since fire on habitat structure, we performed linear regression characterizing the relationship of each structural attribute with time since fire, stratified by severity class.

Results

Summary statistics

Only nine plots (7.96%) met all five desired conditions for nesting habitat simultaneously (Table 3). Of those nine plots, all were either unburned control plots or varying-aged low-severity plots. Still, in each of those categories, only up to 25% of plots of a given category satisfied all five desired conditions (13.2% of unburned, 25% of 1990s–2000s, 20% of 1950s–1960s, and 10% of 1920s). There was a wide spread of slope and aspect within the plots of all disturbance

Table 4 Outputs from the Bonferroni-adjusted post hoc tests for pairwise comparisons between control and severity classes across all plots, regardless of time since fire. The “overall” category refers to a model that evaluates the five considered structure attributes together

Structural attribute	Severity class comparison	Sum of squares	F-model	R ²	Adj P-value
Overall	Low:moderate	8545.518	3.255	0.072	0.258
	Low:high	78036.772	32.366	0.370	0.006*
	Moderate:high	26355.086	12.128	0.205	0.006*
	Low:control	272.683	0.435	0.007	1.000
	Moderate:control	8562.760	3.062	0.054	0.348
	High:control	84592.214	32.696	0.328	0.006*
Canopy cover	Low:moderate	1501.667	7.282	0.148	0.102
	Low:high	10906.306	26.302	0.324	0.006*
	Moderate:high	2875.348	6.154	0.116	0.108
	Low:control	78.190	0.393	0.006	1.000
	Moderate:control	2439.548	11.478	0.175	0.006*
	High:control	15388.415	40.238	0.375	0.006*
Percent large tree basal area	Low:moderate	161.279	0.3619	0.009	1.000
	Low:high	12598.123	21.170	0.278	0.012*
	Moderate:high	7671.233	10.862	0.188	0.024*
	Low:control	589.944	1.3532	0.021	1.000
	Moderate:control	63.933	0.126	0.002	1.000
	High:control	9562.500	15.436	0.187	0.006*
Percent medium tree basal area	Low:moderate	69.178	0.298	0.007	1.000
	Low:high	3775.332	12.383	0.184	0.006*
	Moderate:high	2165.404	7.9240	0.144	0.066*
	Low:control	120.849	0.466	0.007	1.000
	Moderate:control	349.365	1.553	0.028	1.000
	High:control	6252.841	21.860	0.246	0.006*
Large tree density	Low:moderate	5580.730	3.613	0.079	0.468
	Low:high	42389.467	47.0644	0.461	0.006*
	Moderate:high	11549.005	21.168	0.311	0.006*
	Low:control	434.236	0.239	0.004	1.000
	Moderate:control	3784.503	2.305	0.041	0.906
	High:control	41744.328	38.146	0.363	0.006*
Total basal area	Low:moderate	1232.664	6.268	0.130	0.066
	Low:high	8367.544	42.739	0.437	0.006*
	Moderate:high	2094.095	11.583	0.198	0.006*
	Low:control	49.465	0.227	0.004	1.000
	Moderate:control	1925.411	9.262	0.146	0.048*
	High:control	11644.130	56.801	0.459	0.006*

* indicates a p-value considered significant ($p<0.05$)

categories, and no predominant trends in slope or aspect were detected (Figure S5 and Figure S6).

Relationship between fire severity and structural attributes

Across all plots, regardless of time since fire, the results revealed compelling evidence that high-severity plots were different in structure from every other disturbance category in every metric, with the exception of canopy cover between moderate- and high-severity fire plots

(Table 4). When we compared only the control and recent fire plots, the data revealed strong evidence that high-severity plots differed in every structural metric from every other disturbance category, except the percent large tree basal area, for which only control and high-severity plots differed (Table 5). Additionally, data revealed strong evidence that recent moderate-severity fires also differed structurally in both canopy cover and total basal area from control plots (Table 5). In our third PERMANOVA

Table 5 Outputs from the Bonferroni-adjusted post hoc tests for pairwise comparisons between control and severity classes of recent fires (1984–2020). The “overall” category refers to a model that evaluates the five considered structure attributes together

Structural attribute	Severity class comparison	Sum of squares	F-model	R ²	Adj P-value
Overall	Low:moderate	2230.404	1.507	0.067	1.000
	Low:high	34754.769	22.030	0.449	0.006*
	Moderate:high	24283.126	17.103	0.379	0.006*
	Low:control	4336.941	1.592	0.033	1.000
	Moderate:control	13047.101	5.001	0.094	0.054
	High:control	95328.370	37.645	0.411	0.006*
Canopy cover	Low:moderate	1457.999	6.072	0.224	0.150
	Low:high	12122.595	79.887	0.747	0.006*
	Moderate:high	4941.711	36.285	0.564	0.006*
	Low:control	161.305	0.741	0.016	1.000
	Moderate:control	3753.537	18.109	0.274	0.006*
	High:control	26393.865	158.301	0.746	0.006*
Percent large tree basal area	Low:moderate	168.007	0.402	0.019	1.000
	Low:high	4209.613	4.913	0.154	0.186
	Moderate:high	6584.599	7.474	0.211	0.084
	Low:control	0.567	0.001	0.000	1.000
	Moderate:control	293.023	0.610	0.013	1.000
	High:control	7375.293	10.644	0.165	0.024*
Percent medium tree basal area	Low:moderate	96.564	0.313	0.015	1.000
	Low:high	5566.882	17.452	0.393	0.006*
	Moderate:high	4305.043	20.902	0.427	0.006*
	Low:control	10.360	0.0351	0.001	1.000
	Moderate:control	82.074	0.357	0.007	1.000
	High:control	9205.063	37.689	0.411	0.006*
Large tree density	Low:moderate	249.308	0.550	0.026	1.000
	Low:high	9003.152	43.009	0.614	0.006*
	Moderate:high	6360.556	35.718	0.561	0.006*
	Low:control	3101.304	1.990	0.041	0.936
	Moderate:control	6003.947	3.970	0.076	0.300
	High:control	37460.693	29.431	0.353	0.006*
Total basal area	Low:moderate	258.525	4.247	0.168	0.294
	Low:high	3852.526	94.612	0.778	0.006*
	Moderate:high	2091.218	112.600	0.801	0.006*
	Low:control	1063.406	5.456	0.104	0.120
	Moderate:control	2914.520	16.302	0.254	0.006*
	High:control	14893.455	95.714	0.639	0.006*

* indicates a p-value considered significant ($p < 0.05$)

analysis, in which we compared only control and older fire plots, differences in structure were muted. The only compelling evidence for differences in structure detected in this comparison was between high-severity plots and control or low-severity plots, and even these differences were only detected for the percent large tree basal area, large tree density, and total basal area (Table 6).

Temporal trends in structural attributes with time since fire

Canopy cover is believed to be the most important single aspect of forest structure for the Mexican spotted

owl nesting habitat (Ganey et al. 2016; Wan et al. 2017). Distinction in canopy cover between fire severity classes diminished with increased time since fire, demonstrated by low, moderate, and high severity categories all having medians from 62 to 67% canopy cover (all above the minimum desired condition of $\geq 60\%$) within 100 years following fire or sooner (Fig. 4). Following the 2010s fires, canopy cover decreased with increased fire severity and the medians of high- and low-severity classes varied by as much as 30% (and 50% in the 2000s and 1990s group).

Table 6 Outputs from the Bonferroni-adjusted post hoc tests for pairwise comparisons between control and severity classes of older fires (1921–1983). The “overall” category refers to a model that evaluates the five considered structure attributes together

Structural attribute	Severity class comparison	Sum of squares	F-model	R ²	Adj. P-value
Overall	Low:moderate	3869.426	1.229	0.061	1.000
	Low:high	39288.173	18.080	0.410	0.006*
	Moderate:high	8542.091	3.864	0.185	0.174
	Low:control	7595.797	2.574	0.048	0.450
	Moderate:control	674.214	0.215	0.005	1.000
	High:control	24283.026	9.278	0.159	0.006*
Canopy cover	Low:moderate	5.291	0.046	0.002	1.000
	Low:high	295.677	1.100	0.041	1.000
	Moderate:high	119.919	0.396	0.023	1.000
	Low:control	5.453	0.029	0.001	1.000
	Moderate:control	17.224	0.094	0.002	1.000
	High:control	506.037	1.975	0.039	1.000
Percent large tree basal area	Low:moderate	964.180	2.067	0.098	0.900
	Low:high	7555.707	22.096	0.459	0.006*
	Moderate:high	1321.102	2.781	0.141	0.690
	Low:control	1191.618	2.672	0.050	0.678
	Moderate:control	103.678	0.199	0.005	1.000
	High:control	4865.401	10.858	0.181	0.012*
Percent medium tree basal area	Low:moderate	964.180	2.067	0.098	1.000
	Low:high	7555.707	22.096	0.459	1.000
	Moderate:high	1321.102	2.781	0.141	1.000
	Low:control	1191.618	2.672	0.050	1.000
	Moderate:control	103.678	0.199	0.005	0.984
	High:control	4865.401	10.858	0.181	0.720
Large tree density	Low:moderate	2607.619	1.188	0.059	1.000
	Low:high	28892.601	24.193	0.482	0.006*
	Moderate:high	6484.480	6.558	0.278	0.168
	Low:control	5776.369	3.064	0.057	0.594
	Moderate:control	11.523	0.006	0.000	1.000
	High:control	16469.671	11.327	0.188	0.018*
Total basal area	Low:moderate	209.857	0.930	0.047	1.000
	Low:high	2517.234	14.025	0.350	0.012*
	Moderate:high	592.557	2.774	0.140	0.636
	Low:control	278.084	1.302	0.025	1.000
	Moderate:control	18.956	0.081	0.002	1.000
	High:control	1878.720	8.992	0.155	0.030*

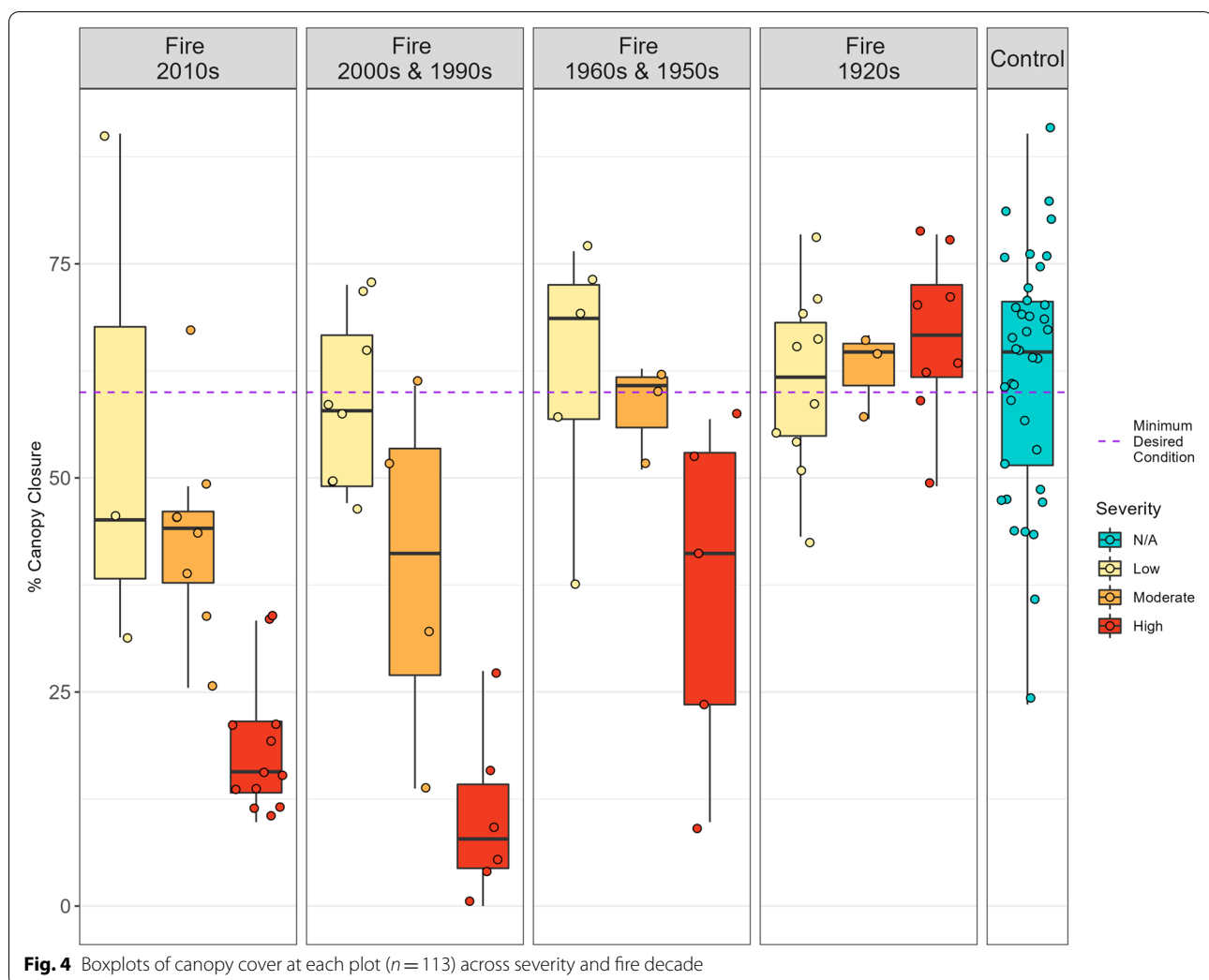
* indicates a p-value considered significant ($p < 0.05$)

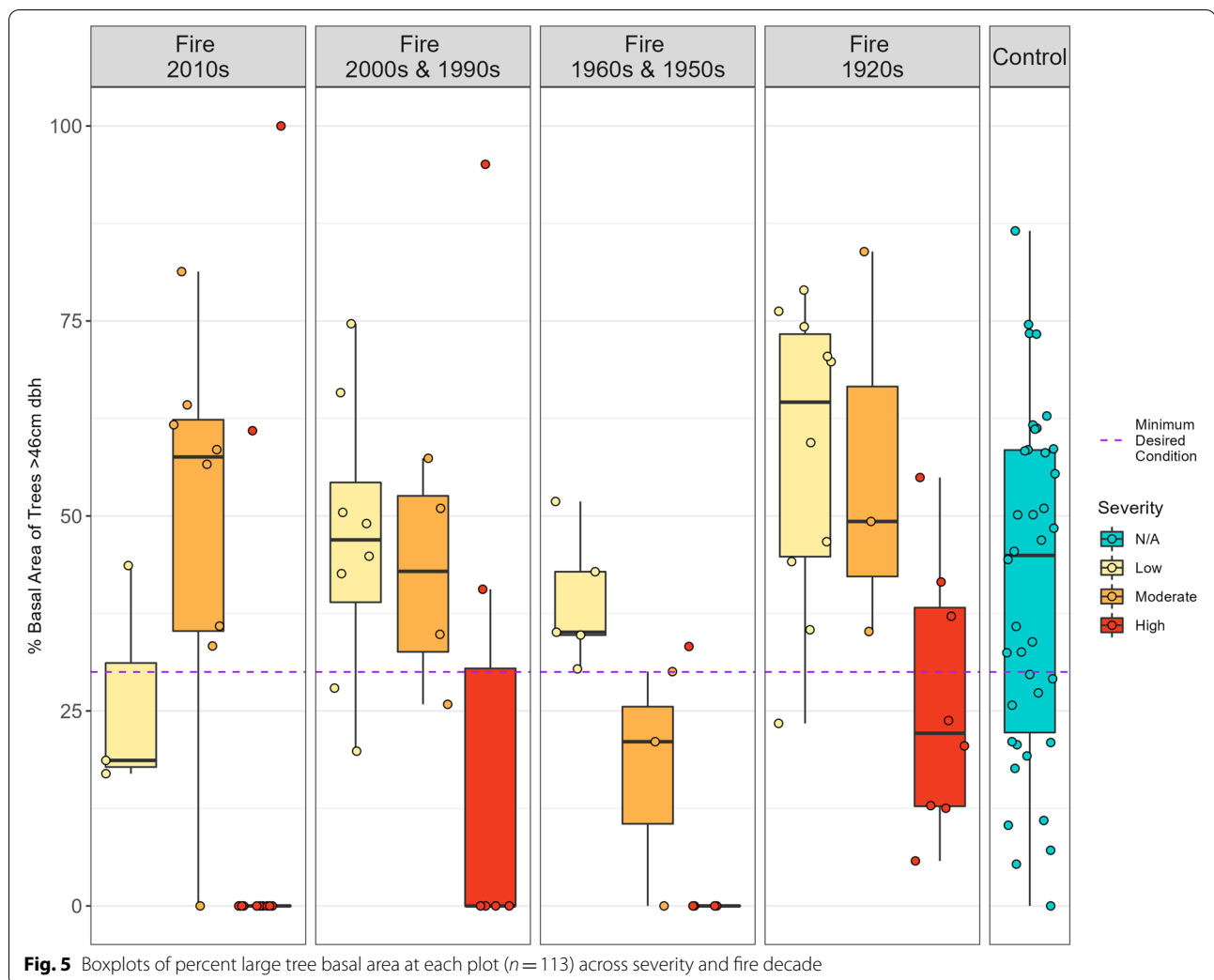
Another important metric of nesting habitat structure, the percent large tree basal area (trees > 46 cm dbh; Table 1), remained low (median < 15%) in high-severity plots relative to the other severity classes and well below the minimum desired condition of 30%, even a century after fire (Fig. 5). For moderate-severity plots, this metric varied greatly across the different fire decades—but the median was only below the minimum desired condition threshold of 30% for fires 50–70 years ago. For low-severity plots, the percent large tree basal area was lowest (and below the desired threshold) after the most recent fires, but median values rose above the threshold after 20–70 years of recovery and increased even higher by 100 years following fire.

The percent medium tree basal area (trees 30–46 cm dbh; Table 1) of high-severity plots increased over time with the median satisfying the minimum desired condition of 30% by a century following fire (Fig. 6). The median of this metric for low- and moderate-severity fire

plots reached the minimum desired condition threshold sooner—low-severity plots exceeding 30% in less than 10 years and moderate exceeding 30% in 20–30 years following fire. However, the median percent medium tree basal area of both low- and moderate-severity plots decreased with time since fire in the absence of repeated fire.

Regarding large tree density (trees > 46 cm dbh; Table 1), plots that burned even at low severity tended to fall short of meeting the minimum desired condition of 37 large trees/ha until 50–70 years following fire, when the median large tree density was 50 trees/ha (Fig. 7). In contrast, median large tree density in moderate-severity plots did not reach the desired threshold until 90–100 years following fire, and median high-severity plots failed to reach the large tree density threshold within the 100-year timeframe (Fig. 7). However, even these plots exhibit a trend in a positive direction (albeit slowly); while medians of sites that burned at high





severity less than 90 years ago remain at zero large trees/ha, by 90–100 years following fire, a few high-severity plots surpassed the large tree density threshold for the first time.

The total basal area of control plots ranged widely, demonstrating the heterogeneity of these forests, but the median value was 37.6%, above the minimum desired total basal area of 30 m²/ha (Fig. 8). After a century of post-fire regeneration, the median values of this metric for low- and moderate-severity fire plots were above the desired threshold, but only one out of eight high-severity plots satisfied that criterion (with the median still below it by 2.5 m²/ha).

Discussion

In the Lincoln National Forest, high-severity fire alters forest structure important for the Mexican spotted owl nest/roost habitat differently than lower severity fire, but this distinction diminishes with time (Fig. 9). Even

so, across the study's 100-year chronosequence, none of the high-severity plots met the desired levels (U.S. Fish and Wildlife Service 2012) of all the structural attributes simultaneously. Forest structure important for the Mexican spotted owl nest/roost habitat is most negatively affected by high-severity fire, and each structural element takes 70 years or longer to recover to a level that provides sufficient nesting habitat structure whereas thresholds for some of the attributes were often met within a single decade in recovery after lower severity fire.

In recent fires, important measures of forest structure at high-severity plots were significantly lower, and therefore less adequate for Mexican spotted owl nesting, than structure at plots of all other severity categories, with few significant differences among the other categories (low severity, moderate severity, and control plots). Sixty or more years after fire, there were no significant differences in the forest structure between moderate-severity classes and high-severity classes—only a distinction between

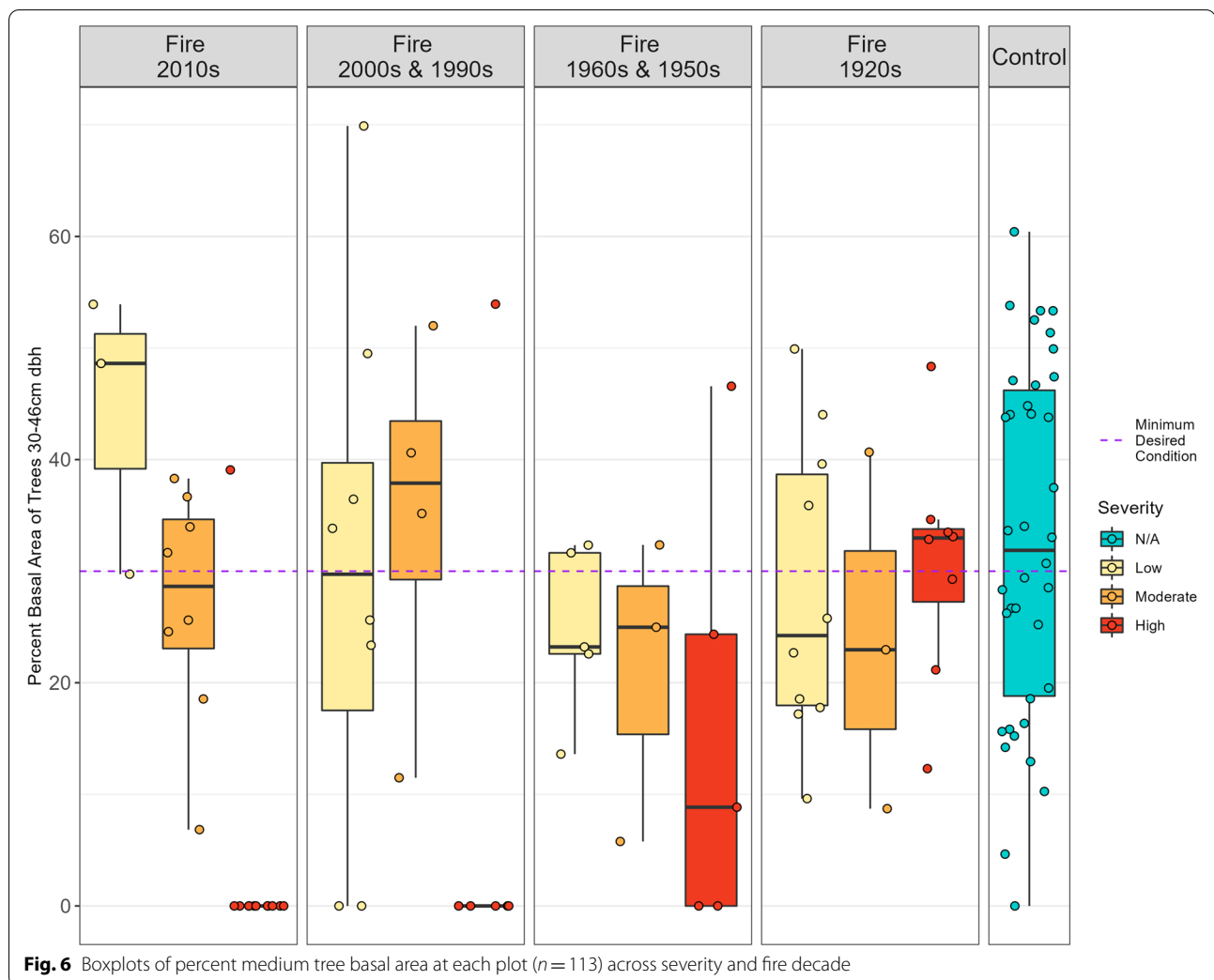


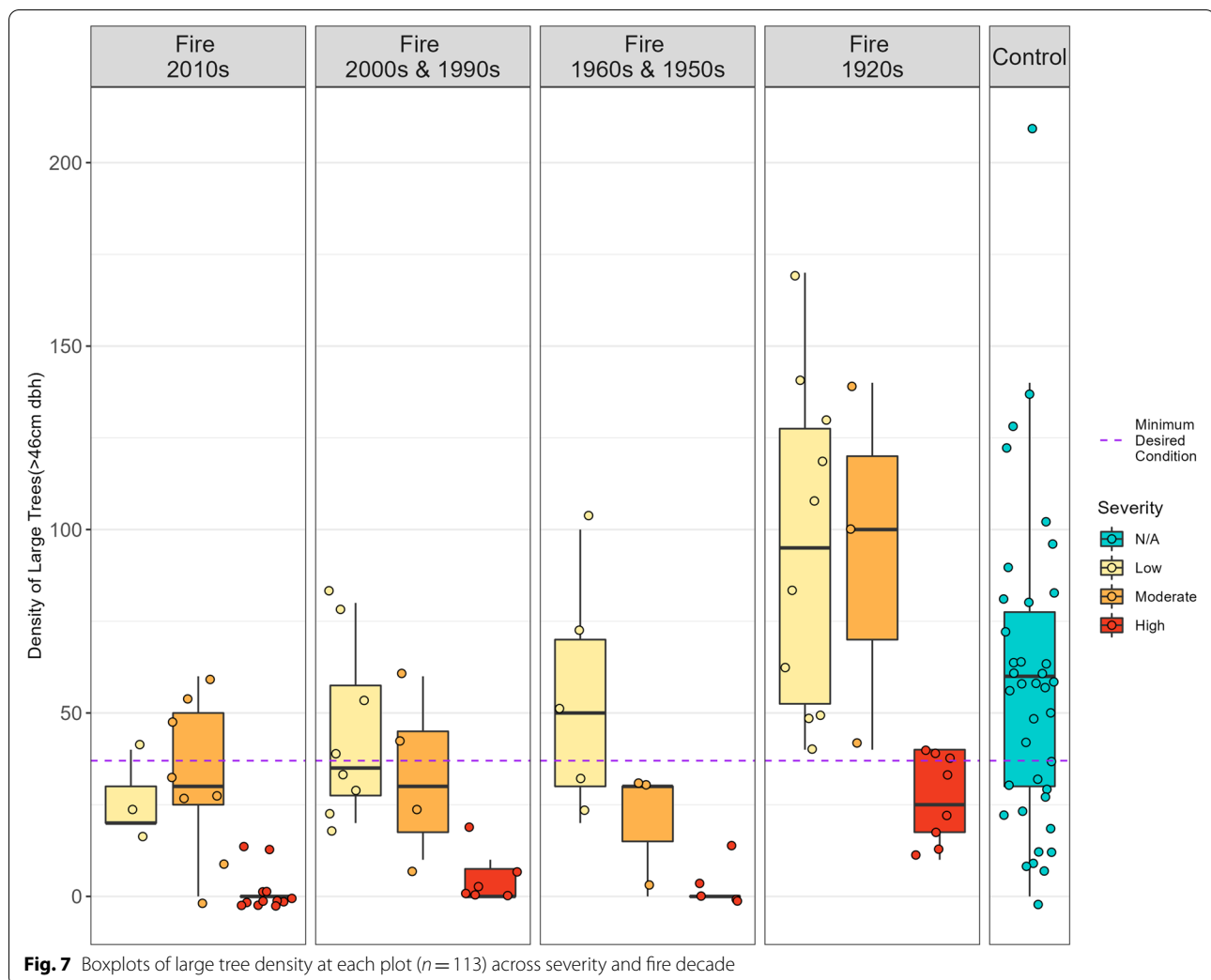
Fig. 6 Boxplots of percent medium tree basal area at each plot ($n = 113$) across severity and fire decade

high-severity and low-severity/control plots—suggesting that high-severity plots that were once different in structure than moderate-severity plots had achieved comparable structure within the timeframe. Canopy cover, the most important of the five attributes we investigated in predicting nesting habitat (Ganey et al. 2016), recovered from stand-replacing fires to levels matching those that are known to support Mexican spotted owls, but only after 90–100 years.

Ganey et al. (2016) found the desired minimum structural thresholds to be much greater than the structure typically observed at successful Mexican spotted owl nest sites in the Sacramento Mountains. However, even if the thresholds were hypothetically set 50% lower, the high-severity burned areas would still take ≥ 40 –50 years to recover, a period of time that is well above the length of the historic mean interval between fires. While the impacts of high-severity fire on forest structure create long-lasting conditions unsuitable for Mexican spotted

owls, management actions can be taken to reduce, though not eliminate, the potential for large, predominantly high-severity fires in the future (Evans et al. 2011; Hurtleau et al. 2014). Additionally, structural recovery following low- and, to a lesser degree, moderate-severity fire is more amenable to the nesting of Mexican spotted owls.

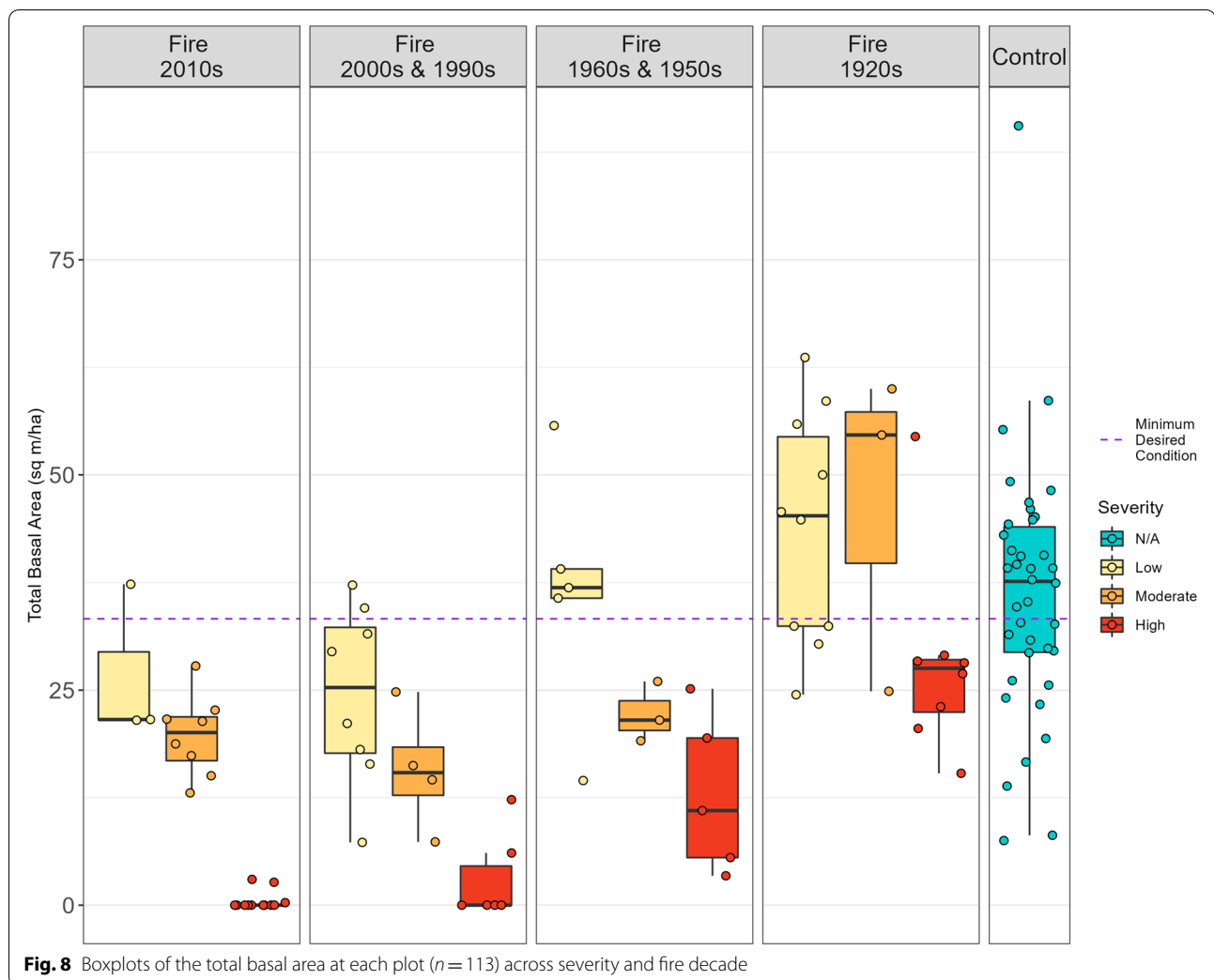
While it is encouraging that forest stands burned at highest severity are eventually recovering to sufficient forest structure to support Mexican spotted owl nesting habitat, the results of the current study suggest the following question: is recovery occurring quickly enough? Before the Euro-American settlement, the fire regime of the study area was characterized by frequent, low-to-moderate-severity fires with a mean return interval of 8–16 years (Azpeleta Tarancón et al. 2018), but the trends we found suggest for the five structural attributes important to Mexican spotted owl nesting habitat, it will take ≥ 80 –100 years for sufficient nesting structure in high-severity burned areas to develop Mexican spotted



owl nesting structure comparable to that of more recent lower severity burns. Given the historic mean fire return interval in dry, mixed-conifer forests and the reality that the status quo of aggressive fire suppression is not sustainable (Dunn et al. 2017; Smith et al. 2018), it is possible that the high-severity burned areas will burn again before adequate recovery to nest habitat structural levels is achieved (Holden et al. 2010). Due to the minimal negative response of nesting habitat structure to low- and moderate-severity fires, setbacks to habitat recovery may be dampened if subsequent fires are of lesser severity than stand-replacing. However, Holden et al. (2010) demonstrated that on a similar landscape, reburns occurring 3–14 years after severe burns have a high probability of reburning at high severity. The study of habitat structure in reburned areas was beyond the scope of the current study, but this represents an important area for future research as stand-replacing fires are expected to increase. Also, fire size and severity have increased throughout

southwestern forests in response to fire suppression and climate change, and conditions for severe fire in these forests are only expected to increase (Fulé et al. 2003; Hurteau et al. 2014; Singleton et al. 2019). Indeed, current predictions are for a predicted 13-fold increase in burned area over time due to climate change alone in the range of the Mexican spotted owl (Wan et al. 2019). These trends, paired with our findings of negative structural effects and slow recovery of severely burned areas, demonstrate an imminent threat to Mexican spotted owls through the reduction of forest with suitable structure for nesting habitat over time.

Mexican spotted owls evolved with and can likely persist alongside wildfire if a fire regime similar to historic patterns can be restored. However, restoration of stand structure is not sufficient for restoring fire regimes, given the rapidly warming climate. If low-severity fire can be promoted through prescribed burning or other means, it can reduce the risk of stand-replacing

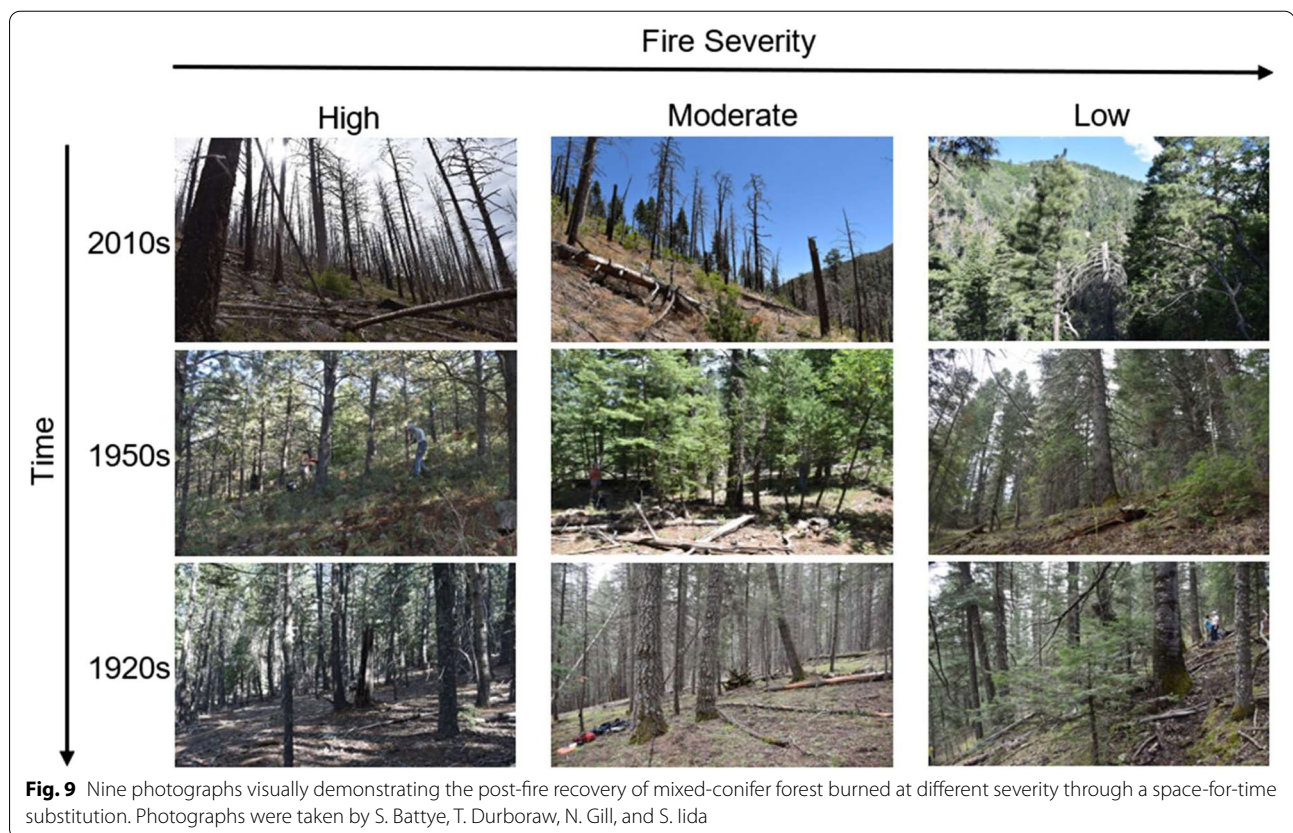


wildfire (Pollet and Omi 2002; Stevens-Rumann et al. 2016) while both minimizing timelines of nesting habitat recovery and creating ecological diversity that benefits Mexican spotted owls and numerous other species. Restoration practices that are intentionally maintaining large, old trees may allow spotted owls to persist while increasing the resilience of the system under a changing climate (Jones et al. 2021a, b).

Fuel reduction efforts that remove fuel ladders and aim to improve the survival of medium and large trees through the next fire are effective in reducing fire hazard and are thus important to broadly maintain the forest structure that provides habitat for nesting Mexican spotted owls and other wildlife (Agee and Skinner 2005; Jones et al. 2022). Restoration activities that focus on plant species composition of the canopy and understory

as well as spatial patterns of open patches and grouped and scattered trees support biodiversity and are expected to improve forest resilience (Reynolds et al. 2013). These restoration activities may include post-fire reforestation (via seeding and/or outplanting), which can accelerate timelines to structural conditions that are suitable for wildlife species (Stevens et al. 2021) including Mexican spotted owls.

Severely burned areas are not completely unusable by Mexican spotted owls; in fact, on the nest site scale, increased pyrodiversity—namely, landscape variation in fire severities—leads to increased persistence of spotted owls (California subspecies; Jones et al. 2021a, b). More open canopy might increase foraging habitat (Bond et al. 2016; Hanson et al. 2018), but our current study shows that nesting habitat will likely be more limited than



foraging habitat given the long period of time associated with post-fire recovery of stand structures. High-quality spotted owl nesting habitat may be found in isolated patches of unburned forest within burn perimeters (Andrus et al. 2021). Such patches may be protected from future high-severity fire (Meddens et al. 2018) and may continue to provide post-fire habitat for Mexican spotted owls, which have high site fidelity (Ganey et al. 2014b). Oftentimes, these patches persist through multiple fires (i.e., fire refugia) because of topographic position and/or high moisture content (Meddens et al. 2018), which also tend to make areas suitable for spotted owl nests. Also, Kramer et al. (2021) found that spotted owls do not avoid high-severity burned areas for foraging per se, but rather avoid *larger patches* of severely burned areas for foraging. However, as fires increase in severity and size (Singleton et al. 2019), our research demonstrates that the landscape will face an overall decrease in the structural conditions needed for nesting habitat, the abundance of which is identified as the primary limiting factor for Mexican spotted owls (U.S. Fish and Wildlife Service 2012). Perhaps the largest threat to the Mexican spotted owl is not necessarily the occurrence of stand-replacing fire, but

rather, the root cause: the absence of lower severity fire and pyrodiversity.

Conclusion

By quantifying how forest recovers following low-, moderate-, and high-severity fires over a century, we were able to show that forest structure important for the Mexican spotted owl nest/roost habitat is most negatively affected by a high-severity fire. After a high-severity fire, each structural element took 70 years or longer to recover to a level that provides the most suitable nesting habitat structure. As fires increase in frequency, severity, and size, the Lincoln National Forest will experience an overall decrease in the structural conditions needed for Mexican spotted owl nesting habitat. Particularly, uncharacteristic high-severity fire, exacerbated by a lack of lower severity fire and pyrodiversity, poses an imminent threat to nesting habitat far into the future.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-022-00158-z>.

Additional file 1: Supplementary tables and figures

Acknowledgements

The authors thank S. Batty, J. Guz, S. Iida, and E. Sanchez who collected the data and L. Cordova, J. Ganey, S. Headwall, G. Jones, and A. Thode for their guidance, expertise, and advice. We also graciously thank the members of the Landscape Ecology and Fire lab that aided in processing the tree-ring collection: M. Garner, T. Grant, R. Hollaway, S. Iida, and A. Sneed.

Authors' contributions

TD and NG conceived and designed the study with input from CB and MF. TD led the acquisition, analysis, and interpretation of the data with contributions from all authors. TD led the writing of the manuscript. All authors contributed to the revising of the manuscript and have approved the submitted version.

Funding

This research was supported by a Pendleton-Rogers Endowed Scholarship award granted to Tara Durboraw.

Availability of data and materials

Data used in this study has been made available in the Texas Tech University Dataverse public repository. The reference information for this dataset is as follows: Gill, Nathan, 2022, "Data: Long-term recovery of Mexican spotted owl nesting habitat after fire in the Lincoln National Forest, New Mexico", <https://doi.org/10.18738/T8/DA6WLM>, Texas Data Repository, V1, UNF:6:5xM2/rUJgt-Kai02LveU2gw== [fileUNF].

Declarations

Ethics approval and consent to participate

This study was solely observational and did not require institutional animal care and use committee approval.

Consent for publication

The authors offer the publishers permission to publish these research findings. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Natural Resources Management, Texas Tech University, Goddard Building Box 42125, Lubbock, TX 79409, USA. ²U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, 1312 Boston Ave, Lubbock, TX 79409, USA. ³U.S. Fish and Wildlife Service, Gulf Restoration Office, 341 North Greeno Rd, Fairhope, AL 36532, USA.

Received: 28 April 2022 Accepted: 21 November 2022

Published online: 19 December 2022

References

- Agee, James K. 1996. *Fire Ecology of Pacific Northwest Forests*. Island Press.
- Agee, James K., and Carl N. Skinner. 2005. Basic Principles of Forest Fuel Reduction Treatments. *Forest Ecology and Management* 211 (1–2): 83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>.
- Allen, Craig D. 2002. *Lots of Lightning and Plenty of People: An Ecological History of Fire in the Upland Southwest*, vol. 143. Washington, DC: Island Press.
- Allen, Craig D., Melissa Savage, Donald A. Falk, Kieran F. Suckling, Thomas W. Swetnam, Todd Schulke, Peter B. Stacey, Penelope Morgan, Martos Hoffman, and Jon T. Klingel. 2002. Ecological Restoration of Southwestern Ponderosa Pine Ecosystems: A Broad Perspective. *Ecological Applications* 12 (5): 1418–1433. [https://doi.org/10.1890/1051-0761\(2002\)012\[1418:EROSP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1418:EROSP]2.0.CO;2).
- Andrus, Robert A., Anthony J. Martinez, Gavin M. Jones, and Arjan J.H. Meddens. 2021. Assessing the Quality of Fire Refugia for Wildlife Habitat. *Forest Ecology and Management* 482: 118868. <https://doi.org/10.1016/j.foreco.2020.118868>.
- Azpeleta Tarancón, Alicia, Peter Z. Fulé, Andrew J. Sánchez Meador, Yeon-Su. Kim, and Thora Padilla. 2018. Spatiotemporal Variability of Fire Regimes in Adjacent Native American and Public Forests, New Mexico, USA. *Ecosphere* 9 (11): e02492. <https://doi.org/10.1002/ecs2.2492>.
- Bond, Monica L., R.J. Gutiérrez, Alan B. Franklin, William S. LaHaye, Christopher A. May, and Mark E. Seamans. 2002. Short-Term Effects of Wildfires on Spotted Owl Survival, Site Fidelity, Mate Fidelity, and Reproductive Success. *Wildlife Society Bulletin* 30 (4): 1022–1028.
- Bond, Monica L., Curt Bradley, and Derek E. Lee. 2016. Foraging Habitat Selection by California Spotted Owls After Fire. *The Journal of Wildlife Management* 80 (7): 1290–1300. <https://doi.org/10.1002/jwmg.21112>.
- Brown, Peter M., Margot W. Kaye, Laurie S. Huckaby, and Christopher H. Baisan. 2001. Fire History along Environmental Gradients in the Sacramento Mountains, New Mexico: Influences of Local Patterns and Regional Processes. *Ecoscience* 8 (1): 115–126. <https://doi.org/10.1080/11956860.2001.11682637>.
- Coop, Jonathan D., Timothy J. Delory, William M. Downing, Sandra L. Haire, Meg A. Krawchuk, Carol Miller, Marc André Parisien, and Ryan B. Walker. 2019. Contributions of Fire Refugia to Resilient Ponderosa Pine and Dry Mixed-Conifer Forest Landscapes. *Ecosphere* 10 (7): e02809. <https://doi.org/10.1002/ecs2.2809>.
- Dunn, Christopher J., David E. Calkin, and Matthew P. Thompson. 2017. Towards Enhanced Risk Management: Planning, Decision Making and Monitoring of US Wildfire Response. *International Journal of Wildland Fire* 26 (7): 551–556. <https://doi.org/10.1071/WF17089>.
- Evans, Alexander M., Rick G. Everett, Scott L. Stephens, and James A. Youl. 2011. Comprehensive Fuels Treatment Practices Guide for Mixed Conifer Forests: California, Central and Southern Rockies, and the Southwest.
- Fornwalt, Paula J., Laurie S. Huckaby, Steven K. Alton, Merrill R. Kaufmann, Peter M. Brown, and Antony S. Cheng. 2016. Did the 2002 Hayman Fire, Colorado, USA, Burn with Uncharacteristic Severity? *Fire Ecology* 12 (3): 117–132. <https://doi.org/10.4996/fireecology.1203117>.
- Fulé, Peter Z., Joseph E. Crouse, Thomas A. Heinlein, Margaret M. Moore, W. Wallace Covington, and Greg Verkamp. 2003. Mixed-Severity Fire Regime in a High-Elevation Forest of Grand Canyon, Arizona, USA. *Landscape Ecology* 18 (5): 465–485. <https://doi.org/10.1023/a:1026012118011>.
- Fulé, Peter Z., Julie E. Korb, and Rosalind Wu. 2009. Changes in Forest Structure of a Mixed Conifer Forest, Southwestern Colorado, USA. *Forest Ecology and Management* 258 (7): 1200–1210. <https://doi.org/10.1016/j.foreco.2009.06.015>.
- Ganey, Joseph L., Darrell L. Apprill, Todd A. Rawlinson, Sean C. Kyle, Ryan S. Jonnes, and James P. Ward. 2013. Nesting Habitat of Mexican Spotted Owls in the Sacramento Mountains, New Mexico. *Journal of Wildlife Management* 77 (7): 1426–1435. <https://doi.org/10.1002/jwmg.599>.
- Ganey, Joseph L., Jose M. Iniguez, Shaulya Hedwall, William M. Block, James P. Ward, Ryan S. Jonnes, Todd A. Rawlinson, Sean C. Kyle, and Darrell L. Apprill. 2016. Evaluating Desired Conditions for Mexican Spotted Owl Nesting and Roosting Habitat. *Forest Science* 62 (4): 457–462. <https://doi.org/10.5849/forsci.15-072>.
- Ganey, Joseph L., Sean C. Kyle, Todd A. Rawlinson, Darrell L. Apprill, and James P. Ward. 2014a. Relative Abundance of Small Mammals in Nest Core Areas and Burned Wintering Areas of Mexican Spotted Owls in the Sacramento Mountains, New Mexico. *Wilson Journal of Ornithology* 126 (1): 47–52. <https://doi.org/10.1676/13-117.1>.
- Ganey, Joseph L., Ho. Y. Wan, Samuel A. Cushman, and Christina D. Vojta. 2017. Conflicting Perspectives on Spotted Owls, Wildfire, and Forest Restoration. *Fire Ecology* 13 (3): 146–165. <https://doi.org/10.4996/fireecology.130318020>.
- Ganey, Joseph L., James P. Ward, Jeffrey S. Jenness, William M. Block, Shaulya Hedwall, Ryan S. Jonnes, Darrell L. Apprill, Todd A. Rawlinson, Sean C. Kyle, and Steven L. Spangle. 2014b. Use of Protected Activity Centers by Mexican Spotted Owls in the Sacramento Mountains, New Mexico. *Journal of Raptor Research* 48 (3): 210–218. <https://doi.org/10.3356/jrr-13-18.1>.
- Ganey, Joseph L., and Scott C. Vojta. 2011. Tree Mortality in Drought-Stressed Mixed-Conifer and Ponderosa Pine Forests, Arizona, USA. *Forest Ecology and Management* 261 (1): 162–168. <https://doi.org/10.1016/j.foreco.2010.09.048>.
- Gutiérrez, R.J., Patricia N. Manley, and Peter A. Stine. 2017. *The California Spotted Owl: Current State of Knowledge*. Gen Tech Rep PSW-GTR-254 Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. <https://doi.org/10.2737/psw-gtr-254>.

- Hanson, Chad T., Monica L. Bond, and Derek E. Lee. 2018. Effects of Post-fire Logging on California Spotted Owl Occupancy. *Nature Conservation*. 24: 93–105. <https://doi.org/10.3897/natureconservation.24.20538>.
- Harvey, Brian J., Daniel C. Donato, William H. Romme, and Monica G. Turner. 2014. Fire Severity and Tree Regeneration Following Bark Beetle Outbreaks: The Role of Outbreak Stage and Burning Conditions. *Ecological Applications* 24 (7): 1608–1625. <https://doi.org/10.1890/13-1851.1>.
- Hessburg, Paul F., Thomas A. Spies, David A. Perry, Carl N. Skinner, Alan H. Taylor, Peter M. Brown, Scott L. Stephens, et al. 2016. Tamm Review: Management of Mixed-Severity Fire Regime Forests in Oregon, Washington, and Northern California. *Forest Ecology and Management* 366: 221–250. <https://doi.org/10.1016/j.foreco.2016.01.034>.
- Holden, Zachary A., Penelope Morgan, and Andrew T. Hudak. 2010. Burn Severity of Areas Reburned by Wildfires in the Gila National Forest, New Mexico, USA. *Fire Ecology* 6 (3): 77–85. <https://doi.org/10.4996/fireecology.0603085>.
- Hurteau, Matthew D., John B. Bradford, Peter Z. Fulé, Alan H. Taylor, and Katherine L. Martin. 2014. Climate Change, Fire Management, and Ecological Services in the Southwestern US. *Forest Ecology and Management* 327: 280–289. <https://doi.org/10.1016/j.foreco.2013.08.007>.
- Jenness, Jeffrey S., Paul Beier, and Joseph L. Ganey. 2004. Associations Between Forest Fire and Mexican Spotted Owls. *Forest Science* 50 (6): 765–772. <https://doi.org/10.1093/forestscience/50.6.765>.
- Jones, Gavin M., H. Anu. Kramer, Shelia A. Whitmore, William J. Berigan, Douglas J. Tempel, Connor M. Wood, Brendan K. Hobart, Tedward Erker, Fidelis A. Atuo, Nicole F. Pietrunti, Rodd Kelsey, R.J. Gutiérrez, and M. Zachariah Peery. 2020. Habitat Selection by Spotted Owls After a Megafire Reflects Their Adaptation to Historical Frequent-Fire Regimes. *Landscape Ecology* 35: 1199–1213. <https://doi.org/10.1007/s10980-020-01010-y>.
- Jones, G.M., H.A. Kramer, W.J. Berigan, S.A. Whitmore, R.J. Gutiérrez, and M.Z. Peery. 2021a. Megafire Causes Persistent Loss of an Old-Forest Species. *Animal Conservation* 24 (6): 925–936. <https://doi.org/10.1111/acv.12697>.
- Jones, Gavin M., Alisa R. Keyser, A. Leroy Westerling, W. Jonathan Baldwin, John J. Keane, Sarah C. Sawyer, John D.J. Clare, R.J. Gutiérrez, and M. Zachariah Peery. 2021b. Forest Restoration Limits Megafires and Supports Species Conservation under Climate Change. *Frontiers in Ecology and the Environment* 20 (4): 210–16. <https://doi.org/10.1002/fee.2450>.
- Jones, Gavin M., Emily K. Vraga, Paul F. Hessburg, Matthew D. Hurteau, Craig D. Allen, Robert E. Keane, Thomas A. Spies, Malcolm P. North, Brandon M. Collins, Mark A. Finney, Jamie M. Lyderson, and A. Leroy Westerling. 2022. Counteracting Wildfire Misinformation. *Frontiers in Ecology and the Environment* 20 (7): 392–393. <https://doi.org/10.1002/fee.2553>.
- Kauffman, Merrill R., Laurie S. Huckaby, Claudia M. Regan, and John Popp. 1998. *Forest Reference Conditions for Ecosystem Management in the Sacramento Mountains, New Mexico*. Gen Tech Rep RMRS-GTR-19 Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Kramer, Anu, Gavin M. Jones, Sheila A. Whitmore, John J. Keane, Fidelis A. Atuo, Brian P. Dotts, Sarah C. Sawyer, Sarah L. Stock, R.J. Gutiérrez, and M. Zachariah Peery. 2021. California Spotted Owl Habitat Selection in a Fire-Managed Landscape Suggests Conservation Benefit of Restoring Historical Fire Regimes. *Forest Ecology and Management* 479: 118576. <https://doi.org/10.1016/j.foreco.2020.118576>.
- Lommler, Michael A. 2019. Mexican Spotted Owl Breeding Population, Site Occupancy, and Habitat Selection 13–15 Years After the Rodeo-Chediski Fire in East-Central Arizona. *Doctoral Dissertation, Northern Arizona University*.
- Martínez Arbizu, Pedro. 2017. PairwiseAdonis: Pairwise Multilevel Comparison Using Adonis. *R package version 0.0*.
- Meddens, Arjan J.H., Crystal A. Kolden, James A. Lutz, Alistair M.S., Smith, C. Alina Cansler, John T. Abatzoglou, Garrett W. Meigs, William M. Downing, and Meg A. Krawchuk. 2018. Fire Refugia: What Are They, and Why Do They Matter for Global Change? *BioScience* 68 (12): 944–954. <https://doi.org/10.1093/biosci/biy103>.
- Monitoring Trends in Burn Severity [MTBS]. 2019. MTBS Project Homepage, USDA Forest Service/U.S. Geological Survey. Available online: <http://mtbs.gov/>. Accessed October 2019.
- National Wildfire Coordinating Group [NWCG]. 2020. Available online: <https://www.nwcg.gov/>. Accessed March 2020.
- Odion, Dennis C., Chad T. Hanson, André Arsenault, William L. Baker, Dominick A. DellaSala, Richard L. Hutto, Walt Klenner, et al. 2014. Examining Historical and Current Mixed-Severity Fire Regimes in Ponderosa Pine and Mixed-Conifer Forests of Western North America. *PLoS ONE* 9 (2): 87852. <https://doi.org/10.1371/journal.pone.0087852>.
- Oksanen, Jari, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGinn, Peter R. Minchin, et al. 2020. *Vegan: Community Ecology Package*. <https://cran.r-project.org/package=vegan>. Accessed January 2021.
- Peery, M. Zachariah., Gavin M. Jones, R.J. Gutierrez, Steve M. Redpath, Alan B. Franklin, Daniel Simberloff, et al. 2019. The Conundrum of Agenda-Driven Science in Conservation. *Frontiers in Ecology and the Environment* 17 (2): 80–82. <https://doi.org/10.1002/fee.2006>.
- Pollet, Jolie, and Philip N. Omi. 2002. Effect of Thinning and Prescribed Burning on Crown Fire Severity in Ponderosa Pine Forests. *International Journal of Wildland Fire* 11 (1): 1–10.
- R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna. <https://www.r-project.org/>. Accessed October 2020.
- Reynolds, Richard T., Andrew J. Sánchez-Meador, James A. Youtz, Tessa Nicolet, Megan S. Matonis, Patrick L. Jackson, Donald G. DeLorenzo, and Andrew D. Graves. Restoring Composition and Structure in Southwestern Frequent-Fire Forests: A Science-Based Framework for Improving Ecosystem Resiliency. 2013. *Gen. Tech. Rep. RMRS-GTR-310*. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 76 p. <https://doi.org/10.2737/RMRS-GTR-310>.
- Ronco, Frank Jr., Gerald J. Gottfried, and Richard Shaffer. 1983. Southwestern Mixed Conifers. In *Silvicultural Systems for the Major Forest Types of the United States*. U.S. Department of Agriculture, Forest Service. 445: 73–76.
- Seamans, Mark E., and R.J. Gutierrez. 1995. Breeding Habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. *Condor* 97 (4): 944–952. <https://doi.org/10.2307/1369533>.
- Simberloff, Daniel. 1987. The Spotted Owl Fracas: Mixing Academic, Applied, and Political Ecology. *Ecology* 68 (4): 766–772. <https://doi.org/10.2307/1938346>.
- Singleton, Megan P., Andrea E. Thode, Andrew J. Sánchez-Meador, and Jose M. Iniguez. 2019. Increasing Trends in High-Severity Fire in the Southwestern USA from 1984 to 2015. *Forest Ecology and Management* 433: 709–19. <https://doi.org/10.1016/j.foreco.2018.11.039>.
- Smith, Alistair M. S., Crystal A. Kolden, and David M. J. S. Bowman. 2018. Biomimicry Can Help Humans to Coexist Sustainably with Fire. *Nature Ecology and Evolution* 2 (12): 1827–1829. <https://doi.org/10.1038/s41559-018-0712-2>.
- Stevens, Jens T., Collin M. Haffey, Jonathan D. Coop, Paula J. Fornwalt, Larissa Yocom, Craig D. Allen, Anne Bradley, et al. 2021. Tamm Review: Postfire Landscape Management in Frequent-Fire Conifer Forests of the Southwestern United States. *Forest Ecology and Management* 502: 119678.
- Stevens-Rumann, Camille S., Susan J. Prichard, Eva K. Strand, and Penelope Morgan. 2016. Prior Wildfires Influence Burn Severity of Subsequent Large Fires. *Canadian Journal of Forest Research* 46 (11): 1375–1385. <https://doi.org/10.1139/cjfr-2016-0185>.
- Stokes, Marvin A., and Terah L. Smiley. 1968. *Introduction to Tree-Ring Dating*. Chicago: University of Chicago Press.
- Swetnam, Thomas W., and Christopher H. Baisan. 1994. Historical Fire Regime Patterns in the Southwestern United States since AD 1700. In *Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium*. Los Alamos, NM: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station, 286: 11–32.
- Syphard, Alexandra D., and Jon E. Keeley. 2016. Historical Reconstructions of California Wildfires Vary by Data Source. *International Journal of Wildland Fire* 25: 1221–1227. <https://doi.org/10.1071/WF16050>.
- U.S.D.A. Forest Service. n.d. Fact Sheet and Information for Timber & Thinning Activities. Available online: <https://www.fs.usda.gov/detail/lincoln/home?cid=STELPRDB5327955>. Accessed September 2022.
- U.S.D.A. Forest Service. 2020. Resolution on Mexican Spotted Owl Litigation Moves Forest Restoration Forward. Available Online: <https://www.fs.usda.gov/detail/r3/home?cid=FSEPRD666433>. Accessed September 2022.
- U.S. Fish and Wildlife Service. 1995. *Recovery Plan for the Mexican Spotted Owl*. U.S. Fish and Wildlife Service, Albuquerque, NM, USA.
- U.S. Fish and Wildlife Service. 2012. *Final Recovery Plan for the Mexican Spotted Owl (Strix occidentalis lucida), first revision*. U.S. Fish and Wildlife Service, Albuquerque, NM, USA.
- Wan, Ho. Y., Kevin McGarigal, Joseph L. Ganey, Valentin Lauret, Brad C. Timm, and Samuel A. Cushman. 2017. Meta-replication Reveals Nonstationarity

- in Multi-scale Habitat Selection of Mexican Spotted Owl. *The Condor* 119 (4): 641–658. <https://doi.org/10.1650/CONDOR-17-32.1>.
- Wan, Ho Y., Samuel A. Cushman, and Joseph L. Ganey. 2018. Habitat Fragmentation Reduces Genetic Diversity and Connectivity of the Mexican Spotted Owl: A Simulation Study Using Empirical Resistance Models. *Genes* 6 (8): 403. <https://doi.org/10.3390/genes9080403>.
- Wan, Ho Y., Samuel A. Cushman, and Joseph L. Ganey. 2019. Recent and Projected Future Wildfire Trends Across the Ranges of Three Spotted Owl Subspecies Under Climate Change. *Frontiers in Ecology and Evolution* 7: 37. <https://doi.org/10.3389/fevo.2019.00037>.
- Wan, Ho Y., Samuel A. Cushman, and Joseph A. Ganey. 2020. The Effect of Scale in Quantifying Fire Impacts on Species Habitats. *Fire Ecology* 16:9. <https://doi.org/10.1186/s42408-020-0068-2>.
- Westerling, Anthony L., Hugo G. Hidalgo, Daniel R. Cayan, and Thomas W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313 (5789): 940–943. <https://doi.org/10.1126/science.1128834>.
- Western Regional Climate Center. 2021. Available online: <https://wrcc.dri.edu/>. Accessed April 2021.
- WildEarth Guardians, Plaintiff, v. United States Fish and Wildlife Service, et al. n.d. Defendants. No. CV-13–00151-TUC-RCC. United States District Court. (District of Arizona 2019).

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article

Submit your next manuscript at ► [springeropen.com](https://www.springeropen.com)