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Fire Ecology

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Fire gives avian populations a rapid and enduring boost in protected forests of California

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Abstract

Background Fire can impact ecosystems and species over both short and long timeframes, resulting in pervasive impacts on the structure of avian communities. While recent research has highlighted the strong impact of fire on bird communities in the short term, there remains a need for understanding long-term population processes following fire, particularly in forested landscapes that are burning more frequently than in the past century. We analyzed avian response to fire using point-count data from 1999–2019 within national parks of the Sierra Nevada Inventory & Monitoring Network, combined with high-resolution estimates of burn severity from fires that burned up to 35 years prior to each count. We used a hierarchical Bayesian framework to account for imperfect detection of birds while estimating the potentially divergent effects of fire on population density over time for each of 42 species. Our models integrated time-varying data on habitat characteristics that would otherwise be confounded with fire history, such as canopy cover and height.

Results In aggregate, bird population density increased rapidly after fire and remained higher in burned areas for at least 35 years relative to unburned areas. Moderate-severity burns typically resulted in more immediate and enduring positive effects than burns of lower severity. Of 42 bird species analyzed, only 13 showed little response to fire, eight responded positively for less than 20 years, 10 showed responses (nine positive) persisting longer than 20 years, and 11 showed positive responses with little or no sign of attenuation even 35 years after a fire. Responses did not align with broad migratory, nesting or foraging traits.

Conclusions A wide variety of birds appeared to benefit—immediately or eventually—from burns at bird point-count stations in two fire-prone parks of the Sierra Nevada. These results offer a rare perspective on long-term avian response to fire and postfire successional processes, in some of the few western forests where effects of fire are relatively unconfounded by anthropogenic habitat loss and resource extraction.

Keywords Fire ecology, Landbirds, Inventory and monitoring, Protected lands, Fire regime, Burn severity, Fire management, Species-specific response to fire, National parks

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Resumen

Antecedentes El fuego puede impactar los ecosistemas y especies tanto en el corto como en el largo plazo, lo que resulta en impactos diversos en la estructura de las comunidades de aves. Mientras que trabajos de investigación recientes han subrayado el fuerte impacto del fuego en comunidades aviares en el corto plazo, permanecen aún no bien comprendidos los procesos que ocurren en estas poblaciones en el largo plazo luego de un fuego, particularmente en ambientes forestales que se están quemando ahora más frecuentemente que en el siglo pasado. Analizamos la respuesta de comunidades aviares al fuego usando datos de puntos de conteo desde 1999 a 2019 dentro de los Parques Nacionales de la red de monitoreo e inventario de la Sierra Nevada, combinado con estimaciones de alta resolución de severidades del fuego en áreas que se quemaros hasta 35 años antes de cada conteo. Usamos un marco de trabajo Bayesiano Jerárquico para detectar las imperfecciones en el conteo mientras que estimamos los efectos potencialmente divergentes del fuego sobre las densidades de las poblaciones en el tiempo para cada una de las 42 especies detectadas. Nuestros modelos integraron datos tiempo-variable sobre características del hábitat, que de otra manera hubiesen sido confundidos con la historia del fuego, como la cobertura y altura del dosel.

Resultados En conjunto, la densidad de las poblaciones de aves se incrementó rápidamente luego de/los fuegos, y permaneció alta por al menos 35 años en relación con áreas no quemadas. Los fuegos que quemaron a moderada severidad resultaron típicamente en efectos positivos más inmediatos y perdurables que los que quemaron a baja severidad. De las 42 especies analizadas, solo 13 mostraron un pequeña respuesta al fuego, ocho respondieron positivamente en menos de 20 años, y 11 mostraron respuestas positivas con muy pocas o sin signos de atenuación aún 35 años después del fuego. Las respuestas no se alinearon con características migratorias, de anidamiento o de forrajeo.

Conclusiones Una amplia variedad de aves parecen beneficiarse – inmediatamente o eventualmente — de los fuegos en las estaciones de conteo en dos parques propensos al fuego de la Sierra Nevada de los EEUU. Estos resultados ofrecen una perspectiva rara sobre la respuesta de comunidades de aves en el largo plazo y los procesos sucesionales post-fuego, en algunos de los bosques del oeste de los EEUU, donde los efectos del fuego son asociados mayoritariamente a la pérdida de hábitat por el hombre y por la extracción de los recursos.

Background

Fire plays a central role in shaping many terrestrial ecosystems (Bowman et al. 2009; McLauchlan et al. 2020; He et al. 2019; Santos et al. 2023) and structuring communities of animal species (Gonzales et al. 2022), including birds (Bowman et al. 2009). Understanding how wildlife populations respond to different kinds of fire is fundamental to habitat management and species conservation, particularly in an era when fire regimes are changing rapidly (Hoecker et al. 2023; Sayedi et al. 2024). Studies of bird population responses during the early years after fire (typically a decade or less; e.g., Fontaine and Kennedy 2012; Tingley et al. 2016) have revealed how species and entire communities respond to variation in fire severity and other fire characteristics that shape ecosystems soon after fire. However, studies of population and community responses to fire over multi-decadal time frames are rare and urgently needed to provide a longer-term perspective on fire- and species-management strategies (Watson et al. 2012).

California's Sierra Nevada is a fire-prone ecosystem (Wright and Heinselman 1973 (reprinted 2014)) where, prior to Euromerican settlement, forests were characterized by frequent low- and mixed-severity fire, often managed by Indigenous people (Taylor et al. 2016; Knight et al. 2022), that tended to maintain relatively open understories with forests dominated by large, old trees (Hessburg et al. 2005). However, fire regimes changed dramatically by 1870, after the loss of Indigenous management practices and with the introduction of livestock grazing that altered available fuels (Kilgore and Taylor 1979; Caprio and Swetnam 1995). During the subsequent era of fire suppression, fire-return intervals increased greatly, often yielding forest stands with uncharacteristically dense understories comprised predominantly of smaller trees, and substantial shifts in tree species composition in favor of shade-tolerant species (Hessburg et al. 2005). More recently, the combination of these and other shifts in vegetation structure (Parks et al. 2018a) with more frequent accidental anthropogenic ignitions (Balch et al. 2017) and a warming climate (Collins 2014; Abatzoglou and Park Williams 2016; Zhuang et al. 2021) are yielding more frequent, extensive, and severe fires throughout the Sierra Nevada and much of western North America (Parks and Abatzoglou 2020; MacDonald et al. 2023).

Fire regime (Gill and Allan 2008) – the general pattern of fire characteristics like fire severity and extent, combined with the history of fire occurrence over time across a geographic area of interest – is known to have profound consequences for the diversity (Arrogante-Funes et al. 2024; Tingley et al. 2016), abundance (Smucker

et al. 2005; García-Redondo et al. 2023), and distribution (Reside et al. 2012) of bird species. Understanding the full implications of a changing fire regime on bird populations in forests of western North America requires a better understanding of how most bird species respond to fire (Brunk et al. 2023). Evidence has accumulated in recent decades that fire plays an important role in creating, maintaining, or enhancing habitat for many species throughout the region (Hanson and North 2008; Taillie et al. 2018; Tingley et al. 2016), creating 'winners' as well as 'losers' within the post-fire bird community (Jager et al. 2021; Brunk et al. 2023). Some habitat specialist species rely preferentially on early post-fire vegetation conditions (Smucker et al. 2005; Hutto 2008; Saracco et al. 2011), but it is becoming increasingly clear that the benefits of fire to birds in western North America extend much more broadly than to just the relatively small number of species considered postfire specialists. Many habitat generalists commonly use recently burned areas (Kirkpatrick et al. 2006; Hutto 1995; Tingley et al. 2016; Taillie et al. 2018), and even some bird species generally thought of as late-seral specialists may thrive after fires, depending on fire characteristics and effects on the local landscape (Lee 2018; Siegel et al. 2019; Schofield et al. 2020; Kramer et al. 2021).

However, the influence of fire and fire regime on bird communities in these fire-prone environments is much more complex than merely the creation of early post-fire habitats. Prior research (e.g., Smucker et al. 2005; Latif et al. 2016; Tingley et al. 2016; Taillie et al. 2018) has made substantial progress elucidating which bird species in western North American forests respond positively or negatively to the immediate effects of fire – like snag creation and understory clearing – but the effects of longer-term, often multi-decadal post-fire processes like deterioration of snags and development of post-fire shrub communities, and how those processes may vary with fire severity, remain poorly studied for most bird species.

Fire initiates dynamic ecological processes, influencing vegetation structure and composition at multiple temporal and spatial scales across the landscape (van Wagtendonk and Fites-Kaufman 2006; Webster and Halpern 2010; Kane et al. 2014). Effects of individual fires on forest structure and composition can persist for many decades or longer, and even relatively subtle differences in forest structure and composition may have profound effects on bird community composition (Siegel and DeSante 2003; Bitani et al. 2023), like the sharp decline in correlation between canopy cover and species diversity—over very small changes in canopy cover—observed by Gil-Tena et al. (2007). Longer-term fire history is therefore likely to be an important factor governing bird distribution and abundance in Sierra Nevada forests – even in mid-seral stands that may not readily be thought of as 'post-fire' habitats.

In the Sierra Nevada, a small number of relatively long-term data sets on bird populations have been leveraged to assess avian responses to fire over more than a decade (Raphael et al. 1987, 2018; Taillie et al. 2018; Steel et al. 2022; Brunk et al. 2023). These studies generally indicate complex, non-linear relationships between bird abundance, fire severity, and time since fire, which is consistent with findings from elsewhere in western North American forests (Hutto and Patterson 2016; Fontaine et al. 2009), though more information is badly needed to support both forest management and bird conservation efforts (Huff et al. 2005; Brunk et al. 2023). An important constraint on recent information from this region is that much of it derives from studies of birds in 'working forests' (Wolf and Klein 2007) that are subject to various forms of resource extraction and relatively intensive ecosystem management, particularly in the aftermath of fire. Salvage logging or other post-fire forest management interventions may be a confounding factor in assessing bird population responses to fire (Hanson et al. 2021). In contrast, U.S. National Parks are well-suited to serve as natural laboratories for studying long-term ecological processes (Silsbee and Peterson 1991; Simons et al. 1999; Siegel et al. 2012), because they are largely devoid of post-fire timber harvest or other confounding forest management interventions. Additionally, through the U.S. National Park Service's Inventory and Monitoring Division, bird populations and other resources in many national parks have been systematically monitored for many years, often using sophisticated, spatially extensive sampling designs that track park populations of many species simultaneously (Sauvajot 2016).

Given the need for analysis of avian population response to fire in the Sierra Nevada, the primary objective of this study was to assess the role of multi-decadal fire history in regulating the local density of individual bird species during the breeding season using Inventory and Monitoring data from this region. Our approach leveraged hierarchical Bayesian models to account for imperfect detection of individuals while modeling the spatially and temporally explicit density of each population as a response to up to 35 years of previous fire history. In addition to fire history, our models accounted for expected fire return interval, physiographic variables, and time-varying habitat characteristics that would otherwise be confounded with fire history, such as canopy cover and height. We expected to identify species whose populations increase or decrease after fire (or after some level of burn severity) as well as those with more nuanced

responses that vary in magnitude and perhaps even direction with time since fire. By revealing how bird populations respond to fire over several decades, these analyses could 1) elucidate longer-term ecological processes that occur in the absence of intensive postfire management interventions, and 2) facilitate better predictions of the effects of fire management policies and actions across the Sierra Nevada and perhaps in similar habitats elsewhere.

Methods

Study areas

We studied two national park units in the Sierra Nevada of California: Sequoia and Kings Canyon National Parks (SEKI—two parks managed as one unit) and Yosemite National Park (YOSE). These large and topographically rugged parks encompass 657,851 ha (SEKI = 350,444 ha, YOSE = 307,407 ha) of the southern and central Sierra Nevada, respectively (Fig. 1). The climate in this region is Mediterranean and includes cool, moist winters and warm summers with only sporadic rainfall. Summer precipitation is associated mainly with thunderstorms at higher elevations. Vegetation across these parks includes annual grasslands, chaparral shrublands, and evergreen woodlands at lower elevations; moist meadows, montane chaparral, mixed conifer forest and groves of giant sequoia at middle elevations; and subalpine forests, alpine and barren areas at higher elevations (Caprio et al. 2002, van Wagtendonk et al. 2020). Both historical and pre-historic fires occurred primarily during the late summer and early fall, and both were more common at lower than higher elevations (Caprio and Swetnam 1995).

We focus here on the effects of burn severity and years since fire in the vicinity of bird point-count stations throughout these parks. Fires occurring between 1984 and 2018 were used to explain the local density of a wide variety of breeding bird species subject to inventory and monitoring in these parks between 1999 and 2019.

Site selection

Survey sites for this study (Fig. 1) derive from breeding-season point counts conducted during a one-time avian inventory (AI) completed during 1999–2004, followed by annual avian monitoring (AM) conducted during 2011–2019. AM surveys were established as part of the National Park Service Inventory & Monitoring Program, using methods detailed in Siegel et al. (2010), which were largely based on methods developed for the AI (Siegel and DeSante 2002; Siegel and Wilkerson 2005).

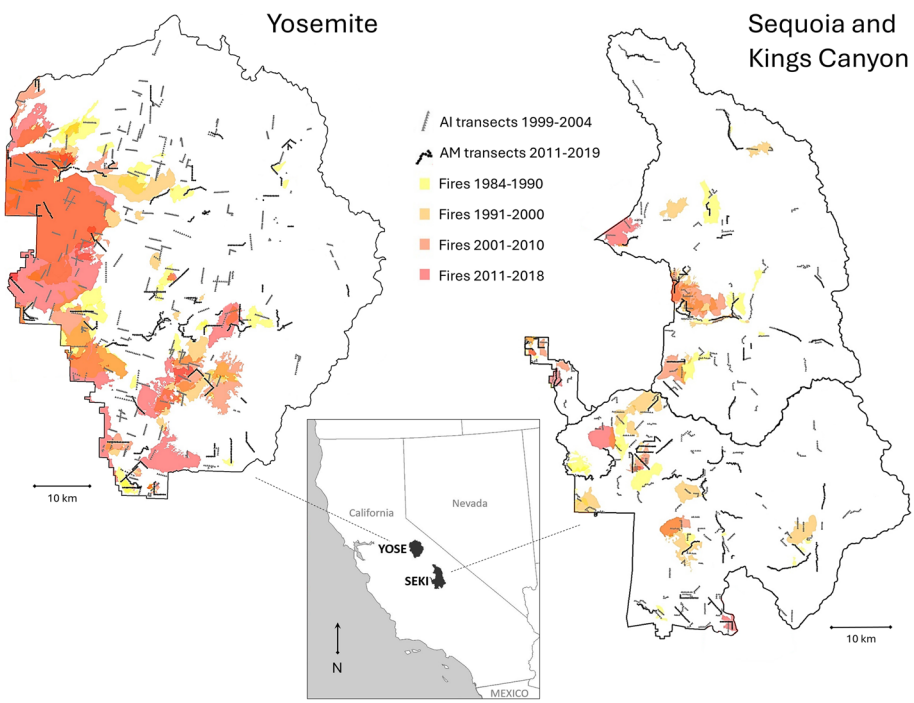


Fig. 1 Fires and bird point-count transects providing data for this study of Yosemite National Park (YOSE) and Sequoia & Kings Canyon National Parks (SEKI), California, USA. Each point-count station along a transect was surveyed once during an avian inventory (AI, gray transects) or repeatedly during a period of avian monitoring (AM, black transects). These maps depict all known fires that burned > 40 ha after 1983 and intersected at least one AI or AM transect. Stations above 2750 m in YOSE and 3000 m in SEKI are not shown and were not included in this analysis due to the rarity of fires at high elevation

The 1999–2004 AI included single surveys of 4138 point-count stations arranged in 496 transects, while the 2011–2019 AM period included repeated surveys of 2428 stations arranged in 148 transects (Fig. 1). AM transects were grouped into five panels, including one panel visited once per year and four panels visited once every five years on a rotating schedule. AI station selection began with a sampling frame that included all areas within 2 km of roads and trails (83% of YOSE and 71% of SEKI). Within this frame, 20 transect origins were selected at random within each of 28 habitat types. Transects were thinned as needed to achieve spacing of at least 3 km, resulting in the retention of 3–18 transects per habitat type. Transects were then added to improve sampling of meadows ($n=46$), human activity centers ($n=14$) and low-elevation riparian areas ($n=4$). The AM sampling frame included all areas within 1.625 km of trails as detailed in Ray et al. (2022). Potential transect origins were identified as a set of points spaced every 50 m along these maintained routes. From these points, a spatially dispersed sample of transect origins was selected for each park using the Generalized Random-Tessellation Stratified (GRTS) sampling method (Stevens and Olsen 2004). To ensure adequate sampling across elevations, transects were distributed across three elevational strata, defined as low-elevation (< 1600 m above sea level in SEKI, < 1800 m in YOSE), medium-elevation (1600–3000 m in SEKI, 1800–2750 in YOSE) and high-elevation (> 3000 m in SEKI, > 2750 in YOSE), to correspond broadly with foothill, montane, and alpine/subalpine habitats, respectively. Point-count stations along each transect were separated by approximately 250 m. Stations above 2750 m in YOSE and 3000 m in SEKI were excluded from the present analysis (Fig. 1). The number of stations along each transect (mean ± SD = 11.64 ± 4.23) varied by year according to field conditions and logistics.

Bird counts

Point-count surveys were conducted during the breeding season (approximately May 20-July 22) by observers trained and tested in the focal parks. Transects at lower elevations were targeted for survey earlier in the season, to track peak breeding season by elevation. During each count, we recorded all bird species heard or seen within a timed survey, along with the time- and distance-to-detection of each bird, enabling analyses that account for birds present but undetected (Royle et al. 2005; Alldredge et al. 2007; Amundson et al. 2014). Potential covariates of detection recorded during surveys included observer, time of day, day of year, ambient noise level and group size (number of birds acting as a unit or flock; usually one bird). All species detected in these surveys were considered for inclusion in this analysis, regardless of presumed relationships with fire. Species were selected for analysis based on whether they met model data requirements and assumptions. Flocking species were excluded because they did not meet the assumption of independent detections, and species detected fewer than 300 times generally did not provide the sample sizes needed for convergence of parameter estimates in our models.

Covariates

We focused on local effects of fire and habitat structure by summarizing covariates within 125 m of each bird point-count station, which represents the mid-point distance between stations and encompasses the maximum detection radius of many bird species in these parks (Ray et al. 2022). Hereafter, 'station' refers to an area of radius 125 m around a point-count station. Covariates considered in this analysis (Table 1) were summarized at the station level using data sources with 30-m resolution, and dynamic covariates were updated annually.

Dynamic covariates (Fig. 2) included two applicable to burned stations (years since fire and burn severity) and two applicable to all stations (forest canopy cover and stand height). Years since fire (YSF) was calculated directly from date-specific fire boundaries available for each park (Folger 2019; van Wagtendonk 2020) as the number of winters since the end of the most recent fire overlapping the station. Only fires that burned > 40 ha after 1983 were used in calculations of YSF and burn severity, because smaller fires rarely intersected our stations and because imagery used to estimate burn severity became available in 1984. By truncating YSF at 1984, we were able to test for effects of its interaction with burn severity in the unified model described below.

Following Parks et al. (2018b, 2021), we used Landsat imagery and Google Earth Engine to characterize burn severity at 30-m resolution within fires that overlapped a station in any year between 1984 and a bird count. This approach allows mean compositing of reflectance from time points before and after a fire, including at least one complete growing season. For a fire in year t, compositing was based on images drawn from the snow-free season in years t-1 and t + 1. Burn severity in each 30-m cell was ranked according to the Relative differenced Normalized Burn Ratio (RdNBR; Miller and Thode 2007), and averaged across the station. Number of fires overlapping a station was considered in preliminary analyses but was not supported as a dynamic predictor of population density.

Forest structure was assumed to affect both individual detection and population density. The Gradient Nearest Neighbor forest structure dataset (LEMMA Lab, Oregon State University, Corvallis, Oregon, USA; lemma.forestry.oregonstate.edu) provided annual canopy cover

Table 1 Covariates considered in models of the observation (Obs) or population (Pop) process when estimating bird population density from point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

Covariate	Definition – at the scale of a bird point-count station	Process
Burn severity	Mean[1] burn ratio[2] based on pre- and post-fire image composites	Pop
Years since fire	Mean number of winters (1–35) since the last burn of any severity	Pop
Fire return interval	Mean expected number of years (2–131) between burns of any severity	Pop
Stand height	Mean height (m) of the forest canopy	Pop
Canopy cover	Residual of a mean canopy cover (%) regression on stand height	Pop
Day of year	Ordinal day of the bird count (140–203 = May 20-July 22)	Obs
Hour of day	Beginning time of the bird count in hours after midnight (5–9)	Obs
Noise	Ambient noise level during the count, coded as low (1–3) or high (4–5)	Obs
Cover count	Number of 30-m cells with forest cover > 40%	Obs

[1] Covariates defined as "mean" values were calculated at the scale of a bird point-count station by averaging values across all 30-m cells within 125 m of station coordinates

[2] Relative differenced Normalized Burn Ratio (RdNBR)

and stand height estimates (Ohmann and Gregory 2002) from 1999 to 2017 for both parks at 30-m resolution. We calculated annual means for cover and height across each station, using values from year 2017 to approximate missing values in years 2018–2019 (Fig. 2). Based on observer experiences in these parks, we assumed a threshold effect of ≥ 40% canopy cover reduced our perception of birds. To characterize this effect at each station, we counted the number of cells with ≥ 40% canopy cover to use as a 'cover count' in models of the observation process.

Static covariates considered in this analysis were latitude at the station center, elevation averaged across the station, and a metric of fire return interval (FRI). In combination with forest structure, these covariates were included to help account for biophysical conditions that might alter or enhance effects of fire history on population density. FRI was based on LANDFIRE 2020 estimates that infer 'reference conditions' regarding vegetation structure given biophysical properties of the landscape and the presumed disturbance regime prior to Euromerican settlement (LANDFIRE 2020). We averaged values of the LANDFIRE (2020) FRI_ALLFIR attribute across all 30-m cells within each station as an estimate of mean FRI based on all fires, regardless of burn severity. Longitude, slope, and aspect were not explanatory in preliminary analyses (Ray et al. 2022) and were not considered here.

Correlation among covariates was low (Pearson's correlation coefficient < 0.34) after replacing canopy cover with the residual of a linear regression of canopy cover on stand height (Graham 2003). Each covariate was standardized by subtracting its mean and dividing by its standard deviation. Two covariates with strong right skew (burn severity and FRI) were log-transformed prior to analyses.

Analysis

We derived population density for each of 42 species using a single-species hierarchical model that estimated abundance as a response to burn metrics, fire timing and landscape features while accounting for imperfect detection (Amundson et al. 2014). As detailed in Ray et al. (2017a), this model involves one level at which the count of birds (y) is influenced by components of detection probability, including the probability that a given bird is available for detection (p_a) and the probability that birds available for detection are detected (p_d). We modeled effects of count timing (day of year and hour of day) on p_a through their effects on q, the per-minute probability of availability, and we modeled effects of noise and observer on p_d through their effects on σ, the scale parameter of a half-normal distribution describing the effect of distance on species perceptibility. These models of p_a and p_d were combined with a model of population size, N, in an N-mixture model of the count y. N-mixture models typically embed a Poisson model of λ (expected N) in a binomial model of y, providing a hierarchical extension of generalized linear models to allow for structure in parameters at each hierarchical level (Royle et al. 2005). We followed Amundson et al. (2014) by linking a Poisson model of λ as a function of environmental covariates with two nested binomial models expressing detection as functions of distance and time, as $y_{st} \sim \text{binomial}(p_{d,st}, n_{a,st})$, $n_{a,st} \sim \text{binomial}(p_{a,st}, N_{st})$, and $N_{st} \sim \text{Poisson}(\lambda_{st})$. The Poisson model of λ was expanded to incorporate metrics of fire history as well as habitat features commonly affected by fire history, such as site-specific

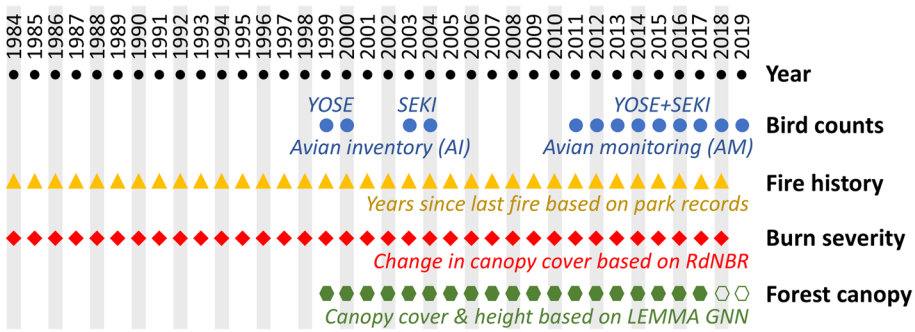


Fig. 2 Time-varying data included in analyses of bird population density in Yosemite (YOSE) and Sequoia & Kings Canyon (SEKI) national parks, California, USA. Open symbols indicate data estimated from the most recent year available. Bird abundance was assumed to lag fire variables by one year

canopy cover and height, to test the role of fire history in determining the pattern of local densities of common bird species while accounting for other habitat characteristics.

The full model included parameters affecting bird availability ($p_a = f(q)$), detection ($p_d = f(\sigma)$) and abundance ($N = f(\lambda)$), with random effects of observer, year and station-within-transect. We used an indicator variable ($\gamma = 0/1$ for burned/unburned) to allow estimation of fire effects for burned stations, as

$$logit(q_{st}) = a_0 + a_D \times DayOfYear_{st} + a_{D^2} \times DayOfYear_{st}^2 + a_H \times HourOfDay_{st} + a_{H^2} \times HourOfDay_{st}^2 \quad (1)$$

$$log(\sigma_{st}) = log(\sigma_0) + b_N \times Noise_{st} + b_C \times CoverCount_{st} + Observer_{st} \quad (2)$$

$$log(\lambda_{st}) = \beta_0 + \beta_H \times StandHeight_{st} + \beta_{H^2} \times StandHeight_{st}^2 + \beta_C \times CanopyCover_{st} + \beta_{C^2} \times CanopyCover_{st}^2 + \beta_E \times Elevation_s + \beta_{E^2} \times Elevation_s^2 + \beta_F \times FRI_s + \beta_{F^2} \times FRI_s^2 + \beta_L \times Latitude_s + \gamma\left(\beta_\gamma + \beta_Y \times YSF_{st} + \beta_{Y^2} \times YSF_{st}^2 + \beta_{YS} \times YSF_{st} \times BurnSeverity_{st} + \beta_S \times BurnSeverity_{st} + \beta_{S^2} \times BurnSeverity_{st}^2\right) + StationInTransect_s + Year_t \quad (3)$$

where lower-case subscripts s and t indicate station and year, while upper-case subscripts distinguish the fitted coefficients of covariates in each submodel.

Models were fitted to data within a Bayesian framework using Markov chain Monte Carlo simulation to estimate the posterior mean and 95% credible interval (CRI) for each parameter. If the 95% CRI on the effect (estimated coefficient) of a covariate did not overlap zero, we reported it here as "supported" with high confidence. To generate and summarize MCMC samples, we used the JAGS program (Plummer 2003) called from the R environment for statistical computing (R Core Team 2024). As detailed in previous analyses (Ray et al. 2017a, b; 2020), we specified vague priors on all parameters, including broad uniform priors on variances and zero-centered normal priors on coefficients; model convergence was evaluated with reference to R-hat and visual inspection of MCMC simulation results; and model fit was evaluated using posterior predictive checks. R and JAGS scripts related to this analysis are available at https://github.com/birdpop/firebird.

The mean effect size of each covariate across species was summarized post-hoc by calculating the mean and 95% confidence interval of its posterior point estimate across the separate models for each species. To further summarize mean effects by life-history traits, species were grouped (Table S1) by migratory status (resident or migrant), nesting substrate (ground, shrub, cavity or tree) and predominant diet (omnivory, invertebrates or plants/seeds) using standard sources (Beedy et al. 2013; Wilman et al. 2014; Billerman et al. 2025). Effects of years since fire, burn severity and their interaction were visualized for each species by fitting generalized additive models to posterior estimates of density using the R package mgcv, and applying similar constraints on model flexibility across species (knots = 6 in most cases).

Results

Point-count surveys during the study period (1999–2019) resulted in the detection of 129,761 individual birds representing 159 landbird species, including 110,560 birds (over 85% of all birds counted) representing 42 species that met our statistical criteria for

Table 2 Species commonly detected in avian point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

Common name	Scientific name	Authority (year)	Code	Count[1]
Mountain Quail	*Oreortyx pictus*	Douglas (1829)	MOUQ	3156
Acorn Woodpecker	*Melanerpes formicivorus*	Swainson (1827)	ACWO	572
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Cassin (1852)	WISA	457
Red-breasted Sapsucker	*Sphyrapicus ruber*	Gmelin (1788)	RBSA	478
Hairy Woodpecker	*Dryobates villosus*	Linnaeus (1766)	HAWO	1193
White-headed Woodpecker	*Dryobates albolarvatus*	Cassin (1850)	WHWO	1304
Northern Flicker	*Colaptes auratus*	Linnaeus (1758)	NOFL	1730
Pileated Woodpecker	*Dryocopus pileatus*	Linnaeus (1758)	PIWO	570
Olive-sided Flycatcher	*Contopus cooperi*	Nuttall (1831)	OSFL	1392
Western Wood-Pewee	*Contopus sordidulus*	Sclater (1859)	WEWP	3039
Hammond's Flycatcher	*Empidonax hammondii*	Xántus (1858)	HAFL	629
Dusky Flycatcher	*Empidonax oberholseri*	Phillips (1939)	DUFL	3988
Western Flycatcher	*Empidonax difficilis*	Baird (1858)	WEFL	434
Cassin's Vireo	*Vireo cassinii*	Xántus (1858)	CAVI	1254
Warbling Vireo	*Vireo gilvus*	Vieillot (1808)	WAVI	2210
Steller's Jay	*Cyanocitta stelleri*	Gmelin (1788)	STJA	5954
Mountain Chickadee	*Poecile gambeli*	Ridgway (1886)	MOCH	9414
Golden-crowned Kinglet	*Regulus satrapa*	Lichtenstein (1823)	GCKI	3637
Red-breasted Nuthatch	*Sitta canadensis*	Linnaeus (1766)	RBNU	5609
Brown Creeper	*Certhia americana*	Bonaparte (1838)	BRCR	2786
Northern House Wren	*Troglodytes aedon*	Vieillot (1809)	NHWR	498
Townsend's Solitaire	*Myadestes townsendi*	Audubon (1838)	TOSO	1357
Hermit Thrush	*Catharus guttatus*	Pallas (1811)	HETH	2582
American Robin	*Turdus migratorius*	Linnaeus (1766)	AMRO	3571
Purple Finch	*Haemorhous purpureus*	Gmelin (1789)	PUFI	675
Cassin's Finch	*Haemorhous cassinii*	Baird (1854)	CAFI	3222
Pine Siskin	*Spinus pinus*	Wilson (1810)	PISI	1533
Chipping Sparrow	*Spizella passerina*	Bechstein (1798)	CHSP	646
Fox Sparrow	*Passerella iliaca*	Merrem (1786)	FOSP	4586
Dark-eyed Junco	*Junco hyemalis*	Linnaeus (1758)	DEJU	10,831
Lincoln's Sparrow	*Melospiza lincolnii*	Audubon (1834)	LISP	579
Green-tailed Towhee	*Pipilo chlorurus*	Audubon (1839)	GTTO	1065
Spotted Towhee	*Pipilo maculatus*	Swainson (1827)	SPTO	1969
Nashville Warbler	*Leiothlypis ruficapilla*	Wilson (1811)	NAWA	3771
MacGillivray's Warbler	*Geothlypis tolmiei*	Townsend (1839)	MGWA	2253
Yellow-rumped Warbler	*Setophaga coronata*	Linnaeus (1766)	YRWA	8746
Black-throated Gray Warbler	*Setophaga nigrescens*	Townsend (1837)	BTYW	1003
Hermit Warbler	*Setophaga occidentalis*	Townsend (1837)	HEWA	2559
Wilson's Warbler	*Cardellina pusilla*	Wilson (1811)	WIWA	757
Western Tanager	*Piranga ludoviciana*	Wilson (1811)	WETA	4947
Black-headed Grosbeak	*Pheucticus melanocephalus*	Swainson (1827)	BHGR	2569
Lazuli Bunting	*Passerina amoena*	Say (1822)	LAZB	1035

[1] For each species, total count of individuals detected across all surveys conducted in this study

analysis (Table 2). Estimates of burn severity at point-count stations between 1984 and 2018 spanned nearly the full range of possible severity values (0–1200 according to Parks et al. 2018b, 2021) and were positively related to estimates of standard deviation in burn severity, especially at lower values of burn severity (Fig. S1).

Influences of fire on bird population density

We found abundant evidence that fire had positive effects on bird density during the study period, including a predominance of higher density populations where fires were more recent and burned at higher severity. The relationship between years since fire (YSF in Fig. S2) and population density was clearly negative in seven species (Hairy Woodpecker, Mountain Chickadee, Northern House Wren, Pine Siskin, Chipping Sparrow, Dark-eyed Junco and Lazuli Bunting) and positive in four species (Steller's Jay, Spotted Towhee, Nashville Warbler and Wilson's Warbler). The relationship between burn severity and population density was clearly positive for 10 species (Mountain Quail, Acorn Woodpecker, Red-breasted Sapsucker, Northern Flicker, Western Wood-Pewee, Northern House Wren, Chipping Sparrow, Fox Sparrow, Green-tailed Towhee and MacGillivray's Warbler) and negative for four species (Golden-crowned Kinglet, Yellow-rumped Warbler, Black-throated Gray Warbler and Hermit Warbler). Point estimates for coefficients of burn severity and years since fire were negatively correlated across species (Pearson's $r = 0.41$, $p < 0.01$).

The interaction between years since fire and burn severity (YSF x Severity in Fig. S2) tended to have a positive effect on population density, indicating that the benefits of higher severity fire increased as time passed following a fire. This interaction was significantly positive (time magnified the effect of burn severity) for five species (Olive-sided Flycatcher, Dusky Flycatcher, Warbling Vireo, Mountain Chickadee and Green-tailed Towhee) and significantly negative (time attenuated the effect of burn severity) only for Lazuli Bunting.

Quadratic effects of years since fire on density were rarely supported. Negative quadratic effects, suggesting a peak in density with years since fire, were supported for three species (Acorn Woodpecker, Purple Finch and Wilson's Warbler). Positive quadratic effects, suggesting a trough in density with years since fire, were supported for four species (Mountain Quail, Black-throated Gray Warbler, Black-headed Grosbeak and Lazuli Bunting).

Stations burned at both the lowest and highest severities observed in our study resulted in positive effects on population density for up to 35 years since fire (Fig. 3). Figure 3 (a) depicts the difference (anomaly) in population density between stations that burned at low severity and unburned stations. Because at least half of our point-count stations did not burn during this study, burn-severity quantiles 0–0.5 represented unburned stations, so population densities at stations in burn-severity quantile 0.6–0.7 were used to depict results from low-severity burns. Conversely, densities at stations in burn-severity quantile 0.95–0.975 were used to depict results from some of the highest-severity burns that we observed in this study (Fig. 3 (b)), although the severity of these burns might be considered "moderate" on the scale presented in Parks et al. (2018b, 2021) and in Fig. S1. Population density at stations that experienced low-severity burns—either because little of the station burned or because any extensive burn was of low severity—remained higher than at unburned stations for decades in most cases (Fig. 3 (a)). This pattern was even more striking at stations that burned at high severity, where population density continued to rise at least modestly in some cases for nearly 35 years after fire (Fig. 3 (b)). Note that neither the median of the population density anomaly (heavy solid curve) nor its interquartile range (dashed region) fell below zero (light solid line) for any post-fire interval.

Plots of the interaction between years since fire and burn severity suggested four classes of demographic response to fire: (1) relatively short-term responses that persisted less than 20 years ($n = 8$, all shown in Fig. 4); (2) relatively long-term responses persisting at least 20 years but attenuating by 35 years ($n = 10$, including eight shown in Fig. 5 plus Northern Flicker and Golden-crowned Kinglet); (3) responses with little sign of attenuation for at least 35 years ($n = 11$, including eight shown in Fig. 6 plus Brown Creeper, MacGillivray's Warbler and Nashville Warbler); and (4) little or no apparent response to burns of any severity at any timescale ($n = 13$, including eight shown in Fig. S3). Populations in class (4) included seven species with no significant effects of fire on density (see Williamson's Sapsucker, Pileated Woodpecker, Hammond's Flycatcher, Cassin's Vireo, Townsend's Solitaire, Hermit Thrush and Cassin's Finch in Fig. S2) and six species with significant but ultimately subtle effects of fire on density (see Red-breasted Sapsucker, Hairy Woodpecker, Olive-sided Flycatcher, Purple Finch, Chipping Sparrow and Wilson's Warbler in Fig. S2). The apparent strength of effects in Fig. S2 was not always a good indicator of the apparent relationship between fire metrics and population density. For example, Chipping Sparrow density clearly decreased with years since fire and increased with burn severity (Fig. S2), but estimates of population density appeared similar at burned and unburned stations (Fig. S3) due to other effects in the complex system represented by our model.

Plotting interactions between burn severity and years since fire helped illustrate the variety of potential effects of fire on population density. For example, we found positive quadratic (concave) effects of years since fire on densities of Mountain Quail, Black-throated Gray Warbler, Black-headed Grosbeak and Lazuli Bunting (Fig. S2). Black-throated Gray Warbler and Lazuli Bunting both spiked immediately after a fire, and their concave effects of years since fire indicated their rapid return to pre-burn density (Fig. 4).

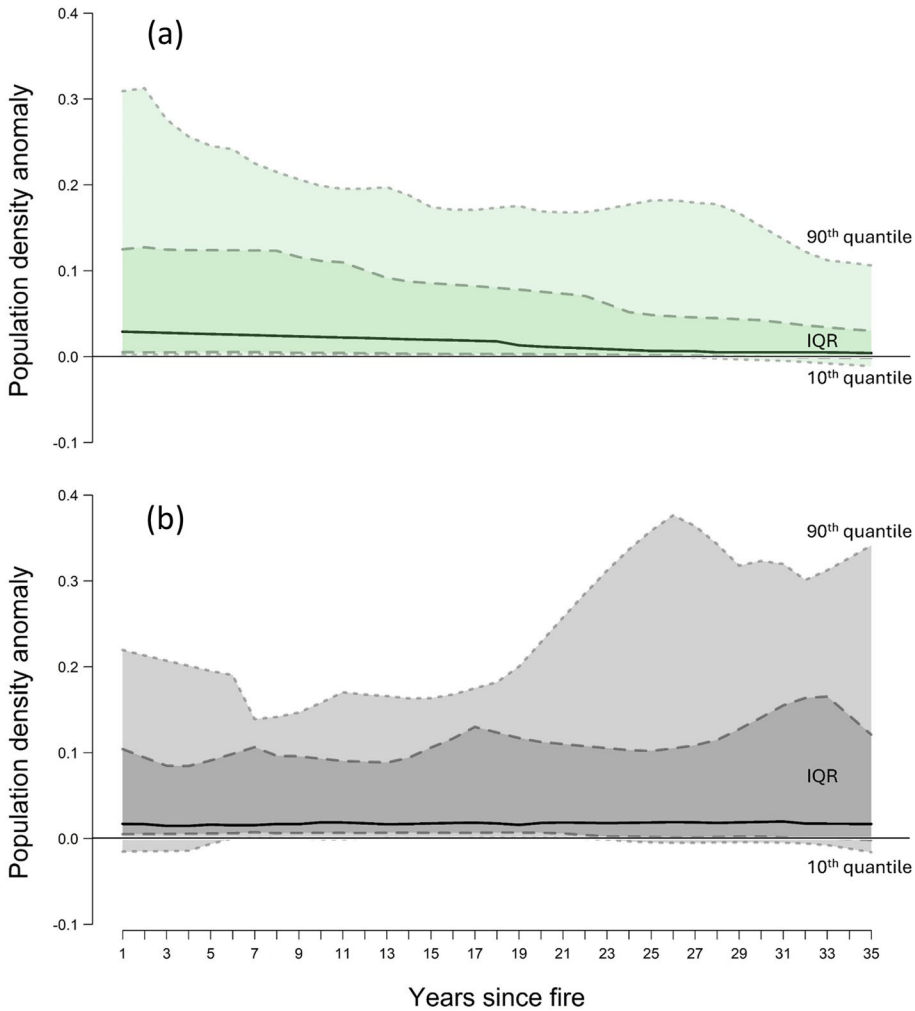
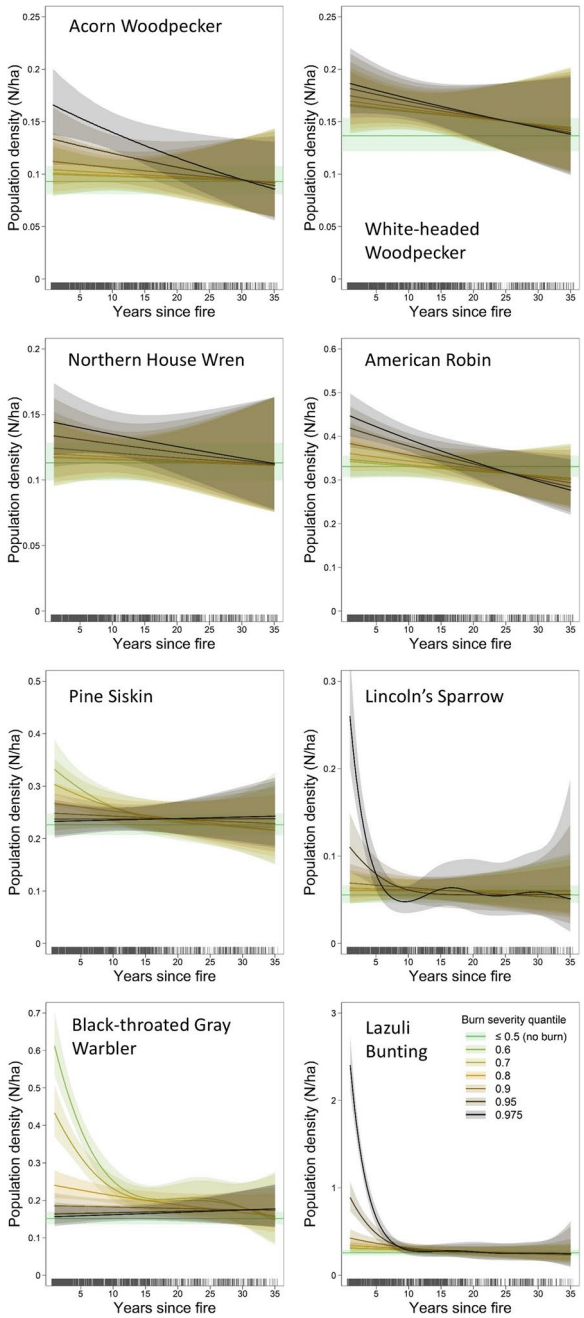


Fig. 3 Anomalies in population density (birds/ha) for each of 42 species at 1–35 years after burns of (**a**) low and (**b**) higher severity. Each panel shows the median (thick solid line) and interquartile range (IQR, dark shaded region), exceeded by the 10th and 90th quantiles of population density relative to density at unburned stations. Outliers (> 1.5 × IQR) were omitted to improve resolution of the IQR, which was mostly positive (above the thin black line of zero anomaly) through all 35 post-fire years, especially at stations in (**b**) where burn severity was higher (quantile 95–97.5 of all burn severities in this study) but also at stations in (**a**) where burn severity was low (quantiles 60–70). All densities were estimated from point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

Conversely, Black-headed Grosbeak was the only species to decline in density immediately after a fire, and its concave effect of years since fire indicated its slow return to pre-burn density (Fig. 5). Mountain Quail density increased immediately after fire but its return to pre-burn density required over 20 years (Fig. 5) and—despite the significant nonlinear effect of YSF apparent in Fig. S2—appeared to decline linearly on average when visualized using additive models with our standard parameterization (knots = 6).

Accounting for non-focal influences on avian density

Stand height and canopy cover effects on population density were commonly significant in our models, with similar numbers of positive and negative effects (Fig. S4). Stand height was particularly explanatory in our analyses, being significantly related to population density for 31 of 42 species, including 18 positive and 13 negative relationships (Fig. S4). Residual canopy cover was also highly explanatory, being significantly related to population density for 20 species, including 10 positive and 10 negative relationships. Although our focus on residual canopy cover eliminated correlation between cover and height, their mean effects were positively correlated across



◀ **Fig. 4** Population density estimates by years since fire and burn severity for eight species with relatively short-term (< 20-year) responses to fire. Each curve represents the fit (mean and 95% confidence interval) of a generalized additive model to posterior density estimates for a population at 1–35 years after burns of the indicated severity. Colors indicate the (relative) average initial burn severity observed at each point-count station, ranging from stations that did not burn (green) to stations that burned most severely (black). Mean population density at unburned stations extends across each panel for ease of comparison with the progression of densities in stations that burned. Densities were estimated from point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

species (Pearson's $r = 0.72$, $p < 0.001$), indicating that populations often responded similarly to both covariates. The one exception to this relationship was the White-headed Woodpecker, which responded positively to stand height and negatively to residual canopy cover (Fig. S4).

In general, the population density of a species at a station was inversely related to the expected length of the fire return interval at that station (FRI in Fig. S4), and a negative effect of FRI was significant for nine species: Dusky Flycatcher, Golden-crowned Kinglet, Fox Sparrow, Green-tailed Towhee, Spotted Towhee, Nashville Warbler, MacGillivray's Warbler, Hermit Warbler and Western Tanager. Warbling Vireo was the only species exhibiting a significant positive effect of FRI on density.

Overall, the covariates with the most consistent effects across species were those related to fire, including expected fire return interval and metrics of years since fire and burn severity (Fig. S5 (a)). Conversely, elevation had strong but divergent effects on density for individual species (Fig. S4), resulting in the weakest apparent effect across species (Fig. S5 (a)). Positive effects of the interaction between burn severity and years since fire were supported only for tree nesters and species that feed on invertebrates (Fig. S5 (c), (d)). Negative effects of the fire return interval were supported for migrant species, tree nesters and both omnivores and species that feed on invertebrates (Fig. S5 (b), (c), (d)). Positive effects of stand height were supported for residents and species that feed on invertebrates (Fig. S5 (b), (d)). Positive effects of elevation were supported for ground nesters and omnivores (Fig. S5 (c), (d)).

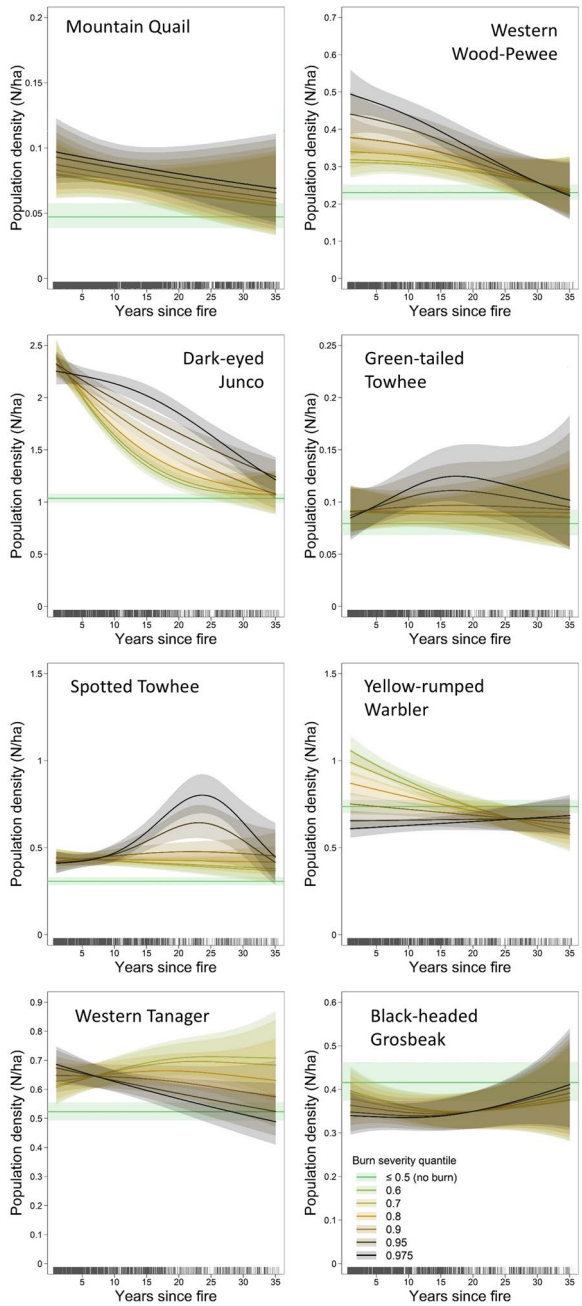


Fig. 5 Population density estimates by years since fire and burn severity for eight species with responses to fire that persisted at least 20 years. Each curve represents the fit (mean and 95% confidence interval) of a generalized additive model to posterior density estimates for a population at 1–35 years after burns of the indicated severity. Colors indicate the (relative) average initial burn severity observed at each point-count station, ranging from stations that did not burn (green) to stations that burned most severely (black). Mean population density at unburned stations extends across each panel for ease of comparison with the progression of densities in stations that burned. Densities were estimated from point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

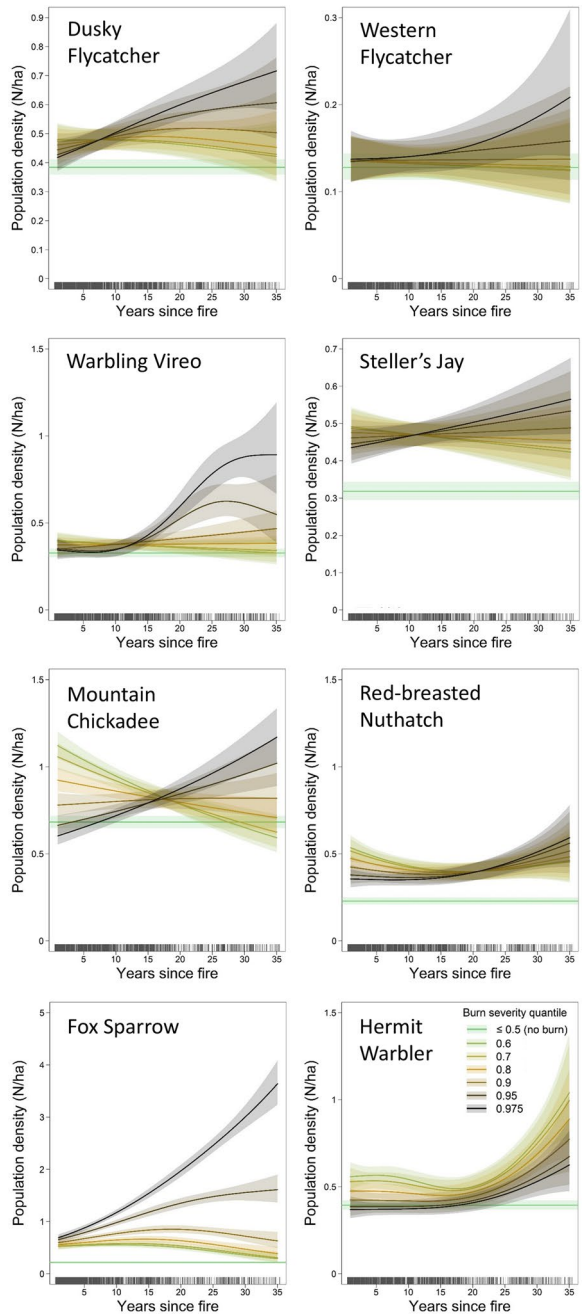


Fig. 6 Population density estimates by years since fire and burn severity for eight species with enduring responses to fire. Each curve represents the fit (mean and 95% confidence interval) of a generalized additive model to posterior density estimates for a population at 1–35 years after burns of the indicated severity. Colors indicate the (relative) average initial burn severity observed at each point-count station), ranging from stations that did not burn (green) to stations that burned most severely (black). Mean population density at unburned stations extends across each panel for ease of comparison with the progression of densities in stations that burned. Densities were estimated from point-count surveys conducted during 1999–2019 in Yosemite and Sequoia & Kings Canyon national parks, California, USA

Discussion

In this study of species common to national parks of the Sierra Nevada, avian populations showed mainly positive and rapid responses to fire, in the form of elevated population densities that frequently endured for decades. For the majority of species we assessed, population density at burned point-count stations increased in the year after fire and remained higher for at least 35 years, relative to unburned stations. Within the range of burn severities we observed (mostly low and moderate), those at the higher end of the range resulted in the most enduring positive effects. Of the 42 species analyzed, 13 showed little or no response to fires of any severity on any timescale, eight responded positively for less than 20 years after fire, ten showed responses (nine positive) persisting longer than 20 years, and 11 showed positive responses with little or no sign of attenuation even 35 years after a fire. Of the 29 species that responded to fire, 28 increased in density at some combination of initial burn severity and years since fire. Only one species (Black-headed Grosbeak) immediately decreased in density at all levels of initial burn severity, and only four additional species experienced notably mixed effects of fire on population density (decreasing at some and increasing at other combinations of initial burn severity and years since fire).

Our results corroborate other studies from western North America that suggest pervasive benefits of fire even for bird species not generally considered to be strongly fire-adapted (Hutto 1995, Raphael et al. 1987, Kirkpatrick et al. 2006, Raphael et al. 2018, Taillie et al. 2018, Hutto et al. 2020, Steel et al. 2022, Brunk et al. 2023). Early comparisons of avian diversity and biomass in two adjacent plots in the Sierra Nevada, one burned and one unburned (Bock and Lynch 1970; Bock et al. 1978), led to the recognition that burned forests could harbor more species and more birds than unburned forests, particularly where burned areas encompass greater habitat heterogeneity. Habitat heterogeneity due to a mixed-severity burn boosted species diversity and density immediately after a fire, followed by a slow decline in diversity and density over time as snags fell and brush closed gaps in the canopy (Bock et al. 1978). When the Bock et al. (1978) study was extended to 25 years (Raphael et al. 1987) and 50 years (Raphael et al. 2018), it became clear that post-fire succession can create a variety of habitats that accommodate a variety of species, and that results derived from short-term studies of fire effects are not necessarily representative of long-term avian responses. Our study of trends in population density during up to 35 years of the post-fire successional process joins several recent studies of bird community structure or habitat occupancy at similar timescales (Steel et al. 2022; Brunk et al. 2023; McGinn et al. 2025).

To the extent that population density correlates with habitat occupancy, the preponderance of species exhibiting an immediate increase in density following fire in our study partially corroborates He et al.'s (2019) general contention that overall biodiversity often peaks immediately after fire and then declines steadily over time. However, we found less reason to suspect a decline in diversity over time, unless the sustained boost in population density that we observed for the relatively common species that we could analyze came at the expense of less common species that we could not analyze (due to small sample sizes). The fact that our findings also contrast with some other studies in temperate forests around the world (e.g., Puig-Gironès et al. 2023) is not overly surprising. Even within temperate forests, responses of bird species and communities to fire may vary substantially depending on fire characteristics, species and community characteristics, and other environmental conditions (Rainsford et al. 2021).

Reponses of bird species may also vary by functional traits of the bird species themselves, so disaggregating results by functional trait groups can yield a better understanding of the mechanisms generating patterns of biodiversity, and may also allow extension of inference to additional species beyond those under study (Guillerme et al. 2025). Results from this part of our analysis did not reveal any striking patterns, but we found greater trait-based differences in effects of non-fire variables, including stand height (more strongly positive for species that forage on invertebrates) and elevation (more strongly positive for ground-nesters and omnivorous birds). The population density of most species analyzed had an inverse and often supported relationship with fire return interval, with the exception of birds that feed primarily on plants and/or seeds. These results may aid hypothesis formulation and suggest future avenues of inquiry.

Hypotheses regarding the importance of interacting effects of burn severity and years since fire in determining the local abundance of individual species have been emphasized in several recent studies of birds in western North America (Smucker et al. 2005, Taillie et al. 2018, Hutto et al. 2020). We found abundant evidence for these interactions, which displayed striking variation across species (Figs. 4, 5, and 6). We can now consider it well established that in this region the abundance of many bird species is likely to reach a higher maximum in burned than unburned sites, and these post-fire maxima are often higher after burns of at least moderate severity, as burn severity and years since fire interact to create conditions that favor particular species (Smucker et al. 2005). Even species not well known to depend on fire have now been shown to have a consistent relationship with burn severity and years since fire: for example,

studies of Mountain Quail occupancy on National Forest lands throughout much of the Sierra Nevada (Brunk et al. 2023) and density in Sierra Nevada national parks (our Fig. 5) both indicate that this species benefits for decades after a high-severity burn.

An important caveat is that our point-count methodology was designed primarily to detect diurnal birds that vocalize frequently during the morning hours (Ralph et al. 1993; Siegel et al. 2010), and therefore effectively excludes nocturnal owls and even diurnal raptors. Some of these species are considered late seral forest specialists within the Sierra Nevada bioregion and may indeed shun recently burned areas (e.g., American Goshawk; Blakey et al. 2019) though recent evidence indicates that other raptors, including Spotted Owl and Great Gray Owl, may persist after fire under some post-fire conditions (Lee 2018; Siegel et al. 2019; Schofield et al. 2020; Kramer et al. 2021; Jones et al. 2024). Automated acoustic monitoring (Brunk et al. 2023), which can improve the detection of raptors by providing a relatively continuous data stream, was used recently to suggest that several owl species in the Sierra Nevada are well-adapted to the "natural" fire regime in this region (McGinn et al. 2025).

Any interpretation of our results should stress that we observed mainly low- and moderate-severity fires during our study period, and many of those fires were associated with appreciable heterogeneity in burn severity. We also focused strictly on effects of fire at a fine scale, within 125 m of individual point-count stations. We did not consider effects of broad-scale fire and landscape characteristics, which include important drivers of species occurrence and abundance, like fire size, pyrodiversity, and proximity to unburned habitat. Past work in the Sierra Nevada and other fire-driven systems has revealed the value of pyrodiversity – particularly the spatial variation in fire severity – for maintaining avian diversity (Tingley et al. 2016; Jones and Tingley 2021), and that even post-fire specialist species like Black-backed Woodpecker may depend on the presence of unburned forest during particular life stages (Stillman et al. 2021). Some of the positive effects of fire on bird populations reported here might therefore depend on a spatiotemporal mosaic of burns that vary in severity and are juxtaposed with unburned or lightly burned habitat patches. If a larger portion of the landscape burns at high severity, habitat heterogeneity and 'edge' areas that include both burned and unburned habitat might reduce to a level that does not benefit avian populations (Steel et al. 2022; Wood et al. 2024).

Indeed, we caution that the fire regime throughout the Sierra Nevada and western North America has changed drastically during the study period and is continuing to change (de Groot et al. 2013; Hessilt et al. 2022; Jain et al. 2022). Particular habitats that are important to birds may be especially vulnerable to high-severity fire, such as Giant Sequoia groves, where many species in the parks occur at their highest densities (Siegel and Wilkerson 2022). Giant sequoias, which are resilient to lower-severity fire but require at least hundreds of years to regenerate, have exhibited high mortality in some recent fires in the parks, and might not be able to regenerate under current and projected future climate conditions (Soderberg et al. 2024). More generally, later-seral forest throughout the region may be at substantial risk of loss as the changing fire regime may be removing or degrading these forests faster than they can regenerate (Stephens et al. 2016). Our results might not capture the effects that pervasive, landscape-level loss of late-seral forest would have on birds.

Fire management – including prescribed fire, vegetation management to alter fire risks, and a range of response options to wildfire – represents the most powerful set of tools available to land managers for maintaining ecosystem function and biodiversity (Parr and Anderson 2006). Using these tools effectively requires knowledge of the pattern of occurrence or abundance of wildlife species with respect to fire history (Driscoll et al. 2010). An improved ability to predict the effects of fire management actions and policies on bird species is necessary for incorporating bird habitat needs into fire management planning (Brunk et al. 2025). Our results provide critical information for this process and demonstrate the surprisingly pervasive value of low- to moderate-severity fire—which likely boosted habitat heterogeneity—for many of the bird species common to national parks in the Sierra Nevada over the past few decades.

Conclusions

Our findings support recent calls for resource management practices that encourage the potential for mixed-severity fire, which generally includes patches burned at high severity, to optimize habitat conditions for diverse species (Smucker et al. 2005, Hutto and Patterson 2016, Rose and Simons 2016, Taillie et al. 2018, Zlonis et al. 2019, Hutto et al. 2020, Roberts et al. 2021). Our results also stand out for revealing the longevity of many species' responses to fire, and the often increasingly positive association between population density and fire severity in historical data from Sierra Nevada national parks. Within the natural range of fire severity in this region—where megafires were historically rare—we found considerable evidence that most of the common bird species experienced a rapid and lasting increase in population density after fire. Although high-severity fire involves a variety of risks that may not be tolerable in many management contexts, the potential for mixed-severity fire to benefit

natural populations warrants further efforts to understand the long-term ecological consequences of fire in national parks and other landscapes.

Abbreviations

AI	Avian inventory completed during 1999–2004
AM	Avian monitoring conducted during 2011–2019
YOSE	Yosemite National Park
SEKI	Sequoia and Kings Canyon National Parks
RdNBR	Relative differenced Normalized Burn Ratio
YSF	Years since fire
FRI	Fire return interval
CRI	Credible interval
CI	Confidence interval
IQR	Inter-quartile range

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00402-2.

Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions
RS, RW, SH, CR and MT conceived the project. SS and KW facilitated data collection. CR, LS and SA conducted analyses. CR and RS drafted the manuscript. All authors edited and approved the final manuscript.

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Data availability
The datasets analyzed here are available in several public repositories. Avian survey data are available through the National Park Service Data Store at https://irma.nps.gov/DataStore/Reference/Profile/2308571. Fire boundaries are available through the National Park Service Data Store at https://irma.nps.gov/DataStore/Reference/Profile/2271857 (for Yosemite) and https://irma.nps.gov/DataStore/Reference/Profile/2258907 or https://irma.nps.gov/DataStore/Reference/Profile/2303745 (for Sequoia and Kings Canyon). Forest structure data for both Yosemite and Sequoia and Kings Canyon are available from LEMMA Lab, Oregon State University, Corvallis, Oregon; https://lemma.forestry.oregonstate.edu. Landfire fire return interval data are available from Earth Resources Observation and Science Center (EROS), U.S. Geological Survey; https://www.landfire.gov/viewer. R and JAGS scripts related to this analysis are available at https://github.com/birdpop/firebird.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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