

# Mixed-severity wildfire and salvage logging affect the populations of a forest-dependent carnivoran and a competitor

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**Abstract.** Effects of historical fire suppression in forested ecosystems, combined with increasingly frequent and prolonged periods of drought due to a changing climate, are predicted to drive increases in the extent and intensity of wildfires in western North America and elsewhere. Understanding the effects of wildfires on forest-dependent species and interactions among species is important for conservation and management decisions. We used data collected from a long-term carnivore monitoring program in northern California and southern Oregon, USA to investigate the effects of three mixed-severity wildfires and salvage logging on a population of fishers (*Pekania pennanti*), forest-dependent carnivoran of conservation concern, and a co-occurring population of gray foxes (*Urocyon cinereoargenteus*), a competitor of similar body size. We developed a spatial capture-recapture population model to estimate the short-term effects of the wildfires and salvage logging on fisher and gray fox abundances, distributions, apparent survival and recruitment, and species interactions using non-invasive genetic data collected three years prior to and three years following wildfires. Fisher abundance decreased significantly in areas of low-, medium-, and high-severity wildfire. Gray fox abundance decreased in the years before the wildfires, but rebounded in subsequent years. Medium-severity wildfire had a negative effect on gray fox density, but high-severity wildfire and fisher density had positive effects on gray fox density. Salvage logging had negative effects on both fisher and gray fox density. Our results suggest that increased severity, extent, and frequency of wildfires in the western USA will affect fisher populations negatively and alter the composition of mesocarnivore communities.

**Key words:** community ecology; fire; fisher; gray fox; Klamath-Siskiyou; mesocarnivore; non-invasive monitoring; *Pekania pennanti*; salvage logging; spatial capture-recapture; *Urocyon cinereoargenteus*.

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## INTRODUCTION

Wildfires influence ecological communities on fire-prone landscapes, and many species have evolved in systems subject to historically variable fire regimes (Noss et al. 2006, Rockweit et al.

2017, Spies et al. 2018). The frequencies, distributions, and intensities of wildfires, however, have increased (Stephens 2005, Lutz et al. 2009, Miller et al. 2009, 2012) often due to decades of fire suppression (Stephens et al. 2009, Calkin et al. 2015), past and current timber harvest practices (Odion

et al. 2004), human encroachment (Bowman et al. 2011, Balch et al. 2017), and a changing climate (Westerling 2006, 2016, Liu et al. 2013, Abatzoglou and Williams 2016). Wildfires impose large-scale losses of natural resources, alter ecological patterns (Adams 2013, Stephens et al. 2014, Spies et al. 2018, Coop et al. 2020), and are becoming increasingly expensive to manage (Calkin et al. 2015). Departures from historical wildfire patterns have prompted calls to restore natural fire regimes via forest restoration and fuels management (Calkin et al. 2015, North et al. 2015, 2019), as the short- and long-term consequences are unclear for wildlife living in these fire-prone landscapes.

Wildfires and post-fire forest management also alter, disrupt, or amplify interspecific interactions within wildlife communities, yet these effects are rarely studied. For medium-sized carnivores (i.e., members of the order Carnivora), wildfires induce changes in vegetation that can make areas uninhabitable due to increases in predation, competition with sympatric species, or loss of forest structure needed to hunt (Nelson et al. 2007, Geary et al. 2018). Salvage logging and replanting following wildfire add additional layers of forest responses to fires and, thereby, increase the lack of understanding of responses of wildlife to fire.

The spotted owl (*Strix occidentalis*) is one of the most extensively studied forest-dependent species and the responses of spotted owls to wildfires appear to reflect the context of the location and each individual owl (Ganey et al. 2017, Rockweit et al. 2017, Lee 2018, Peery et al. 2019, Geary et al. 2020, Jones et al. 2020). Some wildfires have decreased spotted owl survival (Clark et al. 2011), reproduction (Jenness et al. 2004), occupancy, and colonization rates (Clark et al. 2013), especially in high-severity fires (Jones et al. 2016, 2020, Eyes et al. 2017, Rockweit et al. 2017). Other fires, even of high severity, have shown limited to no effects on spotted owl ecology (Bond et al. 2002, 2009, 2016, Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015). A clear understanding of the effects of wildfire on wildlife that occur in mature forests is lacking, and requires further study.

The responses of carnivores to fire are context dependent and vary by ecosystem (Geary et al. 2020). For example, fires may have positive effects on populations of some carnivores by

increasing hunting efficacy (Arjo and Peltscher 2004, Eby et al. 2013), altering the spatial distribution of competitors (Schuette et al. 2014, Green et al. 2015, Geary et al. 2018), or increasing prey availability or distributions (Geary et al. 2020). Fires may have negative effects on carnivores by altering vegetation (Geary et al. 2020) and may make non-apex carnivores more susceptible to predation (Birtas et al. 2012). Thus, a variety of perspectives has emerged regarding the effects of wildfires on wildlife.

Fishers (*Pekania pennanti*) are medium-sized, North American carnivores that are strongly associated with mature forests and are of conservation concern in the western United States (U.S. Fish and Wildlife Service 2016a, b). Fisher populations experienced significant declines and range contractions attributed to over-trapping for their fur, loss or fragmentation of forested landscapes, predator and pest control campaigns, and climate changes at the end of the Little Ice Age in the mid-1800s (Douglas and Strickland 1987, Powell 1993, Ruggiero et al. 1994, Knaus et al. 2011, Krohn 2012, Tucker et al. 2012). The Distinct Population Segment of fishers in the southern Sierra Nevada Mountains of California in the United States was recently listed as Endangered via the Endangered Species Act (U.S. Fish and Wildlife Service 2020) and the increase in frequency and severity of wildfires is considered a potential threat to the population's persistence (U.S. Fish and Wildlife Service 2020). Limited evidence suggests that fire may decrease fisher occupancy (Thompson et al. 2011, Scheller et al. 2011, Garner 2013, Sweitzer et al. 2016) but no study has empirically estimated the effects of wildfires on fisher populations. The Klamath-Siskiyou Ecoregion is the geographic center of the largest population of fishers in the western United States (U.S. Fish and Wildlife Service 2016b, Furnas et al. 2017), and nearly 11,910 km<sup>2</sup> (24%) of their estimated 48,760 km<sup>2</sup> distribution has burned due to fire from 2015 to 2020 (National Interagency Fire Center 2021). Understanding how wildfires of varying intensities affect fishers will aid in fisher conservation (Tempel et al. 2015, Sweitzer et al. 2016). Recent wildfires influenced by drought and beetle-kill-related tree mortality in the southern Sierra Nevada (Stephens et al. 2018, U.S. Fish and Wildlife Service 2020) give urgency to these questions.

Gray foxes (*Urocyon cinereoargenteus*) are generalist canids that compete with fishers and their occupancy can increase in areas where fishers have been removed (Green et al. 2018). Thus, determining the effects of wildfires on gray fox populations and understanding the interactions of gray foxes with fishers may be important for fisher conservation, especially in areas intended for restoration, reintroduction, or management.

We evaluated the effects of mixed-severity wildfire and post-fire forest management in the form of salvage logging and replanting (henceforth, “salvage logging”) on fishers and gray foxes in the Klamath-Siskiyou Ecoregion in northern California and southern Oregon, USA. The Klamath-Siskiyou Ecoregion is a global hotspot for biodiversity (Whittaker 1960, Myers et al. 2000), and it also supports the largest extant population and highest density of fishers in the western United States (Matthews et al. 2011, U.S. Fish and Wildlife Service 2016b, Furnas et al. 2017). To quantify the effects of mixed-severity wildfire on fishers and gray foxes in this system, we took advantage of three wildfires that burned 26% of the area encompassing a long-term fisher monitoring program in the summers of 2014 and 2016 (Green et al. 2018). We hypothesized (H1) that the effects of wildfire on fisher density are inversely proportional to fire severity. Specifically, we tested predictions that (1) low- and medium-severity wildfires have little to no effect on fishers but that (2) high-severity wildfires have negative effects on fishers. For foxes, we hypothesized (H2) that the effects of wildfire would be influenced by fishers and tested the predictions that (1) fishers have negative effects on gray foxes and (2) that the number of foxes will increase in areas where fisher populations decreased due to wildfires. We also hypothesized (H3) that salvage logging has negative effects on fishers but foxes would benefit from the vegetation changes. By leveraging a long-term data set that spans years pre- and post-disturbance, we were able to separate the effects of wildfires and salvage logging from other naturally occurring variation.

## METHODS

### *Study site and data collection*

We monitored fishers and gray foxes on a 465-km<sup>2</sup> portion of the Klamath-Siskiyou Ecoregion

in northern California and southern Oregon (henceforth “Klamath”; Fig. 1a). Klamath was predominantly conifer and mixed conifer-broadleaf forest. Elevation ranged from 472 to 2269 m. Land ownership within Klamath included National Forest Service lands (260 km<sup>2</sup>), private industrial forest (198 km<sup>2</sup>), private non-industrial forest (5 km<sup>2</sup>), and state and local ownership (3 km<sup>2</sup>).

We used track plate boxes to survey non-invasively for wildlife in Klamath annually between mid-September and early December 2006 through 2016 (Green et al. 2018). The Beaver Fire burned 133 km<sup>2</sup> on and adjacent to Klamath from 30 July to 2 September 2014, the Happy Camp Complex burned 558 km<sup>2</sup> adjacent to Klamath from 12 August to 31 October 2014, and the Gap Fire burned 137 km<sup>2</sup> adjacent to Klamath from 27 August to 18 September 2016 (Fig. 1b). All three of these wildfires burned at mixed severity. The Beaver fire burned 37 km<sup>2</sup> at low severity (28%), 46 km<sup>2</sup> at medium severity (35%), and 48 km<sup>2</sup> at high severity (36%). The Happy Camp Complex burned 153 km<sup>2</sup> at low severity (27%), 133 km<sup>2</sup> at medium severity (24%), and 156 km<sup>2</sup> at high severity (28%). The Gap Fire burned 53 km<sup>2</sup> at low severity (39%), 32 km<sup>2</sup> at medium severity (23%), and 30 km<sup>2</sup> at high severity (22%; Fig. 1b). The remaining percentages of each fire that are unaccounted for by these burn categories indicate areas within the fire perimeters that were not burned or lacked appropriate data for estimation of burn severity (Eidenshink et al. 2007). These fires did not affect our sampling. The areas burned by the Happy Camp Complex and Gap Fires were within the mean movement distances for male and female fishers (Green et al. 2018; Fig. 1b). The Beaver and the Happy Camp Complex Fires were ignited by lightning, and the Gap Fire was ignited by humans.

The population of fishers was relatively stable from 2006 to 2013, despite approximately 20% of the population having been translocated in 2009 and 2010 for reintroduction elsewhere (Green et al. 2018). No previous data exist on population trends of the gray fox population in Klamath and our genetic analyses of gray fox samples began in 2011, which is why we start the current analysis in 2011. To disentangle the effects of the fires from naturally occurring variation of populations, we designated 2011 to 2013 as baseline years (i.e., pre-fire) and 2014 to 2016 as treatment



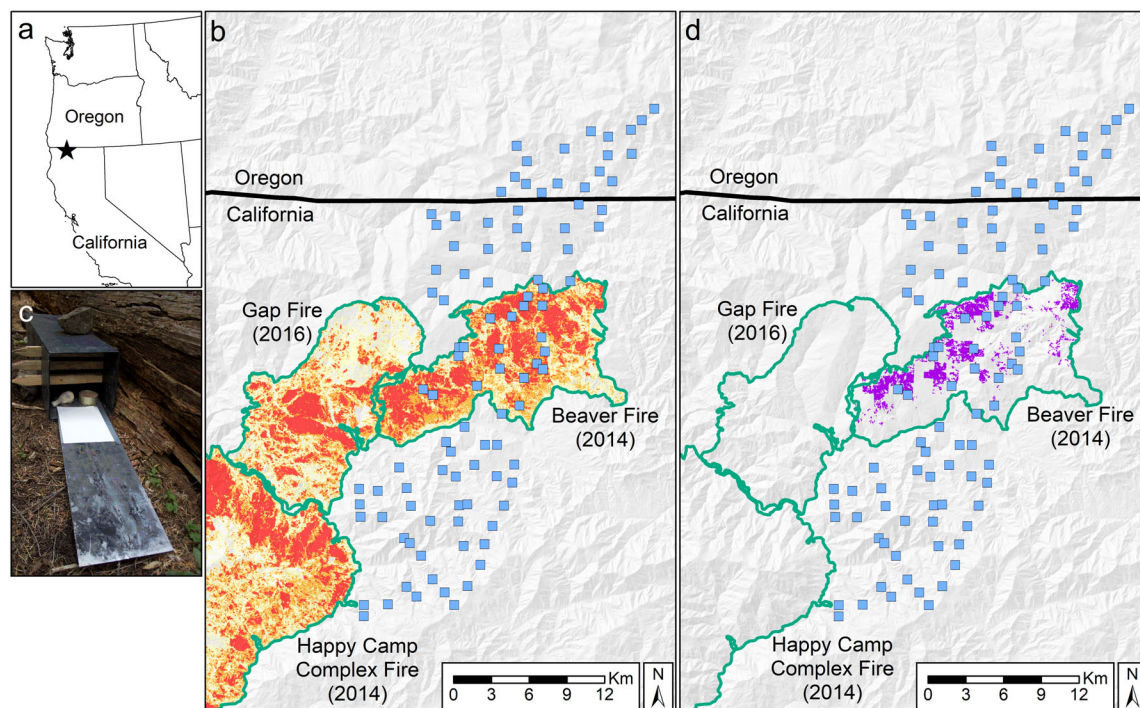


Fig. 1. Study site and methods for monitoring effects of three wildfires on fishers and gray foxes. (a) The Klamath study site in northern California and southern Oregon, USA is shown with a black star. (b) The distribution and severity of the three mixed-severity wildfires that occurred in 2014 and 2016 in Klamath and locations of survey sites. Survey sites are depicted by blue squares and outlines of each fire are shown in green. Areas that burned at low, medium, and high severity are indicated in yellow, orange, and red, respectively. Burn-severity data are from the Monitoring Trends in Burn Severity thematic burn-severity data classification. (c) The non-invasive sampling box used to collect genetic samples from fishers and gray foxes in Klamath. The metal plate extending out the front of the box is fully slid into the box before deployment. (d) The estimated salvage logging that occurred in the Beaver Fire perimeter estimated using Random Forest modeling (see *Methods*).

years (i.e., post-fire) to determine changes to the fisher and gray fox populations that may have resulted from the fires in a Before After Control Impact (BACI) design (Green 1979).

#### *Non-invasive sampling techniques*

We deployed 100 survey stations in Klamath at the same locations each year (Fig. 1b, c). Locations were selected in 2006 based on road access and presumed fisher habitat (i.e., near streams, in areas of dense canopy; Green et al. 2018). Twenty survey stations (20% of all survey stations) were within the Beaver Fire perimeter. Each survey station consisted of a corrugated plastic tunnel with one end covered with  $\frac{1}{2}$  inch (~1.2 cm) hardware cloth and the other end partially obstructed with three wooden slats (Fig. 1c;

Zielinski et al. 2006). We affixed a strip of non-toxic glue board (Catchmaster 72MB, USA) to the underside of the bottom wooden slat so that mammals entering the plastic box would leave a hair sample on the glue strip. Stations were surveyed for 4–6 consecutive weeks each year, baited each week with a raw chicken drumstick and a can of wet cat food (Fig. 1c), and checked weekly for hair samples (Green et al. 2018). Any glue strip with hair attached was put in a 50-mL vial with 5 mL of desiccant. All samples were analyzed at the National Genomic Center for Wildlife and Fish Conservation at the Rocky Mountain Research Station in Missoula, MT, USA. Hair samples were analyzed to species and those identified as fisher or gray fox were further analyzed to sex and individual.

Fisher samples were genotyped using 16 microsatellite loci used in previous mustelid studies: MpP0059, Mp0144, Mp0175, Mp0197, Mp0200, Mp0247 (Jordan et al. 2007), Ma1 (Davis and Strobeck 1998), Mer022, Mvis020, Mvis072 (Fleming et al. 1999), Ggu101, Ggu216 (Duffy et al. 1998), Lut604, Lut733 (Dallas and Pierniey 1998), Gg25 (Walker et al. 2001) Mf1.18 (Basto et al. 2010), and Mvi1321 (Vincent et al. 2003). Genetic sex identification from fisher samples was obtained using the sexing locus SRX/SRY designed for mustelids (Hedmark et al. 2004). Gray fox samples were genotyped using 10 microsatellite loci designed for foxes and other canids: GF-09, GF-14 (Weston et al. 2004), Cph2 (Fredholm and Winterø 1995), C09.250 (Ostrander et al. 1993), FH2001, FH2088, FH2096 (Francisco et al. 1996), AHT137, CO1.424, and REN54P11 (Moore et al. 2010). Genetic sex identification from gray fox samples was obtained using the sexing locus ZFX/ZFY designed for foxes (Ortega et al. 2004). DNA from hair samples was amplified using the multi-tube approach (Eggert et al. 2003, Schwartz et al. 2007). The resultant products were visualized on a LI-COR DNA analyzer (LI-COR Biotechnology). Data were error-checked using program Dropout (McKelvey and Schwartz 2005), GenA-LEx (Peakall and Smouse 2006), and Micro-checker (Van Oosterhout et al. 2004).

#### *Spatial open population capture–recapture model*

We developed a spatial open population capture–recapture model (Efford 2004, Royle and Young 2008, Gardner et al. 2010, Green et al. 2018) to determine the effects of the three fires on the populations of fishers and gray foxes in Klamath. We ran species-specific models for fishers and gray foxes and, in our hierarchical formulation, the spatially explicit detection histories  $y$  for individual  $i$  in year  $t$  at survey station  $j$  in week  $w$  ( $y_{itjw}$ ) were modeled as:

$$y_{itjw} \sim \text{Bernoulli}(\lambda_{itjw} K_{tjw} z_{it}),$$

where  $\lambda_{itjw}$  is the average encounter rate,  $K_{tjw}$  is a binary variable indicating whether or not survey station  $j$  was deployed in week  $w$  of year  $t$ , and  $z_{it}$  is the partially observed latent variable indicating whether or not individual  $i$  was present or estimated to be present in the population in year  $t$ . We modeled the average encounter rate as a

function of the probability of detection  $p0_{itjw}$  and a detection function  $g_{itj}$  based on the distance to an individual's latent activity center  $s_{it}$ , such that  $\lambda_{itjw} = p0_{itjw} g_{itj}$ . Previous research in Klamath and elsewhere has identified sex-specific detection probabilities of fishers (Popescu et al. 2014, Linden et al. 2017, Green et al. 2018) and an increased likelihood of visitation following an initial detection (Sweitzer and Furnas 2016, Linden et al. 2017, Green et al. 2018). Therefore, we modeled the logit-linear mean probability of detection ( $p0_{itjw}$ ) as:

$$\text{Logit}(p0_{itjw}) = \beta0_t + \beta1 \times \text{sex}_i + \beta2 \times \text{previous detection}_{itjw},$$

where the probability of detection is a function of a year-specific intercept ( $\beta0_t$ ), an effect of sex ( $\beta1$ ), and the effect of a binary variable indicating whether the individual visited this survey station in a previous week in the same sampling year ( $\beta2$ ). We modeled the year-specific intercepts,  $\beta0_t$ , by assuming they were random effects, drawn from a uniform distribution.

The detection function  $g_{itj}$  described how the encounter rate of an individual decreases as a function of the distance between their activity center in that year  $s_{it}$  and the location of the survey stations and was modeled with a Gaussian encounter probability such that:

$$g_{itj} = e^{(-d_{itj}^2 / 2\sigma_k^2)},$$

where  $d_{itj}$  is the Euclidean distance between the survey station and an animal's latent activity center, and  $\sigma_k$  is the standard deviation of a bivariate normal distribution reflecting space-use modeled to vary by sex  $k$ . We modeled activity centers for each individual  $i$  in each year  $t$  independently as a homogeneous Poisson point process in the state space  $S$  (Royle et al. 2014). We defined  $S$  as a continuous state space bounded by the outside of a rectangular 4-km buffer around our sampling units (Royle et al. 2014). We initially modeled  $\sigma_k$  to vary by year, but early model runs indicated no significant differences among years (i.e., 95% credible intervals overlapped), so we dropped this parameterization in favor of parsimony. We modeled  $\sigma_k$  as a random variable drawn from a uniform distribution.

We modeled  $z_{i1} \sim \text{Bernoulli}(\Psi_{\text{pop}})$  for year  $t = 1$  and  $z_{it} \sim \text{Bernoulli}(\mu_{it})$  for all years  $t > 1$ , where

$$\mu_{it} = (z_{it-1} \times \Phi_{t-1}) + (A_{it-1} \times \Gamma_t)$$

$$A_{it-1} = 1 - \text{step}(a_{it} - 1)$$

$$a_{it} = \text{sum}(z_{i1:t}).$$

Thus, the probability that an individual is estimated to be in the population in years  $t > 1$  is a function of survival ( $\Phi_{t-1}$ ) from the previous year if already present ( $z_{it-1}$ ) or of the probability that an individual is recruited ( $\Gamma_t$ ) into the population if not already present ( $A_{it-1}$ ). The term  $A_{it-1}$  ensures that individuals are only available to be recruited into the population a single time for the duration of this study. We modeled the year-specific survival and recruitment probabilities by assuming they were random effects, drawn from a uniform distribution. We modeled sex as the Bernoulli distributed partially latent variable,  $\text{Sex}_i \sim \text{Bernoulli}(\Psi_{\text{sex}})$ , where sex was estimated as coming from the population-level sex ratio ( $\Psi_{\text{sex}}$ ).

We fit our models using data augmentation (Royle et al. 2007). We introduced a sufficiently large number of all-zero encounter histories to our population of observed individuals to prevent any truncation of the number of fishers or foxes with activity centers located in  $S$ . The number of individuals  $N$  alive in year  $t$ ,  $N_t$ , was thus:

$$N_t = \sum_{i=1}^M z(i, t).$$

Full model code is provided in Appendix S1.

#### *Post-fire salvage logging model*

We modeled the spatial extent of salvage logging within the 2014 Beaver Fire using a random forest (RF) supervised classification model (Breiman 2001). We only modeled salvage logging in the Beaver Fire because inspection of high-resolution imagery of the Happy Camp Fire did not identify any salvage logging, and any salvage logging following the 2016 Gap Fire occurred after our 2016 field sampling. We created a training data set using 369 random points in the Beaver Fire perimeter by visually interpreting high-resolution (60–100 cm) NAIP aerial imagery from before and after the Beaver Fire occurred. We classified each random point as either being salvage logged ( $n = 147$ ) or unlogged ( $n = 222$ ) using Google Earth Engine (Gorelick et al. 2017). We used Sentinel-2 (10-m resolution) satellite data to aid in the interpretation of training

locations. We used cloud-free short-wave infrared (SWIR) data from the Landsat 8 Surface Reflectance Tier 1 (Band 6) to establish covariates for the model. These were acquired and exported as 30-m resolution raster files from Google Earth Engine. Short-wave infrared reflectance can help separate different types of landscape disturbance (Schroeder et al. 2011, 2012). Salvage logging exposes bare soil such that its spectral signature is distinctive from charred ground in the SWIR region of the electromagnetic spectrum. We extracted SWIR data at each training location for three dates, representing pre-fire forest structure (15 July 2014), post-fire forest conditions (3 October 2014), and post-fire post-salvage logging and before sampling the year following the fires and logging (20 September 2015).

These data were then used to train a RF classification model (Breiman 2001) using the “randomForest” package (Liaw and Wiener 2002) in R v. 3.6.3 (R Core Team 2020). We selected the number of trees in the RF model based on roughly twice the number of trees required for error convergence in an initial model run. We used the tuneRF function from the randomForest package to select the optimal mtry value (i.e., the number of variables randomly chosen to grow each tree). We evaluated model performance using accuracy and kappa statistics calculated from out-of-bag samples. We then used the model to predict logged and unlogged pixels across the Beaver Fire perimeter using the “ModelMap” package in R (Freeman and Frescino 2009). To reduce noise in the map, we then reclassified logged pixel clusters to unlogged pixels where  $\leq 4$  pixels (i.e., 3600 m<sup>2</sup>) were connected (based on the Moore neighborhood). See Appendix S1: Fig. S1 for more information on the salvage logging model.

We created a reference data set to assess the accuracy of the final model of salvage logging in the Beaver Fire. We assigned class values to reference points by interpreting high-resolution imagery using the same technique we used to create the training data. Because class-specific accuracy estimates were of primary interest and equal allocation of samples can lead to imprecise estimates of overall accuracy (Olofsson et al. 2014), we generated a stratified-random sample with 70 and 100 reference samples in the logged and unlogged classes, respectively. Proportional allocations would have required an unfeasibly large



overall sample size to obtain a large enough sample size in the logged class, which accounted for 15% of pixels in the final map. We struck a balance by creating 70 reference samples in the logged class and 100 in the unlogged class (Olofsson et al. 2014). We used the error matrix derived from comparing the reference data to mapped predictions to calculate user's, producer's, and overall accuracy, as well as the kappa coefficient.

#### *Investigating the effects of wildfires and salvage logging on fisher and gray fox density and distribution*

We developed a generalized linear model to test predictions from our a priori hypotheses that the effects of wildfires on fishers would be burn-severity specific, that any effects of fire on foxes would be influenced by fishers and that the effects of salvage logging would be species-specific. We calculated the spatially explicit densities of fisher and fox activity centers from the predicted distributions of activity centers to determine effects of wildfires and salvage logging on fisher and fox density. We overlaid Klamath with a 500 m × 500 m grid of  $R$  cells and calculated the predicted mean density of fisher and gray fox activity centers per each 0.25-km<sup>2</sup> grid cell  $r$  in year  $t$  for each species  $s$  ( $d_{rts}$ ). We used a 500-m grid because this was less than half the size of the smallest estimated sigma values for fishers and gray foxes. We modeled  $d_{rts}$  as:

$$d_{rts} \sim \text{Normal}(\mu_{rts}, \tau_s).$$

For the first year of the study (i.e., 2011), we modeled the densities of fishers and gray foxes in each grid cell  $r$  to vary solely by year  $t$  and species  $s$  specific intercept ( $\alpha_{0ts}$ ):

$$\mu_{r1s} = \alpha_{0ts}.$$

We wanted to account explicitly for the effect of activity center fidelity on fisher and gray fox density and distribution in Klamath. Thus, for all years  $t > 1$  we added an effect of the estimated density of fishers and foxes in each grid cell from the previous year ( $\alpha_{1s}$ ) such that before the wildfires occurred (i.e., 2012 and 2013), we modeled  $\mu_{rts}$  as:

$$\mu_{rts} = \alpha_{0ts} + \alpha_{1s} \times \text{previous density}_{rt-1s}.$$

This allowed us to disentangle any effects of the mixed-severity wildfires and salvage logging

from any naturally occurring variation on the landscape responsible for fisher and gray fox distributions (e.g., habitat covariates). For years following the fires and through the end of the study (i.e., 2014–2016), we modeled  $\mu_{rts}$  as:

$$\begin{aligned} \mu_{rts} = & \alpha_{0ts} + \alpha_{1s} \times \text{previous density}_{rt-1s} \\ & + \alpha_{2s} \times \text{low burn}_{rt} + \alpha_{3s} \\ & \times \text{medium burn}_{rt} + \alpha_{4s} \\ & \times \text{high burn}_{rt} + \alpha_{5s} \times \text{logged}_{rt}, \end{aligned}$$

where the density of fishers and gray foxes in each grid cell  $r$  was modeled to vary as a function of a year and species-specific intercept ( $\alpha_{0ts}$ ), an effect of the estimated density of animals in that grid cell in the previous year ( $\alpha_{1s}$ ), and the effects of the proportion of the grid cell that was burned at low, medium, and high severity ( $\alpha_{2s}$ ,  $\alpha_{3s}$ , and  $\alpha_{4s}$ , respectively), and salvage logged ( $\alpha_{5s}$ ). The effect of salvage logging was only included for years 2015 and 2016 (i.e., after the salvage logging occurred). Previous research has indicated fishers positively affect the colonization of gray fox occupancy and negatively affect the persistence of gray fox occupancy (Green et al. 2018). To retest predictions of this hypothesis here, we coded a 6th term in the gray fox model to determine whether fisher density affects foxes ( $\alpha_6 \times \text{fisher density}_{rt-1}$ ).

We log-transformed  $d_{rts}$  prior to analyses to achieve normality. We standardized all covariates to have a mean of 0 and a standard deviation of 1 and tested them for collinearity prior to analyses; Pearson correlation coefficient was  $< 0.621$  for all relationships. Fire severity data were acquired from the Monitoring Trends in Burn Severity (MTBS) thematic burn-severity data classification (Eidenshink et al. 2007). We modeled  $\alpha_2$ ,  $\alpha_3$ ,  $\alpha_4$ , and  $\alpha_5$  as time series variables to account for any changes to spatially explicit densities that occurred over time due to the fires, burn severity, and salvage logging. Full model code is provided in Appendix S1.

#### *Model fitting and assessment*

We fit our fisher and gray fox models using the Markov chain Monte Carlo (MCMC) methods of JAGS v. 4.2.0 (Plummer 2003). We used uninformative prior distributions for all estimated parameters. Parameter estimates were calculated from 9000 MCMC samples, taken from

3 chains run for 30,000 iterations, thinned by 10, and following a burn-in of 20,000. We assessed model convergence by examining trace plots and  $\hat{R}$  values for convergence (Gelman and Hill 2006, Gelman et al. 2013). We calculated percent probabilities from posterior distributions to determine the significance of parameter estimates, which were calculated as the percent of posterior draws greater or less than zero, depending on the sign of the median value. Values on the normal and logit scales are presented to two decimal places, whereas those on the log scale are presented to three decimal places.

## RESULTS

We sampled 100 systematically placed survey stations annually between 2011 and 2016 for  $474 \pm 48.5$  (yearly mean  $\pm$  SD; total = 2844) trap weeks. We collected  $276 \pm 52$  (total = 1658) samples per year that were submitted for genetic analyses, of which  $258 \pm 51$  (93% of all samples) were of sufficient quality to identify the species of the visitor (total = 1546). We collected  $111 \pm 34$  (total = 664) and  $104 \pm 25$  (total = 621) samples annually from fishers and gray foxes, respectively. Of these samples,  $83 \pm 11\%$  (fishers) and  $83 \pm 10\%$  (gray foxes) were of sufficient quality to determine sex and individual genotype. We identified a total of 123 fishers (51F, 72M) and 205 gray foxes (102F, 103M) from 2011 through 2016, with  $30 \pm 3$  and  $50 \pm 14$  individual fishers and foxes detected each year. Individual fishers were detected at an average of  $1.8 \pm 1.5$  sampling stations each year (range = 1–10), and foxes were detected at an average of  $1.2 \pm 0.5$  sampling stations each year (range = 1–4).

### *Changes in density and distribution of fishers and foxes over time*

Our spatial open population capture–recapture model suggested a 27% decrease in the total number of fishers in Klamath apparent in 2015, a full year after the 2014 wildfires (Figs. 2a, 3). The gray fox population appeared to decrease by 55% from 2011 through 2014 before beginning to rebound in 2015 following the fires (Figs. 2b, 3). The estimated number of female fishers in Klamath decreased in 2015 and remained low in 2016, while the estimated number of male fishers decreased in 2015 but rebounded in 2016 (Fig. 2

c). The total number of fishers with activity centers within the fire perimeters decreased in 2015 and remained low in 2016 (Figs. 2c, 3). The estimated number of male gray foxes exceeded the estimated number of females each year, but both sexes followed the overall population trend (Fig. 2d). Full results from Fig. 2 are presented in Appendix S1: Tables S1, S2. Following the Beaver Fire, fisher density within the burned areas decreased (Figs. 3, 4). Not a single fisher detected in the Beaver Fire perimeter in 2013 was detected there after the fire occurred in 2014 (Fig. 5a). In 2015, we detected a single female in the fire perimeter, but no female fishers were detected there in subsequent years (Fig. 5a). In 2016, we detected a single male in the fire perimeter that was not previously detected in the study area (Fig. 5a). In 2015, we detected many previously undetected gray foxes in the fire perimeter, although few persisted there into 2016 (Fig. 5b).

Baseline detection probabilities for fishers and foxes were consistent over time, but were highest for both species the first full year after the fire in 2015 (Table 1). For fishers, sex and previous detection both had 100% probabilities of affecting detection probability, with males being more likely to be detected than females ( $\beta_1$  median and 95% credible interval on the logit scale for females =  $-1.3$  [ $-1.88, -0.73$ ]) and both sexes more likely to be detected after an initial visit to the survey station ( $\beta_2$  median and 95% credible interval on the logit scale =  $2.54$  [ $2.15, 2.98$ ]). For gray foxes, sex had a 71% probability of affecting detection, with females more likely to be detected than males ( $\beta_1$  median and 95% credible interval on the logit scale for females =  $0.13$  [ $-0.31, 0.57$ ]). Gray foxes had a 100% probability of an increase in detection probability following an initial visit to a survey station ( $\beta_2$  median and 95% credible interval on the logit scale =  $1.84$  [ $1.43, 2.25$ ]). The movement parameter of male fishers was larger than those of females, but the differences between sexes were minor for gray foxes (Table 1). The sex ratio was female dominant for fishers but closer to even for gray foxes (Table 1).

Apparent survival and recruitment for fishers and gray foxes varied over time. Fisher apparent survival was the lowest in 2014, indicating a lower probability of animals remaining or persisting in the study area from 2014 (i.e., the year of the Beaver and Happy Camp Complex Fires)



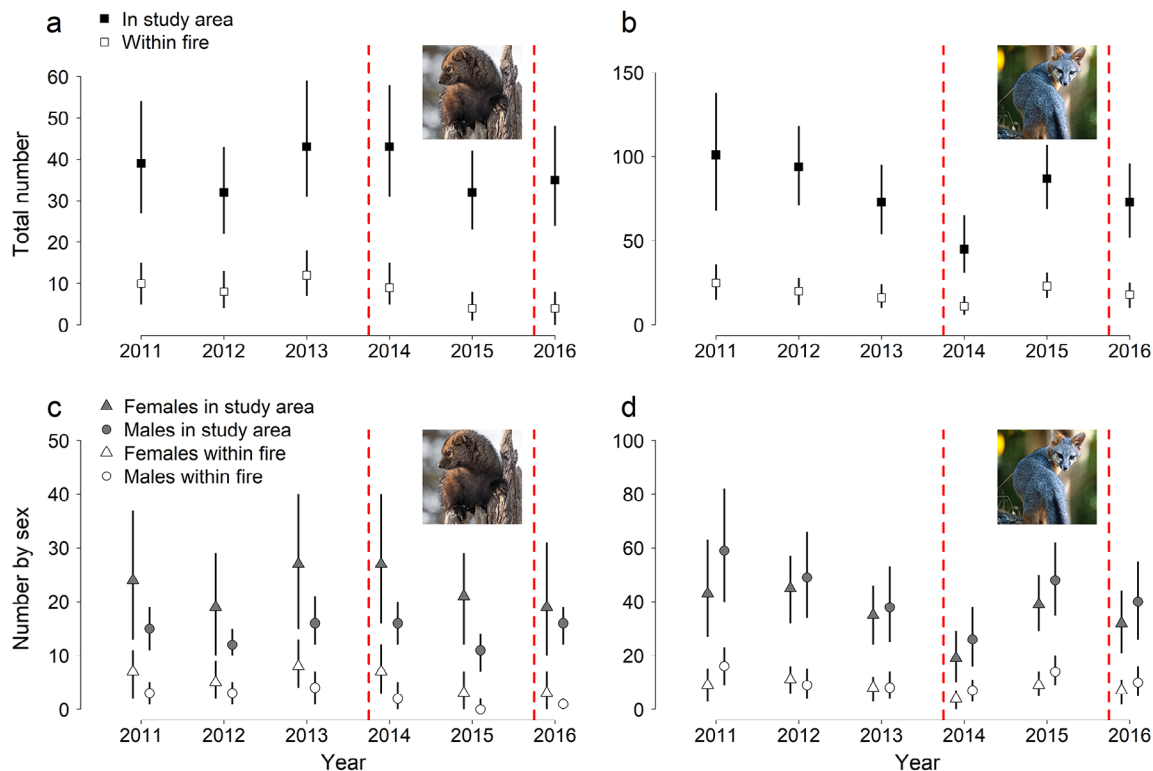


Fig. 2. Fisher and gray fox estimated population abundance over time in the Klamath study area and specific to the Beaver Fire perimeter estimated using a spatial open population capture–recapture model. We present the median and 95% credible intervals for the total number of (a) fishers and (b) gray foxes, and the breakdown of these numbers by sex for (c) fishers and (d) gray foxes. The filled symbols (i.e., black and grays) indicate the number of individuals in the total study area, and the open symbols (i.e., white) indicate the number of individuals located within the Beaver Fire perimeter. In (c) and (d), triangles indicate the predicted number of females and circles indicate the predicted number of males. The red vertical lines indicate the timing of wildfires that occurred during the summer of 2014 (Beaver and Happy Camp Complex Fires) and 2016 (Gap Fire).

to 2015 than in any other year (Table 2). In addition, apparent recruitment was also the lowest in 2015, indicating that fewer fishers were recruited into the population in 2015 than in any other year (Table 2). Gray fox apparent survival generally decreased from 2011 to 2013, before increasing in 2014 and 2015 (Table 2). Apparent recruitment of gray foxes was more than three times greater in 2015 than in any other year, indicating that many animals were detected for the first time the first full year following the Beaver and Happy Camp Complex Fires (Table 2).

#### Salvage logging in the Beaver Fire perimeter

The final RF model was parameterized with 501 trees and two variables randomly selected at

each split (mtry). The overall accuracy of the model based on out-of-bag samples (i.e., not the independent reference data) was 94.8% (kappa = 0.88). The most important variable based on mean decrease accuracy for discriminating salvage logging from other burned areas was the SWIR band from the post-fire post-salvage logging time step.

Since the training data were created in a targeted manner and do not represent a probability sample, we assessed the map accuracy in a separate analysis using the reference data described above. We compared mapped predictions of salvage logging against the independent reference locations. These results showed strong agreement among predicted classes and reference data. Overall accuracy was 90.0% (kappa = 0.79).

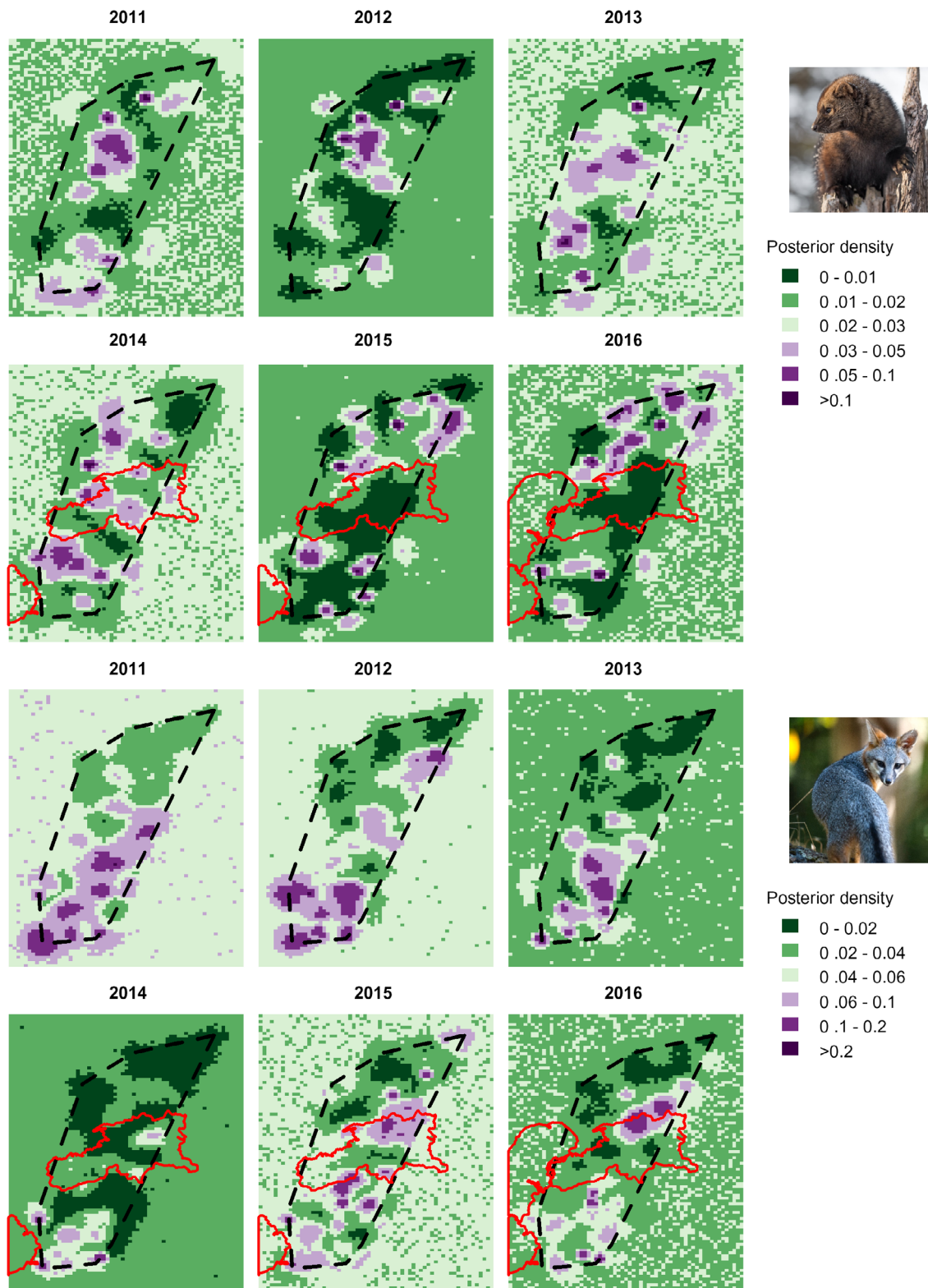


Fig. 3. Predicted density and distribution of fisher and gray fox activity centers in each 500 × 500 m grid cell

(Fig. 3. *Continued*)

in Klamath from 2011 to 2016 determined with an open population spatial capture–recapture model. The dashed black lines indicate the convex hull encompassing our survey sites and what we defined as the Klamath study area. The solid red lines indicate the perimeters of the three wildfires; both the Happy Camp Complex and Gap Fires extend beyond the study area. Green and purple colors indicate relatively fewer and more estimated activity centers in each grid cell each year, respectively. Note the differences in scale between fishers and gray foxes.

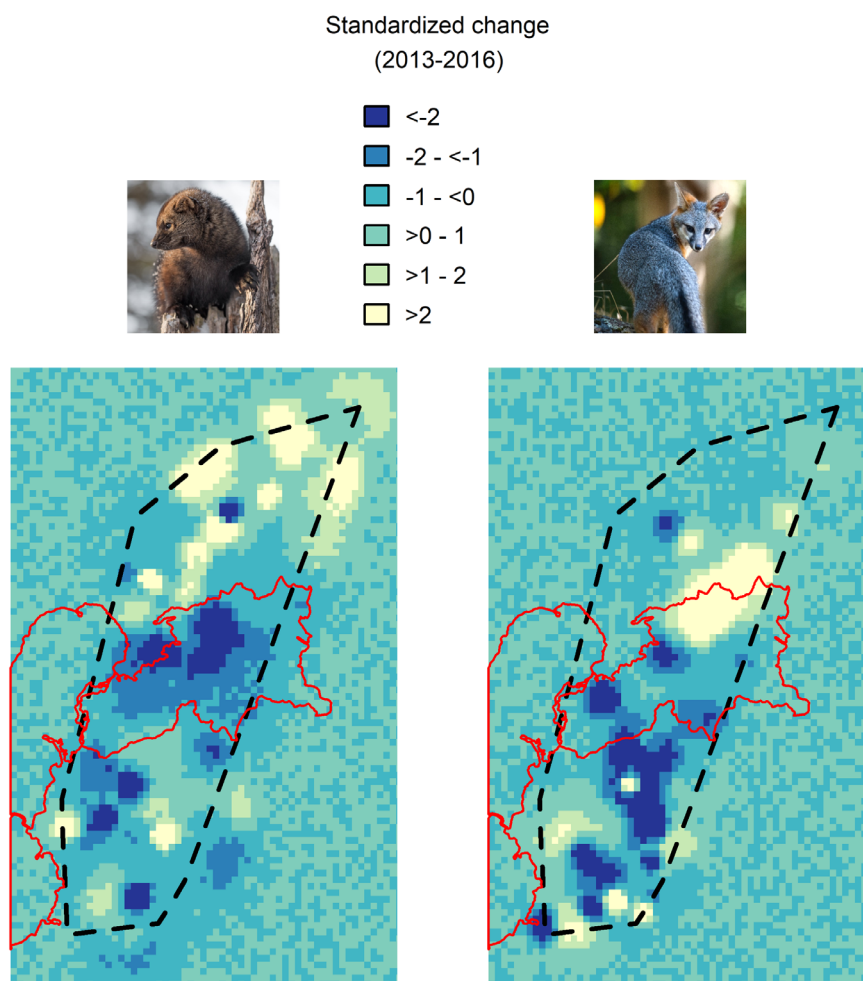


Fig. 4. Predicted change in fisher and gray fox activity center density and distribution from 2013 to 2016. This value was calculated as the difference between the number of estimated activity centers in each  $500 \times 500$  m grid cell in 2013 subtracted from the number of activity centers in 2016. The resulting values were then standardized to have a mean of 0 and a standard deviation of 1. Darker and lighter colors indicate relatively fewer and more estimated activity centers in 2016 compared to the number that were there in 2013, respectively.

User's accuracies were 91.4% and 89.0% for logged and unlogged classes, respectively. Producer's accuracies were 85.3% and 93.6% for logged and unlogged classes, respectively (see

Appendix S1: Table S3 for full results). These results indicated higher errors of omission (14.7%) than commission (8.6%) for the logging class, pointing to a conservative estimate of

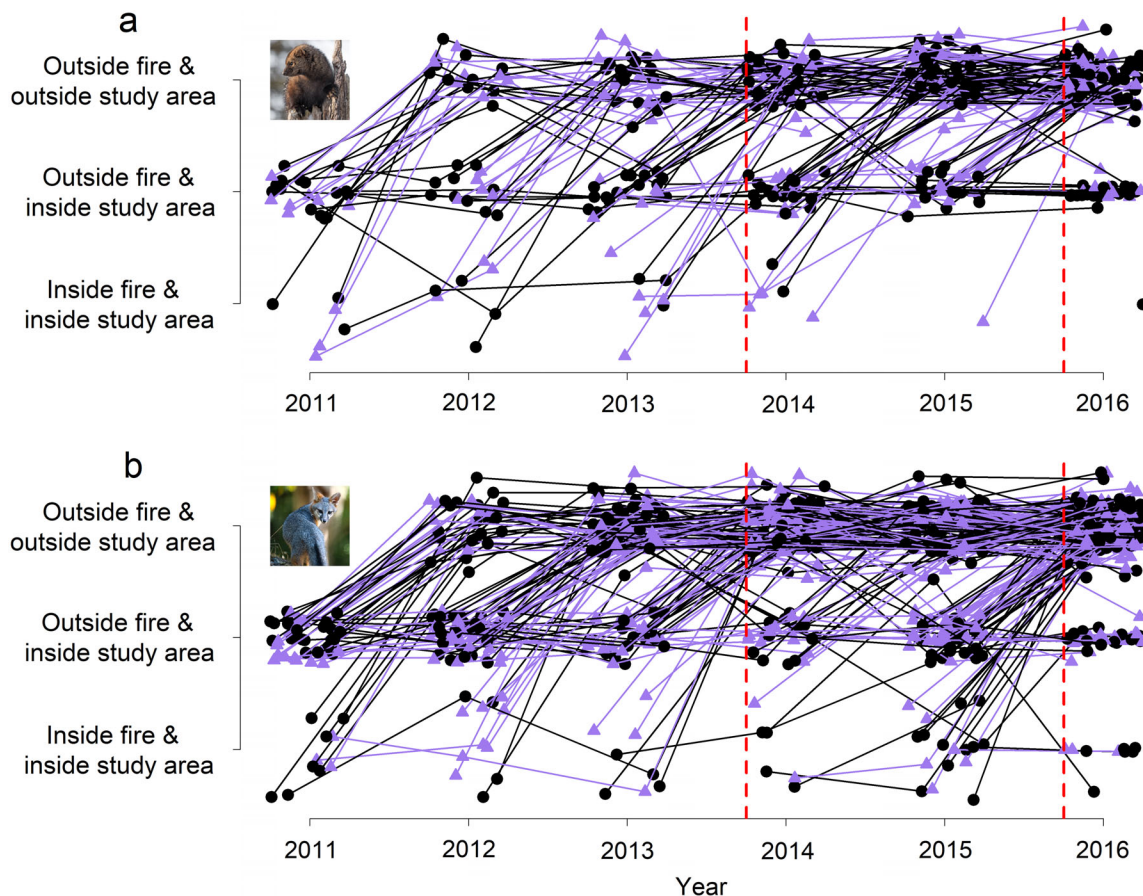


Fig. 5. Average predicted activity center locations of (a) fishers and (b) gray foxes detected at our sampling units broken up by three areas of our study area: (1) outside of the Beaver Fire perimeter and outside of the study area, (2) outside of the Beaver Fire perimeter and inside the study area, and (3) inside the Beaver Fire perimeter and inside the study area. Each purple triangle and black circle represent a female or male individual animal detected at one of our sampling stations, respectively. Individuals are shown starting the year of their first detection through the end of the study. Animals categorized as “Outside fire & outside study area” could indicate that they have died, dispersed, or relocated their activity centers.

salvage logging in our raster prediction. Based on pixel counts in the map, salvage logging occurred in at least 21 km<sup>2</sup> within the Beaver Fire perimeter by September 2015 (Fig. 1d).

#### *Effects of wildfire, salvage logging, and interspecific interactions on fisher and gray fox density and distribution*

For fishers and gray foxes, the predicted density of activity centers in each grid cell from 2012 to 2016 had a 100% probability of being positively correlated with the previous year's density ( $\alpha_1$  median and 95% credible interval on the log

scale = 0.145 [0.141, 0.150] for fisher and 0.189 [0.185, 0.193] for gray foxes; Table 3). The proportion of area burned within each grid cell had significant negative effects on the density of fishers (Table 3, Fig. 6). The probability that low-, medium-, and high-severity fire had negative effects on fisher density was 100% ( $\alpha_2$  median and 95% credible interval on the log scale = -0.013 [-0.016, -0.010],  $\alpha_3$  = -0.020 [-0.024, -0.017],  $\alpha_4$  = -0.023 [-0.026, -0.020]; Table 3, Fig. 6). The probability that low- and medium-severity fire had negative effects on gray fox density was 57% and 99%, respectively



Table 1. Posterior parameter estimates from the spatial open population capture–recapture model for the probability of detection by year intercept ( $\beta_0$ ), the effects of sex ( $\beta_1$ ; female) and previous visit ( $\beta_2$ ) on detection probability, sex-specific movement parameters in m ( $\sigma$ ), and the probability that an individual was a female ( $\psi_{\text{sex}}$ ).

Species	Parameter	Mean	SD	Credible interval		
				2.5	50.0	97.5
Fisher	$\beta_{02011}$	−1.93	0.22	−2.36	−1.93	−1.51
	$\beta_{02012}$	−1.56	0.23	−2.01	−1.57	−1.11
	$\beta_{02013}$	−1.89	0.24	−2.36	−1.89	−1.42
	$\beta_{02014}$	−1.88	0.23	−2.34	−1.87	−1.43
	$\beta_{02015}$	−1.37	0.21	−1.79	−1.37	−0.95
	$\beta_{02016}$	−1.75	0.21	−2.15	−1.75	−1.34
	$\beta_1\text{-sex (F)}$	−1.30	0.29	−1.88	−1.30	−0.73
	$\beta_2\text{-previous}$	2.54	0.21	2.15	2.54	2.98
	$\sigma_m$	1856.08	82.00	1702.80	1852.18	2027.98
	$\sigma_f$	1477.13	182.91	1177.81	1457.57	1891.09
	$\psi_{\text{sex}}$	0.61	0.05	0.50	0.61	0.71
Gray fox	$\beta_{02011}$	−2.55	0.28	−3.10	−2.55	−2.01
	$\beta_{02012}$	−2.22	0.27	−2.74	−2.22	−1.71
	$\beta_{02013}$	−2.35	0.28	−2.90	−2.35	−1.80
	$\beta_{02014}$	−2.28	0.33	−2.91	−2.28	−1.64
	$\beta_{02015}$	−2.17	0.25	−2.66	−2.17	−1.67
	$\beta_{02016}$	−2.61	0.29	−3.15	−2.61	−2.04
	$\beta_1\text{-sex (F)}$	0.13	0.22	−0.31	0.13	0.57
	$\beta_2\text{-previous}$	1.84	0.21	1.43	1.84	2.25
	$\sigma_m$	1152.37	106.12	967.87	1143.15	1380.15
	$\sigma_f$	1241.92	92.75	1076.53	1236.58	1440.39
	$\psi_{\text{sex}}$	0.46	0.04	0.38	0.46	0.54

( $\alpha_2$  median and 95% credible interval on the log scale = 0 [−0.003, 0.002],  $\alpha_3$  median, and 95% credible interval on the log scale = −0.003 [−0.006, 0]), but high-severity fire had a 100% probability of having a positive effect on gray fox density ( $\alpha_4$  median and 95% credible interval on the log scale = 0.008 [0.005, 0.011]; Table 3, Fig. 6). The probability that salvage logging had negative effects on fisher and gray fox density was 97% and 100%, respectively (fisher  $\alpha_5$  median and 95% credible interval on the log scale = −0.005 [−0.010, 0], gray fox  $\alpha_5$  median and 95% credible interval on the log scale = −0.011 [−0.015, −0.007]; Table 3, Fig. 6). The predicted density of fishers in a grid cell had a 93% probability of having a positive effect on the density of gray foxes in the following year ( $\alpha_6$  median and 95% credible interval on the log scale = 0.003 [−0.001, 0.007]; Table 3).

## DISCUSSION

Though measured in the short term, our results are some of the first conclusive evidence

to demonstrate the variable effects of wildfire on the demography of carnivorous species. We found that the wildfires that occurred in Klamath affected fisher density negatively. Density of fisher activity centers decreased in areas that burned regardless of burn severity, while density of gray fox activity centers decreased in areas that burned at medium severity and increased in areas that burned at high severity. We also found that salvage logging following the Beaver Fire affected both fishers and gray foxes negatively. Further information on the long-term effects of fire and salvage logging on carnivores is essential, especially regarding changes in survival or reproduction. The extent and intensity of wildfires are expected to increase under future climate scenarios (Stephens 2005, Lutz et al. 2009, Miller et al. 2009, 2012), and our data suggest that changing fire regimes will have negative effects on fisher populations.

We estimated a 27% reduction in the total number of fishers within our study area following the fires, a decrease that largely occurred

Table 2. Derived posterior parameter estimates for apparent survival ( $\phi$ ) and recruitment ( $\Gamma$ ) for fishers and gray foxes over time in Klamath calculated using a spatial open population spatial capture–recapture model.

Species	Parameter	Mean	SD	Credible interval		
				2.5	50.0	97.5
Fisher	$\phi_{2011}$	0.67	0.14	0.41	0.67	0.95
	$\phi_{2012}$	0.70	0.15	0.41	0.70	0.97
	$\phi_{2013}$	0.68	0.14	0.41	0.68	0.95
	$\phi_{2014}$	0.58	0.13	0.34	0.57	0.87
	$\phi_{2015}$	0.71	0.16	0.39	0.72	0.98
	$\Gamma_{2012}$	0.03	0.03	0.00	0.03	0.10
	$\Gamma_{2013}$	0.14	0.06	0.04	0.13	0.26
	$\Gamma_{2014}$	0.11	0.06	0.01	0.11	0.24
	$\Gamma_{2015}$	0.08	0.05	0.01	0.07	0.18
	$\Gamma_{2016}$	0.15	0.07	0.04	0.14	0.31
Gray fox	$\phi_{2011}$	0.77	0.13	0.50	0.77	0.98
	$\phi_{2012}$	0.74	0.13	0.50	0.73	0.97
	$\phi_{2013}$	0.51	0.12	0.31	0.51	0.77
	$\phi_{2014}$	0.88	0.10	0.64	0.90	1.00
	$\phi_{2015}$	0.78	0.13	0.51	0.80	0.99
	$\Gamma_{2012}$	0.07	0.05	0.00	0.05	0.20
	$\Gamma_{2013}$	0.04	0.04	0.00	0.03	0.13
	$\Gamma_{2014}$	0.08	0.06	0.00	0.07	0.22
	$\Gamma_{2015}$	0.33	0.10	0.16	0.32	0.55
	$\Gamma_{2016}$	0.10	0.09	0.00	0.08	0.33

Notes: Apparent survival estimates indicate the probability that an individual present in that year will survive to the following year and apparent recruitment estimates indicate the probability that a previously undetected individual will be recruited into the population in that year.

within the Beaver Fire perimeter, was irrespective of burn severity, and became apparent the first full year following the fires. We posit that the one-year lag in observed population decline was due to our sampling occurring immediately after the fires occurred in 2014, leaving little time for fishers to alter their home ranges or space-use patterns. Our population estimates were calculated for the entire study area and consequently lack the precision needed to show statistically significant changes in population size due to fire. Nonetheless, we suspect that fishers whose home ranges were burned either partially or completely in the Beaver Fire likely abandoned those home ranges or perished due to indirect negative effects from the fire (e.g., increased susceptibility to predation, altered prey availability). The animals detected within the fire perimeters two or more years following the Beaver Fire (1 female in 2015 and 1 male in 2016) were likely dispersing

individuals attempting to establish home ranges and the female was not detected again. Given fishers' territoriality, and the observed spatial responses of fishers to fires that we have documented here, it stands to reason that the fires caused major rearrangements of the space-use patterns of the fisher population. The effects of wildfires on fisher populations elsewhere may be different and may also be partially explained by forest conditions prior to the occurrence of wildfires.

The population of gray foxes was decreasing in Klamath prior to the wildfires, but rebounded following them. Although we do not have any data to know the mechanism for their declines, one hypothesis is that the gray fox population in Klamath was decreasing due to a disease outbreak before the wildfires occurred. Gray foxes are widely distributed throughout North America and are highly susceptible to population-limiting pathogens that cycle through wildlife communities (Davidson et al. 1992). Although fishers are susceptible to the same diseases that negatively affect foxes (e.g., Keller et al. 2012), it is possible that infection in fishers did not lead to the same rate of mortality as seen in gray foxes. An additional hypothesis for the decrease in the gray fox population is negative effects from the fisher population. Fishers limit the persistence of gray fox occupancy in areas where they co-occur, though foxes are also more likely to colonize areas where fishers are present (Green et al. 2018). Similar to previous research (Green et al. 2018), we also found that gray fox density correlated positively with fisher density in the previous year, indicating that gray fox density increased in areas with high fisher density. Gray foxes and fishers both persist on similar prey and it is possible that this relationship is reflective of this dietary overlap. Gray fox numbers increased in 2015 and 2016 within the fire perimeters. Thus, the gray fox population could have benefited from the direct and indirect negative effects of the wildfires on the fisher population. Yet another hypothesis is that an unknown stochastic event (e.g., decline in prey) could have affected the gray fox population. If the decrease in the number of gray foxes was mediated by some other habitat-related change, however, we might have seen concomitant declines in fisher numbers (Monterroso et al. 2016). Additional monitoring is needed to better understand the

Table 3. Results from the generalized linear model that estimated the effects of burn severity and salvage logging on fisher and gray fox density and distribution in Klamath.

Species	Parameter	Mean	SD	Credible interval		
				2.5	50.0	97.5
Fisher	a0 <sub>2011</sub>	-3.947	0.005	-3.956	-3.947	-3.938
	a0 <sub>2012</sub>	-4.244	0.005	-4.253	-4.244	-4.235
	a0 <sub>2013</sub>	-3.822	0.005	-3.831	-3.822	-3.813
	a0 <sub>2014</sub>	-3.926	0.005	-3.936	-3.926	-3.917
	a0 <sub>2015</sub>	-4.253	0.005	-4.262	-4.253	-4.244
	a0 <sub>2016</sub>	-3.974	0.005	-3.983	-3.974	-3.964
	a1-previous	0.145	0.002	0.141	0.145	0.150
	a2-low fire	-0.013	0.002	-0.016	-0.013	-0.010
	a3-medium fire	-0.020	0.002	-0.024	-0.020	-0.017
	a4-high fire	-0.023	0.002	-0.026	-0.023	-0.020
	a5-logged	-0.005	0.002	-0.010	-0.005	0.000
Gray fox	a0 <sub>2011</sub>	-2.925	0.004	-2.932	-2.925	-2.917
	a0 <sub>2012</sub>	-3.260	0.004	-3.268	-3.260	-3.252
	a0 <sub>2013</sub>	-3.418	0.004	-3.426	-3.418	-3.410
	a0 <sub>2014</sub>	-3.737	0.004	-3.745	-3.737	-3.730
	a0 <sub>2015</sub>	-2.940	0.005	-2.949	-2.940	-2.930
	a0 <sub>2016</sub>	-3.343	0.004	-3.351	-3.343	-3.335
	a1-previous	0.189	0.002	0.185	0.189	0.193
	a2-low fire	0.000	0.001	-0.003	0.000	0.002
	a3-medium fire	-0.003	0.001	-0.006	-0.003	0.000
	a4-high fire	0.008	0.001	0.005	0.008	0.011
	a5-logged	-0.011	0.002	-0.015	-0.011	-0.007
	a6-fisher	0.003	0.002	-0.001	0.003	0.007

*Notes:* We present the posterior parameter estimates for the year-specific intercept ( $\alpha_0$ ), the effect of the density of fishers and gray foxes in the previous year on current density ( $\alpha_1$ ), and the effects of the proportion of a grid cell that burned at low ( $\alpha_2$ ), medium ( $\alpha_3$ ), high severity ( $\alpha_4$ ), and was salvage logged ( $\alpha_5$ ) on the log scale. For foxes, we also included an effect of the density of fishers in the previous year on gray fox density ( $\alpha_6$ ).

mechanisms influencing the gray fox population in Klamath.

The fire regimes in western North American landscapes are changing following decades of fire suppression, timber harvest, and an increasingly warmer and dryer climate (Odion et al. 2004, Calkin et al. 2015, Diffenbaugh et al. 2015, Abatzoglou and Williams 2016, Zald and Dunn 2018). The long-term effects of these changing fire regimes on forest-dependent species are uncertain and require further research. The short-term effects, however, are likely to be negative for some species. For species that persist in restricted distributions and are sensitive from a conservation perspective, such as the fisher, rapid changes to forest structure could threaten long-term persistence. The Klamath-Siskiyou Ecoregion, where we studied fishers, was the geographic center of the largest population of fishers in the western United States (U.S. Fish and Wildlife Service 2016b, Furnas et al. 2017). In

the time since Furnas et al. (2017) estimated an average density of 6.6 fishers per 100 km<sup>2</sup> (i.e., 3196 fishers) in the ecoregion and adjacent areas, nearly 11,910 km<sup>2</sup> (24%) of their 48,760 km<sup>2</sup> estimated distribution has burned through 2020 (National Interagency Fire Center 2021). Although fishers adapted to persist in landscapes that historically experienced periodic wildfires, the increased size and severity of recent fires (Jones et al. 2016, Coop et al. 2020) may have lasting negative effects on their persistence (U.S. Fish and Wildlife Service 2016b).

Empirically evaluating the effects of wildfires on wildlife communities that depend on mature forests is challenging due to the spatial and temporal stochasticity of fires. Further, many studies are unable to disentangle the effects of fires from naturally occurring population variation due to a lack of pre-fire data, small sample sizes, by only examining short-term effects, or by studying only a single species (see Rockweit et al. 2017).

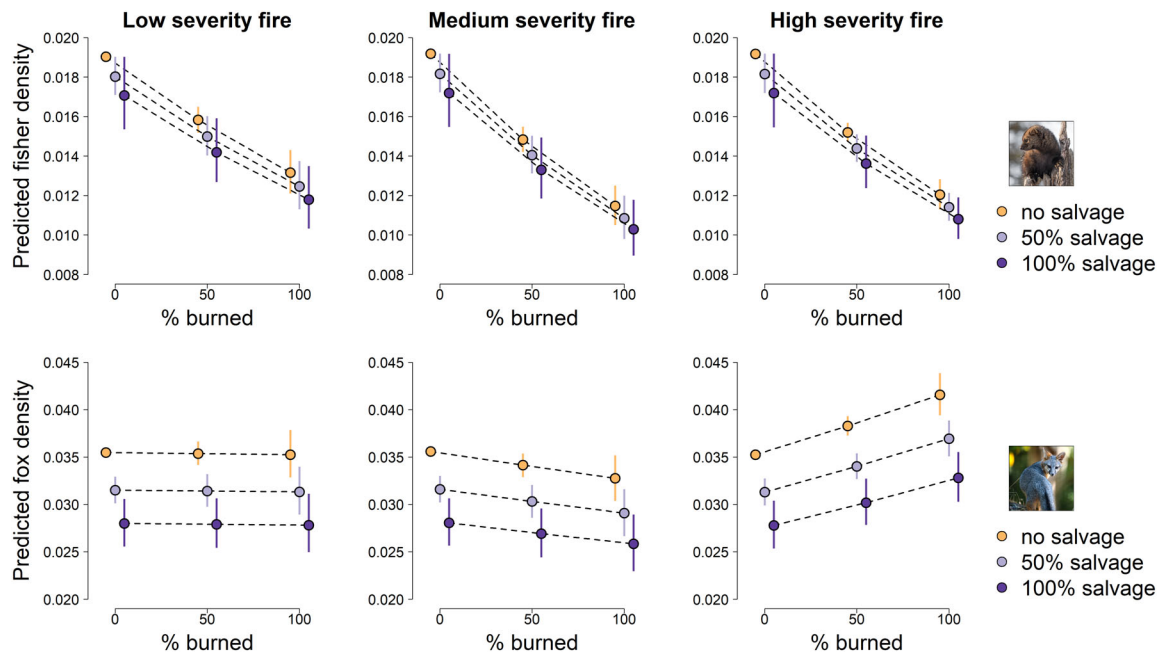


Fig. 6. Predicted density (# of activity centers per 0.25 km<sup>2</sup>) of fishers and gray foxes within the Beaver Fire perimeter by varying amounts of fire (% burned) and salvage logging. The orange, light purple, and dark purple circles indicate the predicted effects of varying amounts of salvage logging on fisher and gray fox density.

By leveraging a unique multi-species data set that spanned the periods before, during, and after disturbance events in Klamath, we were able to elucidate the short-term effects of wildfire and salvage logging on the spatial ecology, demography, and interspecific interactions of two carnivorans of interest. Non-invasive genetic sampling is an efficient method for multi-species monitoring (Golding et al. 2018) and was critical in the current work for evaluating the effects of these stochastic events on two species concurrently. As exemplified by the current work, this technique can provide a powerful approach to evaluate the effects of stochastic events and landscape change on the distribution, demography, and interspecific interactions of wildlife.

Nonetheless, there are some limitations to this work. Our results are limited in that they reflect the effects of three fires on a single study area, consider only the short-term effects of these fires and salvage logging, and estimate the correlation of population changes to the occurrence of fires and salvage logging. As has been documented in reviews of wildlife responses to wildfires (Geary et al. 2020, Volkmann et al. 2020), it is also

possible that the effects of wildfires on species or populations may vary due to spatial or temporal variations in landscape structure and fire characteristics. Reaching a consensus on the effects of mixed-severity wildfires on forest species may require estimating the responses of many taxa to wildfires of varying frequency and severity, and an investment in research on the long-term effects of wildfire on wildlife populations and communities. Given the slow life histories of many carnivorans, including fishers, long-term multi-species monitoring is imperative to understand and to differentiate between short- and long-term effects.

Forest and fuels management, fire, and post-fire forest management under the influence of a changing climate will have an outsized role in the conservation of forest-obligate carnivorans. We found that the estimated 21 km<sup>2</sup> of salvage logging that occurred within the Beaver Fire perimeter had additive negative effects on the density of both fishers and gray foxes (Fig. 6). Logging following wildfires can alter forest succession trajectories and reduce biodiversity (Thorn et al. 2018). Although the short-term effects of fuels management and restoration on



mature forest-dependent species are variable, limited evidence suggests that fuels treatments have negative effects on fisher occupancy and population size (e.g., Thompson et al. 2011, Scheller et al. 2011, Garner 2013, Sweitzer et al. 2016), and alter the movement patterns and physiology of similar mustelid species (Moriarty et al. 2016, Martin et al. 2020). Whether these effects are mitigated by the indirect, positive effects of fuels treatments to reducing the extent and severity of wildfires is unclear. We do not know the effects, if any, of previous fuels management on the population of fishers in Klamath or how fuels treatments influenced the wildfires we studied here.

Continued conservation of fishers and other forest-dependent species will require an understanding of the tradeoffs between short- and long-term effects of fuels management alternatives and varying wildfire severities to habitat and population densities (Tempel et al. 2015, Sweitzer et al. 2016). The negative consequences of fuels management may outweigh the negative effects of increasingly frequent and severe wildfire regimes (Scheller et al. 2011, Sweitzer et al. 2016, Ganey et al. 2017, Rockweit et al. 2017, Banerjee 2020, Stephens et al. 2020, Knapp et al. 2021). For instance, forest conditions used by fishers for reproduction in a fire-suppressed landscape in the southern Sierra Nevada, USA, were also found in a neighboring landscape with a largely restored fire regime, although fishers did not occupy the fire-restored landscape (Blomdahl et al. 2019). Conservation of forest-dependent species in changing wildfire regimes will require a balance between the short-term effects of fuels management and restoration with the negative effects of high-severity wildfires under a changing climate. By disentangling these forces, we may be able to conserve sensitive wildlife communities in a changing world.

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## LITERATURE CITED

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3877/full>