FIRE SEVERITY MEDIATES MARTEN AND FISHER OCCURRENCE: IMPACTS OF THE DIXIE FIRE ON A CARNIVORE COMMUNITY

By

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ABSTRACT

FIRE SEVERITY MEDIATES MARTEN AND FISHER OCCURRENCE: IMPACTS OF THE DIXIE FIRE ON A CARNIVORE COMMUNITY

Christopher James Collier

The consumption of an astounding one million acres resulted from California's largest single fire to date, the 2021 Dixie Fire. The social and economic losses associated with the fire were immediately apparent, but the effects on wildlife remained unknown. While previous research has suggested mixed or low severity fire may be beneficial to certain wildlife species, the responses to megafires are poorly understood for many carnivores. To better understand these responses to severe fire, I used a random sampling design stratified by burn severity to survey in and around the Dixie Fire footprint using baited camera stations. This allowed me to determine the persistence of mesocarnivores of conservation concern including Pacific marten (*Martes caurina*) and fisher (*Pekania pennanti*) in a post-fire landscape. I estimated occupancy at multiple scales using metrics related to burn severity, post-fire forest structure, and prey availability. With increasing levels of burn severity, I found that Pacific marten occupancy increased, and fisher occupancy decreased. Pacific marten may be using burned forest for hunting, as mouse/vole (*Peromyscus/Microtus/Myodes* spp.) species also had a positive relationship with burn severity. Predators and competitors persisted in the burned areas, and coyotes (*Canis latrans*) had a strong positive relationship with burn severity. My results provide insight into how a carnivore community responds to high severity fire and are applicable to regions worldwide that are experiencing a shifting fire paradigm. I equip land managers with forest volumetric information correlated with occurrence data that can inform restoration in large wildfires to benefit carnivore communities.

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District for providing so many cameras worth of data from north of Lassen National Park. Thank you, Colin Dillingham at Plumas NF - Mount Hough District for providing logistical support on the Plumas, teaching us about the fire ecology of the region, and showing us around on our first field day. I also want to thank Colin's crew, Danielle McCauley, Harrison Stoudt, and others, for surveying the Bucks Lake Wilderness and some of the furthest points surrounding it. I thank Jennifer Carlson and Pete Figura with the California Department of Fish and Wildlife for providing marten detections in some key locations for which we did not have permits. I also owe a huge thanks to Bennie Johnson with Collins Pines Company who was instrumental in my sampling. Thank you all for so generously providing your assistance and for sampling locations we would have never been able to access. Furthermore, my crew would not have felt as safe and capable without knowing we could have called upon you.

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INTRODUCTION

The fuelscape has dramatically changed across western North America since the 1800s (Hagmann et al. 2021). This has been attributed to the end of burning and tending of the land by indigenous peoples (Anderson and Moratto 1996, Kimmerer and Lake 2001), which was followed by aggressive timber harvest and intensive grazing (Swetnam et al. 2016). These factors, in combination with widespread fire suppression, often implemented through federal policy (e.g., Stephens and Ruth 2005), led to an increase in the loading and continuity of fuels (Busenberg 2004, Steel et al. 2015). Subsequent warming and drying of forests in the western United States due to climate change further contributed to fire potential (Abatzoglou and Williams 2016, Williams et al. 2019, Parks and Abatzoglou 2020). As a result, wildfires, in much of the western United States, have been increasing in severity and number, with many becoming larger in size (Parks and Abatzoglou 2020).

This new paradigm is especially apparent in the interior forests of California (Miller et al. 2009, Steel et al. 2015, Williams et al. 2019). Prior to European settlement, these forests were characterized by low to moderate intensity fires which occurred at frequent intervals (e.g., Sierra Nevada, Swetnam 1993; Southern Cascades, Miller and Safford 2017). Given that predictions show a continued increase in fire severity and size through the year 2050 (Abatzoglou et al. 2021), assessing the risks and effects of wildfire on ecosystems is warranted and increasingly becoming a priority for land managers (Hagmann et al. 2021).

Fire can affect forested ecosystems through broad changes in structure. It consumes vegetation, including plants that are inedible to animals (Bond and Keeley 2005), which can release nutrients and stimulate new growth (e.g., aspen (*Populus tremuloides*) regeneration, Wan et al. 2014). Depending on severity, fire can either remove understory and dead material or completely kill stands of trees (Bond and Keeley 2005). Over time, pyrodiversity (i.e., fires mixed in severity and frequency) can promote heterogeneous and more biodiverse forests (Jones and Tingley 2022). Larger trees, common in heterogeneous forests, can be more resilient to fire than smaller trees (Ryan and Reinhardt 1988, Hurteau and North 2009) and provide key rest, nest, or den structures for many species of wildlife. Globally, very large trees have declined (Lindenmayer et al. 2012), and tree die-off in general is accelerating from drought stress, climate change, and disease (Anderegg et al. 2013), which is deleterious to the integrity of ecosystems and could leave them more susceptible to fire. These landscape changes to forest structure influence not only vegetation, but they can also have implications for wildlife.

Vertebrate species show varied responses to the environmental modifications caused by fire. Certain species show positive responses, including birds that use snags created by fire for nesting and foraging, such as the black-backed woodpecker (*Picoides arcticus*, Hutto 1995). Other groups are more sensitive to fire and exhibit negative responses through decreases in abundance (e.g., small mammals, cervids, and canids; Fisher and Wilkinson 2005). Gray fox (*Urocyon cinereoargenteus*) experienced fire-associated declines in a study quantifying scat index, while coyotes (*Canis latrans*) remained unchanged (Cunningham et al 2006). Another study found that coyotes selected for recently burned (> 1 year) over unburned forests (Stevenson et al. 2019). Many studies investigating vertebrate species' relationship with fire have focused on small mammals or birds (Fontaine and Kennedy 2012), ungulates, and apex predators (Volkmann et al. 2020), though mesocarnivore responses, in particular mustelids, are relatively understudied (but see Fisher and Wilkinson 2005).

The Pacific marten (*Martes caurina*), formerly understood with a wider geographic distribution as the American marten (*Martes americana*; Dawson et al. 2017), is a medium-sized carnivore and member of the weasel family, Mustelidae. Several subspecies of the Pacific marten occur in California (Schwartz et al. 2020). Specifically, Humboldt martens (*M. c. humboldtensis*) inhabit the coastal temperate forests of southern Oregon and northern California and are listed as endangered by the state of California and federally as threatened (CDFW 2018, USFWS 2020a). Pacific martens in the Sierra Nevada mountains (*M. c. sierrae*; Dawson and Cook 2012) are found in the higher-elevation southern Cascades and Sierra Nevada and are ranked as vulnerable in California (CNDDB 2023). However, a thorough review of phylogenetics is needed to determine the full variation of subspecies (Dawson et al. 2017); my study inference focuses on Pacific martens, drawing new evidence from a study area within the southern Cascade and northern Sierra Nevada mountains.

The Pacific marten has suffered declines across much of its historical range (Laliberte and Ripple 2004, Zielinski et al. 2005, Moriarty et al. 2011), and habitat loss has occurred between the southern Cascade and northern Sierra Nevada populations

(Zielinski et al. 2005). Range reduction may have left the population in Lassen National Forest genetically isolated and at risk of extirpation. It remains uncertain, but marten population declines are suspected to be a byproduct of broad-scale strychnine and 1080 poisoning throughout most of the western states, where airdropped poison-laced carcasses were deployed to access remote montane ridgelines during predator removal campaigns (e.g., Hall 1930, Adams 1930, Leopold et al. 1964). A long history of commercial trapping of martens for fur likely contributed to initial declines (Grinnell et al. 1937), though a ban on hunting them in California was enacted in 1954 (Biberdorf 1982). By 2004, martens had experienced an estimated 21% contraction of their historical home range (Laliberte and Ripple 2004), and in some regions of the Sierra Nevada, this downward trend has persisted (e.g., Moriarty et al. 2011).

Martens are considered specialists, as they are often associated with forests that have late-successional characteristics composed of high percent canopy cover, large trees, snags, and logs, and complex vertical and horizontal structure (Spencer et al. 1983, Tweedy et al. 2019). In the Sierra Nevada, martens occur in higher elevation forests, where wildfires generally occur less frequently (Taylor 2000, Zielinski 2014), but climate change and the shifting fuelscape are increasing the frequency of wildfire.

Few studies have examined the effects of fire on Pacific martens. In the 1970s, researchers in Idaho documented marten avoiding burned stands in winter (Koehler and Hornocker 1977). In Yellowstone National Park, marten were observed using lodgepole pine forest after fire, though burn severity was not directly addressed (Sherburne 1992). A study in Washington, USA and British Columbia, Canada found that Pacific martens persisted in post-fire landscapes, but GPS-collared individuals altered their movement patterns to avoid high-severity burn areas, and they showed preference for low-severity areas (Volkmann and Hodges 2021, 2022). In the Alaskan taiga, it was hypothesized that recent burns were population sinks for American martens because researchers found a higher percentage of juveniles (94%) in burned areas 6-9 years post-fire compared to unburned (63%; Paragi et al. 1996). Combined, evidence largely suggests martens avoid post-fire landscapes or persist only temporarily.

Fuel reduction treatments, which involve the removal of biomass and small-diameter trees, are currently being used to reduce the severity of wildfire (Agee and Skinner 2005). These treatments aim to reduce fire potential and can be beneficial for some species of birds and small mammals (Fontaine and Kennedy 2012), though more research is needed to determine responses for many species of wildlife to treatment (Verschuyl et al. 2011, Kalies and Yocom Kent 2016). Martens were negatively affected by fuel reduction treatments in a study conducted in Lassen National Forest, California (Moriarty et al. 2016), which is further evidence of their sensitivity to disturbance.

Fishers (*Pekania pennanti*) are larger members of the weasel family, more closely related to South American tayra (*Eira barbara*) than they are to martens, providing many similarities but also distinct ecological differences. Like martens, they inhabit late-successional forests, but they are often associated with coniferous forests that are mixed with hardwoods (Zielinski et al. 2005). In the southern Sierra Nevada, fishers are found at lower elevations than martens and in areas that have less spring snowpack and generally warmer temperatures (Zielinski et al. 2017). In the western United States, residing in these areas places fishers in wildland urban interfaces with increased potential human conflict (e.g., encounters with dogs, increased concern of fire risk). Further, fishers may be more at risk from rural development, fuel, and fire thinning (e.g., Sweitzer et al. 2016), and large severe fires (Thompson et al. 2021).

Fishers have declined across much of their historic range (Lewis et al. 2012), including in the Sierra Nevada (Zielinski et al. 2005), which has led to the listing of the species by the State of California as vulnerable and the southern Sierra distinct population segment (DPS) as critically imperiled (CNDDB 2023). In 2020, this population was listed as endangered under the Endangered Species Act (USFWS 2020b). Like martens, fishers were historically affected by trapping for their fur, loss of primary forest, broad-scale poisoning, and human development (Zielinski et al. 2005). Most fishers tested in California (79%) had been exposed to anticoagulant rodenticides often associated with illegal cannabis plantations (Gabriel et al. 2012, Thompson et al. 2014), which reduce fitness and may be furthering population declines.

Conservation concerns for fishers prompted reintroductions that began in 2009 in the northern Sierras (Facka et al. 2016, Green et al. 2022a). Reintroductions occurred on land managed by a private timber entity, Sierra Pacific Industries (SPI). The company’s logging practices employed in this area were designed to retain late-successional features (e.g., snags, large woody debris, wildlife trees). Following reintroductions, it has been estimated this population increased from 54 individuals (95% confidence interval 37-77) in 2011 to 119 (95% confidence interval 96-141) in 2017 (Green et al. 2022a), though surveys were restricted to SPI property. Some fishers dispersed onto the adjacent Lassen and Plumas National Forests, but it is unknown how far or how many.

Given that fishers are specialists of structurally complex forests, they may be exceedingly sensitive to disturbances such as fire. Fishers avoided burned areas that had high-severity fire in the southern Sierra Nevada (Thompson et al. 2021). Similarly, there was a significant decline in fisher abundance with all levels of burn severity three years after a fire in the Klamath Mountains of California (Green et al. 2022b). Green et al. (2022b) documented increases in population density for gray fox with increasing burn severity. This may suggest that specialist species (e.g., fisher) are potentially more negatively affected by fires than generalists (e.g., gray fox, Green et al. 2022b). From the combined literature on fishers and fire, fisher occurrence and use appear negatively correlated with both forest management and large fires, especially high severity fire.

Little is known about how martens and fishers are influenced by fire, especially large spatial extents of high severity fire. The largest single wildfire in California's history, the Dixie Fire, burned in 2021 within Lassen and Plumas National Forests, Lassen Volcanic National Park, and private lands (Figure 1). It consumed 963,309 acres (3,898 km^2; Cal Fire 2022b). Additionally, it was the most expensive fire to combat ($637 million) in U.S. history. The fire ignited from a large tree falling onto a powerline (Cal Fire 2022a) and burned from July 13 until October 25, 2021. Several communities were devastated by the fire, including nearly the entire town of Greenville, California. While the devastation to humans was astronomical, the impacts on wildlife have yet to be determined. The fire burned a large percentage of Pacific marten core habitat in the region (17.9% high severity and 6.9% moderate severity; Moriarty et al., unpublished data) and eclipsed source locations for the reintroduced population of fisher (Facka and Powell 2021, Green et al. 2022a). Given that these mustelids are thought to be among the carnivores most sensitive to disturbance (Zielinski et al. 2005), it is imperative that research be conducted to assess their persistence.

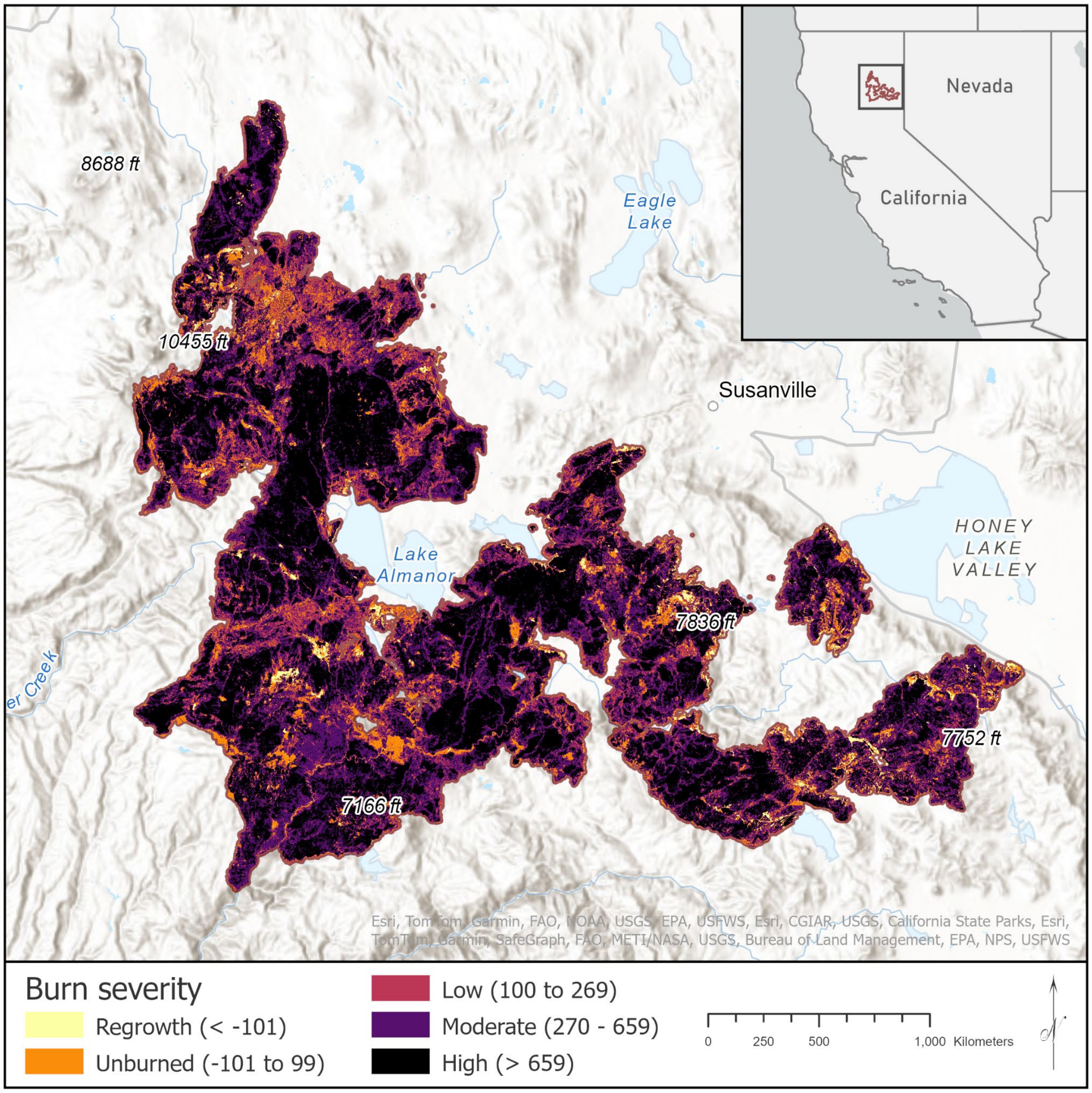


Figure 1. Dixie Fire burn severity as the relativized differenced Normalized Burn Ratio (rdNBR). Shaded colors represent burn severity classes, which were derived from Monitoring Trends in Burn Severity (MTBS.gov) data, and severity classes were determined according to Key and Benson (2006).

In addition to vegetation changes from fire or previous treatment, the occurrence of both potential competitors or predators and prey could influence marten and fisher distributions. Because martens and fishers are relatively small and have large energetic requirements, they are sensitive to both competition (e.g., through resource reduction) and predation. Competitor species in the Dixie Fire area include coyote, gray fox, striped skunk (*Mephitis mephitis*), and western spotted skunk (*Spilogale gracilis*). Carnivores suspected of predating on martens and fishers include coyotes, bobcats (*Lynx rufus*), and mountain lions (*Puma concolor*; Wengert et al. 2014, Delheimer et al. 2021, Martin et al. 2022a). Black bears (*Ursus americanus*) are not known to predate on martens or fishers, but they could have cascading effects through competitors or predators (Prugh et al. 2009; Figure 2).

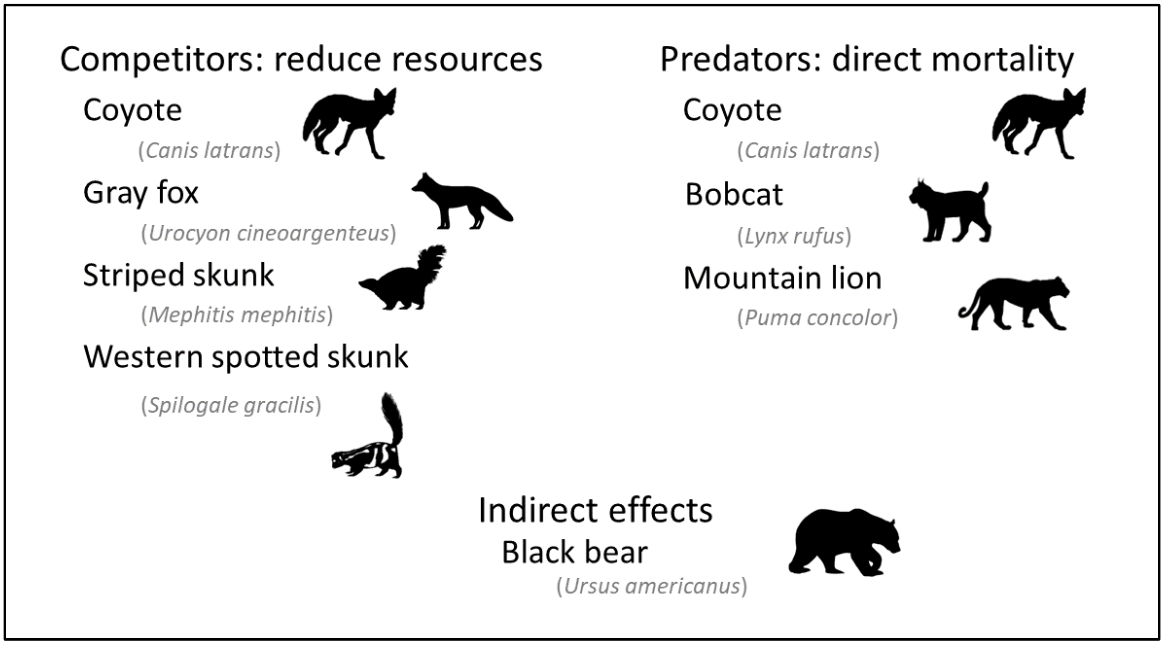


Figure 2. Predicted marten and fisher competitor and predator species present in the Lassen and Plumas National Forests that may have been affected by the 2021 Dixie fire.

One carnivore species that could increase in occurrence following fire is the gray fox (e.g., Borchert 2012, Green et al. 2022b). Little or no relationship with fire severity has been documented for black bears (Lewis et al. 2022), bobcats (Borchert 2012), and coyotes (e.g., neutral, Cunningham et al. 2006; increase, Stevenson et al. 2019). Western spotted skunks could elicit a positive relationship (e.g., association with low fire diversity, Furnas et al. 2022), though this has not been thoroughly studied. A previous study documented a decrease in density with increasing fire severity for striped skunk (Burke 2019), but this study had a very small sample size, so the relationship is uncertain (Figure 3).

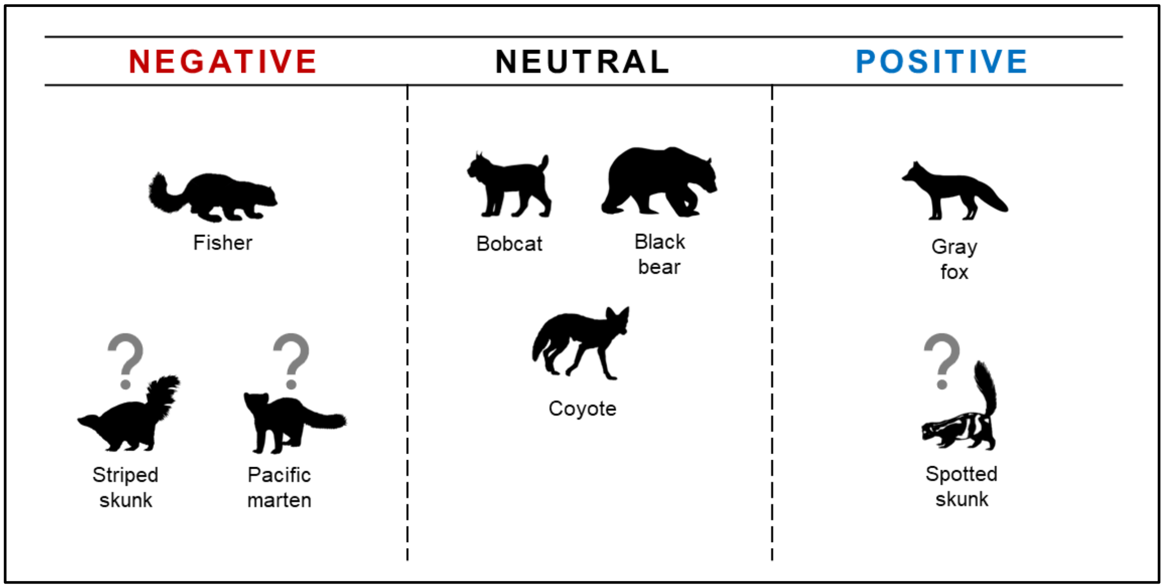


Figure 3. Possible carnivore relationships with increasing burn severity. Negative: fisher. Neutral: bobcat, black bear, and coyote. Positive: gray fox. Uncertain: Pacific marten, striped skunk, and spotted skunk.

Given that marten and fisher consume greater than 25% of their body weight daily with impressive metabolism (Iversen 1972, Worthen and Kilgore 1981), it has been hypothesized that prey availability strongly influences where these animals can survive (e.g., Powell 1982, Bissonette and Broekhuizen 1995). In the area of the Dixie fire, small mammal species that are likely consumed by martens include deer mice (*Peromyscus maniculatus*), voles (*Myodes* and *Microtus* sp.), chipmunks (*Neotamias* spp.), Douglas squirrels (*Tamiasciurus douglasii*), Humboldt's flying squirrels (*Glaucomys oregonensis*), and snowshoe hares (*Lepus americanus*; Martin 1994, Bull 2000, Martin et al., in prep). Likely prey species for fisher include Douglas squirrels, Humboldt's flying squirrels, western gray squirrels (*Sciurus griseus*), woodrats (*Neotoma* spp.), and California ground squirrels (*Otospermophilus beecheyi*; Townsend 2019; Martin 1994).

One prey species that may increase in number or density following high severity fire is the deer mouse (Tevis 1956, Gashwiler 1959, Zwolak and Foresman 2007, Borchert et al. 2014). Conversely, fire severity may reduce the occurrence of chipmunks (Borchert et al. 2014), Douglas squirrels (Roberts et al. 2015, Burke 2019), golden-mantled ground squirrels (*Callospermophilus lateralis*; Burke 2019), Humboldt's flying squirrels (Roberts et al. 2015), western gray squirrels (Roberts et al. 2015), snowshoe hares (Nelson et al. 2008), and woodrats (Zwolak and Foresman 2007, Burke 2019). Increasing fire severity was shown to have no effect on the number of California ground squirrels (Borchert et al. 2014; Figure 4).

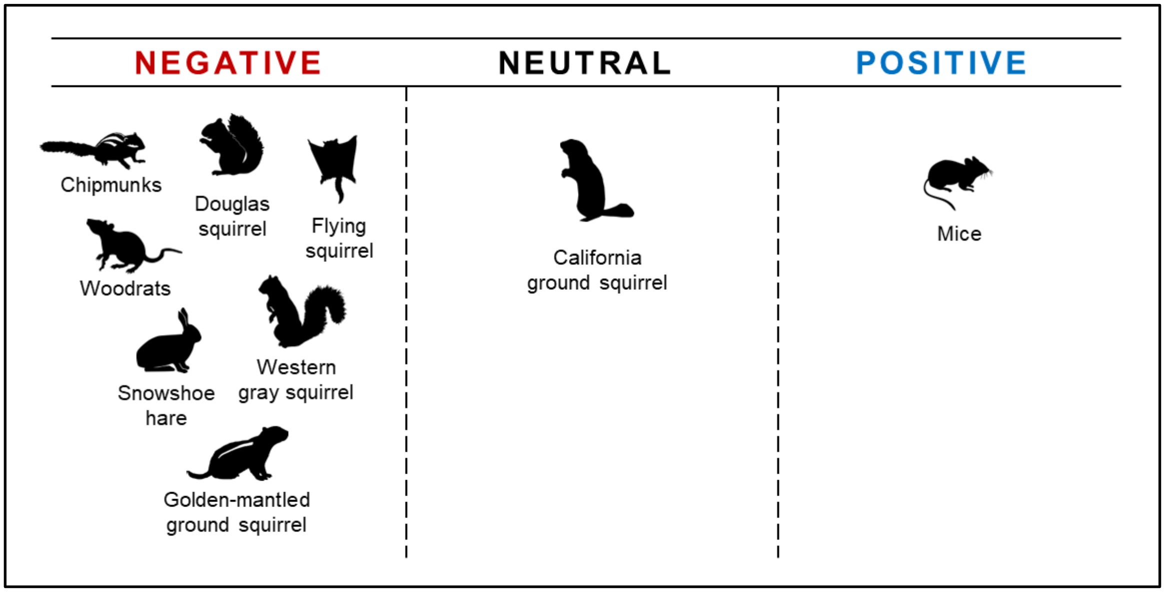


Figure 4. Possible small mammal relationships with increasing burn severity. Negative: chipmunks, Douglas squirrel, flying squirrel, woodrats, snowshoe hare, western gray squirrel, and golden-mantled ground squirrel. Neutral: California ground squirrel. Positive: mice.

My goal for this study was to survey within and surrounding the Dixie Fire footprint with baited camera stations to test whether post-fire occupancy of forest carnivores or their prey was mediated by severity. I aimed to quantify the direction of relationships with fire along a scale of burn severity using occupancy models. This is the first research to estimate occupancy of Pacific martens immediately after a fire (i.e., 1 - 2 years post-fire) and one of relatively few studies evaluating fisher occurrence post fire. I estimated post-fire occupancy relative to forest structural metrics that are important for management recommendations, and I performed scale optimization to determine the scales of these relationships. Additionally, I aimed to determine the post-reintroduction distribution of fishers within Lassen and Plumas National Forests. Post-fire occupancy for carnivore predator or competitor species (e.g., bobcat, coyote, gray fox, skunks) and prey (e.g., mice, squirrels, lagomorphs) was also estimated, with the caveat that the home ranges for some of these species (e.g., bobcat, coyote) were likely larger than the distance between sites, which can lead to overestimated predictions for occupancy.

The high intensity patches of the Dixie Fire likely reduced coarse woody debris and snags that martens and fishers are dependent on for resting and denning. Alternatively, the low to moderate intensity patches may have created new snags, and mixed severity areas have likely become more heterogeneous. I hypothesized that: 1) occupancy of late-seral specialists (martens and fishers) would negatively correlate with burn severity. I predicted that martens and fishers would occur less often in the moderate and high severity patches within the Dixie Fire. 2) Occupancy of generalists (e.g., black bear, gray fox, coyote bobcat, skunks) would either positively correlate or will not correlate with increasing burn severity. I predicted that most generalists would occur equally across the burn severity gradient, but that gray foxes would occur most often in the moderate and high severity. 3) Prey occupancy would differ by species but would positively correlate with burn severity for seed-eating rodents (e.g., mice), and negatively for cone or truffle consuming species (e.g., tree squirrels) except California ground squirrels which would have a neutral correlation. Thus, I predicted that mice would occur more often in moderate and high severity patches, California ground squirrels would occur equally across all severities, and all other prey species would occur more often in unburned and low severity areas.

METHODS

Study Area

The study area was located near (< 6 km) and within the Dixie Fire burn perimeter in Lassen and Plumas National Forests in northern California (Figure 5). This region spans the intersection between the northern Sierra Nevada and southern Cascade Mountain ranges. Mean minimum and maximum temperatures vary from -7.2 °C to 8.5 °C, respectively, in January and 7.8 °C to 32.4 °C in July (PRISM Climate Group 2020; 1991-2020). Locations on the western slope receive an average of 170 cm of precipitation per year, and those on the eastern slope receive approximately 60 cm (PRISM Climate Group 2020; 1991-2020), with most of it accumulating as snow in the winter. Elevations at sampling locations ranged from 1,075 to 2,540 m above sea level, though within the study area, Lassen Peak reaches 3,180 m. Forest cover dominates the region, but meadows, riparian zones, and shrub fields make up some proportion of the landscape. Tree species vary by elevation and aspect, and include ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyii*), lodgepole pine (*P. contorta*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), red fir (*A. magnifica*), incense cedar (*Calocedrus decurrens*), western white pine (*P. monticola*), mountain hemlock (*Tsuga mertensiana*), and quaking aspen (*Populus tremuloides*).

The fire regime in this region was historically characterized by frequently occurring fires that burned at low- to moderate-intensity (Swetnam 1993, Miller and

Safford 2017). Pre-European settlement fire size was influenced by climate, where fires were smaller and more frequent during warmer periods, and larger but less frequent during cooler periods (Swetnam 1993). Before 1905, fires in Lassen National Park burned in the lower elevation Jeffrey pine forest every 24.5 years and in higher red fir-western white pine every 75.9 years (Taylor 2000). Since then, more than a century of fire suppression, warming and drying attributed to climate change (Williams et al. 2019), and forest management practices have led to high fuel loadings and fires becoming larger and higher in severity (Miller and Safford 2017). The Dixie Fire was one such example of an exceedingly large fire burning at high severity in this region, and most of the area (70% or 2,743 km^2) had not burned in more than 37 years (Taylor et al. 2022). Within the past 25 years, the Storrie Fire burned 55,261 acres (223 km^2) in 2000 in both the Plumas and Lassen National Forests. The Moonlight Fire (2007) burned 64,997 acres (263 km^2). Two large fires occurred in the summer of 2012 and included the Reading Fire, which burned 28,079 acres (113 km^2) northeast of Lassen National Park, and the Chips Fire, which burned 75,431 acres (305 km^2) southwest of Lake Almanor.

Sampling Design

I used two data sets for my investigation. First, I created a stratified random design to place cameras proportionally by burn severity. At these locations, I collected site-specific data to validate remotely sensed data. Second, to maximize information from rare and seldom detected species, I compiled all available remote data including my surveys, incorporating surveys completed the year after the fire in previously surveyed locations (2022), and at opportunistic locations set by collaborators during 2022-2023.

I used a random sampling design stratified by burn severity class (i.e., unburned: < 99, low: 100 - 269, moderate: 270 - 659, and high: > 659; Key and Benson 2006). I created locations only on public lands within Lassen and Plumas National Forests or Collins Pines Company property and within a 6 km buffer around the Dixie Fire. I created site locations with the 'Create Random Points' tool in ArcGIS Pro (Version 3.1.2, ESRI, Inc., Redlands, California) with some strategic limitations. I restricted sites to be within 1 km (average distance = 261 m ± 237 SD) of the nearest road to increase efficiency in the field. I enforced a minimum spacing of 3 km (average spacing = 3.8 km ± 0.8 SD) at each site, with a site comprising two camera stations (see "Camera stations" section below for protocol; Figure 5). This average spacing was intentional in hopes of having stations independent for my focal species as the spacing represents an approximate 15 km^2 home range of a female fisher (Zielinski et al. 2004), and would be completely independent for martens with smaller home ranges (e.g., a female home range in this study area was ~2 km^2; Moriarty et al. 2016).

I randomly restricted sites within the burn severity classes with ratios that approximately reflected the area of each class within the study (23% low, 34% moderate, and 31% high severity) and the number of unburned sites to match the high severity ones. To assess burn severity, I created classes using a differenced Normalized Burn Ratio (dNBR) from Monitoring Trends in Burn Severity (MTBS 2023) that I averaged to 400 m resolution using a moving window analysis. I used the 400 m scale because it was the finest scale at which the ‘Create Random Points’ tool generated enough points within the study area. I then classified the raster into polygons using Key and Benson’s (2006) dNBR classes. I created a buffer of 1 km from all roads that occurred on Lassen or Plumas National Forest (TIGER and USFS), which I intersected with the burn severity polygons to restrict the area in which I placed my sites.

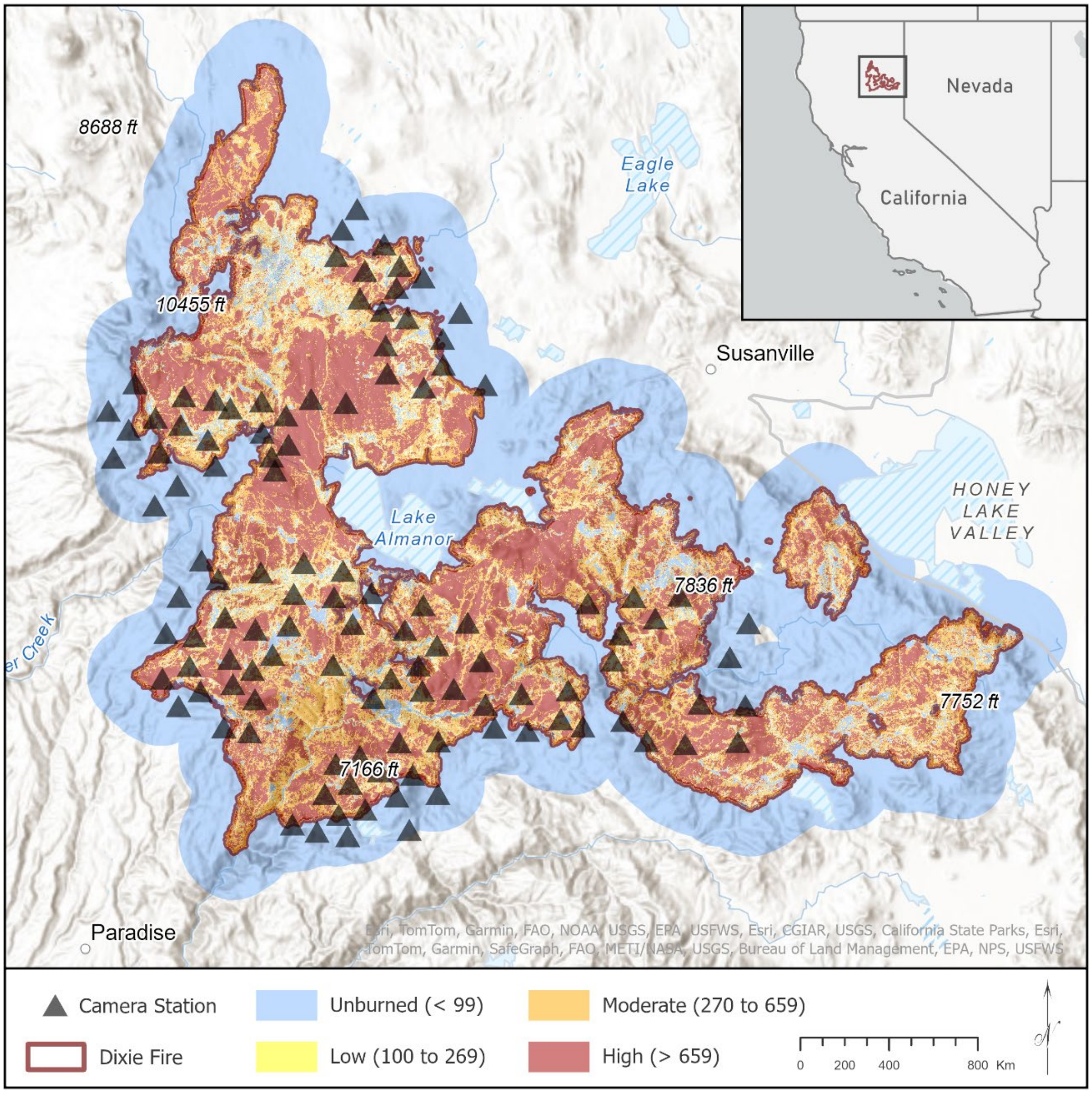


Figure 5. Paired camera locations (*n* = 115) from the summer 2023 Dixie Fire carnivore surveys in northern California. Shaded colors represent burn severity classes (Key and Benson 2006), which were derived from Monitoring Trends in Burn Severity (MTBS.gov) data.

Data Collection

Camera stations

I deployed 230 trail cameras (StealthCam, Irving, Texas, Browning, Morgan, Utah, and Bushnell, Overland Park, Kansas) at 115 sites within the Dixie Fire study area (June 6-August 30, 2023). I placed cameras in a paired configuration to increase detection probability (Pease et al. 2016, Evans et al. 2019), with one camera at the center of the site and another placed in a random compass direction and random distance between 100 and 300 m from the center (e.g., Moriarty et al. 2018). I affixed cameras to a tree, snag, or log approximately 2 meters above the ground and facing north to limit false triggers from direct sunlight. Camera settings included: 8-megapixel resolution, 10 second delay, low or medium LED control, single photo (i.e., not burst), and low sensitivity where applicable. Sensitivity was set to medium if a camera was not being triggered during testing. I collected cameras after a minimum of 28 trap nights.

Because mustelids were assumed uncommon and difficult to detect (e.g., Martin et al. 2022b), I used bait and scent lure to increase likelihood of detection (e.g., for mesocarnivores in general, Ferreras et al. 2018; for mustelids, Buyaskas et al. 2020). We used an olfactory lure called ‘Gusto’ (Minnesota Trapline Products, Inc., Pennock, Minnesota) similar to previous studies in California (Zielinski et al. 2005, 2015, Moriarty et al. 2011, Tweedy et al. 2019). Accordingly, I used a 2 cm^3 sponge coated with approximately 10 mL of Gusto and hung the sponge with flagging tape 1.5 m above ground. We mounted one 156 g (5.5 oz) can of cat food (I Luv My Cat brand, tuna &

salmon, or chicken in gravy) with five holes nailed into it near the lure. To increase detection of small mammal species, I included bait that consisted of half an apple nailed near the cat food can and coated in approximately 30 g (2 tbsp) of chunky peanut butter and a handful of oats. This sampling protocol was reviewed and approved by Cal Poly Humboldt's Institutional Animal Care and Use Committee (IACUC #2022W62-A).

We reviewed and cataloged images, during which a species presence or non-detection was recorded for each camera in a binary fashion, where '1' and '0' represented detection and non-detection, respectively.

Vegetation surveys

To ground-truth the geospatial layers, we measured vegetation characteristics at each camera station using the bait tree as plot center. I used a 20-factor basal area prism to count the number of trees within each plot and estimate the basal area (m/ha and ft.^{2}/acre). I recorded dominant tree species, average percent stem scorch, and average percent tree mortality. I visually estimated canopy closure and shrub cover. I made linear comparisons between my field data and GIS layers for basal area, canopy cover, and percent stem scorch, and I report the R^2 values (Appendix A).

Covariates

I included 12 *a priori* covariates to predict the effects of environmental variation on occupancy and detection and to determine marten and fisher relationships with them (Table 1). These covariates were expected to represent forest characteristics directly affected by the Dixie Fire (e.g., canopy cover, live trees per acre, burn severity), or explain unmodeled variance not captured by fire or structural covariates (e.g., elevation, precipitation; Figure 6). To account for varied effort at individual cameras, I calculated the number of operable trap nights. I considered an ‘operable’ camera to be facing the bait tree with at least some part of the ground in view. For instance, if a bear knocked the camera to face downward, it was no longer considered operable. Additionally, I assumed this effort covariate would serve as a proxy for the decay of lure and bait scent over time.

I used 2022 data for canopy cover and canopy bulk density at 30 m resolution from LANDFIRE (landfire.gov, 2022; Figure 6). I considered using the shrub cover data provided by LANDFIRE, but it was missing values anywhere with canopy and thus would be inaccurate. Based on discussions with managers, I selected forest structural covariates including basal area, stand density index, and live trees per acre. I sourced these post-fire layers at 30 m resolution from the USDA Forest Service as part of the Sierra Nevada Regional Resource Kit (wildfiretaskforce.org). I used a digital elevation model (DEM) derived at 30 m resolution from the National Elevation Dataset (USGS 2022). I acquired annual precipitation data as an 800 m resolution raster, which represented 30-year averages (1991-2020), from the PRISM Climate Group (prism.oregonstate.edu, 2020; Figure 6).

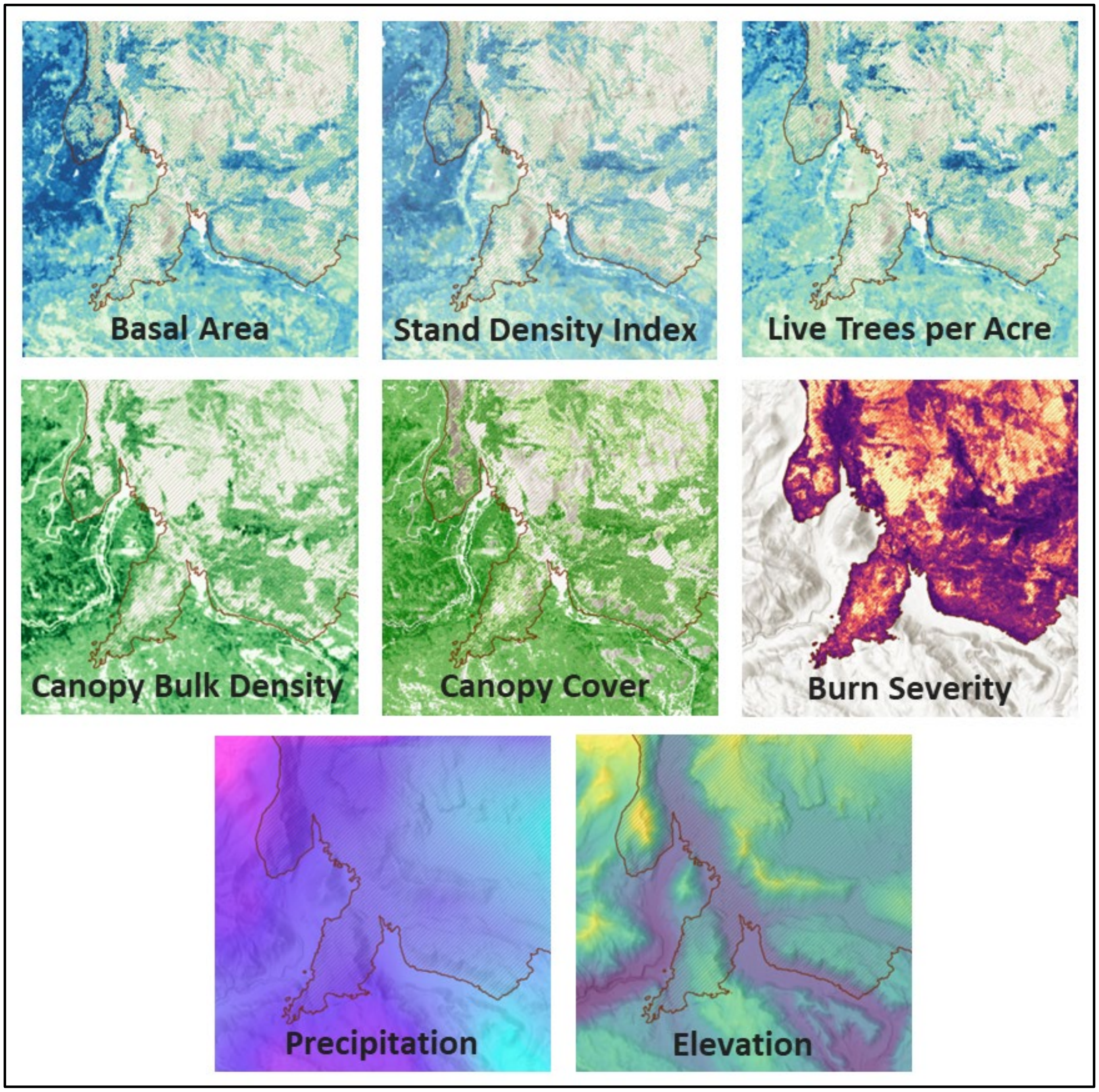


Figure 6. Examples for each forest structural (basal area, stand density index, live trees per acre, canopy bulk density, canopy cover, and burn severity) and abiotic covariates (precipitation and elevation) included in models for marten and fisher occurrence with an outline of the Dixie Fire perimeter.

I created several fire related covariates to estimate carnivore and prey use of post-fire landscapes (Figure 7). Many indices for burn severity are available, including the relativized differenced Normalized Burn Ratio (rdNBR), differenced Normalized Burn Ratio (dNBR), Composite Burn Index (CBI), and Rapid Assessment of Vegetation Condition after Wildfire (RAVG). I acquired copies of each, and visually compared them to images taken in the field. The single year dNBR and rdNBR available from MTBS appeared to best match the photos, but I assumed that forest regrowth taking place between 2022 and 2023 would affect landscape use by carnivores and prey. Thus, I created my own raster representing burn severity 2 years post-fire (Figure 7).

I calculated this 2-year burn severity raster using the differenced Normalized Burn Ratio (dNBR; Key and Benson 2006) at the 30 m resolution. I first sourced a mosaic of cloud-free Sentinel-2A imagery from before (June 1, 2021) and after (July 30, 2023) the Dixie Fire. I then used the high severity patches of burn severity to create the additional covariates of Aggregation Index, Edge Density, and Largest Patch Index with FRAGSTATS software (Version 4.2, McGarigal et al. 2023). All covariates were projected to the NAD 1983 UTM Zone 10N coordinate system and processed in ArcGIS Pro (Version 3.1.2, ESRI, Inc., Redlands, California). The DEM and 2-year dNBR were acquired and processed using Google Earth Engine (Gorelick et al. 2017).

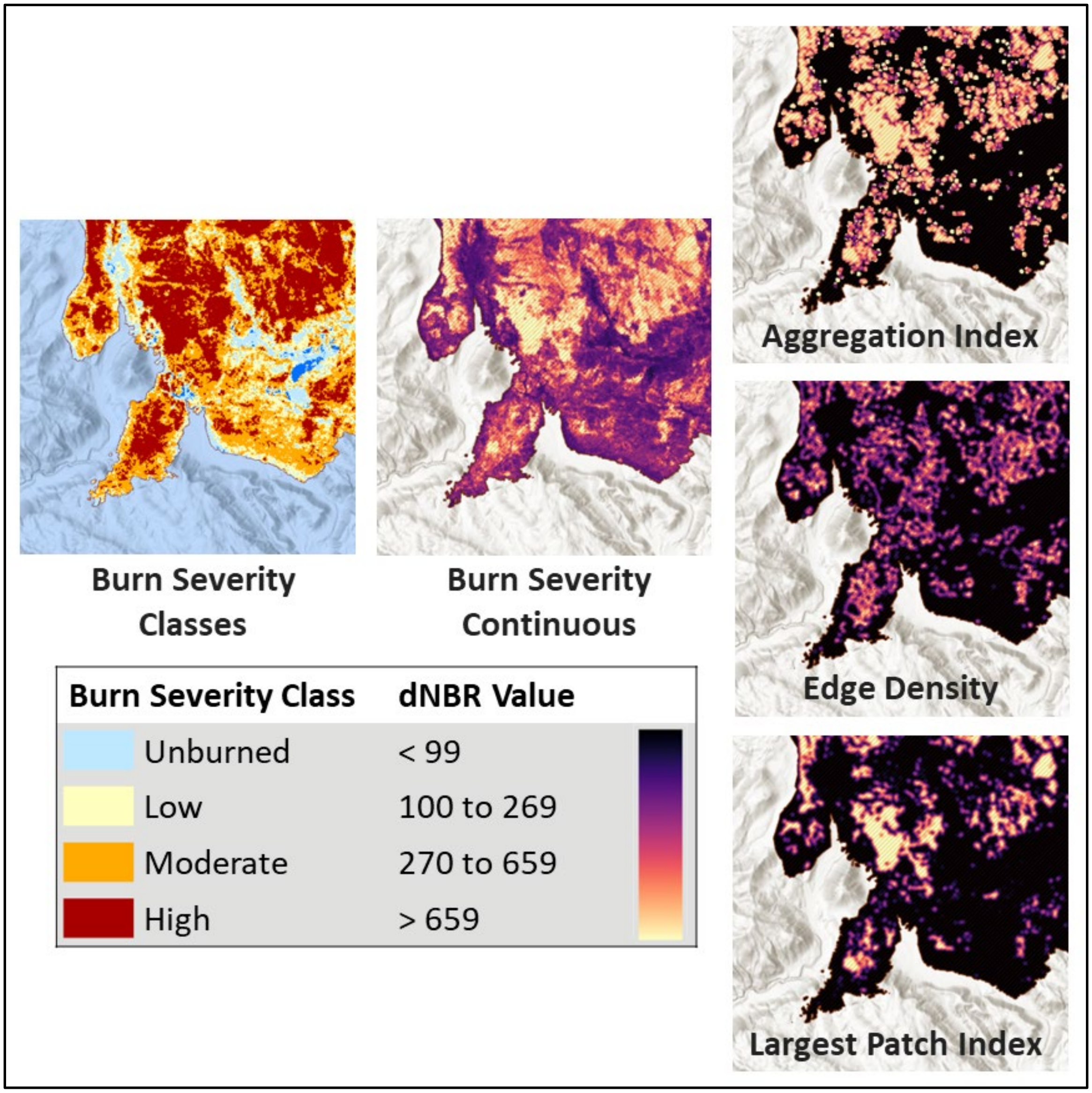


Figure 7. Fire related covariates that were used in this study: 2-year burn severity, aggregation index, edge density, and largest patch index.

Table 1. Independent covariates expected to influence carnivore and prey occupancy or detection and/or expected to be altered by the Dixie Fire in northern California. All environmental covariates were originally provided at a resolution of 30 meters and represent post-fire conditions (Fall 2021 or later) unless otherwise stated.

Covariate	Source	Parameter Type	Description
Trap nights	Collected	Detection	Measurement of effort per camera or occasion.
Canopy cover	LANDFIRE	Occupancy	Percent cover of tree canopy.
Canopy bulk density	LANDFIRE	Occupancy	Density of canopy fuels provided as 100*(kg/m^3).
Elevation	USGS	Occupancy	Derived from USGS 3DEP.
Precipitation	PRISM	Occupancy	Average annual precipitation from 1991-2020 at 800m resolution.
Burn severity (dNBR)	Derived from Sentinel-2A	Occupancy	Burn severity raster representing 2021-2023 conditions, derived from Sentinel-2A imagery.
Aggregation index	FRAGSTATS	Occupancy	Created with the high severity values extracted from the rdNBR.
Edge density	FRAGSTATS	Occupancy	Created with the high severity values extracted from the rdNBR.
Largest patch index	FRAGSTATS	Occupancy	Created with the high severity values extracted from the rdNBR.
Basal area	USFS	Occupancy	Index of live timber provided as sq. ft./acre.
Trees per acre	USFS	Occupancy	Forest density metric provided as live trees/acre.
Stand density index	USFS	Occupancy	Density of a stand provided as trees/acre.

Multi-scale Optimization

The scale at which organisms interact with their environment is essential to making inferences in ecology and is often overlooked (McGarigal et al. 2016). To determine the optimal spatial scales for each species, I first used a moving window analysis to create 7 different scales for each covariate beginning at the 30 m resolution and doubling for each scale from 90 m to 2,880 m radii (i.e., 30, 90, 180, 360, 720, 1,440, 2,880; Figure 8). I selected 2,880 m as the largest scale as it represents the approximate distance between sites and is similar to the diameter of a female fisher home range (Zielinski et al. 2004). I tested all 7 scales for carnivores, but only the finest 4 (30, 90, 180, 360) for small mammals because they have smaller home ranges.

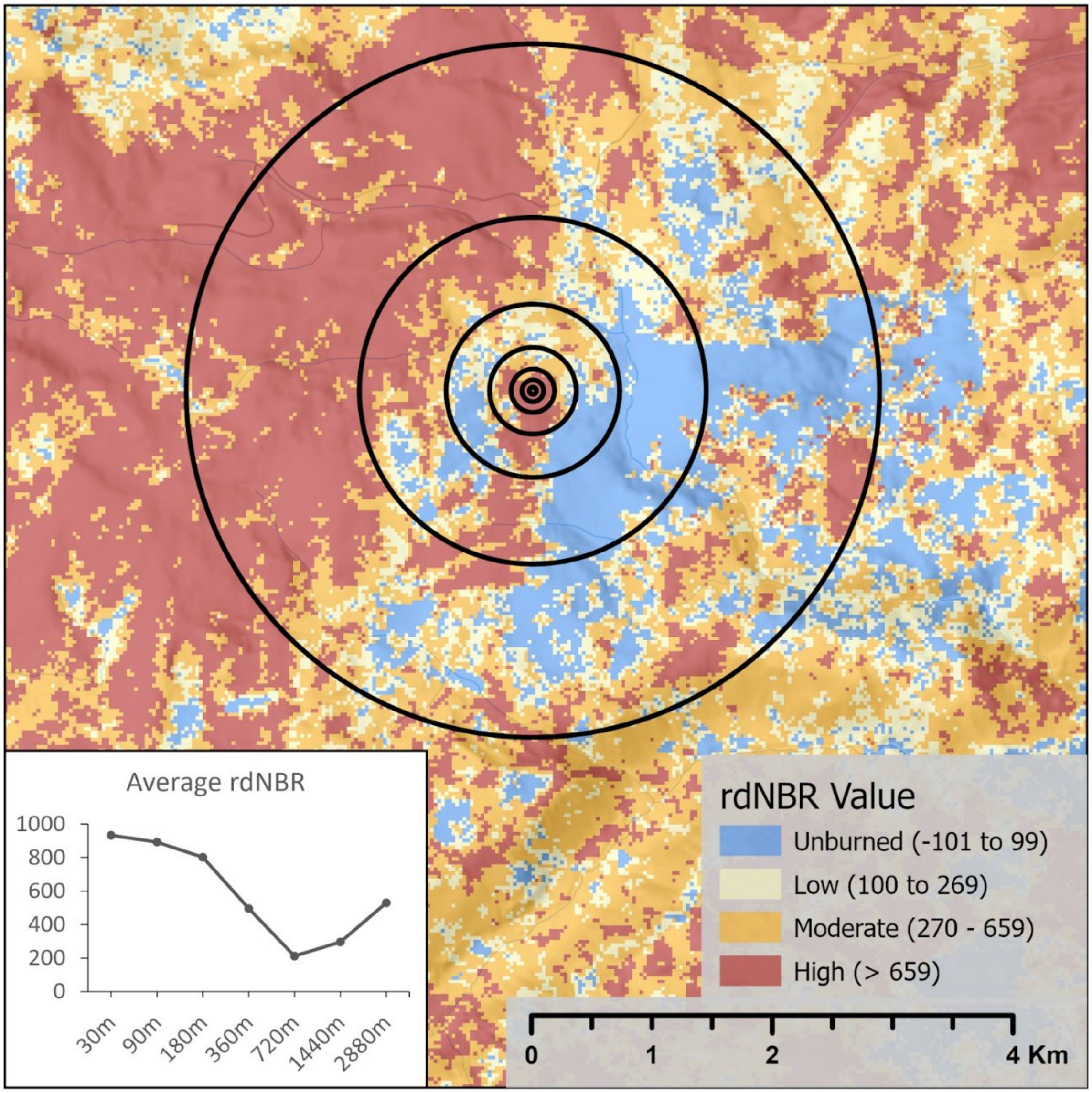
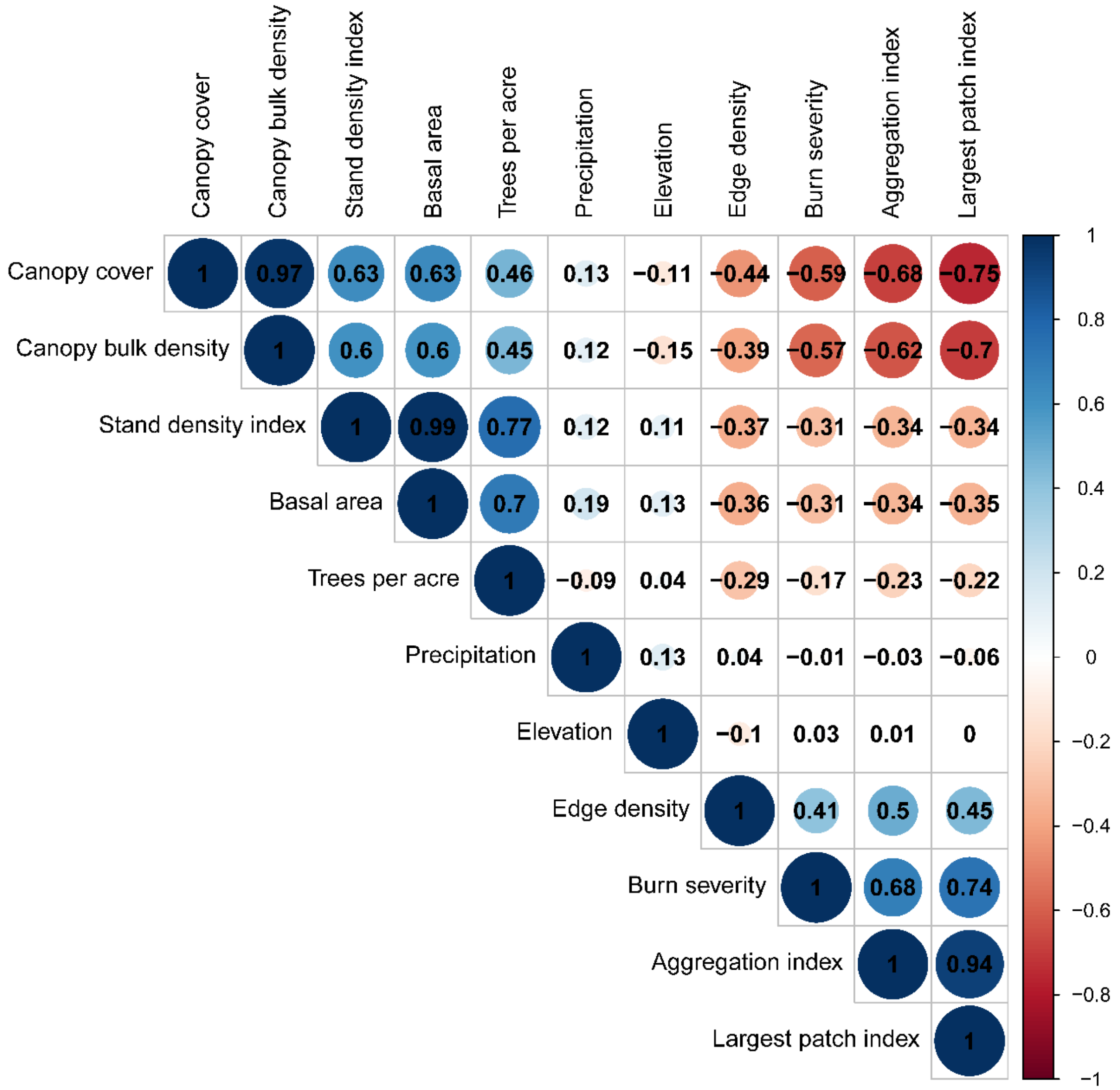


Figure 8. Scales tested for optimization with rdNBR as an example.

I then used presence/non-detection data for each species at each site to fit generalized linear models using the ‘glm’ function in package “stats” built into the R programming software (Version 4.3.1, R Core Team 2023). Models for each covariate were ranked by Akaike Information Criterion for small sample sizes (AICc; Burnham and Anderson 2004), and the scale with the lowest score was carried into occupancy models. I did not scale optimize several covariates including: 1) elevation, because it was assumed fixed at the site level, 2) precipitation, because it was only available at the 800 m resolution, and 3) basal area, trees per acre, and stand density index, because the units would become meaningless at scales other than the stand level.

Once the optimal scale for each covariate was determined for each species, I calculated a Spearman’s Rank correlation coefficient for each pairwise combination of covariates (Figure 9). Correlated covariates were not used within the same model if the absolute value of the coefficient was high (i.e., $| \rho | > 0.6$). The only two covariates that had low correlation values with all other covariates were precipitation and elevation (Figure 9). I then scaled and centered all covariates to have a mean of zero and standard deviation of one, which allowed for direct comparison within models and to promote model convergence.



	Canopy cover	Canopy bulk density	Stand density index	Basal area	Trees per acre	Precipitation	Elevation	Edge density	Burn severity	Aggregation index	Largest patch index
Canopy cover	1	0.97	0.63	0.63	0.46	0.13	−0.11	−0.44	−0.59	−0.68	−0.75
Canopy bulk density		1	0.6	0.6	0.45	0.12	−0.15	−0.39	−0.57	−0.62	−0.7
Stand density index			1	0.99	0.77	0.12	0.11	−0.37	−0.31	−0.34	−0.34
Basal area				1	0.7	0.19	0.13	−0.36	−0.31	−0.34	−0.35
Trees per acre					1	−0.09	0.04	−0.29	−0.17	−0.23	−0.22
Precipitation						1	0.13	0.04	−0.01	−0.03	−0.06
Elevation							1	−0.1	0.03	0.01	0
Edge density								1	0.41	0.5	0.45
Burn severity									1	0.68	0.74
Aggregation index										1	0.94
Largest patch index											1

Figure 9. Correlation matrix for *a priori* covariates at sites within the Dixie Fire study area in northern California. Larger circles correspond to greater correlation coefficients (ρ), with 1 = perfect correlation and 0 = no correlation. I considered covariates highly correlated if | ρ | > 0.6.

Single-species Occupancy Models

Occupancy models allow for the estimation of species occurrence when survey methods involve imperfect detection of the target animal (i.e., detection probability < 1; MacKenzie et al. 2002), which is true for camera trap surveys. This type of model carries the following assumptions: 1) closure, which means the status of occupancy does not change throughout the survey period, 2) constant probabilities of occupancy and detection across all sites, 3) independence in the detection processes at each site, and 4) no false positive detections can be recorded. I created single-species occupancy models (MacKenzie et al. 2002) for carnivores and prey (i.e., small mammals) to determine whether burn severity was associated with occupancy. To avoid problems with model convergence and inference, I only modeled occupancy for species with a sufficient detection probability across the study period ($p \geq 0.15$) and at least 7 stations with detections (MacKenzie et al. 2002).

I used a variation of the single species model that substitutes space in the occasion history for time (hereafter, space for time; MacKenzie et al. 2006, Srivathsa et al. 2018). I accomplished this by simplifying all detections at the camera during the study period to a ‘1’ if the species was detected and ‘0’ if the species was not detected. Given that my sites had paired cameras, each site had two occasions built into the detection history. Another option I considered to estimate occupancy with my paired camera study design was the multi-scale occupancy model (Nichols et al. 2008). This model requires the estimation of a third parameter, theta (θ), and testing it with the marten data from my 2023 surveys resulted in very overfit models and wide confidence intervals that rendered estimates uninformative.

I counted a detection at either camera as presence at the paired site. If a detection occurred at both cameras, the detection history was ‘11’, and it was ‘00’ if neither had a detection. We attempted to set paired cameras within the same class of burn severity, but we occasionally had to place them in different classes due to topographical constraints. To account for differences in camera-level vegetation or environmental characteristics within the same site, I wrote a function in R to select covariate values at the respective camera where detections occurred. For instance, if camera A had a detection and camera B did not (10), the covariate value for the site level would be assigned from camera A. If both cameras had detections (11) or non-detections (00), the mean covariate value of the two cameras would be assigned to the site. In the case of camera malfunction, the covariate value was selected from the remaining operational camera.

I fit space for time occupancy models using R (R Core Team 2023) in package ‘unmarked’ (Fiske and Chandler 2011), which uses maximum likelihood estimation. The latent state, or ecological process, of a given species occurring at site j was modeled as $Z_j \sim \text{Bernoulli}(\psi_j)$, and detection during survey period k was modeled as $y_{j,k} \sim \text{Bernoulli}(Z_j * p_{j,k})$. Logistic regression was used to include covariates in submodels for estimating probabilities of occupancy (ψ) and detection (p) and the logit link function was used to combine the submodels. I provide the p(trap nights) ψ(burn severity) model as an example:

$$\text{logit}(\psi_j) = \alpha_0 + \alpha_1 * \text{Burn Severity}_j$$

$$\text{logit}(p_{j,k}) = \beta_0 + \beta_1 * \text{Trap Nights}_{j,k}$$

First, I built models with the occupancy parameter (ψ) held at the intercept to determine whether ‘trap nights’ (i.e., effort) as a detection covariate improved the model, in which case it was carried into subsequent modeling steps. I then built separate models for each occupancy covariate to determine the optimal occupancy covariates. To assess covariate importance, I ranked models by AICc and compared them to the null model (i.e., no covariates; $p(.)\ \psi(.)$). I then evaluated models for Goodness of Fit (GOF) using the MacKenzie-Bailey test with 2,000 parametric bootstrap simulations (MacKenzie and Bailey 2004). If a fitness test revealed overdispersion ($\hat{c} > 1$), I inflated confidence intervals accordingly when reporting estimates and drawing inferences. For the space for time models, I report mean estimates for alpha and beta parameters and their 95% Confidence Intervals as log-odds ratios.

Unfortunately, my marten space for time model estimates had high error, and I had too few detections to model fisher occupancy. Thus, after fitting space for time models with my survey data attained in summer 2023, I wanted to further explore my hypotheses using all marten and fisher data collected by my team and our collaborators (USDA Forest Service, California Department of Fish and Wildlife, and Collins Pines Company) in 2022 and 2023. These data resulted in 480 camera stations, which included the 230 stations surveyed for this study in 2023. I was concerned about autocorrelation in models using these data because efforts by my collaborators had different spacing between the paired sites (500 - 1,000 m; Figure 10), which could mean detections were not independent of one another. In other words, the same animal could be visiting multiple sites during a detection period, thereby violating the closure and independence assumptions. One way to account for autocorrelation was to account for distance between locations using a spatial occupancy model, or a time-based occupancy model that explicitly accounted for spatial proximity and potential for autocorrelation.

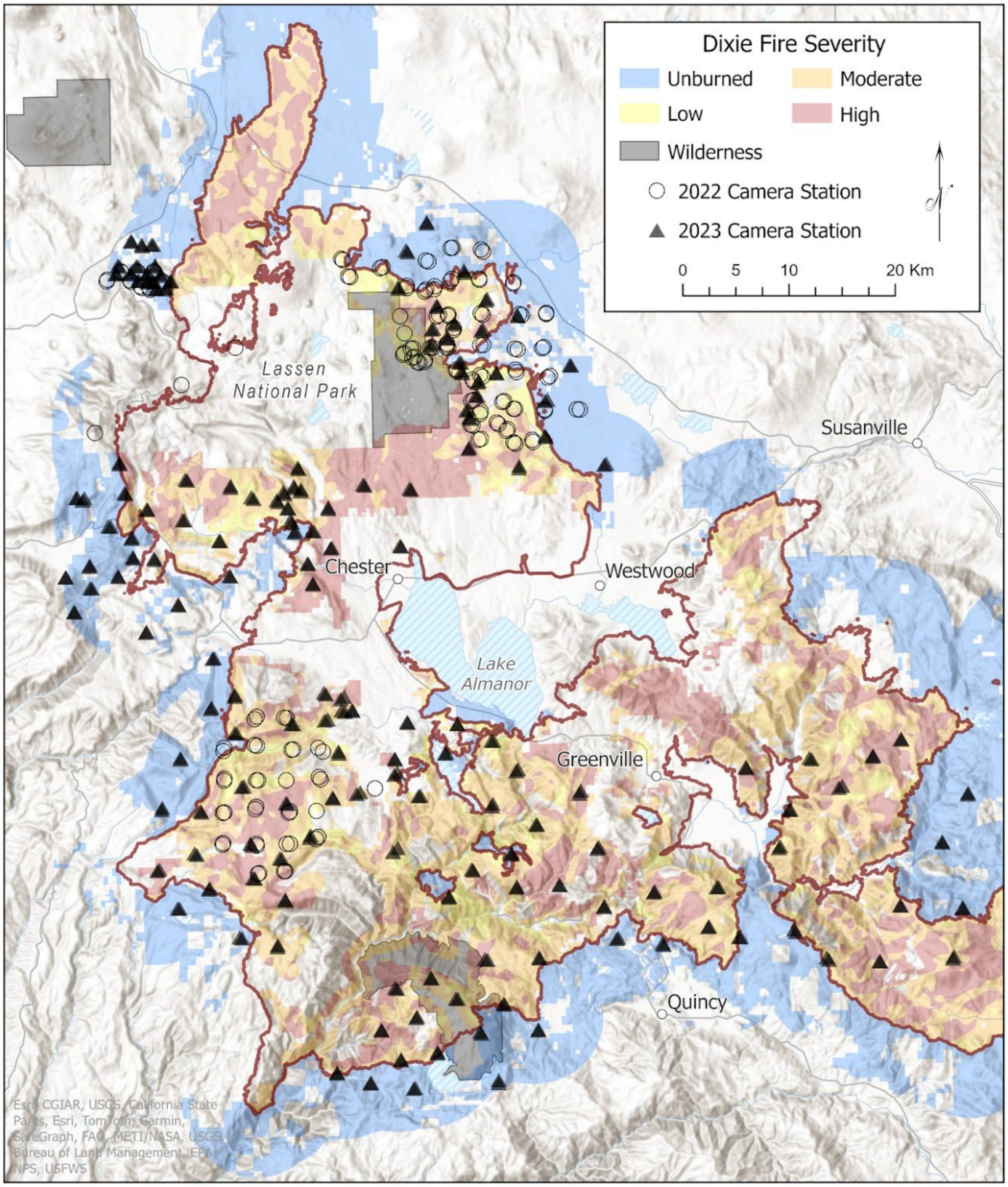


Figure 10. Locations of all camera stations (*n* = 480) deployed during 2022 and 2023 by my team and our collaborators within the Dixie Fire study area in northern California. Shaded colors represent burn severity classes (Key and Benson 2006), which were derived from Monitoring Trends in Burn Severity (MTBS.gov) data.

Spatial Occupancy Models

To further explore marten and fisher use of post-fire forests, and incorporate additional data from my collaborators, I fit spatial occupancy models (Johnson et al. 2013, Doser et al. 2022). This type of model follows the same assumptions and general formula of the non-spatial occupancy model, but it incorporates a matrix of coordinates at each *j* site (s_j) and uses a spatial random effect ($w(s_j)$) that occurs as a Gaussian process with a mean of zero to account for autocorrelation:

$$\text{logit}(\psi(s_j)) = \alpha_0 + \alpha_1 * \text{Burn Severity}_j + w(s_j)$$

$$w(s) \sim N(0, \sum(s, s', \theta))$$

I used the "spOccupancy" package (Doser et al. 2022), within R (R Core Team 2023) to build spatial occupancy models. This package implements occupancy models in a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulation. Additionally, it uses Pólya-Gamma data augmentation (Polson et al. 2013) with a Nearest Neighbor Gaussian Process (NNGP; Datta et al. 2016) to increase efficiency of the sampling process. Minimally informative priors with normal distributions were assumed for the occupancy and detection prior distributions. Issues with model convergence due to clustering of sites (Figure 11) prompted me to restrict the bounds of the uniform prior for the spatial decay parameter (ϕ) to between 100 and 3,000 m, which represented the approximate minimum and maximum distances between camera stations (e.g., Bajcz et al. 2024).

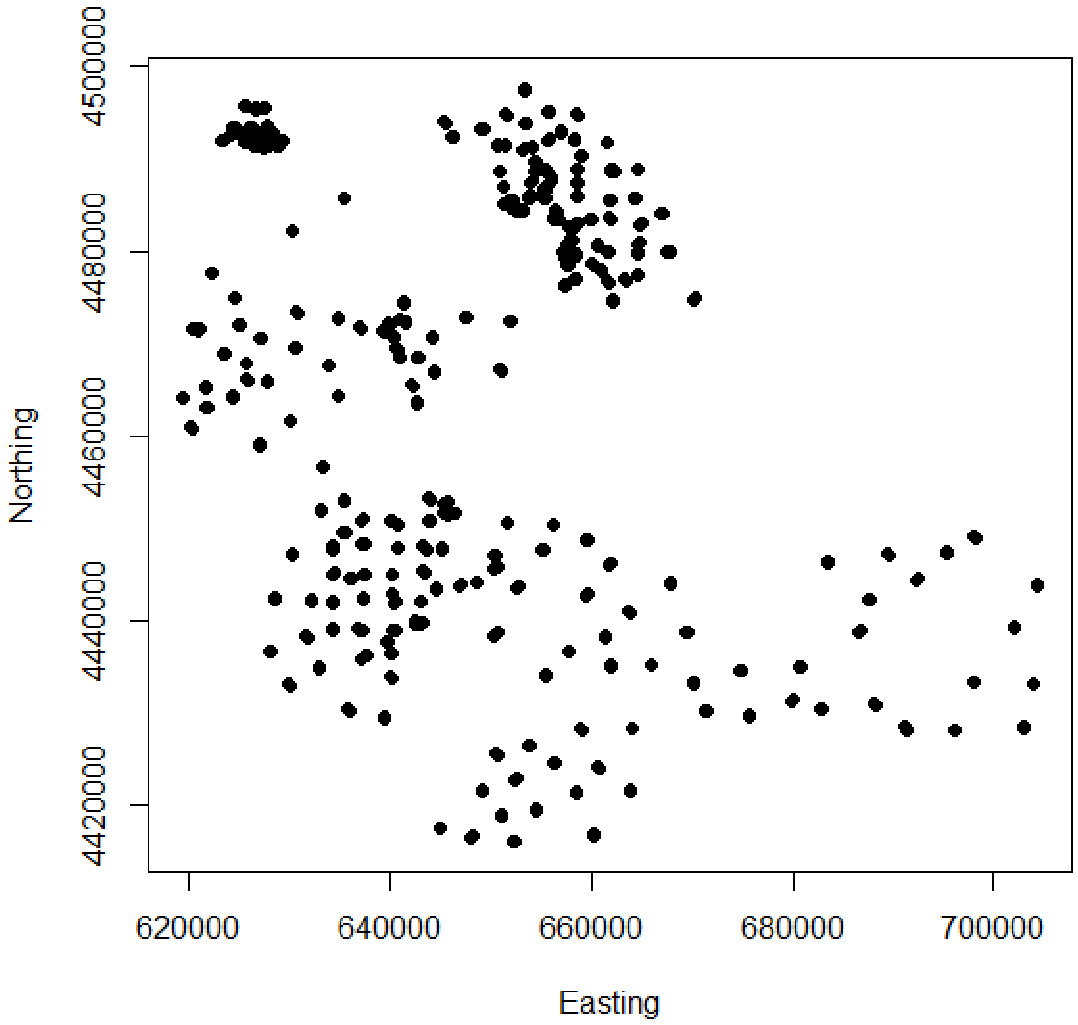


Figure 11. Spatial configuration of camera stations from 2022 and 2023 surveys within the Dixie Fire study area, with easting and northing in meters and the NAD 1983 UTM Zone 10N geographic coordinate system.

For the marten and fisher models, I ran posterior draws on 3 chains and included 6,000 batches of 25 iterations with a thinning rate of 4 and a burn-in period of 2,000 iterations. This resulted in 111,000 total posterior draws per model. I used the exponential spatial dependence function and set the number of nearest neighbors to 15. Model convergence was assessed through visual inspection of traceplots and achievement of acceptable R-hat values (R-hat < 1.1; Brooks and Gelman 1998, Gelman and Shirley 2011). I assessed model fit through comparisons between the observed results and simulated ideal results using the Freeman-Tukey statistic (Kéry and Royle 2016). A Bayesian p-value was then calculated with the most complex model to confirm model fitness (i.e., $0.1 > p > 0.9$; Hobbs and Hooten 2015). For all spatial model estimates, I report the mean values from the posterior samples and their 95% Credible Intervals (CIs). I evaluated the direction of correlations to be strong if the 95% CIs did not overlap zero, weak if only the 50% CIs did not overlap zero, or non-directional if the 50% CIs overlapped zero.

I used the full detection histories, binned into monthly (30 day) occasions for each camera station. I did not model the other carnivore species using the spatial framework for reasons twofold: 1) I did not have the full detection history information or photos from all collaborators, and 2) most Dixie Fire severity relationships were sufficiently modeled in the non-spatial single-species models (i.e., there were sufficient detections). Though we collected data across two years (2022 and 2023), my aim was to estimate occupancy and relationships with covariates (and not colonization or extinction probabilities), so I first considered fitting models in a single-season framework, with each site by year combination as an individual site (e.g., Linden and Roloff 2013, Fuller et al. 2016). However, this “stacked” framework was not possible with the spatial occupancy model because spatial autocorrelation cannot be estimated between two sites with the same coordinates. Only 5 sites operated from the first into the second year because they were left out over winter, so I dropped the second year of detections at these sites (winter/spring months) and proceeded with single-season models.

Spatial models were tested with and without covariates to assess importance following the same methodology as the space for time models. I ranked models by widely applicable information criterion (WAIC; Watanabe 2010), which is useful for comparing models with and without random effects. I then predicted the relationships with covariates by estimating occupancy across the observed range of values. Finally, I created occupancy probability maps for martens and fishers using the top model as determined by the lowest WAIC score. I considered three-covariate models for this step because the univariate models would have created unrealistic predicted occupancy maps. Since precipitation and elevation were the only two covariates not correlated with any of the forest structure or fire covariates, I included them in all models.

RESULTS

With the help of collaborators, I was able to use data from 228 out of 230 cameras (72 unburned, 30 low, 56 moderate, 70 high) at 115 sites. For my first analysis of carnivores and small mammals, I used these data from 228 cameras. Another 79 cameras were set by my colleague Alyssa Roddy (Cal Poly Humboldt) during 2022 (23 unburned, 13 low, 28 moderate, 15 high), and 171 cameras were set by my collaborators during 2022 and 2023 (73 unburned, 53 low, 36 moderate, 9 high; Table 2). For my second analysis of spatial occupancy models for just martens and fishers, I used data combined from these 250 cameras and the 228 from my first analysis for a total of 478 cameras. I could not model the other species in this framework because I only attained photos of martens and fishers, which were needed to create detection histories.

Table 2. Camera deployment counts by burn severity class during 2022 and 2023 surveys within 6 km of the Dixie Fire perimeter. Collaborators included Lassen National Forest - Almanor, Eagle Lake, and Hat Creek Districts, California Department of Fish and Wildlife (CDFW), Plumas National Forest - Mt. Hough District, Collins Pines Company, and Cal Poly Humboldt for 2022.

Organization	Year	Cameras Deployed	Unburned	Low Severity	Moderate Severity	High Severity
Cal Poly Humboldt	2022	79	23	13	28	15
Lassen NF - Eagle Lake District	2022	52	2	21	20	9
Lassen NF - Hat Creek District	2022	16	16	-	-	-
CDFW	2022	5[a]	2	-	3	-
Cal Poly Humboldt	2023	204	64	28	51	61
Collins Pines	2023	14[b]	6	2	1	5
Plumas NF - Mt. Hough District	2023	10[b]	2	-	4	4
Lassen NF - Almanor District	2023	66	22	32	12	-
Lassen NF - Hat Creek District	2023	32	31	-	1	-
Total		478	168	96	120	94

a: Cameras were not paired.

b: Data were used for carnivore and small mammal models.

To provide context for these data sets, I collected 776,914 images, of which 31,720 photos included detections of 27 mammalian taxa (230 cameras set June 06 to August 30, 2023, Table 3). I did not include domestic dogs (*Canis lupus familiaris*) or humans. Cameras operated for 1 to 72 days (x = 29.6 days ± 15.5 SD). Images from one camera were omitted because it stopped capturing photos 5 hours after setup and another because it only captured photos at the end of the survey period, which was after the bait had been taken. This resulted in 228 total cameras I used within occupancy models for all species except martens and fishers.

Black bears (*Ursus americanus*), chipmunks (*Neotamias* spp.), and mule deer (*Odocoileus hemionus*) were the most detected species, and together they accounted for 64% of the total images with wildlife (Table 3). Pacific martens and fishers were detected in 51 and 17 photos, respectively. Mouse and vole species were difficult to differentiate in photos, so I considered them in the same category. However, most of these photos appeared to be deer mice (*Peromyscus maniculatus*). I detected several uncommon species, which, due to low sample size, I could not model their occupancy. These included short-tailed (*Mustela erminea*) and long-tailed (*Neogale frenata*) weasels, North American porcupine (*Erethizon dorsatum*), American badger (*Taxidea taxus*), Sierra Nevada red fox (*Vulpes vulpes necator*), yellow-bellied marmot (*Marmota flaviventris*), ringtail (*Bassariscus astutus*), and Belding’s ground squirrel (*Urocitellus beldingi*; Figure 12).

Table 3. Species detected, including scientific and common names, numbers of photos, and percentages of total out of 31,720 images collected in the summer 2023 Dixie Fire surveys. The table is sorted by the number of photos captured for each species.

Common Name	Scientific Name	Number of Photos	Percent of Total
Black bear	*Ursus americanus*	9,179	28.94
Chipmunk spp.	*Neotamias* (Genus)	6,089	19.20
Mule deer	*Odocoileus hemionus*	5,096	16.07
Golden-mantled ground squirrel	*Callospermophilus lateralis*	2,989	9.42
Gray fox	*Urocyon cinereoargenteus*	1,609	5.07
California ground squirrel	*Otospermophilus beecheyi*	1,565	4.93
Other (bird, bat, lizard, snake)	Vertebrata (Subphylum)	1,526	4.81
Douglas squirrel	*Tamiasciurus douglasii*	1,116	3.52
Mouse/vole spp.	Cricetidae (Family)	873	2.75
Humboldt’s flying squirrel	*Glaucomys oregonensis*	325	1.02
Snowshoe hare	*Lepus americanus*	313	0.99
Coyote	*Canis latrans*	201	0.63
Woodrat spp.	*Neotoma* (Genus)	198	0.62
Black-tailed jackrabbit	*Lepus californicus*	158	0.50
Western gray squirrel	*Sciurus griseus*	125	0.39
Bobcat	*Lynx rufus*	104	0.33
Striped skunk	*Mephitis mephitis*	78	0.25
Pacific marten	*Martes caurina*	51	0.16
Mountain lion	*Puma concolor*	34	0.11
Western spotted skunk	*Spilogale gracilis*	31	0.10
Fisher	*Pekania pennanti*	17	0.05
Weasel spp.	*Mustela/Neogale* (Genus)	13	0.04
North American porcupine	*Erethizon dorsatum*	10	0.03
American badger	*Taxidea taxus*	8	0.03
Sierra Nevada red fox	*Vulpes vulpes necator*	6	0.02
Yellow-bellied marmot	*Marmota flaviventris*	3	0.01
Ringtail	*Bassariscus astutus*	2	0.01
Belding’s ground squirrel	*Urocitellus beldingi*	1	0.003

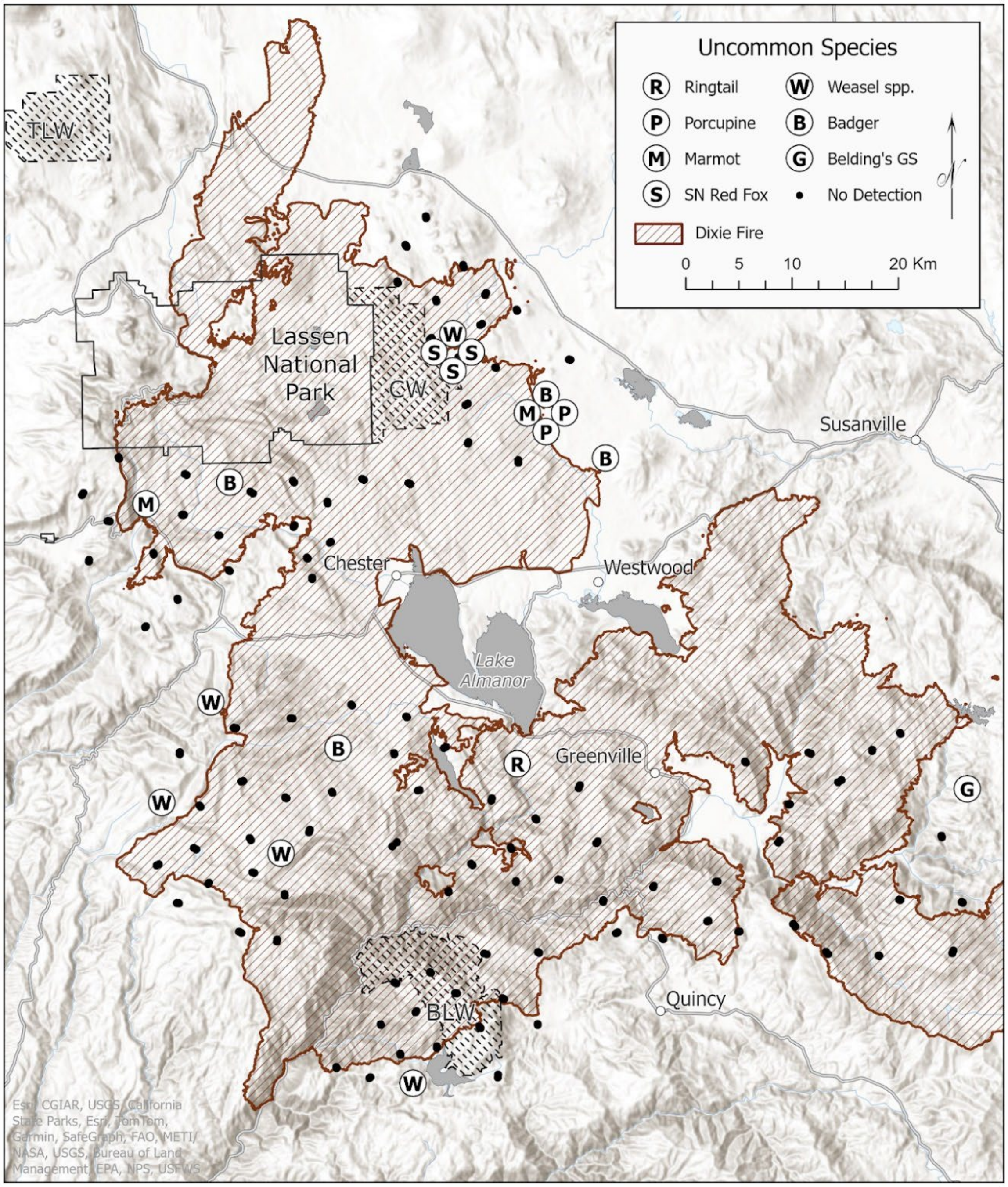


Figure 12. Locations of uncommon species detected in the Dixie Fire study area. Species include short- and long-tailed weasels (W), North American porcupine (P), American badger (B), Sierra Nevada red fox (S), yellow-bellied marmot (M), ringtail (R), and Belding's ground squirrel (G).

Multi-scale Optimization

The optimal scale for martens was 360 m for canopy cover and canopy bulk density, and the coarser scales (1,440 or 2,880 m) for the fire covariates (Table 4). However, many of these models had comparable scales (i.e., within 2 AICc of the top scale). Fishers had the same optimal scales as martens for all covariates except edge density and largest patch index (Table 4). The optimal scales for burn severity were mixed among carnivores and small mammals. Coyote and western spotted skunk showed a correlation with the most coarse burn severity scale. Conversely, the optimal scale for black bear and gray fox was finer (90 and 30 m, respectively), and bobcat and striped skunk had the best association with the intermediate scale of 720 m.

Table 4. Optimal scales for each covariate and each species used in occupancy models. Comparable scales are those that were within 2 AICc of the optimal scale.

Covariate	Species	Optimal Scale	Comparable Scales
Canopy cover	Pacific marten	360	All
	Fisher	360	180, 720
Canopy bulk density	Pacific marten	360	All
	Fisher	360	180, 720
Aggregation index	Pacific marten	2880	All
	Fisher	2880	None
Edge density	Pacific marten	2880	All
	Fisher	360	720, 1440, 2880
Largest patch index	Pacific marten	1440	90 - 2880
	Fisher	30	1440, 2880
Burn severity	Pacific marten	2880	None
	Fisher	2880	All
	Black bear	90	30, 180
	Gray fox	30	All
	Coyote	2880	None
	Bobcat	720	30 - 1440
	Striped skunk	720	All
	Western spotted skunk	2880	All
	Chipmunk spp.	30	None
	Golden-mantled ground squirrel	180	90, 360
	California ground squirrel	180	All
	Douglas squirrel	90	30
	Mouse/vole spp.	30	All
	Humboldt's flying squirrel	180	90
	Snowshoe hare	360	All
	Woodrat spp.	180	All
	Western gray squirrel	90	30

Occupancy and Detection

Black bears had the highest naive occupancy of 77% (175 out of 228 sites; Table 5). Throughout my study area, the naive occupancy rate for martens was 5% (11 out of 228 sites), and for fishers was 2% (5 out of 228 sites; Table 5). I did not collect enough fisher detections to estimate occupancy and detection probabilities in the space for time framework (Table 5). Chipmunk species had the highest naive occupancy of the small mammals (105 out of 228 sites), though Douglas squirrels (98 out of 228 sites) had a similar occupancy probability (Table 6).

Table 5. Carnivore detection histories, including number of cameras that detected or did not detect each species, detection probability (*p*), occupancy probability (ψ) in the Dixie Fire study area during summer 2023 surveys. Species are ordered from the most to least detections. I report estimated values and their standard error (x ± SE).

Species	Cameras With/Without Detections	Detection Probability (*p*)	Occupancy Probability (ψ)
Black bear	175/53	0.86 ± 0.28	0.89 ± 0.03
Gray fox	44/184	0.68 ± 0.08	0.28 ± 0.05
Coyote	39/189	0.37 ± 0.10	0.46 ± 0.12
Bobcat	22/206	0.18 ± 0.11	0.53 ± 0.31
Striped skunk	17/211	0.35 ± 0.15	0.21 ± 0.09
Western spotted skunk	14/214	0.43 ± 0.17	0.14 ± 0.06
Pacific marten	11/217	0.42 ± 0.20	0.12 ± 0.06
Fisher	5/223	–	–
Puma	5/223	–	–
Weasel spp.	5/223	–	–
American badger	4/224	–	–
Sierra Nevada red fox	3/225	–	–
Ringtail	1/227	–	–

Table 6. Small mammal detection histories, including number of cameras that detected or did not detect each species, detection probability (*p*), occupancy probability (ψ) in the Dixie Fire study area during summer 2023 surveys. Species are ordered from the most to least detections. I report estimated values and their standard error (x ± SE).

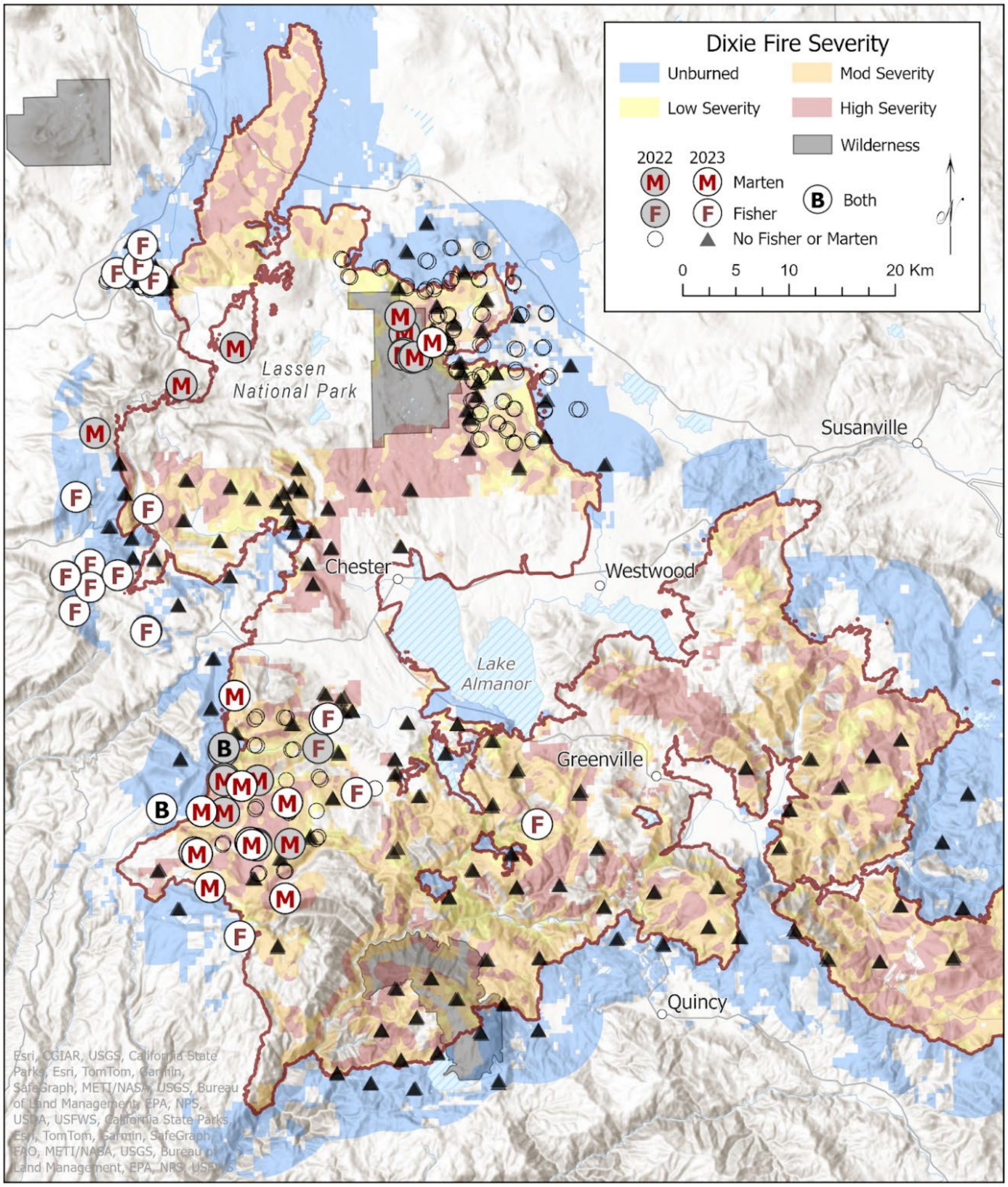
Species	Cameras With/Without Detections	Detection Probability (*p*)	Occupancy Probability (ψ)
Chipmunk spp.	105/123	0.75 ± 0.05	0.61 ± 0.05
Douglas squirrel	98/130	0.69 ± 0.05	0.62 ± 0.06
Golden-mantled ground squirrel	60/168	0.58 ± 0.08	0.46 ± 0.07
Mouse/vole spp.	48/180	0.43 ± 0.09	0.49 ± 0.10
Humboldt’s flying squirrel	44/184	0.50 ± 0.09	0.39 ± 0.07
California ground squirrel	38/192	0.68 ± 0.09	0.24 ± 0.05
Western gray squirrel	30/198	0.60 ± 0.11	0.22 ± 0.05
Snowshoe hare	14/214	0.28 ± 0.16	0.22 ± 0.12
Woodrat spp.	10/218	0.40 ± 0.20	0.11 ± 0.06
Black-tailed jackrabbit	5/223	–	–
North American porcupine	2/226	–	–
Yellow-bellied marmot	2/226	–	–
Belding’s ground squirrel	1/227	–	–

With the additional data from my collaborators binned into 30-day detection histories, I accumulated 41 marten and 24 fisher detections at 30 and 22 camera stations, respectively (Table 7). Martens were most often detected within the perimeter of the Dixie Fire (83.3%) and at higher elevations (average = 1,968 m ± 210 SD, range = 1,538 - 2,540 m) within the study area. The majority of detections occurred southwest of Lake Almanor near Humboldt and Humbug Peaks (e.g., Humboldt Peak study area, Moriarty et al. 2016; Figure 13). Fishers were most often detected in the unburned forests (72.7%) and at the mid elevations (average = 1,625 m ± 155 SD, range = 1,359 - 1,955 m; Figure 13). Martens and fishers were detected by the same camera at only two stations near the edge of the fire perimeter in the Humboldt study area (Figure 13). All marten and fisher detections were in Lassen National Forest, except for one fisher detected south of Lake Almanor in Plumas National Forest (Figure 13).

Table 7. Camera deployment counts, marten, and fisher detections during 2022 and 2023 surveys within 6 km of the Dixie Fire perimeter. Number of detections is reported as the number of cameras with detections. Collaborators provided data for Lassen National Forest - Eagle Lake, Hat Creek, and Almanor Districts, California Department of Fish and Wildlife (CDFW), Plumas National Forest - Mt. Hough District, Collins Pines Company, and Cal Poly Humboldt for 2022.

Organization	Year	Cameras Deployed	Marten Detections	Fisher Detections
Cal Poly Humboldt	2022	79	9	2
Lassen NF - Eagle Lake District	2022	52	4	0
Lassen NF - Hat Creek District	2022	16	0	0
CDFW	2022	5[a]	5	0
Cal Poly Humboldt	2023	204	11	5
Collins Pines Company	2023	14	0	2
Plumas NF - Mt. Hough District	2023	10	0	0
Lassen NF - Almanor District	2023	66	1	9
Lassen NF - Hat Creek District	2023	32	0	4
Total		478	30	22

a: Cameras were not paired and only marten detections were provided.



Esri, CGIAR, USGS, California State Parks, Esri, TomTom, Garmin, SafeGraph, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA, USFWS, California State Parks Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA

Figure 13. Sites with marten (M) and fisher (F) detections (and both [B]) during 2022 and 2023 surveys within the Dixie Fire study area in northern California. Shaded colors represent burn severity classes restricted to Lassen and Plumas National Forest lands. Burn severity raster derived from Monitoring Trends in Burn Severity (MTBS.gov) data. Green represents a 6 km buffer from the fire perimeter.

Burn Severity

Marten predicted occupancy was found to be higher in burned sites than unburned sites in the Dixie Fire, and I found strong evidence that occupancy increased as burn severity increased (β = 0.89, 95% CI [0.19, 1.78]; Figure 14). For every 250 units of increase in burn severity (i.e., dNBR value), which is a value that would change the interpreted severity class, I estimated an increase in the probability of marten occupancy by 19% to 178% (95% CI). Fishers exhibited the opposite relationship, as I found strong evidence of decreasing occupancy as burn severity increased (β = -1.14, 95% CI [-2.28, -0.39]; Figure 14). For every 250 units of increase in burn severity, I estimated a decrease in the probability of fisher occupancy by 39% to 228% (95% CI).

Mixed relationships with fire severity were revealed for the carnivore competitor and predator species (Figure 14). Coyote occupancy had a strong positive correlation with burn severity (β = 0.78, 95% CI [0.07, 1.49]), though they were detected almost evenly across all burn severity classes (Appendix B). I found a weak positive association with burn severity for gray fox (β = 0.19, 95% CI [-0.24, 0.63]) and striped skunk (β = 0.21, 95% CI [-0.41, 0.83]). I estimated that black bears had a strong negative relationship with increasing burn severity (β = -0.74, 95% CI [-1.42, -0.07]). Similarly, I estimated weak negative relationships with increasing burn severity for western spotted skunk (β = -0.26, 95% CI [-0.91, 0.40]) and bobcat (β = -0.82, 95% CI [-2.24, 0.59]). My goodness of fit tests revealed underdispersion for models with gray fox, bobcat and both skunk species, and slight overdispersion for black bear (ĉ = 1.49) and coyote models (ĉ = 1.14; Appendix C).

Most small mammal species had negative correlations in occupancy with increasing values of burn severity (Figure 15). Mouse/vole species had a weak positive relationship with burn severity (β = 0.32, 95% CI [-0.23, 0.87]), and they were detected at 28.4% of the high severity cameras (Appendix B). California ground squirrels had a neutral or slightly positive relationship (β = 0.09, 95% CI [-0.37, 0.55]), but they were detected at moderate severity sites more than any other burn class (29.6%; Appendix B). Aside from the California ground squirrel, all squirrel species had a negative relationship with burn severity (Figure 15) and were most often detected in the unburned or low severity sites (Appendix B).

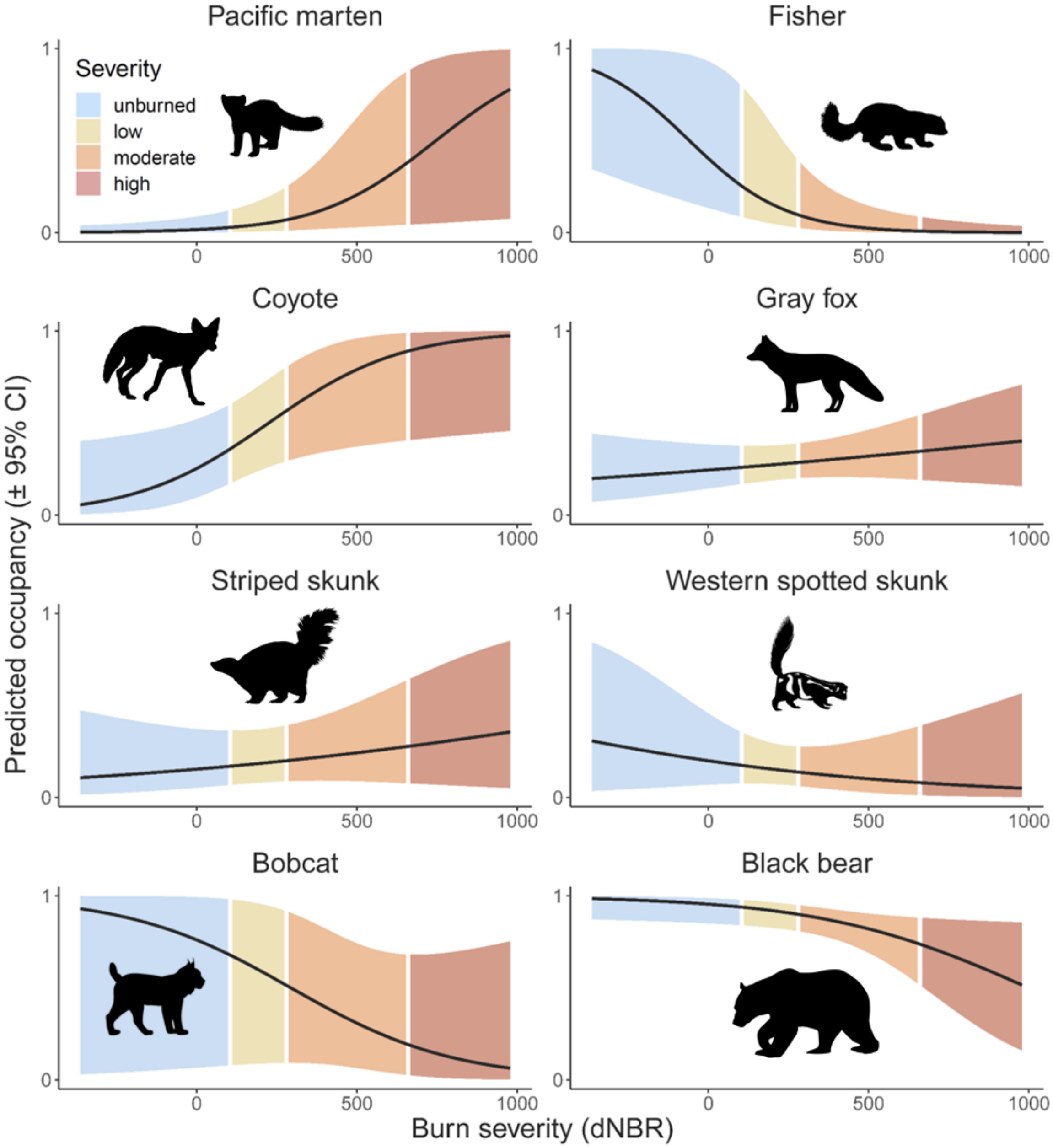


Figure 14. Predicted marginal occupancy (± 95% CI) relative to burn severity as the differenced Normalized Burn Ratio (dNBR) for carnivore species detected in the Dixie Fire study area. Estimates were generated from spatial occupancy models for marten and fisher, and space for time models for all other species.

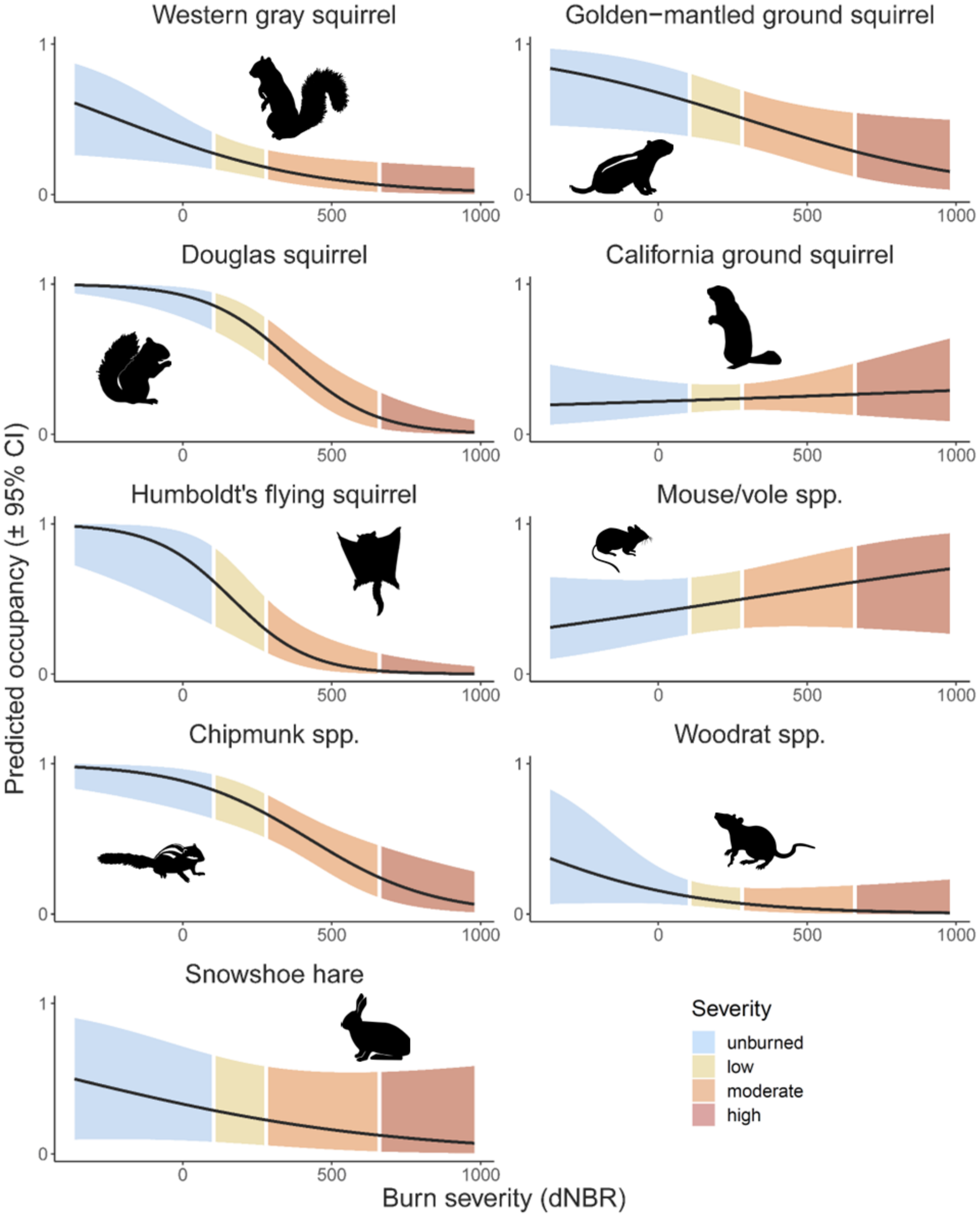


Figure 15. Space for time model estimates for predicted marginal occupancy (± 95% CI) relative to burn severity as the differenced Normalized Burn Ratio (dNBR) for small mammal species detected in the Dixie Fire study area.

Spatial Occupancy Models

Marten occupancy was either weakly or strongly correlated with the fire covariates and elevation, while fisher occupancy had strong negative correlations with them (Figures 16 and 17). Both marten and fisher had strong positive associations with precipitation (Figures 16 and 17), while relationships with post-fire forest structural covariates were mixed. Fisher occupancy was positively correlated with canopy cover (β = 2.06, 95% CI [1.00, 3.52]) and canopy bulk density (β = 2.02, 95% CI [1.01, 3.42]), while marten occupancy showed weakly negative correlations (Figures 16 and 18). Marten showed no correlations with trees per acre or stand density index, but fisher occupancy had a weak positive correlation with stand density index (β = 0.24, 95% CI [-0.13, 1.83]; Figures 16 and 18). Fisher occupancy had a strong positive correlation with basal area (β = 0.87, 95% CI [0.11, 1.92]; Figures 16 and 18). For every 63.2 $ft.^2$ (5.87 m^2) increase in basal area, I estimated an increase in the probability of fisher occupancy by 11% to 192% (95% CI), and I estimated between a decrease of 39% up to an increase of 117% in marten occupancy (95% CI).

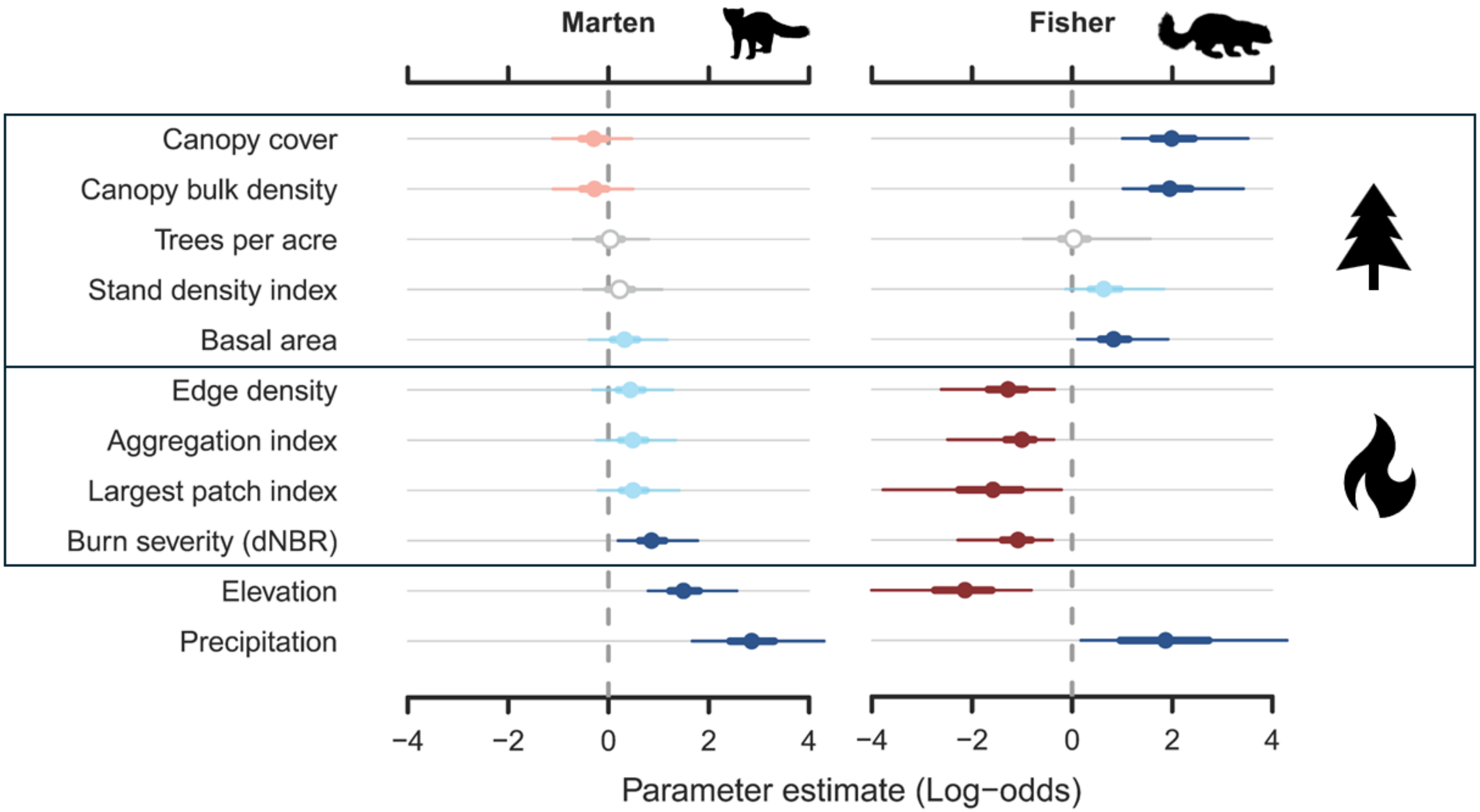


Figure 16. Marten and fisher parameter estimates from univariate occupancy models for post-fire forest, fire, and environmental covariates provided as log-odds (± 50% and 95% CI). Dark blue and red closed circles represent strong positive or negative evidence, light blue or orange closed circles represent weak positive or negative evidence, open gray circles represent no trend.

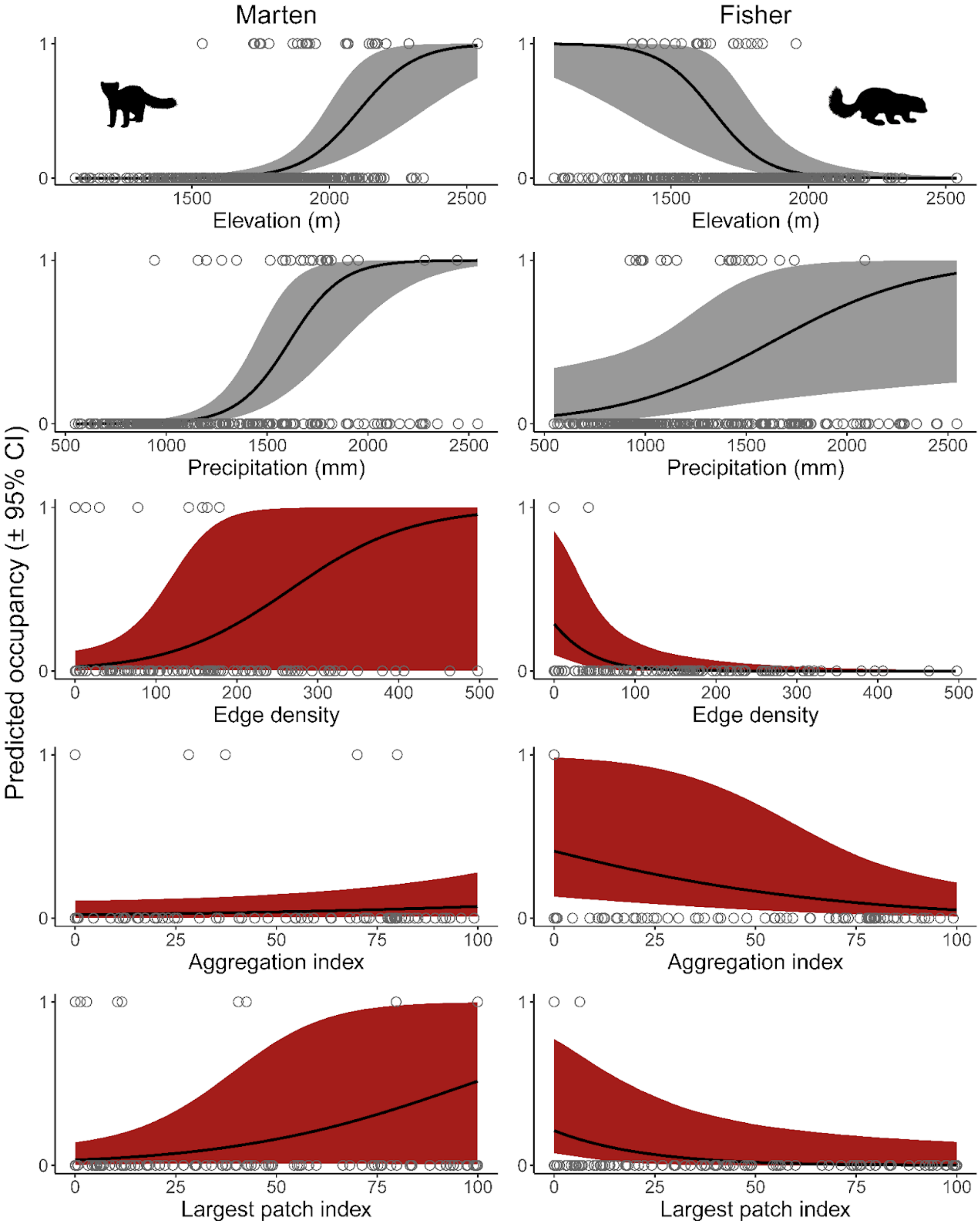


Figure 17. Marten and fisher predicted occupancy (± 95% CI) across the observed range of abiotic (gray) and fire (red) covariates in the Dixie Fire study area. Estimates were generated from univariate spatial occupancy models.

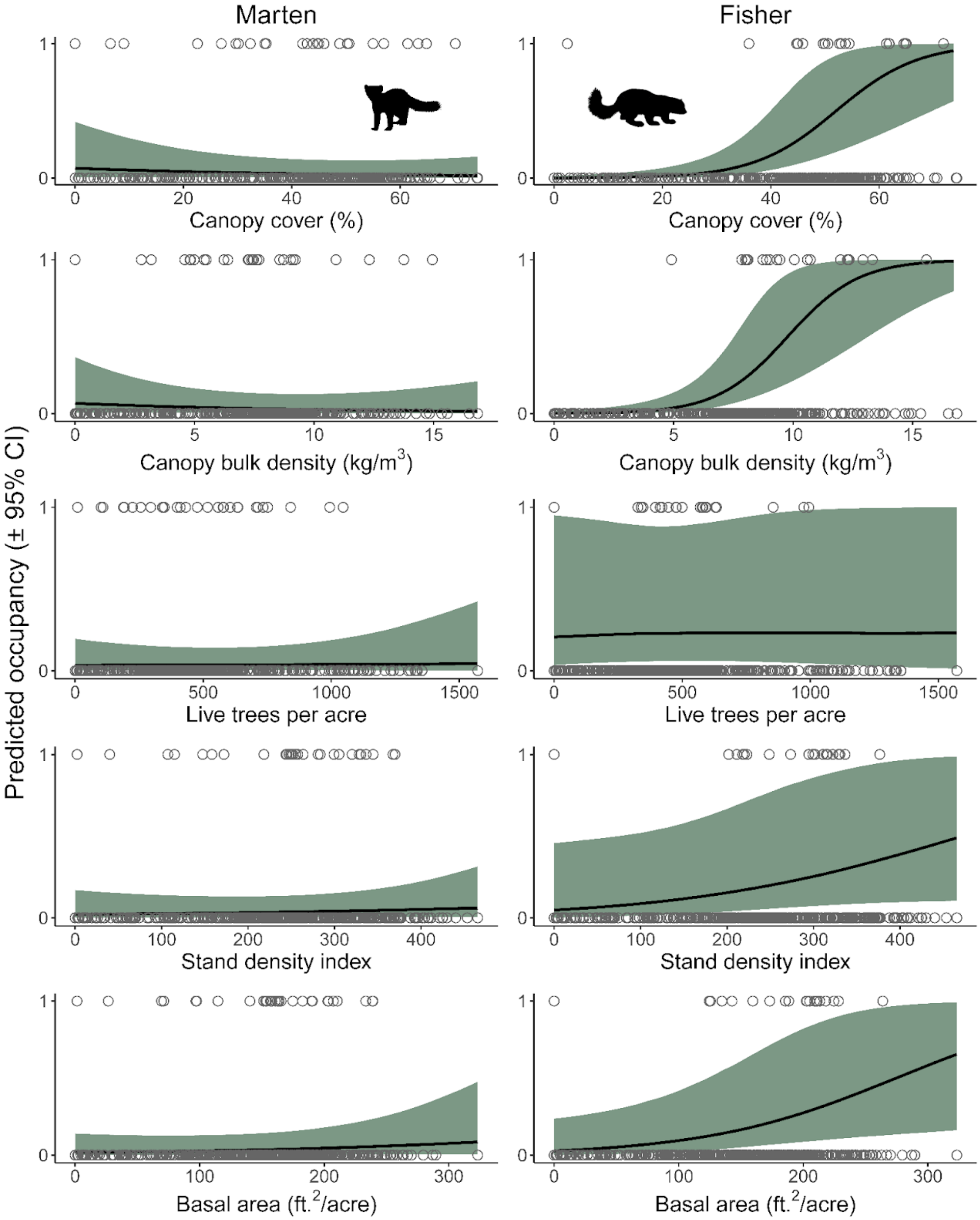


Figure 18. Marten and fisher predicted occupancy (± 95% CI) across the observed range of forest structural covariates in the Dixie Fire study area. Estimates were generated from univariate spatial occupancy models.

The top model for marten occupancy according to WAIC included the null detection submodel (*p*(.)) and the occupancy submodel with elevation, precipitation, and trees per acre as covariates (Table 8). The top model for fisher occupancy included effort as a detection covariate and elevation, precipitation, and canopy cover as occupancy covariates (Table 9). These top models were used to generate the predicted occupancy and standard deviation maps (marten, Figures 19 and 20; fisher, Figures 21 and 22). A goodness of fit test revealed a Bayesian p-value of 0.13 for marten and 0.30 for fisher models, which indicated acceptable model fitness.

Table 8. Marten spatial occupancy models ranked by widely applicable information criterion (WAIC), with effective number of parameters (eK), change in value (ΔWAIC), and model weight suggesting explanatory power. The top model was the one with the lowest WAIC score and was used to make predicted occupancy maps.

Model	eK	WAIC	ΔWAIC	Weight
$p(.)\ \psi$(elev + precip + trees per acre)	5.6	250.47	0	0.203
$p(.)\ \psi$(elev + precip + stand density index)	5.5	250.97	0.50	0.158
$p(.)\ \psi$(elev + precip + basal area)	5.5	251.27	0.79	0.136
$p(.)\ \psi$(elev + precip)	5.5	251.43	0.95	0.126
$p(.)\ \psi$(elev + precip + canopy cover)	5.9	252.31	1.84	0.081
$p(.)\ \psi$(elev + precip + canopy bulk density)	5.9	252.32	1.85	0.081
$p(.)\ \psi$(elev + precip + edge density)	6.1	252.91	2.44	0.060
$p(.)\ \psi$(elev + precip + aggregation index)	6.4	253.00	2.53	0.057
$p(.)\ \psi$(elev + precip + dNBR)	7.2	253.25	2.77	0.051
$p(.)\ \psi$(elev + precip + largest patch index)	6.4	253.37	2.89	0.048
$p(.)\ \psi(.)$	27.5	279.20	28.73	< 0.001
p(effort) $\psi(.)$	27.3	286.05	35.58	< 0.001
$p(.)\ \psi(.)$ non-spatial	3.2	326.13	75.65	< 0.001

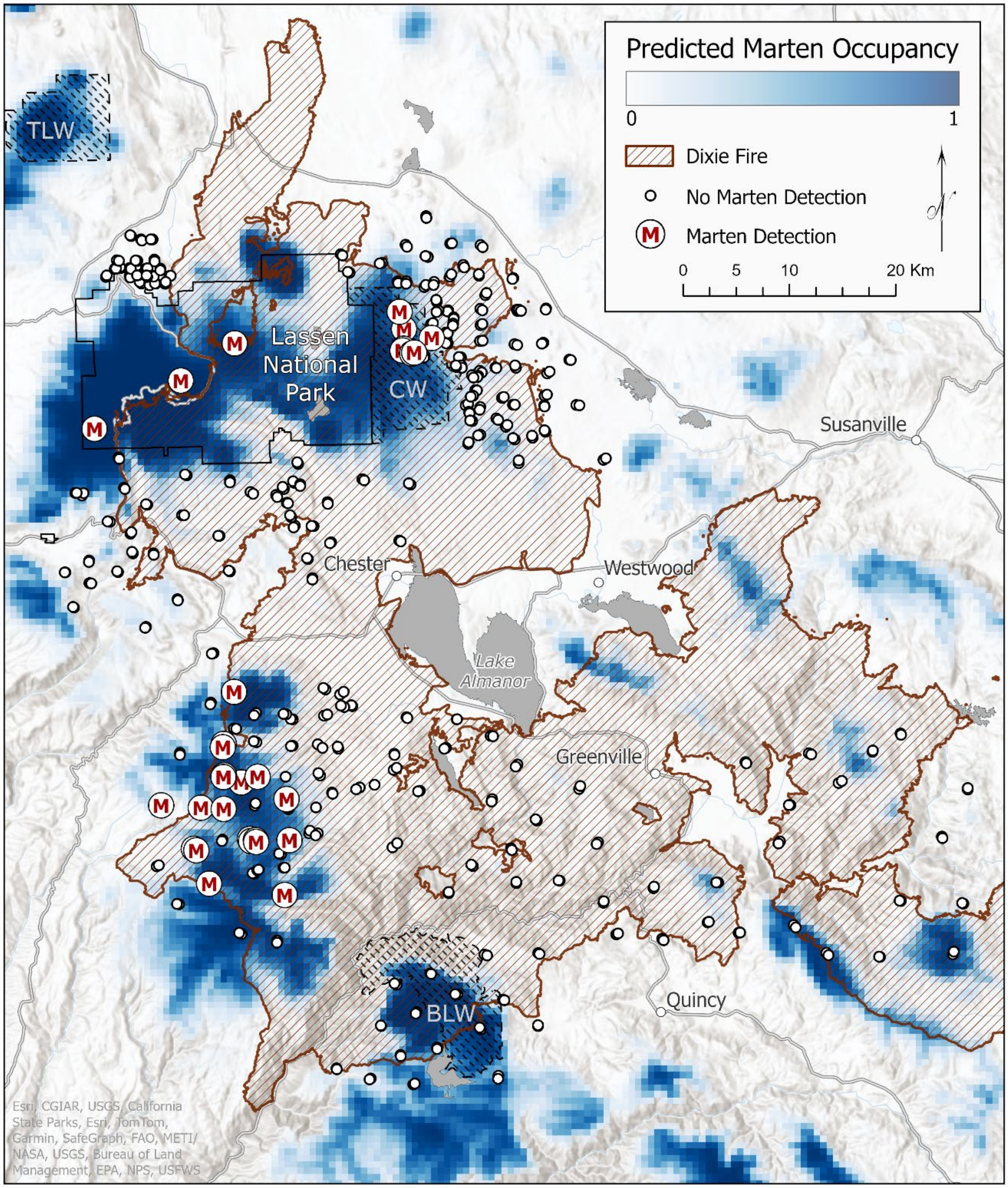


Figure 19. Predicted marten occupancy across the Dixie Fire study area generated from the top spatial occupancy model as ranked by WAIC. This model included no detection covariates and elevation, precipitation, and trees per acre as occupancy covariates. Wilderness areas shown as dashed black polygons are Thousand Lakes Wilderness (TLW), Caribou Wilderness (CW), and Bucks Lake Wilderness (BLW), which have been unmanaged and are relatively high in elevation.

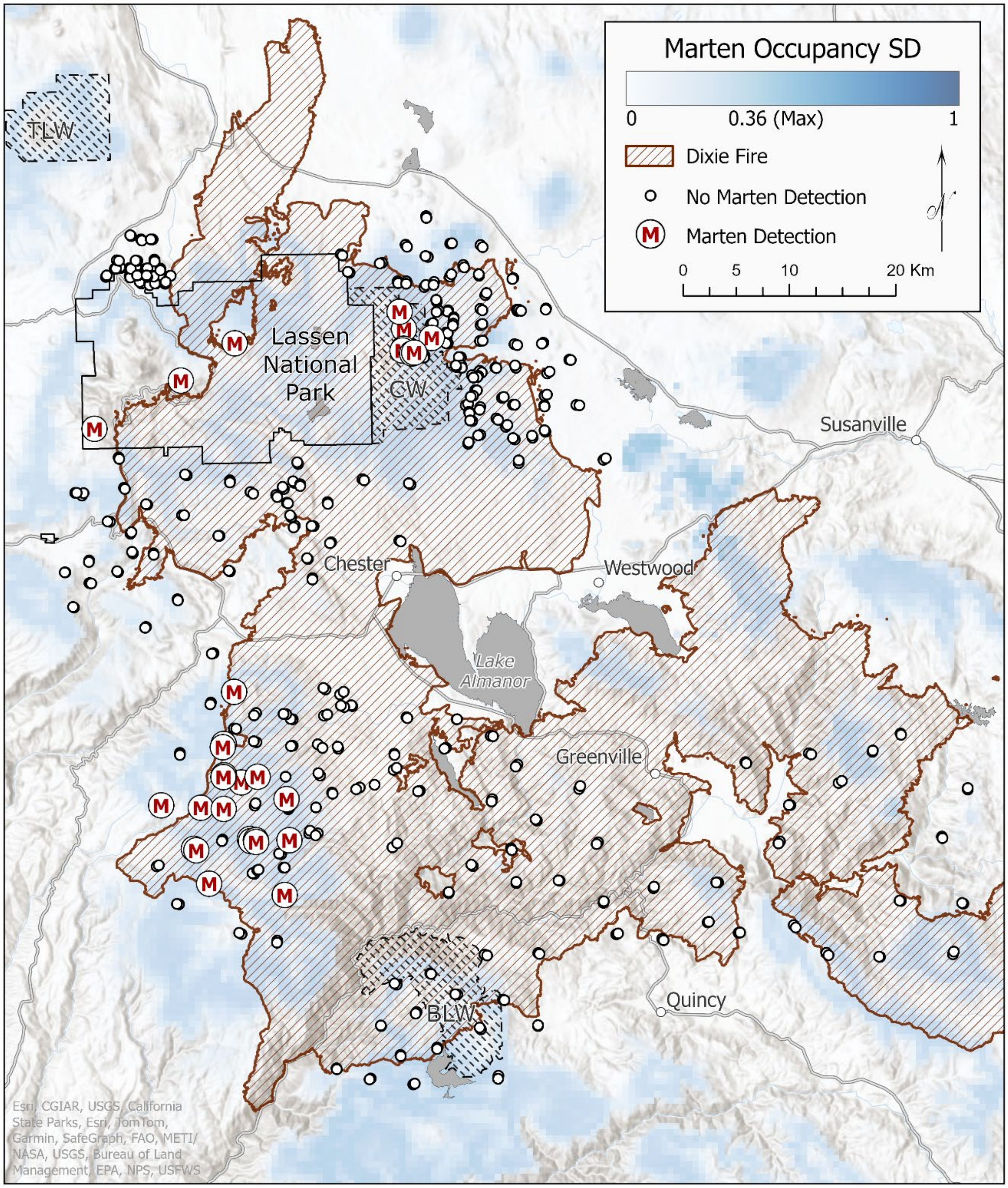


Figure 20. Standard Deviation (SD) of predicted marten occupancy across the Dixie Fire study area generated from the top spatial occupancy model as ranked by WAIC. The maximum SD value was ± 0.36. Wilderness areas shown as dashed black polygons are Thousand Lakes Wilderness (TLW), Caribou Wilderness (CW), and Bucks Lake Wilderness (BLW), which have been unmanaged and are relatively high in elevation.

Table 9. Fisher spatial occupancy models ranked by widely applicable information criterion (WAIC), with effective number of parameters (eK), change in value (ΔWAIC), and model weight suggesting explanatory power. The top model was the one with the lowest WAIC score and was used to make predicted occupancy maps.

Model	eK	WAIC	ΔWAIC	Weight
p(effort) ψ(elev + precip + canopy cover)	6.1	178.02	0	0.554
p(effort) ψ(elev + precip + canopy bulk density)	6.2	178.56	0.54	0.423
p(effort) ψ(elev + precip + aggregation index)	6.5	186.17	8.15	0.009
p(effort) ψ(elev + precip + dNBR)	6.5	186.54	8.52	0.008
p(effort) ψ(elev + precip + edge density)	6.5	187.65	9.63	0.004
p(effort) ψ(elev + precip + largest patch index)	6.5	190.59	12.57	0.001
p(effort) ψ(elev + precip + basal area)	7.4	192.75	14.73	< 0.001
p(effort) ψ(elev + precip + stand density index)	7.2	193.65	15.63	< 0.001
p(effort) ψ(elev + precip)	6.5	196.90	18.88	< 0.001
p(effort) ψ(elev + precip + trees per acre)	6.9	197.94	19.91	< 0.001
p(effort) ψ(.)	10.6	215.33	37.31	< 0.001
p(.) ψ(.)	8.5	226.55	48.53	< 0.001
p(.) ψ(.) non-spatial	1.3	228.41	50.39	< 0.001

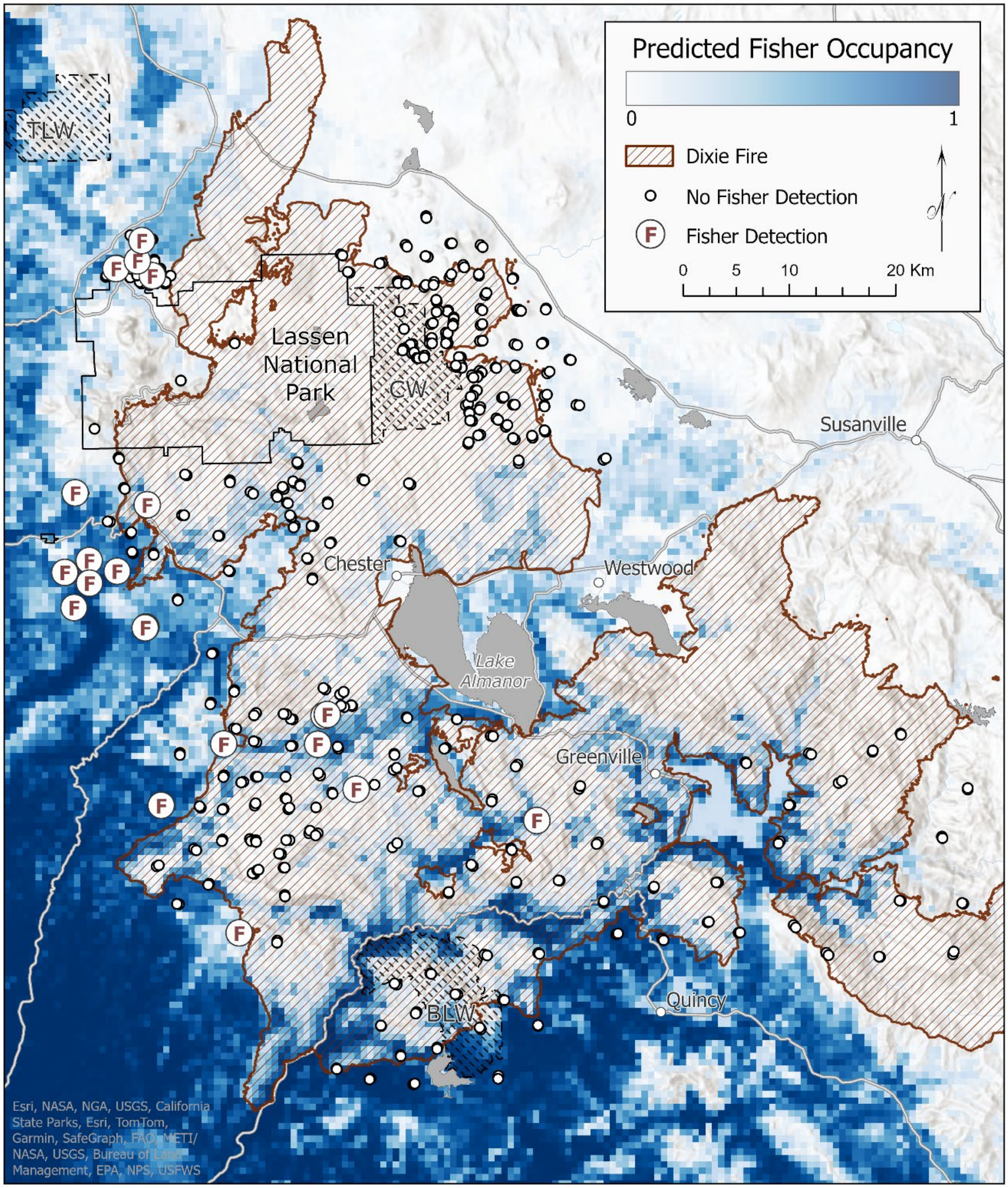


Figure 21. Predicted fisher occupancy across the Dixie Fire study area generated from the top spatial occupancy model as ranked by WAIC. This model included effort as a detection covariate and elevation, precipitation, and canopy cover as occupancy covariates. Wilderness areas shown as dashed black polygons are Thousand Lakes Wilderness (TLW), Caribou Wilderness (CW), and Bucks Lake Wilderness (BLW), which have been unmanaged and are relatively high in elevation.

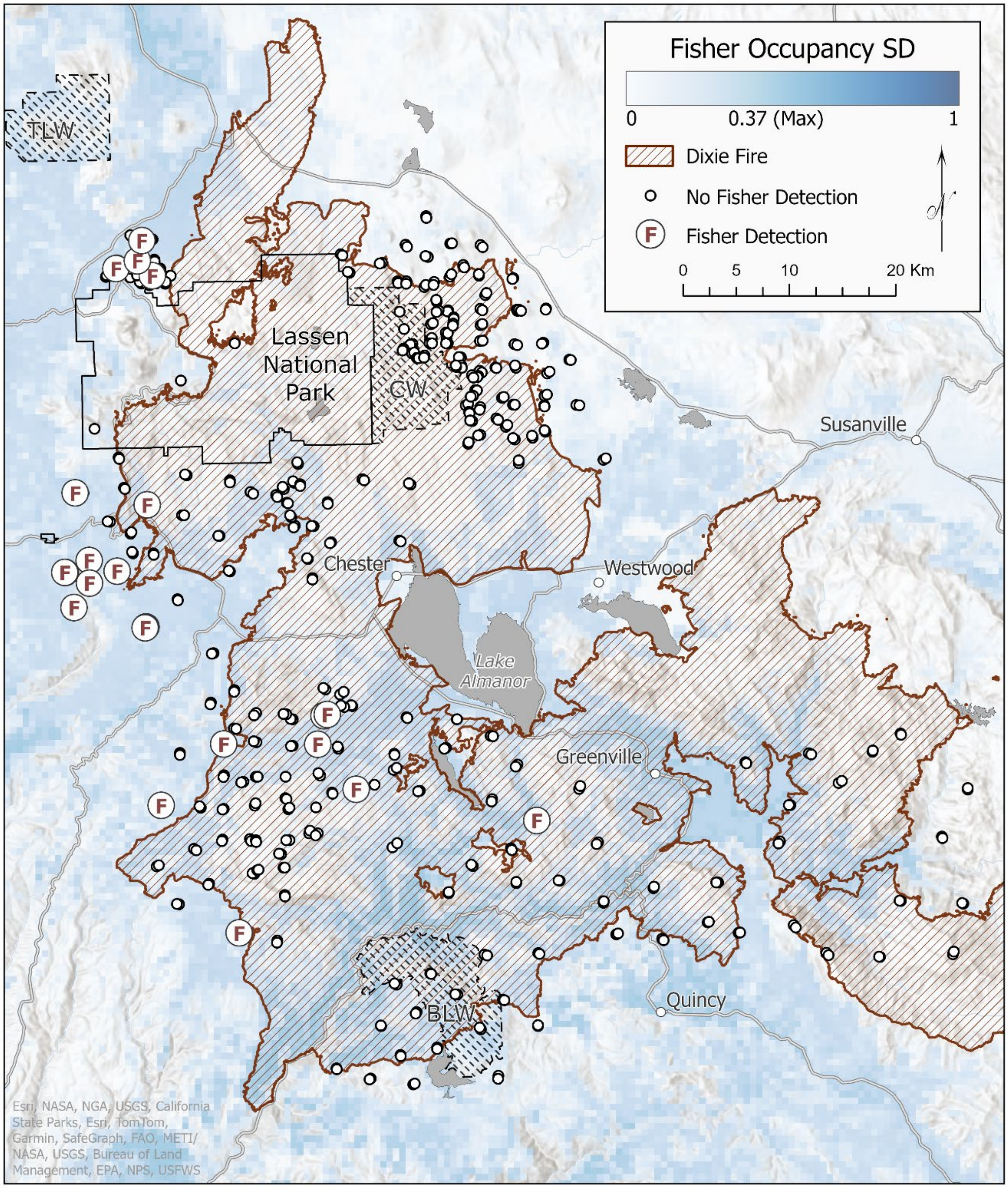


Figure 22. Standard Deviation (SD) of predicted fisher occupancy across the Dixie Fire study area generated from the top spatial occupancy model as ranked by WAIC. The maximum SD value was ± 0.37. Wilderness areas shown as dashed black polygons are Thousand Lakes Wilderness (TLW), Caribou Wilderness (CW), and Bucks Lake Wilderness (BLW), which have been unmanaged and are relatively high in elevation.

DISCUSSION

During this effort, I detected 27 mammalian taxa within or near the largest non-complex fire in California's history. From these data, I was able to model fire severity relationships for 8 carnivore species: Pacific marten, fisher, coyote, gray fox, striped skunk, western spotted skunk, bobcat, and black bear. Additionally, I modeled relationships for 9 small mammal species or groups on which the target carnivores may prey: western gray squirrel, golden-mantled ground squirrel, Douglas squirrel, California ground squirrel, Humboldt's flying squirrel, mouse/vole species, chipmunk species, woodrat species, and snowshoe hare. Pacific marten and coyote occupancy were positively correlated with burn severity, while fisher, black bear, western gray squirrel, golden-mantled ground squirrel, Douglas squirrel, Humboldt's flying squirrel, and chipmunk species were negatively correlated with burn severity. No correlation or relationships were revealed for gray fox, striped skunk, western spotted skunk, woodrat species, and snowshoe hare. Due to lack of data, I was unable to model short-tailed weasel, long-tailed weasel, North American porcupine, American badger, Sierra Nevada red fox, yellow-bellied marmot, ringtail, and Belding's ground squirrel. I provide a repeatable study using remote camera species occurrence data and vegetation surveys 2 years post-fire that can allow future researchers to understand wildlife relationships with fire severity and regeneration of fauna after high severity fire.

This study provides some of the first evidence that Pacific martens use burned forests regardless of severity, and I found no evidence to support my prediction that martens would avoid them. These results corroborate with a recent study in British Columbia which found that martens selected for burned over unburned patches (Volkmann and Hodges 2024). However, in the same study area, martens selected low over high severity burns (Volkmann and Hodges 2021), which is contrary to my finding that marten occupancy increased with burn severity. It is possible that martens could be using burned forests equally without preference for burn severity, and a weaker trend would certainly fit within the 95% Credible Intervals (Figure 14).

I suspect one reason martens had higher occupancy in burned areas may be an increase in small rodent activity or abundance. California ground squirrels and mouse/vole species followed my hypothesis that they would be the only prey species with equal or higher occupancy in the burned areas. The most similar relationship to martens was evidenced in the mouse/vole species, as I estimated they had a strong positive relationship with burn severity. Deer mice are known to increase in number following fire (Tevis 1956, Zwolak and Foresman 2007, Borchert et al. 2014), and they have exhibited a three-fold increase on burned plots compared to plots that were not burned (Gashwiler 1959). Martens north of the study area in Oregon were found to have a diet that was composed of 62.7% vole-sized prey, and that the proportion of voles and chipmunks consumed was higher in summer than in winter (Bull 2000). This may suggest that martens are using these locations for hunting during the summer months, though more research is necessary.

A second explanation for martens using these areas is a lag effect. I found martens in many of the same areas where they were studied before the Dixie Fire (Zielinski et al.

2015, Moriarty et al. 2016, Tweedy et al. 2019, Martin et al. 2021). My predicted occupancy map mirrors Zielinski et al. (2015; Figure 4), likely due to the influence of both precipitation and elevation in both models. Because the Dixie Fire moved through many of these areas quickly (e.g., overnight) it is possible that martens took shelter underground. In this region, 26% of rest locations were underground or subterranean (Delheimer et al. 2023), although fewer subterranean sites were reported in a prior analysis (<1%; Tweedy et al. 2019). Similarly, approximately 50% of Humboldt marten rest locations were subterranean in the Oregon dunes (Linnell, Delheimer, Moriarty, in prep.). Finding underground rest locations is difficult with telemetry, and previous researchers acknowledge potential methods bias (Tweedy et al. 2019). More investigation into the distribution and demographics of persisting marten populations would help inform these interpretations.

Paragi et al. (1996) discovered high rates of juvenile male American martens using burned patches 6-9 years post-fire. They hypothesized these areas could be acting as population sinks due to increased prey biomass, high individual marten turnover rates, and a lack of females. Perhaps the high occupancy probability I estimated in the burned areas is a result of young male martens being attracted by a boon in prey, and these areas could lack suitable kit rearing vegetation structures, such as cover, snags, and large woody material. We detected apparent marten kits at only one site (Figure 23), which was in a low severity patch of forest near Snag Lake. Interestingly, this area was adjacent to a Jeffrey pine plantation with relatively young trees. This observation provides some evidence for reproduction and kit rearing in the burned forest, but surveys which allow for the identification of sex and age are needed for further evaluation.

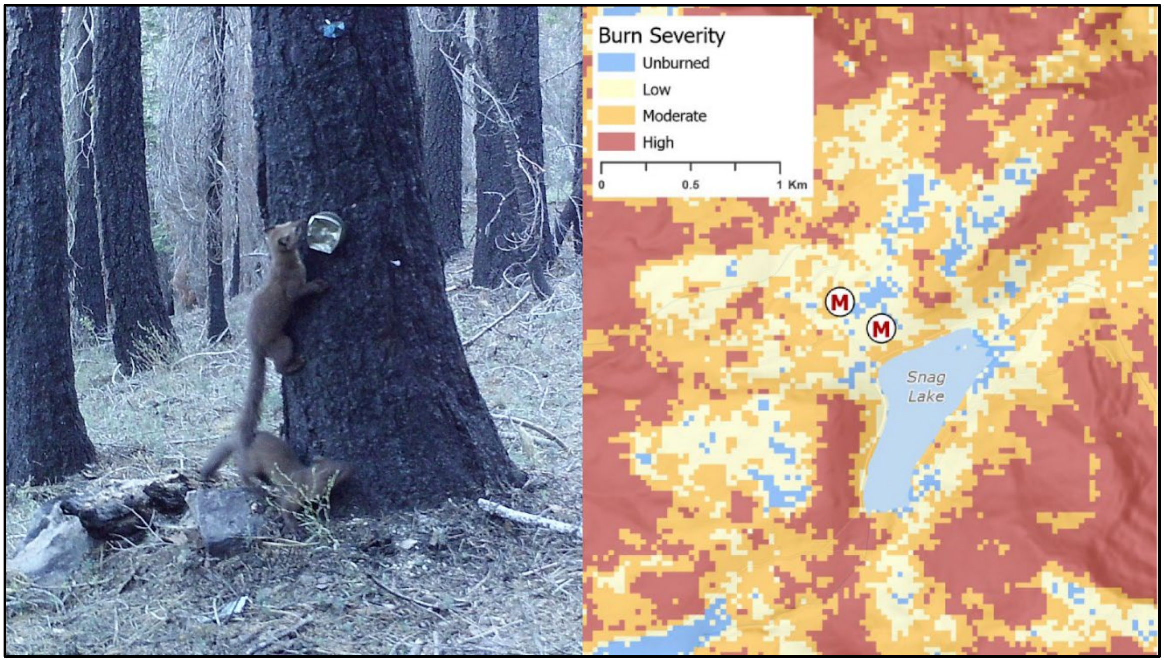


Figure 23. Marten kits using a patch of forest that burned at low severity in the Dixie Fire near Snag Lake in Lassen National Forest, California.

I found that both marten and fisher occupancy strongly correlated with elevation, though they had opposite relationships. This follows a trend observed in the southern Sierra Nevada by Zielinski et al. (2017), where martens and fishers were found more often in higher and lower elevations, respectively, in the northern and wetter portion of their study area. For the precipitation covariate, marten and fisher both exhibited a strong positive association, though for marten the estimate was higher. This relationship is plausible in the context of the study area, where we detected martens and fishers more often in the western slope and higher elevations, which receive more precipitation compared to the drier eastern side of the study area.

Though my models for basal area, stand density index, and trees per acre did not reveal a significant relationship with marten occupancy, they do offer general trends of use. Despite an association with moderate to high severity patches, martens appear to be selecting forests with higher density values even if there are moderate to low numbers of live trees per acre (Figure 24). I found them using forest with relatively high basal area (34 - 57 m^2 per hectare or 150 - 250 ft^2 per acre) and stand density index values (250 - 350) but moderate numbers of live trees (81 - 283 trees per hectare or 200 - 700 trees per acre). These ranges highlight the importance of post-fire forest density, regardless of tree mortality, and they follow current understandings that martens use dense forests with larger trees (e.g., Moriarty et al. 2016, Delheimer et al. 2019, 2023).

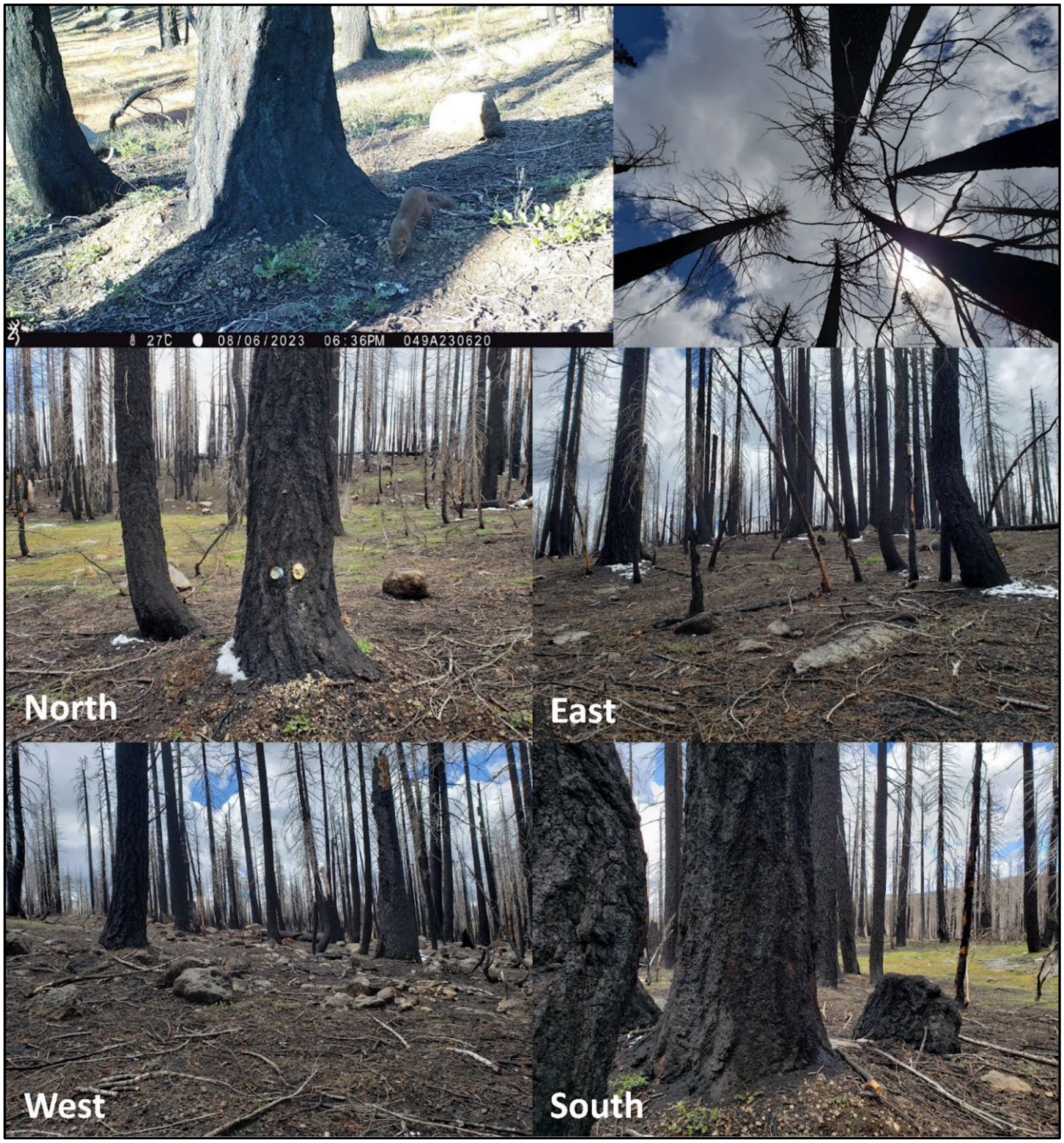


Figure 24. A Pacific marten (top left) using a patch of forest that burned at high severity in the Dixie Fire near Humbug Summit in Lassen National Forest, California. This stand contained large red fir that experienced high mortality and had essentially no remaining canopy, as evidenced by the amount of sunlight reaching the forest floor. Adjacent areas had new forb growth, which may have promoted food available to small mammals.

I found that edge density was positively correlated with marten occupancy, though it was a weak relationship. This appears to contrast with a habitat fragmentation study in Utah, which found that marten capture rates were lower at sites with high values of edge density (Hargis et al. 1999). However, I created the edge density metric using the high severity patches of fire and not proportion of the landscape managed by clearcutting, so my index may reflect pyrodiversity as opposed to notable habitat fragmentation or loss. For instance, my results showed forests with higher basal area values that burned at high severity may offer some form of contiguous habitat for martens. Additionally, martens had a weak positive correlation with the aggregation and largest patch indices, which may suggest martens occupied larger high severity patches that were clustered. However, for all predicted occupancy estimates for landscape variables created through FRAGSTATS, my 95% CIs overlapped zero suggesting my results were inconclusive. A future study could stratify by landscape indices more directly, perhaps using contemporary canopy cover or another structural forest covariate to further explore marten use of differential post-fire landscape configurations.

The scale optimization results revealed that marten occupancy was associated with vegetation structure at the broadest scales (1,440 or 2,880 m) for fire covariates (aggregation index, edge density, largest patch index, burn severity) but a finer scale (360 m) for forest covariates (canopy cover, canopy bulk density). Similarly, Tweedy et al. (2019) found correlations between marten rest sites before the burn with canopy cover at the finest spatial scales (30, 90m) and abiotic factors and measurements at the broadest spatial scales (e.g., 900, 990m). I suspect martens may be selecting for burn severity across their entire home range but may locally cue into forest structural components for fine scale movement. Martin et al. (2021) found marten movement correlated with basal area during summer at the finest spatial scales. Furthermore, Paragi et al. (1996) noted martens did not select post-fire structural components at the stand level. Interestingly, martens and fishers had the same optimal scales for all covariates except edge density and largest patch index, so these sympatric mustelids could be selecting vegetation structure at similar scales.

My results provide evidence that fishers avoid burned areas, which follows patterns documented by recent studies (Thompson et al. 2021, Green et al. 2022b). I documented fishers using mostly unburned and low severity sites (Appendix B). Fishers may be using these areas as “islands” for refugia in the post-fire landscape (Steenvoorden et al. 2019). This relates to a study in the southern Sierra Nevada that found high probability of fisher den sites in low severity burns (Blomdahl et al. 2019), and it is possible that the Dixie Fire created den sites in the low severity patches.

Since their reintroduction, fishers appear to have filled in some of the population gaps identified by Zielinski et al. (2005) in the Lassen area. It appears fishers have spread far beyond the reintroduction sites on adjacent timber lands (Facka et al. 2016, Green et al. 2022a), as I detected one individual approximately 40 km east that was situated south of Lake Almanor. I hypothesize fishers will eventually populate the forests just west of Quincy, where my model also identified high probability of occupancy. We documented fishers using several other low severity sites, including one large individual with an interesting pelage (Figure 25).

Figure 25. A fisher using a patch of forest that burned at low severity in the Dixie Fire near the town of Mineral in Lassen National Forest, California.

Niche partitioning may be occurring between martens and fishers in the study area. This would explain the burn severity relationships I found and how I detected both species at only two sites. A study in southeast Alaska found that martens and fishers temporally partitioned their activity, and the authors suggested that martens are avoiding the larger bodied fishers (Kupferman et al. 2021). However, they found no evidence of spatial partitioning. My results appear to show that spatial partitioning may be happening in the Dixie Fire study area. A future study could perform diel activity analysis to determine whether the relationship that Kupferman et al. (2021) found is expressed in the mustelid guild of Lassen and Plumas National Forests. Similar to Pauli et al. (2022), I would expect competition to be highest in areas lacking snow.

The probability of occupancy maps (Figures 19, 20, 21, and 22) should not be interpreted as habitat suitability, but instead as the probability of a pixel being used at least once during the sampling period (Lele et al. 2013). Nevertheless, they highlight areas that will be important for the conservation of Pacific martens and fishers, and they may help identify locations that offer refugia as the climate and fuelscape shift and more fires occur. Given my finding that martens persisted in burned forests, managers may use the maps to determine appropriate areas for post-fire management plans.

My marten predicted occupancy map is strikingly similar to that of a previous study in the Lassen (Zielinski et al. 2015). Interestingly, their model was generated using detections from summer and winter surveys, whereas mine only included 4 detections that occurred in winter. Perhaps martens shifted their summer activities to encompass more of the wintering range in response to the Dixie Fire. Additionally, the marten habitat suitability model generated by Kirk and Zielinski (2009) classified the Humboldt Peak area (Figure 26, left panel) with low suitability. This could be further evidence that martens are shifting their distribution or summer activities to this location. Post-fire winter surveys are needed to address this hypothesis.

Bucks Lake Wilderness in Plumas National Forest had no marten detections, but it was identified by my predictive model to have high occupancy probability (Figure 19). This location was historically occupied by martens (Grinnell et al. 1937), but by 2002 they were absent (Zielinski et al. 2005). Due to its proximity to the Humboldt Peak population, this wilderness area should be of high priority for marten conservation. It could serve as a key location for restoration or reintroduction efforts to improve connectivity between the Lassen populations and those further south in the Sierra Nevada.

An area that was more recently occupied by martens is the Swain Mountain area east of the Caribou Wilderness (Figure 26), which my models also assigned a high occupancy probability. Martens were often detected at the easternmost sites before the fire (e.g., Kirk and Zielinski 2009, Moriarty et al. 2015, 2016, Zielinski et al. 2015). We surveyed this area extensively in 2022 and 2023, and martens were only detected within the Caribou Wilderness and one site just beyond the perimeter. A recent meta-analysis found that fire severity was the greatest contributor to animal mortality from wildfire (Jolly et al. 2022). Martens have been documented as outrunning fire (Raine 1981), but it is possible that the fire moved both too quickly through this area that it consumed animals and too slowly for them to take refuge underground or in refugia.

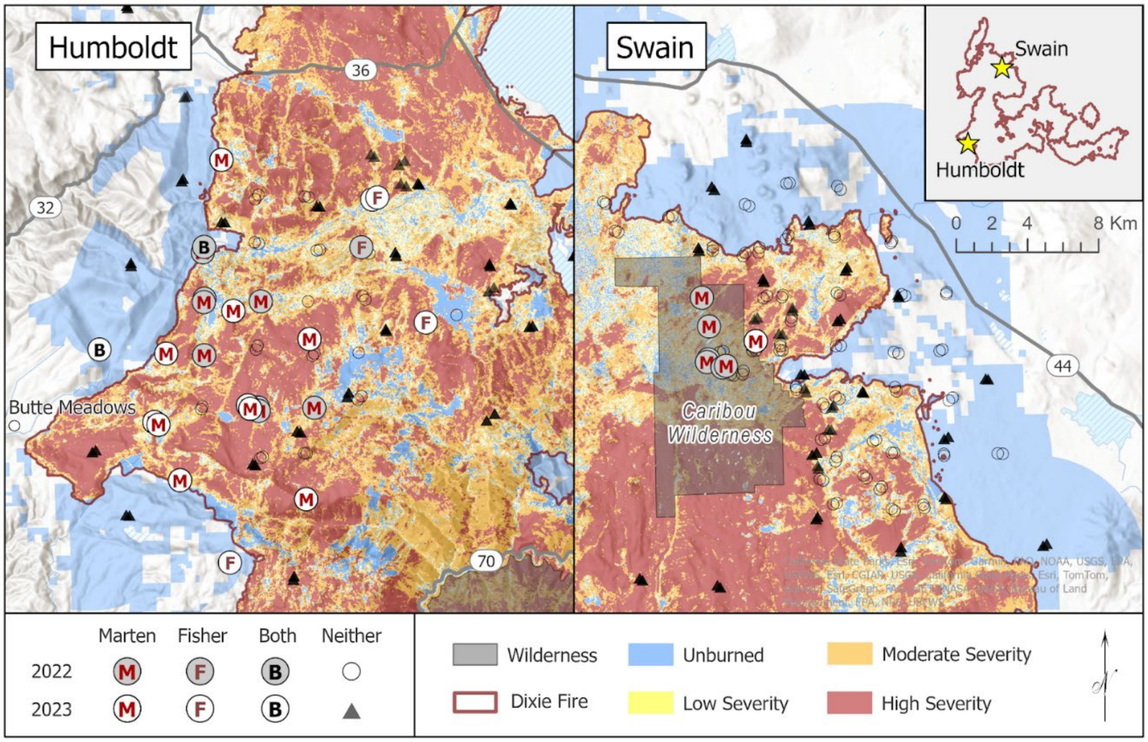


Figure 26. Humboldt Peak and Swain Mountain within Lassen National Forest, California, where previous studies patchily detected martens (e.g., Kirk and Zielinski 2009, Moriarty et al. 2015, 2016, Zielinski et al. 2015).

The Carnivore Community and Fire Severity

The results presented here offer some support for the hypothesis that generalists used burned forests regardless of severity. I found that gray fox and striped skunk occupancy had weak positive correlations with burn severity, and they were detected nearly equally in all levels of burn severity (Appendix B). However, contrary to my hypothesis, coyotes had a strong positive correlation with burn severity, which was similar to the relationship evidenced in martens. My results corroborate with another study that found coyotes selected for recently burned over unburned forests, which was attributed to ease of hunting in areas with less vegetation and higher prey densities (Stevenson et al. 2019). These generalist species using the burned sites may be increasing the threat of competition with or predation on martens and fishers.

We detected bobcats within all classes of burn severity, but I did not uncover a strong relationship in my models. This could indicate that bobcats are using the forest similarly to coyotes and foxes, though we detected them with slightly greater frequency at the unburned sites than the burned sites (Appendix B) or that detectability was too low (18%) to consistently locate bobcat occupancy in all areas. Few studies have explored felid responses to fire (Volkmann et al. 2020). Bobcats were a suspected cause of marten mortality (Delheimer et al. 2021) and later determined to be the most common cause of mortality within the study area before the fire (Martin et al. 2022a), and for fishers in southern Sierra Nevada (Wengert et al. 2014). I suggest more research be conducted to address bobcat responses to fire, and future studies could investigate predator-prey interactions in relation to fire severity or other metrics.

In a meta-analysis that assessed carnivore relationships with fire, Geary et al. (2020) concluded that many species could be resilient to its effects. My results show some support of this suggestion, as gray fox, striped skunk, western spotted skunk, and bobcat were detected at all levels of burn severity and had no strong positive or negative relationship to burn severity. However, marten, fisher, coyote, and bobcat exhibited strong positive or negative associations with burn severity, so these species may be more sensitive to the effects of fire. This discrepancy could be a result of the Dixie Fire burning larger and at higher severity than most other fires.

MANAGEMENT IMPLICATIONS

In summary, Pacific martens appear to be using patches of burned over unburned forests in the Dixie Fire study area. Prey availability or avoidance of the sympatric fisher, which exhibited the opposite relationship with burn severity, may be driving this result. Mouse/vole species had a strong positive relationship with burn severity and occupancy, while other prey species had a negative one. Carnivore species had mixed correlations with burn severity. Coyotes had a strong positive relationship with increasing burn severity, while black bears showed a negative correlation. Bobcats were detected using all classes of burn severity, though my occupancy estimates had high uncertainty. The increased presence of coyotes and persistence of bobcats suggest predator interactions may still exist for martens in post-fire forests. More research is needed to determine if these interactions are mediated by burn severity.

Based on my results, there are 3 obvious inquiries that would benefit from additional research. First, given my finding that marten occupancy increased with burn severity and that they used burned stands more frequently than unburned stands, a study stratified by burn severity in areas with and without salvage logging could help better describe management opportunities. Second, there is evidence of seasonal differences in marten occupancy (e.g., Zielinski et al. 2015) and resource use (e.g., Martin et al. 2021). Conducting similar winter surveys may allow us to understand year-round marten occurrence and relationships with a post-fire landscape. Third, demographic studies that make use of genetic sampling and age estimates would allow comparisons of post-fire home range, densities, and sex ratios to pre-fire studies. Such information could yield evidence as to whether this area is now a population sink (if there were only juveniles or males) or a resilient population (equal sex ratios or increased females and young of the year).

Though martens are using moderate to high severity burned areas, they appear to have experienced reductions in range, especially east of the Caribou Wilderness and north of the town of Mineral. Our detections of fishers show that they have expanded far into Lassen National Forest from the source of reintroduction, but the Dixie Fire appears to have reduced forest quality for them. My occupancy probability maps identify an area west of Quincy that could be populated by fishers in the future. Additionally, the nearby Bucks Lake Wilderness is an important region to consider for marten or fisher establishment. These locations should be surveyed in the future to determine marten and fisher distributions.

The forest inventory values occupied by martens and fishers may be informative to managers for creating post-fire thin, prescription burn plans, or restoration activities. I found that martens and fishers generally used forest with relatively high basal area (34 - 57 m^2 per hectare or 150 - 250 ft^2 per acre) and stand density index values (250 - 350) but moderate numbers of live trees (81 - 283 trees per hectare or 200 - 700 trees per acre). Additionally, a previous study on the Lassen recommended fuels reduction treatments occur below 1,500 m for marten conservation (Moriarty et al. 2016) with no ill effects to fire risk (Credo 2017). The lowest elevation at which I detected them was 1,538 m, so my results support this recommendation. Furthermore, as Moriarty et al. (2016) explained, the historical fire return intervals at lower elevations in the study area are much shorter, so more fuel has built up, and treatments in these locations should take priority over higher elevations, which historically had longer return intervals (Mallek et al. 2013).

Given my finding that marten occupancy was greatest in burned areas and previous research that found martens avoid thinned forests (Moriarty et al. 2016), I suspect prescription burns could be a viable alternative to treatments. Working with indigenous tribes is essential to implementing effective burns. Communication, collaboration, and workshops are supportive options to help build the necessary trust between federal or local agencies and tribes to bring fire back to the landscape using methods informed by traditional knowledge (Lake et al. 2017). However, this type of treatment could negatively affect fishers if it results in high severity fire, so careful planning will be essential to reducing the impacts on mustelid species.

LITERATURE CITED

Abatzoglou, J. T., D. S. Battisti, A. P. Williams, W. D. Hansen, B. J. Harvey, and C. A. Kolden. 2021. Projected increases in western US forest fire despite growing fuel constraints. Communications Earth & Environment 2:1–8.

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113:11770–11775.

Adams, C. C. 1930. Rational predatory animal control. Journal of Mammalogy 11:353–362.

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3:30–36.

Anderson, M. K., and M. J. Moratto. 1996. Native American land-use practices and ecological impacts. Pages 187–206 *in* Sierra Nevada ecosystem project: final report to Congress, vol. II. University of California, Centers for Water and Wildland Resources, Davis, California, USA.

Arvola, T. F. 1978. California forestry handbook. State of California, Department of Forestry. <https://bof.fire.ca.gov/media/8137/california_forestry_handbook_0-ada.pdf>. Accessed 14 Jan 2024.

Bajcz, A. W., W. J. Glisson, J. W. Doser, D. J. Larkin, and J. R. Fieberg. 2024. A within-lake occupancy model for starry stonewort, *Nitellopsis obtusa*, to support early detection and monitoring. Scientific Reports 14:2644.

Biberdorf, A. 1982. Status of the marten in California. Department of Fish and Game, Nongame Wildlife Investigations, California.

Bissonette, J. A., and S. Broekhuizen. 1995. Martes populations as indicators of habitat spatial patterns: the need for a multiscale approach. Pages 95-121 in W. Z. Lidicker, editor. Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, Minneapolis, Minnesota, USA.

Blomdahl, E. M., C. M. Thompson, J. R. Kane, V. R. Kane, D. Churchill, L. M. Moskal, and J. A. Lutz. 2019. Forest structure predictive of fisher (*Pekania pennanti*) dens exists in recently burned forest in Yosemite, California, USA. Forest Ecology and Management 444:174–186.

Bond, W., and J. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20:387–394.

Borchert, M. I. 2012. Mammalian carnivore use of a high-severity burn in conifer forests in the San Bernardino mountains of southern California, USA. Hystrix, the Italian Journal of Mammalogy 23:50–56.

Borchert, M. I., D. P. Farr, M. A. Rimbenieks-Negrete, and M. N. Pawlowski. 2014. Responses of small mammals to wildfire in a mixed conifer forest in the San Bernardino Mountains, California. Bulletin, Southern California Academy of Sciences 113:81–95.

Brooks, S. P., and A. Gelman. 1998. General Methods for Monitoring Convergence of Iterative Simulations. Journal of Computational and Graphical Statistics 7:434–455.

Bull, E. L. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. Northwest Science 74:186–191.

Burke, P. 2019. Climate-mediated wildfire disturbance to a mammal community within protected temperate coniferous forests. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Busenberg, G. 2004. Wildfire management in the United States: the evolution of a policy failure. Review of Policy Research 21:145–156.

Buyaskas, M., B. E. Evans, and A. Mortelliti. 2020. Assessing the effectiveness of attractants to increase camera trap detections of North American mammals. Mammalian Biology 100:91–100.

Cal Fire. 2022a. Cal Fire investigators determine cause of the Dixie Fire. California Department of Forestry and Fire Protection. <https://www.fire.ca.gov/media/edwez51p/dixie_fire_release.pdf/>. Accessed 16 Nov 2022.

Cal Fire. 2022b. Dixie Fire incident. Cal Fire News Release. California Department of Forestry and Fire Protection. <https://www.fire.ca.gov/incidents/2021/7/13/dixie-fire/>. Accessed 16 Nov 2022.

California Department of Fish and Wildlife [CDFW]. 2018. Report to the Fish and Game Commission; a status review of the Humboldt marten (*Martes caurina humboldtensis*) in California. Natural Resources Agency, California Department of Fish and Wildlife, Sacramento, California.

California Natural Diversity Database [CNDDB]. 2023. Special animals list. California Department of Fish and Wildlife. Sacramento, California, USA. <https://wildlife.ca.gov/Conservation/SSC/Mammals/>. Accessed 25 Mar 2023.

Credo, K. 2017. Assessing alternatives for fuel reduction treatment and Pacific marten conservation in the southern Cascades and northern Sierra Nevada. Thesis, Oregon State University, Corvallis, Oregon, USA.

Cunningham, S. C., L. Kirkendall, and W. Ballard. 2006. Gray fox and coyote abundance and diet responses after a wildfire in central Arizona. Western North American Naturalist 66:169–180.

Datta, A., S. Banerjee, A. O. Finley, and A. E. Gelfand. 2016. Hierarchical nearest-neighbor Gaussian process models for large geostatistical datasets. Journal of the American Statistical Association 111:800–812.

Dawson, N. G., J. P. Colella, M. P. Small, K. D. Stone, S. L. Talbot, and J. A. Cook. 2017. Historical biogeography sets the foundation for contemporary conservation of martens (genus *Martes*) in northwestern North America. Journal of Mammalogy 98:715–730.

Dawson, N. G., and J. A. Cook. 2012. Behind the genes: diversification of North American martens (*Martes americana* and *M. caurina*). Pages 23–38 *in* K. B. Aubry, W. J. Zielinski, M. G. Raphael, and G. Proulx, editors. Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, Ithaca, New York, USA.

Delheimer, M. S., K. M. Moriarty, M. A. Linnell, and B. V. Woodruff. 2019. If a tree falls in a forest: implications of forest structure persistence for the Pacific marten (*Martes caurina*). Ecosphere 10:e02819.

Delheimer, M. S., K. M. Moriarty, H. L. Munro, D. A. Early, K. A. Hamm, and R. E. Green. 2023. Structural complexity characterizes fine-scale forest conditions used by Pacific martens. The Journal of Wildlife Management 87:e22388.

Delheimer, M. S., A. M. Roddy, and K. M. Moriarty. 2021. Behavior patterns of denning Pacific martens (*Martes Caurina*). Western Wildlife 8:18–26.

Doser, J. W., A. O. Finley, M. Kéry, and E. F. Zipkin. 2022. spOccupancy: and R package for single-species, multi-species, and integrated spatial occupancy models. Methods in Ecology and Evolution 13:1670–1678.

Evans, B. E., C. E. Mosby, and A. Mortelliti. 2019. Assessing arrays of multiple trail cameras to detect North American mammals. PLoS One 14:e0217543.

Facka, A. N., J. C. Lewis, P. Happe, K. Jenkins, R. Callas, and R. A. Powell. 2016. Timing of translocation influences birth rate and population dynamics in a forest carnivore. Ecosphere 7:e01223.

Facka, A. N., and R. A. Powell. 2021. Intraspecific competition, habitat quality, niche partitioning, and causes of intrasexual territoriality for a reintroduced carnivoran. Frontiers in Ecology and Evolution 9:734155.

Ferreras, P., F. Díaz-Ruiz, and P. Monterroso. 2018. Improving mesocarnivore detectability with lures in camera-trapping studies. Wildlife Research 45:505.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

Fiske, I., and R. Chandler. 2011. unmarked : An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fontaine, J. B., and P. L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22:1547–1561.

Fuller, A. K., D. W. Linden, and J. A. Royle. 2016. Management decision making for fisher populations informed by occupancy modeling: fisher occupancy. The Journal of Wildlife Management 80:794–802.

Gabriel, M. W., L. W. Woods, R. Poppenga, R. A. Sweitzer, C. Thompson, S. M. Matthews, J. M. Higley, S. M. Keller, K. Purcell, R. H. Barrett, G. M. Wengert, B. N. Sacks, and D. L. Clifford. 2012. Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare forest carnivore. PLoS One 7:e40163.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. Journal of Mammalogy 40:128–139.

Geary, W. L., T. S. Doherty, D. G. Nimmo, A. I. T. Tulloch, and E. G. Ritchie. 2020. Predator responses to fire: a global systematic review and meta-analysis. Journal of Animal Ecology 89:955–971.

Gelman A., and K. Shirley. 2011. Inference from simulations and monitoring convergence. Pages 163–174 *in* S. Brooks, A. Gelman, G. Jones, and X. L. Meng, editors. Handbook of Markov Chain Monte Carlo. CRC Press, Boca Raton, Florida, USA.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Green, D. S., A. N. Facka, K. P. Smith, S. M. Matthews, and R. A. Powell. 2022a. Evaluating the efficacy of reintroducing fishers (*Pekania pennanti*) to a landscape managed for timber production. Forest Ecology and Management 511:120089.

Green, D. S., M. E. Martin, R. A. Powell, E. L. McGregor, M. W. Gabriel, K. L. Pilgrim, M. K. Schwartz, and S. M. Matthews. 2022b. Mixed-severity wildfire and salvage logging affect the populations of a forest-dependent carnivoran and a competitor. Ecosphere 13:e03877.

Greenberg, S., and T. Godin. 2019. A tool supporting the extraction of angling effort data from remote camera images. Fisheries Magazine 40:276-278.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing mammals of California. University of California Press, Berkeley, California, USA.

Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, E. E. Knapp, J. M. Lydersen, K. L. Metlen, et al. 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecological Applications 31:e02431.

Hall, E. R. 1930. Predatory mammal destruction. Journal of Mammalogy 11:362–372.

Hargis, C. D., John. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157–172.

Hobbs, N. T., and M. B. Hooten. 2015. Bayesian models: a statistical primer for ecologists. Princeton University Press, Princeton, New Jersey, USA.

Hurteau, M., and M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Frontiers in Ecology and the Environment, 7:409–414.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (USA) conifer forests. Conservation Biology 9:1041–1058.

Iles, K. 1989. Subsampling for VBAR. Inventory Cruising News 8:2–3.

Iversen, J. 1972. Basal energy metabolism of mustelids. Journal of Comparative Physiology 81:341–344.

Johnson, D. S., P. B. Conn, M. B. Hooten, J. C. Ray, and B. A. Pond. 2013. Spatial occupancy models for large data sets. Ecology 94:801–808.

Jolly, C. J., C. R. Dickman, T. S. Doherty, L. M. Van Eeden, W. L. Geary, S. M. Legge, J. C. Z. Woinarski, and D. G. Nimmo. 2022. Animal mortality during fire. Global Change Biology 28:2053–2065.

Jones, G. M., and M. W. Tingley. 2022. Pyrodiversity and biodiversity: A history, synthesis, and outlook. Diversity and Distributions 28:386–403.

Kalies, E. L., and L. L. Yocom Kent. 2016. Tamm review: are fuel treatments effective at achieving ecological and social objectives? A systematic review. Forest Ecology and Management 375:84–95.

Kéry, M., and Royle, J.A., 2016. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS: Volume 1: prelude and static models. Academic Press, Cambridge, Massachusetts, USA.

Key, C. H., and N. C. Benson. 2006. Landscape assessment: ground measure of severity, the composite burn index; and remote sensing of severity, the normalized burn ratio. Pages LA1-51 *in* D. C. Lutes, editor. FIREMON: Fire effects monitoring and inventory system, RMRS-GTR-164. U.S. Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Kimmerer, R. W., and F. K. Lake. 2001. The role of indigenous burning in land management. Journal of Forestry 99:36–41.

Kirk, T. A., and W. J. Zielinski. 2009. Developing and testing a landscape habitat suitability model for the American marten (*Martes americana*) in the Cascades mountains of California. Landscape Ecology 24:759–773.

Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. The Journal of Wildlife Management 41:500–505.

Kupferman, C. A., A. P. Crupi, L. P. Waits, and S. L. Gilbert. 2021. Spatial and temporal partitioning of mustelids in Southeast Alaska. Ecosphere 12:e03827.

Lake, F. K., V. Wright, P. Morgan, M. McFadzen, D. McWethy, and C. Stevens-Rumann. 2017. Returning fire to the land: celebrating traditional knowledge and fire. Journal of Forestry 115:343–353.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

LANDFIRE. 2022. Landscape Fire and Resource Management Planning Tools. U.S. Department of Agriculture and U.S. Department of the Interior. <https://www.landfire.gov>. Accessed 10 Jan 2024.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

Leopold, A. S., S. A. Cain, C. M. Cottam, I. N. Gabrielson, and T. L. Kimball. 1964. Predator and rodent control in the United States. US Fish & Wildlife Publications 254.

Lewis, J. C., R. A. Powell, and W. J. Zielinski. 2012. Carnivore translocations and conservation: insights from population models and field data for fishers (*Martes pennanti*). PLoS One 7:e32726.

Lewis, J. S., L. LeSueur, J. Oakleaf, and E. S. Rubin. 2022. Mixed-severity wildfire shapes habitat use of large herbivores and carnivores. Forest Ecology and Management 506:119933.

Linden, D. W., and G. J. Roloff. 2013. Retained structures and bird communities in clearcut forests of the Pacific Northwest, USA. Forest Ecology and Management 310:1045–1056.

Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012. Global decline in large old trees. Science 338:1305–1306.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H Pollock, L. A. Bailey, and J. E. Hines. 2006. Occupancy modeling and estimation. Academic Press, San Diego, California, USA.

Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4:art153.

Marshall, D. D., K. Iles, and J. F. Bell. 2004. Using a large-angle gauge to select trees for measurement in variable plot sampling. Canadian Journal of Forest Research 34:840–845.

Martin, S. K. 1994. Feeding ecology of American martens and fishers. Pages 297-315 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithica, New York.

Martin, M. E., K. M. Moriarty, and J. N. Pauli. 2021. Landscape seasonality influences the resource selection of a snow-adapted forest carnivore, the Pacific marten. Landscape Ecology 36:1055–1069.

Martin, M. E., M. S. Delheimer, M. W. Gabriel, G. M. Wengert, and K. M. Moriarty. 2022a. Combined field and clinical methods clarify mortality causes and survival patterns of Pacific martens. The Journal of Wildlife Management 86:e22131.

Martin, M. E., M. S. Delheimer, K. M. Moriarty, D. A. Early, K. A. Hamm, J. N. Pauli, T. L. Mcdonald, and P. N. Manley. 2022b. Conservation of rare and cryptic species: challenges of uncertainty and opportunities for progress. Conservation Science and Practice, e12809.

Martin, M. E., M. S. Delheimer, K. M. Moriarty, A. M. Roddy, C. E. Eriksson, M. Szykman Gunther, J. A. Allen, J. A. Hartman, H. Smith, and T. Levi. In prep. From coastlines to mountain crests: regional and continental variation in the diet of North American martens.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McGarigal, K., S. A. Cushman, and E. Ene. 2023. Fragstats v4: spatial pattern analysis program for categorical maps. <https//fragstats.org>. Accessed 15 Jan 2024.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32.

Miller, J. D., and H. D. Safford. 2017. Corroborating evidence of a pre-Euro-American low- to moderate-severity fire regime in yellow pine-mixed conifer forests of the Sierra Nevada, California, USA. Fire Ecology 13:58–90.

Moriarty, K. M., W. J. Zielinski, and E. D. Forsman. 2011. Decline in American marten occupancy rates at Sagehen Experimental Forest, California. The Journal of Wildlife Management 75:1774–1787.

Moriarty, K. M., C. W. Epps, M. G. Betts, D. J. Hance, J. D. Bailey, and W. J. Zielinski. 2015. Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. Landscape Ecology 30:1865–1877.

Moriarty, K. M., C. W. Epps, and W. J. Zielinski. 2016. Forest thinning changes movement patterns and habitat use by Pacific marten. The Journal of Wildlife Management 80:621–633.

Moriarty, K. M., M. A. Linnell, J. E. Thornton, and G. W. Watts. 2018. Seeking efficiency with carnivore survey methods: A case study with elusive martens: discrepancies between detectability and occurrence. Wildlife Society Bulletin 42:403–413.

Moriarty, K. M., J. Thompson, M. Delheimer, B. R. Barry, M. Linnell, T. Levi, K. Hamm, D. Early, H. Gamblin, M. Szykman Gunther, J. Ellison, J. S. Prevéy, J. Hartman, and R. Davis. 2021. Predicted distribution of a rare and understudied forest carnivore: Humboldt marten (*Martes caurina humboldtensis*). PeerJ 9:e11670.

Monitoring Trends in Burn Severity [MTBS]. 2023. MTBS data access: fire level geospatial data. MTBS Project, USDA Forest Service/U.S. Geological Survey. <https://mtbs.gov/direct-download>. Accessed 15 Jan 2024.

Nelson, J. L., E. S. Zavaleta, and F. S. Chapin. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems 11:156–171.

Nichols, J. D., L. L. Bailey, A. F. O'Connell Jr., N. W. Talancy, E. H. Campbell Grant, A. T. Gilbert, E. M. Annand, T. P. Husband, and J. E. Hines. 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. Journal of Applied Ecology 45:1321–1329.

Paragi, T. F., W. N. Johnson, D. D. Katnik, and A. J. Magoun. 1996. Marten selection of postfire seres in the Alaskan taiga. Canadian Journal of Zoology 74:2226–2237.

Parks, S. A., and J. T. Abatzoglou. 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985-2017. Geophysical Research Letters:e2020GL089858.

Pauli, J. N., P. J. Manlick, J. M. Tucker, G. B. Smith, P. G. Jensen, and J. T. Fisher. 2022. Competitive overlap between martens *Martes americana* and *Martes caurina* and fishers *Pekania pennanti*: a rangewide perspective and synthesis. Mammal Review 52:392–409.

Pease, B. S., C. K. Nielsen, and E. J. Holzmueller. 2016. Single-camera trap survey designs miss detections: impacts on estimates of occupancy and community metrics. PLoS One 11:e0166689.

Polson, N. G., J. G. Scott, and J. Windle. 2013. Bayesian inference for logistic models using Pólya–Gamma latent variables." Journal of the American Statistical Association 108:1339–49.

Powell, R. A. 1982. The fisher: life history, ecology, and behavior. University of Minnesota Press, Minneapolis, Minnesota, USA.

PRISM Climate Group. 2020. Time series values for individual locations. Oregon State University, Corvalis, OR. <https://prism.oregonstate.edu/explorer/>. Accessed 11 Nov 2022.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Purcell, K. L., C. M. Thompson, and W. J Zielinski. 2012. Fishers and American martens. Pages 47–60 *in* M. North, editor. Managing Sierra Nevada forests. GTR-PSW-237. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 14 Nov 2022.

Raine, R. M. 1981. Winter food habits, responses to snow cover and movements of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. Thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

Roberts, S. L., D. A. Kelt, J. W. Van Wagtendonk, A. K. Miles, and M. D. Meyer. 2015. Effects of fire on small mammal communities in frequent-fire forests in California. Journal of Mammalogy 96:107–119.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A multispecies occupancy model for two or more interacting species. Methods in Ecology and Evolution 7:1164–1173.

Ryan, K. C., and E. D. Reinhardt. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research 18:1291-1297.

Schwartz, M. K., A. D. Walters, K. L. Pilgrim, K. M. Moriarty, K. M. Slauson, W. J. Zielinski, K. B. Aubry, B. N. Sacks, K. E. Zarn, C. B. Quinn, and M. K. Young. 2020. Pliocene–early Pleistocene geological events structure Pacific martens (*Martes caurina*). Journal of Heredity 111:169–181.

Sherburne, S. S. 1992. Marten use of subnivean access points in Yellowstone National Park, Wyoming. Thesis, Utah State University, Logan, Utah, USA.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. The Journal of Wildlife Management 47:1181–1186.

Srivathsa, A., M. Puri, N. S. Kumar, D. Jathanna, and K. U. Karanth. 2018. Substituting space for time: empirical evaluation of spatial replication as a surrogate for temporal replication in occupancy modelling. Journal of Applied Ecology 55:754–765.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:1-23.

Steenvoorden, J., A. J. H. Meddens, A. J. Martinez, L. J. Foster, and W. D. Kissling. 2019. The potential importance of unburned islands as refugia for the persistence of wildlife species in fire-prone ecosystems. Ecology and Evolution 9:8800–8812.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stevenson, E. R., M. A. Lashley, M. C. Chitwood, J. E. Garabedian, M. B. Swingen, C. S. DePerno, and C. E. Moorman. 2019. Resource selection by coyotes (*Canis latrans*) in a longleaf pine (*Pinus palustris*) ecosystem: effects of anthropogenic fires and landscape features. Canadian Journal of Zoology 97:165–171.

Sweitzer, R. A., B. J. Furnas, R. H. Barrett, K. L. Purcell, and C. M. Thompson. 2016. Landscape fuel reduction, forest fire, and biophysical linkages to local habitat use and local persistence of fishers (*Pekania pennanti*) in Sierra Nevada mixed-conifer forests. Forest Ecology and Management 361:208–225.

Swetnam T. W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885–889.

Swetnam, T. W., J. Farella, C. I. Roos, M. J. Liebmann, D. A. Falk, and C. D. Allen. 2016. Multiscale perspectives of fire, climate and humans in western North America and the Jemez Mountains, USA. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150168.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. Journal of Biogeography 27:87–104.

Taylor, A. H., L. B. Harris, and C. N. Skinner. 2022. Severity patterns of the 2021 Dixie Fire exemplify the need to increase low-severity fire treatments in California's forests. Environmental Research Letters 17:071002.

Tevis, L. 1956. Effect of a slash burn on forest mice. The Journal of Wildlife Management 20:405–409.

Thompson, C., H. Smith, R. Green, S. Wasser, and K. Purcell. 2021. Fisher use of postfire landscapes: implications for habitat connectivity and restoration. Western North American Naturalist 81:225–242.

Thompson, C., R. Sweitzer, M. Gabriel, K. Purcell, R. Barrett, and R. Poppenga. 2014. Impacts of rodenticide and insecticide toxicants from marijuana cultivation sites on fisher survival rates in the Sierra National Forest, California. Conservation Letters 7:91–102.

Townsend, A. M. 2019. Tree squirrels and fishers in northern California: the effects of masting hardwoods on stand use. Thesis, Humboldt State University, Arcata, California, USA.

Tucker, J. M., K. M. Moriarty, M. M. Ellis, and J. D. Golding. 2021. Effective sampling area is a major driver of power to detect long-term trends in multispecies occupancy monitoring. Ecosphere 12:e03519.

Tweedy, P. J., K. M. Moriarty, J. D. Bailey, and C. W. Epps. 2019. Using fine scale resolution vegetation data from LiDAR and ground-based sampling to predict Pacific marten resting habitat at multiple spatial scales. Forest Ecology and Management 452:117556.

U. S. Geological Survey [USGS]. 2022. USGS 3D elevation program. <https://www.usgs.gov/3d-elevation-program>. Accessed 14 Nov 2022.

U. S. Fish and Wildlife Service [USFWS]. 2020a. Endangered and threatened wildlife and plants; threatened species status for coastal distinct population segment of the Pacific marten with a Section 4(d) rule. Federal Register 85:63806-63831.

U. S. Fish and Wildlife Service [USFWS]. 2020b. Endangered and threatened wildlife and plants; endangered species status for Southern Sierra Nevada distinct population segment of fisher. Federal Register 85:29532–29589.

Verschuyl, J., S. Riffell, D. Miller, and T. B. Wigley. 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests – a meta-analysis. Forest Ecology and Management 261:221–232.

Volkmann, L. A., J. Hutchen, and K. E. Hodges. 2020. Trends in carnivore and ungulate fire ecology research in North American conifer forests. Forest Ecology and Management 458:117691.

Volkmann, L. A., and K. E. Hodges. 2021. Post-fire movements of Pacific marten (*Martes caurina*) depend on the severity of landscape change. Movement Ecology 9:1–19.

Volkmann, L. A., and K. E. Hodges. 2022. Residual forest structure influences behaviour of Pacific marten (*Martes caurina*) on post-fire landscapes. International Journal of Wildland Fire 31:329–349.

Volkmann, L. A., and K. E. Hodges. 2024. Effects of burn severity and postfire salvage logging on carnivore communities in montane forests. Journal of Mammalogy: gyad135.

Wan, H. Y., A. C. Olson, K. D. Muncey, and S. B. St. Clair. 2014. Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. Forest Ecology and Management 329:59–68.

Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. Journal of Machine Learning Research 11:3571–3594.

Wengert, G. M., M. W. Gabriel, S. M. Matthews, J. M. Higley, R. A. Sweitzer, C. M. Thompson, K. L. Purcell, R. H. Barrett, L. W. Woods, R. E. Green, S. M. Keller, P. M. Gaffney, M. Jones, and B. N. Sacks. 2014. Using DNA to describe and quantify interspecific killing of fishers in California. The Journal of Wildlife Management 78:603–611.

Williams, A. P., J. T. Abatzoglou, A. Gershunov, J. Guzman-Morales, D. A. Bishop, J. K. Balch, and D. P. Lettenmaier. 2019. Observed impacts of anthropogenic climate change on wildfire in California. Earth's Future 7:892–910.

Worthen, G. L., and D. L. Kilgore. 1981. Metabolic rate of pine marten in relation to air temperature. Journal of Mammalogy 62:624–628.

Zielinski, W. J. 2014. The forest carnivores: marten and fisher. Pages 393-435 *in* Long, J. W., L. Quinn-Davidson, and C. N. Skinner, editors. Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Zielinski, W. J., K. M. Moriarty, J. Baldwin, T. A. Kirk, K. M. Slauson, H. L. Rustigian-Romsos, and W. D. Spencer. 2015. Effects of season on occupancy and implications for habitat modeling: the Pacific marten *Martes caurina*. Wildlife Biology 21:56–67.

Zielinski, W. J., R. L. Truex, F. V. Schlexer, L. A. Campbell, and C. Carroll. 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. Journal of Biogeography 32:1385–1407.

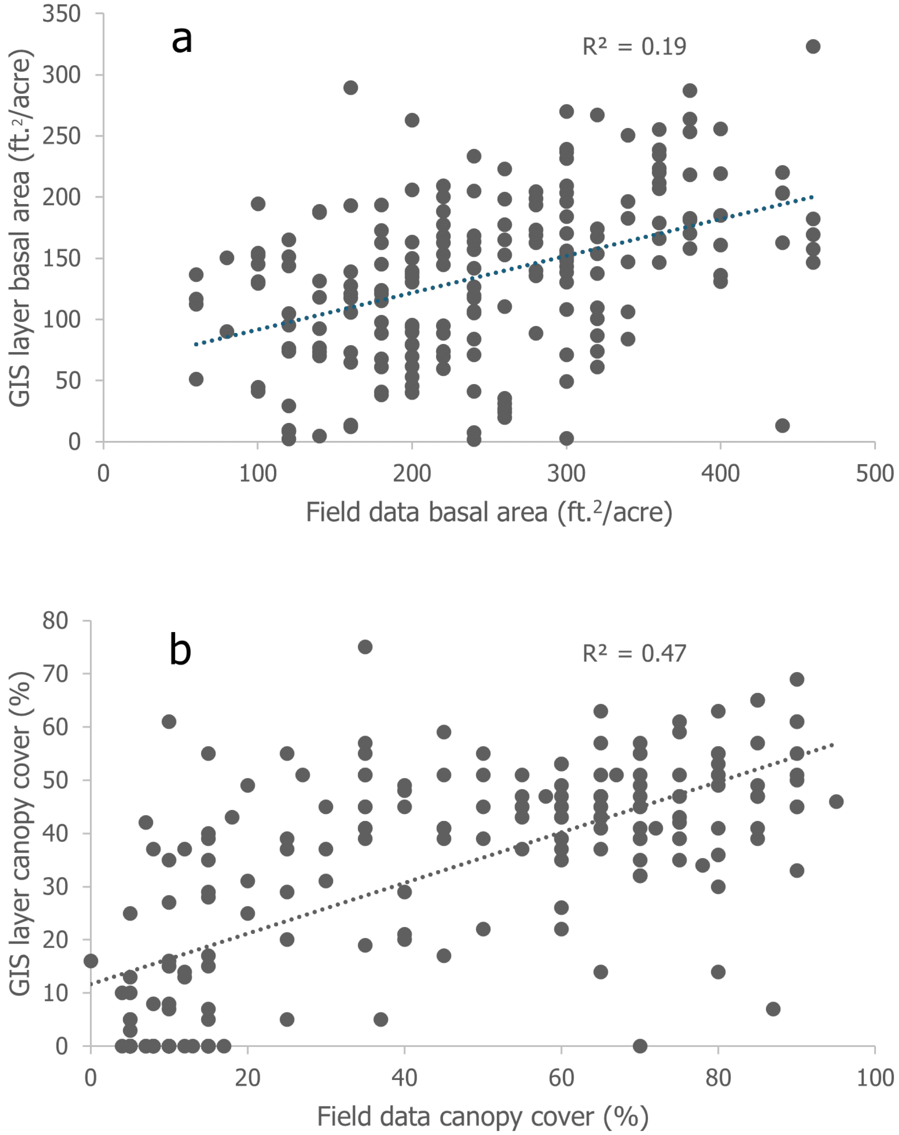
Zielinski, W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. Home range characteristics of fishers in California. Journal of Mammalogy 85:649–657.

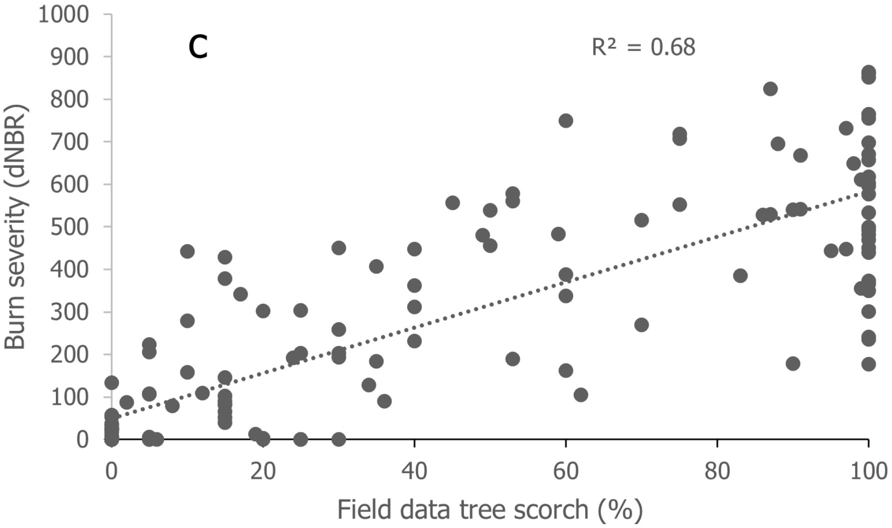
Zielinski, W. J., J. M. Tucker, and K. M. Rennie. 2017. Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. Biological Conservation 209:533–545.

Zwolak, R., and K. R. Foresman. 2007. Effects of a stand-replacing fire on small-mammal communities in montane forest. Canadian Journal of Zoology 85:815–822.

APPENDICES

Appendix A. Comparisons between field data and geospatial layers used in models for basal area (a), canopy cover (b), and percent scorch (c). Negative values in the dNBR were converted to zero for comparisons in panel c because percent scorch cannot exhibit negative values.




c
R² = 0.68
Burn severity (dNBR)
1000
900
800
700
600
500
400
300
200
100
0
0
20
40
60
80
100
Field data tree scorch (%)

Appendix B. Carnivore and small mammal (prey) percentage of cameras with detections out of total surveyed for each burn severity class in the Dixie Fire study area during summer 2023 surveys. Species are ordered from most to least detections. Percentages are bolded if they were greater than the percentage of all cameras (All; *n* = 228) category.

Guild	Species	Unburned	Low	Moderate	High	All
Carnivore	Black bear	**87.8%**	**81.8%**	75.9%	62.7%	76.8%
	Gray fox	13.5%	**27.3%**	14.8%	**25.4%**	19.3%
	Coyote	**17.6%**	**18.2%**	13.0%	**19.4%**	17.1%
	Bobcat	**12.2%**	**15.2%**	7.4%	6.0%	9.6%
	Striped skunk	**9.5%**	**9.1%**	5.6%	6.0%	7.5%
	Western spotted skunk	**6.8%**	3.0%	5.6%	**7.5%**	6.1%
	Pacific marten	2.7%	**6.1%**	**5.6%**	**6.0%**	4.8%
	Pacific marten (all 480 cams)	3.0%	**8.2%**	**10.0%**	5.3%	6.3%
	Fisher	**6.8%**	0%	**3.7%**	0%	3.1%
	Fisher (all 480 cams)	**9.5%**	4.1%	1.7%	0%	4.6%
	Puma	**2.7%**	**9.1%**	0%	0%	2.2%
	Weasel spp.	**5.4%**	0%	1.9%	0%	2.2%
	American badger	**2.7%**	**6.1%**	0%	0%	1.8%
	Sierra Nevada red fox	**2.7%**	0%	**1.9%**	0%	1.3%
	Ringtail	0%	**3.0%**	0%	0%	0.4%
Prey	Chipmunk spp.	**62.2%**	**51.5%**	**51.9%**	20.9%	46.1%
	Douglas squirrel	**67.6%**	**72.7%**	33.3%	9.0%	43.0%
	Golden-mantled ground squirrel	**39.2%**	**33.3%**	18.5%	14.9%	26.3%
	Mouse/vole spp.	20.3%	12.1%	18.5%	**28.4%**	21.1%
	Humboldt's flying squirrel	**35.1%**	**30.3%**	14.8%	0%	19.3%
	California ground squirrel	9.5%	12.1%	**29.6%**	16.4%	16.7%
	Western gray squirrel	**17.6%**	**21.2%**	**14.8%**	3.0%	13.2%
	Snowshoe hare	**9.5%**	3.0%	5.6%	4.5%	6.1%
	Dusky-footed woodrat	**8.1%**	**6.1%**	3.7%	0%	4.4%
	Black-tailed jackrabbit	0%	0%	1.9%	**6.0%**	2.2%
	North American porcupine	**1.4%**	0%	**1.9%**	0%	0.9%
	Yellow-bellied marmot	0%	**3.0%**	**1.9%**	0%	0.9%
	Belding's ground squirrel	**1.4%**	0%	0%	0%	0.4%

Appendix C. Space for time occupancy model selection for carnivore species. Models are ranked by Akaike Information Criterion for small sample sizes (AICc), and I include number of parameters (K), ΔAICc, weight, and the overdispersion parameter, ĉ.

Species	Model	K	AICc	ΔAICc	Weight	ĉ
Black bear	p(effort) ψ(dNBR)	4	229.48	0	0.79	1.49
	p(effort) ψ(.)	3	232.56	3.08	0.17	-
	p(.) ψ(.)	2	235.16	5.68	0.05	-
Gray fox	p(.) ψ(.)	2	193.25	0	0.50	0.25
	p(.) ψ(dNBR)	3	194.61	1.36	0.25	-
	p(effort) ψ(.)	3	194.63	1.38	0.25	-
Coyote	p(effort) ψ(dNBR)	4	198.69	0	0.88	1.14
	p(effort) ψ(.)	3	202.82	4.12	0.11	-
	p(.) ψ(.)	2	207.19	8.50	0.01	-
Bobcat	p(effort) ψ(dNBR)	4	146.62	0	0.44	0.19
	p(effort) ψ(.)	3	147.12	0.50	0.34	-
	p(.) ψ(.)	2	147.97	1.35	0.22	-
Striped skunk	p(.) ψ(.)	2	118.88	0	0.50	-
	p(effort) ψ(.)	3	119.95	1.07	0.29	-
	p(.) ψ(dNBR)	3	120.55	1.67	0.21	0.10
Western spotted skunk	p(effort) ψ(.)	3	99.41	0	0.49	-
	p(.) ψ(.)	2	100.48	1.07	0.29	-
	p(effort) ψ(dNBR)	4	100.97	1.56	0.22	0.09

Appendix D. Study limitations.

I encountered issues with overexposed night images from some of the older Browning cameras. Many photos could not be adjusted (i.e., exposure, brightness, contrast) to identify what triggered the camera. Another problem I faced was that when the newer StealthCams were placed in high severity sites, they triggered repeatedly until the cards were full. These cameras do not have a sensitivity setting, so I had no way to resolve this issue. Thus, some of the high severity sites had tens of thousands of photos to review with few wildlife detections. Another issue I encountered was that bears often took the bait or knocked the lure sponge down before the target mesocarnivore species had visited the station. This is unavoidable in areas with bears, but it could have been ameliorated by checking the stations more often to refresh the bait and lure. That said, we chose a larger study area over sampling more frequently because it can be more efficient in detecting broad changes over time (Tucker et al. 2021).

The basal area measurements my crew and I collected in the field appear to only weakly match the values obtained from the geospatial layer I acquired from the USFS Sierra Nevada Regional Resource Kit ($R^2 = 0.19$, Appendix A). One factor that likely contributed to this difference is that the geospatial layer models live trees with Diameter at Breast Height (DBH) larger than 1 inch, while the basal area factor method I used likely would not count any trees this size as “in” unless they were extremely close to the plot center. Furthermore, my sites often had totals near 20 trees, but more than 4-10 trees per plot compounds the error from missed trees (Iles 1989, Marshall et al. 2004). We also did not correct for slopes, which could have generated biased estimates for slopes greater than 10% (Arvola 1978).

An easily misconstrued aspect of occupancy studies is that, though related, occupancy and selection probabilities are different concepts (Lele et al. 2013). For instance, if many martens inhabit a study area, we may estimate high occupancy (approaching a value of 1) at a given unit even if it contains resources of less desirable quality (i.e., has a low selection probability). Thus, my estimates of high probability of occupancy for marten in the high severity areas could simply be an artifact of high numbers of martens across the Humboldt Peak area, regardless of the burn severity. Alternative survey methods such as hair snares, GPS, or VHF collars will be necessary if we wish to attain estimates of selection probability in my study area.

Though it was not the goal of this study, I compared many different types of occupancy models. This stemmed from a conundrum I encountered that many researchers experience with elusive species. I needed to use a paired design to increase marten and fisher detection probability, but occupancy models that estimate multiple scales or use random effects require more data, and thus more detections, to converge. Furthermore, my results could be biased because I used bait and lure to increase detection probability. A previous study in the Lassen found martens were willing to enter unfavorable forest when motivated by bait (Moriarty et al. 2015). Regardless, when I assessed the relationship between marten occupancy and burn severity, the same positive relationship was estimated among all occupancy model configurations I tested (space for time, multi-scale, standard single-season, and spatial). The spatial model allowed me to use the most data and still estimate occupancy rather than ‘use.’ One drawback to the spatial model was long run times, especially when I generated the occupancy probability maps, which required approximately 80 gigabytes of RAM and 10 hours each, despite their coarse resolution of 600 m.

My colleagues plan to survey within the Dixie Fire study area in 2024, which may allow for better estimates of occupancy and persistence over time. Dynamic hierarchical models could be used to estimate colonization and extinction probabilities of marten and fisher related to burn severity and time since fire. Given my results, I would hypothesize that marten occupancy would either stay the same or decrease over time in the burned areas, and fisher occupancy would increase as canopy closure returns. Interaction models could allow us to estimate the effects of the reintroduced fisher population on martens in the area. Additionally, a subsequent study could generate occupancy probability or habitat suitability maps with future climate scenarios or simulated fires. This would allow for further identification of locations with high conservation priority.