Rapid declines in southern Sierra Nevada fisher habitat driven by drought and wildfire

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Abstract

Forest disturbances are a natural ecological process, but climate and land-use change are altering disturbance regimes at an unprecedented rate, posing significant threats to biological communities and species of concern. Our aim was to develop an automated habitat monitoring system for the Southern Sierra Nevada Distinct Population Segment of fisher (*Pekania pennanti*) in California, USA to investigate long-term habitat trends and the effects of a recent megadrought and numerous megafires on fisher habitat. We used detections of female fishers (n=330) from a standardized monitoring program to develop a dynamic species distribution model using the random forest algorithm in the Google Earth Engine environment. We found that female fisher habitat remained relatively stable from 1985–2011 but declined by nearly half (48%) between 2012 and 2022, corresponding with a period of widespread forest mortality from drought and wildfire. The majority of fisher habitat loss occurred within wildfire perimeters (65%), where declines in habitat quality were associated with moderate- and high-severity fire. Female fisher habitat was more likely to burn at moderate- and high-severity than was expected by chance. Our findings emphasize the urgent conservation needs of this distinct population segment of fishers, highlighting the threat posed by novel disturbance regimes. Our results demonstrate the importance of monitoring for understanding species status, as the status of fisher habitat across the entire southern Sierra Nevada range following recent disturbances was not known. More broadly, our implementation of a cloud-based automated habitat monitoring system shows the necessity of up-to-date habitat information to apply conservation measures in rapidly changing environments and the potential for using habitat monitoring systems to investigate ecological questions of basic and applied relevance (e.g., wildfire-habitat relationships).

Keywords: disturbance, drought, fisher, forest restoration, Google Earth Engine, habitat loss, megafires, *Pekania pennanti*, Sierra Nevada, species distribution model

1. Introduction

Ecosystems are dynamic, and disturbances drive ecosystem dynamics around the globe (Sousa, 1984; Turner, 2010). The frequency, severity, timing and size of disturbances, known as disturbance regimes, play a crucial role in shaping landscape patterns and processes (Pickett & White, 1985; Turner, 1989). Disturbances create spatial and temporal variation in ecosystems and their constituent parts, which in turn influences the structure of biological communities and wildlife habitat. For example, disturbance-driven variation influences species genetic diversity (Banks et al., 2013), vegetation and habitat connectivity (Wimberly, 2006), carbon cycling and storage (Curtis & Gough, 2018), and evolutionary processes in both flora and fauna (Jones, Goldberg, et al., 2023; Keeley & Pausas, 2022). While individual disturbances can be unpredictable, disturbance regimes have remained mostly consistent and predictable in local ecosystems over long periods of time (e.g., centuries to millennia). This long-term predictability and stability of disturbance regimes in local areas has shaped modern vegetation conditions, local- and landscape-scale patterns of biodiversity and species-habitat relationships, as well as contemporary conservation policy.

More recently, however, changes in land use and climate across the world have led to rapid changes to disturbance regimes (Bowman et al., 2020; Johnstone et al., 2016). In western North American forests, a history of fire suppression since the early 1900s and banning of Indigenous fire management since Euro-American colonization have contributed to higher frequency and severity of megafires (Liebmann et al., 2016; Taylor et al., 2016), which are further exacerbated by climate change and drought (Diffenbaugh et al., 2015; S. A. Parks & Abatzoglou, 2020; Westerling, 2016). These dramatic changes in vegetation structure can amplify future disturbances, such as flooding and species invasions, leaving these systems in low-resilience states at risk of type conversion (Coop et al., 2020; Seidl et al., 2017; Stephens et al., 2018). These altered disturbance regimes can cause rapid and unpredictable impacts to ecosystems, increasing uncertainty in how systems—and the wildlife species that depend on them—will respond. Successful conservation of species and ecosystems in this era of rapid change begins with developing approaches to monitor responses to changes in a way that keeps up with the rapid rates of change (Shirk et al., 2023).

The species and ecosystems in the Sierra Nevada, California, USA have seen extraordinary landscape changes over the past decade resulting from fire and drought. From 2012–2016, the Sierra Nevada experienced a 1-in-1000-year drought (Asner et al., 2015) that resulted in the mortality of nearly 150 million trees (Goulden & Bales, 2019). This massive mortality event amplified subsequent bark beetle infestations and large-scale fires (Stephens et al., 2018) resulting in widespread tree mortality at unprecedented scales (Safford et al., 2022). These rapid and widespread ecosystem changes have the potential to influence many wildlife species, including notable species of concern such as the California spotted owl (*Strix occidentalis occidentalis*) and the fisher (*Pekania pennanti*). A recent study estimated that, from 2012–2022, mature forest conditions that are typically associated with habitat for these two species may have declined by at least 50% (Steel et al., 2023). A critical need to facilitate conservation action for threatened and endangered species like the spotted owl and fisher is an understanding of their current habitat distribution, and an ability to rapidly update habitat maps when new disturbances inevitably occur. Such an up-to-date understanding is necessary to determine where, when, and how conservation actions should be implemented to recover the species.

We developed an annually-updating, cloud-based automated habitat monitoring system for the federally-endangered southern Sierra Nevada Distinct Population Segment of fishers (hereafter, SSN fisher) in the Google Earth Engine (GEE) environment (Gorelick et al., 2017). Our habitat monitoring system allowed us to evaluate annual changes to SSN fisher habitat as a function of changes in vegetation and climate. We produced a 38-year time series (1985–2022) of SSN fisher species distribution models (SDMs; Elith & Leathwick, 2009) using fisher detections from systematic non-invasive collection methods (i.e., camera traps, hair snares, and track plates), a combination of topographic and historical climate variables, and multispectral satellite reflectance indices. Using our time series of fisher habitat, we sought to (1) quantify long-term changes in female SSN fisher habitat, (2) evaluate the contribution of wildfires to habitat change over the past three decades, and (3) examine associations between SSN fisher habitat quality and fire risk, specifically how pre-fire habitat quality influenced burn severity, and how burn severity influenced habitat change.

2. Methods

2.1 Study area and fisher detection data

Our study area encompassed the Sierra Nevada ecoregion in California, USA, south of the Tuolumne River and California State Route 120. We divided this area into three subregions (North, Southwest, and Kern Plateau) in which we developed region-specific sub-models, based on local knowledge that these three regions have distinctive environmental, climatic, and topographic differences that influence local fisher habitat-use as well as previous work showing region-specific genetic structure (Tucker et al., 2014) and occupancy rates (W. J. Zielinski et al., 2013). The North subregion included lands north of the middle fork of the Kings River, which encompassed the Sierra National Forest, the majority of Yosemite National Park and Stanislaus National Forest, and the northern part of Inyo National Forest. The Kern Plateau subregion included lands east of the Kern River, which encompassed the eastern part of the Sequoia National Forest and the southern part of the Inyo National Forest. The Southwest subregion included lands between the North and Kern Plateau subregions, which encompassed the majority of Sequoia-Kings Canyon National Parks, the Giant Sequoia National Monument, the western part of Sequoia National Forest, and the central part of Inyo National Forest (Fig. 1). We used spatially and temporally balanced fisher detection data (Fig. 1) obtained through the USFS Region 5 Carnivore Monitoring Program between 2006 and 2022. Detection data were collected using a suite of non-invasive methods, including camera traps, hair snares (to obtain genetic samples), and track plates that were placed at fixed-location 0.8km^2 sampling units. Extensive details are published elsewhere on the sampling methods (B. Zielinski & Mori, 2001; W. J.

Zielinski et al., 2013, 2017). Briefly, fisher sampling units were co-located with USDA Forest Service Forest Inventory and Analysis (FIA) plots that intersected forest-capable lands (i.e., grassland and shrubland-dominated lands were not sampled) and that occurred between approximately 800 and 3400m in elevation. Each sampling unit contained an array of three to six stations located ~500m apart, with each station containing a baited camera trap/hair snare/track plate setup that was deployed between 10 and 21 days. Previous work that focused on occupancy modeling (W. J. Zielinski et al., 2013) aggregated fisher detections to the sampling unit level. For the purposes of our study, we used precise georeferenced detections from individual stations for our presence-only random forest model.

Fishers are described as habitat-specialists and are typically associated with mature, dense forests with multi-layered canopies and large trees (Buskirk & Powell, 1999; Lofroth et al., 2010; Purcell et al., 2009; Weir & Corbould, 2010; W. J. Zielinski et al., 2004a, 2004b). Modeling and conserving these types of fisher habitats are of most concern to wildlife and conservation managers (Spencer et al., 2016) as they are the habitats that are most able to support long-term persistence for SSN fisher occupancy and home range establishment. At least 75% of fisher home ranges are composed of moderate to dense canopy cover (Kordosky et al., 2021; Raley et al., 2017), and even a 5% increase in open areas within fisher home ranges can reduce fisher occupancy probability by 50% (Weir & Corbould, 2010). While these habitats are used by both male and female fishers, male fishers can tolerate a variety of landscape types, while females tend to establish home ranges, and particularly core areas, in areas with dense forests and tall trees (Kordosky et al., 2021; Spencer et al., 2016; Tucker, 2013; W. J. Zielinski et al., 2004a). Furthermore, juvenile females dispersing from their natal dens disperse at much shorter distances than juvenile males, females exhibit high site fidelity once these home ranges are established, rarely disperse once they have reached adulthood, and spend nearly 60-70% of their time in the core areas (7-8km^2) of their home ranges (Spencer et al., 2016; Tucker, 2013). As such, examining fisher habitat using female-only locations is more likely to capture the types of habitats that are of highest conservation-concern, thus we are confident that female detections in our study occur within or in close proximity to high quality core areas. For these reasons, we used only confirmed female detections in our model. Female detections (Total: $n = 330$; North region: $n = 127$; Southwest region: $n = 179$; Kern Plateau region: $n = 24$; Fig. 1) were determined by conducting genetic analysis on the hair samples (Tucker et al., 2014, 2024), using footprint indicators (Tucker et al., 2024), or when a camera trap detected an adult fisher traveling with kits (a behavior limited to females; Thompson, Romsos, et al., 2021).

2.2 Habitat covariates

We selected a suite of 153 environmental covariates to predict fisher locations in our SDMs that fell into three broad categories: topography, climate, and reflectance (Table S1). As with many SDM applications, our primary objective was to develop a model with high local spatial accuracy (i.e., an accurate map). Thus, we were not concerned with model-based inference or exploration, but high spatial predictive capacity instead (Evans et al., 2011; Tredennick et al., 2021). As a result, our local sub-models were overfitted to the data, and we were unconcerned with potential multicollinearity, which affects inference about variable sign or importance but not predictive performance. We included all remotely-sensed variables that we thought could potentially be predictive of female fisher habitat.

We derived topographic variables using a 30m resolution digital elevation model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM; Farr et al. 2007). Variables included slope, heat load index (HLI; characterizes incident radiation), topographic wetness index (TWI; characterizes potential soil moisture), topographic ruggedness index (TRI; characterizes topographic relief), and topographic position index (TPI; characterizes ridge versus valley locations). For slope, HLI, TWI, and TRI, we extracted covariate values at their native scale. For TPI, we extracted covariate values across five scales, representing the radii of circles centered on the focal point: 90, 180, 360, 720, and 1440m. Slope, HLI, TPI, and TRI were derived within the GEE environment, and TWI was derived using ESRI's ArcPro version 2.9.5 (Environmental Systems Research Institute, Redlands, CA).

We derived climate variables using ClimateNA version 7.42 (Wang et al. 2016). We provided the same 30m resolution SRTM DEM that we used to compute topographic variables to the ClimateNA algorithm, which then produced 30m resolution spatial layers of seasonal (winter: December–February; spring: March–April; summer: June–August; autumn: September–November) precipitation, snow-water equivalent, growing degree-days above 5°C, and mean, minimum, and maximum temperature for the 30-year normal historical periods in 10-year increments: 1951–1980, 1961–1990, 1971–2000, 1981–2010, and 1991–2020 and the projected climate for 2011–2040. For each year of fisher locations, we interpolated annual climate values to attribute to the associated year of detection (Shirk et al., 2023). For example, if a location was detected in 2005, we interpolated climate using the 30-year periods of 1971–2000 and 1981–2010.

We derived reflectance variables by applying the Continuous Change Detection and Classification algorithm (CCDC; Zhu & Woodcock 2014) to a 38-year (1985–2022), 30m resolution Landsat 5/7/8 Tier 1 surface reflectance time series within the GEE data repository and workspace. Briefly, CCDC is a change detection algorithm that uses a combination of linear and harmonic models to create robust temporal trend estimation and reliable change detection in remotely sensed data. The CCDC coefficients are then used to generate smoothed annual synthetic Landsat images. We derived a total of 120 covariates for each year from 1985 to 2022 from six synthetic Landsat bands (Blue, Green, Red, NIR, SWIR-1, SWIR-2) and five derived indices (NDVI, NDWI, NDSI, NBR, NBR-2) at two dates (May 1 and August 1 to account for the start of the green-up and the peak of vegetation, respectively). Finally, we used the CCDC model coefficients themselves as predictors, namely the slope coefficient and the 1st/2nd/3rd-degree cosine and sine coefficients for each of the bands and indices. Including the CCDC model coefficients as predictors in the random forest model is effective in reducing a false signal of habitat recruitment following fire events that is produced by rapid vegetation green-up (Witt et al., 2022). We attributed each location with the CCDC variables from that year.

2.3 Species distribution modeling

We modeled the probability of female fisher habitat using random forest models (Breiman, 2001; Cutler et al., 2007; Evans et al., 2011), following similar methods to Shirk et al., (2023). We applied a used-available modeling framework (Elith & Leathwick, 2009), where we randomly generated 10 available locations for every used location in each subregion-year combination. We limited available points to a forest mask, where we labeled a pixel as 'forest' if it was ever classified as deciduous, coniferous, or mixed forest by the National Land Cover Database (NLCD) classification in any period or if the Hansen Global Change Model (Hansen et al., 2013) predicted forest canopy cover >=20%. We used this conservative forest mask to (1) avoid projecting habitat models into areas that were unsuitable for female fishers, such as high montane open areas or shrublands, and (2) to include forest that experienced type conversion to non-forest during our study period from factors including wildfire, drought, timber harvest, bark beetle infestation, etc. For each used and available location, we extracted all habitat covariate values (see above section) at the pixel level (30m cell resolution) by matching the year of habitat data to the year of detection.

We developed three species distribution models within the GEE environment, trained on used-available data from each subregion (Fig. 1) to allow for non-stationarity in habitat selection (Jones, Shirk, et al., 2023). Employing k-fold cross-validation with k = 10, we trained 10 distinct random forest classifiers for each subregion. These classifiers were structured with 50 trees, using 12 variables per split, with a bag fraction of 0.5. Data partitioning allocated 90% for model training, reserving the remaining 10% for model validation. Then, we projected subregion-fold models onto annual environmental data ranging from 1985 to 2022, capturing the evolving characteristics of each subregion. For our final female fisher habitat maps, we projected models onto the region where they were trained, but we also explored the degree to which models were transferable across regions. Utilizing these models, we computed mean and standard deviation probability across 10 model iterations. To evaluate the reliability of our SDMs, we analyzed the mean and standard deviation of the out-of-bag (OOB) error and the area under the receiver operator curve (AUC) across 10 model runs for each subregion.

Before merging our map of female fisher habitat across the entire study area, we performed post-processing, specifically re-scaling, on each sub-regional SDM. Because each SDM was region-specific, this post-processing enabled us to compare across regions and to enhance the consistency of relative probability predictions. Initially, we calculated the true skill statistic (Allouche et al., 2006), which aims to minimize both Type I and Type II errors. This statistic served as the new 0.5 probability value for each sub-model, which we used as a threshold in a subsequent analysis (see annual habitat summaries below). Then, we determined the 5th percentile for points classified as available by the models and the 95th percentile for points classified as used. These percentiles were set as the new 0.0 and 1.0 probabilities, respectively.

2.4 Annual habitat summaries

To calculate the area of available female fisher habitat for each year, we classified each year's SDM into a binary classification of habitat and non-habitat using the afore-mentioned 0.5 threshold. We chose this threshold because it represented the pre-processed true skill statistic and heuristically described areas that were more likely than not to contain elements known to be associated with female fisher habitat. Hereafter, we refer to habitat probability values greater than 0.5 to represent fisher habitat, with relative quality increasing from 0.5 to 1. We summed the total number of cells classified as habitat (i.e., greater than 0.5), multiplied the sum by the area of each cell ($900m^2$) to calculate the area of available habitat for each year and within each subregion. To determine how female fisher habitat trends differed before and after the drought starting in 2012 (Asner et al., 2015), we fitted a linear model for each subregion and the total SSN region, evaluating area as a function of time interacting with an indicator variable of whether the time period was after 2012 or not.

2.5 Fire effects analysis

Within the perimeter of every fire that burned in our study area from 1985–2022, we computed the relativized burn ratio (RBR) with an offset correction to control for tree mortality that was not due to the fire (S. Parks et al., 2014). We then converted RBR values to percent canopy cover loss (Saberi & Harvey, 2023), which we could then classify into burn severity metrics (0-10%: unburned/unchanged; >10-25%: low; >25-75%: moderate; >75%: high).

We computed the annual changes in habitat area that occurred within fire perimeters and compared these fire-associated changes with total annual habitat change across the study area. To estimate fire-associated habitat change for a given year t, we subtracted the total area of habitat within all fire perimeters in year $t-1$ from the total area of habitat within all fire perimeters in year $t+1$. This two-year moving window allowed us to circumvent the problem of fires burning at different times throughout the year during year t. To understand how area burned in each burn severity class changed across the study period, we fitted a linear model measuring the area burned as a function of the year interacting with the burn severity classification for each subregion and the total SSN region.

To measure how habitat quality was impacted by fire, we identified the fire boundary and year the fire burned for each fire and then clipped the associated pre-fire year and post-fire year SDMs to the fire boundary. We then removed any cells that were below the 0.5 probability threshold for both the pre-fire and post-fire periods, i.e., any cells that were never considered 'habitat'. This would ensure that we were including any cells that were above the threshold before the fire but dropped below the threshold after, or vice versa. To examine the relationship between pre-fire fisher habitat and burn severity, we used a binomial test to compare the number of cells of pre-fire fisher habitat that burned in each severity class to a null expectation, which was the observed proportion of cells in each severity class across the whole Sierra Nevada (i.e., regardless of whether it was considered fisher habitat). To examine how burn severity influenced post-fire habitat quality, we calculated the absolute difference in post-fire and pre-fire habitat quality, plotted the distribution of habitat quality difference and corresponding fire severity, and calculated the percentage of cells in each burn severity classification that increased in habitat quality (resulted in >0.05 increase in habitat quality), decreased in habitat quality (resulted in >0.05 decrease in habitat quality), or remained the same post-fire (changes in habitat between −0.05 and +0.05).

3. Results

We predicted the amount and distribution of female SSN fisher habitat over a 38-year period from 1985 through 2022 (Fig. 2). Model fit statistics indicated that our SDMs were highly accurate, with AUC ranging from 0.994 to 0.996 and out-of-bag (OOB) error ranging from 0.0487 and 0.0703 depending on subregion (Table 1). Models performed best when projected to the region in which they were trained, and there was some evidence of non-transferability among regions, particularly the Kern Plateau (Fig. S1). This non-transferability of the Kern Plateau model was more evident when comparing variable importance among subregions (Fig. S2).

3.1 Long-term changes and trends in fisher habitat

In 1985, our model predicted that there were 164,852 ha of female fisher habitat in the southern Sierra Nevada. In 2022, we estimated a total of 86,161 ha, which represents a 48% loss; all of the region-wide net estimated losses occurred between 2012 and 2022 (Fig. 3). Pre-2012, we saw patterns of fluctuating gains and losses in the SSN region as a whole and in the North region (Fig. 3) but with no significant overall losses and gains (Fig. S3), while in the Southwest region we saw an overall slight gain in habitat (Fig. 3, S3). In the North and Southwest subregions, available habitat declined from 97,080 ha and 32,447 ha in 1985 to 48,955 ha (50% loss) and 13,133 ha (60% loss) in 2022, respectively. As with the aggregate region-wide estimates, all of these losses occurred between 2012 and 2022. However, habitat in the Kern Plateau responded differently (Fig. 3). Habitat in this subregion still declined over the study period, dropping from 35,325 ha in 1985 to 24,073 ha in 2022 (32% loss), but only 3% of the total habitat losses in the Kern Plateau occurred in the last decade. Instead, most of the habitat loss in this subregion occurred in the late 1990s and early 2000s, when there were several large wildfires in the area (e.g., the 2002 McNally fire). These patterns were further evident when examining the coefficients of habitat loss pre- and post-2012 (Table S2, Fig. S3), where we observed significant habitat losses from 2012–2022 in the North and Southwest subregions and the southern Sierra Nevada region as a whole, but in contrast the Kern Plateau lost significant habitat in the periods before 2012 and did not show significant change in habitat after 2012.

3.2 Attribution of fire as a driver of habitat change

A large majority of female fisher habitat losses that occurred over the study period appeared to be attributable to wildfire (Fig. 2b, 4). When looking at the entire study area in aggregate, approximately 65% of the total estimated habitat loss occurred within fire perimeters. This number varied depending on subregion, with the North region showing 62.5% of habitat loss occurring within fire perimeters, 89% in the Southwest, and 42% in the Kern Plateau. Across the

SSN region, the amount of area in fisher habitat that burned at low, moderate, and high severity significantly increased across the 38-year study period (β_{low} = 0.543, 95% CI [0.081, 1.006], $\beta_{moderate}$ = 1.479 [0.450, 2.510], and β_{high} = 0.516 [0.191, 0.840]) while unburned/unchanged areas in fire perimeters did not change significantly. However, in the North region, only the area that burned at high severity increased significantly (β_{high} = 0.383 [0.088, 0.677]); there were no significant changes in area burned in any fire severity class in the Kern Plateau; and in the Southwest, all fire severity classes significantly increased from 1985–2022 ($\beta_{unburned/unchanged}$ = 0.133 [0.0493, 0.217], β_{low} = 0.347 [0.127, 0.567], $\beta_{moderate}$ = 0.886 [0.307, 1.466], and β_{high} = 0.323 [0.058, 0.587]; Fig. 5).

3.3 Associations between habitat quality/habitat change and burn severity

When examining pre-fire habitat quality and the classification of fire severity that these cells burned the following year, 207,487 cells were considered unburned/unchanged, 415,205 burned at low severity, 841,489 burned at moderate severity, and 213,689 burned at high severity (Fig. 6a). The number of cells that burned at moderate and high severity within female fisher habitat were greater than expected. For moderate severity, the null (expected) proportion was 0.423 and the actual proportion was 0.502 (95% CI [0.50001, 0.5023]); for high severity, the null proportion was 0.043 and the actual proportion was 0.1273 [0.1269, 0.1279]. In contrast, we found the number of cells within fire perimeters that did not burn/remained unchanged or burned at low severity to be lower than expected, with null proportions of 0.23 and 0.30 respectively but actual proportions of 0.124 [0.1232, 0.1242] and 0.247 [0.2468, 0.2481], respectively.

Female fisher habitat that experienced unburned/unchanged and low burn severity did not experience meaningful changes in habitat quality post-fire, with these two distributions peaked and centered at zero (Fig. 6b). More than 91% of unburned/unchanged areas and nearly 66% of low severity burned areas resulted in fisher habitat changes between −0.05 and +0.05 (i.e., near-zero). On the other hand, female fisher habitat that burned at moderate and high severity experienced substantial declines in post-fire habitat quality (Fig. 6b). Specifically, 90.19% and 98.92% of fisher habitat that burned at moderate and high severity, respectively, decreased in quality (declines of −0.05 or below). The distributions for habitat change in areas affected by moderate and high burn severity both were centered around −0.4, indicating that, on average, habitat quality was reduced by 40% in these two burn severity classes.

4. Discussion

In this paper, we developed a 38-year habitat monitoring system for the southern Sierra Nevada fisher and used this monitoring system to measure how female SSN fisher habitat changed over time and space and quantify fire-habitat interactions. Our study produced four major findings: (i) female SSN fisher habitat declined across the study region by 48%, and a vast majority of that decline at the range-wide scale occurred over just the past decade between 2012 and 2022; (ii) a substantial portion (~65%) of habitat losses occurred inside wildfire perimeters, suggesting wildfires as a major causal agent of habitat change, (iii) moderate and high-severity fire were associated with decreases in post-fire habitat quality, and (iv) female SSN fisher habitat was more likely to burn at high severity and less likely to burn at lower severity than expected by chance alone. Our analysis highlights how rapid, disturbance-driven landscape changes can transform sensitive species habitat and the need for tools that allow us to monitor changes in real-time to support conservation and land management. The dynamic SDM workflow we have developed in GEE allows us to use current data to back-cast as well as rapidly update habitat data in the future to help address such needs.

Losses to female fisher habitat in the southern Sierra Nevada appear to have been recent and swift. For over a quarter century from 1985 to 2011, female SSN fisher habitat remained relatively stable, and even showed evidence of steady and moderate increases in some subregions of the Sierra Nevada (e.g., North and Southwest subregions, Fig. 3). This observation mirrors the results of other studies that concluded relative stability in fisher occupancy (W. J. Zielinski et al., 2013) and fisher resting habitat suitability (W. J. Zielinski & Gray, 2018) prior to 2010. However, in the decade following 2012, fisher habitat declined by nearly half (48% decrease). This period of abrupt decline matched our expectations, occurring concomitantly with an extreme drought from 2012–2016 that resulted in large-scale tree mortality (Asner et al., 2015; Goulden & Bales, 2019) and a series of unprecedented megafires culminating in the 2020–2021 fire season—the most severe in California's modern record (Keeley & Syphard, 2021; Safford et al., 2022)—that together caused widespread changes in forest conditions and loss of habitat for many California wildlife species (Ayars et al., 2023; Fettig et al., 2019). Another study examined recent changes to southern Sierra Nevada forests, showing that between 2011–2020, mature forest extent declined by at least 50% from a combination of drought and wildfire, with many forested areas transitioning to non-tree vegetation (Steel et al., 2023). Our work, which specifically models female fisher habitat that will contain elements of mature forest vegetation, corroborates this evidence by showing a 48% decline in fisher habitat over a similar period, while also adding longer-term context of apparent fisher habitat stability during the pre-drought period from 1985–2011. By monitoring not only habitat trends, but also the pace of those trends and associated drivers, this work can inform management decision-making in times of both relative stability and rapid change.

Severe wildfires have been identified as a major contributor to declines in fisher habitats and mature forest vegetation within the region under study (Jones et al., 2016; Steel et al., 2023). The majority of habitat loss experienced by fishers over the last decade, specifically 65%, could be directly attributed to these fires. However, fire severity played a significant role in determining the extent of habitat losses. In areas where wildfires mainly affected understory vegetation or resulted in low burn severity with only 10-25% overstory canopy mortality, fisher habitat within the fire perimeters remained largely unaffected. Conversely, moderate to high-severity wildfires consistently led to decreases in fisher habitat quality by an average of 40% (Fig. 6b), aligning with previous research that indicated decreased fisher movement, abundance, and colonization rates in areas affected by such fires (Green et al., 2022; Thompson, Smith, et al., 2021). Thus, the combined evidence suggests that expanding wildfire footprints with higher severity could result in detrimental consequences for fisher habitats, demographics, and movement, emphasizing the need for careful consideration of these findings in forest management strategies within the region.

Not only did high-severity fire reduce female fisher habitat quality, but fisher habitat appeared more likely to burn at moderate and high severities than was expected by chance. Observed fire severity class frequencies across the whole southern Sierra Nevada over the study period indicated that 42% and 4% of all burned areas experienced moderate and high burn severities, respectively. However, our analysis showed that 50% and 13% of female fisher habitat burned at moderate and high severity, respectively. Thus, while moderate severity fire occurred in fisher habitat at a rate 1.2× higher than the broader landscape, high severity fire occurred at a rate over 4× higher than the broader landscape. This suggests that fisher habitat may be more at risk of burning than the average vegetation conditions present in the southern Sierra Nevada. This result, while concerning, is not particularly surprising given the widespread perception that fishers tend to occupy dense, fire-prone stands, setting up the possible conflict between forest restoration, fuel reduction, and fisher habitat retention (Jones et al., 2016; Scheller et al., 2011). A similar apparent conflict is well known for another co-occurring old-forest species, the spotted owl (Ganey et al., 2017). Recent work has shown that the perceived forest restoration vs. spotted owl habitat conservation conflict may be a false dichotomy, wherein forest restoration actually increases vegetation heterogeneity in fire-suppressed forests in ways that provide both direct and indirect benefits to spotted owls by generating prey habitat and reducing fire-driven habitat loss (Jones et al., 2022; Kuntze et al., 2023; Wright et al., 2023; Zulla et al., 2022). More work is urgently needed to examine whether similar win-win opportunities exist for the fisher, and where and how potential tradeoffs can best be managed to promote both short-term species conservation and long-term species recovery. For example, our results make it clear that not all fires impact fisher habitat equally, as low severity fires did not significantly impact fisher habitat quality. This suggests that managed, prescribed, or cultural burns that burn at low severity or lower could benefit forest restoration and not conflict with or even aid in fisher conservation. Given the recent extensive habitat loss attributable to fire and the elevated risk of moderate and high severity fire faced by female fisher habitat, combined with the projected increase in severe fire in this area, it is clear that actions to reduce the risk of severe fire to remaining habitat will be essential to species recovery.

Abrupt and large-scale vegetation changes in response to disturbance is indicative of a system that may be experiencing eroded resilience. Seasonally dry forests of western North America (including most of the Sierra Nevada) were historically characterized by tall, old, fire-resistant trees with shifting mosaics of varying densities (Hagmann et al., 2021; Hessburg et al., 2019; Safford & Stevens, 2017). Over many millennia, these forests were highly resilient, sustained by frequent, low-severity fires that were lightning-ignited or managed by Indigenous peoples (Safford & Stevens, 2017). However, Euro-American colonization and associated Indigenous exclusion, selective logging of large trees, and fire suppression policies have transformed these dynamic and diverse landscapes to be characterized more often by dense stands of smaller, shade-tolerant and fire-sensitive trees and shrubs and widespread structural forest landscape homogeneity (Collins et al., 2017; Hagmann et al., 2021; Taylor et al., 2016). These vegetation changes combined with hotter and drier climate conditions have led to larger and more severe fires across the western US, including the southern Sierra Nevada region (Keyser & Westerling, 2019; Steel et al., 2018); Fig. 5b).

As continued increases in severely burned area are expected in the southern Sierra Nevada and throughout the western U.S. (Abatzoglou et al., 2021), management strategies that recognize and account for the rapidly changing landscape are necessary to conserve mature forests that support several species of concern, including the SSN fisher. Rapid habitat losses observed in our study suggest that business-as-usual conservation approaches may not be working or are no longer effective to conserve fisher habitat in the southern Sierra Nevada. Dominant conservation paradigms in much of North America (e.g., conservation reserves, protected areas) were established during an era of apparent environmental stability, and therefore embrace a more ‘static’ view of nature (Gaines et al., 2022). Continued reliance on static conservation paradigms in an era of rapid change could backfire, resulting in increased forest-type conversion and habitat loss. For example, Steel et al. (2023) found that spotted owl protected areas, where many forest management activities intended to increase resilience are restricted, experienced significantly more canopy cover loss than non-protected areas following drought and wildfire. Conservation paradigms that aim to restore a generating process, such as natural disturbance dynamics, as opposed to those that aim to retain an existing pattern, such as maintaining a certain acreage of species habitat in specific locations, may be more likely to succeed in this era of rapid change. The results of this study suggest that conservation approaches for fishers might achieve better outcomes by implementing a transition towards adaptive management and process-based restoration within and adjacent to the best remaining fisher habitat in an effort to reduce fuels and re-introduce natural and Indigenous-managed fire (Jones et al., 2022; Kimmerer & Lake, 2001; Lake et al., 2017; North et al., 2021), in order to reduce risk of abrupt fire- and drought-driven losses to remaining habitat.

Nevertheless, our flexible non-stationary modeling approach also identified some areas that may be acting as larger-scale climate refugia—resisting change or experiencing dampened changes because of their unique geophysical features or other environmental characteristics. In the midst of rapid fire-driven habitat losses for southern Sierra Nevada fishers over the past decade, habitat in our southern-most subregion, the Kern Plateau, remained relatively stable. The Kern Plateau is a high-elevation forested plateau that is geophysically distinct from the much more topographically diverse, rugged Sierra Nevada to the north (Webb, 1946). This remote area is part of a region that is hypothesized to have served as a refugia during a period of intensive logging and fur trapping in the early 1900s (Tucker et al., 2012), and may serve a similar role in the future. The area’s unique features may be producing a climate refugia for the southern Sierra Nevada fisher, buffering remaining habitat in this region from climate- and fire-driven changes (Keppel et al., 2015; Meddens et al., 2018). Other research investigating progressive canopy water loss and drought- and fire-driven forest change in the past decade have suggested congruent dampened effects to this region (Asner et al., 2015; Steel et al., 2023), reinforcing the possibility that the Kern Plateau is acting as a refugia. Until now, very little was understood about the distribution and quality of fisher habitat in this region, and further study is needed to understand the ecology and conservation of fishers in this unique ecoregion. Potential refugia like the Kern Plateau can act as cornerstones for conservation planning by delaying and/or buffering catastrophic losses while also acting as population sources in future recovery efforts.

While our study provides several novel and actionable discoveries about fisher habitat in the southern Sierra Nevada, readers should consider two caveats to better interpret our results. First, we make inferences about changes to high quality fisher habitat of conservation concern from the presence of female fishers detected by genetic methods and camera traps. Applying our modeling approach to other types of data, such as GPS tracking data, den site locations, or incidental detections would likely yield different conclusions about how habitat has changed, but it also would change (e.g., broaden or narrow) the type of habitat that is being modeled. As a test of this possibility, we conducted a parallel analysis in which we used a larger (n = 667) but more spatially biased dataset of fisher den sites; our results differed numerically but not qualitatively (see Appendix B). Thus, we feel our general conclusions about habitat change over time are robust to the type of data used. Second, in attributing the role of wildfire in habitat change (Fig. 4), the effects of drought and fire are confounded to a certain extent (Steel et al., 2023). That is, in the years after the California megadrought began (post-2012), all wildfires occurred within the context of the ongoing drought or post-drought tree mortality. Thus, some unknown fraction of the losses that we attributed to wildfire (65%) may also be partly due to drought. Similarly, without including an analysis of a complete, validated spatial layer of drought-driven tree mortality, we cannot be sure what proportion of the unexplained habitat losses were directly attributable to drought and not other factors such as mechanical activities (e.g., thinning or timber harvest). However, because Steel et al. (2023) showed that over a similar period, a maximum of 4% of total forest losses could be attributed to mechanical activities, we are reasonably confident that a large portion of the remaining 35% of habitat loss that occurred outside fire perimeters in our study area is directly attributable to effects of the extreme drought from 2012–2016 and its subsequent effects on the region's forests rather than thinning or harvest.

5. Concluding remarks

In an era of rapid change, conservation scientists and land managers need tools that can keep up with accelerating rates of change. The automated habitat monitoring system that we developed for southern Sierra Nevada fishers represents such a tool for forest and conservation managers, and such a system could be developed for any species or system, with outputs being used to ask system-specific questions such as those we asked about fire-habitat interactions (see Jones et al. 2023a). It is important to note that these maps are not a replacement for more traditional, classified habitat maps which are slower to produce but more directly interpretable on the ground (e.g., those that relate habitat to specific vegetation metrics, such as canopy cover). Effective conservation and timely habitat restoration planning in this new era of rapid ecological change will require careful integration of both information sources whenever possible.

We hope that recent open-source, fully reproducible Google Earth Engine workflows for dynamic species distribution modeling (Crego et al., 2022; Dobson et al., 2023) will facilitate the more widespread development and uptake of dynamic and automated habitat models in the conservation community. Through innovations first introduced by Shirk et al. (2023) and Jones et al. (2023a), unclassified habitat maps can not only be completed on a timeline much faster than traditional, classified mapping and modeling efforts, but can also be automated, allowing the entire process to run on a schedule with little human intervention. This gives managers the tools they need, updated on a timely basis, and in an accessible form (e.g., see our Google Earth Engine web application to explore results: https://rmrs-dynamic-sdm.projects.earthengine.app/view/ssn-fisher-habitat-area-time-series)

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Data Accessibility Statement

Data supporting the conclusions in this analysis are available here: https://datadryad.org/stash/share/rU1uBJuzt0DKijrqWMccgiHS4oij7R5IWLq8-OfcTSg. With permission from the journal editors, the precision of location data have been reduced to facilitate protection of this threatened distinct population segment.

Tables

Table 1. Predictive statistics for female SSN fisher random forest species distribution models. We report the mean and standard deviation (across all 10 model folds) of the out-of-bag (OOB) error and area under the receiver operator curve (AUC) for each regional sub-model.

Region	OOB Error	AUC
North	0.0523 (0.0039)	0.996 (0.0029)
Southwest	0.0487 (0.0029)	0.996 (0.0024)
Kern Plateau	0.0703 (0.0052)	0.994 (0.0065)

Figures

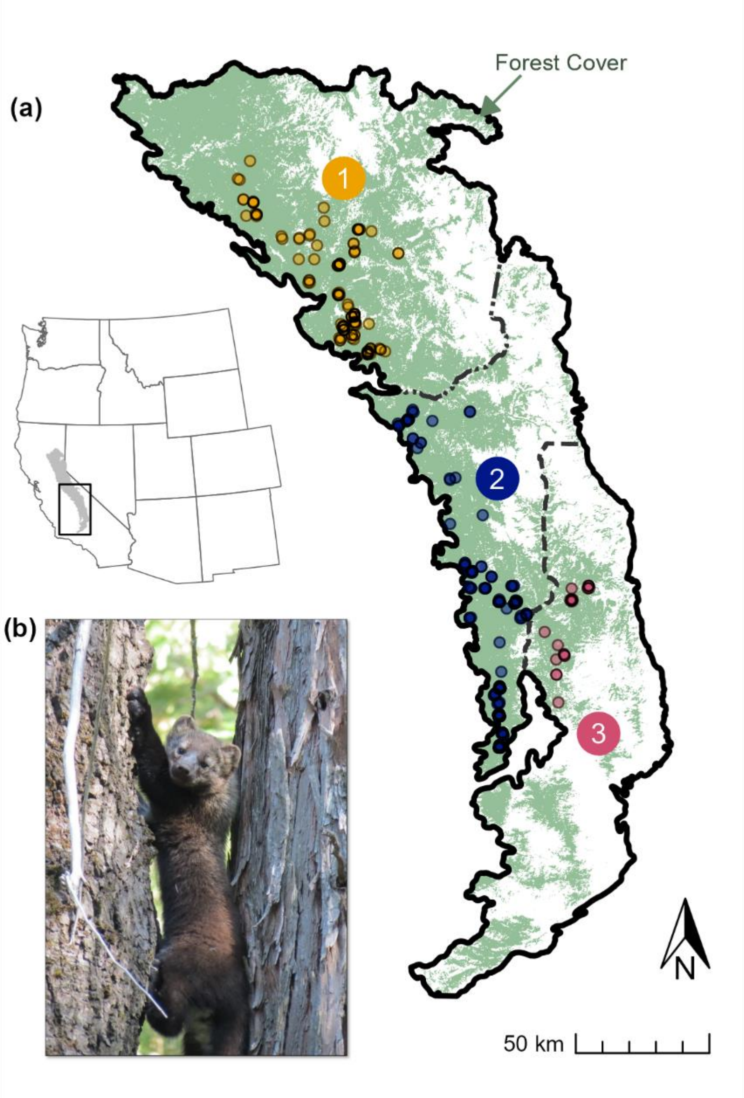

Figure 1. Study area and southern Sierra Nevada fisher location data. (a) Map of female SSN female locations from non-invasive collection methods (colored points) within forested areas (green) in the study area in relation to the Sierra Nevada with the subregions: (1) North, (2) Southwest, and (3) Kern Plateau. (b) Photo of a fisher, *Pekania pennanti*. Photo by Zane Miller, USFS Pacific Southwest Research Station, used with permission.

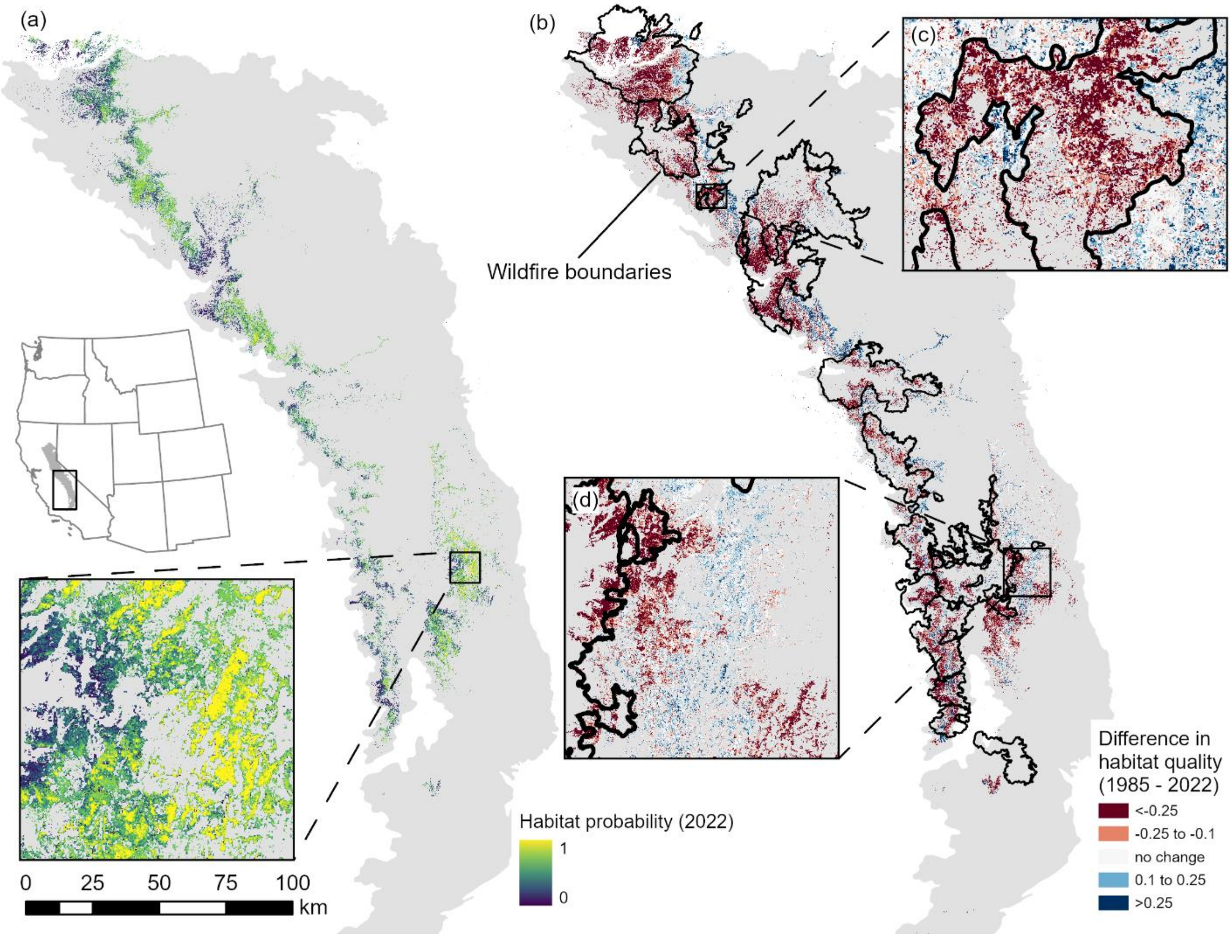

Figure 2: (a) Probability of female fisher habitat in 2022 with an inset of the Kern Plateau and (b) the change in habitat quality from 1985 to 2022, with red cells showing a decrease in quality and blue showing an increase, with black borders indicating wildfire boundaries and insets of (c) the 2017 Railroad fire and (d) the Kern Plateau.

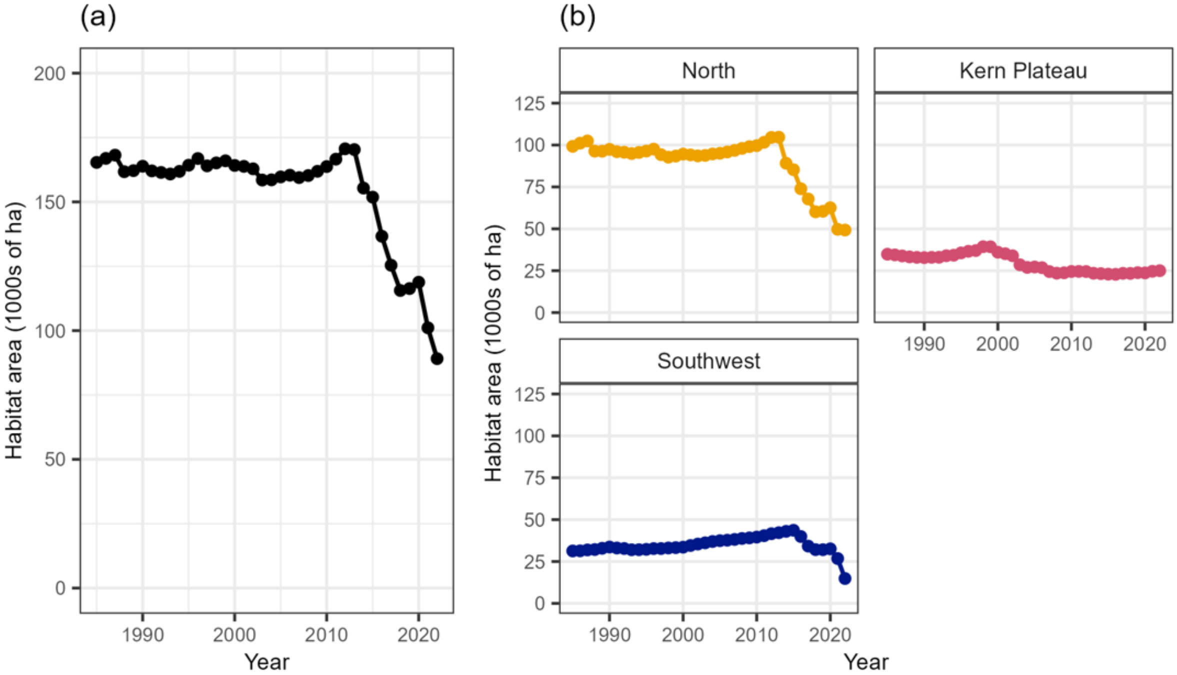

Figure 3. Habitat trends from 1985 to 2022 of (a) the SSN as a whole and (b) by subregion. Values on the y-axis represent area in 1000s of hectares, such that a value of 100 indicates 100,000 hectares.

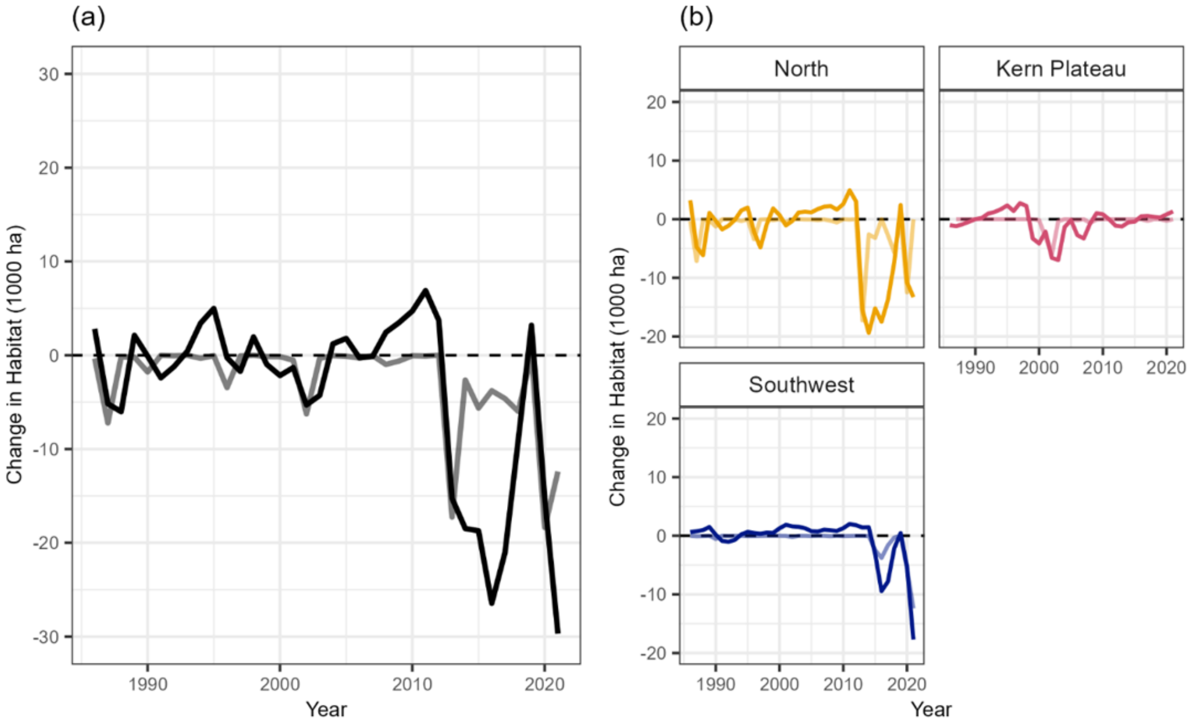

Figure 4. Change in habitat area, where each year marks the difference between the previous year's area from the following year's area. Panel (a) shows the change in habitat in the entire SSN region and panel (b) shows the changes in each subregion's habitat. The darker line indicates change in area in the entire region while the lighter line indicates change specifically within fire perimeters that occurred that year. Values on the y-axis represent change in area in 1000s of hectares, such that a value of 10 indicates 10,000 hectares.

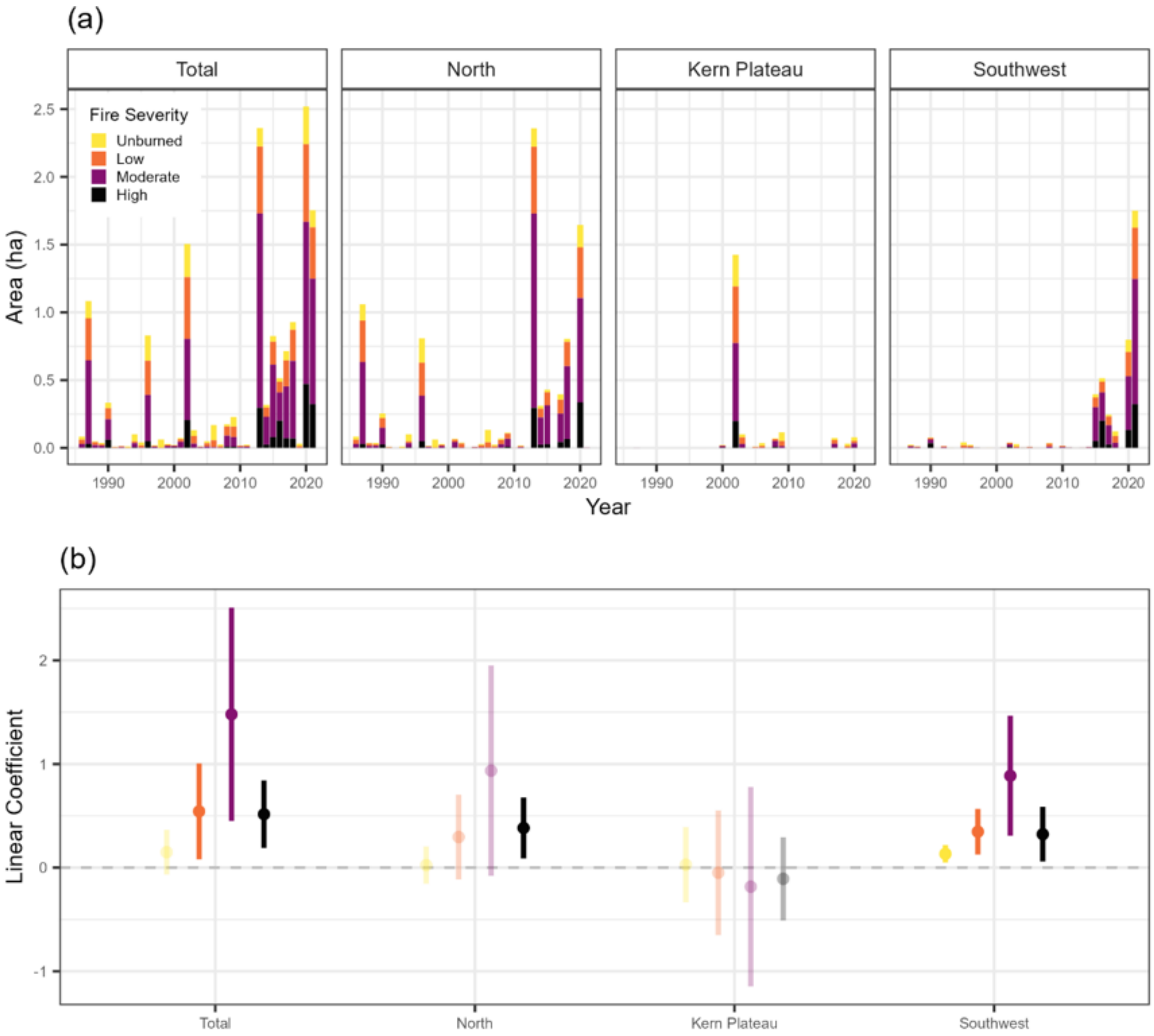

Figure 5. (a) Histogram of area burned in each fire severity class within SSN fisher habitat across the 38-year study period; (b) coefficients and 95% confidence intervals from a linear model of trends in burned area for each burn severity class across the 38-year study period in the SSN region as a whole or by subregion. Semi-transparent points and lines indicate that the 95% confidence intervals overlapped with zero and were thus insignificant.

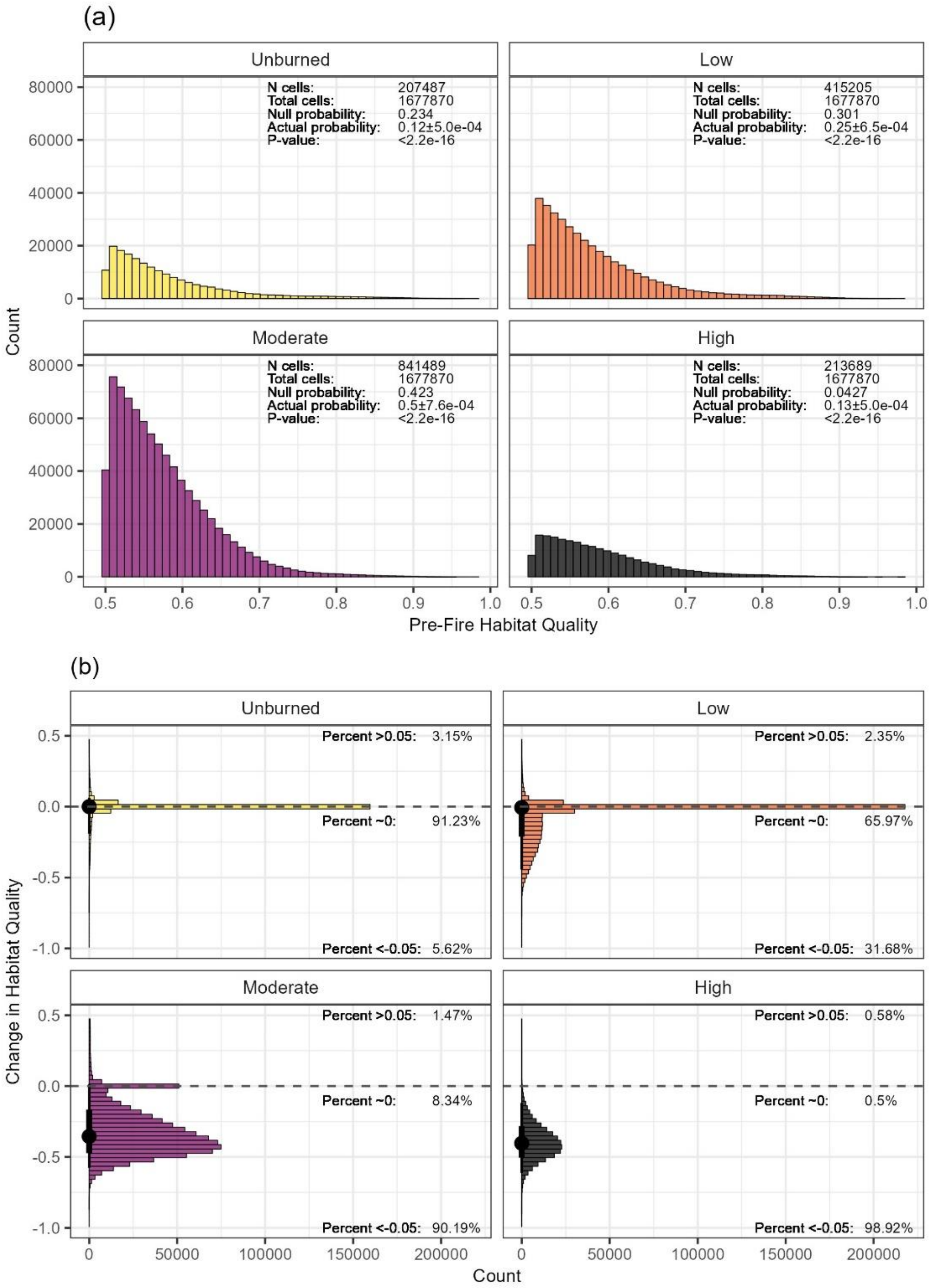

Figure 6. (a) Distribution of pre-fire habitat quality within the fire severity class in which they burned the following year, and the results of the binomial test performed for the number of cells burned in each category compared to the null expectation; (b) distribution of habitat quality change pre- and post-fire within each fire severity class.

Appendix A

Table S1. Covariates used in the random forest species distribution models for SSN fisher.

Covariate class	Covariate name	Abbreviation (Units)
Topography	Topographic ruggedness index	TRI
	Slope	slp (°)
	Heat load index	HLI
	Topographic wetness index	TWI
	Topographic position index	TPI_[90, 180, 360, 720, 1440] (m)
Climate	Average min temperature (spring, summer, autumn, winter; 30-year normal)	Tmin_[sp, sm, at, wt] (°C)
	Average max temperature (spring, summer, autumn, winter; 30-year normal)	Tmax_[sp, sm, at, wt] (°C)
	Mean temperature (spring, summer, autumn, winter; 30-year normal)	Tave_[sp, sm, at, wt] (°C)
	Precipitation (spring, summer, autumn, winter; 30-year normal)	PPT_[sp, sm, at, wt] (mm)
	Precipitation as snow (spring, summer, autumn, winter; 30-year normal)	PAS_[sp, sm, at, wt] (mm)
	Growing degree days (spring, summer, autumn, winter; 30-year normal)	DD5_[sp, sm, at, wt] (°C)
Reflectance	May 1/Aug 1 Landsat bands (CCDC predictions)	blue, green, red, nir, swir1, swir2_[may1, aug1]
	May 1/Aug 1 Landsat bands (CCDC model coefficients)	blue, green, red, nir, swir1, swir2_[SLP, COS(1, 2, 3), SIN(1, 2, 3)]_[may1, aug1]
	May 1/Aug 1 normalized difference vegetation index	NDVI_[may1, aug1]
	May 1/Aug 1 normalized difference water index	NDWI_[may1, aug1]

May 1/Aug 1 normalized difference snow index	NDSI_[may1, aug1]
May 1/Aug 1 normalized burn ratio	NBR_[may1, aug1]
May 1/Aug 1 normalized burn ratio 2	NBR2_[may1, aug1]

Table S2: Beta coefficients (and associated standard error) of the rate of habitat change in the total southern Sierra Nevada as well as each subregion, and how this rate of change differed before or after 2012.

Region	Period	β (SE)
Total	Pre-2012	-0.124 (0.092)
	Post-2012	-8.056 (0.354)
North	Pre-2012	-0.034 (0.088)
	Post-2012	-5.812 (0.339)
Southwest	Pre-2012	0.330 (0.0572)
	Post-2012	-2.343 (0.221)
Kern Plateau	Pre-2012	-0.421 (0.077)
	Post-2012	0.099 (0.299)

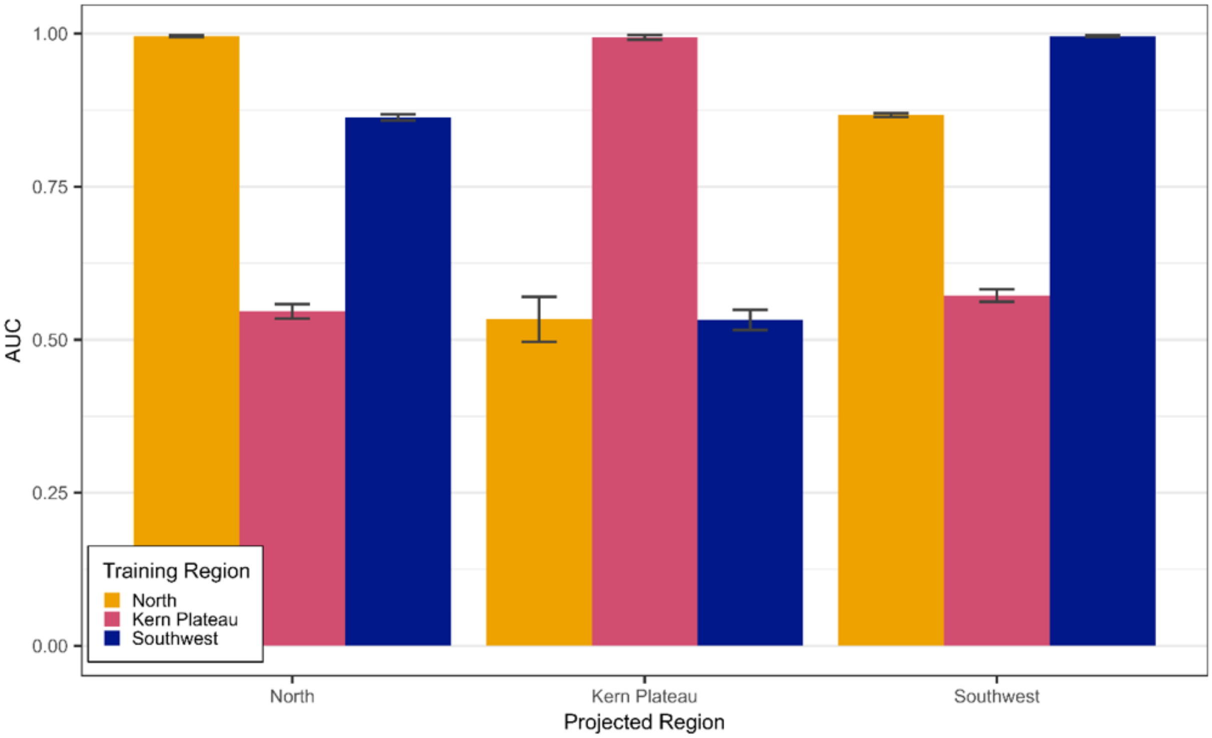

Figure S1. The area under the receiver operator curve (AUC) for each training region and the region its model was projected to. The error bars represent the 95% confidence intervals across the 10 folds.

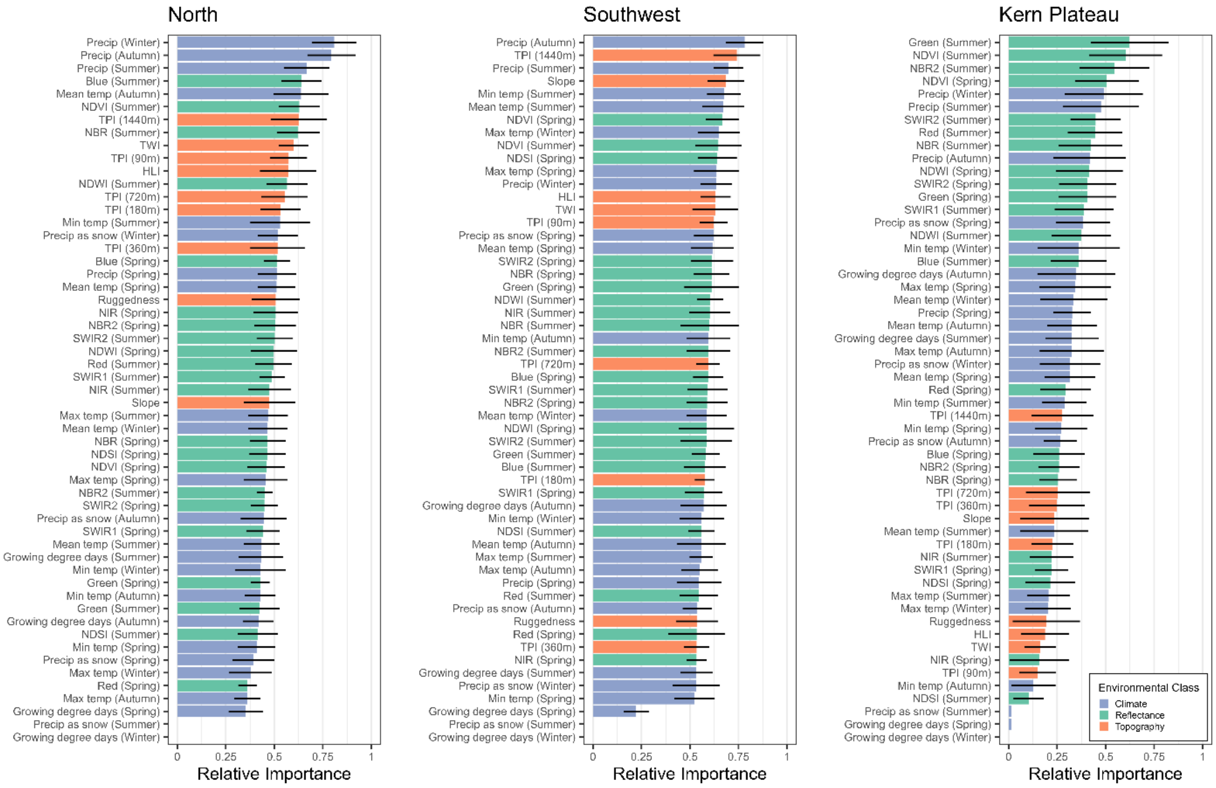

Figure S2. The relative importance of all variables used in each region-model. The colors represent the category of environmental class the variable belongs to and the range lines show the 95% confidence intervals across the 10 folds.

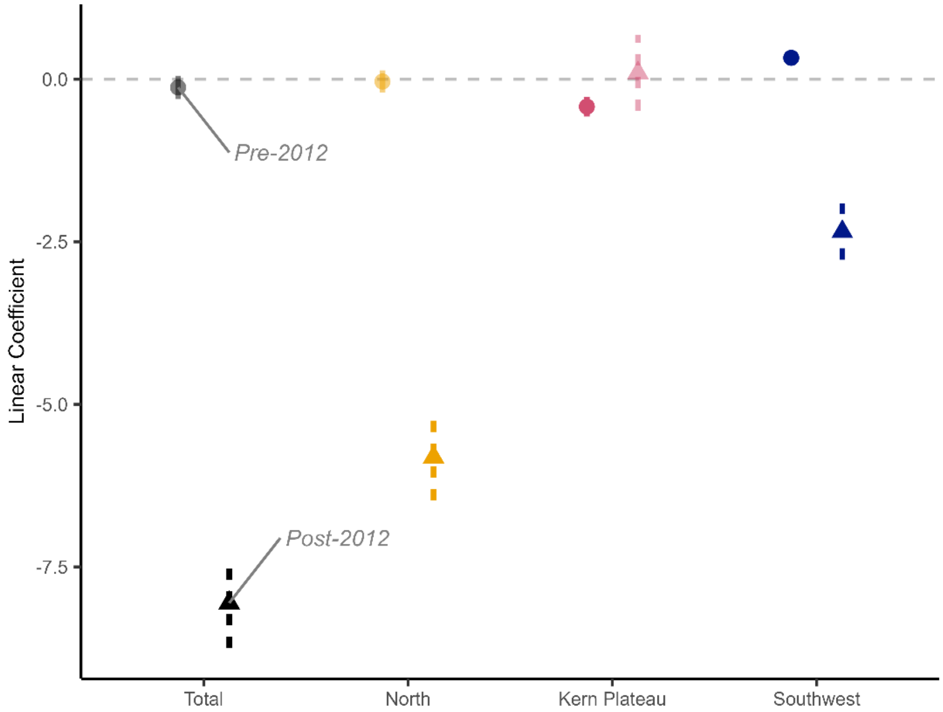

Figure S3. Coefficients and 95% confidence intervals from a linear model of trends in habitat area in the SSN region as a whole (black) or by subregion from 1985–2012 (circle point and solid line) and 2012–2022 (triangle point and dashed line). Transparent points and lines indicate that the 95% confidence intervals crossed 0, meaning insignificant results.

Appendix B: Den site results

We replicated methods explained in the main text with an alternative dataset comprised of known and possible denning sites (n=667, Fig. B1). However, these data are spatially biased, with the majority of locations found in the North region (n=646), only some in the Southwest region (n=21), and none in the Kern Plateau. Because of this, we did not fit a model for each subregion as we did in the main text and instead pooled all locations and fit a single global model and excluded the Kern Plateau from our mapping projections. Besides this modification, all other methods are identical to those in the main text.

We predicted the amount and distribution of SSN fisher denning habitat from 1985 through 2022 (Fig. B2). Similar to the results in the main text, this model was very accurate: across ten folds, the average AUC was 0.997 and the average out-of-bag error was 0.0485 (Table B1).

Our model predicted there was approximately 85,972 ha of potential denning habitat in 1985 and 48,862 ha in 2022, indicating to a loss of nearly 37,109 ha or about 43% decline (Fig. B3a). This decline mostly occurred after 2012 (β=-4.61, SE = 0.0338; Fig. B3b). When examining declines that occurred within fire perimeters compared to total change, about 49.5% of habitat loss occurred within fire perimeters (Fig. B3c).

Across our modeled denning habitat, moderate and high severity fire significantly increased from 1985 to 2022 (moderate: β=1.019, SE = 0.48; high: β=0.641, SE = 0.28) while areas that burned at low or lower severity did not significantly change across the study period (Fig. B4).

When examining burned area and severity across the study period within pre-fire denning habitat, 227,467 cells were considered unburned/unchanged, 266,307 burned at low severity, 659,158 burned at moderate severity, and 448,680 burned at high severity (Fig. B5a). The number of cells that burned at moderate severity within fisher denning habitat was greater than expected, with a null (expected) proportion of 0.300 and an actual proportion of 0.412 (95% CI [0.4108, 0.4123]). In contrast, the number of cells within fire perimeters that did not burn/remained unchanged or burned at high severity was lower than expected, with null proportions of 0.214 and 0.320 respectively but actual proportions of 0.142 [0.1415, 0.1426] and 0.280 [0.2794, 0.2808] respectively. The null compared to the actual probability of cells that burned at low severity was insignificant (Fig. B5a).

Fisher denning habitat that burned at low severity or lower did not experience meaningful changes in habitat quality post-fire, as these two distributions were both centered around zero (Fig. B5b). Areas that burned at moderate or high severity showed two peaks in their distribution, one peak centered at zero and one around -0.4 (indicating a loss of quality of around 40%). However, the percentage of cells that burned at moderate severity fire and showed little to no significant change in quality was around 22%, while this percentage for areas that burned at high severity was around 65%. In contrast, the percentage of cells that burned and significantly changed in habitat quality after was around 75% for moderate severity fires and 32% for high severity fires (Fig. B5b).

Table B1. Predictive statistics for the random forest species distribution models of SSN fisher denning habitat. We report the mean and standard deviation (across 10 model folds) of the out-of-bag (OOB) error and area under the receiver operator curve (AUC) for each regional sub-model.

Model fit statistic	Mean value	Standard deviation
OOB error	0.0485	0.0013
AUC	0.997	0.00050

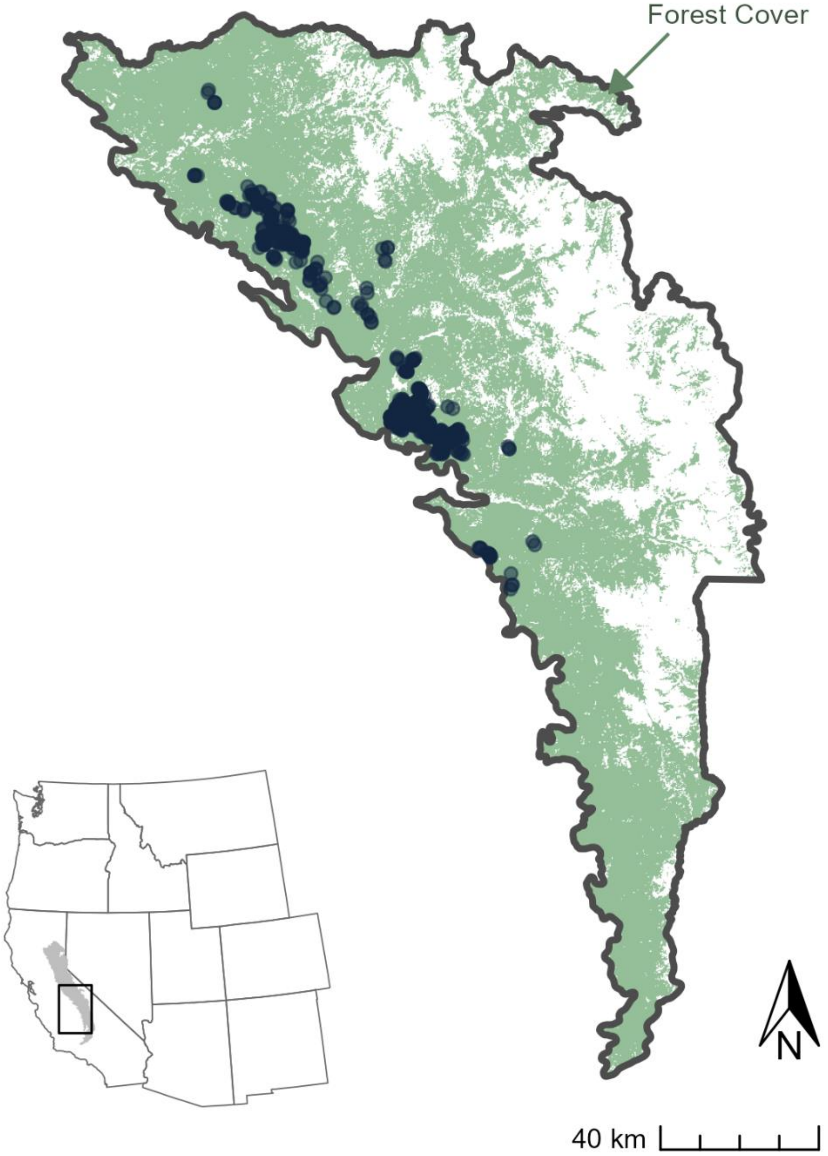

Figure B1: Map of fisher denning locations (n=667) within the southern Sierra Nevada. Note that most locations are found within the North region (n=646), with only some locations found within the Southwest region (n=21) and none in the Kern Plateau (excluded from this figure).

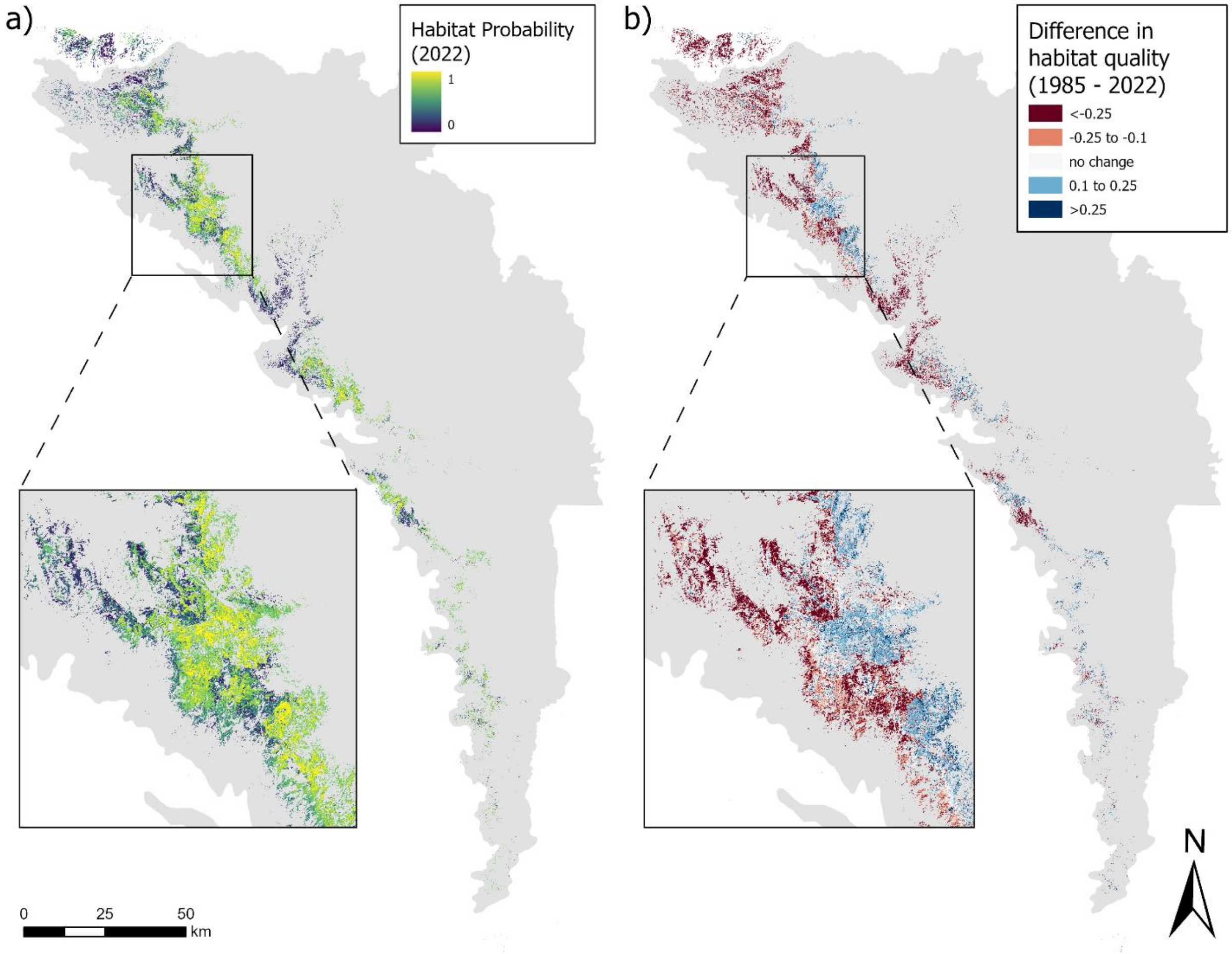

Figure B2: (a) Probability of fisher denning habitat in 2022 and (b) the change in habitat quality from 1985 to 2022, with red cells showing a decrease in quality and blue showing an increase.

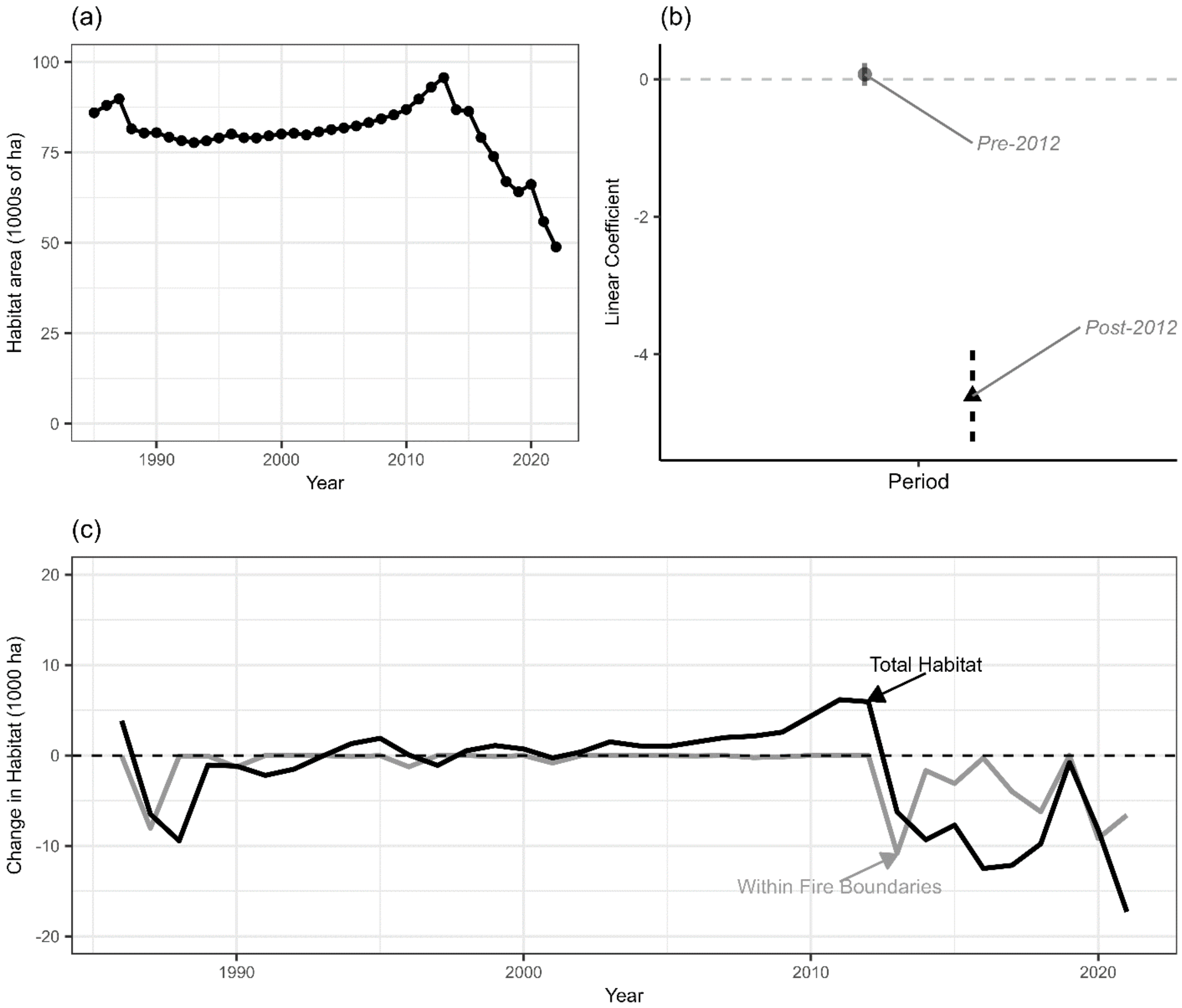

Figure B3: (a) Denning habitat trends from 1985 to 2022; (b) coefficients and 95% confidence intervals from a linear model of trends in denning habitat area in the SSN region from 1985–2012 (circle point and solid line) and 2012–2022 (triangle point and dashed line) with transparency indicating if results were significant or not; (c) Change in habitat area, where each year marks the difference between the previous year's area from the following year's area; the darker line indicates change in area in the entire region while the lighter line indicates change specifically within fire perimeters that occurred that year. Values on the y-axis represent area in 1000s of hectares, such that a value of 100 indicates 100,000 hectares.

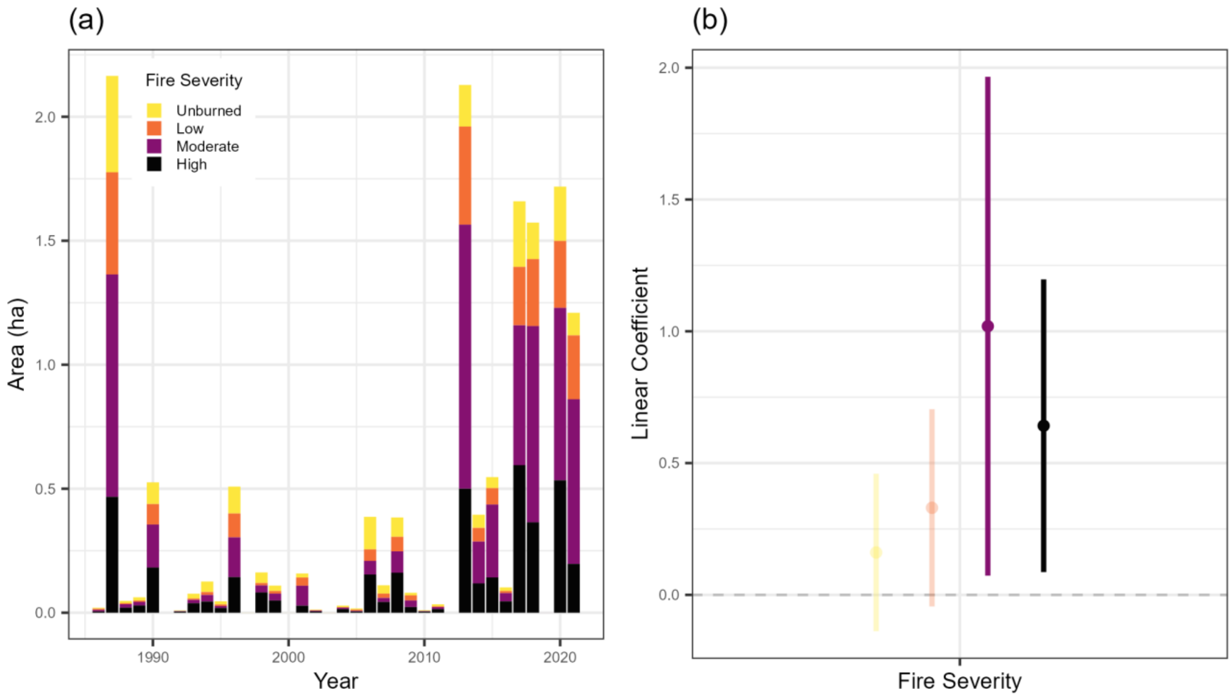

Figure B4: (a) Histogram of area burned in each fire severity class within SSN fisher denning habitat across the 38-year study period; (b) coefficients and 95% confidence intervals from a linear model of trends in burned area for each burn severity class across the 38-year study period; semi-transparent points and lines indicate that the 95% confidence intervals overlapped with zero and were thus insignificant.

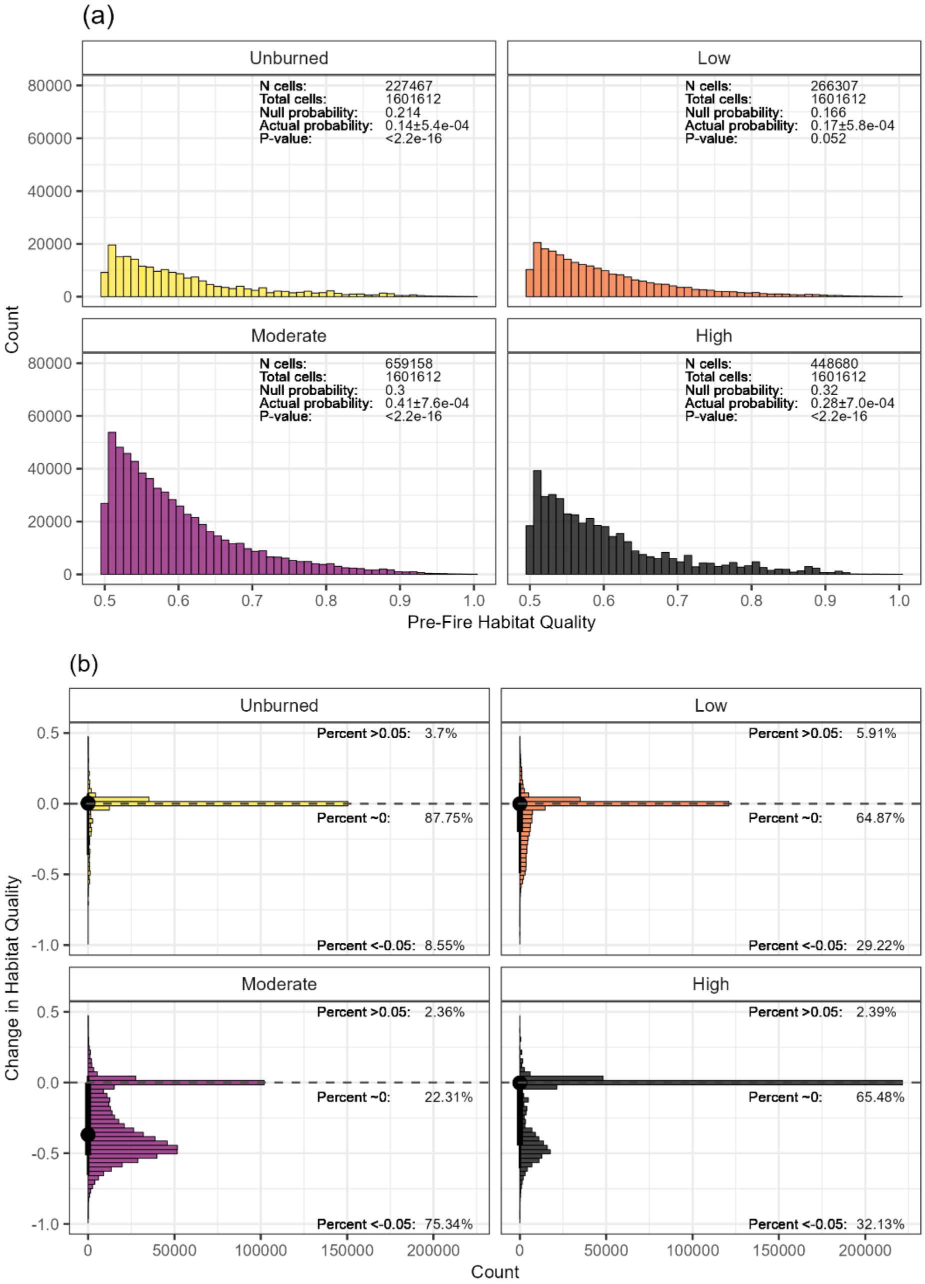

Figure B5: (a) Distribution of pre-fire habitat quality within the fire severity class in which they burned the following year, and the results of the binomial test performed for the number of cells burned in each category compared to the null expectation; (b) distribution of habitat quality change pre- and post-fire within each fire severity class.