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Short communication

Collapse and restoration of mature forest habitat in California

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ABSTRACT

Mature and old-growth forests provide critically important ecosystems services and wildlife habitats, but they are being lost at a rapid rate to uncharacteristic mega-disturbances. We developed a simulation system to project time-to-extinction for mature and old-growth forest habitat in the Sierra Nevada, California, USA. The simulation parameters were derived from a 1985–2022 empirical time-series of habitat for the southern Sierra Nevada fisher (*Pekania pennanti*), an endangered native mammal and old-forest obligate that has seen a 50 % decline in its habitat over the past decade from a combination of extensive drought-related tree mortality and high severity fire. We found that under a continuation of the status quo (extensive tree mortality and severe fire, minimal management intervention), fisher habitat had a 64 % chance of complete loss in the next 50 years (by 2075), a risk that increased to 99 % by 2100. However, under a simulated management regime focused on forest restoration, including expanded use of beneficial fire and mechanical thinning aimed at large tree retention and recruitment, the chances of complete loss were reduced to 2–5 % by 2075 and 2–20 % by 2100, and in some cases resulted in a trend reversal and future habitat increases. Our work suggests that fuels reduction and forest restoration interventions, implemented rapidly and at sufficient scale, could conserve remnant mature and old-growth forest habitat in the southern Sierra Nevada and facilitate its recovery over the next century. Our study serves as an exploratory analysis that aims to help quantify coarse levels of risk and helps to focus future studies and forest restoration investments.

1. Introduction

Mature and old-growth forests are a relatively rare but critically important feature of many ecosystems globally (Spies, 2004; Wirth et al., 2009). Trees within mature and old-growth forests store proportionally large amounts of above- and below-ground carbon (Dean et al., 2020; Hauck et al., 2023), greatly alter nutrient cycling (Ludwig et al., 2004), modify microclimate (Dean et al., 1999), offer a substrate for plant and fungal life (Kartzinel et al., 2013), and provide habitat for numerous wildlife species (Mazurek and Zielinski, 2004; Jones et al., 2018). Mature and old-growth forests have become uncommon because they have been targeted for harvesting due to high economic value and their slow replacement given the long periods of time that they take to develop. Historically, these forests typically developed in contexts where large-scale, high severity ecological disturbances were rare (e.g., refugia or long-interval systems) (Meddens et al., 2018) and/or their constituent tree species had developed adaptations for surviving disturbances (e.g., thick bark, tree crowns well above the forest floor) (Pausas, 2015). Because of their rarity, ecological value, and sociocultural importance, mature and old-growth forests and their constituent large, old trees are often protected (Lindenmayer, 2017; Lindenmayer and Laurance, 2017).

In the United States, land use legacies, climate change, and altered disturbance regimes have led to widespread and abrupt declines of mature and old-growth forests (Steel et al., 2023; USDA Forest Service, 2024). Historical selective logging made large, old trees scarce (Collins et al., 2017); climate change has made them more vulnerable to stress and mortality (Bennett et al., 2015); and fire suppression has placed

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remaining mature and old-growth forests in a vulnerable fire-prone context (Hessburg et al., 2019; Koontz et al., 2020). In the southern Sierra Nevada, California, a once-in-a-millennium drought between 2012 and 2015 killed nearly 129 million trees (Asner et al., 2015; Fettig et al., 2019), with disproportionate mortality among the largest trees (Restaino et al., 2019). Subsequent extreme fire years combined with drought effects led to at least a halving of habitat for mature forest-dependent wildlife since 2011 (Steel et al., 2023) and substantial losses of large, iconic trees (Shive et al., 2022; Stephenson et al., 2024). In the current fire environment, it is not clear how much time is left before mature and old-growth forests disappear, or whether management interventions might slow or reverse observed declines (Hurteau et al., 2025).

Here, we developed an exploratory simulation study to predict time-to-extinction of mature and old-growth forest habitat in the southern Sierra Nevada, California, which is part of the California Floristic Province biodiversity hotspot (Baldwin, 2014). We developed our predictions by drawing on a 38-year habitat time-series for southern Sierra Nevada fisher (*Pekania pennanti*) (Fig. 1a), an endangered distinct population segment closely associated with mature and old forests (Fig. 1b) across their limited geographic range (Purcell et al., 2009). Our objective was to simulate possible losses and gains of mature and old-growth forest habitat for fishers (hereafter, "mature/old-growth forest habitat") under a variety of scenarios that made different assumptions about future wildfire, fuels reduction and forest restoration interventions, and habitat recruitment. We recognize that both the geographic scope of this work and the future scenarios we simulate inherently introduce considerable uncertainty. As such, we explicitly incorporated stochasticity in our simulations in an attempt to bracket this uncertainty. While we focus on fisher habitat in this paper, our results likely mirror issues faced by other species that co-occupy mature and old-growth forest habitat in the broader ecoregion, especially the spotted owl (*Strix occidentalis*) (Gutiérrez et al., 2017). Ultimately, this work suggests that there is still time for management interventions to safeguard mature and old forest habitat in California.

2. Methods

We used a time series of southern Sierra Nevada fisher (hereafter, "fisher") habitat produced by Hart et al. (2025) to derive parameters for our simulation. Briefly, Hart et al. (2025) developed a dynamic species distribution model in the Google Earth Engine environment (Gorelick et al., 2017) using random forest (Breiman, 2001) that predicted the total area of reproductive-capable fisher habitat for each year from 1985 to 2022 using spatially structured survey data and a suite of geospatial environmental covariates (Zielinski et al., 2013). Hart et al. (2025) found that fisher habitat was relatively stable from 1985 to 2012, but then declined by ~50 % between 2013 and 2022 primarily because of vegetation mortality due to severe wildfires and the interacting effects between fire and drought (Steel et al., 2023) (Fig. 1c). Areas that burned at high-severity (>75 % overstory canopy mortality) consistently converted habitat that was previously suitable for fishers to unsuitable conditions. The time-series of fisher habitat, as well as time-series of the area of fisher habitat burned at high-severity, formed the core pieces of our forecasting model (Fig. 2).

The southern Sierra Nevada differs from the broader Sierra Nevada ecoregion and from other mountainous areas in California in some important ways. These distinctions include having experienced the

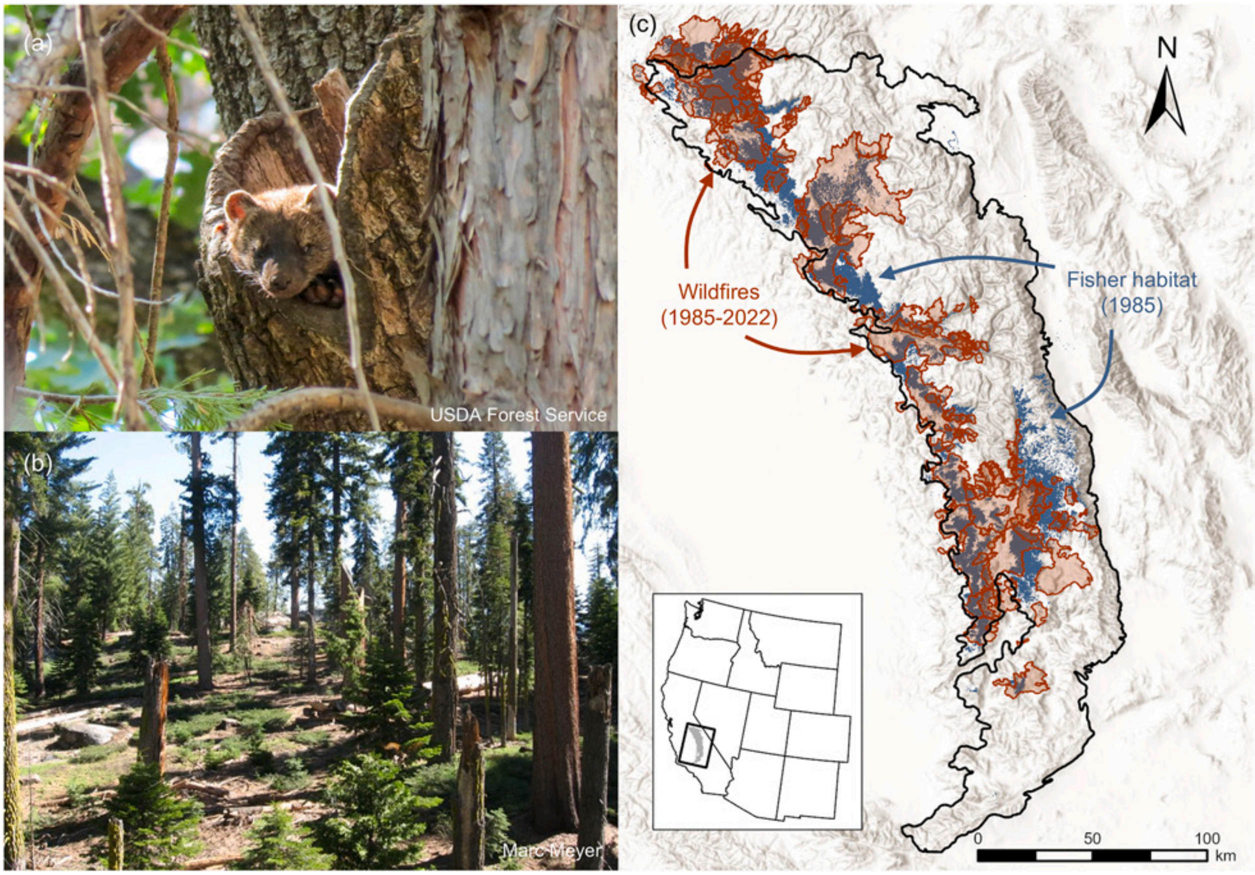

Fig. 1. Mature and old-growth forests provide denning and resting habitat for the southern Sierra Nevada fisher (a), which is often associated with late-seral, structurally diverse, decadent, and well-shaded stands of trees (b). In the past 40 years, fisher habitat has been extensively burned (c), mostly over the past decade. The black outline in panel c shows the approximate boundary of the southern Sierra Nevada bioregion. Photo credit: USDA Forest Service (a); Marc Meyer (b).

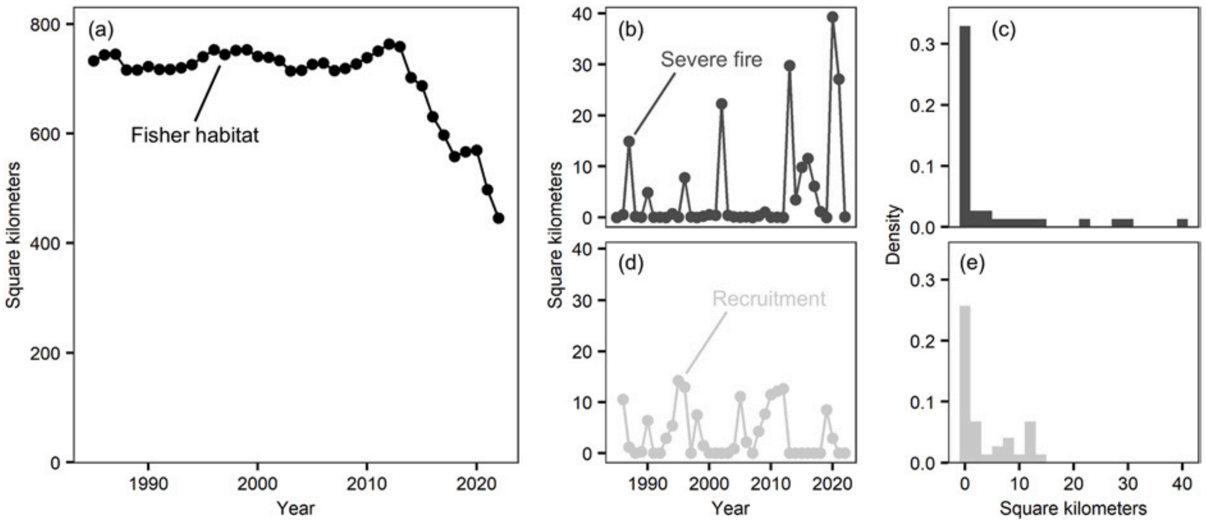

Fig. 2. Empirical trends and data informing the simulation model. Panel (a) shows the long-term trend of southern Sierra Nevada fisher habitat (Hart et al., 2025), with a ~30-year period of stability followed by a recent sharp decline. Panels (b–c) show the annual area of fisher habitat that burned at high-severity (>75 % canopy mortality) over the study period and the distribution of those data; panels (d–e) show the annual area of fisher habitat recruitment over the study period and its distribution.

brunt of an intense statewide drought from 2012 to 2015 (Asner et al., 2015) and the largest and most severe recent fire events (Safford et al., 2022; Ayars et al., 2023), as well as a history of logging that was less intense than the broader Sierra Nevada and northwestern California (Laudenslayer Jr and Darr, 1990; Beesley, 1996). These unique histories make the southern Sierra Nevada an ideal laboratory for understanding rapid changes in disturbance regimes, but also mean that transfer of results and implications to other regions, while at times appropriate, must be done thoughtfully and with caution.

2.1. Simulation system

Our simulation was based on annual accounting of potential habitat losses (severe wildfire) and gains (mature forest recruitment). Starting with the estimated area of fisher habitat occurring in the southern Sierra Nevada in 2022 (445.3 km^2) Hart et al. (2025), we simulated annual habitat change as follows:

$$\Delta habitat_{i,t} = recruitment_{i,t} - fire_{i,t}$$

where $i = 1, 2, \ldots, M$ ($M = 300$) represented a random draw from either an empirical or a simulated probability distribution for each timestep $t = 1, 2, \ldots, K$ ($K = 77$ timesteps were calculated over the period 2023 to 2100). Whether the recruitment or fire distribution was empirical or simulated, and how it changed over time, depended on the scenario examined.

2.2. Scenario development

We developed three scenarios that reflected different assumptions about possible management interventions, future fire activity, and habitat recruitment (Table 1, Table S1). All scenarios included a background rate of fisher habitat recruitment (Fig. 2d–e). We calculated a recruitment distribution by computing the annual rates of fisher habitat change from the 1985–2022 habitat time-series generated by (Hart et al., 2025). We then retained only the values that were positive (i.e., over that year, habitat area increased via recruitment) and used this positive distribution to sample annual recruitment in the simulation (Fig. 2e). While entirely phenomenological and not mechanistic, using this recruitment distribution allowed us to simulate realistic amounts of possible annual increases in habitat.

The first scenario ("business-as-usual" with minimal management intervention) assumed that the observed habitat declines (2013–2022, driven by extensive drought-related tree mortality and uncharacteristically large high severity fires) would continue unabated. This scenario

Table 1
Description of simulation scenarios.

Scenario	Fire	Recruitment
Business-as-usual	Sampling from the empirical severe fire distribution (2013−2022), F_0. $f_{i,t} \sim F_0$	Sampling from the empirical habitat recruitment distribution (1985–2022), R_0. $r_{i,t} \sim R_0$
Restoration	Sampling from F_0 becomes less likely and sampling from a Gamma distribution of historical severe fire $F_1 \sim \text{Gamma}(\alpha = 0.285, \lambda = 0.05)$ becomes more likely over the first 50 years of the simulation. After year 50, sampling exclusively occurs from F_1. $if \begin{cases} t \leq 50, & Bernoulli\left(t/50\right) \begin{cases} 0, f_{i,t} \sim F_0 \\ 1, f_{i,t} \sim F_1 \end{cases} \\ t > 50, & x_{i,t} \sim F_1 \end{cases}$	Sampling from the empirical habitat recruitment distribution (1985–2022), R_0. $r_{i,t} \sim R_0$
Restoration + recruitment	Sampling from F_0 becomes less likely and sampling from a Gamma distribution of historical severe fire $F_1 \sim \text{Gamma}(\alpha = 0.285, \lambda = 0.05)$ becomes more likely over the first 50 years of the simulation. After year 50, sampling exclusively occurs from F_1. $if \begin{cases} t \leq 50, & Bernoulli\left(t/50\right) \begin{cases} 0, f_{i,t} \sim F_0 \\ 1, f_{i,t} \sim F_1 \end{cases} \\ t > 50, & f_{i,t} \sim F_1 \end{cases}$	Sampling from R_0 becomes less likely and sampling from $R_1 = R_0 + \text{sd}(R_0)$ becomes more likely over the course of the full simulation, $M = 77$ years. $Bernoulli\left(t/M\right) \begin{cases} 0, r_{i,t} \sim R_0 \\ 1, r_{i,t} \sim R_1 \end{cases}$

reflects a hypothesis that these forests have crossed a disturbance regime threshold due to climate, fire exclusion, and past timber harvest focused on large tree removal (Pausas and Keeley, 2014; Miller et al., 2019). We first computed the annual area of fisher habitat that burned at high severity in the Google Earth Engine environment from 2013 to 2022, where high severity fire was defined as areas experiencing >75 % canopy mortality determined with the relativized burn ratio (Parks et al., 2014). For the *fire* term of our algorithm, we randomly sampled from this empirical distribution with replacement. We note that annual high severity fire effects were influenced by pre-fire drought-related mortality, which intensified fire effects (Wayman and Safford, 2021; Stephens et al., 2022). Next, we randomly sampled from the *recruitment* distribution described above with replacement.

The second scenario (“Restoration”) reflected the possibility that forest management interventions such as fuels reduction and forest restoration treatments might shift the distribution of high severity fire towards its historical range of variation, or HRV (Agee and Skinner, 2005; Stephens et al., 2020, 2021; Hagmann et al., 2021; Prichard et al., 2021). We developed a high severity fire distribution representing HRV by computing the expected annual area burned at high severity, and simulating a Gamma distribution around this expected value. We computed the expected annual area burned at high severity using information about historical fire regimes in Sierran yellow pine and mixed conifer forests (Safford and Stevens, 2017), which describes the dominant vegetation type in the low- to mid-elevation areas that the southern Sierra Nevada fisher occupies throughout most of its range. Approximately 5 % of yellow pine and mixed conifer forests burned annually, and when they burned, an estimated 5–15 % of the burned area experienced stand-replacing, or high-severity fire. Beginning with the maximum area of fisher habitat observed from 1985 to 2022 (763.2 km^2), we computed that on average, 5 % of this area would burn annually (38.2 km^2) and of that area 5–15 % would burn at high severity (5.7 km^2; we conservatively assumed 15 %).

We then developed a Gamma distribution from which to sample for the Restoration scenario with the distribution mean (μ) equal to 5.7 km^2. The mean of the Gamma distribution is derived from the shape (α) and rate (λ) parameters, where $\mu = \alpha/\lambda$. We explored a suite of possible values for α and λ that produced the mean of 5.7 km^2 but that also approximated the observed range of the empirical fire distribution, such that large observed values (extreme fire years) were still possible but were relatively rarer than they were over the study period (Fig. S1). In the final simulation we selected $\alpha = 0.285$ and $\lambda = 0.05$ that best achieved this objective. This Gamma distribution therefore reflected our approximation of the HRV for area burned at high severity within fisher habitat in the southern Sierra Nevada.

Assuming that HRV could not be instantly attained, we built into the Restoration scenario a transition period of 50 years, where the empirical severe fire distribution used in the business-as-usual scenario was incrementally mixed with the simulated Gamma distribution. Thus, in the first 50 years of the simulation, there was an $t/50$ probability that high severity fire would be drawn from the Gamma HRV distribution, and thus a complementary $1 - t/50$ probability that high severity fire would be drawn from the 2013–2022 empirical fire distribution. Thus, as t approached 50, the probability of drawing from the Gamma HRV distribution approached 1, and sampled exclusively from this distribution thereafter.

The third scenario (“Restoration + recruitment”) was identical to the second scenario in terms of the transition between empirical and HRV high severity fire distributions. However, the third scenario assumed that over time, it would be possible to increase the rate of fisher habitat recruitment, perhaps because a reduction in the density of younger and/or smaller trees that have infilled during the fire suppression era (Steel et al., 2015; Collins et al., 2017) via forest restoration might result in competitive release in medium or large diameter trees that are attempting to access a limited supply of water and other resources (Vernon et al., 2018; Zald et al., 2022; Young et al., 2023). Moreover, treatments could facilitate growth and recruitment of California black oaks (*Quercus kelloggii*) that are important habitat structures of fishers in this region (Thompson et al., 2015). Similar to the transition between the empirical and HRV high severity distributions, we transitioned between drawing from the empirical recruitment distribution and a future distribution that was 1 standard deviation greater than the empirical distribution. The transition was such that there was a $t/100$ probability that annual recruitment would be drawn from the future recruitment distribution, and a $1 - t/100$ probability that the draw would come from the empirical distribution.

We summarized the potential impacts of these three scenarios on mature forest habitat by calculating the proportion of the projected fisher habitat that reached zero (complete loss of habitat) by 2050, 2075, and 2100. We also computed the median fisher habitat area across all iterations to describe expected trajectories within each scenario, and summarized the minimum value, maximum value, and lower and upper 95 % prediction intervals by year 2100. All analyses were conducted using R version 4.4.2.

3. Results

Habitat projections and the probability of complete fisher habitat extinction varied considerably among the three scenarios (Fig. 3). Although following an initial steep downward trajectory, few projections from any of the three scenarios had reached 0 by mid-century; only the business-as-usual scenario saw 1 of 300 projections reach zero before 2050. By 2075, however, 64.3 %, 5.3 %, and 1.7 % of habitat projections reached 0 under the business-as-usual, restoration, and restoration + recruitment scenarios, respectively. By 2100, 99 % of all habitat projections under the business-as-usual scenario had reached 0, while 19.7 % and 2.3 % of projections had reached 0 for the restoration, and restoration + recruitment scenarios, respectively (Table 2).

Fisher habitat trajectories varied among the three scenarios, with the business-as-usual scenario following a straight-line trajectory towards extinction, the restoration scenario showing a shallowing decline closer to 2100, and the restoration + recruitment scenario reversing direction and beginning to show habitat increases by 2100 (Fig. 3). By 2100, no fisher habitat was expected to remain under the business-as-usual scenario; all habitat was expected to disappear by 2071 (95 % prediction interval = [2056, 2093]). Under the restoration scenario, there was an average of 115 km^2 (95 % prediction interval = [0 km^2, 305 km^2]) remaining by 2100. Under the restoration + recruitment scenario, there was an average of 250 km^2 (95 % prediction interval = [9.3 km^2, 672 km^2]) remaining by 2100 (Table 3).

4. Discussion

Under current conditions and the current management paradigm, mature and old-growth forests inhabited by the southern Sierra Nevada fisher in California, USA appear to be vulnerable to complete loss in <50 years. Our statistical simulation study predicts that the likelihood of total fisher habitat extinction is 64 % by 2075 and 99 % by 2100 under the assumption that recent severe fire trends continue and that management interventions remain limited. However, if accelerated fuels reduction and forest restoration efforts are able to move the region's fire regime towards its historical range of variation over the next 50 years, the chances of total loss decrease to 5.3 % by 2075 and 20 % by 2100. Should such restoration also result in increases in tree growth rates and thus recruitment of mature and old-growth forest conditions (Collins et al., 2014; Dagley et al., 2018), the chances of total loss further decrease. Thus, our simulations suggest that a broad range of outcomes, including relatively optimistic ones, for future fisher habitat are possible, depending on social and political will to invest rapidly in broad-scale ecosystem restoration. Such an effort would require revisiting current conservation measures aimed at protecting this critical habitat.

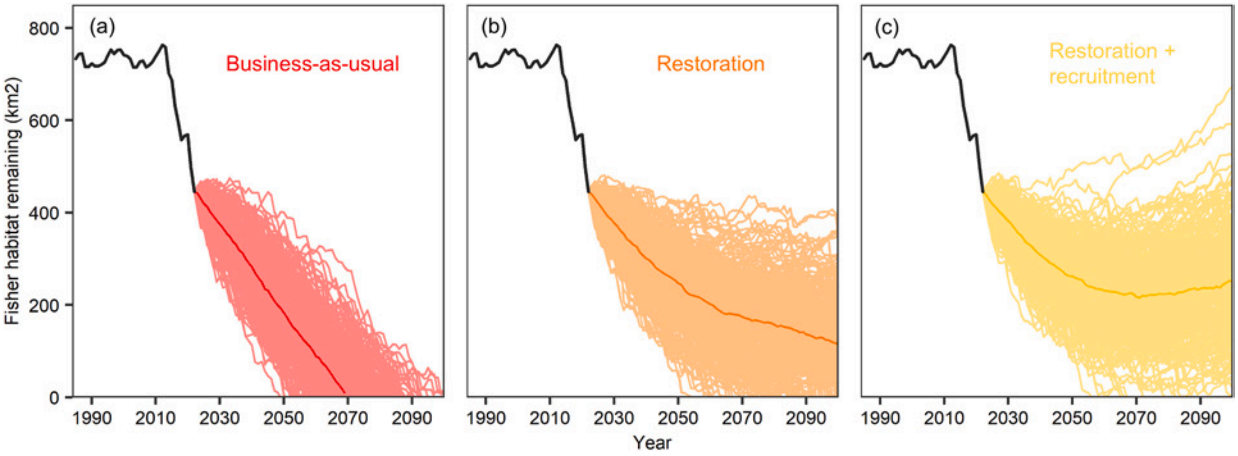

Fig. 3. Simulations of future fisher habitat change across the three scenarios. Panel (a) is the business-as-usual scenario, panel (b) shows the restoration scenario, and panel (c) shows the restoration + recruitment scenario. In all three panels, the black line shows the fisher habitat trend over the period 1985–2022, prior to the simulation period. The dark colored lines (red, orange, or yellow) from 2023 onwards shows the median habitat during the simulation, and the lighter colored lines show individual simulation trajectories ($n = 300$) for each scenario. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Probability of extinction (complete loss) of fisher habitat at different time horizons for the three scenarios examined.

Scenario	Probability of extinction		
	2050	2075	2100
Business-as-usual	0.003	0.643	0.990
Restoration	0	0.053	0.197
Restoration + recruitment	0	0.017	0.023

Table 3
Summary of remaining fisher habitat at the end of the simulation period for each of the three scenarios examined.

Scenario	Habitat area (km^2) remaining at 2100				
	Min	2.5 %	Median	97.5 %	Max
Business-as-usual	0	0	0	0	17.3
Restoration	0	0	115	305	398
Restoration + recruitment	0	9.3	250	459	672

While fuels reduction and forest restoration are known to alter fire behavior and restore lower-severity fire regimes in frequent fire forests that have experienced long-term fire exclusion and suppression (Prichard et al., 2021; Stephens et al., 2024), these activities may also alter important habitat elements for forest-dependent wildlife. Thus, researchers often examine trade-offs between potential direct negative effects of fuels reduction on wildlife habitat and the indirect positive effects of reducing future severe fire-induced habitat loss (Tempel et al., 2015). Previous work has suggested that, on the whole, the benefits of habitat alteration outweigh the costs for both southern Sierra Nevada fishers (Scheller et al., 2011) and another iconic old-forest dependent species, the spotted owl (*Strix occidentalis*) (Jones et al., 2022), particularly in light of recent widespread fire- and drought-driven habitat losses (Steel et al., 2023; Hart et al., 2025). Forest restoration efforts designed to expand the use of beneficial fire, leverage low- and moderate-wildfire burn areas, and promote large trees and other important habitat structures may be particularly effective at increasing the scale of restoration treatments in mature and old-growth forests (North et al., 2021). Fire is a critical ecological process in this and many other ecosystems; rapidly restoring landscapes so that they can accept beneficial fire is likely the best option to facilitate long-term persistence and resilience of wildlife and fire-dependent ecosystems (Gaines et al., 2022; Jones et al., 2025); in fact, it may be the only option with very high chances for success.

In some fire-prone and fire-dependent ecosystems, the accumulation of climatic and land-use changes have led to abrupt and near-irreversible changes to ecosystem dynamics, also referred to as ecosystem collapse (Lindenmayer and Sato, 2018; Canadell and Jackson, 2021). Collapse occurs when ecosystem structure and function become degraded, approach a tipping point or threshold (van Nes et al., 2016), and are subsequently pushed over the tipping point into an alternative and persistent state (Law and Morton, 1993; Beisner et al., 2003). The Sierra Nevada bioregion, by virtue of its long history of natural fire and cultural fire use (Taylor et al., 2016) followed by more recent aggressive fire exclusion (Hagmann et al., 2021) may be particularly vulnerable to collapse and may even be experiencing it now (Guiterman et al., 2022). Evidence for ongoing collapse include abrupt shifts in characteristic patterns and processes, such as rapid declines in snowpack (Mote et al., 2018), altered mixing of high-elevation lakes (Streib et al., 2021), rapid declines in mature and old-growth forests (Steel et al., 2023), and abrupt upticks in severe fire extent and uniformity (Steel et al., 2018). Yet, appropriate interventions can slow or halt collapse (Lindenmayer et al., 2016). Our work here suggests that restoration of natural fire regimes and the forest conditions they create will be necessary to slow and ultimately reverse ongoing declines of mature and old-growth forest habitat in the Sierra Nevada, California (Stephens et al., 2020; Hurteau et al., 2024).

While our paper offers a straightforward simulation approach that examines plausible futures for mature and old-growth forest habitat, its virtue of parsimony is also its vice. First, the simulation system itself is highly simplistic. It is phenomenological, not mechanistic, and thus assumes causality from non-experimental, observational data, and assumes such causal relationships, including climate, will be constant into the future. We do not explore the possibility that large, high-severity fires could become even more prevalent in the coming decades than we have seen recently (Littell et al., 2018; Safford et al., 2022), nor did we account for fire-vegetation feedbacks (Archibald et al., 2018; Hurteau et al., 2019). The simulation system is also entirely aspatial; fire is not allocated across a landscape and intersected with habitat on an annual basis (Tempel et al., 2015; Jones et al., 2022). Instead, we simply draw from a joint fire-habitat distribution, and make no assumptions about, or efforts to account for, spatial variation in fire, habitat, recruitment, or their interactions. Nevertheless, our model results are broadly consistent with spatial models projecting substantial forest habitat and carbon loss in the Sierra Nevada in the 21st century in the absence of increased forest restoration interventions (Krofcheck et al., 2017; Liang et al., 2018; Jones et al., 2022).

Second, despite our explicit attempt to bracket uncertainty, the three scenarios we present here still do not contain all possible realistic outcomes and nor do they fully examine the sensitivity of projections to the simplifying assumptions that we made (Table S1). For example, in the 'restoration' scenario, we assumed HRV could be reached in 50 years, but we could have explored sensitivities to this assumption that reflect varying social and political will, setbacks, delays or accelerations in implementation, or even non-linearities (e.g. a 'ramp up') that have been thoroughly described in the literature (Collins et al., 2010; North et al., 2015). The 'restoration + recruitment' scenario assumed that recruitment could increase by 1 standard deviation over the time horizon, but we could have assumed that was entirely unattainable, or would be far surpassed. However, we emphasize that here, our objective was not to predict the most likely future, nor to be exhaustive of its myriad possibilities, but rather contrast plausible divergent trajectories. In scenario analysis such as this, the focus should be on the relative difference among scenarios, not on the absolute outcomes (Beissinger and Westphal, 1998).

Our work suggests mature and old-growth forest habitat in California finds itself at a critical juncture. On the one hand, continued occurrence of large-scale high severity fire and limited management interventions are predicted to lead to complete loss in the near-term (Safford et al., 2022). On the other hand, it does not appear too late to intervene, slow, or even reverse recent declines in mature and old-growth forest habitat, especially using strategic approaches designed to increase the pace of forest restoration and use of beneficial fire at landscape scales (Meyer, 2015; North et al., 2021, 2024). But such interventions (USDA Forest Service, 2022), namely widespread fuels reduction and forest restoration, will need to be implemented relatively quickly, creatively, and experimentally to reduce the chances that such efforts begin too far down the business-as-usual 'curve' (Fig. 3a) (Stephens et al., 2020; Hurteau et al., 2024; North et al., 2024). The consequences of delay may be irreversible and catastrophic for species, biological communities, ecosystems, and society (Wood and Jones, 2019).

CRediT authorship contribution statement

Gavin M. Jones: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Brandon M. Collins:** Writing – review & editing, Conceptualization. **Lacey E. Hankin:** Writing – review & editing. **Ronan Hart:** Writing – review & editing, Software, Methodology, Data curation. **Marc D. Meyer:** Writing – review & editing, Methodology. **Jon Regelbrugge:** Writing – review & editing, Conceptualization. **Zachary L. Steel:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Craig Thompson:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111241.

Data availability

Data will be made available on request.

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