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Research Article

Long-term benefits of burns for large mammal habitat undermined by large, severe fires in the American West

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Escalating wildfire frequency and severity are altering wildland habitats worldwide. Yet investigations into fire impacts on wildlife habitat rarely extend to the macroecological scales relevant to species conservation and global change processes. We evaluate the effects of wildfire on habitat quality and selection by large mammals spanning three trophic levels in the Western United States. We analyze 12 years of GPS telemetry data for 2966 mule deer *Odocoileus hemionus*, 52 black bears *Ursus americanus*, and 74 cougars *Puma concolor* across Utah and Nevada, USA. Over 800 areas burned between 1990–2022 overlapped with the home ranges of 1892 animals, resulting in almost 23 000 km^2 of burned habitat and representing 12.8% of the total home range area for animals in our sample. Habitat suitability models for 664 mule deer, 14 black bears and 11 cougars indicated that burns improved summer home range quality for mule deer and black bears by 7% and 14%, respectively, highlighting the benefits of fires for nutrient cycling, understory herbaceous growth, and resultant caloric value for animal nutrition. When making fine-scale movement decisions, however, mule deer avoided burned habitats, and all three species generally avoided high-severity burns for up to 30 years post-fire. Thus, the effects of burns on wildlife habitat selection appear to be dependent on spatial scale. Given projected increases in large, severe fires, our results suggest potential reductions in beneficial habitat for wildlife in the long term. However, our results also suggest that prescribed burns, because of their smaller spatial

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footprints and lower severity relative to wildfires, can benefit wildlife habitat quality through improvements in forage, cover, and other vegetation characteristics. Therefore, managing for low-severity burns and limiting large, severe wildfires, e.g. via prescribed burns or fire control policies, could positively impact the habitat quality of these three common species and, therefore, the economic and ecosystem services they provide.

Keywords: carnivore, composite burn index, heterotrophs, prescribed burn, telemetry, ungulates

Introduction

Increasing size, frequency, and severity of wildfires are modifying wildland ecosystems around the world (Abatzoglou and Williams 2016, Mansoor et al. 2022). By changing vegetation structure, composition, productivity, and subsequent sensory cues, wildfires can influence habitat quality and behavior patterns for animals at broad scales (Nimmo et al. 2019, Michel et al. 2023). Such responses might alter habitat use, population dynamics, and wildlife community composition, as well as restructure a host of ecological interactions with subsequent consequences for ecosystem function and services (Kelly et al. 2020, Doherty et al. 2022, Khayati et al. 2023).

Though a number of mammals show resilience to, or even benefit from, burned habitats (Pocknee et al. 2023, Calhoun et al. 2023), such responses are not universal even within the same species (Arthur et al. 2012, Geary et al. 2020, Forney and Peacock 2024, Volkmann and Hodges 2024). Some studies indicate that changing fire regimes are detrimental to habitat suitability for animals (Hale et al. 2016, Jorge et al. 2020), while others suggest fire can enhance habitat use (Cherry et al. 2018, Steel et al. 2019, Cave et al. 2021). In mammals, post-burn effects on habitat use depend on underlying ecological conditions such as vegetation type or altered predation risk, as well as the severity and extent of fire impacts (Culhane et al. 2022, Ganz et al. 2022). However, studies rarely have sufficient data across space and time to thoroughly investigate species' dynamic responses to burns at the broad geographic and temporal extents necessary for effective conservation planning.

Variation in species traits, particularly trophic position, may also lead to unequal adaptability to burned habitats as fires modify resources and habitat structure across space and time (Jones et al. 2023). Predators in higher trophic positions commonly rely on concealment and open sight lines (ambush predators) or high maneuverability (coursing predators) in their hunting strategies, and thus could modify their habitat use due to changes in vegetation structure and terrain (e.g. changes in deadfall) following fires (Geary et al. 2020, Ganz et al. 2022). Fire-induced changes in visibility accompanied by modified plant composition, forage quality, and primary productivity can similarly alter the habitat selection of herbivores as they balance the tradeoffs between increased foraging opportunities (Allred et al. 2011, Proffitt et al. 2019) and predation risks in burned landscapes (Cherry et al. 2017, Doherty et al. 2022). Omnivores or habitat generalists may be more resilient to, or more likely to take advantage of, post-fire changes in resource availability (Cunningham et al. 2003, Santos et al. 2014). Intuitively, species traits should govern animal responses to fire-driven habitat changes, but attempts that use species traits to explain heterogeneity in fire impacts have been largely unsuccessful (van Mantgem et al. 2015, Geary et al. 2020, Calhoun et al. 2023).

Despite numerous studies on dynamic fire impacts and resulting wildlife responses, empirical evidence is scarce for species' long-term responses to burned habitats across spatiotemporal scales and environmental gradients. Here, we assessed the macroecological impacts of burns on wildlife habitat selection using 12 years (2010–2022) of high-resolution GPS telemetry data for three common mammals native to montane ecosystems – mule deer *Odocoileus hemionus*, black bears *Ursus americanus* and cougars *Puma concolor* – across Utah and Nevada in the USA. These species have long inhabited fire-prone landscapes, but the growing extent of wildfire impacts projected in this region may outpace their capacities to adjust (Turner et al. 2019). These species' large ranges and high mobility enable them to exploit dynamic resources across heterogeneous post-fire landscapes (Nimmo et al. 2019). We hypothesized that trophic position would mediate animal responses to burned habitats. Specifically, we predicted that mule deer would respond most strongly to burned habitats because they are most directly reliant on early successional vegetation for foraging, with diminishing responses to burned habitats at higher trophic levels. Moderate responses by black bears and weak responses by cougars could arise because their use of burns is likely influenced by both vegetation changes and the distribution of herbivore prey, leading to less predictable or consistent selection patterns. We also expected larger, more severe, and more recent fires to elicit the strongest responses from wildlife.

Methods

Study system

Our study region encompassed large portions of Utah and Nevada, USA, including portions of the Great Basin, Sierra Nevada, Rocky Mountains, Mojave Desert and Colorado Plateau ecoregions. We used GPS telemetry data from collared mule deer (n = 2966), black bears (n = 52), and cougars (n = 74) collected by researchers and state and federal agencies across this region between 2010 and 2022 (Fig. 1a). Additional details are available in the Supporting information.

Across the American West, the annual number of fires has doubled and the area burned has quadrupled since the 1990s (Iglesias et al. 2022). Additionally, intervals between wildfires

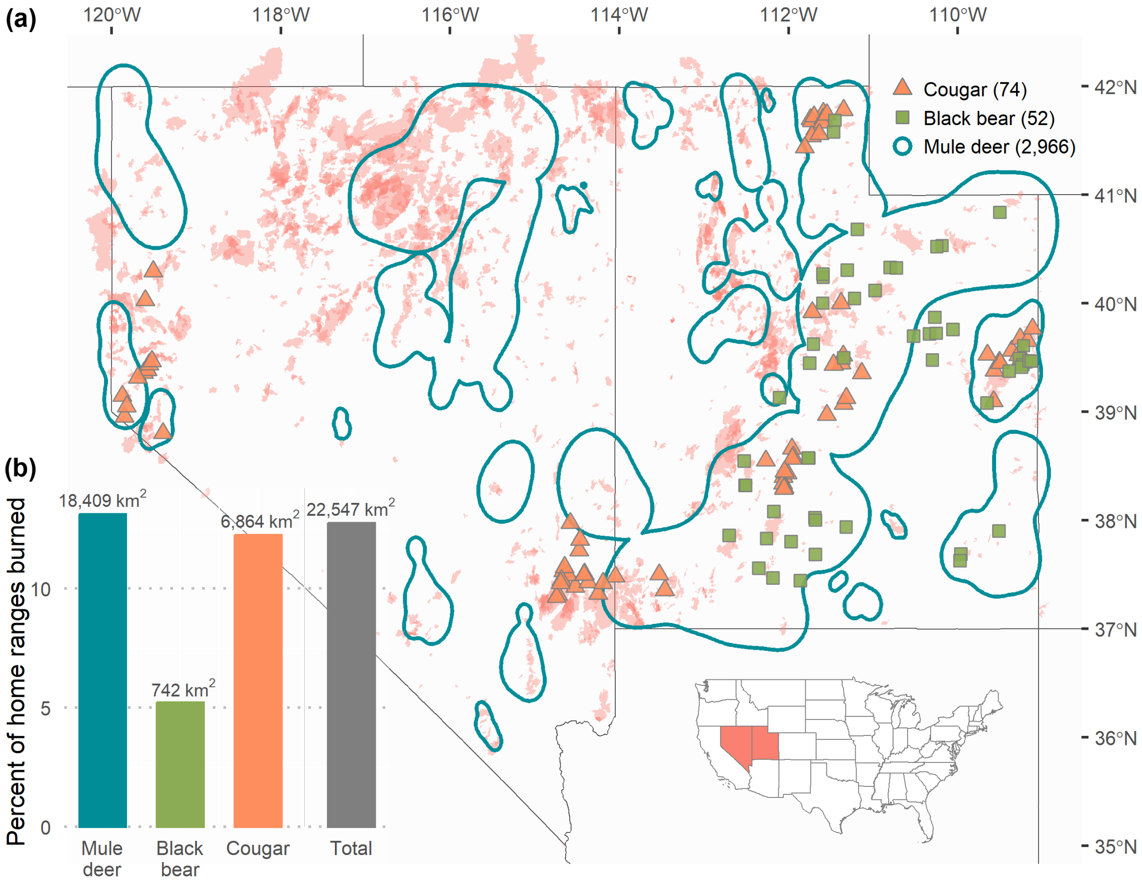

Figure 1. The overlap of burned areas with wildlife telemetry data across the study area in Utah and Nevada, USA. (a) The distribution of collared animals across the study area from 2010–2022. Points represent the 95% home range centroids for collared cougars and black bears (summer HRs for animals collared in summer and winter). Because the mule deer data are too dense to visualize using points, the blue outlined areas represent the distribution of mule deer data generated by estimating the 95% kernel density contours around the centroids of deer home ranges. Parentheses denote the number of individuals collared for each species. The red shaded areas are polygons representing fires in the Monitoring Trends in Burn Severity fire perimeter database since 1990. (b) The proportion (and total area) of wildlife home ranges that were impacted by burns. Proportions and area represent the overlap between the animals' aggregated 95% home ranges and burn data occurring prior to each animal's collaring dates.

are decreasing across the USA, which reduces the ability of landscapes to recover to pre-fire conditions (Turner et al. 2019, Coop et al. 2020). Warming and drying climates in this region are forecasted to worsen in the coming century (Garfin et al. 2013, Seager et al. 2013), which will modify or exacerbate current fire regimes.

We analyzed GPS data collected during early summer (May–July) and winter (December–February), separately, to account for seasonal changes in home range size and environmental conditions. For deer, the summer period encapsulates the last stages of gestation, fawning, and lactation, and the peak of foraging necessary for survival. There is no winter black bear data because of their denning cycle. Seasonal home ranges for each individual animal were delineated using a 95% kernel density estimator in the R package 'adehabitatHR' (www.r-project.org, Calenge 2024). The habitats encompassed by the combined ranges of all the animals were predominantly comprised of shrub/scrub (55.7%), forests (27.5%), and herbaceous (9.8%) land cover types (USGS National Land Cover Dataset; Dewitz 2021), with only 1.5% and 2.4% of their home ranges occurring in developed or agricultural land use types, respectively.

Burn data

We overlaid wildlife location data with the Monitoring Trends in Burn Severity (MTBS) dataset (Eidenshink et al. 2007), which maps fires ≥ 400 ha. Given the large home range sizes and movement capacity for these large mammals, we do not expect the exclusion of small fires to skew our results. To calculate the total area and percentage of species' home ranges previously impacted by burns, we overlaid individual home ranges with burn perimeters. We included only burn extents that occurred before the median year of each individual's data collection. For species-level assessments, we aggregated the home ranges and burned extents for each species.

For habitat selection modeling, we filtered the wildlife movement dataset to only include individuals with 5–95% of their GPS locations in areas that had burned since 1990 and prior to each GPS location's timestamp to enable comparisons in habitat selection between burned vs. unburned habitats. We created a raster surface of burn severity as measured by the composite burn index (CBI, 100 m resolution) within each fire perimeter with Google Earth Engine (Gorelick et al. 2017) sensu Parks et al. (2019). This burn severity method was developed for forested areas where vegetation recovers relatively slowly, and so burn severities measured in more rapidly recovering habitat types (e.g. grasslands) likely produce conservative estimates of fire impacts.

For all GPS locations, we extracted: 1) burn status ('burned' versus 'unburned'), defining whether the location experienced a fire prior to the location timestamp; 2) burn distance, defining the distance in kilometers (km) of the location from the nearest perimeter of a burned area; 3) burn time class, indicating the time since the most recent burn if the location was burned prior to its timestamp, and 4) burn severity, the CBI pixel value of the most recent fire at that location. CBI continuously ranges from 0 (no vegetation change) to 3 (complete vegetation loss), and unburned locations were assigned CBI values of 0. Given wide variation in fire timing across our study animals' sampling periods, with each animal overlapping with ~ 2 burns on average (range: 1–11), burn time class was categorized as 'unburned', 'early successional' (0–9 years post-fire), and 'late successional' (10–30 years post-fire) to account for sample size limitations (Fisher and Wilkinson 2005, Ganz et al. 2022).

Habitat data

We included a suite of habitat characteristics commonly used to measure large mammal habitat selection to control for underlying habitat preferences irrespective of fire impacts. For all GPS locations in the analyses, we extracted elevation (USGS 30 m elevation data) and the terrain ruggedness index (TRI, calculated with the *terrain* function in R package 'terra'; Hijmans 2025), as well as the following dynamic habitat characteristics that vary over time: 1) annual aboveground biomass (Sexton et al. 2013, 30 m resolution, see the Supporting information), generally representative of habitat structure and cover; 2) the normalized difference vegetation index (NDVI) for summer GPS locations; and 3) the normalized difference snow index (NDSI, representing the likelihood of snow cover; Hall et al. 1995) for winter locations to represent forage availability, movement impedance, and other seasonal factors. NDVI and NDSI were derived from 500 m, daily resolution imagery from MODIS (MCD43A4 ver. 6.1). We also included the log-distance to the nearest road based on the USGS National Transportation Dataset to account for anthropogenic impacts on wildlife habitat selection.

Habitat selection and quality

We fit resource selection functions (RSFs) and step-selection functions (SSFs) to evaluate home range habitat quality and fine-scale habitat selection, respectively, for individuals with sufficient GPS data to compare use of burned and unburned areas.

RSFs are logistic regression models that compare relative resource selection between used and available locations within home ranges. Available locations for RSFs were randomly generated across each animal's 95% home range (excluding open water) at a density of 20 per km^2 (mean = 4 points per used location) and were assigned a timestamp sampled from the corresponding animal's GPS data, ensuring that we effectively sampled dynamic habitat characteristics (NDVI, NDSI, biomass) over space and time.

SSFs are conditional logistic regression models that compare relative resource selection between used and available locations at each movement 'step', a set of used and random available end locations from a given starting location. We generated 10 available locations per step sampled from the empirical distributions of step lengths and turning angles for an individual's movement steps (Thurfjell et al. 2014, Avgar et al. 2016, Signer et al. 2019).

The different scales in availability compared to used locations in the two model types allows us to distinguish landscape-level habitat associations from behavioral responses to local habitat features. Thus, we interpret the RSF coefficients as broad-scale preferences that reflect overall habitat quality across an individual's home range, whereas SSF coefficients capture fine-scale selection associated with movement decisions. GPS data were filtered based on sample sizes to limit poor model fits, and the requirements for an individual's inclusion in each model type are outlined in the Supporting information.

In the RSFs and SSFs, we investigated the effects of burn characteristics on habitat selection by creating global models that included fixed linear effects of scaled habitat characteristics and the burn-related variables described below. RSFs additionally included a quadratic term for the effect of elevation. We included the fixed effect of burn time class (reference class: unburned) to evaluate overall selection for burned habitats. To assess selection relative to burn perimeters, we included the interaction between burn status and distance to burn edge, producing separate coefficients for response to distance to the burn perimeter for locations inside and outside of the burned area. We also used an interaction between burn severity and burn time class to assess the combined effects of burn severity and ecosystem recovery, resulting in model coefficients representing selection for varying levels of burn severity within burn perimeters at early and late successional time periods.

Unconverged models and those with poor fit were removed from the final model sets (see Supporting information for more details). All continuous variables were evaluated for collinearity (correlation < 0.7) and scaled across the entire dataset (mean = 0, SD = 1) to enable comparisons of effects among variables. To assess the population-level effects of burned habitats on habitat selection, we used a non-parametric bootstrap with 19 999 iterations to calculate the median SSF and RSF model coefficients ($\tilde{\beta}$) with 95% confidence intervals (CIs) per species and season.

Burn effects on home range habitat quality

We evaluated the overall impacts of burns on wildlife habitat quality by using the individual RSF model coefficients to predict the relative probability of selection per pixel (habitat quality, 100 m resolution) within an animal's 95% home range under two scenarios: 1) 'real-burn' conditions represented by fire metric variables, and 2) 'unburned' conditions in which the fire layers were manually transformed to represent 'unburned' classifications for each fire metric variable (e.g. burn status = 'unburned'; burn severity = 0), thereby nullifying the effects of those variables in the habitat quality predictions (Fig. 2). In 'unburned' scenarios, values for distance to burn were set to the median value for the individual's dataset inside and outside of the burned area. Because we cannot predict values of NDVI, NDSI, or biomass in a scenario where a burned area was never burned, all non-fire habitat variables were held constant between the two scenarios. Thus, a pixel in a previously burned habitat has the same NDVI value in the 'real-burn' and 'unburned' scenarios, but the burn-related variables differ. To populate the scenario landscapes, all habitat variables were extracted from the original data sources for the median survey year for a given individual, representing the habitat at the time corresponding to the GPS data collection and RSF model.

We then calculated the per pixel difference in habitat selection probabilities between the 'real-burn' and 'unburned' scenarios. Within the area of an individual's home range intersecting with each burn polygon, we extracted the median pixel value of the difference surface. The extracted value of RSF difference for each burn/animal combination is termed here as the median quality difference (MQD), which represented the change in habitat quality due to burns, and is used as the response variable in the subsequent modeling analyses (Fig. 2). Because non-fire habitat values were not changed between scenarios, we accounted for the additive effects of underlying habitat characteristics and therefore assumed that difference between scenarios represents the marginal effects of burns on habitat selection. We evaluated population-level averages of burn-induced changes to habitat quality (MQD) using intercept-only (representing the population mean) linear mixed effects models that included random effects of animal ID and study area.

We evaluated how MQD was influenced by burn characteristics and habitat types using global generalized additive mixed-effects models (GAMM), with MQD as the response variable and random effects for animal ID and study area. The models included fixed effects for habitat type and smoother terms for burn severity, years since the burn, and log-transformed area burned (km^2) by the fire within the home range. Additional details on calculating MQD and the modeling approach are available in the Supporting information.

Prescribed burns versus wildfires

Because prescribed fires are an increasingly common management approach to improve wildlife habitat, we compared the effects of prescribed burns and wildfires on RSF-derived MQD using a linear mixed effects model for each species and season that included a fixed effect of fire type and a random effect of study area. We also used t-tests to compare average burn severity (median CBI pixel) and size (log-km^2) between wildfires (n = 755) and prescribed burns (n = 35) for all fires that intersected with wildlife habitat in our analyses.

Results

The home ranges used by 3092 mule deer (n = 2966), black bears (n = 52) and cougars (n = 74) overlapped with habitats previously burned by 807 fires from 1991 to 2020 (Fig. 1a). These burns ranged widely in both area (1.6 km^2 to 2296.2 km^2, median = 14.0 km^2) and severity as measured by the median value of CBI within the burn perimeter (0.001–2.87, median = 1.07) (Supporting information). The total home range area of the three species covered 176 670.5 km^2, of which 22 546.5 km^2 (12.8%) had been burned between 1991 and the time represented by that animals' home range (Fig. 1b). In summer, burns impacted 11.9% (16 458.0 km^2) of the total summer home range area (138 243.1 km^2) of all three species. Over 60% (1892 out of 3092) of individual home ranges overlapped burned areas (54.6% or 1605 animals for summer home ranges, 47.6% or 1,370 for winter).

The largest proportion of burned habitat occurred in mule deer home ranges (18 409.0 km^2, 13.1%), with a similar proportion for cougars (6863.9 km^2, 12.3%) but much lower for black bears (741.6 km^2, 5.2%) (Fig. 1b). Cougars were most likely to overlap with burned habitat, likely because of their much larger home ranges; 85.1% of collared cougars overlapped with at least one previous burn, compared to 63.5% of black bears and 60.6% of mule deer.

Home range habitat quality

We created RSFs evaluating population-level burn impacts on home range-scale habitat selection for 664 mule deer, 13 black bears, and 38 cougars. All three species showed positive habitat selection for higher NDVI locations and those farther from roads, though responses were more varied among species and seasons for habitat characteristics such as TRI and biomass (Supporting information).

Mule deer ($\tilde{\beta}_{\text{early}} = -1.44$, 95%CI: −2.07, −0.54) and black bears ($\tilde{\beta}_{\text{early}} = -0.52$, 95%CI: −0.86, −0.26) avoided burned areas in early successional stages (burned 0–9 years ago) within their home ranges in the summer. In contrast, cougars selected habitats in late successional stages (burned 10–30 years ago; $\tilde{\beta}_{\text{late}} = 2.70$, 95%CI: 0.82, 3.19) during the winter. Across remaining seasons and fire time class combinations, the three species did not show significant responses to burned versus unburned habitats (Supporting information).

During summer within early succession burned habitats, black bear avoided areas with higher burn severity ($\tilde{\beta}_{\text{CBI:early}} = -0.24$, 95%CI: −0.73, −0.07). Cougars selected lower severity burn locations in late succession burned habitats within their summer home ranges ($\tilde{\beta}_{\text{CBI:late}} = -0.30$, 95%CI: −0.49, −0.003), whereas mule deer were less responsive to burn severity at either time scale. In winter, cougars and mule deer both selected less severely burned locations when in more recently burned habitats (mule deer $\tilde{\beta}_{\text{CBI:early}} = -0.34$, 95%CI: −0.49, −0.14; cougar $\tilde{\beta}_{\text{CBI:early}} = -0.62$, 95%CI: −0. 97, −0.32).

Burn effects on habitat quality

On average, burned areas had higher habitat quality compared to their expected quality in hypothetical unburned

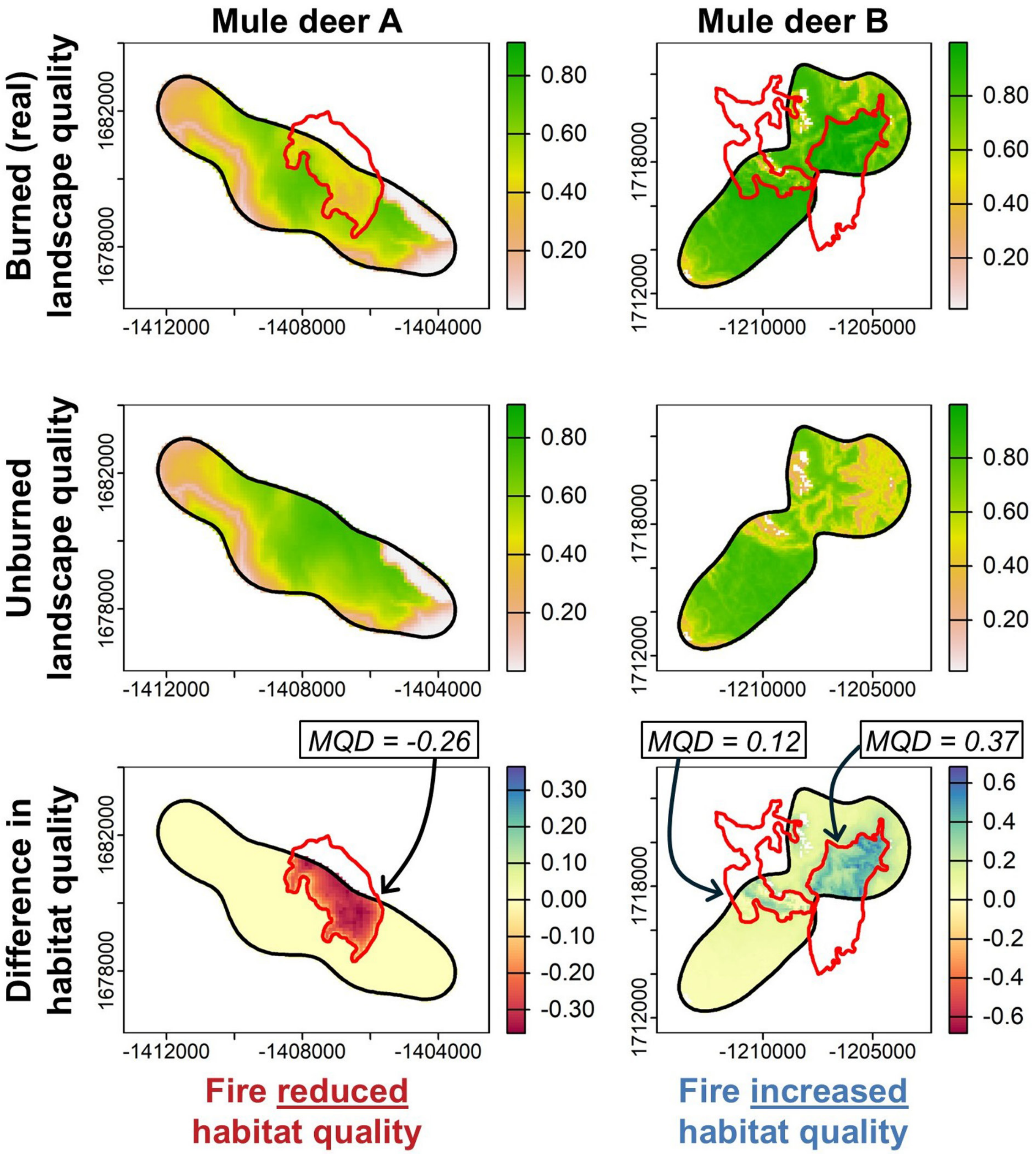

Figure 2. Examples of habitat quality surfaces produced by resource selection function (RSF) models for two mule deer in southern Utah in 'real-burn' versus 'unburned' scenarios. Black outlines show the mule deer 95% home range and red outlines delineate fire perimeters. Top row: real habitat scenario predicted quality, given current (time frame of collar data/RSF model) habitat conditions (normalized difference vegetation index, biomass, etc.) and burn data. Middle row: hypothetical 'unburned' habitat scenario predicted quality, given current environmental conditions but no burn present on the landscape (composite burn index = 0, burned categories = 'unburned', and distance to burn = constant held at median value in animal's dataset). Bottom row: difference in predicted quality between real and 'unburned' habitat surfaces, representing the contribution of fire-specific variables to predicted habitat quality within the burned area. Negative values (red within the burn perimeter in Mule deer A) indicate the burn reduced quality more than expected given current habitat conditions and positive values (blue within the burn perimeter in Mule deer B) indicate the burn improved habitat quality.

landscapes for mule deer ($\overline{\text{MQD}} = 0.07$, 95%CI: 0.02, 0.12) and black bears ($\overline{\text{MQD}} = 0.14$, 95%CI: 0.01, 0.28) in summer (Fig. 2). Burns did not significantly change habitat quality for cougars in the summer ($\overline{\text{MQD}} = -0.03$, 95%CI: −0.15, 0.10) or winter ($\overline{\text{MQD}} = -0.03$, 95%CI: −0.12, 0.07), nor mule deer in the winter ($\overline{\text{MQD}} = -0.01$, 95%CI: −0.07, 0.04).

Across species, heterogeneity in MQD was most commonly explained by the time since a fire occurred (Fig. 3a, Supporting information). Both cougars (EDF = 1.00, F = 5.32, p-value = 0.03) and black bears (EDF = 1.00, F = 6.26, p-value = 0.04) experienced linear decreases in habitat quality as the time since a burn increased on summer ranges, while mule deer habitat quality was reduced by early successional burns on winter ranges (EDF = 1.60, F = 7.78, p-value = 0.004). Mule deer habitat quality was most strongly reduced by fires that burned larger areas of a deer's summer home range (EDF = 1.88, F = 7.22, p-value = 0.002), with burn size leading to negative effects at a threshold area of approximately 16 km^2; however, a nearly significant effect of burn area on mule deer MQD in the winter suggested large fires were more beneficial (EDF = 1.37, F = 2.01, p-value = 0.09) (Fig. 3a). Additionally, we detected a marginal negative effect of burn severity on mule deer MQD in the winter (EDF = 1.66, F = 2.50, p-value = 0.052).

After accounting for burn characteristics, the average effect of burns on mule deer habitat quality was dependent on a deer's predominantly used habitat type (Fig. 3b, Supporting information). Mule deer occupying forested (β = 0.08, 95%CI: 0.01, 0.15) and herbaceous (β = 0.20, 95%CI: 0.07, 0.32) habitats in the summer experienced average increases in habitat quality (MQD > 0), while those in shrub/scrub habitat did not (β = 0.04, 95%CI: −0.02, 0.10). MQD for mule deer in the winter and cougars year-round was not significantly influenced by habitat type.

Prescribed burns versus wildfires

The type of burn had significant effects on mule deer MQD in both summer and winter, but did not affect cougar or black bear MQD. Mule deer habitat quality values increased more with prescribed burns relative to wildfires in the summer ($\beta_{prescribed}$ = 0.10, 95%CI: 0.004, 0.20), but was somewhat lower for prescribed burns in the winter ($\beta_{prescribed}$ = −0.25, 95%CI: −0.51, 0.01) (Fig. 4a). Across our dataset of burn perimeters, we found that prescribed burns were smaller on average than wildfires (t = −6.74, df = 43.34, p-value < 0.01), but not lower in severity (t = −0.88, df = 38.17, p-value = 0.38) (Fig. 4b). Prescribed burns mostly occurred in forested areas (57% of prescribed fires), whereas wildfires occurred most often in herbaceous (67% of wildfires) and shrub (22% of wildfires) habitats where severity is likely to be underestimated.

Fine-scale habitat selection

SSFs for 688 mule deer, 14 black bears, and 11 cougars showed that avoidance of burned areas was strongest at lower trophic levels (Fig. 5a). All species also generally selected locations with higher values of NDVI, biomass, and distance to roads (Supporting information).

In the summer, mule deer ($\tilde{\beta}_{early}$ = −0.52, 95%CI: −0.86, −0.26) and black bears ($\tilde{\beta}_{early}$ = −0.50, 95%CI: −1.41,

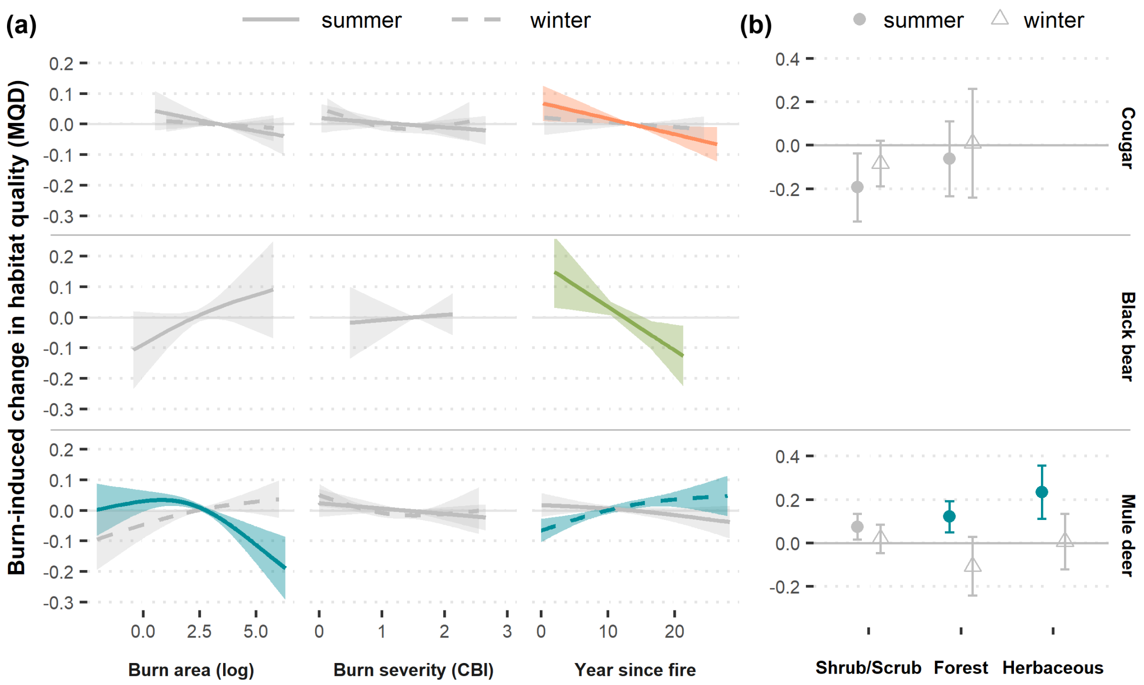

Figure 3. For each of the three focal species (cougar [top row], black bear [middle row], mule deer [bottom row]), the influence of burn characteristics and habitat type on the median quality difference (MQD) in Utah and Nevada, USA, from 2010–2022. MQD is derived from comparisons of burned and hypothetical unburned landscapes for fire/home range overlap areas, predicted by generalized additive mixed effects models. Values less than 0 indicated fire reduced habitat quality and values greater than 0 indicate fire improved habitat quality. Results in color indicate significant model effects (p-value < 0.05). Models were created separately for summer (solid lines, circles) and winter (dashed lines, triangles). (a) Partial effects of burn area, burn severity, and years since fire on MQD. Values on the y-axis represent term contributions to the MQD. (b) MQD by habitat type, with stars denoting significant effects (MQD ≠ 0). A habitat model was not created for black bears because all individuals except one occurred in forested habitat. CBI = composite burn index.

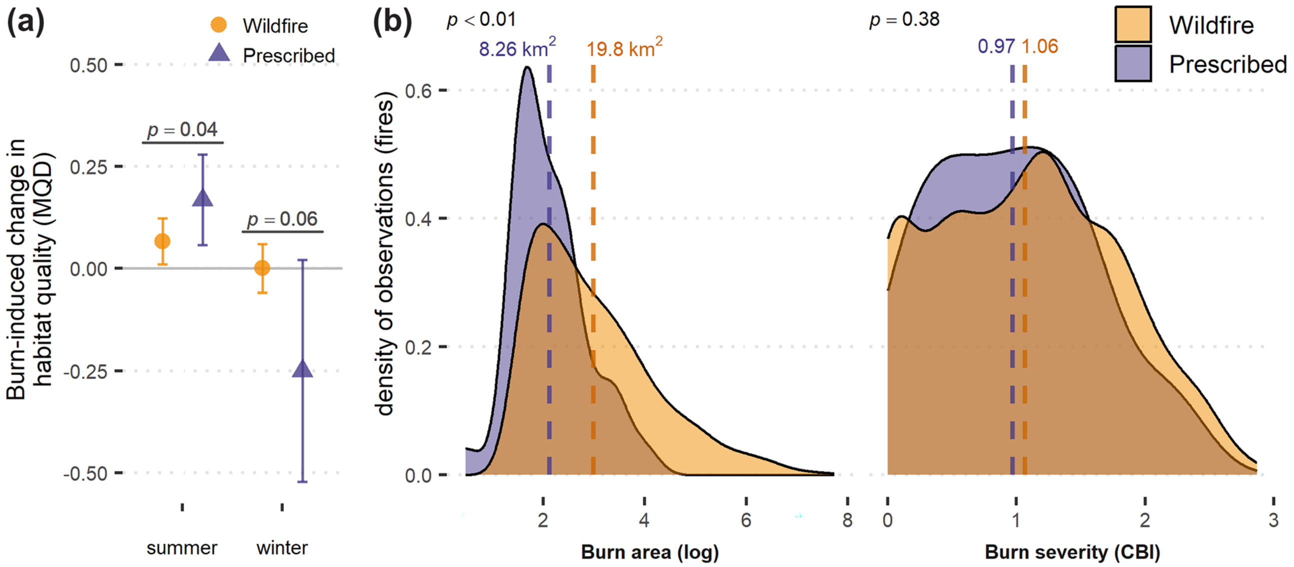

Figure 4. (a) The effects of wildfires versus prescribed burns on mule deer changes in habitat quality due to burns (median quality difference, MQD) in the summer (circles) and winter (triangles) in Utah and Nevada, USA, from 2010–2022. Predicted mean effects with 95% CI and p-values were produced by linear mixed effects models. (b) Comparisons of the distribution of burn size (log-transformed area in square kilometers) and severity (median CBI pixel value per fire) between wildfires and prescribed burns intersecting with GPS data for all mule deer, black bears, and cougars, with p-values representing t-tests evaluating differences in averages between groups. CBI = composite burn index.

−0.14) both avoided areas burned within the last nine years (early successional), with mule deer's avoidance of burns persisting even for late successional burned habitats ($\tilde{\beta}_{\text{late}} = -0.71$, 95%CI: −0.94, −0.41). Mule deer also avoided late successional burned habitats in the winter ($\beta_{\text{late}} = -0.31$, 95%CI: −0.55, −0.12), though they showed no avoidance of early succession habitats in winter. Cougars, however, did not avoid burns, and even selected early successional areas in the summer ($\beta_{\text{early}} = 0.71$, 95%CI: 0.14, 3.43).

When moving in burned areas, all three species generally selected locations with lower burn severity compared to higher severity, regardless of the amount of time since the fire occurred (Fig. 5b). In summer, black bears were least likely to choose a higher severity location for early successional burns ($\tilde{\beta}_{\text{CBI:early}} = -0.19$, 95%CI: −0.41, −0.02) and late successional burns ($\tilde{\beta}_{\text{CBI:late}} = -0.20$, 95%CI: −0.40, −0.04). Cougars showed a similar selection for lower burn severity for both early ($\tilde{\beta}_{\text{CBI:early}} = -0.18$, 95%CI: −0.24, −0.06) and late successional burns ($\tilde{\beta}_{\text{CBI:late}} = -0.23$, 95%CI: −0.52, −0.09). Mule deer, however, did not respond to burn severity during the summer, with similar responses between early ($\beta_{\text{CBI:early}} = -0.05$, 95%CI: −0.09, 0.002) and late successional burns($\beta_{\text{CBI:late}} = -0.02$, 95%CI: −0.07, 0.01).

Mule deer avoided moving towards high-severity burn areas more strongly in winter, particularly for more recently burned locations ($\beta_{\text{CBI:early}} = -0.22$, 95%CI: −0. 31, −0.15; $\tilde{\beta}_{\text{CBI:late}} = -0.09$, 95%CI: −0.14, −0.03). Cougars overlapping with older burns, however, failed to show a pattern in winter responses to burn severity ($\tilde{\beta}_{\text{CBI:late}} = -0.24$, 95%CI: −0.66, 0.35), driven by diverse responses for each of the four cougars with winter data. The only cougar to interact with an early successional burn in winter showed no response to severity ($\beta_{\text{CBI:early}} = -0.03$, 95%CI: −0.15, 0.09). Species-level responses to distance to burn edges are reported in the Supporting information.

Discussion

With nearly 23 000 km² of burned habitat in the home ranges of mule deer, black bears and cougars across our study region, our findings demonstrate the pervasiveness of burned areas in wildlife habitats across several ecoregions of Western North America. Burns overlapped with the home ranges of almost two-thirds of animals in our study, but none of our study species experienced a reduction in habitat quality in burned areas. Rather, burns led to improved habitat quality on average for mule deer and black bears, whose diets are directly reliant on vegetation productivity and palatability. Our findings corroborate reports of the benefits of burned habitats for herbivore foraging opportunities at a regional scale (White et al. 2023, Forney and Peacock 2024, Snobl et al. 2024).

Despite this overall positive effect, the effects of burns on mule deer habitat quality declined drastically when burns reached over 16 km² (Fig. 3a). Large fires likely have a homogenizing effect on landscape habitat structure, and avoidance of these aligns with mule deer preference for heterogeneous habitats that provide improved foraging opportunities and more complex vegetation structure that can be

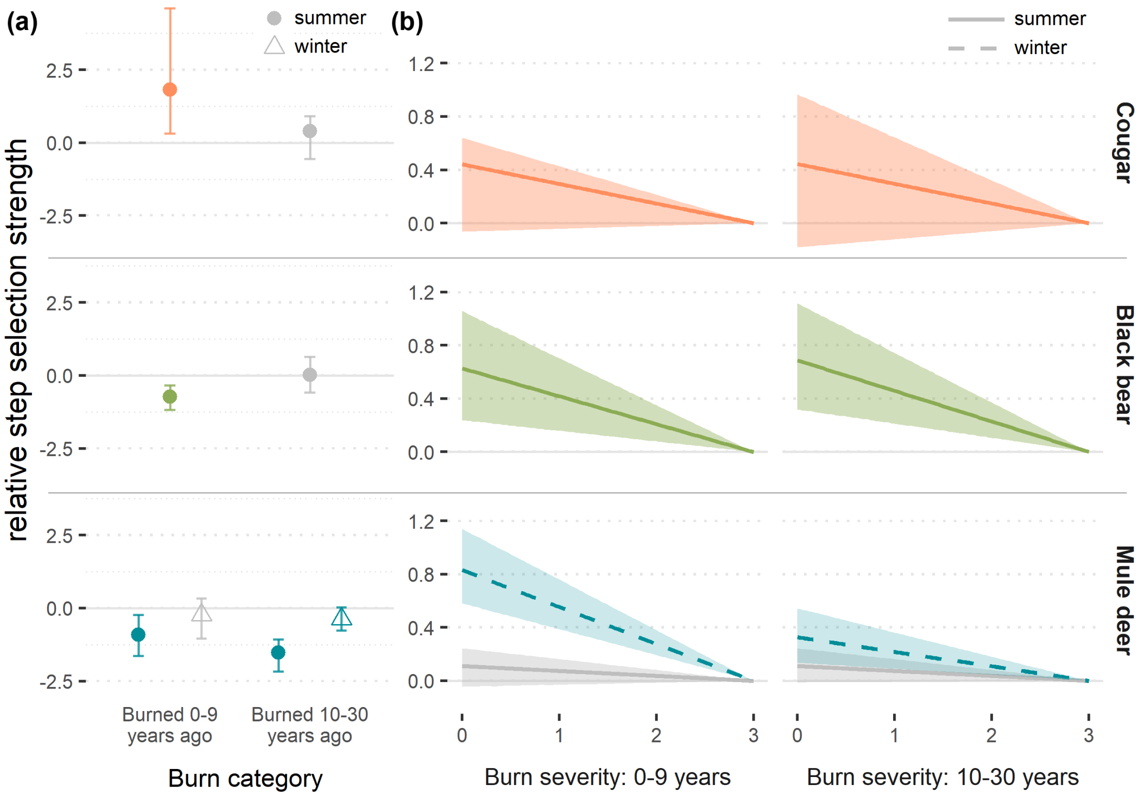

Figure 5. Integrated step-selection model results for cougars (top row), black bears (middle row), and mule deer (bottom row) in Utah and Nevada, USA, from 2010–2022 revealing how burned areas affect fine-scale habitat selection. All y-axis values represent bootstrapped median and 95% CIs of SSF model-predicted log-odds of habitat selection relative to reference locations. Results in color (not gray) represent significant effects based on 95% CIs of population-level model coefficients. (a) Relative selection for habitats burned < 9 years prior and 10–30 years prior, relative to unburned habitats. (b) Relative selection in response to burn severity (measured by composite burn index) given an individual is within a fire. We present results for animal responses in summer (solid lines, circles) and winter (dashed lines, triangles). Log-odds values of selection are relative to an alternative movement step endpoint for which burn severity = 3. Cougar results for winter models were excluded from plot due to low sample sizes (n = 4 cougars) and wide confidence intervals, but all results were non-significant.

used to conceal fawns from predators or provide thermal cover (Kie et al. 2002, Bond and Keeley 2005, Smit et al. 2010, White et al. 2023). A functional response to burned habitats, in which mule deer avoid burns more strongly when burns are larger, could explain the observed population-level avoidance of burned habitats at finer spatiotemporal scales (Fig. 5a). Although fires improved mule deer habitats overall, avoidance at fine scales signals short-term disadvantages to using burned habitats (Signer et al. 2019). In our study, habitats were burned an average of ~ 12 years prior to mule deer use and had likely experienced substantial regrowth, which simultaneously increases foraging opportunities and predation risks from ambush predators (Cherry et al. 2017, Lendrum et al. 2018). Our results suggest that mule deer avoid this amplified predation risk in regenerating burned areas, though they may benefit from access to burns that improve foraging and concealment. Yet this balance shifts to reduce overall habitat quality when burns constitute a large portion of their habitat and preferred unburned areas are less available.

Unlike mule deer, cougars and black bears experienced increases in habitat quality in early successional burned habitats (Fig. 3a). Early vegetation regeneration quickly supports new growth post-fire, particularly in forests, offering foraging opportunities and cover for wildlife (Allred et al. 2011, Proffitt et al. 2019, Zong and Tian 2022). Specifically, post-disturbance landscapes can have increased fruit production for black bears (Brodeur et al. 2008) and attract herbivore prey that in turn increases cougar use (Allred et al. 2011, Smith et al. 2019, Puig-Gironès and Pons 2020, Miritis et al. 2024). However, cougar habitat quality was the least impacted by burns in our study, both in terms of burns' overall effect on cougar habitat quality and the effects of fire characteristics (Fig. 3a). As fires most directly impact the primary producers, it's unsurprising that the effects of fire are strongest for herbivores and attenuate at higher trophic levels (Bowman et al. 2016, Bardales et al. 2024). However, limited sample sizes for cougars and black bears impeded our ability to precisely detect their responses to burned habitats. Thus, higher trophic levels may be more affected by burned habitats than our findings indicate, though it is possible they are simply less responsive to burns.

Our results provide insight into potential mechanisms by which burned habitats modulate predator–prey interactions. We observed notable differences in the responses of mule deer, the key prey species for cougars in this region (Pierce et al. 1999, Stoner et al. 2018), to burned habitats between summer and winter. In the winter, mule deer habitat quality was lower in early successional habitat (Fig. 3a) and mule deer avoided high-severity burns when compared to summer (Fig. 5b), which is similar to findings in Ganz et al. (2022). This could be a result of loss of thermal cover and increased snow accumulation, which increases energetic costs and predation risks, where severe burns have removed vegetation cover (Parker et al. 1984). Although we did not explicitly examine joint responses, cougar and mule deer habitat use in burned areas is likely shaped by complex relationships between vegetation changes and each other's responses to fire.

Our findings of improved habitat quality following prescribed burns, but not wildfires, for mule deer align with recent findings that suggest prescribed burns benefit herbivore habitat quality in the summer (Fig. 4a) (Roerick et al. 2019). This is particularly crucial information for large mammal conservation in the Western United States as land management agencies scale up use of fuel treatments to counter changing fire regimes (USDA Forest Service 2022, US Bureau of Land Management 2024). Wildfires are typically much larger than prescribed burns (Fig. 4b; Fernandes 2015), which could be driving the reduced mule deer habitat quality in wildfires relative to prescribed burns given our finding that large fires reduce mule deer habitat quality. Our results also support evidence that prescribed burns increase forage nutrition for ungulates (Hobbs and Spowart 1984) and have been linked to longer-term benefits of cover and forage opportunities (Andrus et al. 2021); including for omnivores such as bears (Stratman and Pelton 2007). Prescribed burns could therefore aid U.S. management agencies addressing mule deer population declines due to habitat loss, degradation from land development, or plant community succession (Johnson et al. 2017, Morano et al. 2019, Murphy et al. 2023). Future studies leveraging quasi-experimental burn treatments could further quantify the relative benefits of wildfires and prescribed burns, improving on our limited sample size of prescribed burns, as well as fitness benefits for mammal species at higher trophic levels.

Although burns largely led to improved habitat quality, we also found that all three species consistently avoided high-severity locations within burned areas (Fig. 5b). Low-severity burns promote new growth of palatable, herbaceous species without altering basic habitat structure (e.g. most woody plants survive the burn), whereas high-severity burns reduce woody vegetation, change plant species dominance, alter habitat structure, and sterilize soils (Stephens et al. 2021, Hayes et al. 2022, Weeks et al. 2023). Detrimental effects of severely burned areas have been documented for large mammals elsewhere (Bardales et al. 2024), including cougars in southern California (Blakey et al. 2022), black bears in Arizona (Crabb et al. 2022), and deer in northern California (Kreling et al. 2021). The potential fitness consequences for primary consumers foraging in severely burned areas may help explain mule deer and black bear avoidance of burned areas. Our results suggest that severely burned areas may present diminished foraging opportunities, increased predation risks to neonates, or reductions in other preferred habitat characteristics.

However, some wildlife communities may be more resilient to severe fires, including other generalist species such as coyotes *Canis latrans* and racoons *Procyon lotor* (Calhoun et al. 2023). Though mule deer showed population-level avoidance of burns at fine scales, there was wide variation in individual mule deer responses to burns. Some studies show positive effects of burn severity on mule deer habitat use, generally after vegetation recovers to optimal foraging levels or when burns improved visibility, reducing predation risks (Bristow et al. 2020, Calhoun et al. 2024). However, these effects are mostly observed over short time-scales post-fire (< 2 years) relative to the time scales represented in our data. Omnivores and carnivores can also display positive responses to high-severity burns, increasing in both habitat use and diversity (Furnas et al. 2022, Lewis et al. 2022). More studies are needed to further examine how the combinations of species and burn characteristics can lead to improved habitat quality for as many species as possible, as well as to assess body condition, reproductive fitness, and overall population impacts of animals living in fire-impacted areas.

As climate change and human impacts increase the severity and frequency of fires around the world (Barbero et al. 2015, Ellis et al. 2022, Hantson et al. 2022), our findings provide evidence of how three habitat generalists respond to the multifaceted impacts of fire across broad spatiotemporal extents. We highlight the pervasiveness of burned habitats across mule deer, black bear, and cougar ranges and the mixed consequences of this increasingly common and influential disturbance. While low-severity burns appear to promote habitat quality for herbivorous species, the increase in high-severity fires in the American West could lead to fine-scale avoidance of burned habitats across trophic levels. Prescribed burns can reduce severe fire risks while promoting pyrodiversity that improves habitat for large mammals and other wildlife (Jones and Tingley 2022, Steel et al. 2024, Brodie et al. 2024). Although large mammals may generally benefit from fires, there remains a crucial need to understand and manage the impacts of increasingly severe wildfires that could lead to long term reductions in habitat quality (González et al. 2022, Bardales et al. 2024).

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fqz612k4d (Mills et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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