



Fire disturbance and severity shape Canada lynx behavior: fine-scale movements and unburned island refugia

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Abstract

Context Increased fire frequency and severity in subalpine forests causes uncertainty regarding how forest-dependent species may respond to fire-disturbed landscapes relative to burn heterogeneity and severity.

Objectives We tested individual-level habitat-use response of Canada lynx to fire severity, heterogeneity, patch characteristics, and unburned island refugia.

Methods We instrumented 22 Canada lynx (27 lynx years, 2018–2020) in the Northern Rocky Mountains, U.S.A. to investigate selection behavior in recent (≤ 3 yrs) fire-impacted landscapes using resource selection (RSF) and integrated step selection models (iSSF), functional response analyses, and hurdle models.

Results Canada lynx increasingly avoided burned landscapes as disturbance became more prevalent within home ranges. At a finer scale (iSSF), lynx

traversing burns selected high post-fire normalized burn ratio (NBR; i.e., low severity), high heterogeneity of severity, and near fire perimeters. Lynx exhibited strong selection for unburned islands, with 22.8% of random locations in islands compared to 42.5% of lynx locations. Lynx traveled an average of 720 m (range: 42–2293 m) inside fire perimeters to access unburned islands. Islands with higher post-fire NBR, lower perimeter to area ratio (simpler shape), and greater surrounding fire heterogeneity were more likely to be used. Snowshoe hares were more abundant in unburned islands in fires compared to controls outside fires.

Conclusions Canada lynx were sensitive to the extent of fire-impacted landscapes in home ranges and to patterns of fire severity and heterogeneity, including their use of unburned islands of fire refugia. Trends of increased fire severity in subalpine forests may reduce habitat suitability for Canada lynx.

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Introduction

Forested ecosystems are being transformed globally (Millar and Stephenson 2015) through complex interactions involving drought, forest utilization, fire, urbanization, insect pathogens, climate, and other

factors (Seidl et al. 2017; Sommerfeld et al. 2018; Biedermann et al. 2019; Steel et al. 2022). Thus, a central challenge at the intersection of conservation biology and landscape ecology is to understand how these accelerated environmental changes impact species' persistence and ecosystem-level biodiversity. The extent to which disturbance impacts biodiversity depends on the life histories and habitat requirements of individual species (Viljur et al. 2022) and community responses. Globally, fire is an ecological process influencing species composition and diversity as well as habitat heterogeneity and structure (Wright and Bailey 1982). However, fire that burns outside the historic range of variation for a particular habitat type may act as a disturbance agent that significantly impacts biodiversity (Fontaine and Kennedy 2012; He et al. 2019) and habitats for specific species (Agee 1993). For example, combinations of fire severity and time since fire occurrence can promote species richness for some avian guilds (Hutto and Patterson 2016), whereas forest-dependent species like spotted owls (*Strix occidentalis*) (Jones et al. 2021) and woodland caribou (*Rangifer tarandus caribou*) (Konkolics et al. 2021; Palm et al. 2022) may experience substantial habitat loss and declines in occupancy and fecundity following fire.

The resilience of forested ecosystems to disturbance depends on ecological memory, which forms through legacies of a system's information (e.g., the combination of species life history traits) and materials (e.g., abiotic attributes and biotic structure) remaining after disturbance (Johnstone et al. 2016). Ecological resilience is reduced if legacies are altered beyond ecological thresholds due to uncharacteristic or novel disturbance patterns. Thus, a current conservation need is to understand how species respond to changes in forest heterogeneity from disturbance, especially given the recent increase in area burned and severity of fire disturbance that can stress ecosystem resilience and associated species assemblages (Abatzoglou and Williams 2016; Parks and Abatzoglou 2020).

Canada lynx (*Lynx canadensis*; interchangeable "lynx") is a mid-sized federally-threatened carnivore under the U.S. Endangered Species Act, evolved to hunt primarily snowshoe hares (*Lepus americanus*) in deep-snow environments (Aubry et al. 2000;

Mowat et al. 2000). Snowshoe hares, in turn, are mostly found in mixed-conifer subalpine forests that provide high horizontal cover (i.e. woody vegetation touching the ground or snow surface) that offers forage and protective cover from predation (Hodges 2000; Ivan et al. 2014, 2018). Species, like lynx and snowshoe hares, that occupy cool, moist subalpine forests are at heightened risk from disturbance given the vulnerability of these forests to climate impacts and increased wildfire (Price et al. 2013; Gauthier et al. 2015; Millar and Stephenson 2015). Paleofire records indicate that subalpine forests in the Southern Rocky Mountains, USA are burning more than at any point in the last 2,000 y and already exceed the variability found in past climate extremes (Higuera et al. 2021). However, despite the sharp increases in fire size and severity, the proportion of unburned area in fires of the northwestern United States between 1984 – 2014 remained relatively unchanged (Meddens et al. 2018a). These unburned patches provide refugia of intact forest vegetation (hereafter "unburned islands") within fire perimeters that provide habitat for species to retreat to, persist in, and/or then expand from following disturbance (Meddens et al. 2018b). In addition, overstories in unburned islands provide seed sources that support forest recovery (Meddens et al. 2018b, a; Sommers and Flannigan 2022). Keystone habitat features, like forest patches of high horizontal cover, also allow a specialist carnivore like Canada lynx to occupy naturally disturbed landscapes (Squires et al. 2022; Olson et al. 2023). Conservation actions that effectively promote species persistence in subalpine forests require nuanced understanding of how gradients of fire severity and characteristics of forest refugia shape resource use and habitat suitability during this period of rapid change.

In this study, we instrumented Canada lynx in recent (≤ 3 y old), large fires with GPS collars to document their habitat selection behavior. We assessed if they generally avoided fire disturbance in home-ranges and how individuals responded to the post-fire landscapes based on the extent of burned areas within home ranges. We predicted that Canada lynx (Squires et al. 2010; Simons-Legaard et al. 2013; Ivan and Shenk 2016) and their primary prey, snowshoe hares (Hodges 2000; Holbrook et al. 2017a) would generally avoid burns given their strong selection for high

horizontal cover which is reduced after recent burns. Next, we evaluated fine-scale selection behavior of Canada lynx to understand how elements of environmental heterogeneity in burns impacted habitat use. Specifically, we tested the prediction that fire severity and patch-level spatial characteristics would be important drivers of lynx movement in burned landscapes. We based our prediction on the knowledge that silviculture treatments, both pre- and post-fire, impact the timing of how lynx use burns (Olson et al. 2023), and that fire severity influences habitat suitability (Vanbianchi et al. 2017). Finally, we evaluated lynx selection behavior for unburned islands in burns, specifically how lynx intensity of island use was influenced by island characteristics including island size, proximity to fire perimeter, and the surrounding fire heterogeneity (i.e., average fire severity around islands). We also sampled the relative abundance of snowshoe hares in both unburned islands and controls to evaluate prey availability as a potential motivation for island use. Based on field observations and previous research (Vanbianchi et al. 2017), we predicted that Canada lynx would preferentially select unburned islands within fire perimeters. Here, we extend this knowledge with nuanced responses of Canada lynx to fire disturbance across severity gradients and unburned island refugia in ways that better inform silvicultural practices and fire management within the conservation context of a federally listed species.

Methods

Study area

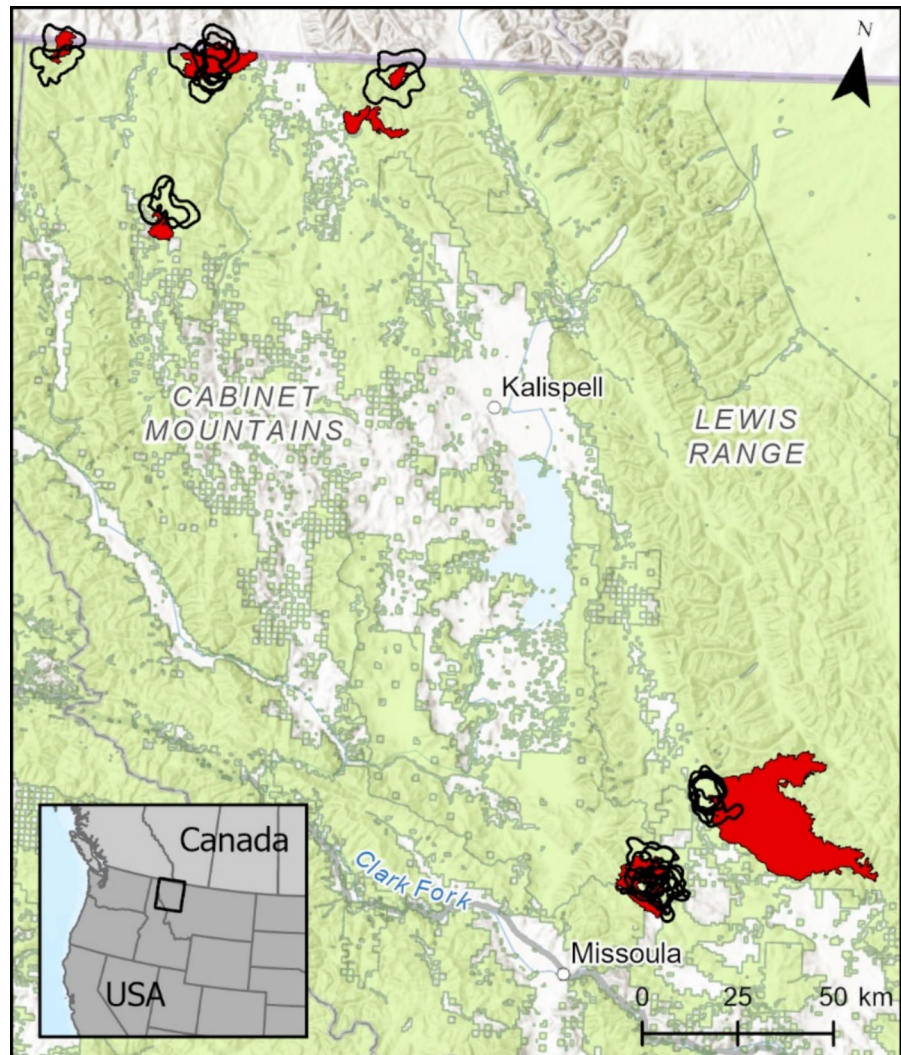
We conducted our study in the occupied range of Canada lynx across the Northern Rocky Mountains (interchangeably “Northern Rockies”) of Montana, USA (Fig. 1) (Squires et al. 2013; Olson et al. 2021). Topography of the Northern Rockies was characterized by steep mountain valleys and high peaks within an elevation range of 550 to 3400 masl. This topographic relief imposed a mosaic of subalpine montane forests interspersed with meadows and avalanche chutes extending to alpine tundra. Generally, forests were mixed conifers that included ponderosa

pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). However, the cool, moist subalpine forests that lynx mostly occupy primarily contained subalpine fir, Engelmann spruce, and lodgepole pine (Squires et al. 2010; Holbrook et al. 2017b). The study area included mostly federal ownerships ($\approx 80\%$) that were managed for multiple uses including recreation, timber production, grazing, wildlife and water management under the Multiple-Use Sustained-Yield Act of 1960, but it was also intermixed with private, state, and tribal lands. The level of human-caused disturbance varied across ownerships from extensive tree harvest on commercial forestry lands to large, protected areas like the Bob Marshall Wilderness complex and Glacier National Park where mechanical harvest was prohibited. Similar to other forests in the western contiguous US (Abatzoglou and Williams 2016; Parks and Abatzoglou 2020), forests across the study area were patterned by large-scale fire disturbance that increased recently, consistent with continued climate change, past management history, and landscape homogeneity. For example, in mapped lynx habitat as defined by Olson et al. (2021), 148 km² of our study areas burned from 1984–1999 compared to 1644 km² in the same areas from 2000–2024. The general climate was characterized by cold winters with deep snow followed by warm dry summers. The study area is ecologically unique within the continental United States in supporting a full complement of mid- and large-sized carnivores including grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), Canada lynx, wolverines (*Gulo gulo*), gray wolves (*Canis lupus*), and coyotes (*Canis latrans*).

GPS (global positioning system) data

From 2018–2020, we captured and collared (TGW-4277–5, Telonics, Mesa, AZ) Canada lynx in and adjacent to the Caribou (2017 ignition, 11,372 ha), Davis (2018, 2874 ha), Liberty (2017, 11,222 ha), Rice Ridge (2017, 69393 ha), and Weasel (2017, 1595 ha) fires. We surveyed for lynx activity inside and adjacent to fire perimeters, and set box traps to

Fig. 1 Map of western Montana, USA, showing lynx home ranges (black outlines) and fire perimeters (red polygons) on public land (green shading). Inset map shows the location of the study area (black square) in the US. Background image credit: ArcGIS software by Esri



target these individuals (Kolbe et al. 2003). We captured 22 individual lynx with 5 of these animals monitored in 2 consecutive years ($N=27$ lynx years). Lynx capture and handling was conducted under the direction of the U.S. Forest Service, Institutional Animal Care and Use Committee (USFS IACUC-2018–5). We collected hourly GPS movement data for lynx from approximately late January through August each year, with collars programmed to drop off individuals in September. Collar fix success rate averaged 93.8% (range: 88.7–97.0%).

Selection behavior – broad and fine-scale

At a broad scale, our first goal was to evaluate the prediction that Canada lynx would exhibit avoidance behavior of fire-impacted landscapes within home-ranges. We used Manly's selection ratio (Manly et al. 2002) as a metric to evaluate selection behavior at this broad scale based on the proportion of used and available locations in and outside fires. We created 95% kernel home ranges with a reference bandwidth for each lynx-year combination using package

‘adehabitatHR’ (Calenge 2006). We counted separately per lynx the number of GPS locations inside versus outside fire perimeters, as determined using Monitoring Trends in Burn Severity (MTBS) fire boundaries (Picotte et al. 2020). We then generated a set of random locations that consisted of 20 times the number of lynx use locations per home range to quantify the proportion inside versus outside the fire. We calculated a selection ratio (proportion of used points in a category/proportion of available points in a category) to evaluate selection or avoidance of fires within home ranges.

Selection of a given resource (or avoidance) can vary depending on how much is available to an individual, especially for disturbance-related predictors that may be tolerable up to a certain threshold (Knopff et al. 2014; Olson et al. 2018). Therefore, we further examined if lynx use of burned areas depended on the amount of burned area within the home range, known as a functional response (Mysterud and Ims 1998; Holbrook et al. 2019a). We tested if lynx use of burns was linearly related to the proportion of fire-impacted landscape in their home ranges using a linear regression model, with the proportion of use as the dependent variable and the proportion of availability as the independent, including each individual in the model as a single data point. We considered statistical deviation from a slope=1 as evidence of a functional response, in that the proportion of fire disturbance in home ranges impacted lynx selection behavior at a broad scale.

To evaluate fine-scale habitat selection of lynx in fires, we performed an integrated step-selection function (iSSF) analysis (Avgar et al. 2016). We used conditional logistic regression to compare used locations, defined by hourly GPS points of lynx on movement paths in burns, to multiple available locations, characterized by empirical step lengths and turn angles. We used the R package ‘amt’ (Signer et al. 2019) to select available locations based on a gamma distribution applied to step lengths and a von Mises distribution applied to turn angles. To ensure adequate sampling of available habitat we selected 20 available locations per use location that we verified as adequate by re-runs of our final models with varying ratios (1 to 20) of used to available locations to confirm that

coefficients were stable (Northrup et al. 2013; Fieberg et al. 2021).

We evaluated fine-scale habitat selection of lynx within fire perimeters using predictors that represented burn severity, fire heterogeneity, distance to fire edge, and patch-level area and/or shape metrics within fires. Predictors were considered at three spatial scales, a 30 m original resolution and two scales generated as neighborhood averages (means for continuous covariates, modes for categorical) at 150 m (50% hourly step distances) and 1 km (90% hourly step distances) radii. We initially considered 32 covariates at our three spatial scales, created from 15 unique covariates within these broad categories (Appendix – Table 4). Since predictors were highly correlated across scales and within categories, we initially ran univariate models for each predictor at each scale. We then ranked univariate models within categories using AIC and kept the single best-performing in each category; there was no model uncertainty within categories, with $\Delta AIC \geq 12$ for all categories (Appendix, Table 4). This resulted in four predictors that we included in the final iSSF model: post-fire NBR (normalized burn ratio), fire heterogeneity using a Shannon Diversity Index (SHDI, (McGarigal et al. 2023)), distance to fire perimeter, and severity patch area. We used post-fire NBR as an index of fire severity based on remotely sensed spectra that related to vegetation condition (Parks et al. (2019)), with higher values of NBR representing lower fire severity. The NBR index provided a valid predictor of fire severity (Escuin et al. 2008), particularly in boreal forest environments (Epting et al. 2005). Fire heterogeneity was measured using SHDI, an index commonly used for biodiversity (Crotteau et al. 2020) and burn heterogeneity (Jones et al. 2020) and which considers the number and area of categories, here defined as MTBS fire severity classes, within a 1 km neighborhood. We calculated SHDI using the formula $-\sum(P_i * \ln P_i)$, where P_i is the proportion of fire severity class i in a given neighborhood, following McGarigal et al. (2023). Distance to fire perimeter was calculated using MTBS wildfire boundaries, with distance equal to 0 at the boundary and then increasing with distance from the boundary inside the burn. Patch area was determined by converting the composite burn index

(CBI) raster associated with the MTBS RAVG (Guay 2011) into like polygons and then calculating the area (m^2).

We then built a global iSSF model composed of the best-performing scale of all four predictors (burn severity, fire heterogeneity, distance to fire edge, and patch-level area) within fires to determine how lynx responded to these specific aspects of wildfires on movement paths as they traversed burns. To consider non-linear relationships, we included quadratic forms of fire severity, fire heterogeneity, severity patch size, and distance to fire edge with inclusion based on likelihood ratio tests ($p \leq 0.05$) (Zuur et al. 2009; Jones et al. 2020). We evaluated a set of 5 candidate models: (1) the global additive model as well as 4 models chosen to address potentially important interactions between fire characteristics, fire severity, and lynx behavior. These interaction hypotheses included: (2) selection for fire characteristics will interact with the availability of a given covariate in a home range; (3) patch size will interact with burn severity because lynx would prefer large patches of low fire severity; (4) fire heterogeneity will interact with severity because greater homogeneity will be favored when fire severity is low; and (5) step length and turn angle will interact with fire covariates, indicating a change in movement patterns depending on fire characteristics.

We followed Muff et al. (2020) and used a generalized linear mixed model with a Poisson distribution and strata (step-ID) included as a random intercept with the variance set arbitrarily large to force estimation similar to fixed-effects parameters. This model parameterization provides a way to fit a mathematical equivalent to a conditional logistic regression model while allowing for the inclusion of random effects for slope and intercept by individual (Muff et al. 2020). We included individual-specific random slopes on each predictor to account for individual variation. We assessed support for the inclusion of these random slopes using a likelihood ratio test of models with the random term to those without. We ranked models by AIC and considered the most parsimonious as the top-performing. We considered individual covariates in the final model significant if the 95% CI of their beta coefficients did not overlap zero.

Selection behavior for unburned islands in fires

We first used a resource selection function (RSF) within fires to test whether lynx exhibited preferential selection for unburned islands in burns. For the sake of repeatability, we used an existing and publicly available dataset to delineate unburned islands, the USFS RAVG (Rapid Assessment of Vegetation Condition After Wildfire) (Guay 2011) composite burn index (CBI). This four-category index was created using remotely sensed pre- and post-fire Landsat imagery and has a category of ‘Unchanged’, corresponding to a $\text{CBI} < 0.1$, which we set as our measure of unburned islands. However, we acknowledge this classification may include fire impacts of low severity in understory vegetation that were undetectable by remotely-sensed imagery. Our sample of forest vegetation in unburned islands (see below; Appendix Table 6) confirmed low fire impacts, but we also acknowledge that islands could be surrounded by gradients of low severity areas. We did not consider islands < 0.4 ha (1 acre) in our analyses, as we deemed these islands too small to support most prey species for lynx. In the RSF analysis, we compared lynx use locations to randomly available locations within lynx home ranges and in fire perimeters at a ratio of 1 to 20. We considered a single covariate, whether a location was in an island or not. Following Muff et al. (2020), we used a generalized linear mixed model with a binomial distribution and random slope for each individual. We weighted used locations with $W=1$ and available locations with $W=1000$, the equivalent of using a very large number of available points to provide a better approximation of the heterogeneous point process likelihood (Muff et al. 2020).

Once we had determined that lynx selectively used islands within fires (See Results – Selection behavior for unburned islands in fires), we focused our analysis on island polygons to determine whether factors related to island quality, shape, or location influenced their intensity of use by lynx. For all islands within fire perimeters and lynx home ranges, we counted the number of lynx locations per island, which we used as our dependent variable. We initially considered 25 covariates at our three spatial scales, created from 19 unique covariates including measures of island shape

(area, perimeter, and area/perimeter ratio), island quality (as indexed by NBR – higher values correlate to lower fire severity), and island surroundings (the average fire severity and heterogeneity surrounding an island) (Appendix Table 5). For island surroundings, we considered similar spatial scales as those used in the iSSF analysis (150 m and 1 km) and took the mean or mode of covariates within this distance of an island. We used hurdle models to explore the relationship between these covariates and lynx use of islands. Hurdle models include two model components, binomial to model use/non-use, and truncated count to model use intensity of counts ≥ 1 ; this model type allows the simultaneous investigation of what factors influence a lynx to use some islands and not others, as well as what factors influence greater use of some islands. We fit hurdle models with the ‘glmmTMB’ package in R, with a negative binomial count model, an offset term of log of island size, and random slopes and intercepts for all covariates to allow them to vary across individual fires. We first considered univariate hurdle models for each of our covariates. We ranked univariate models by AIC and selected all uncorrelated covariates; if two covariates were correlated ($r \geq 0.6$) we selected the one with the lower AIC score (Appendix, Table 5). This resulted in a global model containing 6 covariates: the perimeter to area ratio, a metric which increases with increasing island shape complexity; island perimeter length, a measure of island size; island distance to burn edge; mean post-fire NBR in the island, a metric indicating the vegetation quality, with greater values equal to greater quality (Epting et al. 2005; Escuin et al. 2008); the mean surrounding CBI within 150 m, indicating surrounding burn severity; and the standard deviation of the surrounding composite burn index within 150 m, indicating surrounding burn heterogeneity. We tested the following hypotheses regarding unburned islands using 6 candidate models derived from these 6 covariates, chosen to investigate interactions between fire characteristics: (1) island use is influenced by all covariates additively (Vanbianchi et al. 2017); (2) surrounding heterogeneity interacts with burn severity surrounding the island, since vegetation structure can constrain lynx habitat selection at the southern range periphery (Koehler et al. 2008; Squires et al. 2010; Simons-Legaard et al. 2013; Ivan and Shenk 2016);

(3) island shape complexity mediates distance from a fire edge, since lynx use of burned landscapes is impacted by stand shape (i.e., core area shape, Olson et al. 2023); (4) island size mediates distance from a fire edge, since lynx may prefer larger patches of contiguous forests (Kosterman et al. 2018; Holbrook et al. 2019b); (5) island vegetation quality mediates distance from a fire edge, since lynx prefer habitat with high horizontal cover (Mowat et al. 2000; Holbrook et al. 2017b); and (6) island vegetation quality mediates island shape complexity, given lynx and hare sensitivity to forest structure (Squires et al. 2010; Ivan and Shenk 2016).

Given the prey dependence of Canada lynx on snowshoe hares (Mowat et al. 2000; Squires and Ruggerio 2007; Ivan and Shenk 2016), we hypothesized that hare abundance was an important driver of lynx selection of unburned islands in fire perimeters. We sampled pellet plots to index snowshoe hare relative abundance in unburned islands within burn perimeters and at control locations outside of fires but inside lynx home ranges. Many studies document the positive relationship between pellet counts and relative snowshoe hare abundance (Krebs et al. 1987; Mills et al. 2005; Murray et al. 2005; Hodges and Mills 2008; Berg and Gese 2010). We focused on four fires (Caribou, Liberty, Rice Ridge, Weasel Fires) that had unburned islands of varying sizes, but that were easily accessible. For each fire, we sampled four sites inside unburned islands, and four control sites located outside fire perimeters but within 6 km of each perimeter (average distance from fire perimeter: 1.72 km, range: 0.11 – 5.82 km) and in a lynx home range; a total of 8 sample sites per fire. At each site, we sampled a square grid of 25 pellet plots (5 plots wide $\times$ 5 plots long) spaced 10 m apart and at least 30 m from any island edge. We then counted hare pellets on 1 m² circular plots (Murray et al. 2002); plots were uncleared and represent cumulative hare use over the previous year. At each corner plot of the grid, we also quantified the species, density and diameter at breast height (DBH) of large (> 7.62 cm DBH) and small (< 7.62 cm DBH) trees (> 1.4 m tall) in nested circular plots (large tree radius plots = 5.67 m, small trees plots = 3.59 m).

For analysis we averaged pellet counts across all 25 plots at each of the 32 sampling sites. For each site,

we also calculated large trees per hectare, small trees per hectare, and the basal area of large spruce and fir trees combined. Basal area is a metric of tree density that is weighted by tree size for an improved estimate of site occupancy (Kershaw et al. 2017, p221). We based our covariate selection on known habitat characteristics previously determined to be important to lynx and hares and purposely chose few covariates due to our small sample size of sites. We used a generalized linear mixed model to quantify the effect of site type (control vs island) and vegetation variables to relative hare abundance (i.e. pellet counts) on sites. We used R package ‘glmmTMB’ (Brooks et al. 2017) with a Poisson distribution and included individual fire as a random intercept to control for the dependence of plots within and near the same fire. Since hare use might also depend on factors intrinsic to islands, we ran a second model on a subset of our data including only plots inside islands to test whether island size, distance to fire perimeter, and the density of lynx use an island received (as quantified by the number of lynx GPS locations inside the island divided by island size) was also related to pellet density.

For all models, we standardized covariates for easier model fitting and ease of interpretation by subtracting the mean and dividing by the standard deviation. We assessed model fit using QQ plots and model residuals plotted against predicted values with the R package ‘DHARMA’ (Brooks et al. 2017). We ranked all models by AIC and considered individual coefficients in models significant if their 95% confidence intervals did not overlap 0.

Results

Selection behavior – broad and fine-scale.

The spatial extent of fire disturbance in Canada lynx home ranges varied from 10 to 78% of home range area. Of lynx monitored (N=22), 6 individuals (27%, 5 males, 1 female) abandoned their winter (January – April) home ranges during the monitoring period; the median proportion of area burned in these abandoned home ranges was 49.5% (range: 10.7–69.8%). An additional female lynx engaged in 2 exploratory movements outside her home range, before

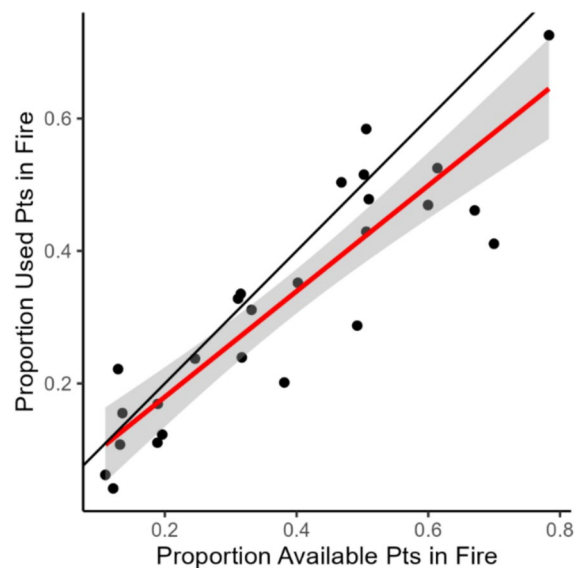


Fig. 2 Functional response of Canada lynx to the proportion of burned area used versus available within home ranges ($\beta=0.798$, 95% CI: 0.63–0.97); black line indicates use in proportion to availability, red line indicates modeled slope of lynx use, black dots represent individual lynx. Canada lynx used fire-impacted landscapes in proportion to availability when burn spatial overlap within home ranges was low, but avoidance behavior increased as fire-impacted area increased in home ranges

succumbing to mortality from unknown causes on return to her original territory.

At the individual level, Canada lynx validated our prediction by exhibiting avoidance behavior to recent fires (≤ 3 yrs post-disturbance) at the home-range scale (Selection Ratio W_i in fires: 0.86 [95% CI: 0.77–0.96] compared to out of fires: 1.08 [95% CI: 1.02–1.14]). Thus, Canada lynx generally used areas outside but often adjacent to fire perimeters. However, Canada lynx also exhibited high individual variation in their use of recently burned areas at the home-range scale, with 7 individuals using burns in slightly greater proportion than availability (Selection Ratio > 1 ; Fig. 2). Canada lynx also exhibited a functional response to fire disturbance ($\beta=0.798$, 95% CI: 0.63–0.97; Fig. 2). Lynx increasingly avoided fire-impacted landscapes as burned areas became more prevalent within home ranges. When lynx used burned landscapes within fire perimeters, they selected areas of unburned and low fire severity

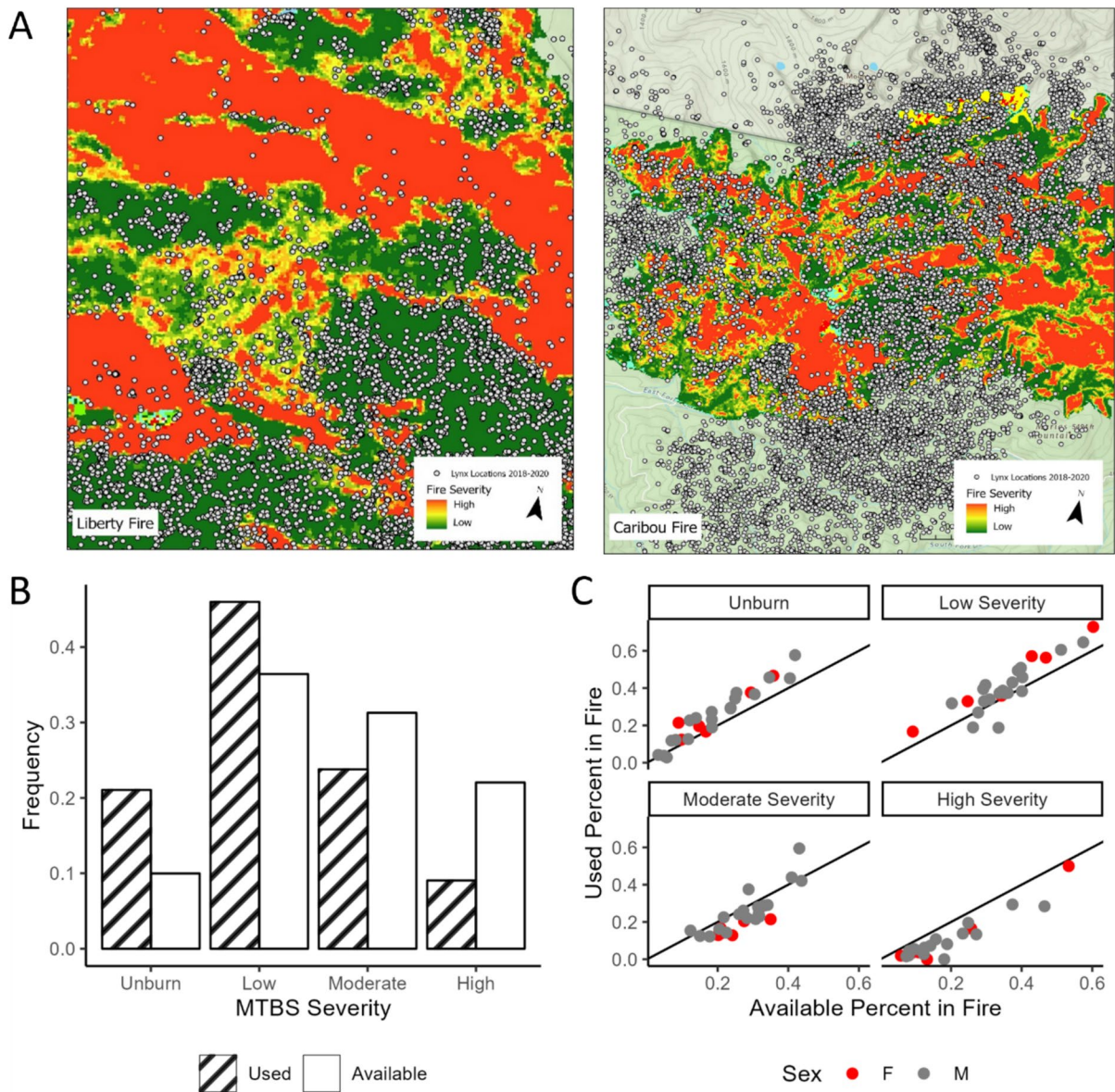


Fig. 3 Response of Canada lynx to gradients of fire severity. Panel A) landscape perspective illustrating selection behavior (GPS locations) of lynx for unburned patches or low severity fire in recent (≤ 3 yrs post-disturbance) burns, Northern Rocky Mountains, Montana, USA; Panel B) Frequency of lynx use

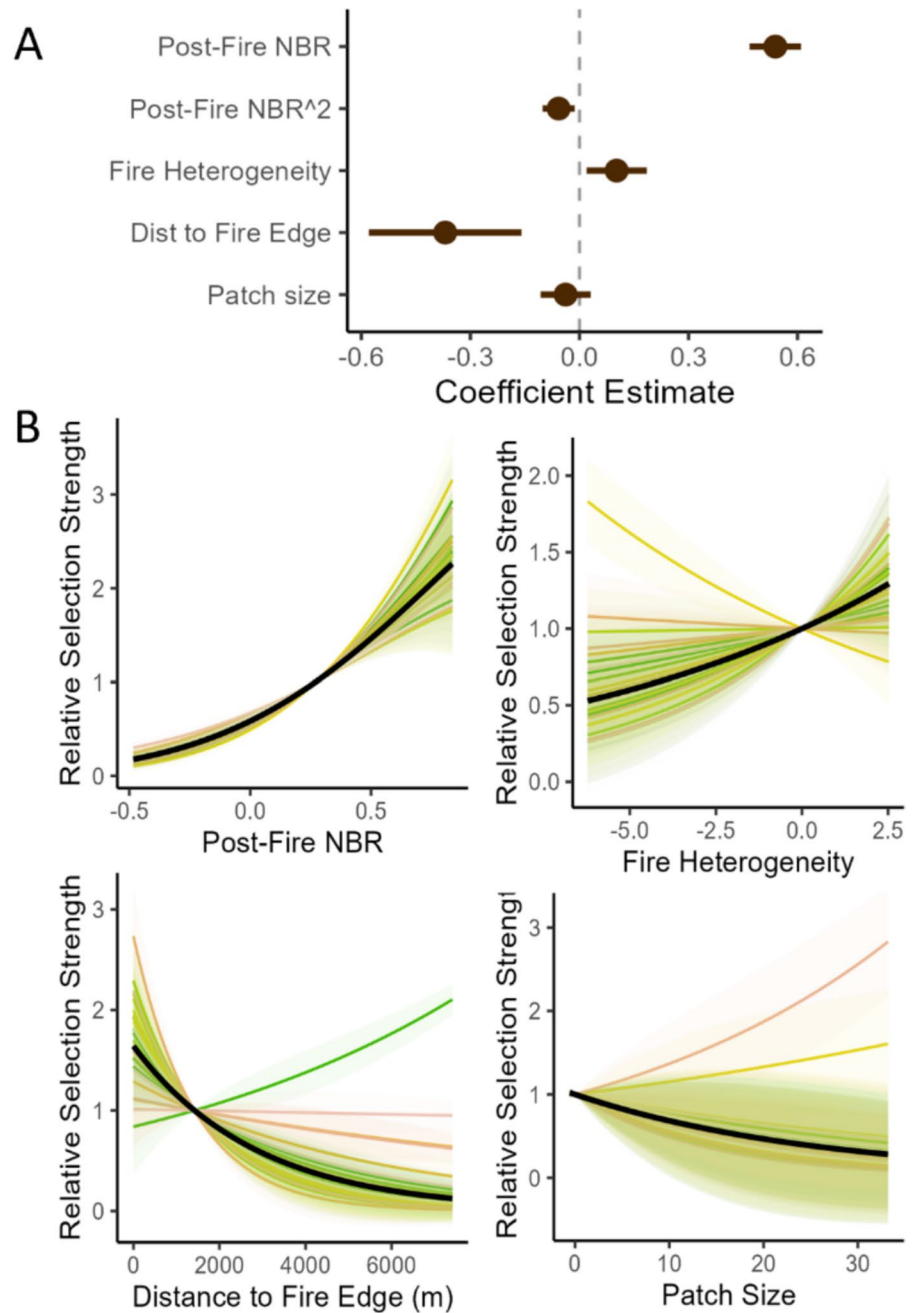
compared to available across fire severity classes; and C) lynx use compared to availability of each fire severity class with black line representing slope=1; red dots indicate females while gray are males

(Fig. 3, panels A, B). The response of lynx to gradients of fire severity was highly consistent across individuals (Fig. 3, panel C): almost all individuals preferentially used patches of unburned and low severity

fire and avoided patches of moderate and high severity (Fig. 3, panel C).

At the fine scale along travel paths of Canada lynx traversing recent fires, results from the iSSF

Fig. 4 Integrated step-selection function (iSSF) of Canada lynx to fire characteristics in burns, Northern Rocky Mountains, Montana, USA: Panel A) Coefficient estimates (and 95% confidence intervals) from the mixed-effects iSSF models of lynx movement in recent wildfires. The strength of the covariate is indicated by the distance from the dotted horizontal line at 0; coefficients that cross the 0 line are not considered significant. Panel B shows marginal response plots of Canada lynx selection for post-fire NBR, fire heterogeneity, distance to fire perimeter, and severity patch size while traversing wildfires. Black line shows the population response, while colored lines show random effects of individuals



model indicate that three of four predictors characterizing landscape heterogeneity in burns were significant. These included: post-fire NBR, fire heterogeneity, and distance to fire edge. Patch area was the only landscape metric not significantly related to lynx selection behavior (Fig. 4A). The global

model with no interactions was the most parsimonious model, as indicated by AIC, and included a quadratic term for fire severity (Table 1). Competing models with an interaction between patch size and severity as well as fire heterogeneity and severity performed within 4 AIC units of this top model

Table 1 Step-selection models of Canada lynx traversing fire-impacted landscapes (≤ 3 yrs post-disturbance) from 2018 – 2020 in the Northern Rocky Mountains of Montana, USA.

Models are ranked by AICc, and the number of model parameters (K), delta AICc, AICc weight, and log likelihood (LL) for each model are given. Most supported model is shown in bold

Hypothesis number	Model	K	AICc	Delta_AICc	AICcWt	LL
4	Severity ² *FireHet + DistoEdge + PatchSize	14	123,226.1	0	0.47	–61,599.03
3	Severity ² * PatchSize + FireHet + DistoEdge	14	123,226.5	0.4	0.38	–61,599.23
1	Severity² + FireHet + DistoEdge + Patch-Size	12	123,228.5	2.42(*)	0.14	–61,602.24
2	Severity ² *Available Sever-ity + FireHet*Available Fire-Het + DistoEdge*Average Dist-toEdge + PatchSize	19	123,234.6	8.48	0.01	–61,598.27
5	Severity ² *(TurnAngle + StepLength) + Fire-Het * (Turn Angle + StepLength) + Dist-toEdge * (TurnAn-gle + StepLength) + PatchSize * (TurnAngle + StepLength)	18	123,236.5	10.42	0	–61,600.24

Severity: Fire severity as measured by post-fire normalized burn ratio

FireHet: Fire heterogeneity, measured by Shannon's diversity index applied to categorical fire severity

DistoEdge: Distance to the fire perimeter

PatchSize: Measure of the area of categorical fire severity patches

TurnAngle: The change in movement direction of a lynx from one path segment to the next

StepLength: The log distance between subsequent steps in the lynx movement path

Shape Complexity: Perimeter/area ratio of an island

(Table 1) and the number of model parameters differed by only 2 degrees of freedom from the global model. Thus, AIC values of the more parameterized models were likely influenced by non-informative terms (Arnold 2010), so we chose the global model with no interactions as most parsimonious. Based on this model, Canada lynx at the individual level when traversing recent fire-impacted landscapes selected movement paths in patches of low fire severity (higher values of post-fire NBR), through neighborhoods of higher fire heterogeneity (SHDI based on number of fire severity classes), and at closer distances to fire perimeters (Fig. 4).

Canada lynx traveled an average median distance of 613 m from the fire perimeter (range: 103–2348 m) into burns; the average maximum distance lynx traveled into a burn was 2314 m (range: 1021 – 6615 m). For comparison, random locations within home ranges averaged 714 m (range: 254–1848) from the perimeter; the average maximum distance was 2473 m (range: 1139–6983 m).

Selection behavior for unburned islands in fires.

Validating our prediction, Canada lynx exhibited strong selection behavior for unburned islands of forest vegetation within fires ($\beta = 1.01$, $SE = 0.08$, 95% CI: 0.84–1.17); 42.5% of all within-fire lynx locations were found in unburned islands as compared to 22.8% random locations in fire perimeters. A visualization of Canada lynx GPS locations demonstrates not only their extensive use of unburned islands within a fire perimeter, but how they use corridors of unburned forest to access patches within a burn perimeter (Fig. 5). Unburned forest islands (> 0.4 ha) in fires, in general (both inside and outside lynx home ranges), were small (median = 0.9 ha, IQR = 0.5–2.3); 90% were smaller than 6.2 ha. The maximum island size in any fire in our study was 408.3 ha ($n = 5289$). The median number of spatially distinct islands (> 0.4 ha) per fire was 326 (IQR 47–351). The median size of islands that Canada lynx used was 1.7 ha (IQR: 0.72–4.23 ha, $n = 406$), whereas the median size of unused islands in home ranges was 0.72 ha (IQR: 0.54–1.35 ha, $n = 363$). Lynx traveled a median distance of 720 m

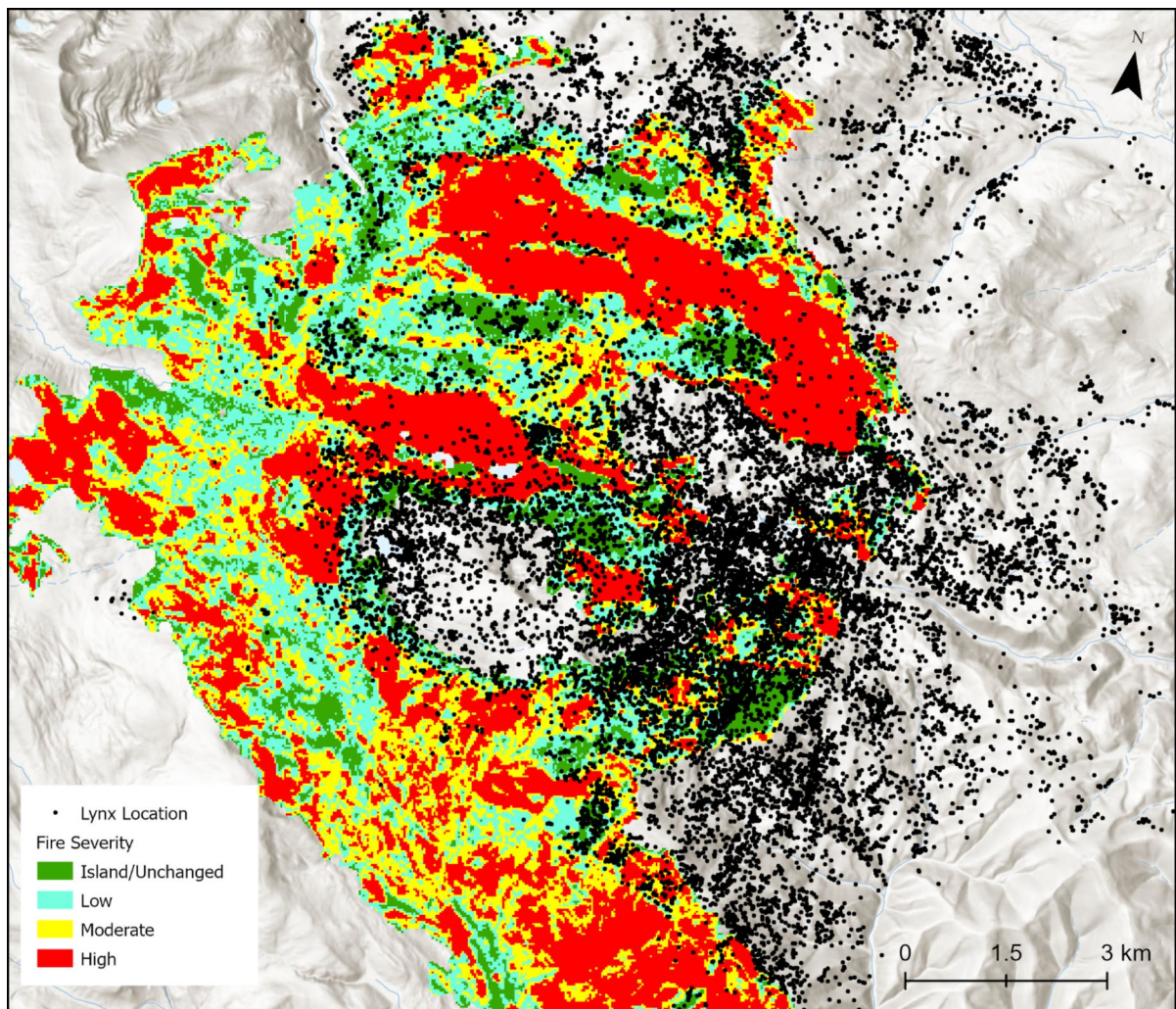


Fig. 5 An example of Canada lynx using patches of unburned islands and forest-corridor connections to the fire perimeter, Liberty fire, Montana, USA, 2019. Lynx use occurred in 2018

and 2019; fire burned in 2017. Background image credit: ArcGIS software by Esri

(range: 42–2293 m) from a fire perimeter to access unburned islands in burns; the maximum they traveled to an island was 6885 m. Thus, Canada lynx in general traveled further from the fire perimeter when using islands, as compared to their general penetration of burn-impacted landscapes (average median distance: 613 m [range: 103–2348 m]).

The global hurdle model with no interactions was the top-performing model of lynx use of islands (Table 2). Canada lynx were more likely to use islands with greater vegetation quality (post-fire

NBR), lower perimeter to area ratio (simpler, more compact shape), and greater surrounding fire heterogeneity within 150 m of the island (Fig. 6A). Also, the intensity of lynx use was greater in islands with greater vegetation quality (post-fire NBR) and greater surrounding fire heterogeneity within 150 m of the island (Fig. 6). In general, the intensity of island use by lynx did not respond consistently to island size, distance to fire edge, and surrounding island severity when using unburned islands in fires (Fig. 6). There was some uncertainty in the model selection process,

Table 2 Candidate hurdle models used to evaluate the intensity of use of unburned islands by Canada lynx in fire perimeters. Models are ranked by AICc, and the number of model

parameters (K), delta AICc, AICc weight, and log likelihood (LL) for each model are given. Most supported model is shown in bold

Hypothesis number	Model	K	AICc	Δ_{AICc}	AICcWt	LL
1	ShapeComplexity + PostNBR + SurrHet + Perimeter + SurrSev + DisttoEdge	29	3171.75	0	0.49	− 227,827
2	ShapeComplexity + PostNBR + Perimeter + SurrHet * SurrSev + DisttoEdge	31	3172.56	0.81	0.33	− 227,982
6	Perimeter + DisttoEdge + PostNBR * ShapeComplexity + SurrHet + SurrSev	31	3174.93	3.18	0.1	− 228,241
3	ShapeComplexity * DisttoEdge + PostNBR + Perimeter + SurrHet + SurrSev	31	3175.49	3.75	0.08	− 228,720
5	DisttoEdge* PostNBR + ShapeComplexity + SurrHet	25	3182.77	11.03	0	− 229,166
4	Perimeter*DisttoEdge + PostNBR + SurrHet	23	3191.73	19.98	0	− 231,601

Shape Complexity: Perimeter/area ratio of an island polygon

PostNBR: Post-fire normalized burn ratio, index of island quality

SurrHet: Surrounding fire heterogeneity in a 150 m radius around island polygon

Perimeter: Measure of the distance around an island, index of island size

SurrSev: Mean surrounding fire severity in a 150 m radius around island polygon

DisttoEdge: Distance from the island to the fire perimeter

with the model containing an interaction between surrounding fire severity and surrounding heterogeneity (both within 150 m of the island) also receiving 33% of the model weight, although the interaction term itself was not significant (Table 2).

Pellet counts of snowshoe hares were significantly higher (15.2 mean pellets/m², 10.3–20.0 95% CI) in unburned islands than in control sites in home ranges (5.0 mean pellets/m², 3.7–6.2 95% CI), but with variation across fires (Fig. 7). After application of the Mills (2005) equation ($\exp(-1.67 + 0.77 \cdot \log(\text{mean pellets}))$) derived in the Northern Rockies, the relative abundance of snowshoe hares, as indexed by pellets, was 1.43 hares/ha (95% CI: 1.07–1.79) in islands versus 0.62 hares/ha (95% CI: 0.49–0.74) in control stands that were adjacent to the fire perimeter while in a lynx home range. We found that site type (islands versus control sites) had a strong effect on relative hare abundance, whereas our vegetation predictors did not (Table 3), possibly due to little difference in forest vegetation characteristics in islands versus controls (Appendix Table 6). At sites in unburned

islands (not controls), we found a weak relationship between lynx use and hare pellets, with more hare pellets found in islands with greater lynx use (β coefficient 95% CI: 0.05–0.61, Table 3). There were more pellets in islands closer to the fire perimeter (β coefficient 95% CI: −0.95–0.01, Table 3) with no effect of island size on pellet counts. Collectively, our pellet analyses suggest that Canada lynx selected unburned islands in fire-impacted landscapes, at least in part, to access higher densities of snowshoe hares.

Discussion

A central issue facing landscape ecology is to understand how the habitat requirements of species are impacted by natural disturbance across spatial and temporal scales (Viljur et al. 2022). Here, we validated our original prediction that Canada lynx, at the individual level, exhibited avoidance behavior of recent (≤ 3 yrs old) fires in their home ranges. In addition, they exhibited a functional response to fire

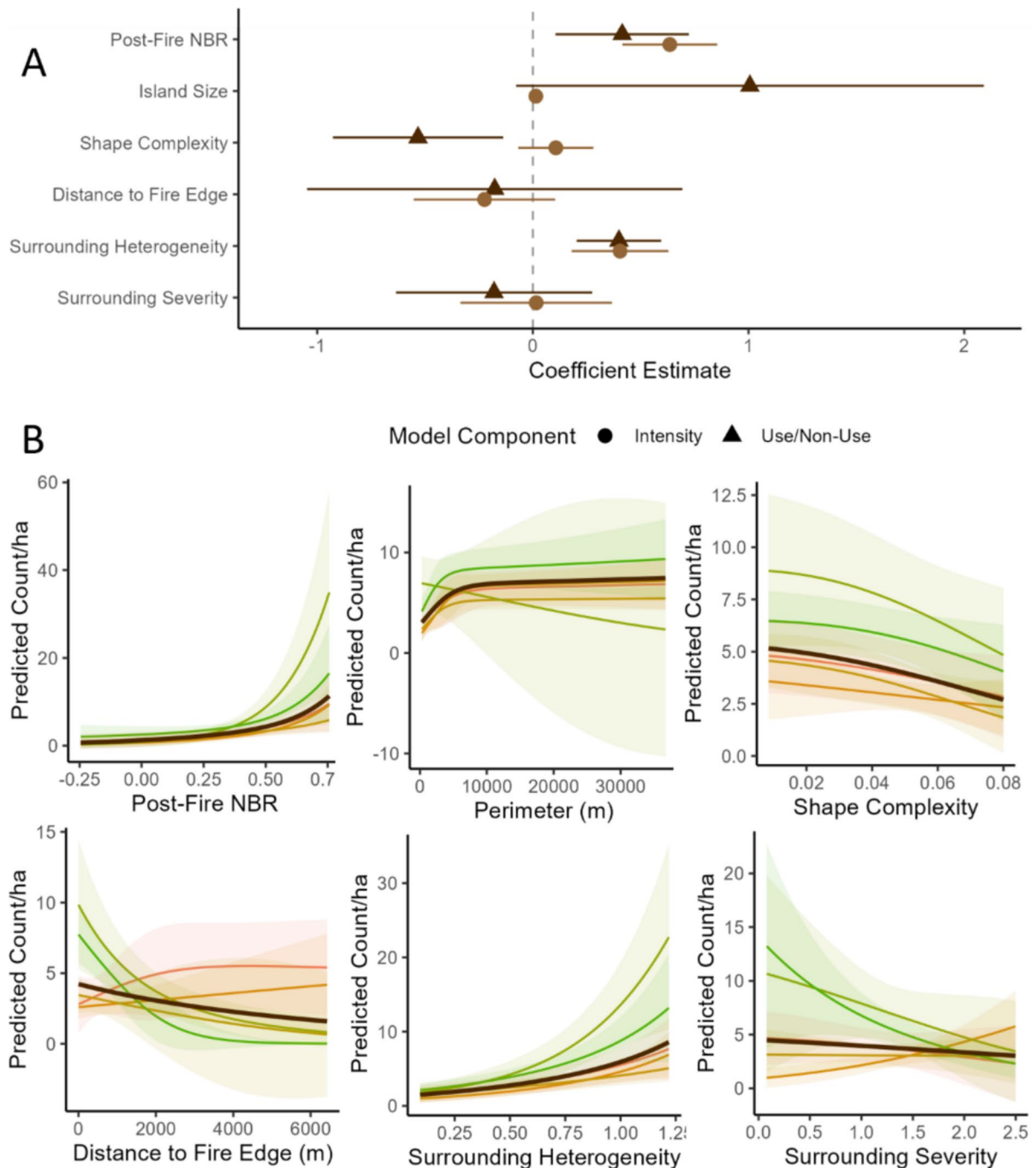


Fig. 6 Response of Canada lynx to patch characteristics of unburned islands in fires, Northern Rocky Mountains, Montana, USA: Panel A) Coefficient estimates (and 95% confidence intervals) of a hurdle model that describes how patch characteristics of islands related to the intensity of island use. The strength of the covariate is indicated by the distance from the dotted horizontal line at 0; coefficients that cross the 0 line are not considered significant. Panel B): marginal response

plots from the hurdle model that show the predicted number of lynx GPS points per hectare within an island in response to changes in post-fire NBR (high values indicate low fire severity), perimeter length, island shape complexity (low values equate to simple shapes), distance to fire edge, surrounding heterogeneity, and surrounding severity in of islands within fires, while holding all other model covariates at their mean

Fig. 7 Snowshoe hare density, as indexed by hare fecal pellets, in unburned islands in fires compared to control sites outside and adjacent to fire perimeters, but inside home ranges of Canada lynx; four fires were sampled (Caribou (2017 ignition, 11,372 ha), Liberty (2017, 11,222 ha), Rice Ridge (2017, 69,393 ha), and Weasel (2017, 1595 ha), Montana, USA, 2023

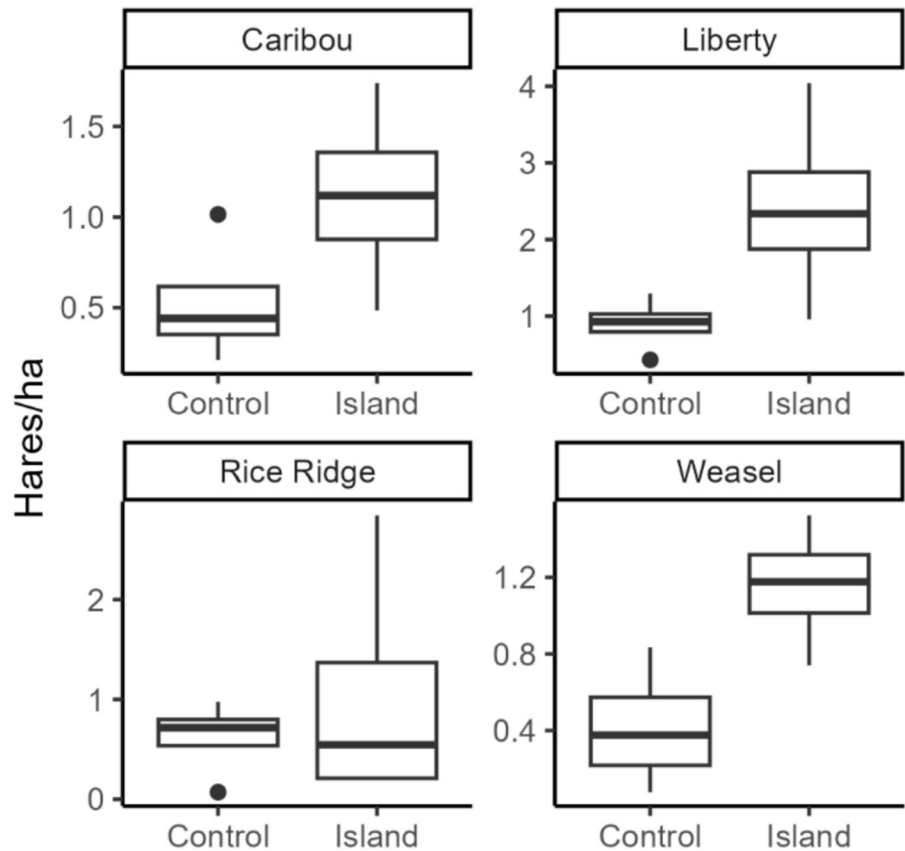


Table 3 Coefficients for generalized linear mixed models that evaluate relative snowshoe hare abundance in unburned islands in fires compared to control sites outside burn perimeters. “All Sites” considers relative hare abundance (i.e. pellet counts) at island versus control sites with associated vegetation metrics (Small TPA: small (<7.6 cm) trees per hectare, Large TPA:

large trees (>7.6 cm) per hectare, Spruce/Fir BA: spruce-fir tree basal area); “Islands only” considers relative hare abundance relative to island patch characteristics (island size, distance to fire perimeter, rate of lynx use in island (number of lynx GPS locations inside the island per ha) in only unburned forest islands. Significant covariates are shown in bold

	Estimate	Std. error	2.50%	97.5%
<i>All sites</i>				
(Intercept)	1.64	0.31	1.04	2.24
Site type (island vs control)	0.99	0.30	0.40	1.57
Small TPA	0.30	0.20	−0.09	0.69
Spruce/Fir BA	0.08	0.20	−0.31	0.47
Large TPA	−0.10	0.19	−0.46	0.27
<i>Islands Only</i>				
(Intercept)	2.60	0.19	2.22	2.94
Island size	0.45	0.20	−0.24	0.55
Lynx density	0.33	0.14	0.05	0.61
Island Dist to edge	−0.48	0.24	−0.95	−0.01

disturbance by increasing their avoidance of burned areas in home ranges that experienced higher levels of fire disturbance, but with variation across individuals (Fig. 2). The general avoidance that we observed occurred across the range of fire impacts we measured in home ranges (10%–80% spatial overlap, Fig. 2). Thus, at the landscape scale, recent fire disturbances reduced the amount of preferred lynx habitat, especially with higher amounts of disturbance/home range overlap (i.e., a functional response). We also documented that fire disturbance in home ranges may exert other ecological “costs” in that 27% (6/22 individuals) of our lynx study population dispersed from their disturbed territories, as well as an additional individual that returned and died; this rate of extra home range movement was higher than we have observed for this population in over 25 years of sampling (J. Squires, unpublished data).

Despite general avoidance behavior, Canada lynx in the Northern Rockies did frequently use recently burned landscapes, similar to other southern populations (Vanbianchi et al. 2017). Their patterns of selection were influenced at the home range- and patch-scales by gradients of environmental heterogeneity in fires. At a home range scale, fire severity affected how Canada lynx used fire-impacted landscapes (Fig. 3). Lynx concentrated their use of recent burns in unburned or low-fire severity areas within fire perimeters (Fig. 3). We also validated our prediction that patch-level characteristics affect how Canada lynx traverse fire-impacted landscapes at a fine spatial scale. Canada lynx selected movement paths in burns in patches of low fire severity (as indexed by post-fire NBR), but they were also responsive to the distance to fire perimeter and the heterogeneity of fire severity in the travel neighborhood (Fig. 4). Finally, we validated our prediction that Canada lynx would preferentially select unburned islands within fire perimeters. We demonstrated that lynx were sensitive to the characteristics of unburned islands by selecting island patches of greater vegetation quality (i.e., higher post-fire NBR consistent with lower fire severity) and higher burn heterogeneity surrounding the island’s periphery (Fig. 6). We further demonstrated a higher snowshoe hare density in unburned islands within a fire perimeter compared to adjacent completely unburned areas in home ranges. This pattern of prey abundance could explain, in part, why lynx exhibited

such strong patterns of selection for these patches of forest-island refugia in burns (Fig. 7). Collectively, this study advances the conservation and management of Canada lynx by demonstrating their response to fire across spatial scales; this is especially important at the southern range periphery of this federally listed species during this new period of rapid change in fire severity and frequency with climate change.

A challenge to natural resources conservation and management, especially given the preponderance of burn-impacted landscapes, is to understand how species respond to gradients of fire severity and heterogeneity (Fontaine and Kennedy 2012; Steel et al. 2023). For example, before our research, biologists in our study area were asked where to focus tree salvage operations with respect to fire severity and Canada lynx, which led to uncertainty when prescribing and implementing management actions. At the individual level, Canada lynx generally used unburned and low severity areas within fire perimeters (Appendix Table 6; Fig. 3, panel B) in a highly consistent manner across individuals (Fig. 3, panel C) and moderate and high severity areas were mostly avoided. At the finer spatial scale of a travel path (iSSF), all individuals selected areas of low fire severity that supported greater amounts of forest vegetation (post-fire NBR, Fig. 4, panel B) and all but one individual traversed paths through burned areas with greater fire heterogeneity (Fig. 4, panel C). Lynx populations at their southwestern range periphery depend on mixed conifer subalpine forests dominated by Englemann spruce and subalpine fir (Aubry et al. 2000; Squires et al. 2010; Ivan and Shenk 2016; Vanbianchi et al. 2017). These forests provide the horizontal cover (conifer boughs touching the ground or snow surface) necessary to support Canada lynx (Squires et al. 2010; Ivan and Shenk 2016) and snowshoe hares (Hodges 2000; Holbrook et al. 2017a; Ivan et al. 2023). Subalpine forests that support dense horizontal cover are likely to burn at high severity due to abundant horizontal and ladder fuels, and in recent years, at higher frequency (Higuera et al. 2021) in a manner consistent with other conifer forests across the western United States (Parks and Abatzoglou 2020; Hagmann et al. 2021; Coop et al. 2022). Thus, understanding how lynx respond to fire severity gradients is particularly important within forests of the Northern Rockies.

We acknowledge that fire effects to mammal communities are variable across severity and temporal gradients, depending on the life histories of different species (Forney and Peacock 2024). How species respond to low- versus high-fire severity is highly variable in terms of their resilience to increased fire disturbance (Jager et al. 2021). An important caveat to our results is that we investigated lynx use of fire severity and heterogeneity gradients at a single point in time of forest succession (≤ 3 -yr post-disturbance). Thus, we acknowledge that non-linear and interacting effects of burn severity across time since disturbance could impact lynx use of fire-impacted landscapes (Taillie et al. 2018; Olson et al. 2023). It was also beyond the scope of this study to investigate any long-term or demographic impact of fire disturbance to Canada lynx.

Importance and management of unburned islands

Canada lynx in the Northern Rockies exhibited strong selection behavior for unburned islands, similar to other southern populations in the contiguous USA (Vanbianchi et al. 2017). Thus, the management of unburned islands as disturbance refugia in fire perimeters is important to lynx conservation, like for many other species (Andrus et al. 2021; Sommers and Flannigan 2022). The unburned islands selected by lynx were generally small (median 1.7 ha, IQR: 0.72–4.23 ha) in area, but the islands that lynx selected were approximately twice as large as those randomly available (0.72 ha (IQR: 0.54–1.35 ha) in home ranges. We also demonstrated the island's vegetation quality or greenness as indexed by higher post-fire NBR values (Fig. 6) and the heterogeneity of burn severity surrounding the island perimeter impacted the intensity at which Canada lynx used island patches.

In the landscape context, the preservation and maintenance of unburned islands (or low-severity patches) in fire-impacted landscapes supports post-fire ecosystem function and disturbance resilience (Meddens et al. 2018a, b). In spruce-fir forests especially, surviving trees and unburned islands are critical in providing stepping stones for tree seed dispersers and pollinators that speed the time of forest recovery, and provide beneficial mature forest influences such as tree structure, tree seeds, and temperature regulation to fire-disturbed landscapes (see

review, Sommers and Flannigan 2022). Thus, the opportunity for forest and fire managers to conserve unburned islands and low severity patches in fire-impacted landscapes remains an important issue for Canada lynx in ways that also promote many other ecological benefits.

Snowshoe hare abundance in unburned islands

Different ecological factors could influence the extent and timing of how mobile species like Canada lynx use unburned islands in fire perimeters including interspecific interactions, food abundance, predator avoidance, and landscape fragmentation. We demonstrated that snowshoe hare abundance may be an important driver of why Canada lynx selected unburned islands in fires. Snowshoe hare abundance, as indexed by pellet counts, was over twice as high (1.43 hares/ha, 95% CI:1.07–1.79) in islands compared to control points (0.62 hares/ha, 95% CI:0.49–0.74) adjacent to but outside fire perimeters (Fig. 7). Snowshoe hare populations tend to decline immediately following fire disturbance due to reductions in vegetation cover (Wolff 1980; Hodges et al. 2009; Cheng et al. 2015; Kelly and Hodges 2020). Therefore, it was surprising that forest vegetation covariates in unburned islands were not predictive of hare abundance in the islands we sampled (Appendix, Table 6). We also found that landscape context or intrinsic island attributes, such as island size, had no effect on hare abundance. The island distance from the fire perimeter had a weak negative impact, but none of these environmental factors strongly impacted hare abundance (Table 3). So, why was snowshoe hare abundance higher in unburned islands? One possible explanation is that unburned islands were surrounded by less vegetation cover that reduced hare dispersal and created a type of ecological “fence effect” (Krebs et al. 1969; Ostfeld 1994). Another possible explanation was that predation on hares, in general, was lower in unburned islands compared to similar habitat outside the fire perimeter. However, we documented a weak relationship between lynx use of islands and hare pellet counts suggesting that lynx actively selected islands with higher relative hare abundance. Additional research is needed to understand the potential mechanism(s) behind the observed higher snowshoe hare density that we found in unburned islands.

Management implications for fire-impacted landscapes

Boreal and mixed-conifer subalpine forests that support Canada lynx populations were structured by fire disturbance for millennia (Agee 2000). Thus, Canada lynx evolved in landscapes shaped by fire, and these disturbed landscapes are used by populations across the species distribution (Mowat et al. 2000; Vanbianchi et al. 2017; Olson et al. 2021, 2023). It takes approximately 25 yrs post-disturbance for Canada lynx in the Northern Rockies of Montana, USA, to increase their use of landscapes severely impacted by fire, and active forest management following disturbance can speed habitat recovery (Olson et al. 2023). This time frame (≈ 25 yrs) is similar to how lynx use areas that experienced complete forest resets from clearcutting (Holbrook et al. 2018). Therefore, management actions that retain live forest structures can help bridge the gap between high-severity disturbances and subsequent succession and will have enduring benefits on the continuity of lynx habitat. Broadly, this amounts to maintaining a diversity of forest structures on the fire-impacted landscape and providing for connectivity at varying spatial and temporal scales. These principles have direct benefit to lynx and snowshoe hare, but also to reforestation, resilience, and ecological recovery following disturbance. Prior to wildfire, active forest management can create and maintain a patchwork mosaic of varying forest composition and structural stages that may reduce the impact of large-scale fire disturbance. For example, Olson et al. (2023) found that pre-fire silviculture can reduce fire severity and post-fire habitat recovery time of lynx use, while post-fire management can speed the recovery of lynx use in burned landscapes.

Previously, we mapped forest structure (Mature, Advanced Regeneration, Sparse, Stand Initiation) on our study areas based on remotely-sensed imagery and trained on field plot data (Savage et al. 2018). We then demonstrated that lynx in the Northern Rockies, USA, were responsive to these mapped forest structures in terms of habitat selection and the proclivity of females to produce kittens (Holbrook et al. 2017b, 2019a; Kosterman et al. 2018). However, we did not include pre-fire forest structure in our step-selection models because of correlation with post-fire NBR, especially for the advanced regeneration structure class that was present prior to fire disturbance

(Appendix, Fig. 8). This correlation suggests that Canada lynx when selecting patches of high post-fire NBR on movement paths (Fig. 4), used patches that were in part the result of active forest management or other vegetation resets approximately 20–30 yrs before fire disturbance (Holbrook et al. 2019b); this change in forest structure resulted in higher post-fire NBR or lowered fire severity. When managing forests in the Northern Rockies at the lynx's southern range periphery, it is important for managers to consider that lynx benefit from unburned, dense, multi-layered mature forest in their habitat use and their proclivity to produce kittens (Squires et al. 2010; Kosterman et al. 2018; Holbrook et al. 2019b) as a core element of landscape habitat mosaics.

In addition, wildfire suppression activities in the Northern Rockies could enhance lynx conservation and encourage forest recovery, if applied thoughtfully. We have observed common wildfire suppression activities such as burning out unburned islands of forest vegetation within fire perimeters and extensive use of backfires around fire perimeters in important lynx habitat. Although these practices may be necessary under extreme fire conditions or to ensure crew safety, these actions also alter or remove critical forest patches that support the establishment, movements and persistence of species in fire-impacted landscapes (Backer et al. 2004; Krawchuk et al. 2016; Meddens et al. 2018b). Thus, incident management teams would serve lynx conservation if they reduced the use of suppression activities that homogenize post-fire forest structures whenever safe and prudent to do so.

Following wildfire suppression, managers frequently consider post-fire clearcut and salvage operations. Since lynx preferentially avoid wildfire immediately post-disturbance, it follows that forest management in burns may be preferred over removing unburned quality habitat elsewhere. Among the many tradeoffs for managers to consider in this context, we suggest three important considerations for post-fire activities with respect to Canada lynx. First, since lynx preferentially use the outer 2000 m (average maximum travel distance into burns, 2314 m) of a burn edge in the early years following fire, the best practice would be to minimize timber removal within that burn edge and instead prioritize management and tree salvage areas in the

interior of the burn footprint while realizing that how far lynx penetrate inside fire perimeters may vary in size depend on burn severity and size. For example, the contrasting burn patterns in the Caribou versus the Davis fires illustrate how patterns of burn severity will alter how lynx use the interior portions of burns (Appendix, Fig. 9). In addition, tree removal adjacent to the recent burn may further reduce lynx habitat and access to the burn edge. Second, because lynx tend to avoid patches of high severity with low post-fire vegetation heterogeneity (i.e., homogeneous neighborhoods), timber activities are best focused on dead tree removal in large high-severity patches with little understory. Third, and as aforementioned, lynx seek access to fire refugia, or unburned green-tree islands. Protecting island refugia and corridors during post-fire management serves lynx conservation, especially simple-shaped patches of high vegetation quality that are surrounded by moderate-to-high-severity patches. Canada lynx are willing to travel farther into burned landscapes to access quality island refugia. Thus, it is wise to maintain regular pockets of unburned refugia within the interior of burn footprints.

Since low severity and unburned forest refugia remain present in burns (Meddens et al. 2018a, b) despite the increase of fire size and severity (Price et al. 2013; Gauthier et al. 2015; Millar and Stephenson 2015; Higuera et al. 2021), our research of how Canada lynx use fire-impacted landscapes supports the more general understanding and appreciation of managing areas for low burn severity within the context of landscape ecology (Jones and Tingley 2022; Steel et al. 2023). For example, like Canada lynx, large ungulates and carnivores avoided areas of high severity burns for up to 30 years across the western United States, resulting in lower habitat availability for many species (Mills et al. 2025). Similarly, the probability of site extirpation of spotted owls (*Strix occidentalis*) was seven times higher in areas of high fire severity (Jones et al. 2016). Thus, new understandings of how Canada lynx respond to burn severity and unburned island refugia demonstrated in this study support the importance of managing mosaics of low fire severity and unburned islands in burn perimeters to species conservation.

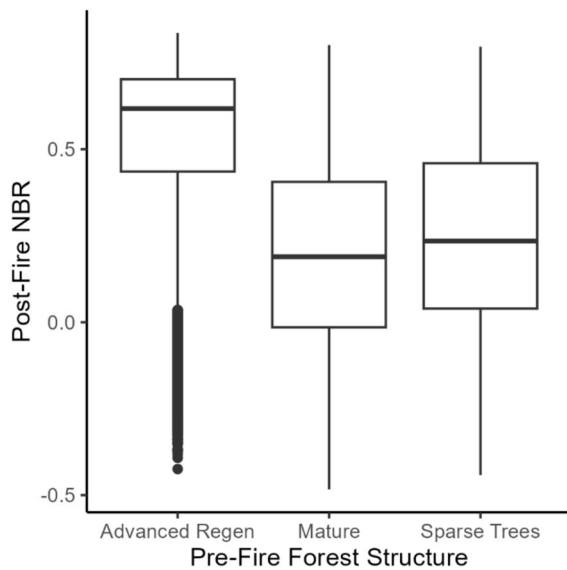


Fig. 8 Boxplot showing the average post-fire NBR value associated with pre-fire forest structure class (Savage et al. 2018). Structure classes were derived from remotely-sensed imagery collected in 2013 and trained on field plot data. Forests that were in an advanced regeneration structure class before a fire resulted in lower burn severity than forests that were mature or sparse. Canada lynx selected high values of post-fire NBR (low fire severity) on movement paths within wildfires

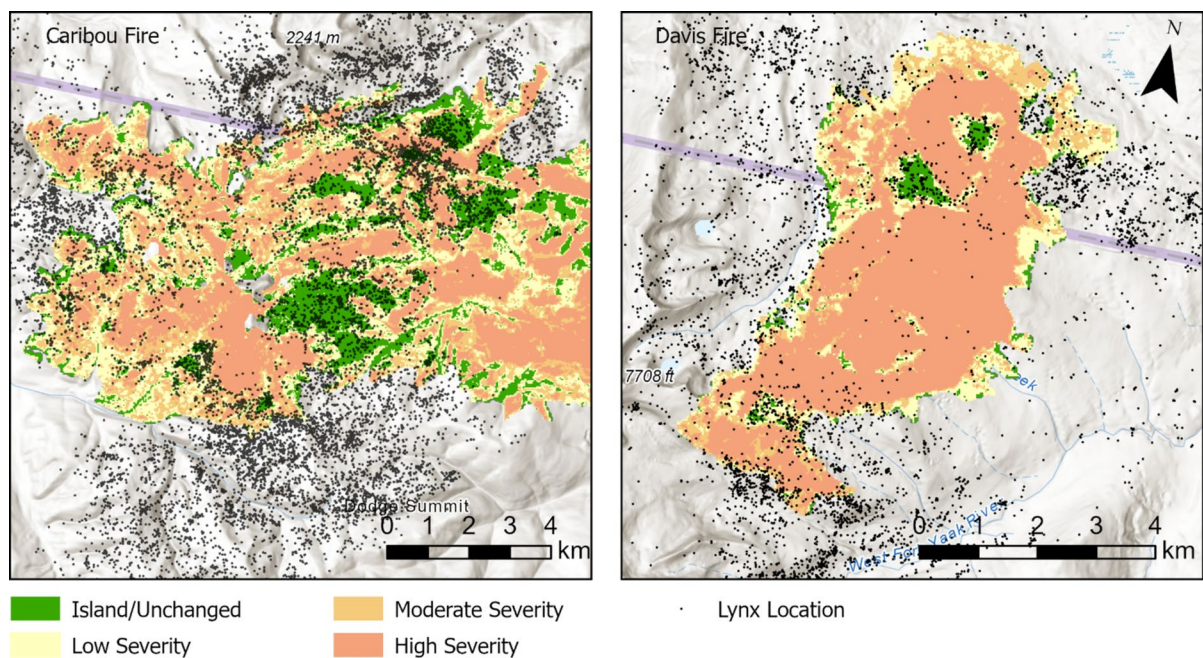


Fig. 9 Examples that illustrate the high variability in patterns of unburned islands in wildfires used by Canada lynx in the Northern Rocky Mountains due to variation in patterns of burn severity on fire-disturbed landscapes

Table 4 Predictor variables considered in iSSF models that evaluated patterns of selection for Canada lynx in fire-impacted landscapes

Name	Scale	Derived FROM	Category	Median	Min	Max	AIC	ΔAIC
Post-fire NBR	30 m	Post-fire NBR	burn severity	0.39	−0.398	0.816	123,320	0
Composite burn index	30 m	Continuous CBI	burn severity	1.14	0	3	123,459	−139
Normalized burn ratio	30 m	Differenced NBR	burn severity	181	−377	1082	123,484	−164
Composite burn index	30 m	RAVG CBI	burn severity	Categorical: Unchanged($0 < \text{CBI} < 0.1$), Low Severity($0.1 < \text{CBI} < 1.25$), Moderate Severity ($1.25 < \text{CBI} < 2.25$), High Severity($2.25 < \text{CBI} < 3.0$)			123,490	−170
Percent change in basal area	30 m	RAVG BA	burn severity	Categorical: 0%, 0–10%, 10–25%, 25–50%, 50–75%, 75–90%, > 90%			123,497	−177
Percent change in canopy cover	30 m	RAVG CC	burn severity	Categorical: 0% canopy loss, 0–25%, 25–50%, 50–75%, > 75%			123,502	−182
Post-fire NBR	150 m	Post-fire NBR	burn severity	0.313	−0.372	0.76	123,503	−183
Composite burn index	150 m	Continuous CBI	burn severity	1.32	0	2.97	123,564	−244
Moisture index	30 m	Differenced Moisture Index	burn severity	150	−372	784	123,579	−259
Fire severity	30 m	MTBS Severity	burn severity	Categorical: Unburned, Low, Moderate, High			123,596	−276
Normalized burn ratio	150 m	Differenced NBR	burn severity	249	−133	950	123,605	−285
Moisture index	150 m	Differenced Moisture Index	burn severity	192	−111	723	123,674	−354
Composite burn index	150 m	RAVG CBI	burn severity	Majority value of categorical composite burn index			123,707	−387
Fire severity	150 m	MTBS Severity	burn severity	Majority value of categorical MTBS fire severity			123,749	−429
Post-fire NBR	1 k	Post-fire NBR	burn severity	0.194	−0.254	0.599	124,088	−768
Composite burn index	1 k	Continuous CBI	burn severity	1.63	0.244	2.77	124,106	−786
Normalized burn ratio	1 k	Differenced NBR	burn severity	343	−11.6	869	124,119	−799
Moisture index	1 k	Differenced Moisture Index	burn severity	252	−8.54	631	124,128	−808
Fire severity	1 k	MTBS Severity	burn severity	Majority value of categorical MTBS fire severity			124,138	−818
Distance to fire edge		MTBS Boundary	distance to fire edge	1170	0	6615	124,143	0
Shannon diversity index	1 k	MTBS Severity	fire heterogeneity	1.16	0.183	1.56	124,144	0
Severity standard deviation	150 m	MTBS Severity	fire heterogeneity	0.591	0	1.85	124,156	−12
Shannon diversity index	150 m	MTBS Severity	fire heterogeneity	0.884	0	1.54	124,160	−16
Severity standard deviation	1 k	MTBS Severity	fire heterogeneity	0.879	0.438	1.29	124,180	−36
Area (m²)		RAVG CBI	shape metric	191,700	900	1.4E+07	124,033	0
Perimeter (m)		RAVG CBI	shape metric	5460	120	141,180	124,100	−67

Table 4 (continued)

Name	Scale	Derived FROM	Category	Median	Min	Max	AIC	Δ AIC
Area (m2)		MTBS Severity	shape metric	744,300	900	4.4E+07	124,114	– 81
Perimeter to area ratio		RAVG CBI	shape metric	0.032	0.00588	0.133	124,132	– 99
Polygon shape		RAVG CBI	shape metric	3.01	1	16.6	124,149	– 116
Perimeter (m)		MTBS Severity	shape metric	15,420	120	987,240	124,168	– 135
Polygon shape		MTBS Boundary	shape metric	4.76	1	37.2	124,175	– 142
Perimeter to area ratio		MTBS Severity	shape metric	0.0275	0.00677	0.133	124,178	– 145

Metrics for predictors included: median, minimum, and maximum for each continuous variables. Also included: predictor name, the scale of consideration, original data product from which it was derived, the predictor category where it was considered, and the AIC and Δ AIC values calculated in univariate model testing (see text for more details). A total of 32 covariates were calculated at different spatial scales, derived from 15 unique covariates (see 'Name' column). Covariates in bold were selected for inclusion in final models

MTBS Monitoring Trends in Burn Severity, *RAVG* Rapid Assessment of Vegetation Condition after Wildfire, *CBI* Continuous burn index, *NBR* Normalized Burn Ratio, *BA* Basal Area, *CC* Canopy Cover

Table 5 Predictor variables considered in hurdle models that evaluated the intensity of use by Canada lynx for unburned islands in fire perimeters

Name	Scale	Derived from	Category	Median	Min	Max	AIC	ΔAIC
Perimeter to area ratio		RAVG CBI	Island Shape	0.05	0.01	0.08	3329.86	0.00
Mean pNBR	30 m	Continuous pNBR	Island Quality	0.50	−0.17	0.76	3330.33	−0.47
Mean CBI	30 m	Continuous CBI	Island Quality	0.47	0.00	2.40	3332.37	−2.51
SD CBI	150 m	Continuous CBI	Island Surroundings	0.80	0.24	1.22	3340.18	−10.32
SD pNBR	150 m	Continuous pNBR	Island Surroundings	0.22	0.08	0.40	3349.45	−19.59
Perimeter (m)		RAVG CBI	Island Shape	840	300	36,720	3350.36	−20.50
Area (ha)		RAVG CBI	Island Shape	1.71	0.45	408.00	3357.74	−27.88
Mean CBI	150 m	Continuous CBI	Island Surroundings	1.27	0.08	2.26	3369.29	−39.43
Distance to edge		MTBS Boundary	Island Quality	191	0	5166	3372.74	−42.88
Mean NBR	30 m	Continuous dNBR	Island Quality	83.90	−365	665	3375.76	−45.90
Mean CBI	1 km	Continuous CBI	Island Surroundings	1.34	0.24	2.53	3379.75	−49.88
Mean MTBS severity	150 m	MTBS Severity	Island Surroundings	2.17	1.06	3.34	3383.10	−53.24
Mean MTBS severity	1 km	MTBS Severity	Island Surroundings	2.24	1.21	3.48	3387.54	−57.68
Mean pNBR	150 m	Continuous pNBR	Island Surroundings	0.30	−0.26	0.69	3390.66	−60.80
Mean dNBR	150 m	Continuous dNBR	Island Surroundings	248	−51.40	565	3390.82	−60.96
Mean dNBR	1 km	Continuous dNBR	Island Surroundings	290	−7.20	731	3391.31	−61.45
Majority category MTBS severity	150 m	MTBS Severity	Island Surroundings	Categorical: Unburned, Low, Moderate, High			3396.74	−66.88
SD MTBS severity	150 m	MTBS Severity	Island Surroundings	0.76	0.24	1.34	3398.29	−68.43
SD MTBS severity	1 km	MTBS Severity	Island Surroundings	0.98	0.58	1.36	3398.59	−68.73
Variety (count of unique categories) MTBS	150 m	MTBS Severity	Island Surroundings	4.00	2.00	5.00	3404.84	−74.98
Majority category MTBS severity	1 k	MTBS Severity	Island Surroundings	Categorical: Unburned, Low, Moderate, High			3412.74	−82.88
SD dNBR	150 m	Continuous dNBR	Island Surroundings	245.0	131.0	385.0	3414.98	−85.12
Majority category % MTBS severity	30 m	MTBS Severity	Island Quality	42.2	29.4	88.0	3415.32	−85.46
Mean pNBR	1 km	Continuous pNBR	Island Surroundings	0.25	−0.17	0.55	3420.96	−91.10
Majority category % MTBS severity	150 m	MTBS Severity	Island Surroundings	50.0	27.6	94.1	3422.80	−92.94

MTBS Monitoring Trends in Burn Severity, *RAVG* Rapid Assessment of Vegetation Condition after Wildfire, *CBI* Continuous burn index, *pNBR* Post-fire Normalized Burn Ratio, *dNBR* Differenced Normalized Burn Ratio (before and after fire), *SD* Standard deviation

Metrics for predictors included: median, minimum, and maximum for each continuous variables. Also included: predictor name, the scale of consideration, original data product from which it was derived, the predictor category where it was considered, and the AIC and ΔAIC values calculated in univariate model testing (see text for more details). A total of 25 covariates were calculated at different spatial scales, derived from 19 unique covariates (see ‘Name’ column). Covariates in bold were selected for inclusion in final models

Table 6 Forest structure in unburned islands used by Canada lynx within fire perimeters

Metric	Plot Type	Min	Median	Max	SD	2.5% CI	97.5% CI
Large tree basal area	Control	63.2	107	232	47	104	138
	Island	52.4	112	200	49	98.9	134
Maximum DBH (in)	Control	9	12	28	6.06	12.1	16.4
	Island	6	11	39	8.52	12.1	18.3
Large plot trees per acre	Control	210	415	1120	250	385	565
	Island	220	530	890	165	450	569
Small plot trees per acre	Control	25	1200	4450	1236	939	1830
	Island	50	888	2325	759	756	1303

The density and diameter at breast height (DBH) of Large (> 7.62 cm DBH) and Small (< 7.62 cm DBH) trees (> 1.4 m tall) as quantified in nested circular plots (large tree radius = 5.67 m, small trees = 3.59 m) at each plot corner of a 50 m by 50 m grid where we quantified hare pellets to estimate snowshoe hare abundance (see Fig. 7)

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Author contributions All authors contributed to the study conception and design. Research management, hiring, and oversight of field work was provided by John Squires and Joseph Holbrook. Data analysis, graphic preparation, and statistical modeling were conducted by Lucretia Olson. The first draft was written mostly by John Squires, with substantial help from Lucretia Olson and Justin Crotteau. All authors commented on previous drafts of the manuscript. All authors read and approved of the final draft.

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Data availability Data are publicly available in Figshare <https://doi.org/10.6084/m9.figshare.31382932>.

Declarations

Competing interests The authors declare no competing interests.

Appendix

See Figures 8, 9 and Tables 4,5,6.

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