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Effects of compound disturbance on Canada lynx and snowshoe hare: Wildfire and forest management influence timing and intensity of use

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ABSTRACT

Wildfires are increasing in scale and impact on the landscape, altering large amounts of wildlife habitat and forest ecosystems. The reduction of fuels through forest management is considered a primary way to reduce the extent and severity of wildfires before they occur but may lead to a decrease in tree density prohibitive of some species' habitat. Alternatively, management actions undertaken after a fire may speed the trajectory of burned areas back into quality habitat but may also impede this development if the wrong type of treatment is undertaken. Thus, information on how different management actions, applied either pre- or post-fire, can influence the timing of a burned area's return to suitable habitat will help managers conserve species on the landscape. Our study aims to understand how a rare carnivore, Canada lynx (*Lynx canadensis*), uses stands managed with different silviculture actions at different times relative to wildfire. We used GPS locations from 39 individual lynx collected from 2004 to 2015 to examine the response of lynx to wildfire compounded by active forest management, where time since fire at time of use ranged from 1 to 27 years. To understand the drivers behind lynx use of wildfires, we also focused on the primary prey of Canada lynx, snowshoe hares (*Lepus americanus*), using pellet counts across a similar range of post-fire treatment types in fires between 22 and 28 years old. We also assessed vegetation recovery and forest structure over time since wildfire using remotely sensed data and field measurements. We found that lynx intensity of use differed based on timing and type of management action, with the greatest lynx use ~25 years after a wildfire managed with post-fire regeneration cuts (removal of the majority of the canopy). Lynx use was likely driven by hare abundance, which was also highest in post-fire regeneration cuts, characterized at time of use by dense lodgepole pine stands. We conclude that managing landscapes with a mosaic of active (pre- and post-fire treatments) and passive (hands-off) management will best conserve a desirable range of lynx habitat in an increasingly fire-impacted landscape.

1. Introduction

Wildfire is one of the largest sources of habitat disturbance in forested ecosystems at a global scale (Curtis et al., 2018), and the continued effects of a warming climate and increased area of wildland urban interface, which can lead to increased human-caused ignitions and greater fuel availability through land-use change and fire-suppression around habitations (Pausas and Keeley, 2021; Radeloff et al., 2018), will only increase its impact. Decades of fire suppression and forest management decisions have led to changes in forest species composition, structure, and fuel loads, and combined with the effects of a warming climate result in forests that may not be able to withstand the severity, extent, and frequency of contemporary wildfire disturbances (Stephens and Ruth, 2005). This increase in wildfire severity and frequency (Pausas and Keeley, 2021; Shvidenko and Schepaschenko, 2013; Williams et al., 2019) has rendered forests that were once ecologically resilient to fire susceptible to large-scale homogenization, such as through stand replacement of subalpine species with lower elevation heat tolerant species (Cassell et al., 2019), or permanent type conversion to non-forested ecosystems (Coop et al., 2020). This, in turn, may have cascading negative effects on some wildlife habitat (Driscoll et al., 2021), forest ecosystem services (Harris et al., 2021; Vukomanovic and

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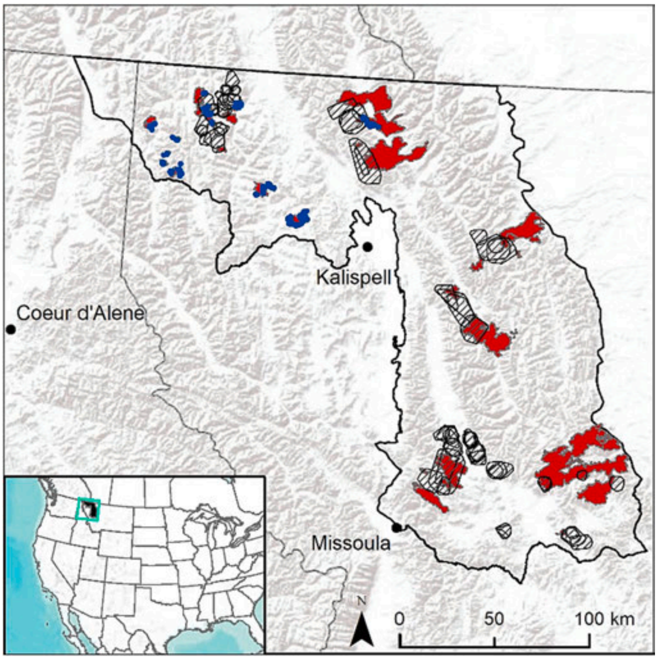

Fig. 1. The location of fires (red; n = 25) from 1988 to 2015 included in our study that overlapped with Canada lynx 95 % minimum convex polygon home ranges (black cross-hatching, n = 69) and hare pellet plots (blue dots, n = 178 plots) within the distribution of lynx (black outline) in the northern Rocky Mountains in western Montana, USA. Inset shows the location of the study polygon within the western United States. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Steelman, 2019), and human habitations and structures (Radeloff et al., 2018). Thus, there is a current strong motivation to apply forest management practices at large spatial scales to reduce fire extent and severity.

Extensive fuel reduction treatments are currently proposed for the western United States, with a plan by the United States Forest Service to treat up to 20 million acres on National Forest lands and 30 million acres across all other ownerships over the next 10 years (Wildfire Crisis Strategy, 2022). Forest management treatments mediate fire through the removal or redistribution of forest fuels, including live trees, standing dead, downed woody material, and shrubs or undergrowth (Stephens et al., 2012). A common management practice to reduce fire extent and severity is reduction of fuels using mechanical removal or prescribed burning to decrease tree densities and surface fuels before a wildfire takes place (Agee and Skinner, 2005; Stephens et al., 2021). However, fuels reduction can have deleterious effects on wildlife, especially those species that require dense or structurally complex forest. California spotted owls (*Strix occidentalis*; Tempel et al., 2014) and fisher (*Pekania pennanti*; Truex and Zielinski, 2013) both exhibit short term negative effects to fuel reduction treatments, although evidence indicates that these effects ameliorate over time and may be less destructive than high severity fire. Management actions chosen specifically to protect habitat can also mitigate negative effects on wildlife; for example, thinning by removing only small trees and removing debris from around specific nesting trees before a prescribed burn were both successful in mitigating fisher habitat destruction while decreasing fuels (Truex and Zielinski, 2013). These fine-scale pre-fire actions are time-consuming and difficult, however, and will thus be prohibitively expensive to impose at large spatial scales.

Once an area has experienced a wildfire, post-fire management actions are often carried out to attempt to speed landscape recovery or recoup financial losses through the harvest of remaining marketable timber. Similar to pre-fire management, post-fire actions shape the trajectory of vegetation recovery and thus the temporal and spatial response of wildlife to burned areas (Jones et al., 2020; Kelly and Hodges, 2020; Nappi et al., 2004). Common post-fire management practices include removal of all or the majority of the canopy (clear-cutting) to reduce remaining fuels and regenerate a new cohort of trees, removal of large or marketable trees without emphasis on regeneration (salvage logging), or remedial actions such as planting or erosion control (Beschta et al., 2004). These different types of management actions differentially impact the amount and distribution of remaining vegetation, and thus impact wildlife habitat in turn. In addition, the spatial extent and arrangement of management actions is also important. Smaller, more heterogeneous actions may favor species that forage among edges or require dense cover, while larger patches, specifically those resulting from severe management actions, may be avoided by some species of wildlife (Smith, 2021; Squires et al., 2013). Current management drivers are such that the desire to reduce fuels over extremely large areas and to salvage timber in recent megafires are preeminent objectives, while the costs of these potentially compounding disturbances to wildlife communities is not well understood.

Subalpine forest species that rely on dense forest, mature trees, and complex forest structure are likely to be particularly impacted by both wildfire and widespread, simplifying forest management to mitigate wildfire. The subalpine forest ecosystem, composed primarily of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) at mid-elevations in the western United States (Agee, 1999) is experiencing increased burned area and fire frequency due to increased temperature and decreased precipitation (Higuera et al., 2021). Species such as fisher, spotted owls, and Canada lynx (*Lynx canadensis*) are known to depend on specific structural components related to mature and old-growth forests, elements which are lost through both severe wildfire and simplifying forest management. Here, we focus on Canada lynx, a threatened forest carnivore whose habitat is characterized by mature forest, high horizontal cover (dense cover of vegetation resulting from horizontal vegetation elements, such as tree boughs, saplings, and shrubs), and multi-storied vegetation that supports snowshoe hares (*Lepus americanus*), their primary prey (Holbrook et al., 2017; Ivan and Shenk, 2016; Squires et al., 2010). Lynx in the western United States are negatively affected at an immediate and often multi-decadal temporal scale by forest management actions such as clearcuts (removal of all trees) or selection cuts (patchy removal of some trees) (Holbrook et al., 2018), but less is known about their response to burned areas, especially in conjunction with forest management. Snowshoe hares avoid burned areas immediately after wildfire (although some use may take place within two years after the burn, with the return of understory vegetation [Keith and Surrendi, 1971]), but increase their use as shrub cover, dense young trees, and understory cover increase, generally 20–30 years post-fire (Cheng et al., 2015). Hare habitat is negatively impacted by forest management actions which remove understory and decrease tree density (Ferron et al., 1998; Griffin and Mills, 2007). Post-fire, hares were shown to avoid salvage logged areas (Kelly and Hodges, 2020) which removes remaining live trees and horizontal cover after a burn.

The goal of this work was to understand how the compound disturbances of forest management and wildfire influenced the timing and intensity of lynx use of burned areas. Previous research has shown lynx to use stands approximately 20–40 years after forest management, depending on the intensity of the harvest (Holbrook et al., 2018), and to use burned areas more if severity was low or date of fire older than 20 years (Vanbianchi et al., 2017b). The compound effect of forest management combined with wildfire is not well understood. To address this issue, we used GPS locations collected from 39 individual lynx in western Montana, USA from 2004 to 2015 combined with spatial data from 25 wildfires and 900 forest management stands. We also performed an evaluation of snowshoe hare abundance across various post-fire management actions in the same study areas. Since snowshoe hares are the primary prey of Canada lynx, this second data source complements our analysis of lynx use of fires by providing information on the prey mechanism behind the observed patterns of lynx use. We evaluated the following primary hypotheses in our work: 1) the timing of forest management with regard to wildfire (i.e., management before versus after a fire) will alter lynx use intensity, with pre-fire management leading to lower severity fire and increased lynx use after a burn, and 2) less severe management action types (i.e., those that remove fewer trees) combined with wildfire will become useable more quickly for hares and lynx. To further explain lynx and hare response to the combination of fire and management, we investigated whether a suite of other fire-related characteristics influenced the timing and intensity of lynx and hare use of burned areas. Finally, we evaluated remotely sensed indices of forest vegetation recovery and forest structure to characterize forest vegetation conditions as they relate to management type and timing.

2. Methods

2.1. Study area

Our study area was located in the northern Rocky Mountains of northwestern Montana, USA, covering approximately 36,000 km^2 and delineated by previously estimated boundaries of current lynx distribution, as described in Squires et al. (2013; Fig. 1). Elevation within the study area ranges from 550 to 3400 m and climate is characterized by cold snowy winters and warm dry summers. Lynx habitat in this area is predominantly subalpine and mixed coniferous forest, composed of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudostuga menziesii*) at drier low elevations and Engelmann spruce, western larch (*Larix occidentalis*), subalpine fir, and lodgepole pine at higher, more mesic, elevations. Land use in our study area is primarily (~80 %) federally owned multiple use public land, which allows management for timber harvest, recreation, water and wildlife conservation, and grazing (Multiple-Use Sustained-Yield Act of 1960) plus some private and state-owned land. Much of observed lynx habitat in the northwestern Rocky Mountains historically had mixed severity fire regimes, with an estimated 20 % of forested area burned in stand-replacement fire, 30 % in nonlethal severity, and 50 % in mixed severity (Arno et al., 2000). For the past several decades, however, fires have occurred on the landscape with increasing frequency, size, and severity (Jolly et al., 2015; Salguero et al., 2020), with an estimated increase of 889 % in the number of wildfires and 2966 % in the amount of burned area from 1973 to 2012 on public lands in the Northern Rocky Mountains (Westerling, 2016).

3. Lynx locations

Our lynx dataset was initially composed of 69 adult individuals collared in western Montana, USA, from 2004 to 2015. Of these, 39 individuals (17 females and 22 males) had home ranges that overlapped with wildfires, resulting in 17,660 GPS locations considered for our analysis (individual distribution across years, some animals collared in multiple years: 2004 n = 1, 2005 n = 8, 2006 n = 8, 2007 n = 5, 2009 n = 1, 2010 n = 2, 2011 n = 4, 2012 n = 8, 2013 n = 9, 2014 n = 2, 2015 n = 3). All lynx were live-trapped using specially designed box-traps (Kolbe et al., 2003) and fitted with store-on-board GPS collars (Lotek Wireless, Newmarket, Ontario, Canada or Sirtrack ltd., Havelock North, New Zealand) weighing < 3 % of lynx bodyweight. Lynx capture and handling methods were approved under University of Montana IACUC permits 4–2008 and TE053737-1. Lynx were primarily captured in January through March, with GPS collars programmed to collect one location every 30 min for 24 h on alternate days until the programmed drop-off date. On average, collars collected a mean of 129 days (range: 4–362) of data, and a mean of 2342 locations (range: 44–7626) during this time, with an average fix success of 86 %.

4. Lynx response to management type and timing

We defined the spatial extent of our analysis as the intersection of lynx home ranges, wildfires, and forest management actions, with the management polygon (or stand) as our individual sample unit. To estimate lynx home ranges, we used 95 % minimum convex polygons (MCP) for each lynx (n = 39) from 2004 to 2015; home ranges averaged 69 km^2 (range: 13–330 km^2). We used the MTBS (Monitoring Trends in Burn Severity; MTBS Project, 2015) dataset to determine the extent and severity of wildfires that overlapped with lynx home ranges within our study area; we included 25 fires from 1988 (the oldest fire in the MTBS dataset to overlap a lynx home range) to 2015 (to coincide with our most recent year of lynx locations); fires were 1 to 27 years old at the time of lynx use. To determine spatially co-occurring management actions, we used the FACTS (Forest Activity Tracking System) database, which is compiled by the U.S. Forest Service (USFS) and records the type and date of management action that took place (spatially limited to USFS land ownership and temporally spanning ~ 1960 to present), as well as the shape and location of the stand in which they occurred. For all analyses, we used this stand-based approach, with dependent and independent variables summarized to a given FACTS-based polygon.

For our study area, the FACTS database contained 48 unique categories of management actions that we determined would influence vegetation in some way. Previously, Holbrook et al. (2018) examined the response of Canada lynx in our study population to forest vegetation management, and developed a classification of management actions into categories based on a strong and differential signature of NBR (normalized burn ratio) across time that indicated variation in severity of vegetation removal and thus also of post-management vegetation recovery. The NBR correlates strongly with overstory and understory vegetation covariates, such as percent canopy cover (Hudak et al., 2004) and has been shown to reflect long-term vegetation recovery after a burn (Chen et al., 2011). Therefore, we adopted this same categorization, which classifies vegetation altering management actions depending on the severity of vegetation removal, into "Thinning", "Selection Cut", and "Regeneration Cut", from least to most severe, respectively (see Appendix A for the classification of all actions). In addition, we added the categories "Salvage Cut" and "Planting", as these were unique management actions that were associated with fires but were not represented in Holbrook et al. (2018). In general, Thinning treatments reflected partial canopy removal, generally of small trees ~ 15 cm, to improve stand growth; Selection Cut treatments included removal of overstory or competing trees to release remaining trees from competition; Regeneration Cut treatments were even-aged regeneration harvests such as clearcuts that removed all or most of the canopy; Salvage Cut treatments removed marketable timber after fire or insect loss without emphasizing regeneration; and Planting treatments were actions that introduced artificial regeneration.

We limited our dataset of management stands to post-fire actions ≤ 10 yrs after a fire and pre-fire actions ≤ 25 yrs before a fire, since we reasoned that actions that occurred >10 yrs after a fire were increasingly unrelated to the original fire conditions, and actions that occurred >25 yrs before a fire were old enough at the time of fire to be difficult to distinguish from unmanaged stands. Furthermore, we did not include stands with management both before and after a fire, which would confound our pre- versus post-treatment analysis. We also included stands where no active management occurred to serve as a comparison group. This resulted in a total of n = 900 stands for analysis. For each unique FACTS polygon, our initial thought was to assign a single management category to represent the management that had occurred there. As we assembled the dataset, however, we realized that many stands had multiple actions which occurred over a span of decades, and that these combinations would make the effects of individual management categories difficult to interpret. Therefore, we created a second, limited dataset with which to examine the effects of management category, since limiting FACTS polygons to one or two management categories resulted in the removal of as much as 58 % of the managed stands. For this limited dataset, we discarded stands that had more than two types of management categories throughout their history and removed any categories with less than n = 30 stands. Thus, we examined lynx response to pre-fire Salvage (n = 34) and Thinning (n = 36) and post-fire Salvage (n = 81), Planting (n = 48), Regeneration Cut (n = 52), and Regeneration Cut with Planting (n = 46). For both pre- and post-fire management type datasets, we included a random sample of stands with no management action ("No Action") as a comparison; the number of No Action stands was set equal to the management category with the largest sample size (i.e., in pre-fire dataset, No Action n = 36; in post-fire dataset, No Action n = 81). To determine the lynx response to management timing (either pre- or post-fire), or other fire-related covariates, we did not limit stands by management type and included stands that had multiple management actions, resulting in a full dataset of n = 900 stands (Pre-Fire n = 312, Post-Fire n = 276, No Action n = 312).

In addition to the type and timing of management relative to wildfire, we also evaluated other fire-related covariates that we hypothesized might influence lynx use of burned areas. We hypothesized that lynx use intensity would take longer to increase in high severity fire compared to low severity fire, since lynx prefer dense canopy cover and high horizontal cover (Squires et al., 2010). To measure burn severity, we calculated the mode of the MTBS fire severity raster, which uses the differenced normalized burn ratio (dNBR) to categorize burn severity into unburned (17 % of the stands), low (23 %), moderate (24 %), and high (36 %) severity. We hypothesized that stands promoting landscape homogeneity (i.e., larger area and lower perimeter to area ratio) would receive less lynx use over time than stands associated with landscape heterogeneity (smaller area and greater perimeter to area ratio). To determine the importance of stand shape and arrangement for lynx use, we used a series of landscape metrics defined in the Fragstats package (McGarigal and Marks, 1995) and implemented with the 'landscapemetrics' package in R (Hesselbarth et al., 2019). Thus, for each stand we calculated patch-level Fragstat metrics including perimeter, fractal dimension, and core area index. The 'perimeter' value is the perimeter of a polygon in m, the 'fractal dimension' statistic is a measure of shape complexity, with larger values indicating more complexity (i.e., greater perimeter to area ratio), and 'core area index' is a metric indicating the percent of a stand (patch) that is a given distance (we chose 50 m, a distance shown to be sufficient to avoid edge effect differences in temperature and moisture in subalpine managed stands; Redding et al., 2003) from a stand of a different category, with greater core area in larger, less complex stands. Stand sizes averaged 0.13 km^2 (range: 0.01 – 9.14 km^2), perimeter values averaged 2.0 km (range: 0.3 – 108 km), core area index values averaged 26.4 (range: 0 – 91.1), and fractal dimension averaged 1.05 (range: 0.98 – 1.56) with lower (less complex) values associated with stands averaging 0.06 km^2 in area and higher values associated with stands averaging 0.19 km^2 in area. We hypothesized that intensity of lynx use of a stand would increase more quickly if the surrounding landscape contained less burned or managed area (i.e., the managed stand was in a matrix of good habitat, as in Holbrook et al. [2018]). To determine the importance of the surrounding landscape on lynx use across time, we calculated the percentage of the area surrounding a given stand that was burned (i.e., inside the wildfire boundary) and the percentage that received any type of vegetation altering management action. We used a 4 km buffer around each management stand, chosen as the radius of average lynx home range size, as calculated in Holbrook et al. (2017). Percentages of surrounding burned area averaged 57.3 % (range: 9.3 % – 100 %) and surrounding management area averaged 30.2 % (range: 0 – 80 %). We hypothesized that since cooler, more moist areas are adapted to infrequent, severe fire, these vegetation types would recover more quickly than hot, dry forest types which are adapted to low-severity understory burns but now experience high-severity crown fires (Turner et al., 2003). We included potential vegetation type (PVT; Pfister and Arno, 1980), a descriptor of what vegetation is likely to grow on a specific site based on abiotic conditions, as a broad index of likely vegetation trajectory after fire. We used a categorical raster of PVT (Milburn et al., 2015) and determined the majority category for each stand, resulting in four levels: Cold (5 %), Cool Moist (84 %), Warm Dry (5 %), and Warm Moist (6 %).

For all analyses, we used generalized linear mixed models (Bolker et al., 2009) with a random intercept of individual fires to control for spatial non-independence of stands within a given fire. We fitted all models using the 'glmmTMB' package (Brooks et al., 2017) in program R (R Core Team, 2019) and standardized all continuous variables by subtracting the mean and dividing by the standard deviation using the package 'MuMIn' (Barton, 2015) for ease of model fitting and interpretability. Our dependent variable was intensity of lynx use, quantified as the count of all GPS locations inside a given treatment stand. Given the known differences in seasonal lynx habitat selection (Squires et al., 2010), we compiled intensity of use counts separately for summer (April – October) and winter (November – March). Since the number of lynx GPS locations inside a given stand is likely to be influenced by the size of the stand as well as the number of lynx locations in the general area, we calculated a correction term for each stand using the log of the stand area multiplied by the number of GPS locations inside the 4 km radius buffer around the stand (Holbrook et al., 2018; Lesmerises et al., 2013), and included this as an offset in the model to account for these stand-specific differences. For each stand we also calculated time since fire as the difference between the year of the wildfire and the year that lynx use occurred in that stand. If lynx use occurred over more than a single year, we calculated the median year based on all GPS locations inside that stand; we discarded any stands with a span of lynx use > 5 yrs. If stands had no lynx use (GPS locations n = 0), we calculated time since fire using the median of lynx use years within the 4 km buffer around the stand.

We initially tested several probability distributions to determine the best-fitting model for the data. Since our data were counts, we fitted a Poisson and a negative binomial, and since there were frequent zeroes in the data, we also considered zero-inflated and hurdle models fitted with a Poisson and negative binomial distribution (Brooks et al., 2017). We compared a base model consisting only of time since fire and each of these distributions using AIC (Akaike, 1974) and assessed goodness of fit by comparing the distribution of predicted and observed counts using a hanging rootogram (Kleiber and Zeileis, 2016); we determined the best-fitting distribution was the negative binomial and used this in all further models.

To address our first question of how timing of management relative to wildfire, either pre- or post-fire, influenced lynx use of burned areas, we fit a model with the interaction of management timing (categorical: Pre-Fire, Post-Fire, or No Action) and time since fire. Since lynx habitat use varies seasonally (Squires et al., 2010), we fit 2 models, a summer and a winter model, separately. To answer our second question of how the type of management action influences lynx use of burned areas, we fit a model with the interaction of management category and time since fire, using our limited dataset. We fit separate models for pre-fire and post-fire management, and for summer and winter, resulting in a total of 4 models of lynx response to management action. Finally, to understand any additional fire-related factors that might better explain differences in lynx use after a wildfire, we considered a set of 6 candidate models, constructed to address our hypotheses regarding fire severity, patch or shape characteristics, and landscape characteristics around a patch. Due to the limited dataset required for investigating type of management action, we did not include type of management action as a covariate in the set of candidate models. We used AIC to discriminate among these candidate models and select the best performing. For all selected models, we tested for model over or under-dispersion, zero-inflation, and the goodness of fit of our data to the modeled distribution using QQ plots and Kolmogorov-Smirnov tests in the 'DHARMa' package (Hartig, 2022). In addition, we investigated the presence of spatial autocorrelation in model residuals using Moran's I index from the R package 'pgirmess' (Giraudoux, 2022).

Table 1
The management timing model parameter estimates from a negative binomial generalized linear mixed model of the interaction of management timing (No Action, Pre-fire, Post-fire) with time since fire on lynx use intensity. Separate models for summer and winter are presented. Bold type indicates terms with 95% confidence intervals that do not overlap 0.

	Estimate	Std. Error	95 % Confidence Interval	
Summer Timing				
(Intercept)	−17.92	0.32	−18.54	−17.30
Post-fire	**−0.64**	**0.33**	**−1.29**	**0.01**
Pre-fire	0.39	0.28	−0.15	0.94
Time Since Fire	0.00	0.02	−0.04	0.04
Post*Time Since Fire	**0.05**	**0.02**	**0.02**	**0.08**
Pre*Time Since Fire	0.02	0.02	−0.01	0.06
Winter Timing				
(Intercept)	−18.58	0.40	−19.37	−17.78
Post-fire	**−1.24**	**0.51**	**−2.24**	**−0.24**
Pre-fire	**1.19**	**0.46**	**0.29**	**2.09**
Time Since Fire	0.04	0.02	−0.01	0.09
Post*Time Since Fire	**0.09**	**0.02**	**0.05**	**0.14**
Pre*Time Since Fire	−0.04	0.03	−0.11	0.03

5. Hare response to management type

As an additional step to further understand the drivers behind lynx use of burned and managed areas, we analyzed the relative abundance of their primary prey, snowshoe hares, relative to wildfire and forest management. We used the results of our lynx-based analyses to direct our focus on hares to wildfires with only post-fire management.

In 2015 and 2016, we sampled hare pellets and measured vegetation once per year in summer (June – Aug) at 178 plots in FACTS delineated polygons. To spatially align our hare data with our lynx area of inference, we sampled pellets on 13 fires within the distribution of lynx in our study area. We focused on fires between 22 and 28 years old at the time of sampling (fire year between 1985 and 1995) to allow time for post-fire management actions and vegetation recovery to take place. Fires ranged in size from approximately 1 km^2 to 137 km^2 and varied in severity. Within these fires, we sampled five categories of FACTS post-fire management actions, including clearcut (n = 28), clearcut and planted (n = 39), salvaged (n = 35), planted (n = 43), or no action (n = 33).

Within each plot, technicians sampled 36 subplots arranged in 3 linear transects of 12 subplots each, spaced 30 m apart, oriented to cover as much of the management stand as possible. At each subplot, we counted all hare pellets within a 1 m^2 uncleared (i.e., old and new pellets were counted) circular area (Murray et al., 2002); these subplots provide an index of relative hare abundance which has been shown to correlate strongly with actual hare density (Hodges and Mills, 2008; Mills et al., 2005). In addition, we recorded summer vegetation data at each plot to further determine what factors corresponded with greater hare abundance. We estimated the percentage of grass and forb ground cover inside each circular pellet subplot. We also estimated horizontal cover (vegetation cover resulting primarily from tree boughs, saplings, and shrubs; Squires et al., 2010) at the beginning, middle, and end of each transect, for a total of 9 cover estimates per plot. Cover was estimated using a 0.5 m by 2 m rectangular canvas sheet, divided into four 0.5 m squares. The sheet was held by the short side and suspended perpendicularly to the ground, with the bottom of the sheet touching the ground, in a random direction 10 m away from subplot center. For each 0.5 m square, we estimated the percent covered by vegetation and averaged these for a single measure of cover per board and averaged all 9 subplot cover estimates for a single estimate of horizontal cover per plot. For plots sampled in 2016, we collected two additional measures of vegetation at the beginning, middle, and end of transects: within a 6.8 m radius plot, we recorded the species and DBH (diameter at breast height, 1.37 m) of all trees > 2.5 cm and the species and number of all shrubs with a DBH of > 1.3 cm.

To test for differences in pellet abundance depending on forest management action type, we used the same approach as in the lynx analysis with a generalized linear mixed model with a negative binomial distribution and a random intercept of plot nested within individual fires to control for spatial non-independence. We fit the count of pellets at each subplot as the dependent variable and the management action as the independent. We used the Mills et al. (2005) equation ($y = 0.63x - 1.14$), which was developed on our study area, to convert our modelled pellet counts into hares per hectare for ease of interpretation. To provide further comparison with lynx results, we evaluated the response of hare pellet abundance to the other fire related covariates that we explored for lynx, including severity, type of management action, proportion of fire and management in the surrounding neighborhood, potential vegetation type, and size and shape of management stands. Since hares have small home ranges (3 ha [Keith et al., 1993] to <10 ha [Dolbeer and Clark, 1975] in the continental United States) and are less mobile than lynx (maximum movement distance 730 m in a Montana population [Griffin, 2004]), we considered both 4 km and 1 km buffers when evaluating hare response to the proportion of fire and management in the surrounding neighborhood. We fit 7 candidate models to the hare data and used AIC to determine the best performing. We also summarized our vegetation measurements within the five categories of management actions. Within each management type, we calculated the mean (±SD) percent horizontal cover, grass cover, and forb cover across all plots. We also calculated mean trees per acre by size class (5.1–12.7 cm [2–5 in], 12.7–25.4 cm [5–10 in], 25.4–38.1 cm [10–15 in], >=38.1 cm [>=15 in]) and by species (five groups: *Larix occidentalis; Pinus contorta; Pseudotsuga menziesii; Abies lasiocarpa/Picea engelmannii;* and all other species). For all vegetation metrics, we used non-parametric Kruskal-Wallace tests, chosen because our data did not meet the normality assumption necessary for one-way analysis of variance, to test for differences in mean vegetation metrics among management activities, and pairwise Wilcoxon rank sum tests to test for differences among individual groups (Kutner et al., 2005).

6. Forest vegetation and management type and timing

Finally, we investigated satellite-derived forest vegetation dynamics to verify that differences in vegetation relating to the type and timing of management in burned areas were present and to provide further understanding of the forest successional drivers behind differences in lynx and hare use. We examined two raster time-series of remotely sensed indicators of vegetation from 1972 to 2015: annual normalized burn ratio (NBR) and modeled forest structure classes. The normalized burn ratio is a measure of vegetation reflectance created using the near infrared (NIR) and shortwave infrared (SWIR) bands, calculated here using Landsat data series 1 through 8. The forest structure classes were taken from Savage et al. (2018), and represent four structure classes ("Stand Initiation", "Advanced Regeneration", "Mature", and "Sparse") which were modeled at 30 m resolution using all bands of the above-mentioned Landsat data and machine learning classification methods (see Savage et al. [2018] for detailed methods). Briefly, Stand Initiation structure class is marked by stands with few, generally young trees due to recent disturbance; Advanced Regeneration is early to mid-seral stands of ~ 25–40 yrs; Mature is multi-storied stands of ≥40 yrs; and Sparse is stands with few trees (see Holbrook et al. [2017] Table 2 for a detailed silvicultural description of the structure classes). For each forest management stand in our dataset, we calculated the mean value of NBR and the percent of each of the four structure classes within the stand per year across the entire time series (1972 to 2015). We then averaged the stands by year based on when the wildfire occurred (i.e., year of wildfire = year 0, subsequent years = year 0 + t, where t = 1–27) to generate a mean (±90 % confidence interval) vegetation trajectory across time to visualize differences in vegetation impact immediately after a fire and vegetation recovery post wildfire. To assess the impact of management

Table 2
The management type model parameter estimates from a negative binomial generalized linear mixed model of the interaction of pre-fire management action type (No Action, Salvage, Thinning) or post-fire management action type (Non-Managed, Planting, Planting/Regeneration Cut, Regeneration Cut, Salvage) with time since fire on lynx use intensity. Separate models for summer and winter are presented. Bold type indicates terms with 95% confidence intervals that do not overlap 0.

	Estimate	Std. Error	95 % Confidence Interval	
Summer Pre-fire				
(Intercept)	−17.98	0.56	−19.08	−16.87
Salvage	−0.85	1.02	−2.85	1.15
Thinning	0.67	0.77	−0.84	2.18
Time Since Fire	0.01	0.03	−0.06	0.06
Salvage*Time Since Fire	0.11	0.08	−0.05	0.27
Thinning*Time Since Fire	0.01	0.05	−0.08	0.10
Winter Pre-fire				
(Intercept)	−22.02	2.27	−26.47	−17.57
Salvage	3.65	2.44	−1.14	8.44
Thinning	4.93	2.55	−0.08	9.95
Time Since Fire	0.14	0.10	−0.05	0.33
Salvage*Time Since Fire	−0.20	0.14	−0.48	0.09
Thinning*Time Since Fire	−0.25	0.17	−0.58	0.08
Summer Post-fire				
(Intercept)	−18.17	0.32	−18.81	−17.54
Planting	−0.55	0.96	−2.42	1.33
Planting/Regen Cut	−0.88	0.72	−2.28	0.53
Regen Cut	**−1.69**	**0.71**	**−3.09**	**−0.29**
Salvage	−0.23	0.54	−1.30	0.83
Time Since Fire	**0.03**	**0.02**	**0.00**	**0.07**
Plantin*Time Since Fire	0.02	0.04	−0.06	0.10
Planting/Regen Cut*Time Since Fire	**0.06**	**0.03**	**0.00**	**0.12**
Regen Cut*Time Since Fire	**0.09**	**0.03**	**0.03**	**0.16**
Salvage*Time Since Fire	0.01	0.03	−0.05	0.07
Winter Post-fire				
(Intercept)	−18.65	0.45	−19.54	−17.76
Planting	0.24	1.42	−2.55	3.02
Planting/Regen Cut	−0.76	1.02	−2.77	1.24
Regen Cut	−0.50	0.89	−2.25	1.24
Salvage	−0.85	0.76	−2.33	0.63
Time Since Fire	**0.09**	**0.02**	**0.05**	**0.13**
Planting*Time Since Fire	−0.03	0.06	−0.15	0.09
Planting/Regen Cut*Time Since Fire	0.03	0.05	−0.06	0.12
Regen Cut*Time Since Fire	0.03	0.04	−0.05	0.11
Salvage*Time Since Fire	0.03	0.04	−0.05	0.11

action type and timing on vegetation trajectories, we grouped averages by action type (No Action, Salvage, Thinning, Planting, Regeneration Cut) and timing (Pre-Fire, Post-Fire, or No Action). In addition, to determine whether we observed differences in fire severity based on management timing in our study area, we calculated the number of our sample stands in each MTBS fire severity category (Unburned, Low, Medium, High) by management timing group (Pre-Fire, Post-Fire, or No Action).

7. Results

7.1. Lynx response to management type and timing

Our results indicate that both the timing of management actions relative to fire and the type of management action influenced lynx intensity of use after a wildfire. In winter and summer, lynx use of stands with management that occurred after the fire (post-fire management) increased over time, while use in pre-fire managed and non-managed stands remained largely constant over time and did not differ from each other (Table 1). Similarly, the type of management action also influenced lynx intensity of use, but only for post-fire management; stands that had been salvage logged or thinned pre-fire did not significantly differ in lynx use over time from stands that received no management (Table 2). Post-fire management actions, however, differed significantly in lynx use over time: post-fire regeneration cuts increased use more quickly compared to non-managed stands. This effect of management action was present in summer but not in winter (Table 2).

Fire severity as well as timing of management action relative to wildfire were the most predictive of lynx use intensity (Table 3). In winter, lynx intensity of use increased more quickly over time given post-fire management, and lynx used high severity fire stands significantly less than unburned; we found no difference in use among unburned and low or moderate severity (Table 4; Fig. 2). In summer, the same model of fire severity and management timing was the most predictive, although there was some model uncertainty, with the candidate model containing shape characteristics of a management stand within 2 ΔAIC of the top performing model (Table 3). In summer, lynx use intensity was again influenced by severity, with low and high severity fire used less intensely than unburned, and by timing, with intensity of use in post-fire managed stands increasing more steeply over time than pre-fire or non-managed stands (Table 4; Fig. 2). In the second-most supported model, lynx use intensity differed based on stand shape characteristics; when stand core area was low (i.e., small or less compact shapes) lynx use was greater and did not differ between managed and non-managed stands; when core area was high (i.e., larger or simpler shapes) lynx used managed stands more intensely than non-managed stands (Appendix B Fig. B.1).

Model validation metrics indicated good fit of all selected models. QQ plots showed no deviation from the expected distribution, with non-significant ($p \geq 0.05$) Kolmogorov-Smirnov tests for all models. Similarly, there was no evidence of consistent spatial autocorrelation among residuals for any models, with all Moran's I coefficients ≤ 0.1 ($p \geq 0.05$).

8. Hare response to management type

The relative abundance of hares showed a clear response to post-fire management in 22–28-year-old fires. Model predictions showed the greatest number of pellets in clearcut stands ($\beta = 1.13$, SE = 0.29, $p < 0.01$), while planted ($\beta = 0.73$, SE = 0.26, $p = 0.01$) and clearcut with planting ($\beta = 0.61$, SD = 0.27, $p = 0.02$) both also had significantly more pellets than non-managed stands, and salvaged stands did not differ from non-managed stands ($\beta = -0.07$, SE = 0.28, $p = 0.81$; Fig. 3). Based on these modeled values, in clearcuts, plots had a predicted 1.9 hares/ha; planted had 1.5; planted with clearcut had 1.4; salvaged had 0.9; and non-managed had 0.9 hares/ha. We found no consistent patterns of difference in ground cover (grass or forbs) or horizontal cover relative to our management type categories (see Appendix C). Based on vegetation results from 2016, however, the tree density differed significantly among management categories for all size classes and species groups (except spruce/fir). Most significant differences occurred between clearcut and all other categories, notably with more midsize (12.7–25.4 cm [5–10 in] DBH) trees and more lodgepole pine trees in clearcuts compared to all other groups (see Appendix C Table C.1 for results from Wilcoxon ranked sum tests). The evaluation of candidate models with other fire-related factors revealed the strongest predictor of hare pellet abundance was the proportion of managed area surrounding the stand at the 4 km scale (Table 5). There was a significant interaction between the type of management in a stand and the proportion of managed area surrounding that stand. Specifically, the abundance of hares in non-managed stands increased when the surrounding landscape had greater amounts of management; this was also true for stands with salvage logging, but not for any other management actions, which did not differ based on the surrounding landscape (Table 6) (see Table B1).

Table 3
Candidate model selection results of other fire-related characteristics from negative binomial generalized linear mixed models that examine the influence of fire-related covariates on lynx intensity of use of burned and managed areas. Table shows the Hypothesis that the model was created to test, the Model Specification shows additive or interactive model covariates, K is the number of model parameters, AICc is the AIC score for small sample sizes, ΔAICc is the change in AIC from the top model to each other model, and AICcWt is the weight of each model. Results for summer and winter models are shown separately.

Hypothesis	Model Specification	K	AICc	ΔAICc	AICcWt
Summer					
Severity and Timing	Severity+ Timing*Time Since Fire	11	2938.27	0	0.63
Stand Characteristics	Fractal*Timing + CAI*Timing+ Perimeter*Timing	10	2939.37	1.1	0.36
Timing	Timing*Time Since Fire	8	2946.36	8.09	0.01
Landscape Characteristics	Pct Mgmt 4 k*Time Since Fire + Pct Fire 4 k*Time Since Fire	8	2959.57	21.3	0
Habitat Type and Severity	PVT*Time Since Fire+ Severity	13	2960.9	22.63	0
Severity	Severity*Time Since Fire	10	2964.78	26.52	0
Winter					
Severity and Timing	Severity+ Timing*Time Since Fire	11	1909.17	0	0.89
Timing	Timing*Time Since Fire	8	1913.4	4.23	0.11
Stand Characteristics	Fractal*Timing + CAI*Timing+ Perimeter*Timing	10	1920.62	11.46	0
Habitat Type and Severity	PVT*Time Since Fire + Severity	13	1937.52	28.35	0
Severity	Severity*Time Since Fire	10	1940.9	31.74	0
Landscape Characteristics	Pct Mgmt 4 k*Time Since Fire+ Pct Fire 4 k*Time Since Fire	8	1953.88	44.72	0

Table 4
Model parameter estimates from the 'Severity and Timing' top-performing candidate model of other fire-related covariates on lynx intensity of use for summer and winter. For both seasons, the top-performing model included an interaction effect between management timing (Non-Managed, Pre-fire, Post-fire) and time since fire plus a categorical measure of fire severity. Bold type indicates terms with 95% confidence intervals that do not overlap 0.

	Estimate	Std. Error	95 % Confidence Interval	
Summer				
(Intercept)	−17.71	0.33	−18.35	−17.07
SeverityLow	**−0.29**	**0.15**	**−0.58**	**−0.01**
SeverityMedium	−0.24	0.16	−0.56	0.08
SeverityHigh	**−0.58**	**0.16**	**−0.89**	**−0.28**
Postfire	−0.56	0.33	−1.21	0.10
Prefire	0.41	0.28	−0.15	0.96
Time Since Fire	0.01	0.02	−0.04	0.05
Postfire*Time Since Fire	**0.05**	**0.02**	**0.02**	**0.08**
Prefire*Time Since Fire	0.02	0.02	−0.02	0.05
Winter				
(Intercept)	−18.5	0.42	−19.32	−17.69
SeverityLow	−0.21	0.22	−0.65	0.22
SeverityMedium	−0.11	0.23	−0.57	0.35
SeverityHigh	**−0.71**	**0.24**	**−1.19**	**−0.24**
Time Since Fire	**0.06**	**0.02**	**0.01**	**0.10**
Postfire	**−1.22**	**0.52**	**−2.24**	**−0.20**
PreFire	**1.31**	**0.47**	**0.39**	**2.23**
Post*Time Since Fire	**0.1**	**0.02**	**0.05**	**0.15**
Pre*Time Since Fire	−0.05	0.03	−0.12	0.01

9. Forest vegetation and management type and timing

The vegetation analyses provided a better understanding of the mechanisms behind lynx use of burned and managed areas. Pre-fire management resulted in less initial impact (smaller drop in NBR) to vegetation immediately after a fire, and thus a faster (approximately 10–15 years) return to the range of NBR values found in unburned lynx home ranges (Fig. 4). Stands that were thinned before a fire (n = 36) demonstrated the least impact to vegetation immediately post-fire and recovered the most quickly, while stands with pre-fire salvage logging (n = 34) took slightly more time to recover; both types of managed stands experienced less immediate vegetation impact and faster recovery than stands that were burned but not managed (n = 36; Fig. 4). Post-fire managed stands experienced a large initial drop in NBR due to fire and vegetation removal activities, and thus took longer (~20–25 years) to return to conditions favored by lynx. The type of post-fire management did not apparently influence vegetation recovery, with stands that had been planted (n = 48), salvage logged (n = 81), regeneration cut (n = 52), regeneration cut and planted (n = 46), or not managed (n = 81) all displaying overlapping NBR trajectories. However, ~15–20 years after a fire, stands with any type of post-fire management began to outpace non-managed stands in recovery, and ~ 25 years after a fire the NBR values for some management categories (regeneration cuts alone and with planting) became higher than any found in pre-fire managed stands (Fig. 4).

The analysis of forest structure also indicated differences resulting from the timing (Pre- or Post-Fire) of management actions (Fig. 5). Before the onset of fire, pre-fire management resulted in stands with greater amounts of sparse forest and less mature forest than non-managed or post-fire managed stands. After the fire, for ~ 10 years, stand initiation increased sharply, especially in post-fire managed stands. At ~ 20–25 years after the fire, the advanced regeneration structure class began to peak, particularly for the pre- and post-fire managed groups; non-managed stands did not see a large increase in advanced regeneration structure, but instead an increase in sparse forest structure. Mature forest was low for all groups after the wildfire, but highest in non-managed stands. We also found differences in fire severity based on when management action took place. Pre-fire management had an almost even split among severity groups across stands (unburned 29 %, low 28 %, medium 24 %, high 19 %), while non-managed and post-fire stands had more high severity (non-managed: unburned 19 %, low 19 %, medium 22 %, high 40 %; post-fire: unburned 5 %, low 20 %, medium 28 %, high 47 %). Based on these results and the slow recovery trajectory of non-managed stands, we also performed a post-hoc investigation of non-managed stands to verify that there were no intrinsic differences in stand accessibility (such as slope or elevation) or vegetation productivity (such as precipitation, soil pH, or past NBR) that might confound the response to fire and found no evidence this was the case (see Appendix D for full details of this analysis).

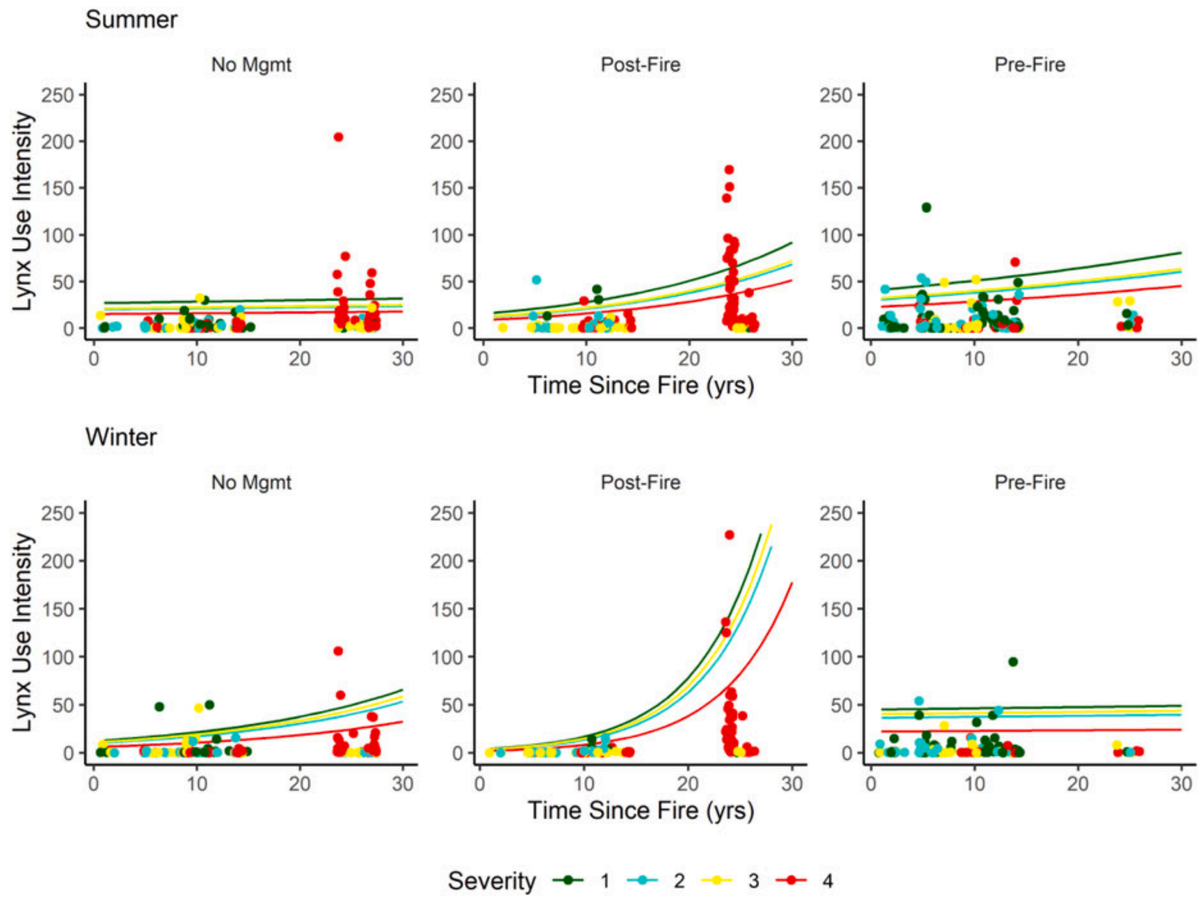

Fig. 2. Predicted intensity of lynx use over time in burned and managed stands as an effect of management timing relative to fire (No management, Post-Fire, Pre-Fire) and the severity of the fire inside the polygon (Severity 1 = Unburned, 2 = Low, 3 = Moderate, 4 = High). Dots show actual counts of lynx GPS points inside stands, lines show modeled predictions.

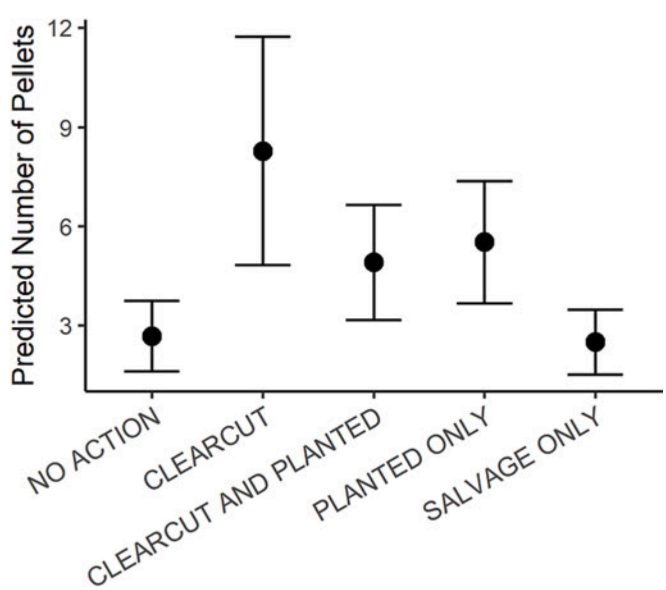

Fig. 3. The modeled estimate of hare pellet counts (±95 % Confidence Interval) in each of the categories of post-fire management actions across which hare pellets were sampled in western Montana, 2015 and 2016. Compared to the "No Action" group, hare pellets were significantly more abundant in "Clearcut", "Clearcut and Planted", and "Planted Only"; there was no difference between "No Action" and "Salvage" groups.

10. Discussion

Understanding how rare carnivores respond to a combination of wildfire and forest management actions intended to prevent or ameliorate fire damage is important given the current widespread conditions of increased warming temperatures, drought, and fire. Our work showed that management actions can improve the outcome of wildfire for lynx and provides novel insights into the relative impacts of pre- and post-fire active management and passive management as well as the type of action influencing the timing and intensity of lynx use. Stands that received forest management action up to 25 years before a wildfire tended to burn at lower severity and were used more by lynx immediately after a wildfire and consistently thereafter. Burned areas that were managed after a fire were used by lynx at very low intensity for at least 10 years after a wildfire but experienced a steep increase in use intensity by approximately year 25, to achieve the greatest lynx use that we documented during the study period. Our hare results offer a clear driver for this pattern: snowshoe hares were found at their highest abundance in clearcut stands approximately 25 years after a wildfire, and mid-sized lodgepole pines, a preferred food item for hares (Ellsworth et al., 2013), were also more abundant in this category. Taken together, these results can inform the actions managers take to improve the outlook of lynx habitat given increased pressure from wildfires. Importantly, our findings stress the need to maintain a mosaic of forest management on the landscape to provide favorable lynx habitat in the short and long term after a wildfire.

The influence of the timing of forest management relative to wildfire

Table 5
Candidate model selection table for other fire-related covariates on hare pellet counts in polygons with 22–28 year old fires and post-fire management using negative binomial generalized linear mixed models. Table shows the Hypothesis that the model was created to test, Model Specification shows additive or interactive covariates, K is the number of model parameters, AICc is the AIC score for small sample sizes, ΔAICc is the change in AIC from the top model to each other model, and AICcWt is the weight of each model.

Hypothesis	Model specification	K	AICc	ΔAICc	AICcWt
Landscape Characteristics	Pct Mgmt 4 k*Treatment+ Pct Fire 4 k*Treatment	18	22,419	0	0.92
Severity and Type	Severity*Treatment	13	22423.9	4.91	0.08
Landscape Characteristics	Pct Mgmt 1 k*Treatment+ Pct Fire 1 k*Treatment	18	22430.3	11.31	0
Severity	Severity	5	22432.2	13.24	0
Type	Treatment	8	22438.6	19.61	0
Habitat Type and Severity	PVT*Treatment	18	22442.1	23.14	0
Stand Characteristics	Fractal*Treatment + CAI*Treatment+ Perimeter*Treatment	23	22454.7	35.72	0

Table 6
Model parameter estimates from the ‘Landscape Characteristics’ hypothesis top-performing candidate model of other fire-related covariates on hare pellet counts. The model included an interaction effect between management type and the proportion of management in the 4 km neighborhood and a non-significant interaction between management type and the proportion of burned area in the 4 km neighborhood. Bold type indicates terms with 95 % confidence intervals that do not overlap 0.

	Estimate	Std. Error	95 % Confidence Interval	
(Intercept)	1.26	0.22	0.84	1.69
Pct Mgmt 4k	**0.79**	**0.27**	**0.26**	**1.32**
Clearcut	**0.84**	**0.31**	**0.24**	**1.44**
Clearcut and Planted	0.42	0.27	−0.11	0.96
Planted	0.41	0.27	−0.12	0.93
Salvage	−0.07	0.29	−0.63	0.49
Pct Fire 4k	0.07	0.26	−0.44	0.57
Pct Mgmt 4k* Clearcut	**−0.73**	**0.33**	**−1.37**	**−0.08**
Pct Mgmt 4k*Clearcut and Planted	**−0.63**	**0.33**	**−1.27**	**0.01**
Pct Mgmt 4k*Planted	**−0.70**	**0.33**	**−1.35**	**−0.05**
Pct Mgmt 4k*Salvage	0.13	0.34	−0.53	0.80
Pct Fire 4k*Clearcut	−0.13	0.34	−0.79	0.54
Pct Fire 4k*Clearcut and Planted	0.24	0.30	−0.35	0.84
Pct Fire 4k*Planted	0.07	0.31	−0.55	0.68
Pct Fire 4k*Salvage	0.12	0.34	−0.55	0.78

Table B1
This table shows model parameter estimates from the ‘Stand Characteristics’ hypothesis second-ranked candidate model of fire-related covariates on summer lynx use intensity. The interaction between core area index (CAI) and the presence or absence of management (Active Mgmt) is weakly significant. Bold type indicates terms with 95% confidence intervals that do not overlap 0.

	Estimate	Std. Error	95 % Confidence Interval	
(Intercept)	−17.76	0.18	−18.11	−17.41
Fractal	−0.10	0.15	−0.40	0.19
Active Management	**0.44**	**0.11**	**0.22**	**0.67**
CAI	**−0.40**	**0.13**	**−0.65**	**−0.15**
Perimeter_m	0.09	0.11	−0.14	0.31
Fractal*Active Mgmt	0.07	0.20	−0.33	0.46
CAI*Active Mgmt	**0.34**	**0.18**	**−0.01**	**0.69**
Perimeter_m*Active Mgmt	−0.26	0.17	−0.60	0.08

on lynx use intensity is one of the most important findings of this work, given the current U.S. plan to address the national wildfire crisis with active management strategies (Wildfire Crisis Strategy, 2022). A reduction in forest fuels is one of the main tools used in the U.S. to reduce fire severity (Stephens et al., 2021) and has been applied effectively in dry forest (Strom and Fulé, 2007) and mixed conifer types (Prichard et al., 2010; Waltz et al., 2014). Treated areas in these studies showed lower tree mortality (Prichard et al., 2010; Strom and Fulé, 2007) and greater retainment of large trees (Prichard et al., 2010; Waltz et al., 2014). Ecological and outcome-driven justification for fuels removal in subalpine forests is more complex; these forests are generally considered to have a climate limited fire regime, with accumulated fuels a threat only when they have dried out sufficiently due to weather conditions, resulting in historically infrequent and mixed to severe wildfires (Bessie and Johnson, 1995; Coop et al., 2020). Thus, fuel

Table C1
This table shows the results of non-parametric Kruskal-Wallace tests for differences between means across types of management groups (Non-Managed, Clearcut, Clearcut/Planted, Planted, and Salvaged) for each measure of vegetation recorded at hare pellet sample plots. Vegetation metrics include percent horizontal cover, percent grass cover, and percent forb cover sampled in 2015 and 2016, and measures of trees per acre (TPA) across size class (5.1–12.7 cm [2–5 in], 12.7–25.4 cm [5–10 in], 25.4–38.1 cm [10–15 in], >=38.1 cm [>=15 in]) and by species (grouped into 5 categories: LAOC = *Larix occidentalis;* PICO = *Pinus contorta;* PSME = *Psuedotsuga menziesii;* ABLA/PIEN = *Abies lasiocarpa/ Picea engelmannii;* and Other = all other species). The group numbers are used in Table C.2 to indicate differences between specific management groups.

Group Number	Vegetation Metric	Chi sq	DF	P-value
	Horizontal Cover	10.71	4	0.03
	Grass	15.53	4	<0.01
	Forbes	10.03	4	0.04
1	TPA 2–5	22.54	4	<0.01
2	TPA 5–10	33.34	4	<0.01
3	TPA 10–15	17.49	4	<0.01
4	TPA > 15	11.77	4	0.02
5	LAOC	18.29	4	<0.01
6	PICO	25.45	4	<0.01
7	PSME	18.80	4	<0.01
8	ABLA/PIEN	4.33	4	0.36
9	Other	18.69	4	<0.01

Table C2
This table indicates significant pairwise differences as determined by Wilcoxon rank sum tests between management groups for each tree per acre size class and species group. The number listed in a given cell indicates a significant difference between those management groups for that vegetation metric (refer to Table C.1 for group numbers and the vegetation metrics they denote). For example, a ‘2′ in the first row and first column indicates a significant pairwise difference in trees per acre for size class 12.7–25.4 cm [5–10 in] DBH between non-managed polygons and clearcut polygons. Refer to Figs. C.1-C.3 for boxplots illustrating the direction of the differences.

	Non-Managed	Clearcut	Clearcut/Planted	Planted
Clearcut	2,6,7			
Clearcut/Planted	3,5	2,6,7,9		
Planted	5	1,2,6,7,9	1,4	
Salvaged		2,6,9	3	1

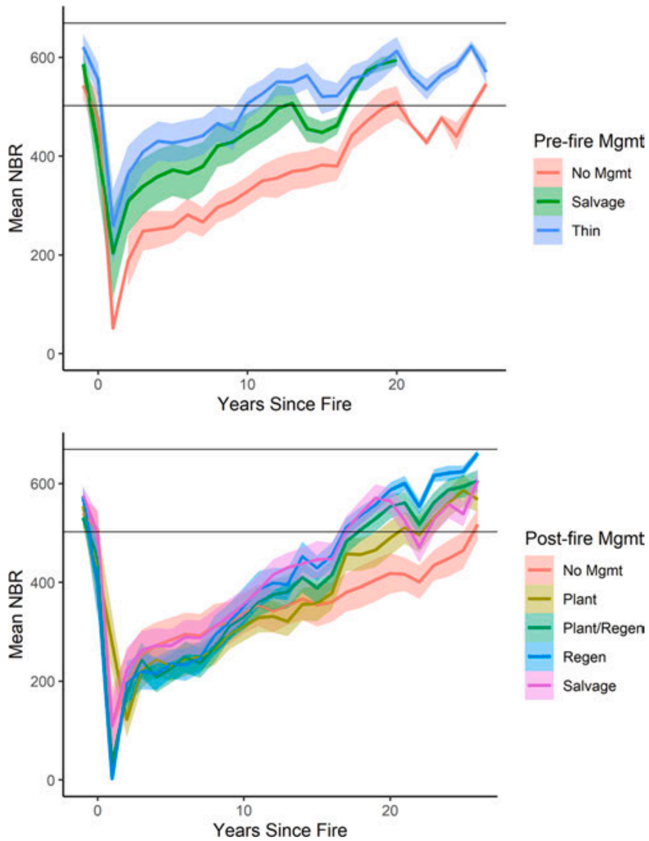

Fig. 4. The mean (±90 % Confidence Interval) normalized burn ratio (NBR) trajectory over time since fire for different types of management actions that occurred either pre- (top panel) or post-fire (bottom panel). Different colors represent different management actions. Solid horizontal black lines represent the interquartile range of NBR values at actual lynx GPS locations.

removal in mesic mixed conifer and subalpine forests may be a lower management priority given greater need in dry type forests (Agee and Skinner, 2005; Brown et al., 2004), although this may change as climate conditions continue to warm and dry (Jolly et al., 2015). Our work showed that management applied before a wildfire in mesic mixed conifer and subalpine spruce-fir forests reduced the proportion of high severity burned stands and resulted in wildfires that showed a smaller initial decrease of NBR, an indicator of vegetation greenness and recovery (Chen et al., 2011), and a faster return to the NBR values found in undisturbed lynx home ranges. We therefore expected that lynx would

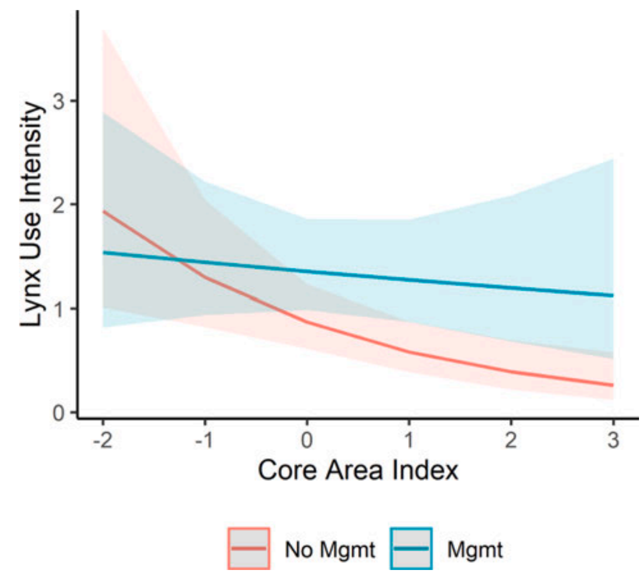

Fig. B1. This plot shows the predicted response of summer lynx use intensity to the interaction between core area index (CAI), a measure of polygon complexity, and whether a burned polygon received any type of forest management or not. Lower CAI indicates smaller stands or greater shape complexity, while higher values indicate larger, less complex stands.

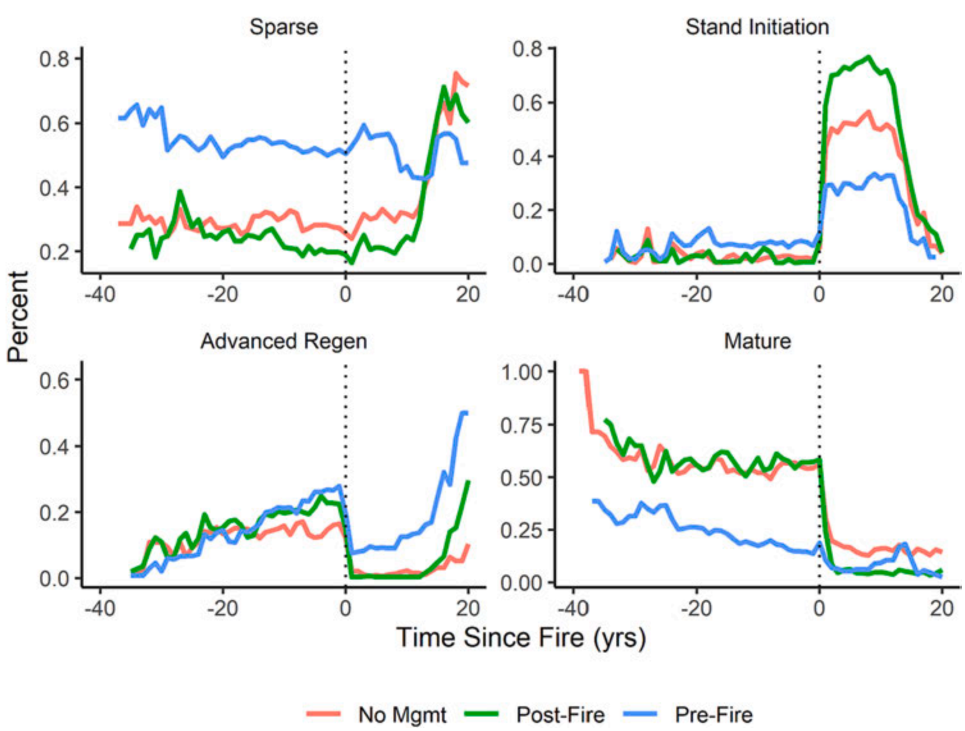

Fig. 5. The percent of all stands in a given management timing category (Non-Managed, Post-fire, Pre-fire) that are made up of each forest structure class (as classified by Savage et al. 2018) in a given year relative to the wildfire. Year '0' indicates the year that a wildfire occurred and is indicated by a vertical dashed black line. For reference, before a fire, non-managed polygons (red line) in our study averaged ~ 30 % sparse structure, <10 % stand initiation, ~10 % advanced regeneration, and ~ 60 % mature. After a fire, non-managed polygons showed an immediate increase in stand initiation, a sharp drop in mature, and an increase over time in sparse and advanced regeneration structure classes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

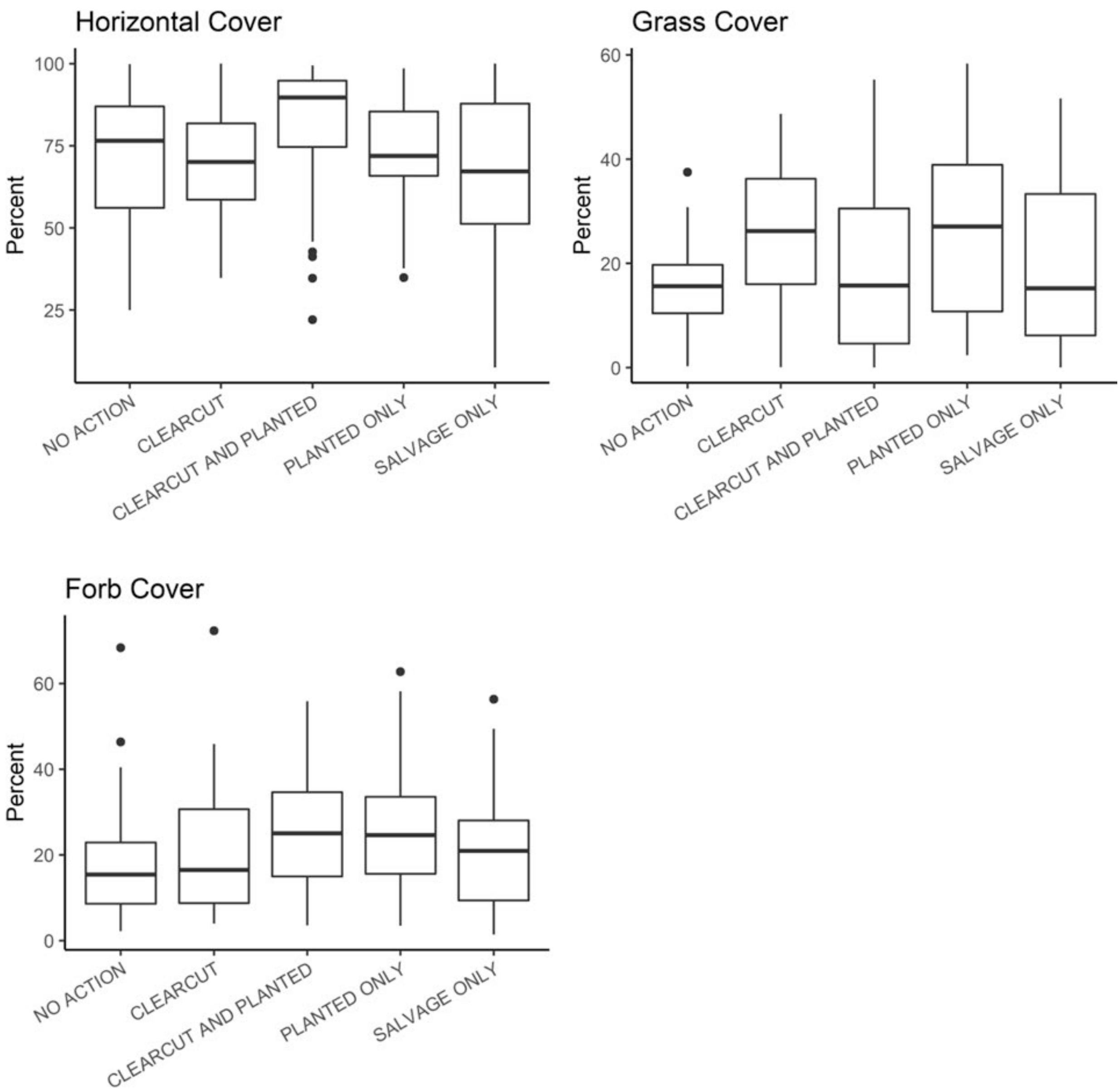

Fig. C1. Boxplots of horizontal cover, grass cover, and forb cover sampled at hare pellet plot locations across various categories of post-fire management actions in 22–28 year old fires in western Montana, 2015 and 2016. No consistent pattern of differences is demonstrated across these measured variables across post-fire management types.

use these areas at greater intensity after a wildfire. Interestingly, however, we found that while lynx use of these areas was consistently greater than non-managed areas (although not statistically so), their use remained relatively low over time and was dwarfed by the high use of post-fire managed stands ~ 25 years after the fire. Lynx have been shown to prefer dense forest with high horizontal cover (Holbrook et al., 2017; Squires et al., 2010), and thus while pre-fire management appears to reduce burn severity and allow the persistence of more vegetation and therefore more hare habitat, it does not appear to be sufficient to encourage high lynx use. However, this type of management may provide a crucial temporal bridge for lynx, generating enough habitat for prey immediately after a wildfire that lynx are able to maintain occupancy of burned areas while waiting for other areas to become suitable.

The type of management action had less of an effect on lynx use of burned stands than we initially predicted. We expected lynx use intensity to be influenced by the severity of the management action, with more severe vegetation removal (i.e., regeneration cuts) leading to increased time to lynx use. In a previous study on the same population of lynx, Holbrook et al. (2018) found an effect of treatment severity on lynx use of managed forest, with quicker use of areas that had been thinned versus those that had been subject to more severe selection or regeneration cuts. When combined with wildfires, however, we did not find a similar effect; differences in treatment type before a wildfire did not influence lynx use after the fire, and after a wildfire, we found greater lynx use over time only in the summer in the more severe regeneration cuts. Our investigation of snowshoe hares and forest characteristics supports a prey-related driver of this pattern of lynx use, as we found a greater abundance of snowshoe hares in post-fire clearcut (i.e., regeneration cut) stands, which are characterized by a complete removal of forest canopy post-wildfire, and subsequently result in a rapid development of a new tree cohort and a large proportion of advanced regeneration forest structure (i.e., saplings) ~ 25 years post-management. Clearcut stands were characterized at the time of hare and lynx use by a predominance of lodgepole pine in small and medium size classes (5.1–25.4 cm DBH). Snowshoe hares have been shown to prefer lodgepole pine as forage (Ellsworth et al., 2013; Wirsing and

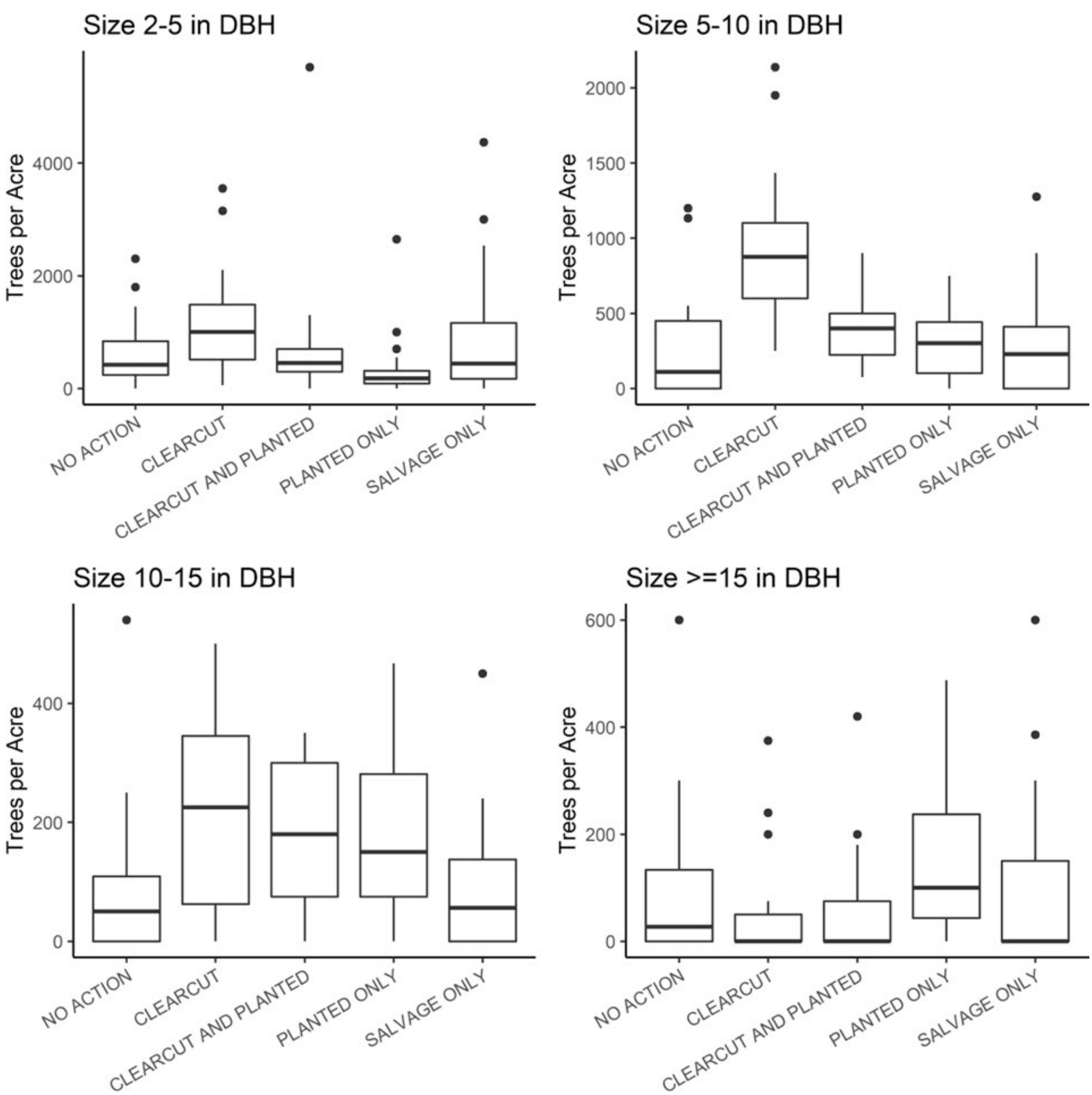

Fig. C2. Boxplots of four size classes of trees (5.1–12.7 cm [2–5 in], 12.7–25.4 cm [5–10 in], 25.4–38.1 cm [10–15 in], >=38.1 cm [>=15 in]) sampled at hare pellet plot locations across various categories of post-fire management actions in 22–28 year old fires in western Montana, 2015 and 2016. The 'Clearcut' category has greater median trees per acre for all size classes < 38.1 cm [15 in] DBH.

Murray, 2002) and to select mid-successional forest with dense stem counts, with high use generally 20–30 years after disturbance: hares were most numerous 15–40 years after disturbance in Idaho (Thornton et al., 2012), 17 years after fire in Montana (Cheng et al., 2015), and 20 years after disturbance in Washington (Koehler, 1990). In the Alaskan taiga, Canada lynx and snowshoe hares both showed a preference for 25–28 year old burns, in forests with ~ 9000 saplings/ha and 900 live trees/ha (Paragi et al., 1997). A caveat to our results, however, is our small sample size, particularly for pre-fire management actions. Stands in our study area tended to be subject to multiple forest management actions over time; to avoid confounding different silvicultural actions, we did not include stands with more than two management categories, which severely limited our sample size and thus our ability to detect patterns in lynx use relative to pre-fire management type over time. Furthermore, lynx response to pre-fire management actions may be mediated by disturbance to the understory, with treatments that preserve understory trees likely to favor faster recovery of snowshoe hare and lynx habitat (Squires et al., 2020; Sullivan et al., 2010). Anecdotally, we have observed stands in our study area that were treated pre-fire with a management action that removed small understory trees and were then generally avoided by lynx due to low horizontal cover for more than two decades post-treatment. Thus, while our results did not detect a difference in lynx use depending on the type of pre-fire management action, we recommend that managers consider the importance of the understory to lynx and hares when planning large fuel removal treatments.

Fire severity was also an important factor in lynx use of previously burned areas: lynx used high severity fire less over time compared to non-burned areas. Severity is a key factor influencing the impact of wildfire on wildlife habitat. Marten (*Martes caurina*) and lynx have been shown to select sites with lower burn severity 1–13 years after fires in Washington and British Columbia (Volkmann, 2021; Volkmann and Hodges, 2022), while spotted owls (Jones et al., 2020) and bighorn sheep (*Ovis canadensis canadensis*; Donovan et al., 2021) were shown to

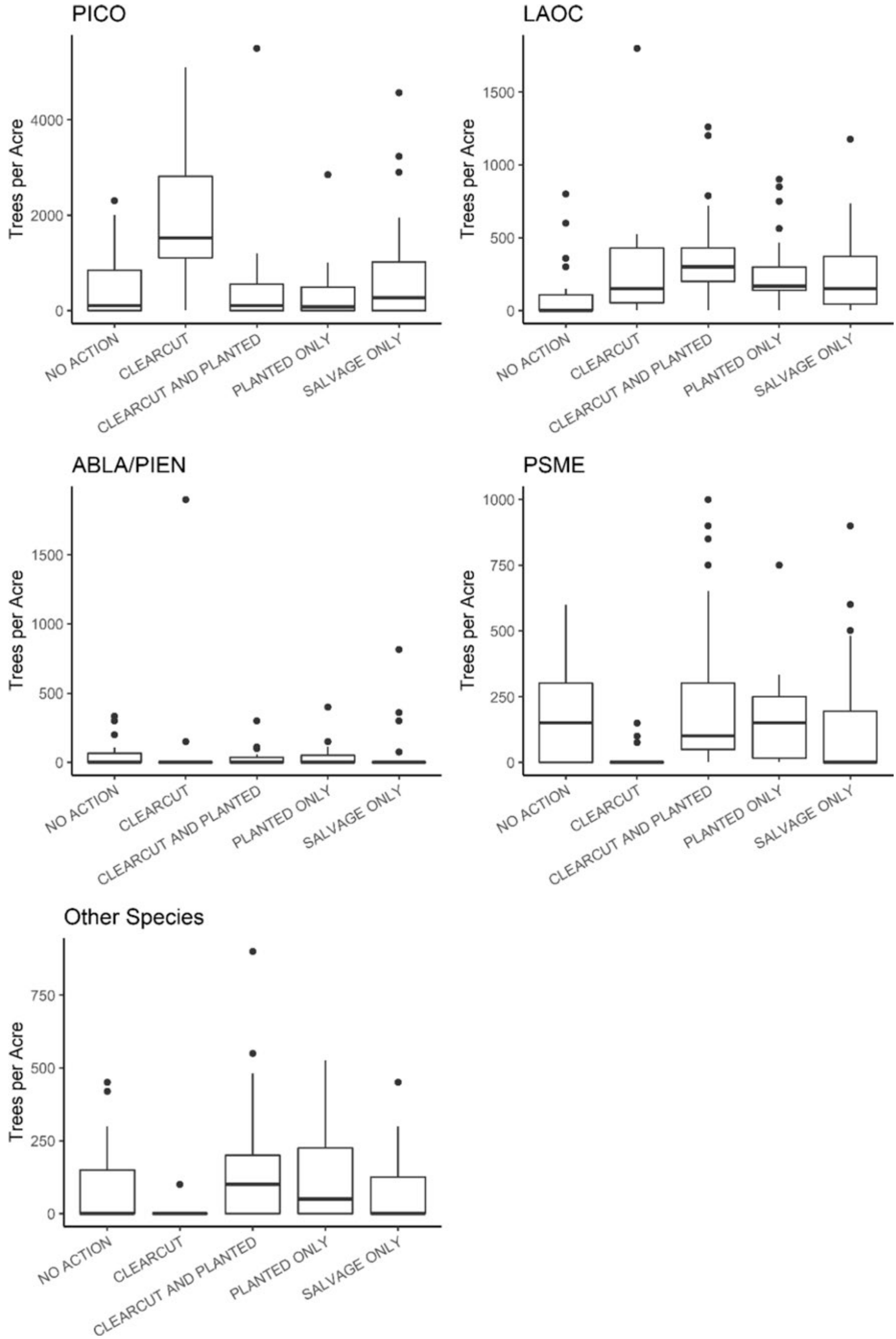

Fig. C3. Boxplots of five species categories (LAOC = *Larix occidentalis;* PICO = *Pinus contorta;* PSME = *Psuedotsuga menziesii;* ABLA/PIEN = *Abies lasiocarpa/Picea engelmannii;* and Other = all other species) sampled at hare pellet plot locations across various categories of post-fire management actions in 22–28 year old fires in western Montana, 2015 and 2016. The 'Clearcut' category is made up almost entirely of *Pinus contorta* and *Larix occidentalis*.

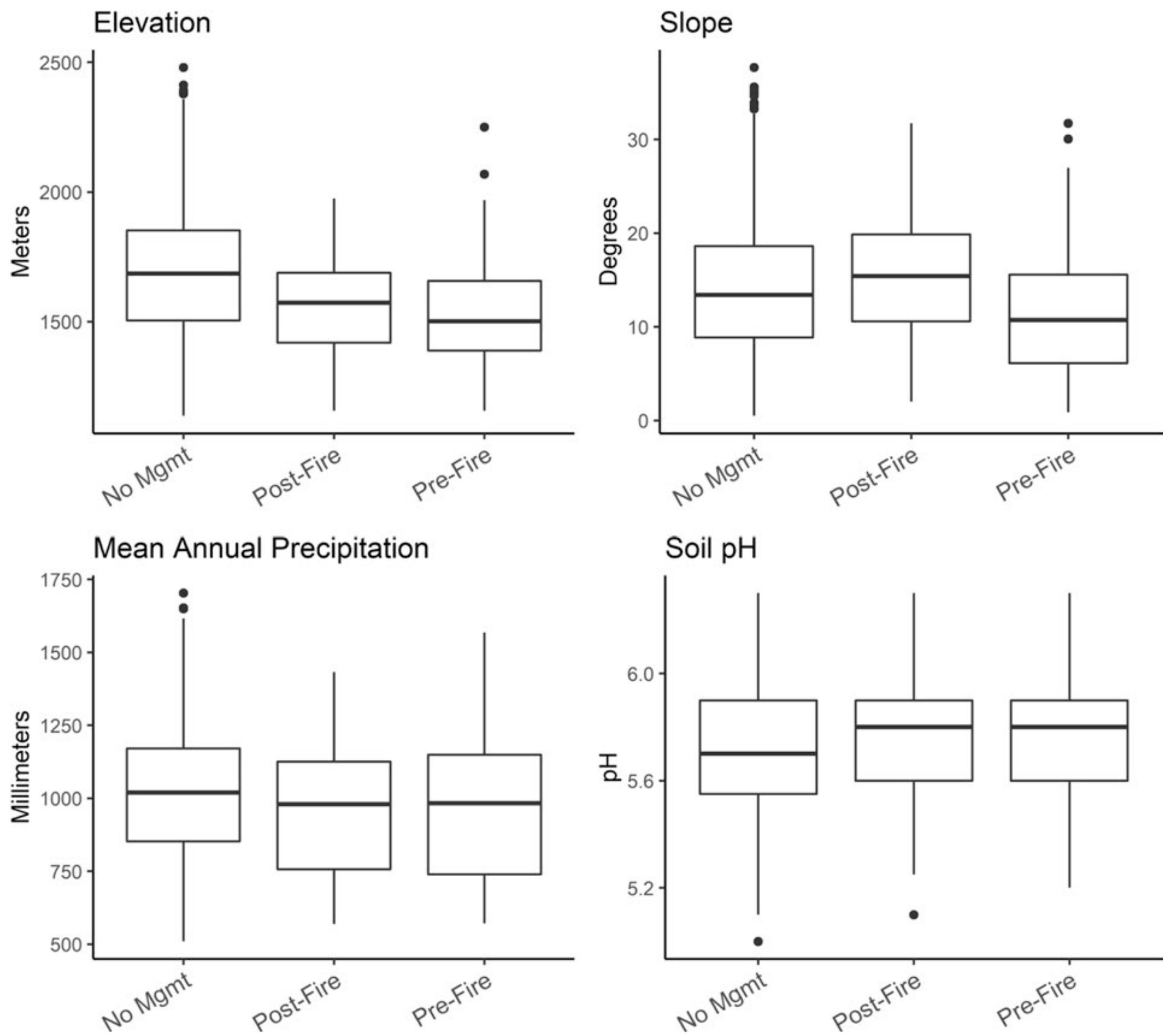

Fig. D1. Boxplots showing differences in elevation, slope, mean annual precipitation, and soil pH for burned stands that have no active management, post-fire, or pre-fire management within the distribution of Canada lynx in western Montana.

select severely burned areas, provided that sufficient heterogeneity in fire severity was present. Vanbianchi et al. (2017b) found that lynx in Washington were more likely to use low severity burned areas or unburned vegetation within burns and emphasized the importance of maintaining any remaining live trees inside fires to provide hare habitat. Our work agrees with these results and stresses the importance of maintaining forest heterogeneity when implementing forest management actions to both mitigate wildfire and conserve lynx. While lynx responded positively to regeneration cuts implemented post-fire, use was lower than stands that received no management or pre-fire management for approximately 10–15 years. Thus, while this type of management is likely to lead to good lynx habitat in ~ 25 years, stands that are not actively managed or that were managed before the fire are also required to provide useable post-burn habitat immediately and in the short-term after a fire. Previous work on this (Holbrook et al., 2019) and other populations of lynx (Ivan and Shenk, 2016; Koehler and Brittell, 1990; Vanbianchi et al., 2017a) have also demonstrated the importance of maintaining a mosaic of forest structure classes within a lynx home range, with the greatest reproductive success of lynx in our study area found when a home range is composed of ~ 50–60 % mature and ~ 20 % advanced regeneration (Holbrook et al., 2019). Lynx in our study also showed some response to the size and shape of managed stands, with greater use of small or more complex shapes in both managed and non-managed stands, indicating further support for a heterogenous mosaic of forest patches.

Differences in hare relative abundance also highlighted the importance of a managed landscape mosaic, showing the most predictive characteristics were related to the 4 km landscape around a given stand. Hares were more abundant in salvaged or non-managed stands when a high proportion of management was in the surrounding neighborhood. Our investigation into forest structure relative to wildfire indicated that managed stands had a greater proportion of advanced regeneration lodgepole pine forest that hares prefer. Thus, we may see higher abundance of hares in non-managed stands in this case because surrounding stands have high hare abundance. Lewis et al. (2011) found a similar response to neighboring conditions in hares in Washington, with more hares in patches surrounded by high quality habitat.

An unexpected result of this work was the slower trajectory of vegetation recovery and the low lynx and hare use of non-managed burned areas. We initially expected that vegetation removal through forest management, particularly post-fire management, would compound the wildfire disturbance and result in longer time to use and lower quality of lynx habitat. Instead of a compounding effect, we found an opposite disturbance mitigating effect, with non-managed stands showing the slowest NBR recovery and both pre- and post-fire managed areas used more intensely by lynx over time. We found no evidence to

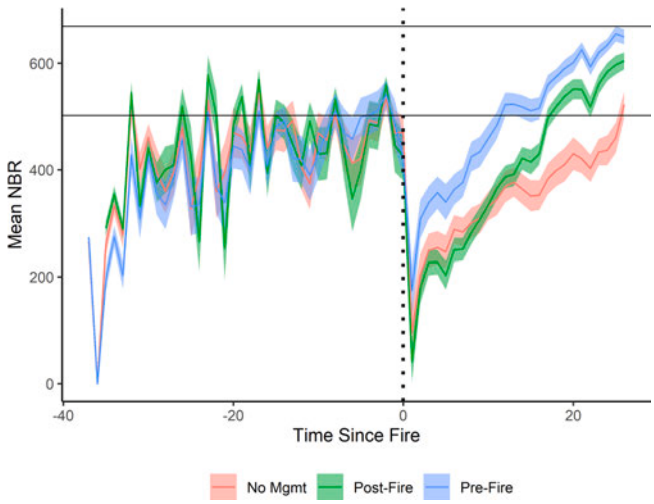

Fig. D2. The average (±90 % confidence interval) vegetation trajectory before and after a wildfire in stands that have active or passive management within lynx distribution in the northern Rocky Mountains, Montana. The colors represent when management occurred relative to the wildfire, solid black horizontal lines indicate the range of NBR values in unburned lynx home ranges, and dotted vertical line indicates the year that wildfire occurred. This plot demonstrates that before the wildfire, all stands in our analysis followed a relatively level NBR trajectory with some stochasticity between years, but after a wildfire, these trajectories differed significantly based on the timing of active management in the stand.

indicate that differences in accessibility or growing conditions existed between managed and non-managed stands (see Appendix D for details), thus, one possible reason for this is our result that more non-managed stands burned at high severity than those with pre-fire management. High severity fire in subalpine forests can result in decreased ground cover and shrub cover a decade or more after a fire (Turner et al., 2003), as well as high tree mortality (Hood et al., 2018) and reduced tree regeneration (Hansen et al., 2018; Turner et al., 2019), contributing to slow vegetation recovery. Furthermore, increasingly warm temperatures and greater drought caused by global climate change are contributing to greater fire severity, particularly in forests in the western United States, which may lead to a loss of lynx habitat through a change from mesic higher elevation subalpine species to species tolerant of hot and dry conditions (Cassell et al., 2019), or a conversion to non-forest (Coop et al., 2020). However, our results also showed that non-altered stands maintained more mature forest structure immediately after a burn than stands that had been silviculturally managed either pre- or post-fire, and Vanbianchi et al. (2017b) confirm the importance of non-managed areas to lynx in recent fires. Mature forest is an important element of lynx habitat, particularly in the winter (Ivan and Shenk, 2016; Squires et al., 2010), providing consistent forage and cover for hares. The presence of mature forest has also been shown to relate to reproductive success of female lynx in our study population, with the most successful females maintaining core home ranges with ~ 60 % mature forest in large, connected patches (Holbrook et al., 2019; Kosterman et al., 2018). Moreover, while we found that pre-fire management did reduce the proportion of stands that burned at high severity, these stands also had less mature forest structure and more sparse forest after a fire, indicating that pre-fire management is not a panacea for lynx habitat. Therefore, while passively managed stands may be slower to provide lynx habitat after a wildfire, they still play an important role in the forest mosaic needed to support lynx.

11. Conclusions

This work illuminated the importance of the timing of forest management with respect to wildfire, highlighted the role of spatial and temporal scale when considering management mosaics on the landscape, and suggested bottom-up processes underlying carnivore behavior in the face of large-scale compound disturbances. The conservation of lynx habitat given the challenge of large and severe wildfires depends on the maintenance of stand heterogeneity through a thoughtful management approach that includes pre- and post-fire treatments, while keeping in mind that most silvicultural treatments will render the area unfavorable to lynx for at least the next 10 years. Thus, a mosaic of active and passive managed stands in different age classes is important at the home range scale, which for lynx in our study area has averaged between 33 km^2 (Holbrook et al., 2019) to 69 km^2 (this study). Within a home range, female lynx had between 0 and 16 % of their entire home range in stand initiation (Holbrook et al., 2019); based on our analysis, we found 30–70 % of the managed and non-managed stands in our study reverted to stand initiation immediately after a wildfire (Fig. 5), illustrating the difficulty that managers face in maintaining acceptable levels of non-favorable structure classes at the home range scale when fires are large. At the temporal scale, our work speaks to the importance of temporal connectedness among land managers, given that the benefits of treatments for hares and lynx will be realized over the course of an entire career for most people (~25–30 years). Therefore, ensuring current management decisions consider the actions of both past and future managers will be essential to fully embrace the spatio-temporal detail underlying the patterns we uncovered with Canada lynx and snowshoe hares.

Declaration of Competing Interest

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

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Appendix A

The list of U.S. Forest Service FACTS database activity classes and the management category into which they were grouped for analysis. Categories correspond to those used in Holbrook et al. (2018).

FACTS Activity Name	Category
Seed (Trees)	Planting
Plant Trees	Planting
Fill-in or Replant Trees	Planting
Wildlife Habitat Seeding and planting	Planting
Broadcast Burning - Covers a majority of the unit	Prescribed Fire
Underburn - Low Intensity (Majority of Unit)	Prescribed Fire
Wildfire - Fuels Benefit	Prescribed Fire
Site Preparation for Planting - Burning	Prescribed Fire
Site Preparation for Seeding - Burning	Prescribed Fire
Site Preparation for Natural Regeneration - Burning	Prescribed Fire
Shelterwood Removal Cut (EA/NRH/FH)	Regen Cut
Seed-tree Removal Cut (w/ leave trees) (EA/NRH/FH)	Regen Cut
Shelterwood Staged Removal Cut (EA/NRH/NFH)	Regen Cut
Two-aged Shelterwood Final Removal Cut (w/res) (2A/NRH/FH)	Regen Cut
Patch Clearcut (EA/RH/FH)	Regen Cut
Stand Clearcut (EA/RH/FH)	Regen Cut
Stand Clearcut (w/ leave trees) (EA/RH/FH)	Regen Cut
Shelterwood Establishment Cut (with or without leave trees) (EA/RH/NFH)	Regen Cut
Seed-tree Seed Cut (with and without leave trees) (EA/RH/NFH)	Regen Cut
Seed-tree Final Cut (EA/NRH/FH)	Regen Cut
Two-aged Seed-tree Seed and Removal Cut (w/res) (2A/RH/FH)	Regen Cut
Two-aged Shelterwood Establishment and Removal Cut (w/ res) (2A/RH/FH)	Regen Cut
Salvage Cut (intermediate treatment, not regeneration)	Salvage
Single-tree Selection Cut (UA/RH/FH)	Selection Cut
Group Selection Cut (UA/RH/FH)	Selection Cut
Liberation Cut	Selection Cut
Thinning for Hazardous Fuels Reduction	Thinning
Tree Release and Weed	Thinning
Prune	Thinning
Seed-tree Preparatory Cut (EA/NRH/NFH)	Thinning
Improvement Cut	Thinning
Commercial Thin	Thinning
Precommercial Thin	Thinning

Appendix B

The results from the second-ranked candidate model of lynx use intensity in summer in response to other fire-related covariates. This model received 36 % of the candidate set AICc weight.

Appendix C

These figures show boxplots (median and interquartile range) across categories of post-fire management action types (No Action, Clearcut, Clearcut/Planted, Planted, Salvaged) for field sampled vegetation measures taken at hare pellet survey plots in western Montana, USA, in 2015 and 2016.

Appendix D

The results from our analyses of lynx use intensity in response to type or timing of forest management in burned areas consistently indicated a low level of use over time in non-managed (burned only) polygons. Vegetation recovery trajectories showing changes in normalized burn ratio (NBR) over time since fire appeared to confirm this, with a slower return to the range of NBR values used by lynx in non-managed polygons compared to polygons with management (see Fig. 4 in main paper). Since this result was counter to our initial hypotheses, we carried out two post-hoc analyses to verify this unexpected finding. We evaluated management timing groups (Non-managed, Pre-fire, Post-fire) for underlying differences in variables unrelated to fire but that might confound the effect of management actions due to polygon accessibility (such as slope or elevation) or vegetation productivity (such as precipitation or soil pH). For all polygons in our study ($n = 900$) we extracted a mean value of slope, mean annual precipitation, elevation, and soil pH. We constructed boxplots showing the median and interquartile (IQR) ranges of each covariate; if inherent differences were present in non-managed stands, we expected this group to show differences in these values as compared to the groups with management. We also averaged NBR across all polygons within management timing groups for individual years relative to wildfire (i.e. wildfire became year = 0 for all polygons, and values were averaged according to years before and after this event). We then constructed a graph showing the mean NBR values across time for each category of management action; if inherent differences were present in non-managed polygons, we expected to see differences in NBR values in this category before a wildfire occurred.

Based on these analyses, we did not find evidence of any strong differences between non-managed (burned-only) polygons compared to those with management before or after fires. Of the four covariates considered, only elevation showed some difference, with the mean of non-managed stands slightly higher than stands with management, although the IQRs of both overlapped considerably (Fig. D.1). The NBR vegetation trajectories also showed no obvious differences between the three groups before a fire took place, with some variability between years but considerable overlap of the 95 % CI of each group leading up to the fire (Fig. D.2). After the fire, however, differences became apparent, with pre-fire managed polygons demonstrating higher values of NBR and faster return to unburned NBR values, and non-altered polygons initially higher than post-fire managed polygons but showing slower increase over time to end with the lowest NBR values of the three groups at ~ 30 years after the fire (Fig. D.2).

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