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## Multi-scale habitat selection by Northern Goshawks (*Accipiter gentilis*) in a fire-prone forest

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### ABSTRACT

Increasing frequency and severity of wildfire may jeopardize persistence of large tracts of late seral forest, raising concerns over population viability of forest-dependent species like the Northern Goshawk (*Accipiter gentilis*). We tracked 20 adult Northern Goshawks with GPS loggers over 4 years to investigate roosting (nocturnal) and foraging (diurnal) habitat selection in a heterogeneously burned forest landscape of the Sierra Nevada mountains of California, United States. Goshawks selected late seral forest attributes for both roosting and foraging at multiple spatio-temporal scales, although at the finest (daily) scale, goshawks selected more diverse forest structure that included small trees and medium canopy cover. Less than 6% of roosts were in areas burned in the last 50 years and goshawks avoided areas burned at high severity when roosting and when foraging across spatial scales. Four goshawks (3 males, 1 female) undertook forays > 5 km from their nest location, two of which forayed into burned areas during at least one season. High severity fire is likely to make forests unsuitable foraging or roosting habitat for Northern Goshawks, although lower severity fire may provide foraging opportunities for this generalist predator. Eighty percent of foraging space use and 87% of roost locations were considered high fire hazard potential, suggesting that goshawk habitat in western North America is likely to be reduced by predicted increases in fire frequency and severity in the region.

### 1. Introduction

Changes in fire regime, including regional increases in large, high severity fires, are transforming forests globally (Dennison et al., 2014; Ferreira-Leite et al., 2015; Flannigan et al., 2009; Karavani et al., 2018). In dry forests of western North America fire regimes are changing, driven by climate change, drought, fire suppression and human land-use change (Jones et al., 2016). Although opinions differ on characteristics of historical fire regimes in the region (Baker, 2014; Stephens et al., 2015), the number and extent of high severity fires are increasing (Keyser and Westerling, 2019; Safford and Stevens, 2017). Many forest ecosystems in western North America historically have been maintained by mixed severity fire regimes that promote forest heterogeneity (DellaSala et al., 2015). Fire-adapted specialists like the Black-backed

Woodpecker (*Picoides arcticus*) and Northern Hawk Owl (*Surnia ulala*) colonize burned areas soon after high severity fire (Hannah and Hoyt, 2004; Tingley et al., 2016b), and a variety of other species take advantage of later successional stages of post-fire vegetation (Hutto and Patterson, 2016; Sollmann et al., 2015).

Concern is growing about the impact of a changing fire regime on wildlife associated with late seral forest, also known as mature or old-growth forest (Jones et al., 2016; Wan et al., 2019). In forests in western North America, these species require features such as abundant large trees and snags, diverse tree size classes, and abundant downed woody material (Davis et al., 2015). Late seral forests already are fragmented, and are declining at a rate of 2.5% per year worldwide (Morales-Hidalgo et al., 2015). In western North America, wherein 4.2–5.4% of late seral forest was lost to wildfire alone between 1994 and 2013, the

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rate of habitat loss is likely greater (Davis et al., 2015). After high severity fire, late seral attributes may take centuries to develop and fire can interact with other disturbances to delay its regeneration (Lindenmayer et al., 2014). Nevertheless, some old-forest dependent wildlife appear to be resilient to severe fire in late seral forest stands, at least in the short-term (Hanson, 2015; Siegel et al., 2019).

Relationships between fire and life history needs of avian predators associated with late seral forest are likely complex. Predicted increases in fire extent and severity may substantially reduce nesting habitat (Ray et al., 2014; Stephens et al., 2016). Conversely, prey populations may ephemerally increase on post-fire landscapes, providing increased foraging opportunities for raptors (Hovick et al., 2017; Hutto and Patterson, 2016). The Northern Goshawk (*Accipiter gentilis*) is an apex avian predator in forests across North America and Eurasia (Squires and Reynolds, 1997), nesting in dense forest with late seral forest attributes across its range (Penteriani, 2002). The American subspecies (*A. g. atricapillus*) ranges widely across Alaska, Canada, western US and Mexico, but favors mature montane coniferous forest with high canopy cover and large trees for foraging, roosting and nesting (Greenwald et al., 2005; Squires and Kennedy, 2006). We know of only one empirical study that assessed Northern Goshawk response to burned landscapes, indicating a negative effect of high severity fire on breeding territory occupancy with neutral effects of low severity fire (Reynolds et al., 2017). No study has yet examined effects of fire of any severity on foraging or roosting behavior, or on any aspects of goshawk habitat use during the non-breeding season.

We studied roost-site selection and multi-scale foraging habitat selection of goshawks in a fire-prone forest of California's Sierra Nevada. We used GPS loggers to track 20 individual goshawks over four years (2015–2018) during both the breeding (1 April–31 August) and non-breeding (1 September–31 March) seasons, and across a mosaic of forest conditions including recently burned areas. Our objectives were to: 1) assess roosting and foraging habitat selection at multiple spatio-temporal scales relative to variation in forest structure and fire regime; and, 2) evaluate fire risk to goshawk habitat and designated protected habitat in our study area. We predicted negative effects of high severity fire on roosting and foraging habitat selection of Northern Goshawks, and positive effects of low severity fire on foraging habitat selection.

## 2. Materials and methods

### 2.1. Study area

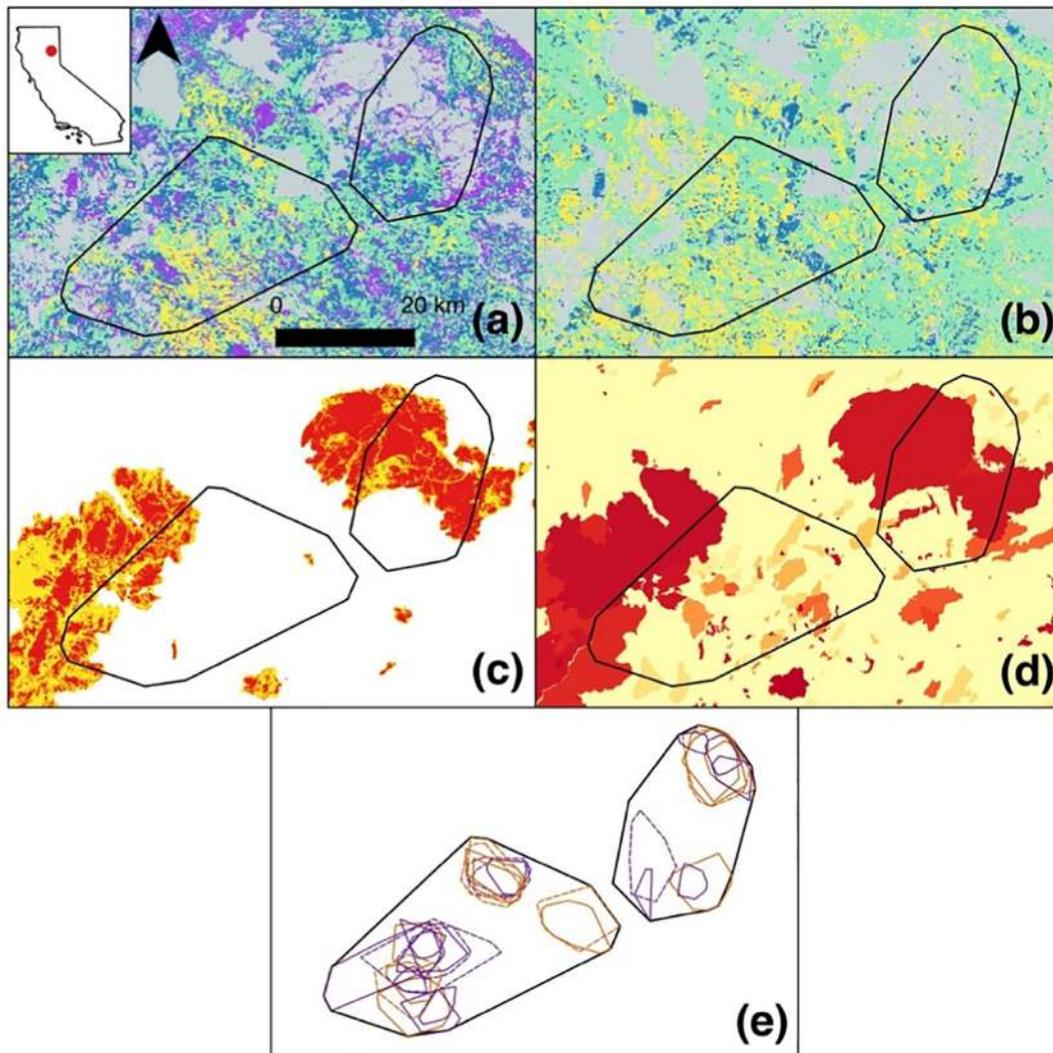
We studied Northern Goshawks on Plumas National Forest, within the Sierra Nevada mountain range (“Sierra Nevada”) in northern California within an area spanning > 100,000 ha (40°00′01″N 120°40′05″W, Fig. 1). Plumas National Forest has an elevation gradient of 311 to 2433 m and a Mediterranean and montane climate with dry, warm summers and cool, wet winters with mean annual precipitation of 1036 mm, and mean temperature ranging from  $1.3 \pm 2.4$  °C in January to  $19.3 \pm 1.5$  °C in July (1895–2017, Western Regional Climate Center, 2017). Vegetation is dominated by lower and upper montane forest with stands of ponderosa pine (*Pinus ponderosa*) - mixed conifer, white fir (*Abies concolor*) - mixed conifer, and red fir (*Abies magnifica*) (Fites-Kaufman et al., 2007). Mixed severity fire regimes dominated historically, though studies vary in their estimates of high severity fire extent (Baker, 2014; Stephens et al., 2015). Mixed severity fire regimes exist where the combination of fires over time result in a complex mix of patches of different severity, including unburned patches, low severity patches (e.g. underburn), moderate severity patches (up to 2/3 vegetation killed), and high severity patches (almost all the vegetation is killed) (Agee, 2005). Within the last 20 years, five extensive (> 20,000 ha) wildfires have been recorded within the study area (USDA Forest Service, 2017).

### 2.2. Goshawk movement surveys

During 2015–2018 we marked and tracked 20 goshawks (12 females and 8 males) from 11 territories during 35 goshawk-seasons (we tracked 7 individuals during multiple sampling periods, Appendix S1). Goshawks were captured across range of locations, representative of the range of environmental conditions (elevation, vegetation, microclimate) that goshawks occur in throughout the study area and all territories found to be occupied were included in the study. We used United States Department of Agriculture Forest Service data on known nests to locate goshawks in May and June of 2015–2018. We used the Dho-gaza technique, in which a raptor is attracted into a mist net which is placed near a non-releasable ‘lure bird’ (*Bubo virginianus*) (Bloom et al., 2007), to capture goshawks. We fit 3 goshawks with Skua-M GPS-GSM-UHF tracking devices, and 17 individuals with Harrier/Kite-M GPS-UHF tracking devices (Ecotone Telemetry, Sopot, Poland), both unit types were solar-powered. Each tracking unit also contained a VHF transmitter (Advanced Telemetry Systems, Isanti, USA), and the entire package was attached using a back-mounted Teflon ribbon harness (total package mass = 14–18 g). Tracking units recorded locations at defined intervals within daily duty cycles, and stored locations until a connection was established with a cellular network (Skua units) to which locational data were transmitted. We placed stationary base stations (Kite/Harrier units; EP-BS base station, Ecotone Telemetry) near nests or in areas commonly transited by goshawks to collect location data downloads as goshawks moved through the area.

We collected a mean of 791 ( $n = 27,885$ , range = 76–3833) foraging locations and 34 ( $n = 604$ , range = 12–78) night-time roost locations per goshawk-season across > 100,000 ha of forest. We defined foraging locations (diurnal movements) as locations recorded between sunrise and sunset, and roost locations (nocturnal roosting) as locations recorded between 2h after sunset and 2h before sunrise. We acknowledge that not all movements and behaviors during the day were consistent with the broad definition of “foraging”, though the majority of nightly activity was likely to be “roosting”. During the breeding period, units were programmed to collect data at a frequency of one location every hour from approximately 06:00 to 19:00 Pacific Standard Time, and then at a tracking frequency of one location every 240 min during the remainder of the year when less light was available to charge unit batteries. Additionally, 10 units were set to record locations every 1–6 min for 3–5 days for higher resolution tracking (5 females, 5 males, 11 summer and 1 winter goshawk-season). One male was not frequently encountered, and associated challenges reprogramming his unit resulted in collection of a mean of 49 locations per day throughout the non-breeding season. We fit three additional goshawk females with transmitters in the summers of 2015, 2017 and 2018, but these individuals dispersed or disappeared in less than a week, and so we excluded them from the study. Though every effort was made to minimize package weight and stress to goshawks during handling in this study, we cannot rule out the possibility that transmitter attachment detrimentally impacted individual goshawks. Given the value of GPS tracking devices in understanding raptor ecology, future studies should assess the effect of carrying transmitters on raptor movements, survival and breeding success. We did not use all individuals or goshawk-seasons for every analysis (e.g. not all goshawk-seasons including high resolution daily data); see specific sample sizes for each analysis in the scale sections of the Foraging Habitat Selection methods.

We quantified movement data during the breeding (1 April–31 August) and non-breeding season (1 September–31 March) based on goshawk behavior and reports on breeding phenology (Squires and Reynolds, 1997). All goshawks either bred or attempted to breed during each breeding season in which they were tracked. We tagged goshawks under authorization from the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645) and the USFWS Bird Banding Laboratory (Permit #22423).



**Fig. 1.** Study area in Plumas National Forest, California where 20 Northern Goshawks were tracked during 2015–2018 during the breeding (1 April–31 August) and non-breeding (1 September–31 March) seasons. All panels depict two study landscapes (eastern and western, large black polygons) which represent the overall MCP of goshawk locations in the two separate areas and were used to estimate landscape-scale habitat availability. The two study landscapes are overlaid on: (a) canopy cover (high = yellow, medium = green, low = blue, very low = purple, no canopy = grey); (b) dominant tree size (large = yellow, medium = green, small = blue, no trees = grey); (c) burn severity (high = red, medium = orange, low = yellow and unburned = white); (d) time since last fire (TSLF) in years (ranging from 0 to 110 years: red to yellow); (e) Minimum convex polygons (MCPs) of goshawk locations in eastern and western landscapes within the study area (female = purple, male = orange, breeding season = solid line, non-breeding season = dashed line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3. Foraging habitat selection

To evaluate foraging habitat selection, we tested whether goshawks used areas with particular characteristics disproportionately to the amount available by comparing intensity of use to availability using methods described in detail in (Blakey et al., 2019). We selected this method because it allowed us to compare continuous measures of habitat use integrating both recorded locations and paths between them (intensity of use), rather than limiting our analysis to point locations. We restricted our analysis to four metrics with the potential to influence goshawk habitat selection (Greenwald et al., 2005; Reynolds et al., 2017), including two measures of forest structure (canopy cover and dominant tree size) and fire history (burn severity and time since last fire in years (TSLF)). We assessed habitat selection by foraging goshawks at four spatio-temporal scales: landscape (2nd order), home range (3rd order), foray (movements > 5 km from the nest and temporally extending for  $\geq 10$  locations and  $\geq 1$  h), and daily (Johnson, 1980). While foraging movements were included in our investigations of

habitat selection, we acknowledge that these movements do not necessarily imply foraging and may be exploratory movements (see Discussion). We conducted all analysis within the R environment for statistical computing (R Development Core Team, 2016) using: the *adehabitatHR* v3.3.0 package to fit minimum convex polygons (MCPs), *adehabitatLT* v3.3.0 to building movement trajectories, *adehabitatHS* v0.3.13 to evaluate roost habitat selection, *BBMM* v3.0 to fit utilization distributions and *lme4* v1.1–12 to fit generalized linear mixed effects models. We report and 95% confidence intervals (95% CI) where appropriate.

#### 2.3.1. Landscape scale

To evaluate foraging habitat selection at the landscape scale, we tested whether goshawks used areas disproportionately to those available by comparing habitat use at the home-range scale to that available within the eastern or western landscapes of the study area (Fig. 1). We characterized vegetation structure using vegetation mapping data (USDA Forest Service, 2015) based on the CALVEG (“Classification and

Assessment with Landsat of Visible Ecological Groupings”) classification (Nelson et al., 2015) and fire regime mapping from the USDA Forest Service (Miller and Thode, 2007; Safford et al., 2016; USDA Forest Service, 2017). From these data we extracted five categories of canopy cover (cover from above of all trees) and three categories of dominant tree size (diameter at breast height, DBH, of uppermost canopy layer), treating them as eight separate datasets (Fig. 1). Canopy cover categories included high (> 70%), medium (50–70%), low (30–50%), very low (< 30%) cover and treeless areas (0%). Dominant tree size was based on the mean size (DBH) of the dominant trees in the mapping unit, and categorized as large (> 50 cm), medium (25–50 cm), or small (< 25 cm) (USDA Forest Service, 2015).

We also extracted time since last fire (TSLF) and burn severity categories. We used time since last fire in years with a maximum TSLF of 109 years marking the commencement of the dataset (1908). We included three categories (recent = burned < 10 years ago (2008–2017), medium-term = burned 10–50 years ago (1968–2007) and long-term unburned = burned > 50 years ago (before 1968)). We binned burn severity into four categories of percent change in canopy cover: unburned, low (burned with canopy loss < 25%), medium (canopy loss 25–75%) and high (canopy loss > 75%). We treated each category within all variables as a separate variable in the foraging habitat selection analysis, with up to 15 variables investigated at each spatio-temporal scale. Associations between habitat categories are provided in Appendix S2. We excluded categories from analyses for a particular goshawk-season, day or foray if they could not be tested for selection (e.g. availability was either 100 % or < 1%) (Arthur et al., 1996).

We identified the landscape available in our study as the MCP bounding foraging locations obtained for all goshawks in our study, separated into eastern and western landscapes to account for two clusters of MCP home ranges in our study area (Fig. 1). To quantify habitat use at the landscape scale, we derived the volume of the Brownian bridge utilization distribution (UD) for each goshawk-season, with a spatial accuracy of 30 m (corresponding to estimated accuracy of our GPS units) and a grid cell size of 50 m (Horne et al., 2007; e.g. Blakey et al. (2019)). We chose to use Brownian bridges to characterize use because they take into account both recorded locations and paths in between locations (Horne et al., 2007). When calculating UD, we excluded time lags longer than 4 h, and thinned our data to one location per hour (higher resolution data addressed below), using the *adehabitatLT* v3.3.0 package. Within each UD, we calculated the volume of use within 15 habitat categories for each goshawk-season.

We produced a landscape-scale dataset for each of the 15 habitat categories, each with 33 goshawk-seasons of proportional used habitat, and corresponding measurements of proportional goshawk-season available area (representing either the eastern or western landscape). We developed seven generalized linear mixed effects models to test hypotheses on foraging habitat selection (Table 1, models 1–7). We fit models using proportion (including both used and available) as the response variable, with the Gaussian family and the log link. The focal predictor variable in all models was a categorical variable with two levels: used and available. Therefore, we interpreted strength and directions of these coefficients as evidence of selection for or against the habitat category in question. Random effects included individual for landscape and home-range scale models, and goshawk-season for foray and daily scale models. We retained the model with the lowest AIC<sub>c</sub> (Akaike’s information criterion, adjusted for sample size) and interpreted variables using parameter estimates from this best-approximating model (Burnham and Anderson, 2002). Small sample sizes prevented us from running a true cross validation. To check model robustness and influence of outliers on our results, we divided datasets into 10 equal sections and re-ran the model 10 times, each time excluding one of the 10 sections. We interpreted models that were not robust (direction or significance of selection coefficients changed) as non-significant.

### 2.3.2. Home-range scale

We used methods similar to those described above to compare proportional habitat use within the UD and available habitats within the home range. We estimated home-range size for 33 goshawk-seasons using the MCP method (Worton, 1987). We produced a home-range dataset for each of the eight habitat categories in the MCPs (available area) and 33 goshawk-seasons of proportional habitat use. We used the same habitat variables described above, the same alternative models (Table 1, models 1–7) and model selection process.

### 2.3.3. Foray scale

The mean distance to nearest neighboring nest of study subjects was 5 km, so we defined forays as movements > 5 km from the nest and temporally extending for ≥ 10 locations following Blakey et al. (2019). We examined habitat selection during forays, which we observed in three males and one female. Foray periods ended when a goshawk returned to within 5 km of the nest, with a median duration of 40 h (1 h to 6 days), and 14 forays exceeding 24 h. We estimated the proportional used area for each habitat with UD for each foray period ( $n = 34$  in 6 goshawk-seasons), and compared those to the proportional area of each habitat within the MCP home range for the goshawk-season using a generalized mixed effects model that included individual as a random effect. We used the same habitat categories described above with a similar model fitting and selection process, but examined only the effect of the selection (used/available) due to the small number of individuals ( $n = 4$ ) (Table 1, models 1–2).

### 2.3.4. Daily scale

High-resolution location data (locations recorded every 1–6 min) were available for 12 goshawk-seasons, enabling analysis of habitat use at a daily scale. Daily records ranged from 2 to 16 h periods over 134 goshawk\*days (median 8 h). We obtained a median of 85 (range 24–458) locations per goshawk per day and 1–47 days per goshawk-season (median = 6). We derived a UD for each goshawk day and estimated the proportional used area by habitat. We used the same estimate of available area as in the home range analysis, the MCP, and included goshawk-season as a random effect. We used the same habitat categories described above, the same model fitting and selection process, and tested for an effect of sex on habitat selection, but not season, given only one individual was tracked at high resolution during the non-breeding season (Table 1, models 1–3, 5, 8).

## 2.4. Roost habitat selection

We defined roost locations as the location temporally closest to midnight for each goshawk from the set of locations recorded between 1 h after sunset and 1 h before sunrise. We summed the number of roost locations within each habitat category for each goshawk-season to define use and only included goshawk-seasons when we recorded > 10 roost locations ( $n = 16$  goshawks,  $n = 27$  goshawk-seasons,  $n = 1024$  total roost nights). We defined available roost habitats as the proportion of each habitat category within the corresponding MCP home range. Given < 6% of goshawk roosts were located in areas burned within the last 50 years, we did not analyze roost selection by fire category further. We calculated Manly selectivity measures for each habitat category and tested overall habitat selection using a type III log-likelihood test statistic (Khi2L) (Manly et al., 2007) because use and availability were measured for each goshawk-season (Thomas and Taylor, 1990). We treated canopy cover and dominant tree size as separate categorical variables where both included open treeless areas as a variable level. We interpreted Manly selection ratios as indicating selection for a habitat if the ratio and its confidence interval was > 1 and selection against a habitat if the ratio and its confidence interval was < 1.

**Table 1**

Alternative hypotheses and corresponding models representing Northern Goshawk habitat selection on the Plumas National Forest during 2015–2017 at the landscape and home-range (1–7), foray (1–2) and daily (1–3,5,8) scales. The response variable is proportion of each habitat category within each goshawk-season. Habitat use is represented by a categorical variable (used\_available) and selection is tested by comparing proportion across these two categories. Models were fitted as generalized linear mixed effects models with a Gaussian response distribution and log link function, territory ID is included as a random effect for landscape and home-range scales and individual as a random effect for the foray and daily scales. At each scale we tested 8 habitat categories related to canopy cover (high, medium, low, very low) and dominant tree size (large, medium, small) and open treeless (0%). The random effect (1|random) was individual goshawk for landscape and home-range scales and goshawk-season for daily and foray scales. The scale column indicates the scales at which the hypotheses were tested (L: landscape, HR: home range, F: foray, D: daily).

Hypothesis	Model equation	Scale
1. Goshawks use habitat in proportion to availability (no habitat selection)	Proportion $\sim \beta_0 + (1 \text{random})$	L, HR, F, D
2. Goshawks use habitat disproportionately to availability (habitat selection)	Proportion $\sim \beta_0 + \beta_1 * \text{used\_available} + (1 \text{random})$	L, HR, F, D
3. Goshawks use habitat in proportion to availability, but habitat availability differs between sexes	Proportion $\sim \beta_0 + \beta_1 * \text{sex} + (1 \text{random})$	L, HR, D
4. Goshawks use habitat in proportion to availability, but habitat availability differs between seasons	Proportion $\sim \beta_0 + \beta_1 * \text{season} + (1 \text{random})$	L, HR
5. Goshawks select habitat and habitat availability differs between sexes	Proportion $\sim \beta_0 + \beta_1 * \text{used\_available} + \beta_2 * \text{sex} + (1 \text{random})$	L, HR, D
6. Goshawks select habitat and habitat availability differs between seasons	Proportion $\sim \beta_0 + \beta_1 * \text{used\_available} + \beta_2 * \text{season} + (1 \text{random})$	L, HR
7. Goshawks select habitat and habitat availability differs between sexes and between seasons	Proportion $\sim \beta_0 + \beta_1 * \text{used\_available} + \beta_2 * \text{sex} + \beta_3 * \text{season} + (1 \text{random})$	L, HR
8. Female and male goshawks select habitat differently, or one sex selects habitat, whereas the other does not	Proportion $\sim \beta_0 + \beta_1 * (\text{used\_available} * \text{sex}) + (1 \text{random})$	D

### 2.5. Analysis of fire risk

We used categorical measures of wildfire hazard potential from a USDA Forest Service raster product at 270-m resolution (USDA Forest Service, 2018). Wildfire hazard potential combines wildfire likelihood and intensity with information on spatial fuels, vegetation type and point locations of historical fires to calculate the relative potential for wildfire that would be difficult to contain (USDA Forest Service, 2018). We used the categorical version of the product, which separates fire risk into five categories (very low, low, moderate, high, very high). We combined high and very high fire risk areas (hereafter ‘high’) and calculated the proportion of overlap between goshawk foraging space use, roost locations and Protected Activity Centers (PACs). PACs are areas where forest management activities are limited with the intention of conserving Northern Goshawk nesting habitat in known use areas. Within Plumas National Forest, PACs were delineated in previous years by Forest Service biologists to comprise the best available 81 ha of goshawk habitat surrounding known and suspected nests.

## 3. Results

### 3.1. Foraging habitat selection

Northern Goshawks used habitats selectively at landscape, home-range, daily and foray scales (Fig. 2, Appendices S3 & S4) after accounting for differences between sexes and seasons (breeding/non-breeding). Goshawks selected for habitats with late seral forest attributes (high canopy cover and large trees) at landscape, home-range and foray scales (Fig. 2). Goshawks selected against un-forested areas at all scales, and selected against areas with very low canopy cover (< 30%) at all scales except the daily scale (Fig. 2). We detected some diversions from these trends at finer scales, i.e. foraging goshawks selected areas with both low and high canopy cover, and at the daily scale goshawks selected for stands dominated by small but not medium-sized trees (Fig. 2, Appendix S4). Daily scale was the only spatio-temporal scale with sufficient sample size to test for influence of sex on foraging habitat selection. Females were more likely than males to select high canopy cover, but conversely, they were more likely to select areas with small trees, whereas males were more likely to select areas of medium cover (Appendix S4).

Across all scales, goshawks selected against high burn-severity areas, and in all but the foray scale, selected against areas burned

10–50 years prior to the study (Fig. 2). Goshawks selected for unburned areas (burned > 50 years prior) at the landscape and daily scales (Fig. 2). Females also were more likely than males to select low- and medium-severity burned areas and areas burned within the past 10–50 years at the daily scale (Appendix S4). Of the four individuals that conducted forays, two forayed into burned areas, with one female foraging > 15 km from her nest into an adjacent burned area (Fig. 3).

### 3.2. Roost habitat selection

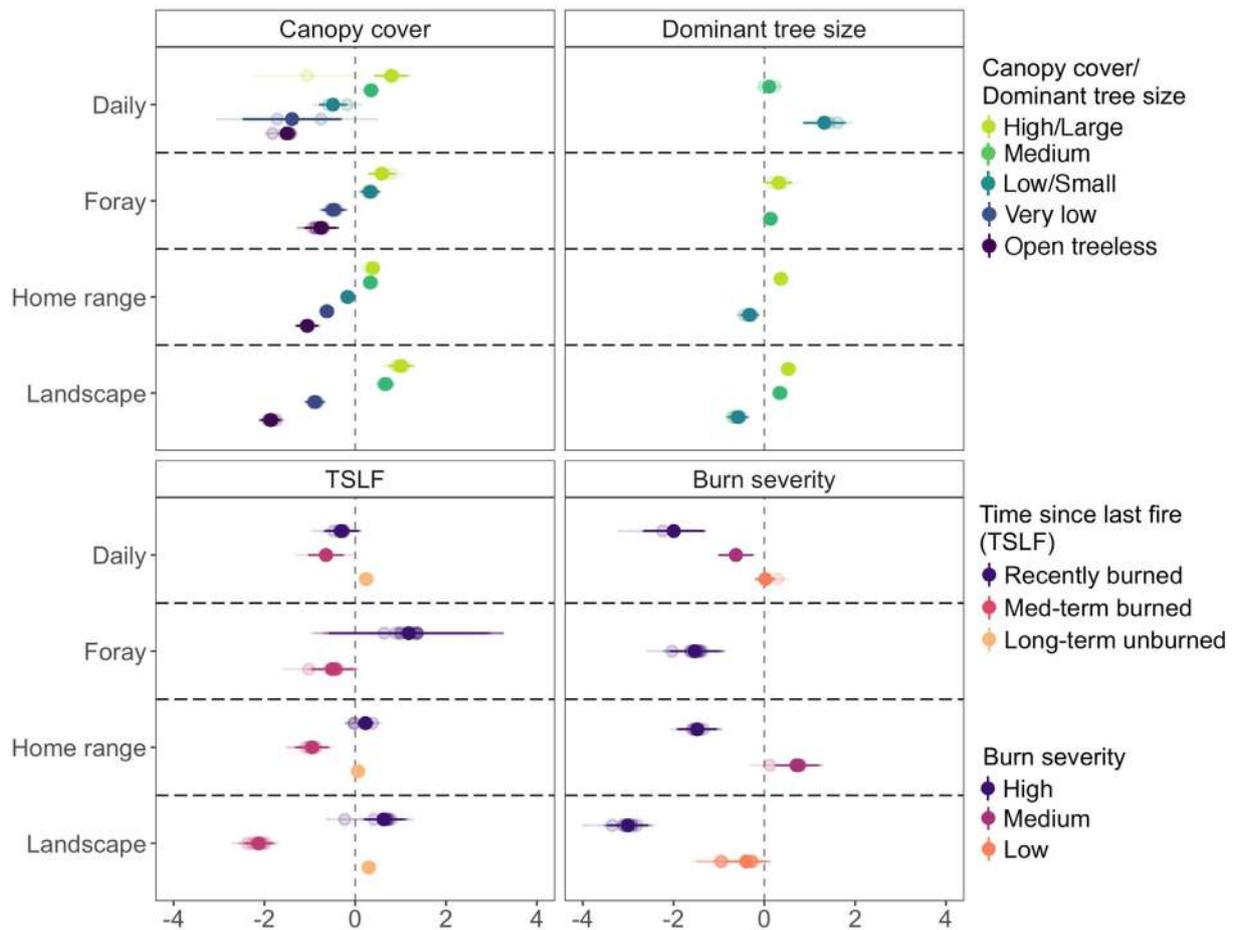
Goshawks selected roost sites based on canopy cover (Khi2L = 448, df = 61,  $p < 0.001$ ) and dominant tree size (Khi2L = 313, df = 49,  $p < 0.001$ ) where canopy cover was > 50% and in stands dominated by large trees (> 50 cm DBH) (Fig. 4). Goshawks selected against areas with canopy cover < 50% and used small to medium trees (< 50 cm DBH) in proportion to their availability in the home range (Fig. 4). We did not have sufficient sample size to formally test for selection of fire habitat variables because use of burned areas for roost sites was limited; among 1024 roost night locations, < 6% were burned in the last 50 years, with < 1% of roosts within medium-severity burned areas and none in high-severity burned areas. Additionally, 75% of goshawk roosts were within areas where fires have not been recorded for over 100 years.

### 3.3. Analysis of fire risk

The majority of foraging space use and roost locations in the study area overlapped with areas designated as high risk of large wildfires (Fig. 5). Across goshawk-seasons, high fire-risk areas overlapped with 41–99% of foraging space use with a mean of 80% (2 SE). Roost-site overlap with high fire-risk areas ranged from 36 to 100% across goshawk-seasons, with a mean of 87% (3 SE). The network of protected areas designated for goshawks (PACs) in the study area had 86% overlap with areas of high fire risk. Goshawk foraging and roosting activity, and PAC areas, overlapped with greater proportions of high fire-risk areas compared to the whole of Plumas National Forest (68%) and the broader Sierra Nevada (48%).

## 4. Discussion

Our study indicated movements and habitat selection of Northern Goshawks were influenced by the fire-mediated landscape that they

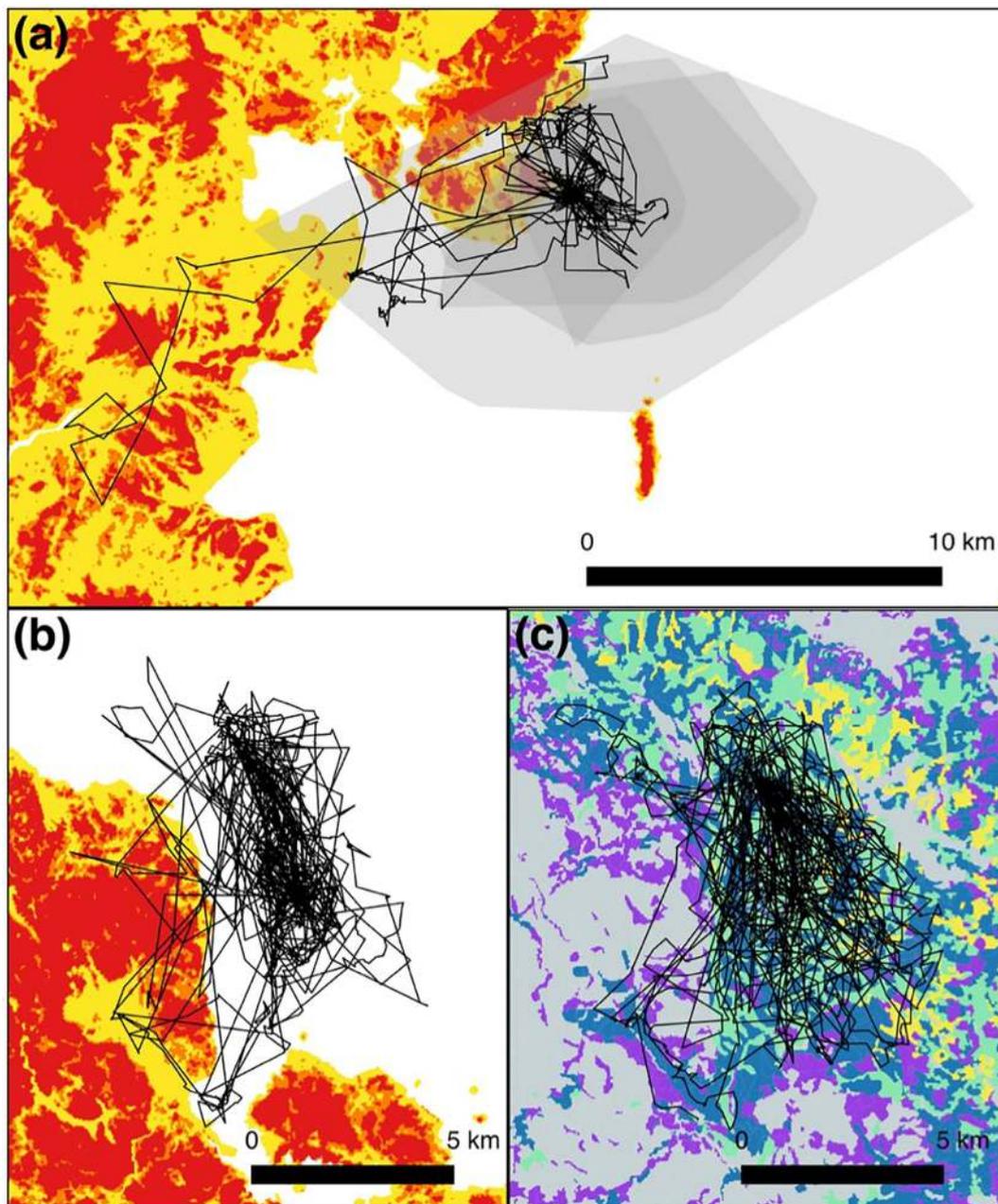


**Fig. 2.** Coefficient estimates and 95% CI (whiskers) for best-approximating models relating habitat selection at four spatio-temporal scales, including landscape, home range, daily and foray. Where the best-approximating model did not include the selection coefficient, no coefficient appears for that category. Coefficient estimates and confidence intervals for full model (all data) are opaque whereas subset models fit during model validation are transparent. Positive coefficients indicate selection for a habitat category and negative coefficients indicate selection against. Estimates with confidence intervals crossing zero were not significant, and models were not considered robust when subset models provided estimates differing in direction of selection or significance. Habitat categories are shown in four groups, including canopy cover (high: 70%, medium: 50–70%, low 30–50%, very low < 30%, open treeless areas: 0%), dominant tree size (large: DBH > 50 cm, medium: 25–50 cm, small: < 25 cm) and two fire variable categories: time since last fire (TSLF; recently burned, last fire < 10 years ago; medium-term burned, last fire 10–50 years ago; long-term unburned, last fire > 50 years ago) and burn severity (change in canopy cover after fire: unburned 0%, low < 25%, medium 25–75%, high severity > 75%).

inhabit via selection for late seral forest attributes and avoidance of high-severity burned areas when roosting and foraging. These relationships suggest the increasing wildfire risk presents substantial concern for management and conservation of the goshawk population in the region, as high fire-hazard-potential areas overlapped with 80% of foraging space use and 87% of roost locations in our study. Goshawks selected late seral forest attributes (high canopy cover and large trees) at greater spatiotemporal scales (landscape, home range and foray) when foraging, and when roosting, consistent with prior studies (Greenwald et al., 2005). However, foraging-habitat selection differed at the finest (daily) scale, where selected attributes included dominance of small trees and medium canopy cover, potentially indicating finer-scale selection within the home range for prey (Reynolds and Graham, 2008), as prey diversity may increase with habitat heterogeneity (Tews et al., 2004). Foraging habitat selection at the daily scale may indicate selection for features not accounted for at coarser scales of movement (Keane and Morrison, 1994). While our study defined diurnal movements as foraging, some of the variability in habitat selection was likely due to the variety of other behaviors conducted by goshawks during this time, including social, territorial and breeding related activities or additional environmental covariates not measured in this study.

Our finding that areas burned at high severity (> 75% canopy loss)

were avoided by foraging and roosting goshawks was consistent with predictions from a simulation study (Ray et al., 2014) and findings in Arizona, where similar rates of canopy loss (> 64%) led to territory abandonment (Reynolds et al., 2017). Similarly, other predators associated with late seral conifer forests have exhibited a negative association with high severity fire (e.g. American Martens, *Martes americana atrata* and Spotted Owls, *Strix occidentalis*; Gosse et al., 2005; Lee et al., 2013). We cannot rule out an interactive effect of wildfire and logging in driving goshawk avoidance of high-severity burned areas (Leverkus et al., 2018) as some post-fire logging occurred within portions of our study area. Post-fire logging reduces hunting perches and prey habitat (Hutto and Patterson, 2016), and there is evidence that the California Spotted Owl (*S. o. occidentalis*), a sympatric avian predator that also depends on late seral forest, is adversely affected by post-fire logging (Hanson et al., 2018). However, the extent of post-fire logging was minimal within the burned areas of our study area; of the four large fires recorded in our study area over the past 20 years, it was conducted only in the Chips and Moonlight Fires, where 5% and 13%, respectively, of the burned area intersecting Plumas NF was treated with post-fire logging (USDA Forest Service, 2017). Thus, post-fire logging impacted minimal amounts of burned areas and we consider the underlying driver of habitat selection for northern goshawk in this study to be



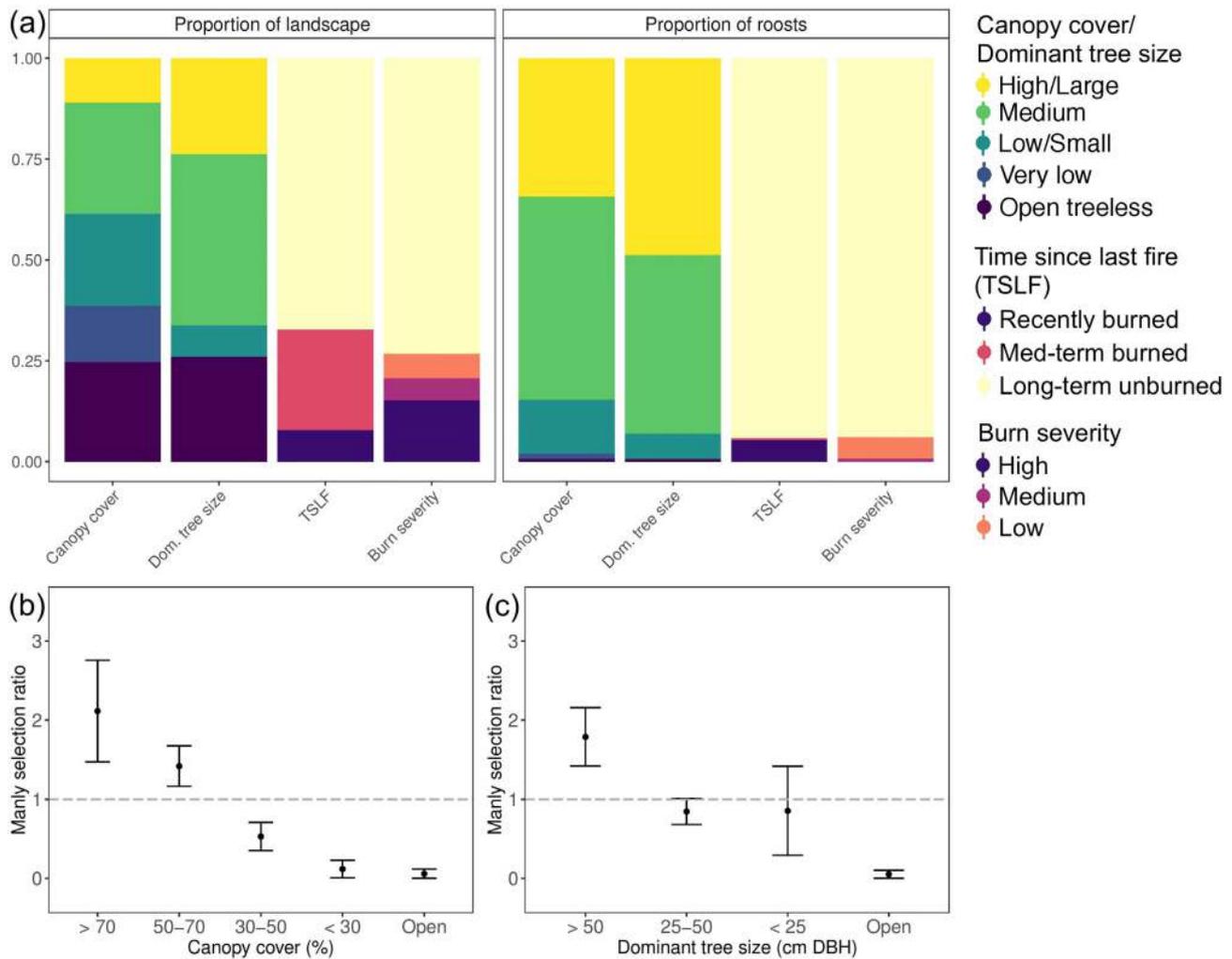
**Fig. 3.** Movement paths depicting long-range movements of a (a) female Northern Goshawk during the 2018 breeding season and (b) a male goshawk during the 2016 breeding season and (c) non-breeding season. Breeding-season (a, b) paths (solid lines) are overlaid on burn severity (high = red, medium = orange, low = yellow) and (c) the non-breeding season path is overlaid on canopy cover: > 70% (high) is yellow, 50–70% (medium) is green, 30–50% (low) is blue, and < 30% (very low) is purple and 0% (open) is grey. Panel (a) shows shaded MCPs of previous seasons for the same individual, with breeding and non-breeding seasons for 2016 and 2017. Burned areas in panel (a) were from the Bucks (1999) and Storrie (2000) fires whereas burned areas in panel (b) resulted from the Moonlight fire (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wildfire and subsequent alternations to vegetation structure.

Effects of timber harvest, including thinning, on goshawks are debated, with several studies indicating negative effects of timber harvest (Crocker-Bedford, 1990, 1995) while a recent long-term study indicates more frequent breeding by goshawks in thinned areas (Reynolds et al., 2017). In a global meta-analysis, Northern Goshawk nest sites or territories with larger trees and less timber harvest close by were more likely to be occupied, however, no effects of timber harvest or tree size were found on productivity (Rodríguez et al., 2016). Despite lack of consensus in the literature, the avoidance of open areas and low canopy cover by goshawks in our study indicate that harvesting activities that result in these conditions may detrimentally impact Northern

Goshawks.

We also observed long-distance foraging behavior (travel 5–15 km from nest location) in both sexes. In contrast to other spatial scales, foraging goshawks selected habitat with both low canopy cover (30–50%) and high canopy cover (> 70%). Use of relatively open vegetation structure while foraging by goshawks and sympatric California Spotted Owls (Blakey et al., 2019) may minimize transit times, avoid conspecific or interspecific interactions, or relate to prey availability. Foraging behavior, which may vary among individuals, may be explained by prospecting for new territories, seeking extra-pair copulations, or simply exploiting ephemeral or alternative foraging opportunities (Reed et al., 1999). Goshawks foraging into burned areas may



**Fig. 4.** Analysis of Northern Goshawk roost distribution and selection across vegetation structure and fire regime categories in Plumas National Forest, Sierra Nevada, CA. Panel (a) shows the proportion of the landscape covered by each habitat category (left) with the proportion of total roosts recorded in each habitat category (right). Panels (b) and (c) show Manly selection ratios indicating positive ( $> 1$ ) and negative ( $< 1$ ) selection of canopy cover and tree size categories by roosting goshawks across 1024 total roost nights (16 individuals, 8 females and 8 males, 27 goshawk-seasons).

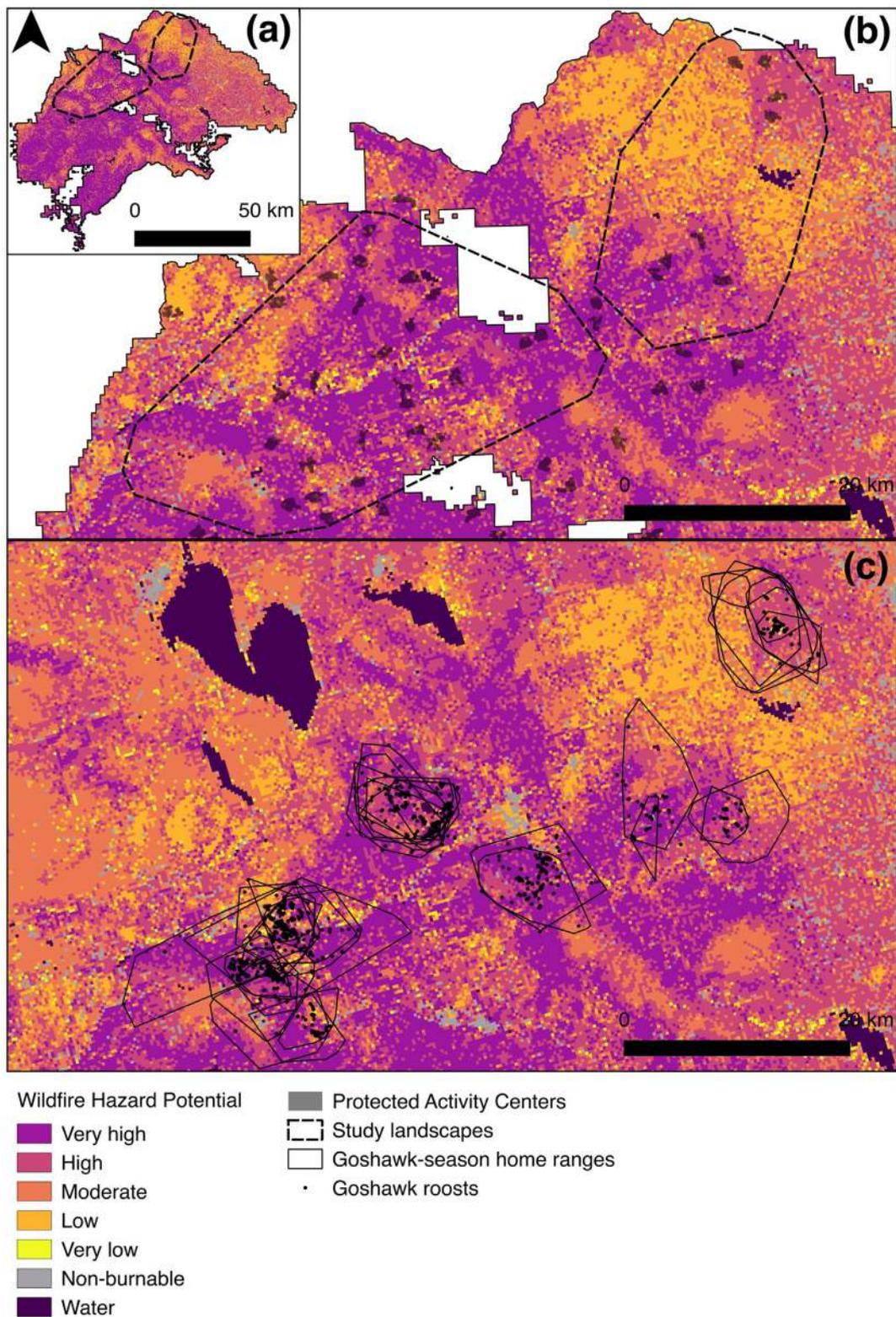
have been seeking alternative prey (Fontaine and Kennedy, 2012; Roberts et al., 2015) or making use of habitat conditions created by low severity fire such as open understory and intact canopy (Squires and Kennedy, 2006). Use of burned landscapes for foraging also has been observed in other late seral forest predators (Spotted Owls, (Bond et al., 2009) Pacific Fishers, *Pekania pennanti*, (Hanson, 2015)) and mosaics of habitat burned at varying times and severities are likely to provide productive landscapes and meet the life history needs of many species (Tingley et al., 2016a).

#### 4.1. Management implications

Across the global range of the Northern Goshawk, changing fire regimes are resulting in longer fire seasons and conversion of forest to shrublands and grasslands (Jolly et al., 2015; Karavani et al., 2018). Given the variety of fire regimes and vegetation types across the range of the Northern Goshawk in North America and indeed across its global distribution in Europe and Asia, our findings warrant further regional investigation and are likely to be most relevant to the dry coniferous forests of western North America. As is the case for other late seral forest dependent species (Wan et al., 2019), high-severity fires are likely to increase in areas occupied by Northern Goshawks in western North America and subsequently reduce the extent and/or quality of roosting and foraging habitat for Northern Goshawks. Efforts to reduce

risk of high-severity fire, including forest thinning and prescribed fire, also may reduce goshawk foraging and roosting habitat quality if they decrease canopy cover and fragment late-seral forest. However, high resolution diurnal tracking indicated that goshawks use areas with smaller trees and medium canopy cover while foraging and two individuals foraged into burned areas. Additional study is required to establish whether mixed severity fire may improve goshawk foraging habitat by creating a mosaic of habitat structures conducive to prey diversity.

Global declines in late seral and old forests (2.5% per year) are exacerbated in western North America by loss through recent increases in wildfire extent and severity (Davis et al., 2015; Morales-Hidalgo et al., 2015; Ray et al., 2014; Stephens et al., 2016). Forest management directed at creating vegetation patterns maintained by wildfire has been proposed in the Sierra Nevada to reduce the risk of large-scale stand-replacing wildfire (North et al., 2009; Sherlock, 2007) and specifically to restore Northern Goshawk habitat in the Southwest U.S. (Reynolds et al., 2013). Concentrating relatively larger-scale fuels treatments (forest thinning) and prescribed fire in mid seral and young forest patches across the landscape may simultaneously reduce risk of large scale high-severity wildfire and promote development and maintenance of wildfire-maintained vegetation patterns, reducing risk to Northern Goshawk roosting and foraging habitat.



**Fig. 5.** Overlap of Fire Risk or Wildlife Hazard Potential (USDA Forest Service, 2018) with (a) Northern Goshawk study landscapes, (b) Protected Activity Centers and (c) roost sites and home ranges.

## Data availability

We will provide base data for collaborations and investigations at the conclusion of our work on the Plumas National Forest.

## Declaration of competing interest

We have no competing interests or conflicts of interest to declare.

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