



Anthropogenically protected but naturally disturbed: a specialist carnivore at its southern range periphery

John R. Squires¹ · Lucretia E. Olson¹ · Jacob S. Ivan² · Peter M. McDonald³ · Joseph D. Holbrook⁴

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Abstract

Understanding how species distributions and associated habitat are impacted by natural and anthropogenic disturbance is central for the conservation of rare forest carnivores dependent on subalpine forests. Canada lynx at their range periphery occupy subalpine forests that are structured by large-scale fire and insect outbreaks that increase with climate change. In addition, the Southern Rocky Mountains of the western United States is a destination for winter recreationists worldwide with an associated high degree of urbanization and resort development. We modeled habitat for a reintroduced population of Canada lynx in the Southern Rocky Mountains using an ensemble species distribution model built on abiotic and biotic covariates and validated with independent lynx locations including satellite telemetry, aerial telemetry, camera traps, den locations, and winter backtracking. Based on this model, we delineated Likely and Core lynx-habitat as thresholds that captured 95% and 50% of testing data, respectively. Likely (5727 km²) and Core (441 km²) habitat were spatially limited and patchily distributed across western Colorado, USA. Natural (e.g., insect outbreaks, fire) and anthropogenic (e.g., urbanization, ski resort development, forest management) disturbance overlapped 37% of Likely lynx-habitat and 24 % of highest quality Core. Although overlap with fire disturbance was low (5%), future burns likely represent the greatest potential impact over decades-long timeframes. The overlap of publicly owned lands administratively classified as “protected” with Likely (62% overlap) and Core (49%) habitat may insulate lynx from permanent habitat conversion due to direct human disturbance (urbanization, ski resort development).

Keywords Fire · Insect outbreaks · Protected landscapes · Canada lynx · Ski resorts · Species distribution models

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Extended author information available on the last page of the article

Introduction

Forests provide the fabric of goods and services required by natural ecosystems and human societies. Yet, forests that will provide ecological and human welfare now and in the future are declining globally due to complex and varied interactions involving climate change and associated drought, harvest and deforestation, urbanization, disease and insect pathogens, and other natural and anthropogenic disturbances (Millar and Stephenson 2015; Seidl et al. 2017; Sommerfeld et al. 2018; Biedermann et al. 2019; Steel et al. 2022). For example, persistent warming and drying trends from climate change contributed to a doubling of area burned in the western continental United States from 1984 to 2015 (Abatzoglou and Williams 2016) and to an eightfold increase in areas burned at high severity (Parks and Abatzoglou 2020). Forest management and fire suppression actions may have compounded this impact through increased forest homogenization (Hagmann et al. 2021; Hessburg et al. 2021), whereas these same actions may enhance landscape restoration and resilience depending on field prescriptions (Stephens et al. 2018; Fettig et al. 2019). In addition, disturbance from outbreaks of tree-killing bark beetles (Coleoptera: Scolytinae) strongly impact forest structure and composition at broad scales, especially given how climate change impacts basic ecological drivers that regulate insect populations (Bentz et al. 2010; Seidl et al. 2017; Rodman et al. 2021). Finally, forest management is a significant source of forest disturbance as well (Gauthier et al. 2015; Kuuluvainen and Gauthier 2018) with harvest effects on forest structure that range from those somewhat similar to insect outbreaks (e.g., uneven-aged harvest) to outcomes more closely resembling fire (e.g., complete overstory removal via clearcut; Graham & Jain 1998; Savilaakso et al. 2021). In general, individual harvest disturbances impact forests at smaller scales than fire or insect outbreak (Smith 2000).

Forest disturbance is compounded by an expanding human footprint that includes high human density, land transformation (e.g., agriculture, urbanization, transportation systems, hydrologic modification), power infrastructure (e.g., sustainable and non-sustainable energy development) and other interrelated factors (Sanderson et al. 2002). Human impacts are also heightened by the demand for nature-based recreation that has increased sharply across the same natural landscapes required for conservation of species dependent on public lands in the United States (USA) (Larson et al. 2016).

Forests in the Southern Rocky Mountains of the western USA (interchangeably, “Southern Rockies”) support ecosystems with diverse natural disturbance regimes from fire and insects as well as anthropogenic caused disturbance. In general, increased temperatures from climate change in Rocky Mountain forests result in increased rain as winter precipitation, earlier snowmelts, and increased severity and duration of the fire season (Rocca et al. 2014). The historical fire regime in subalpine forests is characterized by infrequent but extensive stand-replacing fires that result in high tree mortality (Agee 2000; Schoennagel et al. 2004; Sibold et al. 2006). However, there has been a decades-long trend of increased fire in the Rocky Mountains since 1984, and fire is currently occurring at a higher rate than at any time over the past two millennia (Higuera et al. 2021). Heightened levels of fire disturbance were especially acute in 2020 across the western United States with 2.5 million ha burned in some of the largest recorded fires (Higuera and Abatzoglou 2020). Additionally, 39.5% (10,256 km²) of montane and subalpine forests across the Southern Rockies were impacted by tree-killing bark beetles with 19.3% of stands experiencing > 70% tree mortality from 1997 to 2019 (Rodman et al. 2021). Colorado, which includes most of the Southern Rockies, also has a rapidly expanding human footprint and supports the

9th fastest growth rate of human populations in the US from 2022 to 2023 (U. S. Census Bureau 2023). In addition, Colorado supports 28 developed ski resorts that are located primarily on public lands administered by the U.S. Forest Service, and the state experienced the highest economic contribution in the USA from winter sports that generated \$2.56 billion in annual economic value and 43,000 jobs in 2016 (Hagenstad et al. 2018). However, climate impacts from mid to late century may reduce snow-related visitations from 40 to 60% (Parthum and Christensen 2022).

The challenge of managing these complex patterns of natural and human-caused disturbance is especially daunting in the western USA where forest managers must also promote the conservation of snow-dependent species like Canada lynx (*Lynx canadensis*; interchangeably “lynx”) in high elevation, subalpine forests. For these species, extant patches of high quality habitat that resist climate impacts through elevation and topography provide “stepping stones” of refugia that enhance the persistence of vulnerable species during periods of severe and extensive disturbance (Michalak et al. 2020; Morelli et al. 2020). As pressures mount on forested ecosystems, understanding the distribution, extent, and status of habitat refugia for species is fundamentally important for their continued existence with climate change (Keppel et al. 2012; Krawchuk et al. 2020; Morelli et al. 2020). An important initial step in identifying disturbance and climate refugia for vulnerable species is to delineate the current extent and configuration of high-quality habitat within a disturbance context.

From 1999 to 2006, Colorado Parks and Wildlife (CPW) reintroduced 218 wild-caught Canada lynx into Colorado with the goal of establishing a viable population at the species’ southern-most range periphery in the Southern Rockies (Devineau et al. 2010). All lynx currently present in the Southern Rockies are the result of this reintroduction. As a federally listed species in the contiguous USA under the U.S. Endangered Species Act (ESA; Federal Register. 2000. Vol. 65, No 58, 16052–16086), land managers must consider the conservation of Canada lynx populations in the design and implementation of management actions. Lynx in both northern boreal forests and populations at the range periphery preferentially use boreal or subalpine forests with high horizontal forest cover (e.g., conifer boughs at the snow or ground surface) (Mowat et al. 2000; Koehler et al. 2008; Squires et al. 2010; Simons-Legaard et al. 2013; Ivan and Shenk 2016); forests with high horizontal cover support populations of snowshoe hare (*Lepus americanus*), the primary prey of lynx (Hodges 2000; Mowat et al. 2000; Squires and Ruggiero 2007; Ivan and Shenk 2016). In the western USA, lynx preferentially use mosaics of spruce-fir forests dominated by mature and advanced regenerating (≈ 20 –40 yr old trees) structure classes (Holbrook et al. 2017). Canada lynx may also use landscapes disturbed by large-scale fire (Vanbianchi et al. 2017) and forest insects (Squires et al. 2020), but with time-lags that depend on the nature of disturbance and management actions (Holbrook et al. 2018, 2019; Olson et al. 2023). Lynx also exhibit functional (Squires et al. 2019) and behavioral responses to motorized and non-motorized winter recreation, including an avoidance of high recreation-related disturbance at developed ski resorts (Olson et al. 2018).

Canada lynx in the Southern Rockies provide a valuable case study of managing a sensitive species in landscapes that are increasingly structured by complex disturbance patterns accelerated by climate change. Here, we model the distribution of lynx habitat in the Southern Rocky Mountains of the western United States based on GPS telemetry and environmental covariates that we validated with independent lynx detections (i.e., den locations, camera photos, telemetry data collected a decade prior to this study). We then spatially delineated a lynx habitat threshold that captures 95% of testing data to represent the extent and spatial configuration of high-quality lynx habitat

in the Southern Rocky Mountains. Next, we determined how patterns of disturbance from fire, forest insects, past active forest management (e.g., tree harvest, thinning, controlled burning), and urbanization and ski resort development may overlap current lynx habitat, as well as determined how administratively protected landscapes, such as designated Wilderness areas, roadless areas, and national parks and monuments, relate spatially to lynx habitat. Thus, we evaluated how natural and human-caused disturbance overlaps high-quality, in situ habitat required by lynx to identify areas of highest conservation concern for management, as a foundation for the recognition of potential lynx refugia that resist disturbance and climate impacts.

For this research, we predicted the following: (1) lynx habitat in the Southern Rockies would consist of relatively small and spatially isolated patches given the complex mountain topography; (2) natural disturbance from fire and insect outbreaks are primary ecological forces that are impacting the current spatial and temporal configuration of lynx habitat; and (3) the expanding human footprint from urbanization, ski-resort development, and forest management is reducing the spatial extent of lynx habitat, and, as such, protected landscapes offer an important buffer to human-caused direct impacts.

Methods

Study area

Our study area included the southernmost range periphery of Canada lynx within the continental United States; western Colorado, southern Wyoming, and northern New Mexico (approximately 145,000 km²; Fig. 1). Mean temperatures in the Southern Rocky Mountains average -4.8°C (range: -13 – 2.3°C) in winter and 14.8°C (range: 4.5 – 23.5°C) in summer. Mean annual precipitation is primarily from snowfall, and averages 58.3 cm (range: 19.2–182.2 cm) per year (AdaptWest Project 2015; Wang et al. 2016). Human settlements and agricultural/ranching areas are primarily in the lower-elevation valleys. Lynx occupy mid-range elevations (mean: 3261 m, range: 2574–4169 m) above valley bottoms but below open alpine tundra on mountain tops and high ridges. Lower elevations within the lynx-occupied zone were dominated by lodgepole pine (*Pinus contorta*) with the cool, moist higher elevations supporting subalpine forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Large stands of aspen (*Populus tremuloides*) were interspersed throughout subalpine forests. Due to lodgepole pine reaching its range limit in our study area, the southern one third of our research area was dominated by subalpine spruce-fir forest and the northern two thirds dominated by lodgepole pine or mixed lodgepole-spruce-fir. Developed ski resorts in Colorado and associated towns and urbanization were distributed across the study area. Canada lynx have successfully produced kittens since their reintroduction (Ivan and Shenk 2016), and they primarily occupy the San Juan Mountains (location centroid 37.554°N , -106.868°W) of southern Colorado and the Mosquito Range near Vail and Leadville, Colorado, USA (approximate centroid coordinates 39.45°N , 106.30°W Buderman et al. 2018; Ivan et al. 2018; Olson et al. 2018; Squires et al. 2019).



Fig. 1 Study area to investigate the distribution of Canada lynx at the species' southern range periphery in the Southern Rocky Mountains of the western United States, including portions of Wyoming, Colorado, and New Mexico, USA

Lynx capture and location data

From 2010 through 2013, we captured Canada lynx on and adjacent to the Vail Pass Winter Recreation Area as part of previous research that investigated potential impacts of winter recreation on lynx movements and resource-use (Olson et al. 2017, 2018; Squires et al. 2019). In 2012 and 2013, we then expanded our lynx trapping to the Sawatch Range near Leadville, CO, USA, and south to the San Juan Mountains near Silverton and Telluride, CO, USA. We captured lynx ($N = 18$) using box-traps (Kolbe et al. 2003), and we fitted each individual with a store-on-board GPS collar (≈ 255 g) that was $<3\%$ of body mass. All capture and handling protocols were performed in accordance with Institutional Animal Care and Use Permit CDOW-ACUC File #13-2009 from

Colorado Parks and Wildlife and Institutional Animal Care and Use Permit AUP-062-13MHWB-122013 from the University of Montana. We believed that captured lynx represented a large proportion of individuals present on trapping areas based on snow tracks and recaptures of collared individuals. Collars were programmed to collect locations every 20 min, 24 h per day in 2010, 2012, and 2013, and every 30 min, every other day in 2011. The GPS data set characterized winter use (Jan–Apr), which is the season that lynx are most constrained in their habitat (Squires et al. 2010). The timing of our lynx sample provided a snapshot of habitat use generally before the surge in large-scale disturbance from fire and insects in these study areas (Ivan et al. 2018; Squires et al. 2020).

We screened location data from lynx collars for errors following Bjørneraas et al. (2010) and Hurford (2009), based on the removal of erroneous movement ‘spikes’ with calculated movement speeds greater than 3 kph and turning angles between 166° and 194°. To reduce autocorrelation and facilitate use of large GPS datasets in species distribution models (Boria and Blois 2018), we first converted GPS locations to presence data at the resolution of our environmental covariates (i.e., one to many GPS data points were reduced to a single presence location per 120 m raster cell) and then presence locations were subsampled to include 30% of the dataset for model training, with the other 70% of the data withheld for model testing, a reduction in data previously determined to balance model performance and overfitting (Boria et al. 2014; Olson et al. 2021). We defined the extent of the study area using the ‘Southern Rocky Mountains’ level 3 ecoregion, an area characterized by steep high-elevation mountains and largely coniferous forest (Omernik and Griffith 2014). We buffered the ecoregion by 5 km to ensure the background sample was large enough to reduce edge effects and include habitat transition zones on the edges of the forested mountains (Northrup et al. 2013).

Environmental covariates

We initially considered 42 environmental covariates for species distribution models (SDMs) based on known lynx-habitat relationships from the literature and our field experience. These represented the general categories of climate, topography, vegetation, and anthropogenic influences on lynx distribution (Appendix 1). For final models, we narrowed the number of covariates to 18 based on variable selection procedures outlined below. Covariates selected for final models included the climate variables comprised of: (1) mean annual relative humidity; (2) mean temperature in the coldest month; (3) precipitation as snow; and (4) summer precipitation (Jun to Aug). All climate variables were 1981–2010 averages downloaded from ClimateNA (AdaptWest Project 2015; Wang et al. 2016) with a native (original) resolution of 1 km.

Topographic covariates included (5) slope; (6) surface ratio (an index of topographic roughness, calculated by surface area divided by planimetric area; Jenness 2013); (7) topographic position index (an index of surface concavity or convexity; Jenness et al. 2013); and (8) compound topographic index (an index of landscape wetness, calculated based on slope and upstream area; Evans et al. 2014). All topographic covariates were calculated based on a digital elevation model with a native resolution of 10 m (Gorelick et al. 2017).

Soil covariates included: (9) soil bulk density, with lighter soil potentially related to more organic matter and increased water holding capacity (Ilek et al. 2017); and (10) soil pH, with the wetter conditions of subalpine forests, a common lynx habitat type, expected

to have lower pH (Hengl et al. 2017). Soil layers were downloaded from SoilGrids (Hengl et al. 2017) at 250 m native resolution.

Vegetation data consisted of: (11) normalized difference vegetation index (NDVI), an index of vegetation productivity (Pettorelli et al. 2005); and (12–15) the presence of certain categories of forest species composition (see Appendix 1), as delineated using LandFire Existing Vegetation Type (LANDFIRE 2018), both at native resolutions of 30 m. An index of forest heterogeneity (16) was also included, calculated as the standard deviation of forest cover (0–100% cover, resolution 30 m; Hansen et al. 2013) within a given neighborhood (neighborhood sizes defined below).

Finally, two anthropogenic covariates were considered, (17) an index of nighttime visible lights from persistent light sources such as cities and towns (National Oceanic and Atmospheric Administration, 2014; resolution 1 km), and (18) a measure of road density including highways, local roads, and open forest roads (OpenStreetMap Foundation 2017). To make covariates consistent for modeling, we reprojected all rasters to a common spatial projection and resampled them to 120 m resolution using bilinear interpolation for continuous data and nearest neighbor for discrete data.

To accommodate the potential for lynx to select and respond to covariates at different spatial scales (DeCesare et al. 2012), we evaluated all covariates at three spatial scales, determined by the observed movement characteristics of lynx in our study: a local scale of 400 m, the average distance lynx moved in an hour; a mid-scale of 4 km, the average lynx movement distance in 12 h; and a large-scale of 8 km, the average movement distance in 24 h (which also corresponds to roughly the dimension of a home range if home ranges were square). Spatial scales were calculated for each covariate using a neighborhood analysis with a circular radius equal to the scale distance.

Distribution modeling

We used the R package ‘biomod2’ (Thuiller et al. 2009) to create ensemble SDM models (Araújo and New 2007) of Canada lynx distribution across the study area. Ensemble models combine the predicted results of multiple modeling methods to produce predictions that are generally superior or equal to single models (Marmion et al. 2009; Hao et al. 2020). First, we screened all covariates to determine the scale at which to include them in final models. We determined the predictive ability and best performing scale of each covariate using a limited ensemble species distribution model including only machine-learning (Maxent) and regression modeling (general linear regression) methods (Araújo & New 2007) to minimize computation time. For each covariate at each scale, we calculated univariate model performance using the receiver operating characteristic (ROC; Peterson et al. 2008) area under the curve (AUC) based on the 70% testing location data and our background availability sample, and considered only the top-performing scale (highest AUC) for each covariate in further models. Additionally, for each covariate, we created a response plot showing the change in relative probability of lynx distribution as an effect of the given covariate (Elith et al. 2005; Thuiller et al. 2009). This allowed us to compare the effect size of the modeled response for each covariate. Next, we screened all covariates at previously selected scales for Pearson pairwise correlations of $r > 0.71$. We carried forward all covariates that had AUC above 0.5; when two covariates had pairwise correlations above $r > 0.71$, we chose the covariate with a greater effect on lynx distribution, as determined by response plots. Using this method, we grouped plausible covariates to create three candidate SDMs for consideration: the “Literature” model focused on biotic and abiotic covariates

determined in previous studies to be most predictive of lynx habitat (Squires et al. 2010, 2013; Holbrook et al. 2017); the "Abiotic" model used only abiotic covariates, (i.e., climate, topography, and soil) to provide a model suitable for future climate predictions if desired; and the third model ("Combined") included both biotic and abiotic covariates in a manner consistent with the variables used in a previously developed SDM model for lynx in the Pacific Northwest (Cascade Range, Northern Rockies, Greater Yellowstone Areas) of the USA (Olson et al. 2021).

The ensemble models for the final Literature, Abiotic, and Combined models used five modeling methods commonly used in an SDM framework: random forest, multivariate adaptive regression splines, generalized boosted model, general additive model, and generalized linear regression (Elith and Graham 2009; Hao et al. 2019). Ensembles were created using a weighted average, with weights determined by the AUC of each individual model, validated on the 70% testing data. Background (random) locations were sampled across the study area at a density of 1 point per km², then randomly subsampled to equal 20 times the number of presence locations. Since models run using the default 'biomod2' modeling parameters validated highly on testing data, we accepted the default parameters for all models. We assessed individual covariate contribution to the top-performing model using a permutation procedure in which each variable in turn was randomized (5 permutations per variable), new model predictions were generated, and the correlation between the permuted predictions and the original model predictions was calculated (Thuiller et al. 2009; Olson et al. 2021). If a given covariate had a greater contribution to the model, correlations between the prediction sets would be low. We performed this procedure for each of the five modeling methods in the ensemble and combined the results into a single boxplot for interpretation. Thus, in total, we fit 3 SDMs (Literature, Abiotic, and Combined) with different sets of covariates, each of which consisted of an ensemble of 5 modeling methods.

Model validation

We quantified model performance using two datasets and three validation methods. First, we validated our model using the 70% withheld location data set aside at the beginning of the modeling process. However, given the frequently high correlation between model training and withheld model testing data, and the high impact of a federally listed species like the Canada lynx on land management, we also evaluated model performance using independent location data for lynx collected by Colorado Parks and Wildlife after the species reintroduction from 1999 to 2021 (Devineau et al. 2010). We believed that model validation based on these independent field data provides the best evaluation of model performance for conservation planning. These independent location data included: conventional VHF telemetry from fixed-wing aircraft ($n=3889$), camera trap detections ($n=25$), lynx snow tracks ($n=104$), and dens ($n=49$). Prior to 2012, Colorado Parks and Wildlife monitored lynx movements using Argos satellite telemetry. Therefore, for completeness, we also reported how Argos lynx locations performed relative to model testing ($n=673$) using only the most accurate, class-3 locations. This result was reported in Appendix 2 but not included in the overall model evaluation due to the inherent high variability in location accuracy of Argos telemetry. We screened VHF and Argos telemetry locations to only include resident animals that were ≥ 1 year post-release, to avoid heightened movement behavior immediately post-reintroduction (Buderman et al. 2018). We evaluated independent data by season, winter (November through April) and summer (May–October), since

the SDM model was based on winter GPS locations from January through April and thus depicts a lynx's more constricted winter space use (Squires et al. 2013).

We used two primary validation methods for both withheld test data and independent lynx detections: AUC, as a widely used metric to evaluate model performance, and the continuous Boyce index (Hirzel et al. 2006) from the R package 'ecospat' (Di Cola et al. 2017) as a secondary method given some criticism of AUC when applied to SDMs (Lobo et al. 2008). The continuous Boyce index compares the distribution of model predictions at lynx presence locations to the distribution of model predictions at background locations. Results from these validation metrics generated values from 0 to 1: an AUC of 0.5 indicated model performance similar to random and 1 indicated perfect prediction; a continuous Boyce index of 1 indicated a strong correlation between the distribution of modeled testing and background predictions. Additionally, for independent field data only, we used a third method of model validation, the percent of independent lynx locations that were captured above a 95% probability threshold generated by the 70% withheld data (see below). Higher percentages indicated more independent data points occurred above the validation threshold and signified better model performance (Holbrook et al. 2017; Olson et al. 2023); this approach was similar to the 'minimum predicted area' methodology developed in Engler et al. (2004).

Habitat-use thresholds and disturbance overlap analysis

To identify the most appropriate areas on which to focus conservation planning and resource management, we created 3 habitat classes: Unlikely, Likely, and Core habitat based on the underlying continuous predicted distribution. We used the withheld testing data to delineate habitat-quality thresholds. The Likely threshold captured 95% of withheld testing data and defined all habitat that most likely supported breeding populations of Canada lynx. The Core threshold is nested within the Likely habitat threshold and defined by the highest 50% isopleth of withheld testing data, which delineated the highest quality habitat with greatest probability of use. We chose these thresholds to roughly conform to core (50%) and high-use (95%) areas as defined in the home range literature (Fieberg and Kochanny 2005). The Unlikely habitat threshold included areas outside the 95% distribution of withheld data and defined areas of poor habitat quality with a low chance of sustained lynx occupancy.

A central motivation for this research was to evaluate how natural and anthropogenic disturbance potentially impacted lynx habitat in the Southern Rockies. Here, we calculated the area (km²) and percent of spatial overlap for multiple disturbance categories to the Likely (95%) and Core (highest 50%) habitat thresholds. To provide a more complete context of these disturbances across the study area, we also evaluated the extent that disturbance impacted landscapes in the low-probability use (Unlikely; > 95% distribution isopleth) threshold. The categories that we considered included: forest disturbance (insect outbreaks, wildfire, timber harvest); human-foot print disturbance (ski resorts, urbanization), and protected areas (Wilderness, roadless areas, national parks/monuments).

We calculated overlap from mountain pine and spruce beetle disturbance using the U.S. Forest Service's National Insect and Disease Detection Survey, which employs annual aerial and ground surveys from 1997 to 2022 to delineate forest patches impacted by forest insects (United States Forest Service Forest Health 2022) in a polygon-based dataset of disturbance by year. We determined the spatial extent of fire disturbance based on polygons of burn perimeters delineated in the Monitoring Trends in Burn Severity dataset (MTBS

Project 2022) from 1990 to 2022. We evaluated how forest management impacted lynx habitat based on the publicly available Forest Service Activity Tracking System (FACTS) dataset (U.S. Forest Service Natural Resource Manager 2022) using data from 1990 to 2022. These data include spatial polygons that delineate the extent, timing, and type of forest management activity across U.S. National Forests. We focused on forest management actions in the FACTS database that altered forest structure and composition, including timber harvest, stand improvement cuts, and hazardous fuel reductions.

We estimated the spatial overlap of urbanization to lynx habitat using the North America Microsoft Building Footprints database (Microsoft 2021), a freely available online dataset of polygons representing building footprints delineated using a machine-learning process (Microsoft Corporation 2023). We recognized that impacts of urbanization included not only the actual house and building footprints, but also the disturbance buffer around structures based on lynx avoidance behavior. Based on an analysis of avoidance behavior of Canada lynx to buildings/structures (see Appendix 3), we included a 200 m buffer around each building polygon to better encompass the actual area of urbanization disturbance. We used spatial layers provided by U. S. Forest Service, Region 2 to evaluate the spatial extent that established ski resorts, including other infrastructure associated with developed recreation, overlapped lynx habitat, excluding Nordic ski tracks/areas.

We evaluated the spatial overlap of protected areas on habitat of Canada lynx, given their role in buffering human disturbance. We evaluated how designated ‘National Wilderness Areas’ identified in the U.S. National Wilderness Preservation System overlapped lynx habitat. Wilderness areas exclude all mechanized use, development, road-building, forest management, or extractive activities (Dietz et al. 2015). We also considered habitat overlap by national parks and monuments, while acknowledging these public lands may support greater human use than Wilderness areas given high visitation rates, motorized travel, extensive park infrastructures, and some limited forest management (Lemons and Stout 1982). Finally, we determined the extent that “roadless areas” overlapped lynx habitat based on the Colorado Roadless Rule of 2012; we used the US Roadless Rule of 2001 for areas outside of Colorado. Designated roadless landscapes typically support little forest management, despite some exceptions (U.S. Forest Service Natural Resource Manager 2022).

Results

Model validation

Model validation from withheld and independent data indicated that all 3 candidate models (Literature, Abiotic, and Combined) were effective in predicting lynx locations with only small differences in model performance and spatial delineations. Based on the 70% withheld dataset, model performance was similar based on AUC with values of 0.995 for the Literature-based model (abiotic and biotic covariates), 0.993 for the Abiotic model (abiotic covariates), and 0.995 for the Combined model (abiotic and biotic covariates; Olson et al. 2021). Similarly, continuous Boyce index values equaled 1 for all three models indicating strong model validations.

Model performance when evaluated with independent lynx location data was more varied as expected, given these independent data spanned the life history of reintroduced lynx including denning behavior, winter foraging, dispersal, and within home range movements (Table 1). We also expected varying levels of model performance across the classes of

independent data due to variation in location accuracy (e.g., lower location accuracy = aerial telemetry; high location accuracy = den locations, field cameras, winter backtracks plotted with GPS). All three SDM models (Literature, Abiotic, Combined) were highly predictive (>0.95 AUC) when evaluated with AUC on independent data. The Boyce index was 0.93, 0.93, and 0.91 for the Literature model, the Combined model, and the Abiotic model, respectively (Table 1). The Abiotic model included the highest percentage (81%) of independent data in Likely lynx habitat, with the Combined model close (77%) in performance (Table 1). Models correctly predicted from ~71 to 79% for lynx locations documented with VHF telemetry and summer cameras, and ~85–89% of lynx locations documented through winter cameras, snow tracks, and den locations (Table 1). Although we did not use ARGOS satellite locations in formal model testing, these locations performed with high accuracy with AUC and continuous Boyce validations, but at lower accuracy (~45–59%) for the 95% threshold (Appendix 2). Since models validated essentially equal on AUC and the continuous Boyce index, and the Abiotic and the Combined models were similar in performance based on independent data prediction, we chose the Combined model as the best

Table 1 Validation of species distribution models (SDMs) for Canada lynx based on independent location data (i.e., not used to build SDMs) evaluated with AUC, Continuous Boyce Index, and the percentage of independent location data above the 95% “Likely” habitat threshold

	Validation Dataset	Literature	Abiotic	Combined
AUC Validation	VHF Winter	0.95	0.95	0.95
	VHF Summer	0.95	0.96	0.96
	Camera Winter	0.95	0.96	0.96
	Camera Summer	0.97	0.97	0.97
	Snow Tracks	0.98	0.98	0.98
	Dens	0.96	0.97	0.97
	Average	0.96	0.97	0.97
Continuous Boyce Index Validation	VHF Winter	1.00	0.99	0.99
	VHF Summer	1.00	0.97	1.00
	Camera Winter	0.85	0.73	0.84
	Camera Summer	0.87	0.88	0.89
	Snow Tracks	0.97	0.96	0.90
	Dens	0.93	0.94	0.98
	Average	0.94	0.91	0.93
Percent of Independent Locations in 95% Threshold	VHF Winter	0.57	0.71	0.67
	VHF Summer	0.59	0.76	0.71
	Camera Winter	0.78	0.89	0.86
	Camera Summer	0.65	0.79	0.69
	Snow Tracks	0.73	0.86	0.84
	Dens	0.71	0.88	0.84
	Average	0.67	0.81	0.77

SDM model “Literature” was built on abiotic and biotic literature-informed covariates; “Abiotic” from abiotic-based covariates, and “Combined” based on abiotic and biotic covariates consistent with Olson et al 2021

Validation data were divided into winter (Nov–Apr) and summer (May–Oct) seasons. Samples sizes for each validation dataset are: VHF winter = 3360 locations, VHF summer = 2874, Camera trap winter = 36, Camera trap summer = 48, Snow tracks = 86, Dens = 49

spatial depiction for the distribution of habitat required by Canada lynx in the Southern Rocky Mountains of the western United States; this model also had the advantage of providing continuity with a previous SDM for the Pacific Northwest, USA (Olson et al. 2021) and together with those outputs provide spatial depiction of habitat required by the Canada lynx across the western U.S.

Distribution

Based on the Combined SDM model, the distribution of Canada lynx habitat in the Southern Rocky Mountains of the western USA included mid-range elevations in primarily the San Juan, Sawatch, Never-Summer and Mummy Mountain Ranges of western Colorado (Fig. 2), similar to predictions of the Literature and Abiotic models (Appendix 4). The Combined SDM was only considered from here on. Isopleths for Likely habitat and highest quality Core habitat encompassed 5,727 km² and 441 km², respectively (Fig. 3). The land ownership for Likely lynx-habitat included 83.5% U. S. Forest Service (4811 km²), 7.3% private (420 km²), 4.3% Bureau of Land Management (248 km²), 3.5% National Park Service (201 km²), 0.8% state (45 km²), and <0.1% non-government organizations (1.6 km²). Current “in situ” habitat for Canada lynx at the species’ southern range periphery consists of relatively small areas of Likely and high-quality Core habitat that were limited spatially and patchily distributed across the Southern Rockies within a matrix of unlikely habitat. The shape of lynx habitat was convoluted due to the complex mountain topography that dominates the region (Fig. 3). Plots of covariate importance in the best-performing Combined model indicated that variables related to climate and topography had the greatest contributions to the model predictions (Fig. 4). The covariate *Precipitation as snow* was the most important covariate, followed by *relative humidity*, *soil pH* (an indicator of the presence of moist boreal-type forests; Hengl et al. 2017), *summer precipitation*, *topographic position index* (a metric of terrain convex or concavity), and *mean temperature in the coldest month*. All other covariates had relatively little impact on model predictions (Fig. 4).

Disturbance overlap

In total, natural and human-caused disturbance impacted approximately 37% of Likely habitat for Canada lynx in the Southern Rockies; 24% of this area was impacted when high-quality habitat was considered separately (Table 2). Consistent with our prediction, natural disturbance was the primary force impacting lynx habitat, especially forest insects that altered forest structure in 31% of Likely habitat and 19% of high-quality Core habitat (Table 2, Fig. 5); insect impacts were mostly confined to the southernmost extent of the species’ distribution, including the San Juan Mountains of southern Colorado (Fig. 5). Spruce beetles overlapped 25% of Likely habitat and 17% of Core habitat. In contrast, mountain pine beetles overlapped 7% of Likely habitat and 3% of Core habitat (Appendix 5). Fire disturbance across the Southern Rockies from 1990 to 2022 overlapped 5% of Likely lynx habitat, with most large-scale burns in Unlikely (8% overlap; Table 2, Fig. 4). Similarly, urbanization from house/building structures including buffers that accounted for lynx avoidance behavior (Appendix 3) and developed ski resorts impacted 4% of Likely lynx habitat. Current levels of disturbance associated with forest management, such as tree

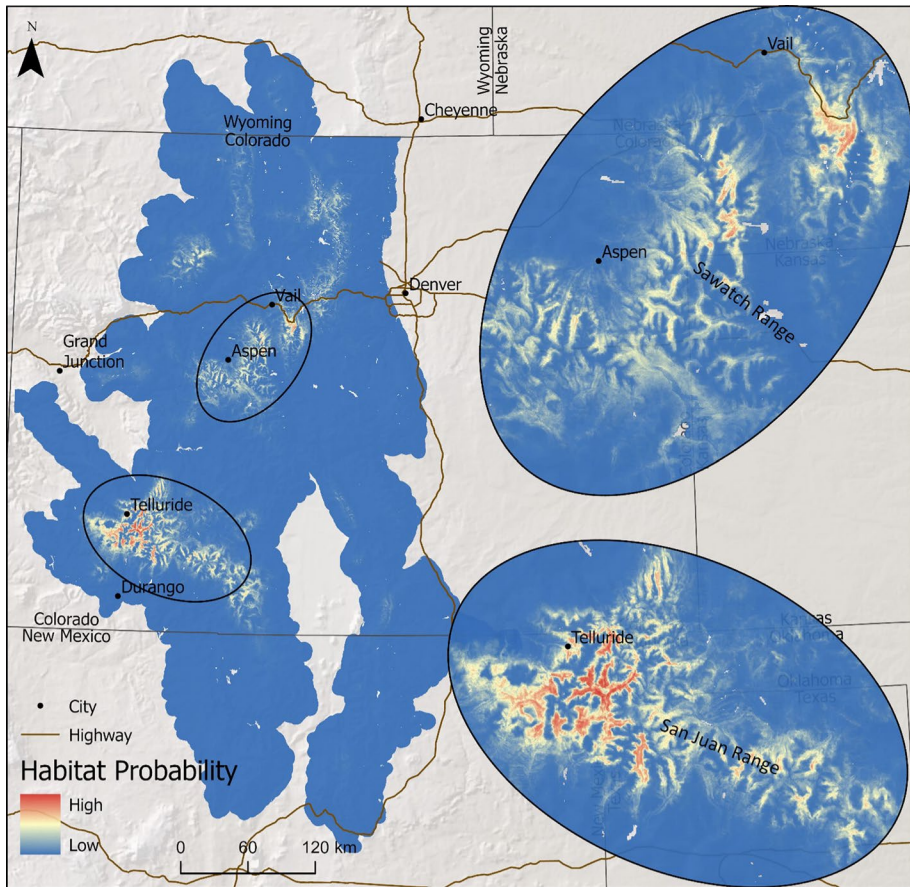


Fig. 2 Distribution of Canada lynx habitat across the Southern Rocky Mountains of the western United States, as estimated with the Combined species distribution model. The color ramp indicates a habitat-quality gradient from poor (blue) to good (red). Inserts are enlargements of areas outlined in black

harvest and controlled burning had limited spatial impacts ($\sim 3\%$) to Likely lynx habitat (Appendix 5 and 6).

Consistent with the original prediction, lands that were legally (i.e., national parks, Wilderness areas) or administratively (i.e., state and federal roadless areas) designated as protected landscapes overlapped significant portions of lynx habitat in the Southern Rockies. Specifically, protected landscapes overlapped 62% of Likely lynx habitat, with 49% overlap in highest-quality Core (Table 2). The remaining state and federal lands that overlapped lynx habitat were administered for multiple use (e.g., recreation, tree harvest, grazing). Designated “roadless” landscapes overlapped 21% of *Likely* habitat and 26% of *Core* within protected landscapes, whereas wilderness areas and national parks combined covered 42% and 23% of Likely and Core habitat, respectively (Appendix 5). Qualitatively, habitat connectivity appeared high within protected landscapes that overlapped Likely habitat (Fig. 6). However, disturbance from developed ski resorts and urbanization occurs in many of the non-protected interstices between protected landscapes (Fig. 6).

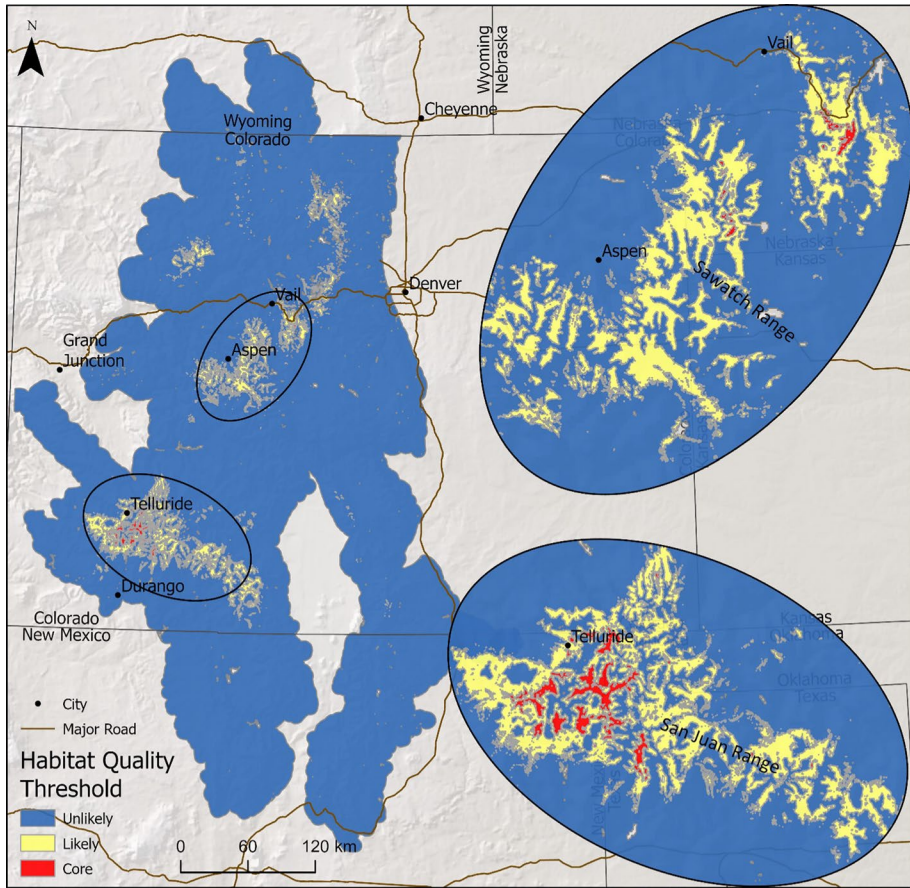


Fig. 3 Threshold isopleths that delineate current habitat for Canada lynx across the Southern Rocky Mountains of the western United States; the Likely threshold captured 95% of withheld data and the Core threshold of best habitat captured 50%. Inserts are enlargements of areas outlined in black

Discussion

The distribution of Canada lynx habitat at the species' range periphery in the Southern Rocky Mountains of the western U.S. is spatially restricted to relatively small landscape patches of southwestern and central Colorado, within a larger matrix of unlikely habitat. Consistent with our original prediction, the Likely habitat (5,727 km²) was restricted to narrow bands of subalpine forests arranged in convoluted shapes, due to the complex mountain topography and the narrow elevation gradient that supports the subalpine forests preferred by lynx and their primary prey, snowshoe hares. The quality of lynx habitat followed a general pattern of good to poor from southern to northern extents of the Southern Rocky Mountains in western CO. The San Juan Mountains at the near southernmost extent of the Southern Rockies supported the highest quality habitat (e.g., the largest blocks of Likely habitat and Core habitat) characterized by cool moist subalpine forests dominated by subalpine fir and Engelmann Spruce. Habitat quality then declined to the

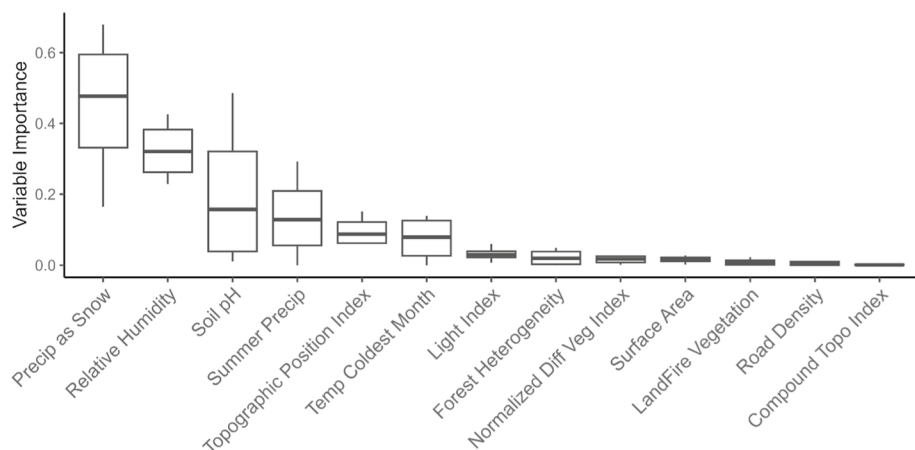


Fig. 4 Relative importance of covariates used in SDM models to predict the distribution of Canada lynx in the Southern Rocky Mountains of the western United States

Table 2 The spatial overlap between current habitat for Canada lynx (from the Combined SDM habitat quality thresholds Unlikely, Likely, and Core) and natural and human-caused disturbed or protected areas in the Southern Rocky Mountains of the western United States

Overlap Type ¹	Years	Area (km ²)			Percent Overlap (%)		
		Unlikely	Likely + Core	Core	Unlikely	Likely + Core	Core
Fire	1990–2022	12,265	291	5	8	5	1
Insect Outbreak	2000–2022	22,192	1756	86	15	31	20
Developed Recreation		236	109	10	0.2	2	2
Forest Management	1990–2022	4638	168	12	3	3	3
Urbanization		11,445	159	13	8	3	3
Total Disturbed (all sources)		43,642	2128	108	29	37	24
Protected		32,174	3578	217	21	62	49
Total Lynx Habitat		150,421	5727	441	–	–	–

The amount of habitat (km²) impacted by each disturbance type and the percent out of the total area in each lynx habitat threshold that this equates to is shown. Overlap between protected and disturbed areas, as well as areas that are neither protected nor disturbed, prevents percents in each threshold category from summing to 1

¹Disturbance classification: Fire (recent fire events), Insect Outbreaks (spruce beetle and pine bark beetle combined); Developed Recreation (ski resorts), Forest Management (hazardous fuel treatments, forest thinning, and tree harvest), Urbanization (spatial footprint of house/buildings including lynx-avoidance buffer) and Protected (state and federal roadless areas, designated wilderness areas, national parks, and monuments)

north as dry forest became more dominant, comprised mostly of climax lodgepole pine or pine-dominated mixtures of lodgepole-spruce-fir forests.

The subalpine forests that sustain Canada lynx have been structured by natural disturbance from fire and insect outbreaks for millennia (Vioreck 1973; Price and Apps 1995; Agee 2000). In recent years, these disturbance agents have increased in impact, particularly

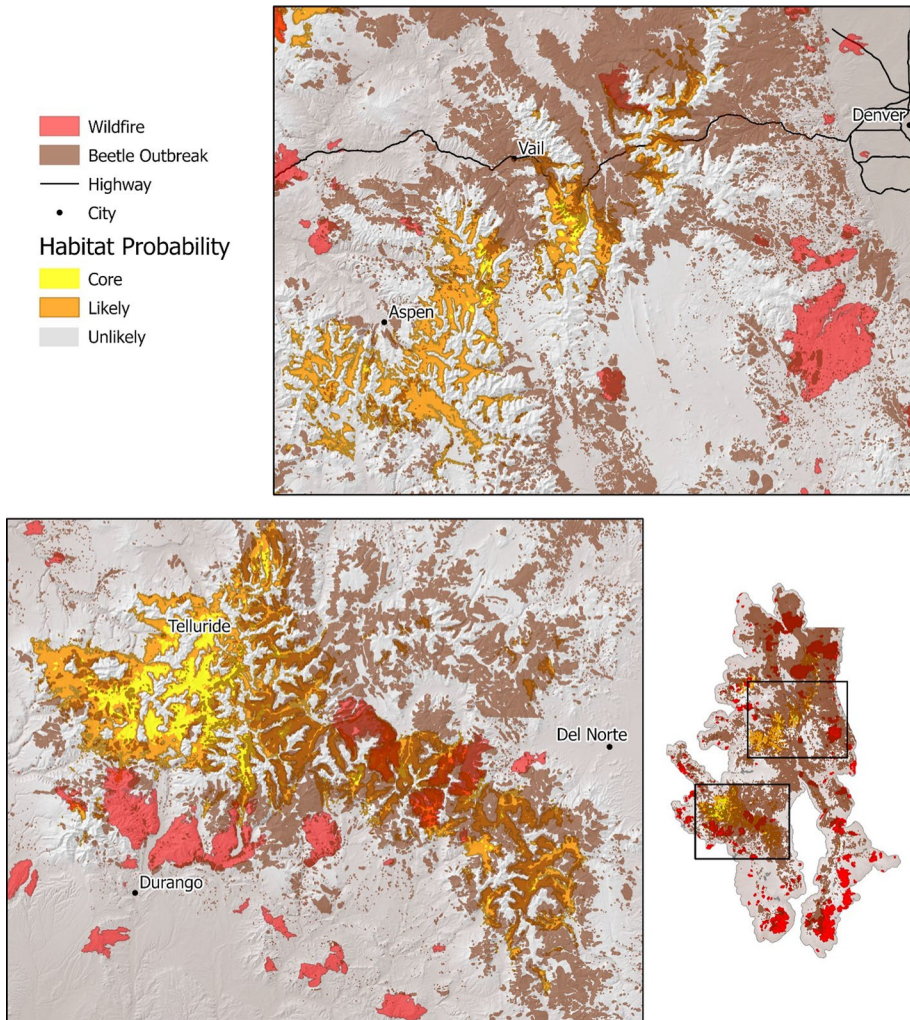


Fig. 5 The overlap of natural disturbance from fire and beetle outbreaks over habitat for Canada lynx in the Southern Rocky Mountains of the western United States as defined by Likely (95% withheld data) and Core (50% of withheld) habitat thresholds. Insets are enlargements of areas outlined in black

in extent and severity, associated with climate change (Bentz et al. 2010; Abatzoglou and Williams 2016; Parks and Abatzoglou 2020; Johnson and Haynes 2023). Thus, the pressing challenge for lynx in the Southern Rockies is the extent, frequency, and severity of impacts on habitat from these disturbances in a relatively short time frame of decades. For any given year, populations of lynx require habitat that promotes their prey species, snowshoe hare and red squirrels (*Tamiasciurus hudsonicus*). Current undisturbed patches of habitat and those previously disturbed but with vegetative recovery (e.g., > 25 years post-disturbance; Kosterman et al. 2018; Holbrook et al. 2019; Olson et al. 2023) will be the stronghold of lynx habitat in the coming decades. With current trends in temperature, precipitation, and drought linked to climate change, the main concern for lynx in the Southern Rockies is the persistence of these relatively few, and somewhat isolated, patches

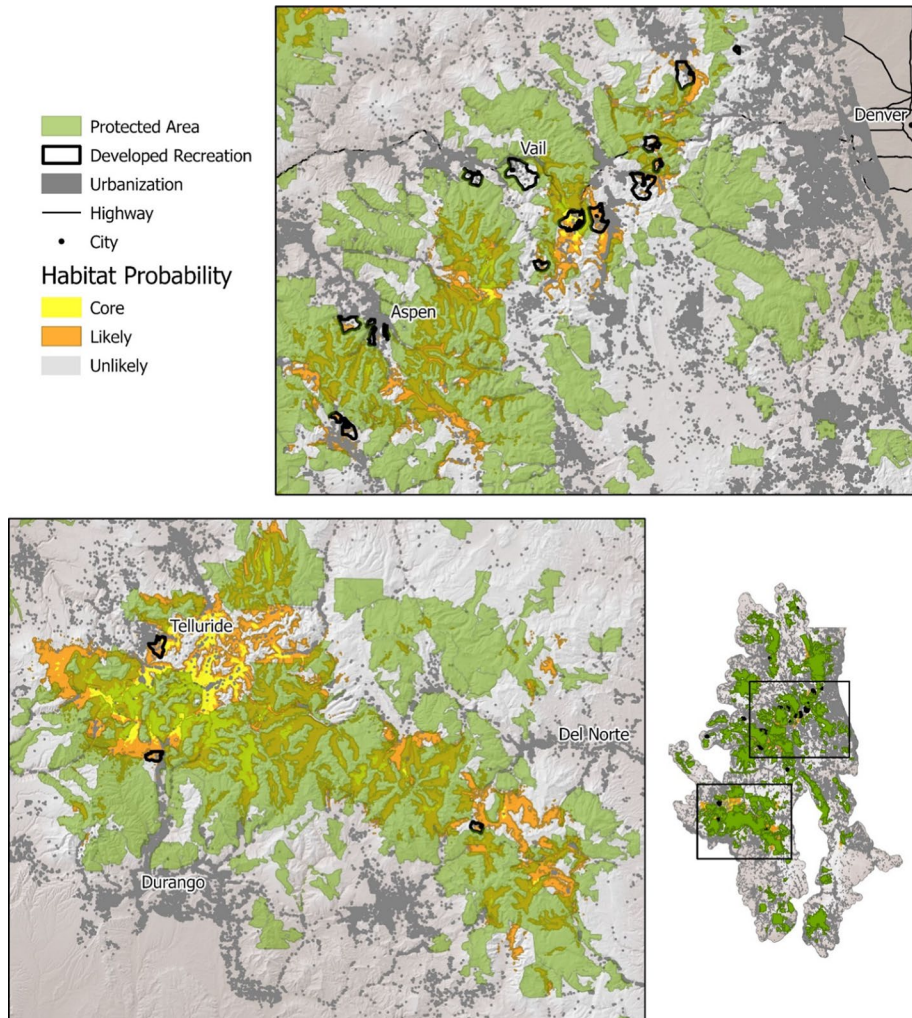


Fig. 6 The overlap of disturbance from developed recreation (i.e., ski resorts), urbanization and protected landscapes (i.e., roadless areas, designated wilderness, national parks) with habitat refugia for Canada lynx in the Southern Rocky Mountains of the western United States as defined by Likely (95% withheld data) and Core (50% of withheld) habitat thresholds. Inserts are enlargements of areas outlined in black

of habitat within a time window that is sufficient to have demographic, and thus, conservation consequences (Meddens et al. 2018; Morelli et al. 2020). A natural question, then, is can we implement forest- and fire-management frameworks in and around lynx habitat to instill habitat mosaics that promote resistance to disturbance? If so, what might that framework look like? Our work presents a static depiction of lynx habitat relative to disturbance agents, which provides the important fundamental information to guard against shifting baseline syndrome (Soga and Gaston 2018). Spatial depictions of Likely, in situ habitat are also needed to focus management and conservation actions in areas most apt to be effective. Thus, the next step for lynx conservation in the Southern Rockies is to understand the

efficacy and ecological constraints associated with forest and fire/fuels management strategies that promote the dynamic spatial assortments of relatively small and isolated patches of Likely habitat mosaics that sustain lynx populations (Holbrook et al. 2019) across space and time in ways that are necessary for persistence within a backdrop of human-caused climate change.

Currently, natural and human-caused disturbance overlaps 37% of likely lynx habitat in the southern Rockies, and 24% of Core (Table 2). This result supported our prediction that disturbance factors are important considerations in conservation planning for the species, but the impact of specific disturbance elements to lynx habitat varied. Natural disturbance was the primary factor that overlapped current lynx habitat, whereas the spatial overlap of human-caused disturbance to lynx habitat was low. However, we recognize that natural and anthropogenic disturbances impact lynx habitat at different spatial and temporal scales, and to different degrees. For example, disturbance to forest structure and composition from fire and insects recover through successional processes, albeit over potentially very long-time frames, while human disturbance from developed recreation at ski resorts and urbanization from building structures represent permanent habitat loss.

Spruce beetle outbreaks were the primary disturbance factor (25%) overlapping Likely lynx habitat (Table 2; Appendix 5) and were most prominent in the south-most extent of the Southern Rockies. However, the legacy forests following insect outbreaks tend to retain an understory that provides high horizontal cover (conifer boughs touching the snow or ground surface) sufficient to support adequate snowshoe hare abundance (Ivan et al. 2018, 2023). Subalpine forests in the coming decades may shift increasingly to subalpine fir following beetle disturbance (Rodman et al. 2022) that may benefit snowshoe hare and lynx populations, given the positive association of both species to subalpine fir in the forest understory (Squires et al. 2020; Ivan et al. 2023). Canada lynx in the Southern Rockies preferentially select locations with higher proportions of beetle-killed trees in insect-impacted landscapes across spatial scales (Squires et al. 2020). The distribution of Canada lynx in the Southern Rockies has changed little before and after large-scale spruce beetle outbreaks primarily due to keystone habitat features, such as high horizontal forest cover that promote habitat suitability (Squires et al. 2022). Thus, despite high spruce-beetle overlap with Likely lynx habitat, these landscapes still provide the forest structure necessary for continued occupancy.

An important caveat to how beetle disturbance may impact lynx long-term is that red squirrels (*Tamiasciurus hudsonicus*), which provide > 70% of the lynx diet during periods of low hare abundance (Ivan and Shenk 2016), are negatively impacted by changes in forest structure from spruce-beetle outbreaks (Ivan et al. 2018, 2023). Thus, potentially for decades, Canada lynx are at heightened risk from reduced prey density, starvation, and potential increased dispersal movements until spruce-fir forests attain an age following insect outbreaks that cone-bearing trees are sufficient to support squirrel populations as alternative prey (Ivan et al. 2018, 2023; Squires et al. 2020, 2022). Area of forests impacted annually by spruce beetles in Colorado has steadily dropped from a peak of around 200,000 ha during 2014 to 12,000 ha in 2022 (Colorado State Forest Service 2022), and there are relatively few unimpacted areas into which the irruption can spread. Thus, effect of disturbance due to bark beetles on lynx habitat is likely waning, and most spruce-fir stands in the Southern Rockies will be in a recovery phase from forest insects over the next several decades.

We predicted a priori that fire would represent a primary disturbance factor impacting the extent and configuration of lynx habitat across the Southern Rockies. Our opinion was shaped by the fact that three of the largest fires recorded in Colorado (e.g., Cameron

Peak—84,545 ha, East Troublesome—78,433 ha, and Pine Gulch—56,254 ha) burned during the 2020 fire season (Higuera and Abatzoglou 2020). However, burns from 1990 to 2022 overlapped just 5% of Likely habitat, with large-scale fires mostly at elevations below lynx occupancy and in Unlikely habitat that occurred primarily in northern portions of the Southern Rockies. However, the West Fork Fire Complex (Papoose, West Fork, and Windy Pass fires) burned at high severity across 442 km² of the San Juan Mountains in 2013 (MTBS Project 2022), impacting one of the most important patches of lynx habitat in the Southern Rockies. This wildfire illustrates the potential vulnerability of lynx habitat to fire impacts, given the limited spatial extent of lynx across the Southern Rockies (Fig. 3). In general, lynx avoid fire impacted landscapes for at least ~25 yrs (Olson et al. 2023), likely because stand-replacing fires of high severity that are common in subalpine systems reset much of the impacted area to a stand initiation stage (Agee 2000; Schapira et al. 2021). In the North Cascades Ecosystem of Washington, USA, fires in 2013 and 2020 burned 32% of lynx habitat, and fire disturbance from 2000 to 2020 reduced estimated carrying capacity of lynx by 66–73% despite active fire suppression (Lyons et al. 2023). That said, Canada lynx do use burns across spatial and temporal scales (Vanbianchi et al. 2017; Olson et al. 2023), including immediately after fire disturbance depending on site conditions. The degree that fires impact the persistence of populations is dependent on extent, frequency, and severity of disturbance events, given that lynx demography and resource-use are impacted by mosaics of forest structure and pattern at the range periphery (Holbrook et al. 2017, 2019; Kosterman et al. 2018). Therefore, despite low current overlap, a central conservation issue for lynx and forest management in the Southern Rockies is how to “defend” Likely, in situ habitat from frequent fire disturbance with climate change.

Like large carnivores (Carter and Linnell 2016), Canada lynx in the Southern Rockies occupy a mosaic of protected and multiple-use lands, mostly administered by the U.S. Forest Service (83.5%, 4811 km²). Protected areas in fragmented landscapes can promote larger patches of forests in ways that support species occurrence and conservation (Timmers et al. 2022). As originally predicted, both multiple-use lands and protected landscapes are central to the conservation of Canada lynx at the range periphery. Yet, the high degree (62% overlap) that protected areas insulated Likely and Core habitat from direct human disturbance (i.e., ski resort development, urbanization) was unexpected, given that many protected areas in the Southern Rockies include high-elevation landscapes dominated by alpine vegetation that lynx avoid. The interstitial areas between patches of Likely habitat are subject to permanent alteration from housing/building urbanization and ski-resort development (Fig. 6). Of protected landscapes that overlapped Likely lynx habitat, 21% of these lands (1,191 km²) are administered by the U. S. Forest Service as “roadless” areas (Appendix 5). Thus, the management of roadless areas in ways that enhance the conservation of lynx is important at the southern-most range periphery. As the name implies, “roadless” areas represent landscapes where the emphasis is to minimize new road construction. However, managers still have some flexibility in the management of roadless areas, such as tree harvest and potentially controlled burning, if done in the context of maintaining or restoring habitat for *threatened* or *endangered* species under the ESA. Therefore, active management in protected landscapes might reduce the risk of large-scale natural disturbance, especially large-scale fire, if consistent with the landscape mosaics that sustain lynx occupancy (Holbrook et al. 2017, 2019; Kosterman et al. 2018).

At the population level, movement paths for lynx in the Southern Rockies extended along the western Continental Divide through the Sawatch, Mosquito, and Front Ranges of western Colorado (Buderman et al. 2018). This population-level corridor crosses several important patches of Likely lynx habitat. Dispersing lynx often traverse large portions

of non-typical habitat (i.e., xeric shrublands, lodgepole pine) during long-distance movement (Buderman et al. 2018). In addition, despite a general avoidance of developed ski resorts, lynx in the Southern Rockies can traverse these high-disturbance recreation sites at night and during snow-free periods (Olson et al. 2018). Finally, lynx in the Southern Rockies also readily cross linear features on the landscape, like 2-lane highways and on occasion, 4-lane interstate highways with high traffic volumes (Baigas et al. 2017). Therefore, we believe that connectivity among the relatively small and isolated patches of habitat within protected and multiple-use landscapes is intact at the population-level with current levels of human disturbance (Fig. 6). An important caveat is that higher human density in the future could curtail or block connectivity movements for Canada lynx. We demonstrated that lynx exhibit some avoidance behavior to building structures (Appendix 2) and anecdotal observations from the Northern Rocky Mountains suggest that lynx circumvent rather than cross suburban-type neighborhood developments (J. Squires, personal communication, 2023). Thus, future expansion of human-caused disturbance from urbanization and resort development in the relatively low-elevation valleys that intersect patches of lynx habitat in the Southern Rockies may threaten population connectivity and persistence, but that disturbance threshold is unknown.

The conservation insights gained from our overlap analyses are heavily reliant on the predictive ability of the underlying SDM model. While SDM models are a common method to estimate habitat suitability (Elith and Leathwick 2009) with modeling methods that are well-studied (Elith et al. 2006; Watling et al. 2015) and easy to implement (Thuiller et al. 2009), rigorous validation of their results is frequently lacking (Sofaer et al. 2019). This is often because small sample sizes preclude withholding testing data or, more importantly, there is a lack of independently collected test data. Spatially independent data collected from other data sources or in other areas provide a rigorous test of model performance when applied to common model assessment metrics such as AUC or other measures of model discrimination (Fourcade et al. 2018). A rich independent dataset thus provides this work, and a similar model we created for the Northwest Rocky Mountains (Olson et al. 2021), with a rare opportunity for rigorous model testing and validation. Using independent data and multiple model assessment metrics, we were able to discriminate among several models based on predictive performance as well as to demonstrate that the predictions of our three different model hypotheses were highly spatially consistent, which increased our confidence in model outputs. Further, the different types of independent data, including different seasons and behaviors such as denning, long-distance movements, and movements within territories, allowed us to better understand the predictive strengths and weaknesses of our model to future field applications (Smeraldo et al. 2018). We also stress the importance of collaboration across different agencies and conservation organizations in assembling independent datasets, as was done for this study, since independent data is often expensive and time-consuming to collect. Furthermore, this study and Olson et al. (2021) benefited from data that were collected consistently across a long time period, primarily for other projects, which was then able to be fortuitously used for model testing. The conservation importance of collecting this type of multiple-use long-term data is high, especially given current rapidly changing environmental conditions due to climate change and human encroachment.

In conclusion, the combined SDM from this study for the Southern Rockies, in conjunction with Olson et al. (2021) for the Pacific Northwest, provides updated spatial understandings of the distribution of habitat required by Canada lynx across the species' range periphery in the western United States. These remapping efforts are important because they focus conservation planning and management actions in areas that spatially and temporally

have the greatest impact on the persistence of sensitive species, like Canada lynx at the range periphery. This is particularly important for the conservation and management of lynx in the continental USA because habitat was broadly mapped with limited data in 2000 when the species was federally listed under ESA (McKelvey et al. 2000; Interagency Lynx Biology Team 2013). In addition, Canada lynx at the time of federal listing were just being reintroduced into the Southern Rockies (Devineau et al. 2010). Over the intervening two decades, considerable research on the ecology of Canada lynx and key prey in the Southern Rockies justifies new models that spatially delineate the extent and pattern of lynx habitat across the region. We conclude that Canada lynx in the Southern Rockies depend on habitat that is small and relatively spatially isolated, with complex configurations determined by mountainous topography with little contiguous core habitat. We also conclude that natural disturbance, primarily from spruce beetles, has the greatest spatial overlap with lynx habitat. However, despite current low overlap, fire is likely the greatest threat to lynx habitat over a decades-long timeframe, given the current increase in fire size, severity, and frequency from climate change. Therefore, management approaches for Canada lynx in the Southern Rockies will require an integration of disturbance ecology with the species' ecological requirements. Canada lynx, and their primary prey snowshoe hares, require sub-alpine forests with high horizontal cover, which are susceptible to large-scale fire. Therefore, an emerging challenge for lynx conservation in the Southern Rockies is to address the ecological risk of large scale disturbance in ways that sustain habitat mosaics (Holbrook et al. 2017, 2019; Kosterman et al. 2018) across spatial and temporal scales within the complex assortment of multiple-use and protected landscapes. Given that large-scale fire in subalpine forests are stand-replacing events driven by complex interactions of climate, topography, and fuel (Andrus et al. 2016; Hagmann et al. 2021; Prichard et al. 2021), fire management that reduces risk to these cool, moist forests is less about within-stand tree characteristics and more about instilling landscape-scale patterns across north and south aspects, forest openings, and moisture gradients from vegetation that reduce fire spread (Hessburg et al. 2015, 2019; Prichard et al. 2021). Finally, we conclude that although current human-caused disturbance (tree harvest, resort development, urbanization) overlaps little with Likely lynx-habitat in the southern Rockies, future permanent habitat loss from heightened development could limit population connectivity between habitat patches, especially in the southern and central portions of the Southern Rockies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02978-8>.

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Author contributions All authors contributed to the study conception and design, manuscript preparation, editing, and science interpretation. John Squires and Lucretia Olson wrote the first draft of the manuscript with additional narrative provided by all authors. Lucretia Olson provided species distribution modeling and GIS analysis. All authors read, discussed, and approved the final manuscript.

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Data availability Data for species distribution modeling are available in Figshare (<https://figshare.com>). Data for disturbance overlap analysis are publicly available (see Appendix 1).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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References

- Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proc Natl Acad Sci USA* 113:11770–11775. <https://doi.org/10.1073/pnas.1607171113>
- AdaptWest Project (2015) Gridded current and projected climate data for North America at 1km resolution, interpolated using the ClimateNA v5.10 software
- Agee JK (2000) Disturbance ecology of North American boreal forests and associated northern mixed/sub-alpine forests. *Ecol Conserv lynx United States* 39–82
- Andrus RA, Veblen TT, Harvey BJ, Hart SJ (2016) Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. *Ecol Appl* 26:700–711. <https://doi.org/10.1890/15-1121/supinfo>
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- Baigas PE, Squires JR, Olson LE et al (2017) Using environmental features to model highway crossing behavior of Canada lynx in the Southern Rocky Mountains. *Landsc Urban Plan* 157:200–213. <https://doi.org/10.1016/j.landurbplan.2016.06.007>
- Bentz BJ, Régnière J, Fettig CJ et al (2010) Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *Bioscience* 60:602–613. <https://doi.org/10.1525/bio.2010.60.8.6>
- Biedermann PHW, Müller J, Grégoire JC et al (2019) Bark beetle population dynamics in the anthropocene: Challenges and solutions. *Trends Ecol Evol* 34:914–924. <https://doi.org/10.1016/j.tree.2019.06.002>
- Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I (2010) Screening global positioning system location data for errors using animal movement characteristics. *J Wildl Manage* 74:1361–1366. <https://doi.org/10.1111/j.1937-2817.2010.tb01258.x>
- Boria RA, Blois JL (2018) The effect of large sample sizes on ecological niche models: Analysis using a North American rodent, *Peromyscus maniculatus*. *Ecol Modell* 386:83–88. <https://doi.org/10.1016/j.ecolmodel.2018.08.013>
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Modell* 275:73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>
- Buderman FE, Hooten MB, Ivan JS, Shenk TM (2018) Large-scale movement behavior in a reintroduced predator population. *Ecography (Cop)* 41:126–139. <https://doi.org/10.1111/ecog.03030>
- Carter NH, Linnell JDC (2016) Co-adaptation is key to coexisting with large carnivores. *Trends Ecol Evol* 31:575–578. <https://doi.org/10.1016/j.tree.2016.05.006>
- Colorado State Forest Service (2022) Report on the health of Colorado's forests: insects and diseases. Fort Collins
- DeCesare NJ, Hebblewhite M, Schmiegelow F et al (2012) Transcending scale dependence in identifying habitat with resource selection functions. *Ecol Appl* 22:1068–1083. <https://doi.org/10.1890/11-1610.1>
- Devineau O, Shenk TM, White GC et al (2010) Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. *J Appl Ecol* 47:524–531. <https://doi.org/10.1111/j.1365-2664.2010.01805.x>

- Di Cola V, Broennimann O, Petitpierre B et al (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography (Cop)* 40:774–787. <https://doi.org/10.1111/ecog.02671>
- Dietz MS, Belote RT, Aplet GH, Aycrigg JL (2015) The world's largest wilderness protection network after 50 years: an assessment of ecological system representation in the U.S. National Wilderness Preservation System. *Biol Conserv* 184:431–438. <https://doi.org/10.1016/j.biocon.2015.02.024>
- Elith J, Graham CH (2009) Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. *Ecography (Cop)* 32:66–77. <https://doi.org/10.1111/j.1600-0587.2008.05505.x>
- Elith J, Leathwick J (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst* 40:677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith J, Ferrier S, Huettmann F, Leathwick J (2005) The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. *Ecol Modell* 186:280–289. <https://doi.org/10.1016/j.ecolmodel.2004.12.007>
- Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop)* 29:129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Engler R, Guisan A, Rechsteiner L (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *J Appl Ecol* 41:263–274
- Evans JS, Oakleaf J, Cushman SA, Theobald D (2014) An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0
- Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB (2019) Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For Ecol Manage* 432:164–178. <https://doi.org/10.1016/j.foreco.2018.09.006>
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manage* 69:1346–1359. [https://doi.org/10.2193/0022-541x\(2005\)69\[1346:qho-tio\]2.0.co;2](https://doi.org/10.2193/0022-541x(2005)69[1346:qho-tio]2.0.co;2)
- Fourcade Y, Besnard AG, Secondi J (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Glob Ecol Biogeogr* 27:245–256. <https://doi.org/10.1111/geb.12684>
- Gauthier S, Bernier P, Kuuluvainen T et al (2015) Boreal forest health and global change. *Science* 349:819–822. <https://doi.org/10.1126/science.aaa9092>
- Gorelick N, Hancher M, Dixon M et al (2017) Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens Environ* 202:18–27. <https://doi.org/10.1016/j.rse.2017.06.031>
- Graham RT, Jain TB (1998) Silviculture's role in managing boreal forests. *Conserv Ecol* 2:8
- Hagenstad M, Burakowski E, Hill RL (2018) The economics of snow for recreation in a changing climate. *Proc Int Snow Sci Work Innsbruck, Austria 2016*:531–536
- Hagmann RK, Hessburg PF, Prichard SJ et al (2021) Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol Appl*. <https://doi.org/10.1002/eap.2431>
- Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853. <https://doi.org/10.1126/science.1244693>
- Hao T, Elith J, Guillera-Arroita G, Lahoz-Monfort JJ (2019) A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Divers Distrib*. <https://doi.org/10.1111/DDI.12892>
- Hao T, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2020) Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography (Cop)* 43:549–558. <https://doi.org/10.1111/ecog.04890>
- Hengl T, De Jesus JM, Heuvelink GBM, et al (2017) SoilGrids250m: Global gridded soil information based on machine learning
- Hessburg PF, Churchill DJ, Larson AJ et al (2015) Restoring fire-prone Inland Pacific landscapes: seven core principles. *Landsc Ecol* 30:1805–1835. <https://doi.org/10.1007/s10980-015-0218-0>
- Hessburg PF, Miller CL, Parks SA et al (2019) Climate, environment, and disturbance history govern resilience of Western North American forests. *Front Ecol Evol* 7:1–27. <https://doi.org/10.3389/fevo.2019.00239>
- Hessburg PF, Prichard SJ, Hagmann RK et al (2021) Wildfire and climate change adaptation of western North American forests: a case for intentional management. *Ecol Appl*. <https://doi.org/10.1002/eap.2432>

- Higuera PE, Abatzoglou JT (2020) Letter to editor - record-setting climate enabled the extraordinary 2020 fire season in the western. *Glob Chang Biol* 27:1–2. <https://doi.org/10.1111/gcb.15388>
- Higuera PE, Shuman BN, Wolf KD (2021) Rocky Mountain subalpine forests now burning more than any time in recent millennia. *Proc Natl Acad Sci USA* 118:1–5. <https://doi.org/10.1073/pnas.2103135118>
- Hirzel AH, Le Lay G, Helfer V et al (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecol Modell* 199:142–152. <https://doi.org/10.1016/j.ecolmodel.2006.05.017>
- Hodges KE (2000) Ecology of snowshoe hares in southern boreal and montane forests. In: Ruggiero LF, Aubry KB, Buskirk SW et al (eds) *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, pp 163–206
- Holbrook JD, Squires JR, Bollenbacher B et al (2018) Spatio-temporal responses of Canada lynx (*Lynx canadensis*) to silvicultural treatments in the Northern Rockies, U.S. *For Ecol Manage* 422:114–124. <https://doi.org/10.1016/j.foreco.2018.04.018>
- Holbrook JD, Squires JR, Bollenbacher B et al (2019) Management of forests and forest carnivores: relating landscape mosaics to habitat quality of Canada lynx at their range periphery. *For Ecol Manage* 437:411–425. <https://doi.org/10.1016/j.foreco.2019.01.011>
- Holbrook JD, Squires JR, Olson LE et al (2017) Understanding and predicting habitat for wildlife conservation : the case of Canada lynx at the range periphery. *Ecosphere* 8:e01939. <https://doi.org/10.1002/ecs2.1939>
- Hurford A (2009) GPS measurement error gives rise to spurious 180 degree turning angles and strong directional biases in animal movement data. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0005632>
- Ilek A, Kucza J, Szostek M (2017) The effect of the bulk density and the decomposition index of organic matter on the water storage capacity of the surface layers of forest soils. *Geoderma* 285:27–34. <https://doi.org/10.1016/j.geoderma.2016.09.025>
- Interagency Lynx Biology Team (2013) Canada lynx conservation assessment and strategy, 3rd edn. USDA Forest Service, USDI Fish and Wildlife Service, USDI Bureau of Land Management, and USDI National Park Service. Forest Service Publication R1-13-19, Missoula
- Ivan JS, Shenk TM (2016) Winter diet and hunting success of Canada lynx in Colorado. *J Wildl Manage* 80:1049–1058. <https://doi.org/10.1002/jwmg.21101>
- Ivan JS, Seglund AE, Truex RL, Newkirk ES (2018) Mammalian responses to changed forest conditions resulting from bark beetle outbreaks in the southern Rocky Mountains. *Ecosphere* 9:e02369. <https://doi.org/10.1002/ecs2.2369>
- Ivan JS, Newkirk ES, Gerber BD (2023) Differential impacts of spruce beetle outbreaks on snowshoe hares and red squirrels in the southern Rocky Mountains. *For Ecol Manage* 544:121147. <https://doi.org/10.1016/j.foreco.2023.121147>
- Jenness J (2013) DEM Surface Tools for ArcGIS (surface_area.exe). In: Jenness Enterp
- Jenness J, Brost B, Beier P (2013) Land Facet Corridor Designer: Extension for ArcGIS. In: Jenness Enterp
- Johnson DM, Haynes KJ (2023) Spatiotemporal dynamics of forest insect populations under climate change. *Curr Opin Insect Sci* 56:101020. <https://doi.org/10.1016/j.cois.2023.101020>
- Keppel G, Van Niel KP, Wardell-Johnson GW et al (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404. <https://doi.org/10.1111/j.1466-8238.2011.00686.x>
- Koehler GM, Maletzke BT, Von Kienast JA et al (2008) Habitat fragmentation and the persistence of lynx populations in Washington State. *J Wildl Manage* 72:1518–1524. <https://doi.org/10.2193/2007-437>
- Kolbe JA, Squires JR, Parker TW (2003) An effective box trap for capturing lynx. *Wildl Soc Bull* 31:1–6. <https://doi.org/10.2307/3784442>
- Kosterman MK, Squires JR, Holbrook JD et al (2018) Forest structure provides the income for reproductive success in a southern population of Canada lynx. *Ecol Appl* 28:1032–1043. <https://doi.org/10.1002/eap.1707>
- Krawchuk MA, Meigs GW, Cartwright JM et al (2020) Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. *Front Ecol Environ* 18:235–244. <https://doi.org/10.1002/fee.2190>
- Kuuluvainen T, Gauthier S (2018) Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *For Ecosyst*. <https://doi.org/10.1186/s40663-018-0142-2>
- LANDFIRE (2018) LANDFIRE Existing Vegetation Type layer. In: U.S. Dep Inter Geol Surv [Online]
- Larson CL, Reed SE, Merenlender AM, Crooks KR (2016) Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE* 11:1–21. <https://doi.org/10.1371/journal.pone.0167259>
- Lemons J, Stout D (1982) National parks legislative mandate in the United States of America. *Environ Manage* 6:199–207. <https://doi.org/10.1007/BF01866883>

- Lobo JM, Jiménez-valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. *Glob Ecol Biogeogr* 17:145–151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>
- Lyons AL, Gaines WL, Lewis JC et al (2023) Climate change, wildfire, and past forest management challenge conservation of Canada lynx in Washington, USA. *J Wildl Manage* 87:1–23. <https://doi.org/10.1002/jwmg.22410>
- Marmion M, Parviainen M, Luoto M et al (2009) Evaluation of consensus methods in predictive species distribution modelling. *Divers Distrib* 15:59–69. <https://doi.org/10.1111/j.1472-4642.2008.00491.x>
- McKelvey KS, Aubry KB, Ortega YK (2000) History and distribution of lynx in the contiguous United States. In: Ruggiero LF, Aubry KB, Buskirk SW et al (eds) *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, pp 207–264
- Meddens AJH, Kolden CA, Lutz JA et al (2018) Fire refugia: what are they, and why do they matter for global change? *Bioscience* 68:944–954. <https://doi.org/10.1093/biosci/biy103>
- Michalak JL, Stralberg D, Cartwright JM, Lawler JJ (2020) Combining physical and species-based approaches improves refugia.pdf. *Front Ecol Environ* 18:254–260. <https://doi.org/10.1002/fee.2207>
- Microsoft (2021) Building Footprints
- Microsoft Corporation (2023) Building footprints: an AI-assisted mapping deliverable with the capability to solve for many scenarios. <https://www.microsoft.com/en-us/maps/bing-maps/building-footprints/>. Accessed 1 Feb 2023
- Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826
- Morelli TL, Barrows CW, Ramirez AR et al (2020) Climate-change refugia: biodiversity in the slow lane. *Front Ecol Environ* 18:228–234. <https://doi.org/10.1002/fee.2189>
- Mowat G, Poole KG, O'Donoghue M (2000) Ecology of lynx in northern Canada and Alaska. In: Ruggiero LF, Aubry KB, Buskirk SW et al (eds) *Ecology and conservation of lynx in the United States*. Unive, Boulder, pp 265–306
- MTBS Project (2022) MTBS data access: fire level geospatial data. In: USDA For Serv Geol Surv National Oceanic and Atmospheric Administration (2014) *Global radiance calibrated nighttime lights*
- Northrup JM, Hooten MB, Anderson CR, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456–1463. <https://doi.org/10.1890/12-1688.1>
- Olson LE, Squires JR, Roberts EK et al (2017) Modeling large-scale winter recreation terrain selection with implications for recreation management and wildlife. *Appl Geogr* 86:66–91. <https://doi.org/10.1016/j.apgeog.2017.06.023>
- Olson LE, Squires JR, Roberts EK et al (2018) Sharing the same slope: behavioral responses of a threatened mesocarnivore to motorized and non-motorized winter recreation. *Ecol Evol*. <https://doi.org/10.1002/ece3.4382>
- Olson LE, Bjornlie N, Hanvey G et al (2021) Improved prediction of Canada lynx distribution through regional model transferability and data efficiency. *Ecol Evol* 11:1667–1690. <https://doi.org/10.1002/ece3.7157>
- Olson LE, Croteau JS, Fox S et al (2023) Effects of compound disturbance on Canada lynx and snowshoe hare: wildfire and forest management influence timing and intensity of use. *For Ecol Manage* 530:120757. <https://doi.org/10.1016/j.foreco.2022.120757>
- Omernik JM, Griffith GE (2014) Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environ Manage* 54:1249–1266. <https://doi.org/10.1007/s00267-014-0364-1>
- OpenStreetMap Foundation (2017) OpenStreetMap
- Parks SA, Abatzoglou JT (2020) Warmer and drier fire seasons contribute to increases in area burned at high severity in Western US forests From 1985 to 2017. *Geophys Res Lett* 47:1–10. <https://doi.org/10.1029/2020GL089858>
- Parthum B, Christensen P (2022) A market for snow: modeling winter recreation patterns under current and future climate. *J Environ Econ Manage*. <https://doi.org/10.1016/j.jeem.2022.102637>
- Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol Modell* 213:63–72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>
- Pettorelli N, Vik JO, Mysterud A et al (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510. <https://doi.org/10.1016/j.tree.2005.05.011>
- Price DT, Apps MJ (1995) The boreal forest transect case study: global change effects on ecosystem processes and carbon dynamics in boreal Canada. *Water, Air Soil Pollut* 82:203–214

- Prichard SJ, Hessburg PF, Hagsmann RK et al (2021) Adapting western North American forests to climate change and wildfires: 10 common questions. *Ecol Appl* 31:1–30. <https://doi.org/10.1002/eap.2433>
- Rocca ME, Brown PM, MacDonald LH, Carrico CM (2014) Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. *For Ecol Manage* 327:290–305. <https://doi.org/10.1016/j.foreco.2014.04.005>
- Rodman KC, Andrus RA, Butkiewicz CL et al (2021) Effects of bark beetle outbreaks on forest landscape pattern in the southern rocky mountains, U.S.A. *Remote Sens* 13:1–21. <https://doi.org/10.3390/rs13061089>
- Rodman KC, Andrus RA, Carlson AR et al (2022) Rocky Mountain forests are poised to recover following bark beetle outbreaks but with altered composition. *J Ecol* 110:2929–2949. <https://doi.org/10.1111/1365-2745.13999>
- Sanderson EW, Jaiteh M, Levy MA et al (2002) The human footprint and the last of the wild. *Bioscience* 52:891–904. [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- Savilaakso S, Johansson A, Häkkinen M et al (2021) What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. *Environ Evid* 10:1–38. <https://doi.org/10.1186/s13750-020-00215-7>
- Schaphira Z, Stevens-Rumann C, Shorrock D et al (2021) Beetlemania: is the bark worse than the bite? Rocky Mountain subalpine forests recover differently after spruce beetle outbreaks and wildfires. *For Ecol Manage* 482:118879. <https://doi.org/10.1016/j.foreco.2020.118879>
- Schoennagel T, Veblen TT, Romme WH (2004) The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience* 54:661–676. [https://doi.org/10.1641/0006-3568\(2004\)054\[0661:TIOFAJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFAJ]2.0.CO;2)
- Seidl R, Thom D, Kautz M et al (2017) Forest disturbances under climate change. *Nat Clim Chang* 7:395–402. <https://doi.org/10.1038/nclimate3303>
- Sibold JS, Veblen TT, González ME (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *J Biogeogr* 33:631–647. <https://doi.org/10.1111/j.1365-2699.2005.01404.x>
- Simons-Legaard EM, Harrison DJ, Krohn WB, Vashon JH (2013) Canada lynx occurrence and forest management in the Acadian Forest. *J Wildl Manage* 77:567–578. <https://doi.org/10.1002/jwmg.508>
- Smeraldo S, Di Febbraro M, Bosso L et al (2018) Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: lessons from bats. *Biodivers Conserv* 27:2425–2441. <https://doi.org/10.1007/s10531-018-1545-7>
- Smith FW (2000) Forestry practices and forest fragmentation in the Southern Rocky Mountains. In: Knight RL, Smith FW, Buskirk SW et al (eds) *Forest fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, pp 123–134
- Sofaer HR, Jarnevich CS, Pearse IS et al (2019) Development and delivery of species distribution models to inform decision-making. *Bioscience* 69:544–557. <https://doi.org/10.1093/biosci/biz045>
- Soga M, Gaston KJ (2018) Shifting baseline syndrome: causes, consequences, and implications. *Front Ecol Environ* 16:222–230. <https://doi.org/10.1002/fee.1794>
- Sommerfeld A, Senf C, Buma B et al (2018) Patterns and drivers of recent disturbances across the temperate forest biome. *Nat Commun*. <https://doi.org/10.1038/s41467-018-06788-9>
- Squires JR, Ruggiero LF (2007) Winter prey selection of Canada lynx in northwestern Montana. *J Wildl Manage* 71:310–315. <https://doi.org/10.2193/2005-445>
- Squires JR, DeCesare NJ, Kolbe JA, Ruggiero LF (2010) Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. *J Wildl Manage* 74:1648–1660. <https://doi.org/10.2193/2009-184>
- Squires JR, DeCesare NJ, Olson LE et al (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biol Conserv* 157:187–195. <https://doi.org/10.1016/j.biocon.2012.07.018>
- Squires JR, Olson LE, Roberts EK et al (2019) Winter recreation and Canada lynx: reducing conflict through niche partitioning. *Ecosphere* 10:e02876. <https://doi.org/10.1002/ecs2.2876>
- Squires JR, Holbrook JD, Olson LE et al (2020) A specialized forest carnivore navigates landscape-level disturbance: Canada lynx in spruce-beetle impacted forests. *For Ecol Manage* 475:118400. <https://doi.org/10.1016/j.foreco.2020.118400>
- Squires JR, Ivan JS, Paolini KE et al (2022) Keystone structures maintain forest function for Canada lynx after large-scale spruce beetle outbreak. *Environ Res Ecol*. <https://doi.org/10.1088/2752-664X/ac8eb7>
- Steel ZL, Jones GM, Collins BM et al (2022) Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecol Appl*. <https://doi.org/10.1002/eap.2763>

- Stephens SL, Collins BM, Fettig CJ et al (2018) Drought, tree mortality, and wildfire in forests adapted to frequent fire. *Bioscience* 68:77–88. <https://doi.org/10.1093/biosci/bix146>
- Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography (Cop)* 32:369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>
- Timmers R, van Kuijk M, Verweij PA et al (2022) Conservation of birds in fragmented landscapes requires protected areas. *Front Ecol Environ* 20:361–369. <https://doi.org/10.1002/fee.2485>
- U. S. Census Bureau (2023) U. S. population trends return to pre-pandemic norms as more states gain population. <https://www.census.gov/newsroom/press-releases/2023/population-trends-return-to-pre-pandemic-norms.html>
- U.S. Forest Service Natural Resource Manager (2022) Download National Datasets. In: Website. <https://data.fs.usda.gov/geodata/edw/datasets.php>
- United States Forest Service Forest Health (2022) Insect and Disease Detection Survey Data. In: Website
- Vanbianchi CM, Murphy MA, Hodges KE (2017) Canada lynx use of burned areas: Conservation implications of changing fire regimes. *Ecol Evol* 7:2382–2394. <https://doi.org/10.1002/ece3.2824>
- Viereck LA (1973) Wildfire in the Taiga of Alaska. *Quat Res* 3:465–495. [https://doi.org/10.1016/0033-5894\(73\)90009-4](https://doi.org/10.1016/0033-5894(73)90009-4)
- Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11:e0156720. <https://doi.org/10.1371/journal.pone.0156720>
- Watling JI, Brandt LA, Bucklin DN et al (2015) Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. *Ecol Modell* 309–310:48–59. <https://doi.org/10.1016/j.ecolmodel.2015.03.017>

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Authors and Affiliations

John R. Squires¹ · Lucretia E. Olson¹ · Jacob S. Ivan² · Peter M. McDonald³ · Joseph D. Holbrook⁴

✉ John R. Squires
john.squires@usda.gov

¹ USDA Forest Service, Rocky Mountain Research Station, Missoula, MT, USA

² Colorado Parks and Wildlife, Fort Collins, CO, USA

³ USDA Forest Service, Rocky Mountain Region, Lakewood, CO, USA

⁴ Department of Zoology and Physiology, Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY, USA