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Synthesis of habitat models for management of wolverine (*Gulo gulo)*: Identifying key habitat and snow refugia in the Columbia and Rocky Mountains, Canada

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ABSTRACT

The wolverine is a wide-ranging and frequently at-risk or data-deficient species with dramatic range contractions across the northern hemisphere. Recent reports of low population densities inside and outside protected areas in western North America highlight the need for better conservation practice, policy, and planning across large landscapes. To assess broad habitat needs, we synthesized available wolverine habitat models in the Columbia and Rocky Mountains (63,000 km^2), Canada. We used coefficients from four existing models to create spatial predictions over environmental datasets including snow, landcover, and roads. We averaged predictions using the distance-weighted mean of equal-area percentile habitat values and validated the output by comparison to independent data. Because persistent spring snow is tightly correlated with high-quality habitat, we assessed 2080 spring snow cover forecasts (under Representative Concentration Pathway (RCP) 8.5 high emissions scenario) to identify potential habitat refugia in British Columbia. Our synthesized habitat model identified high-quality habitat along mountain ranges, notably in the Purcell Mountains and the Columbia Icefield in the Rocky Mountains. Mean habitat value was 0.70 (SD: 0.19) inside protected areas and 0.55 (SD: 0.28) outside protected areas. The British Columbia side of the study area is forecasted to lose 44% of persistent spring snow cover by 2080, with declines identified inside many protected areas. By synthesizing existing habitat research and climate forecasts, we provided new insights at the broad spatial scale needed to conserve wide-ranging species like wolverine and to inform land-use planning for recreational access and the establishment and management of protected and conserved areas.

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1. Introduction

Globally, large carnivore populations and ranges have dramatically declined in recent centuries due to habitat loss, degradation, and fragmentation, as well as persecution, harvest, and depletion of prey (Ripple et al., 2014). North American carnivore ranges have contracted as a result of colonial settlement and development, which affects members of large and meso-carnivores (Laliberte and Ripple, 2004). Wolverine (*Gulo gulo*), the largest terrestrial species of the Mustelidae family is no exception; data from the United States and Canada indicate declining wolverine populations in southern parts of its range (Fisher et al., 2022), and a 39% loss of historic range (Laliberte and Ripple, 2004). Extant North American wolverine distributions occur in the western mountains, the boreal forest, and the Arctic (Aubry et al., 2007). Wolverine in the western mountains live in the southern part of their range (Laliberte and Ripple, 2004) and are the focus of this research due to the interest and immediacy of management needs.

Today, wolverines are often associated with areas of low human disturbance and industrial footprints (Heim et al., 2017; Stewart et al., 2016) such as large parks and protected areas. Wolverine populations can be fragmented by human disturbance (Sawaya et al., 2019), though dispersal through this poor habitat is key to connecting metapopulations (Carroll et al., 2020). In mountainous areas, protected areas can provide secure habitat (Kortello et al., 2019), where wolverine densities in the Canadian Rocky Mountains was three times higher in protected areas relative to unprotected areas (Barrueto et al., 2022). However, density estimates for Canada's Rocky Mountain national parks have declined over the past decade and were lower than expected for an unharvested population in high-quality habitat (2.1 wolverines /1000 km^2; Barrueto et al., 2022). Climate may also be a factor in wolverine population success; females have been observed denning in areas where snow is present through the late spring (Copeland et al., 2010) as snow dens are thought to provide insulation and protection from predators (Magoun and Copeland, 1998). Despite a number of studies (reviewed in Fisher et al., 2022), there is no consensus as to whether wolverine is a snow-dependent species per se (see Brodie and Post, 2010; McKelvey et al., 2011), as snow extent can be difficult to disentangle from other environmental features such as terrain and human disturbance. As such, there is a need for evidence-weighted studies that can robustly predict key wolverine habitat among often correlated environmental drivers.

A common challenge in wolverine management is the lack of reliable long-term monitoring data, particularly at the broad spatial scale needed to conserve this wide-ranging species. This information gap is reflected in the status of wolverine in North America. In the contiguous United States, wolverine is classified as 'Proposed Threatened' under the Endangered Species Act (U.S. Fish and Wildlife Service, 2022). The inability to define wolverine critical habitat has been called a primary impediment to listing (U.S. Fish and Wildlife Service, 2013), and this lack of clarity in defining critical habitat represents a data deficiency across large spatial extents. Wolverine was not listed as a threatened species in the contiguous United States in 2020 under the assumption that it would not experience a significant loss of habitat due to climate change before 2055 (U.S. Fish and Wildlife Service, 2020). In Canada, wolverine is listed as a species of Special Concern under the Species At Risk Act (Environment and Climate Change Canada, 2017) with significant threats from increased habitat fragmentation from industrial activity, trapping pressure, and climate change, particularly along their southern range (Committee on the Status of Endangered Wildlife in Canada, 2014) where snow cover is projected to markedly decrease (Barsugli et al., 2020; Peacock, 2011). Wolverine status and management also differs among provinces and territories in Canada. In Alberta, wolverine is designated as Data Deficient (Alberta Conservation Association, 2020); the provincial management plan is over 20 years old and based on data from the 1990s (Petersen, 1997). In British Columbia, mainland wolverine is a species of Special Concern (Weir, 2004) and the provincial management plan is over 30 years old (Hatler, 1989).

This study combines existing data across jurisdictional boundaries and a range of land tenures to identify consistent habitat patterns across a large landscape and create an accessible habitat data product. Such syntheses are valued by environmental professionals to inform decisions about conservation-related policy and planning (Thomas-Walters et al., 2021). Further, synthesized spatial predictions can be valuable for conservation by identifying areas where many models agree, increasing the certainty in those findings and avoiding the risk of basing management decisions on a single model (Jones-Farrand et al., 2011).

To better understand wolverine habitat use in a 63 000 km^2 area in western Canada, we completed a systematic review of published wolverine research to define habitat suitability parameters, weighing the relative role of habitat drivers in a mountainous region. We conducted our research with the following objectives:

1) Condense habitat studies into a single product useful for conservationists and managers;
2) Evaluate habitat quality across protected and unprotected areas; and,
3) Identify quality habitat likely to persist under forecasted snow loss.

This research is timely for several reasons. First, the status of wolverine will be reviewed federally in Canada in 2024 (Committee on the Status of Endangered Wildlife in Canada, 2022), and the Government of Alberta is conducting a review of the science to consider formally re-assessing the status of wolverine (Ellis, 2022). Our work can also provide a template for the synthesis of wolverine habitat data in regions beyond our study area, such as the contiguous United States where the status of wolverine is not yet finalized (U.S. Fish and Wildlife Service, 2022). Second, wolverine population density and occupancy have declined steeply over the last decade in this part of western Canada – both inside and outside protected areas (Barrueto et al., 2022). Because it is challenging to study wolverines, sound management and policy decisions must make efficient use of finer scale information at the broad landscape extent that the species needs.

2. Methods

2.1. Study area

Our area of interest covered multi-jurisdictional management areas, spanning the Canadian Rocky Mountain Parks and adjacent private and public lands in Alberta and British Columbia (Fig. 1)., Canada. It included provincial, federal, Indigenous, and private protected areas, as well as towns, private land, industrialized landscapes, and significant recreation activities. The area of interest encompassed mountainous landscapes on the west and east sides of the Continental Divide. The area of interest was bisected by the Trans-Canada Highway, a major east-west transportation corridor (Fig. 1). Our study area is also part of the greater Yellowstone-to-Yukon (Y2Y) region, which is the most intact large mountain system in the world (Theobald et al., in prep) and overlaps with much of present wolverine range in southern Canada and the contiguous United States.

The study area falls within the montane cordillera ecozone, which comprises alpine, subalpine and montane regions (Holland and Coen, 1983; Statistics Canada, 2017). Forested areas include Engelmann spruce *(Picea englemannii),* subalpine fir *(Abies lasiocarpa),* trembling aspen *(Populus tremuloides),* and lodgepole pine *(Pinus contorta)* (Downing and Pettapiece, 2006). Mean annual precipitation declines from west (1200 mm) to east (590 mm) (ClimateData.ca, 2022), with average maximum winter snow depth ranging from 200 cm in the Purcell and Rocky Mountains to 30 cm in the Eastern foothills (Natural Resources Canada, 2006). Elevation ranges from 350 m to 3600 m (Natural Resources Canada., Series, 2019). Mean winter temperatures range from – 11 °C to – 6 °C, with frosts occurring through to June (ClimateData.ca, 2022).

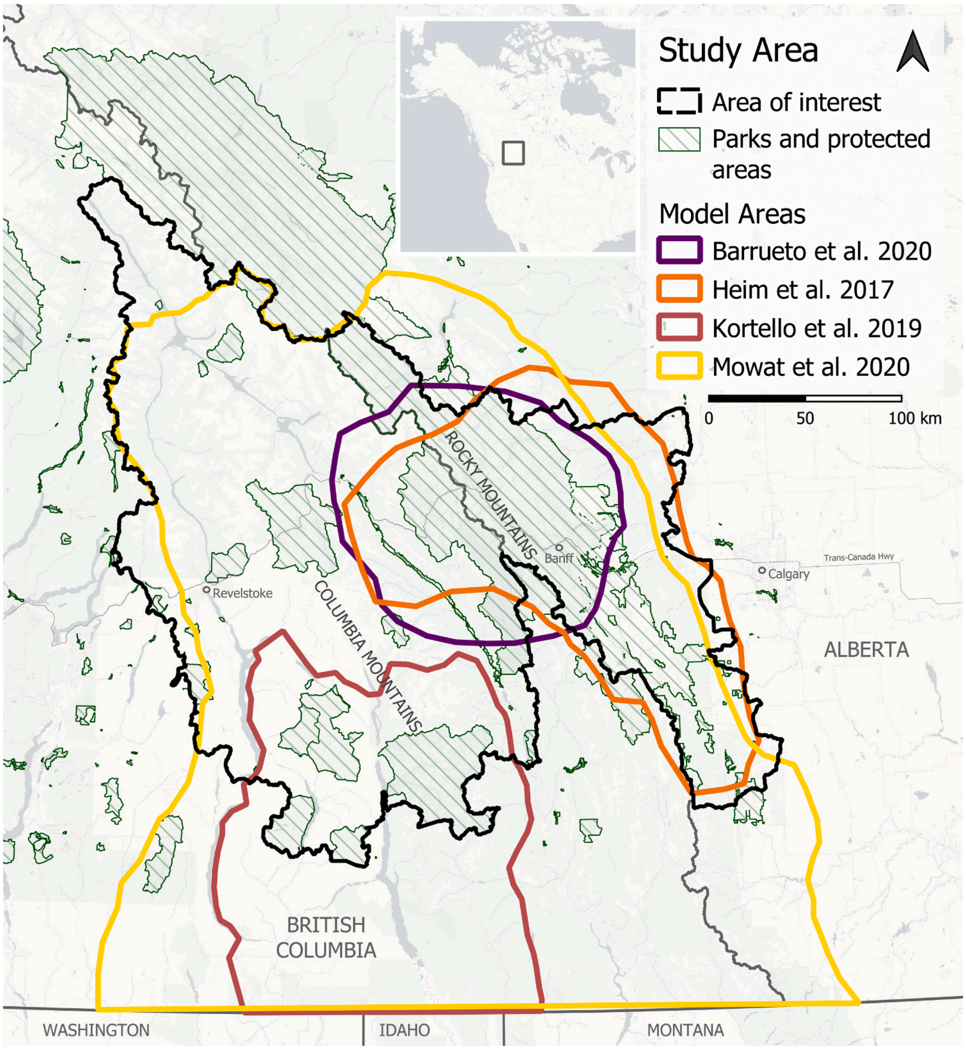

Fig. 1. The study area, which is located in the Columbia and Rocky Mountains, Canada. Shown in hashed black outline is the area of interest for model synthesis, along with coloured outlines of the areas of the four models chosen for synthesis. The area of interest encompasses parks and protected areas (green), as well as public and private lands.

2.2. Study species

Although wolverine trapping is permitted outside of protected areas in British Columbia and Alberta, a ban on trapping in the B.C. portion of the study area was enacted in 2020 following documentation of unsustainable harvest (B.C. Ministry of Forests, Lands, 2020; Mowat et al., 2020). Winter trapping (Nov-Jan) is permitted in Alberta (Alberta Environment and Parks, 2022). Mean wolverine density within our area of interest is estimated at 2 individuals/1000 km^2, with a maximum density of 4.4 individuals/1000 km^2 (Mowat et al., 2020), but has declined by 39% between 2011 and 2020 (Barrueto et al., 2022). Wolverine primary food resources either through direct predation or scavenging include moose *(Alces alces),* woodland caribou *(Rangifer tarandus),* hoary marmots *(Marmota caligata),* mountain goats *(Oreamnos americanus)* and porcupine *(Erethizon dorsatum)* (Lofroth et al., 2007).

2.3. Literature review

To synthesize wolverine habitat research in our area of interest, we conducted a systematic literature search in Web of Science. Keywords searched were TOPIC:(wolverine) AND TOPIC:(model) AND TOPIC:(habitat OR resource selection function OR RSF) AND TOPIC:(British Columbia OR Alberta). Of the 17 papers returned by the search, we filtered papers to meet our criteria based on their relevance, study design, and study area. We excluded papers that focused on spatial covariates of stress, mortality, physiology, or demography because they did not explicitly address wolverine habitat. We only considered papers that fell entirely or partially within the area of interest because we did not want to extrapolate research from nearby but significantly different ecosystems, such as the boreal forest.

For the subset of nine papers that we deemed relevant, we further assessed the statistical methods and, when appropriate, took note of top model summaries. If relevant papers did not report full model summaries including coefficients, we followed up with the corresponding author by email. The habitat models we considered were regressions based on detections across a spatial extent, including methods of resource selection (Manly et al., 2002), occupancy (MacKenzie et al., 2005), spatial capture recapture (Royle and Young, 2008), or spatially explicit capture recapture (Efford, 2011). Model outputs were probability of use, probability of occupancy, the probability of detection, and the density of individuals, respectively. While the model outputs differed, all models contained wolverine detections as a function of habitat surrounding the detection site. For each habitat variable (e.g. snow, road density, vegetation) a beta coefficient describes the relationship to wolverine detections. We used beta coefficients from habitat variables in each paper's top model to describe the relationship between habitat and wolverine landscape use.

Four studies met our criteria (Table 1, Fig. 1). Each of these studies used non-invasive hair-snagging to collect wolverine DNA data (Fisher et al., 2013) and assessed habitat variables as a function of the number of individuals to visit each hair snare station. All four models assessed environmental variables using a 10-km radius of the detection site, as this approximates a female home range (Mowat et al., 2020).

Data from baited hair snares can be limited by the individuals not detected in hair snares, behavioral responses of individual wolverines, and genotyping errors (Augustine et al., 2014). In three of the four studies we selected, effort was taken to reduce bias associated with hair snares. To account for non-detection where a wolverine did not leave a hair sample, camera traps were set up at all hair snare stations in Barrueto et al. (2020) and Heim et al. (2017), and some stations in Mowat et al. (2020). As wolverines may be trap

Table 1
Four studies used for synthesis of wolverine habitat models.

Lead author and title	Variables in top model	Type of model	Response variable
Barrueto et al. (2020). Low wolverine density in a national park complex of the Canadian Rocky Mountains	• Persistent spring snow • Shrub	Spatial capture-recapture	Population density
Heim et al. (2017). Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine	• Persistent spring snow • Shrub • Mixed-wood forest • Coniferous forest • Industrial cut line density	Generalized linear regression	Probability of use
Kortello et al. (2019). Mechanisms influencing the winter distribution of wolverine in the southern Columbia Mountains, Canada	• Persistent spring snow • Industry road density • Protected area • Talus / moraine landforms	Occupancy	Occupancy probability
Mowat et al. (2020). The sustainability of wolverine trapping mortality in Southern Canada	• Persistent spring snow • Road density	Spatially explicit capture-recapture	Population density

shy or become 'trap happy', behavioral responses were included in the modelling process as a 'local trap response' in Barrueto et al. (2020), and as a site-level detection covariate in Mowat et al. (2020). During genotyping, Barrueto et al. (2020), Mowat et al. (2020), and Heim et al. (2017) explicitly corrected for lab-based errors associated with low-quantity DNA samples.

2.4. Environmental data

To predict habitat quality from published models, we obtained and processed spatial environmental data which closely replicated the data used in the original modelling process. Spatial data were selected to best match the top model terms, where reproducible descriptions were given (Table 1; Table S1). For example, Barrueto et al., 2020 defined 'persistent spring snow cover' as snow lasting until May 15th averaged over the study years; thus, we used snow cover data from those dates over the most recent three years (i.e., 2019–2021) from the same source (Hall and Riggs, 2021). We used publicly available vegetation land cover (Hermosilla et al., 2016), and extracted coniferous forest, mixed-wood forest (both coniferous and deciduous), and shrub areas. Shrub cover within our study area includes avalanche paths and similar habitat (Barrueto et al., 2020), which can be home to wolverine prey (Heim et al., 2017). We also included protected areas (UN Environment World Conservation Centre, 2021), and moraine surficial landforms (Natural Resources Canada, Series, 2021) which can be a proxy for marmot habitat (Kortello et al., 2019). We calculated the linear density (km/km^2) of industrial features (seismic lines, transmission lines, pipelines), resource roads, and motorized trails from public databases in Alberta and B.C. (Alberta Biodiversity Monitoring Institute, 2018; Alberta Environment and Parks, 2021; BC Oil and Gas Comission, 2016; GeoBC Branch, 2017b, 2017a). We followed data transformations (e.g. log(), 0–1) and averaged spatial data over a 10-km radius surrounding each raster cell, as described in the original studies. To ensure alignment of many environmental layers of incompatible original dimensions, we resampled spatial data for each model to a template extent and resolution of 500 m. We processed all data in R (R Core Team, 2021) using rgdal (Bivand et al., 2021) and raster packages (Hijmans, 2020). We produced final maps in QGIS (QGIS Association, 2022).

2.5. Habitat predictions

We re-created habitat prediction rasters for the top models in Barrueto et al. (2020), Heim et al. (2017), and Kortello et al. (2019). We obtained the original model prediction raster from Mowat et al. (2020), which provided the broadest coverage over the area of interest. For the three remaining models, we re-created habitat predictions by multiplying the reported beta estimate (β_i) by the standardized habitat data (x_i), summed across each variable in the model $f(x) = \exp(x_1\beta_1 + x_2\beta_2 \ldots)$, where x is the explanatory variable and β is the model coefficient. Since later binning of model predictions renders model constants trivial, we did not include the reported intercept in the model predictions. To ensure coefficients were compatible with the spatial data range, we standardized ($(X - \mu)/\sigma$) the raw data to the original study extents.

2.6. Predictions synthesis

We synthesized an ensemble of species distribution models by using distance-weighted means to create a more robust prediction that acknowledges model uncertainty (Jones-Farrand et al., 2011; Marmion et al., 2009) as opposed to using a single model with a more limited range of predictors, and known and unknown errors. To compare habitat predictions across the four study designs and locations, we transformed raw model outputs into equal-area percentile values for 21 bins between 0 and 1 (i.e., 0, 0.05, 0.10, …, 1). This produced a uniform binned distribution of predicted values, which standardizes interpretation of spatial habitat predictions (Morris et al., 2018). For example, a value >0.8 represents the top 20th percentile habitat in each model. We undertook this binning transformation within each original model extent to maintain the range of values associated with the original models (i.e., we did not want to extrapolate beyond the spatial extent). While individual model outputs differ (e.g., density estimates, occupancy probability), we assumed that binned spatial predictions would be comparable between studies because all models use the same form of wolverine detection data (i.e. detection / non-detection from hair snares). To assess the assumption of comparable values at each cell, we computed a weighted coefficient of variation ($CV = \sigma/\mu$). A high coefficient of variation represents dissimilarity of values, while low CV would indicate similar values. As 93% of our CV values were less than the proposed threshold value of 0.5 (Jones-Farrand et al., 2011), we found it reasonable to synthesize these binned spatial predictions. We mapped CV values to assess areas with high variance and greater uncertainty in synthesized model predictions.

We synthesized model predictions in two ways: 1) using continuous percentile values (0−100) and 2) binary (0,1) values. Using percentile values, we synthesized predictions by computing a distance-weighted mean for each pixel. We calculated weights as the inverse of the distance (km) from each original study area. If a pixel occurred in the original model area, it was assigned a value of 1. As a coarse metric of agreement among individual model predictions, we transformed cell values greater or equal to 0.5, which represents areas with top 50th percentile habitat quality, to binary values ($1 = \geq 0.5$; $0 = < 0.5$) at each cell. We summed values for all models, resulting in a range of values from zero (i.e., all models predict habitat < 0.5) to four (i.e., all models predict habitat ≥ 0.5). This method can be understood as a 'frequency histogram' of the number of models predicting above a certain threshold at each cell (Araújo and New, 2007).

As a post-hoc exploration of the most important environmental features that contributed to the synthesized wolverine habitat map, we examined Pearson's correlation between the spatial covariates and the resulting synthesized habitat values. To compute 95% confidence intervals, we conducted a pair-wise bootstrap over 1000 iterations.

2.7. Prediction assessment

To validate the synthesized habitat predictions, we compared habitat values to two independent wolverine occurrence datasets. First, we used wolverine detection locations at remote camera sites in Banff, Yoho, and Kootenay national parks, Canada (Barrueto et al., 2022) and extracted the mean habitat value within a 100-m radius of each camera site. Second, we extracted mean habitat values for predicted wolverine denning habitat in the Kananaskis-Ghost region, the eastern part of our study area, Alberta, Canada (Heim et al., 2019). We visually examined the relationship between the independent occurrence locations and synthesized habitat values via histograms, with the expectation that higher quality synthesized habitat values should experience greater wolverine detections and overlap with high-quality denning habitat. While this does not explicitly test the validity of the habitat raster, it provides a useful range of habitat values where one could expect wolverines to occur.

2.8. Persistent spring snow forecasts

As persistent spring snow cover has been identified as important to wolverine habitat (Mowat et al., 2020; Heim et al., 2017; Kortello et al., 2019), we assessed future spring snow cover forecasts to identify habitat refugia. We obtained snow water equivalent (SWE) forecasts for British Columbia for May 1 2080 under Representative Concentration Pathway (RCP) 8.5 high-emissions scenario (Pacific Climate Impacts Consortium, 2022). We took the ensemble mean of six available snow water equivalent forecasts (Pacific Climate Impacts Consortium, 2022) to create one snow water equivalent raster. Similar data for Alberta were not publicly available after extensive searching. We selected the high-emissions scenario (RCP 8.5) for future snow cover as we wanted to identify snow areas most likely to persist under climate warming, i.e., to have greater certainty of identifying lasting refugia. As snow water equivalent forecast data (e.g., numeric values) differs from binomial remote sensing snow cover (e.g., snow cover presence/absence), which we used in our habitat modeling, we calibrated the two data types using MODIS snow cover *MOD10A2* from May 2020 (Hall and Riggs,

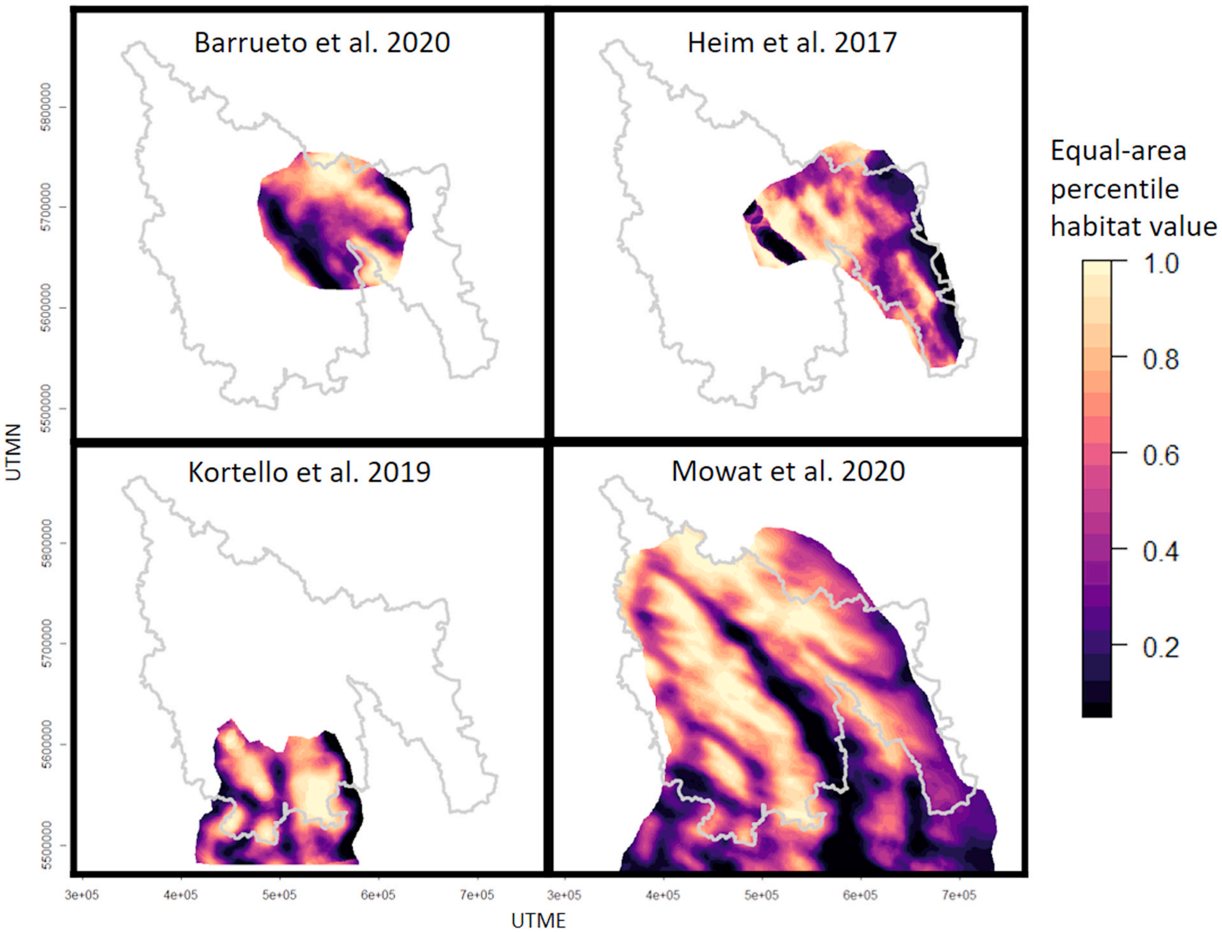

Fig. 2. Wolverine habitat model predictions, scaled to equal-area percentile values. Dark colors represent poor quality habitat whereas light colors represent high quality habitat. Each map panel represents the original habitat model predictions, mapped to the original study area extents, with the area of interest border overlain in grey.

2021). To identify an approximate threshold for binomial snow cover, we took the inflection point of a logistic regression between snow water equivalent data and its respective binomial MODIS snow cover data (inflection at SWE = 390 mm). This calibration method produced an 81% accuracy in binomial classification for 2020 snow datasets. We then used this value to classify 2080 snow water equivalent forecasts into binomial data comparable to spring snow cover. With the 2080 RCP 8.5 binomial snow cover data, we visually assessed areas where snow persistence overlapped with high quality habitat. For each protected area within the snow forecast extent, we calculated a snow cover value for 2020 and 2080 RCP 8.5.

3. Results

3.1. Habitat predictions

The model prediction equations and equal-area percentile transformations produced estimates of wolverine habitat quality ranging from 0 to 1 in four original study areas (Fig. 2). We combined the four model predictions using a distance-weighted mean. The resulting synthesized habitat map (Fig. 3) can be explored with a freely accessed web-based interactive viewer (https://y2yrececol.shinyapps.io/Wolverine_Habitat_Suitability/). Extrapolation was infrequent: within the area of interest, only 8% of cells were not covered by an original model area, with a maximum extrapolation distance of 36 km. Residuals between model predictions and the synthesized values were normally distributed for all four models (Supplementary Material Fig. S2).

The synthesized habitat map (Fig. 3) predicted poor habitat in the Alberta Eastern Slopes (i.e., foothills of the Rocky Mountains) and in wide low-elevation, populated valleys of the upper Columbia River. The highest quality habitat was predicted along mountain

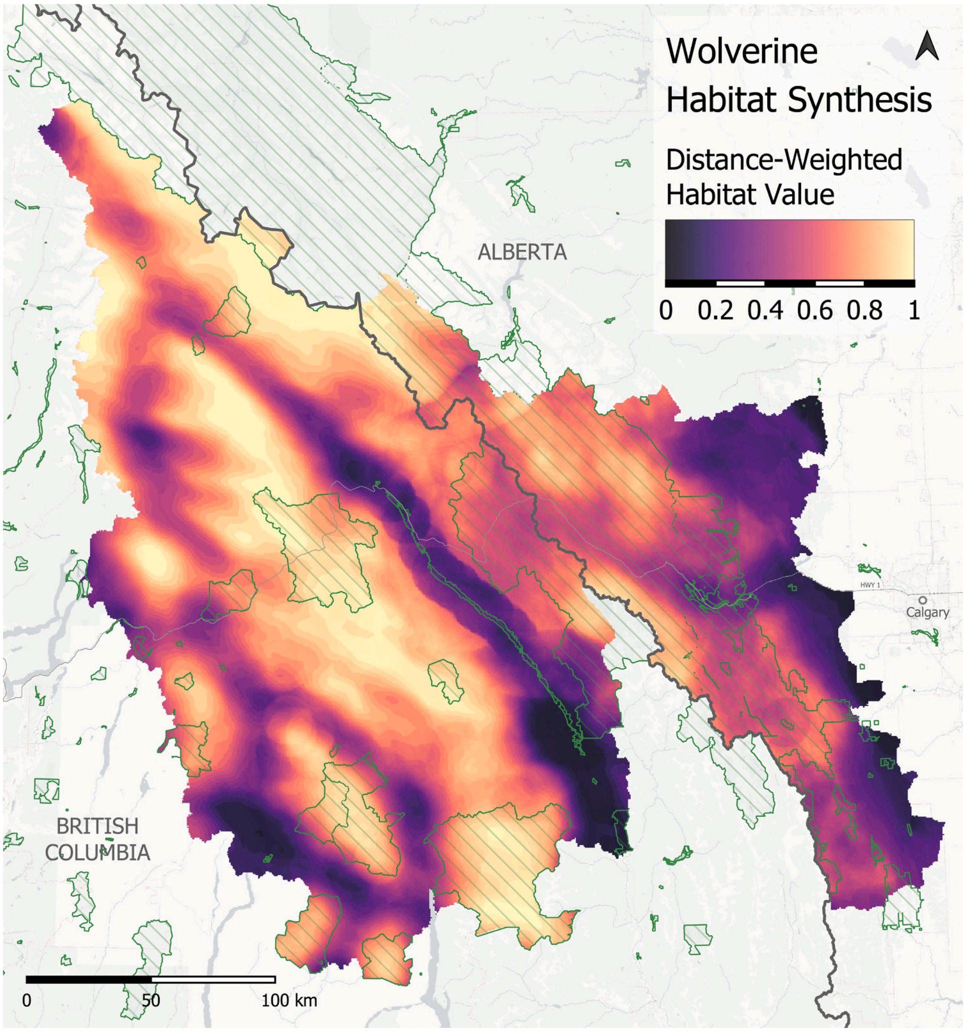

Fig. 3. Predicted wolverine habitat created by distance-weighted synthesis of four original models transformed to equal-area percentile values. Dark colors represent poor quality habitat whereas light colors represent high quality habitat. The habitat predictions span protected areas (green outline), and unprotected lands in Alberta and British Columbia.

ranges, notably in the Purcell Mountains and the Columbia Icefield in the Rocky Mountains. Mean habitat value inside protected areas was 0.70 (SD: 0.19), as compared to 0.55 (SD: 0.28) outside protected areas.

3.2. Prediction assessment

The weighted coefficient of variation (Fig. 4) demonstrates relative similarity among habitat predictions. In 98.5% of cells, the standard deviation (SD) was smaller than the mean (coefficient of variation < 1). The coefficient of variation was highest in the Columbia River valley, where models produced the most dissimilar predictions.

Within the area of interest, 26% of habitat was unanimously predicted at ≥ 0.5 equal-area percentile habitat value by all four models, and 19% of habitat was unanimously predicted to be < 0.5 (Fig. 5). Areas of majority agreement where at least three models predicted good habitat align with higher elevation areas that were identified as high-quality habitat in the synthesized map. Areas unanimously identified as poor habitat are the foothills of Alberta, and valleys of the Columbia River. The southwestern part of the study area contains isolated patches of good quality habitat, notably in Goat Range and Kokanee Glacier provincial parks.

All environmental variables used during the original modelling remain correlated with the synthesized habitat map (Table 2). The most strongly correlated variable to wolverine habitat is persistent spring snow (r=0.82), followed by a negative relationship with resource road density ($r = -0.60$). Protected areas within a 10 km radius did not have a strong linear relationship to habitat quality ($r = 0.30$).

Comparison of the synthesized wolverine habitat map with independent datasets showed support for its predictive ability within the area of interest. Eighty-seven percent of wolverine denning areas occurred at synthesized habitat value > 0.5 (Fig. 6a). In Banff,

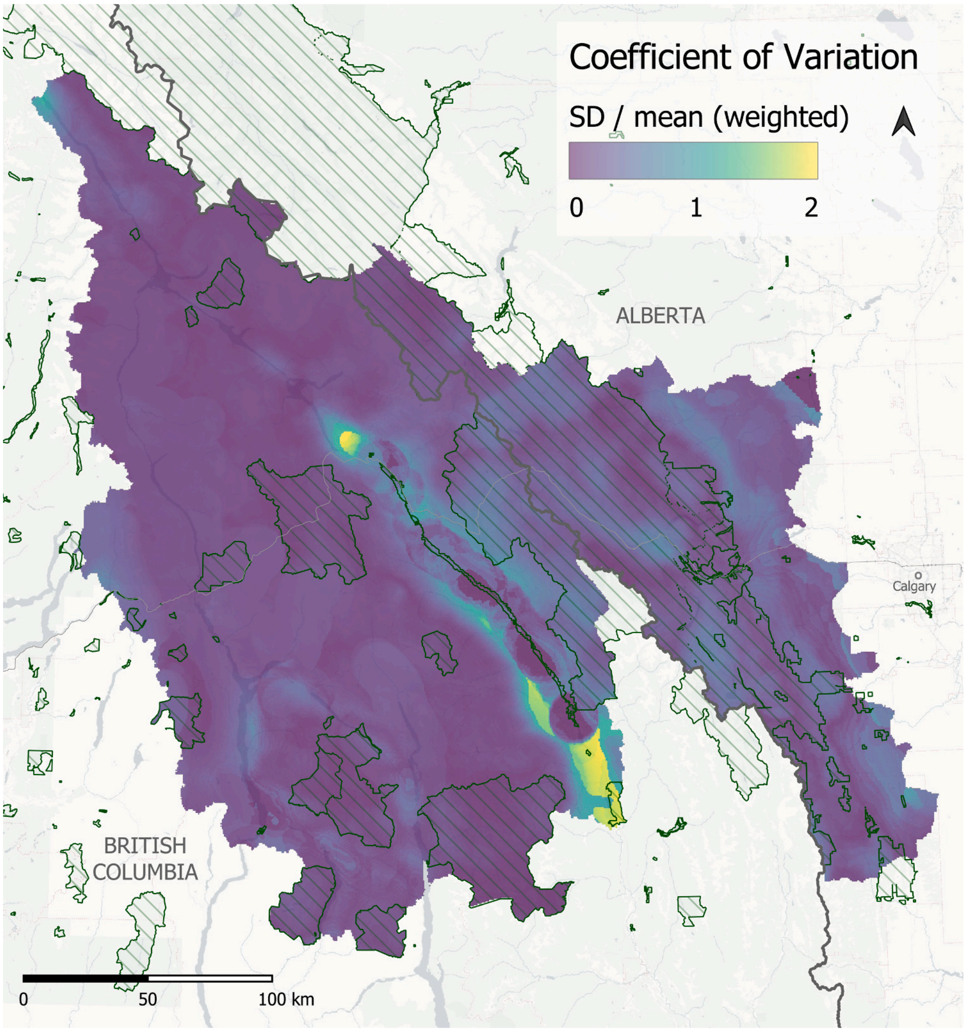

Fig. 4. Weighted coefficient of variation (mean over standard deviation) of the four model predictions creating the synthesized wolverine habitat map. Dark blue represents areas of small difference between individual model predictions, whereas light colors represent larger differences. The model synthesis spans protected areas (green outline), and unprotected lands in Alberta and British Columbia.

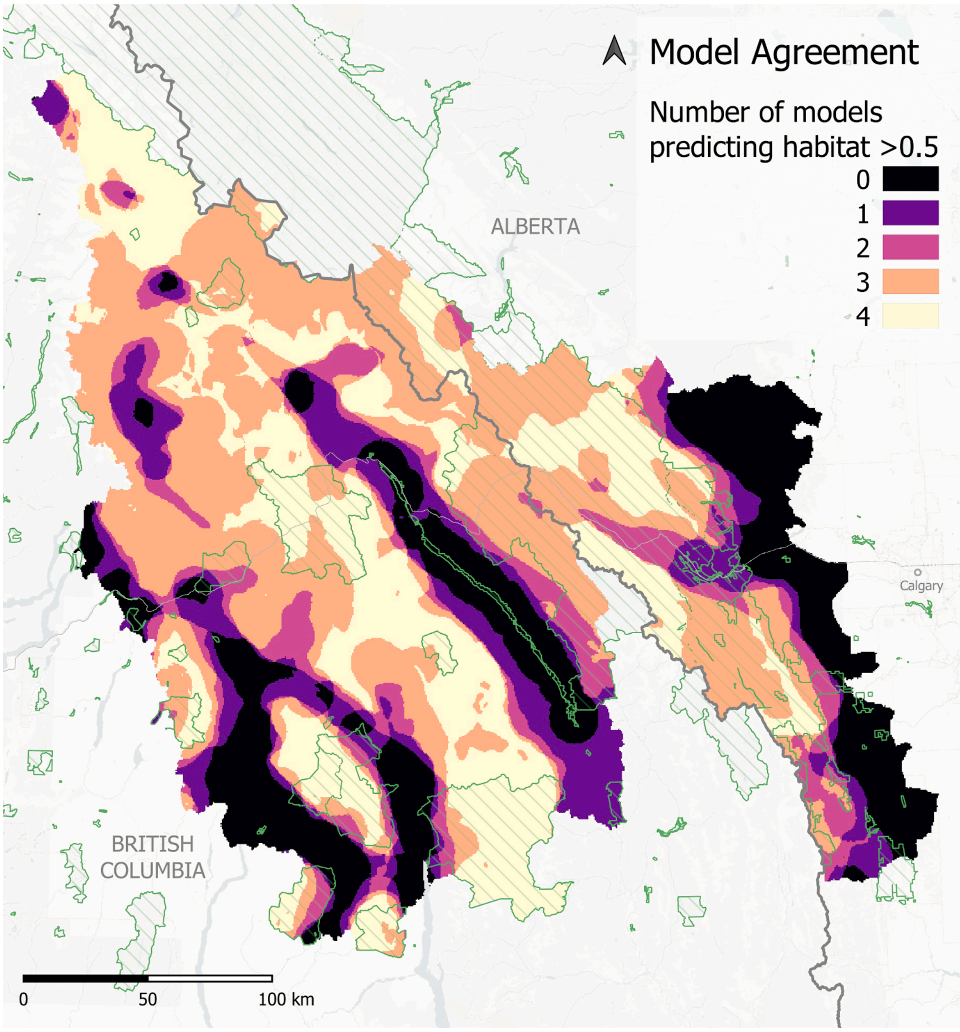

Fig. 5. Model agreement of four model predictions. Values (0 through 4) represent the number of models predicting a habitat value of greater than 50th percentile, which we define as 'good habitat'. Dark (0) represents areas where all models predict poor habitat, whereas yellow (4) represents areas where all four models predict good habitat. The model synthesis spans protected areas (green outline), and unprotected lands in Alberta and British Columbia.

Table 2
Post-hoc examination of environmental variables contributing to synthesized wolverine habitat map, by linear correlation index Pearson's r. Confidence intervals were computed by pairwise bootstrap over 1000 iterations.

Variable	Pearson's *r*	95% Confidence Interval		
Persistent spring snow	0.82	0.81	—	0.84
Resource road density	–0.60	–0.64	—	–0.55
Landcover: shrub	–0.51	–0.55	—	–0.46
Landcover: conifer	–0.50	–0.57	—	–0.43
Industrial linear features density	–0.50	–0.54	—	–0.46
Moraines	0.31	0.27	—	0.35
Protected areas	0.30	0.26	—	0.35
Landcover: mixedwood	–0.24	–0.29	—	–0.19

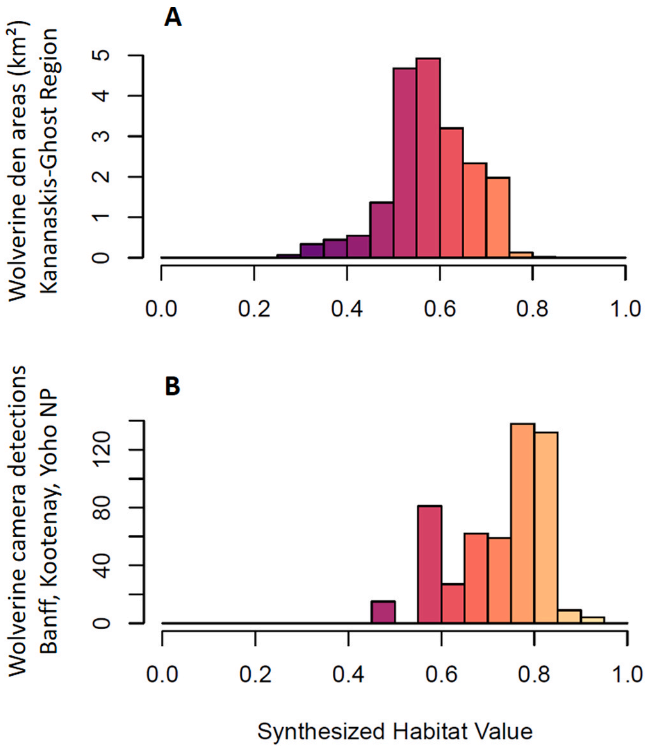

Fig. 6. Synthesized habitat values of independent wolverine datasets: A) predicted denning habitat in Kananaskis – Ghost (Alberta Parks), and B) camera detection locations in Banff, Kootenay, and Yoho National Parks 2017–2019 (Parks Canada).

Yoho, and Kootenay national parks, 98% of wolverine detections on remote cameras occurred at synthesized habitat value > 0.5 (Fig. 6b).

3.3. Persistent spring snow forecasts

Under RCP 8.5 forecasts, 44% of persistent spring snow cover will be lost between 2020 and 2080 in the British Columbia part of the study area. Forecasted snow persistence for May 1, 2080 coincides with high quality habitat predictions in the Columbia Mountains, and near the Columbia Icefields (Fig. 7). Areas without spring snow persistence are the Columbia River valley, as well as high-elevation

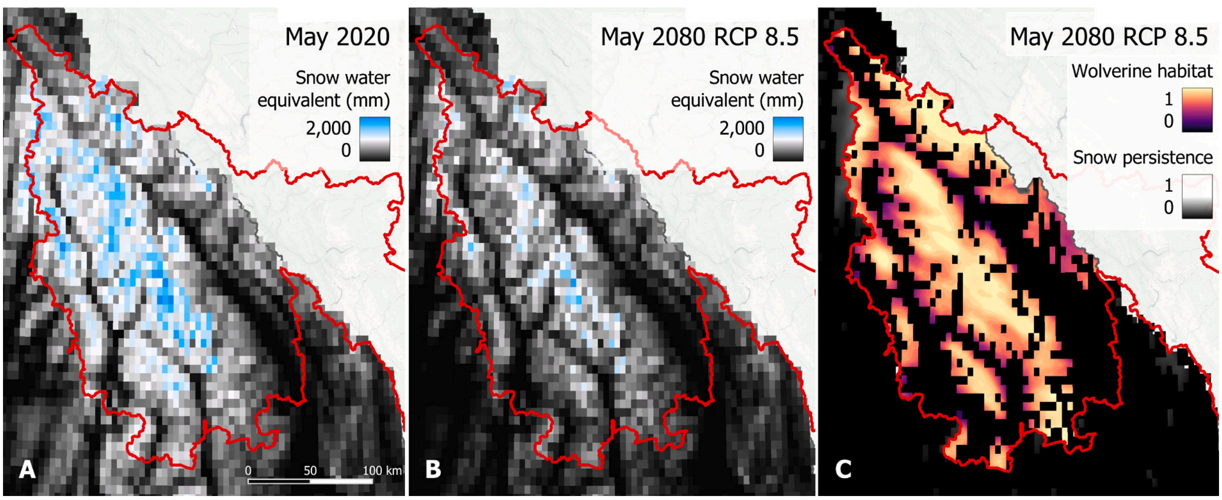

Fig. 7. Persistent spring snow cover (May 1) in British Columbia part of study area. Snowpack depth as modelled snow water equivalent (SWE; mm) in **A:** May 2020, and **B:** May 2080 under RCP 8.5 high-emissions climate forecast. **C:** Wolverine habitat clipped to snow persistence based on calibration to satellite data (black areas SWE < 390 mm).

terrain on the southwestern side of the study area. While Yoho and Kootenay national parks have some areas of forecasted spring snow persistence, the current habitat quality in these refugia is modest. Protected areas with a forecasted decline of 2080 spring snow cover include Mount Revelstoke National Park, Bugaboo, Goat Range, Purcell Wilderness Conservancy provincial parks, and Hamling Lakes Wildlife Management Areas (Supplementary Material Table S2). Kokanee Glacier Provincial Park and Glacier National Park retain greater than 80% persistent spring snow cover under 2080 RCP 8.5 forecasts, indicating potential habitat refugia.

4. Discussion

By synthesizing four independent wolverine habitat models, we estimated habitat values across a broad landscape, clarified locations and descriptors of high-quality wolverine habitat, and avoided spatial extent and modelling limitations associated with single studies. Wolverine is a wide-ranging species, and recent reports of low and declining population densities within protected areas (Barrueto et al., 2020, 2022) highlight the importance of broad-scale management planning that considers wolverine habitat needs across large landscapes, including areas inside and outside parks and protected areas. Wolverine are often considered data deficient (Alberta Conservation Association, 2020), both formally in status assessments and informally by researchers and managers; here we used available data to fill in gaps across a large landscape. Our synthesis of habitat models produced a continuous surface of habitat quality predictions, taking into account multiple drivers identified in the literature including landcover, climate, and landscape disturbance (Fisher et al., 2022).

We found that persistent spring snow cover (lasting until May 15) was the most tightly correlated variable to wolverine habitat quality estimates in our study area. Wolverine often select snow-covered areas for denning (Copeland et al., 2010; Magoun et al., 2017), and persistent spring snow influences wolverine density in the study area (Mowat et al., 2020). Spring snow cover is the most important driver of genetic structure in a neighbouring U.S. wolverine population, followed by topography and human density (Balkenhol et al., 2020). While our work does not disentangle the inversely related effects of snow cover and human disturbance (Heim et al., 2017), both climate and anthropogenic variables were included in our synthesis.

While our study area included a range of protection levels, protected areas contained higher quality habitat than unprotected areas across our study area. Barrueto et al. (2022) found that wolverine densities inside protected areas were three times higher than outside. However, these protected areas were not population refugia because wolverine density inside protected areas was not stable and decreased over a 10 year period (Barrueto et al., 2022), suggesting a need for increased protections across vast landscapes greater than 10,000 km^2. Our work identifies high quality wolverine habitat that could be prioritized for future protection, conservation, and/or improved management, such as the western slopes of the Rocky Mountains adjacent to Jasper National Park, and near Glacier National Park. These unprotected areas may be prone to future recreation expansion, and existing research points to strong negative impacts of motorized and non-motorized recreation on wolverine occurrence and density (Barrueto et al., 2022; Heinemeyer et al., 2019).

To support conservation initiatives, we have created an interactive RShiny online application to share habitat synthesis results with managers, which may be used in decision-making (Thomas-Walters et al., 2021). The application displays wolverine habitat quality, which users can view overlaid on base maps or satellite imagery, along with the options to zoom and to toggle on protected area boundaries. This application and its interactive features assist map users in viewing habitat information for their area of interest, without GIS software or training, which can be limitations for non-specialized workers. Some parts of our study area have better model agreement and thus more confidence for decision-making; we provide users with a coefficient of variation map to assess model agreement in their area of interest. The coefficient of variation was below the proposed threshold (Jones-Farrand et al., 2011) in most areas, making it suitable for use. We note that the Columbia River valley has high model dissimilarity; predictions are most likely limited by a lack of appropriate habitat variables in that area. In a management context, users are cautioned that the map represents predicted habitat quality based on environmental features; in situ habitat quality may be affected by unmapped variables such as human activity.

In protected and unprotected areas, high-quality wolverine habitat can be supported by limiting human disturbance. Wolverine are sensitive to winter recreation; they avoid areas of motorized and non-motorized recreational activities, which contributes to indirect habitat loss (Heinemeyer et al., 2019). Winter recreation management, such as limiting snowmobile and heli-skiing activities, already occurs in some parts of the study area as a measure to limit disturbance for caribou (B.C. Ministry of Forests, Lands, 2022). Small areas of sensitive wolverine habitat in Kokanee-Glacier Provincial Park have designated winter closures (B.C. Ministry of Environment and Climate Change Strategy, 2021) where wolverine were detected in recent habitat research (Kortello et al., 2019). Our habitat quality estimates can help identify candidate areas for winter recreation management and spot closures that would support wolverine populations at a broad scale.

Various climate change scenarios predict a loss of spring snow cover in wolverine's southern range (Barsugli et al., 2020). We identified key habitat areas where spring snow cover is likely to persist under an RCP 8.5 future climate scenario. As spring snow cover is the variable that best explains wolverine habitat selection, management of snow refugia will be essential to ensure the security of wolverine populations in mountainous environments. Snow refugia may experience increased disturbance, for instance due to snow loss at former winter recreational areas (Steiger et al., 2019), concentrating recreationists in areas with remaining snow. A climate change–induced shortening of the recreational season and shrinking of the area available for skiing and snowmobiling (Wobus et al., 2017) risks straining wolverine habitat in snow refugia especially during the late spring months.

For large-scale management of wolverine, a continuous surface of habitat predictions can be used as a tool to support connectivity between key habitat areas. For example, our habitat synthesis predicts poor habitat quality in the valley between the Columbia and Rocky Mountains, which could isolate populations. Dispersal of wolverine through low-quality habitat can be important to maintain gene flow in a metapopulation (Carroll et al., 2020). Even inside protected areas, wolverine populations can be fragmented by low-quality habitat, especially major transportation corridors (Sawaya et al., 2019). Future development in the study area, such as proposed ski development (Brent Harley and Associates, 2021) in a key connectivity corridor between Goat Range and Kokanee Glacier provincial parks, could further isolate areas of high-quality habitat and reduce animal movement between core habitat and farther afield.

Improving ecological connectivity and expanding and managing protected areas are global conservation goals and targets (Goal A and Target 3; Secretariat of the United Nations Convention on Biological Diversity, 2022), as well as a priority for government (Parks Canada, 2022). Movement of wide-ranging carnivores such as wolverine can represent broad-scale ecosystem connectivity, and wolverine can act as a focal species to support landscape management (Carroll et al., 2001) i.e., between Glacier and Mount Revelstoke national parks (Cumming and Tavares, 2022). Climate change is also an important consideration for connectivity: species require corridors for successful dispersal into future high-quality habitat provided by climate analogues (Littlefield et al., 2017). Current protected areas may not adequately encompass future critical habitat; both Banff and Jasper national parks are predicted to experience ecoregion transition to some of their area by 2050 under 2 °C warming (Dobrowski et al., 2021). While the Rocky Mountains are sensitive to mid-21st century ecological transitions, the Columbia Mountains are predicted to be more static (Dobrowski et al., 2021), pointing to the importance of maintaining connectivity to facilitate climate-induced migration between the ranges.

Further transboundary collaboration is needed to assess and respond to threats in the wolverine's southern mountainous range (Fisher et al., 2022). Here we have outlined a framework to synthesize existing habitat research across the broad scale necessary to manage this wide-ranging carnivore. We developed an interactive web interface for managers to visualize wolverine habitat information within the study area. Our wolverine habitat predictions can be used as a valuable tool to support evidence-based land-use planning and conservation.

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Declaration of Competing Interest

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

Data Availability

Environmental data layers, output data layers, and R script are available at https://doi.org/10.5281/zenodo.7806631. Due to the sensitive nature of camera and denning data, they are not available.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02540.

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