ORIGINAL RESEARCH

A framework to support the identification of critical habitat for wide-ranging species at risk under climate change

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Abstract

To recover species at risk, it is necessary to identify habitat critical to their recovery. Challenges for species with large ranges (thousands of square kilometres) include delineating management unit boundaries within which habitat use differs from other units, along with assessing any differences among units in amounts of and threats to habitat over time. We developed a reproducible framework to support identification of critical habitat for wide-ranging species at risk. The framework (i) reviews species distribution and life history; (ii) delineates management units across the range; (iii) evaluates and compares current and (iv) potential future habitat and population size and (v) prioritizes areas within management units based on current and future conditions under various scenarios of climate change and land-use. We used Canada Warbler (*Cardellina canadensis*) and Wood Thrush (*Hylocichla mustelina*) in Canada as case studies. Using geographically weighted regression models and cluster analysis to measure spatial variation in model coefficients, we found geographic differences in habitat association only for Canada Warbler. Using other models to predict current habitat amount for each species in different management units, then future habitat amount under land use and climate change, we projected that: (1) Canada Warbler populations would decrease in Alberta but increase in Nova Scotia and (2) Wood Thrush populations would increase under most scenarios run in Quebec, New Brunswick and Nova Scotia, but not in Ontario. By comparing results from future scenarios and spatial prioritization exercises, our framework supports identification of critical habitat in ways that incorporate climate and land-use projections.

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Introduction

Habitat protection is key to the recovery and conservation of species at risk (Taylor et al. 2011; Langpap and Kirkvliet 2012; Geldmann et al. 2013). Identifying and designating habitat that is necessary for the survival and recovery of species at risk (hereafter "critical habitat") is a central component of conservation legislation around the world (e.g., United States: Endangered Species Act 1973; Australia: Environment Protection and Biodiversity Conservation Act 1999; Canada: Species at Risk Act (SARA) 2002). In the United States, critical habitat is defined as: "(1) specific areas within the geographical area occupied by the species at the time of listing that contain physical or biological features essential to conservation of the species and that may require special management considerations or protection and (2) specific areas outside the geographical area occupied by the species if the agency determines that the area itself is essential for conservation." In Australia, under section 207A of the Environment Protection and Biodiversity Conservation Act, the government is authorized to declare critical habitat for species or ecological communities based on habitat that is: (1) used during periods of stress; (2) used to meet essential life cycle requirements; (3) used by important populations that are necessary for a species' long-term survival and recovery; (4) required to maintain genetic diversity and long-term evolutionary development; (5) required for use as corridors to allow the species to more freely between sites used to meet essential life cycle requirements; (6) required ensure the long-term future of the species or ecological community through reintroduction of re-colonisation or (7) critical for a species or ecological community in any other way. In Canada, critical habitat is legally defined as habitat that is: (1) necessary for the survival or recovery of a listed wildlife species and (2) is identified as such in a recovery strategy or an action plan for the species (SARA 2002). In the case of migratory species, Canada is legally obligated to identify critical habitat for the part of the life cycle on Canadian territory, to ensure there is sufficient habitat to support a recovering population or intended future population size (SARA 2002). In the European Union, the Habitats Directive is analogous to federal endangered species laws in Australia, Canada, the United States, and requires that the Union's member states each establish protected areas within the continental Natura 2000 network for animal and plant species listed in Annex IV of this directive. These protected areas are analogous to critical habitat (Habitats Directive 1992).

Assumptions implicit to legal definitions of critical habitat are that: (i) a positive relationship exists between available habitat and a species' population size, and (ii) a minimum habitat amount is required to meet a species' recovery goals (Rosenfeld and Hatfield 2006). There is some evidence that habitat protection reduces species declines and/or aids species recovery (Taylor et al. 2011; Langpap and Kirkvliet 2012; Geldmann et al. 2013). Therefore, methods to identify critical habitat should evaluate population size, extinction risk, and/or amount of habitat needed to achieve species' population and distribution objectives at different spatial and temporal scales (Rosenfeld and Hatfield 2006; Camaclang et al. 2015). Although habitat loss or degradation has been identified as the most or second-most important threat to most species at risk (e. g., 85% of species in the United States (Wilcove et al. 1998); 62% of species on the IUCN Red List (Maxwell et al. 2016) 82% of species at risk in Canada (Woo-Durand et al. 2020)), few recovery strategies have evaluated relationships between habitat quantity and species abundance, demography or population viability (Lemieux Lefebvre et al. 2018).

Current approaches to defining critical habitat may underestimate the habitat needed for recovery, especially for wide-ranging species (e.g., caribou (*Rangifer tarandus*), migratory

landbirds) because of spatial variation in data availability, habitat associations and threats (Camaclang et al. 2015; Crosby et al. 2019). Identification of critical habitat is often based on where individuals are or were known to occur, and a set of specific habitat characteristics within a specified area around occurrence locations (species at risk in Canada, the United States, and Australia (Camaclang et al. 2015); Canadian vertebrate species at risk (Lemieux Lefebvre et al. 2018)). Key limitations of this approach are that inaccessible habitats are poorly sampled and thus inadequately represented in species-habitat relationships (Wilgenburg et al. 2020), animals may be observed while passing through unsuitable habitats (e.g., tigers (Thinley et al. 2021)), habitats may be unoccupied at the time of sampling (Thomas and Kunin 1999) and/or species with low detectability may not be observed despite being present (Dénes et al. 2015). Species distributions may also be overestimated if those distributions are based on the extent of occurrence locations, causing vulnerability of species to extinction to be underestimated (e. g., bird species in southern Africa, Australia, and the United States (Jetz et al. 2008)). As a result, identifying critical habitat based only on known locations of species may underestimate the amount of critical habitat, or incorrectly identify it (Camaclang et al. 2015, Thinley et al. 2021). Critical habitat should also not be overestimated, to reduce management costs and maximize the use of available resources for more species (Martin et al. 2018).

An additional challenge for wide-ranging species is variation in habitat selection across their ranges (e. g., rodents, Holarctic birds (Miller 1942); snakes (Carfagno and Weatherhead 2006); European birds (Wesolowski and Fuller 2012); caribou/reindeer (Yannic et al. 2016; Webber et al. 2022); boreal forest songbirds (Crosby et al. 2019)), combined with the reality that habitat protection and management actions are often undertaken at different levels of jurisdiction (international, national, subnational, Indigenous: (Hessami et al. 2021)). As such, important habitats may need to be identified and managed at scales smaller than national distributions (Waples 1991; COSEWIC 2020a). Systematically assessing abundance and habitat relationships across multiple management units can address range wide differences in a species' habitat requirements, extinction risk, genetic structure, ecological structure and/or reproductive isolation (e. g., Distinct Population Segments (Waples 1991), Evolutionarily Significant Units (Crandall et al. 2000), Designatable Units (Green 2005)), along with differences in habitat use and other ecological aspects of species within individual jurisdictions. While management units based at least partially on biological evidence have been defined for some well-studied species based on ecological and genetic data (e. g., caribou (Yannic et al. 2016)), there remain many challenges and disagreements among biologists on how to use such data to delineate management units within jurisdictions and below the species level for many wide-ranging species at risk (Green 2005; Whitehead et al. 2023).

Identification of critical habitat is also challenged by the dynamic nature of habitat suitability over time as influenced by natural and human disturbance and ecosystem succession (Stralberg et al. 2015a, b). Climate change is altering these processes and as such, habitat suitability and amounts of available suitable habitat are changing for many species (Stralberg et al. 2015a; Taylor et al. 2017; Tremblay et al. 2018; Cadieux et al. 2020; St-Laurent et al. 2022; Leblond et al. 2022). Temperature increases associated with current climate change are predicted to increase with latitude, however tropical species, especially ectotherms, may be more vulnerable to local extinctions related to habitat loss or degradation from climate change, due to a narrower range of thermal tolerances in these species relative to those at higher latitudes (Deutsch et al. 2008; Grinder and Wiens 2023) or due to increases in pathogens (e.g., chytrid fungi infecting amphibians (Pounds et al. 2006)). Some tropical species may adapt by shifting their range towards cooler refugia like

mountains; however, using all extant mammals as an example, distance to the nearest cool refugium exceeded 1000 km for 20% of tropical species, in contrast to 4% of extratropical species (Wright et al. 2009). Even within tropical mountainous regions, high-altitude species are experiencing population declines and range contractions with global warming, while lowland species are expanding their ranges to higher altitudes (e.g., Australia (Shoo et al. 2005); India (Adve 2014); New Guinea (Freeman and Freeman 2014); South America (Freeman et al. 2018)). Finally, for many temperate and tropical species, the poleward edges of their ranges may shift towards higher latitudes, potentially increasing future habitat for them polewards (Parmesan and Yohe 2003; Hickling et al. 2006; Chen et al. 2011). Thus, methods to identify critical habitat should consider changes in the distribution of suitable habitats that could occur in the short and long term.

Given the current pace of species loss, declines in suitable habitat, and environmental change (Powers and Jetz 2019; Rosenberg et al. 2019; Winkler et al. 2021), any delays associated with lengthy and complicated processes for critical habitat identification are certain to result in continued exacerbated losses (Martin et al. 2018; Ward et al. 2019). We build on a conceptual model previously developed for boreal caribou in Canada (Environment Canada, 2011) to construct a generalizable modeling framework that can inform identification of critical habitat for wide-ranging species of conservation concern, both in the present and under future scenarios. We describe this framework and demonstrate how the quantitative output of this framework can support decision-making and planning related to identifying critical habitat or analogous protected areas, in support of species' population and distribution objectives, using two wide-ranging migratory landbirds in Canada (Canada Warbler [*Cardellina canadensis*] and Wood Thrush (*Hylocichla mustelina*)) as case studies.

Methods

Both Canada Warbler and Wood Thrush were assessed by COSEWIC as Threatened (COSEWIC 2008, 2012) and both are listed as Threatened on Schedule 1 of the Species at Risk Act in Canada as of October 2023 (https://www.sararegistry.gc.ca/species/schedules_e.cfm?id=1), although Canada Warbler was recently reassessed as of Special Concern (COSEWIC 2020b). Both species have broad distributions encompassing many different habitats and are exposed to a variety of natural and anthropogenic stressors. Thus, both are suitable to illustrate a framework for delineating critical habitat for wide-ranging bird species in Canada. The framework encompasses five steps (Fig. 1).

Step 1 Review distribution and life history characteristics

Understanding basic habitat associations across the species' distribution and life stages is a priority (Rosenfeld and Hatfield 2006) and is required to identify environmental variables and spatial data for population modeling. Information about life history, habitat associations, conservation status and distribution can be assembled from a range of sources including scientific and gray literature as well as expert opinion. For understudied and/or culturally important species, best practice would involve establishing an advisory committee to consolidate expert opinions (e.g., of species biologists, Indigenous and other knowledge-holders, conservation practitioners); otherwise, decisions and input could potentially be limited to 1–2 people. All available location data for the species should be assembled,
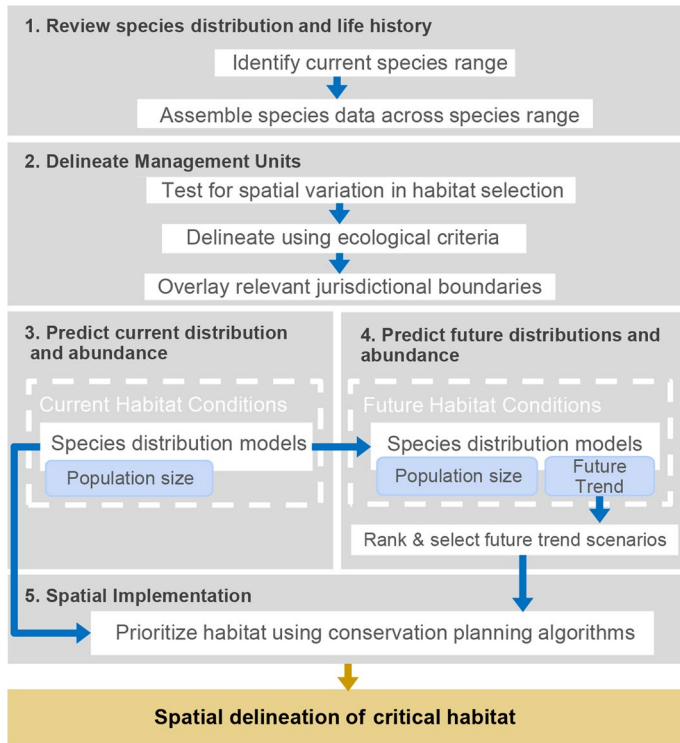
Fig. 1 Analytical framework to inform the identification of critical habitat for wide-ranging species at risk

integrated, and compared with the known distributional range to assess the degree to which the available data are likely to represent the entire geographic range and to identify areas where the data and analyses should extend beyond the known range.

Step 2 Delineate management units

Delineating management units fulfills multiple purposes in the identification and implementation of critical habitat, including: (i) defining the scale and extent of analysis; (ii) representing differential habitat associations or needs across a species' range (i.e., niche separation), (iii) reflecting geographic inconsistencies in environmental data (e.g., forest classifications) and (iv) representing variation in species' and habitat management amongst jurisdictions. Management unit boundaries may vary with or within jurisdictions and may also be defined based on ecological data using a number of methods (COSEWIC 2020a), but some of these (e.g., genetic markers, morphological measurements) may only be available for well-studied species (e.g., caribou). For less well-studied species, species distribution models (*hereafter*, 'SDMs') based on surveys of unmarked animals may be used. In SDMs, a species metric (e. g., occupancy, relative abundance, or density) is related to a suite of environmental variables to elucidate habitat associations and predict species distribution. The choice of SDM approach depends on the survey data available (Elith and Leathwick 2009; Dénes et al. 2015; Fois et al. 2018). If abundances (e. g., avian point-count data) are used as the input variable and appropriately standardized for detectability

(Sólymos et al. 2013), the SDM model outputs can be interpreted as predicted population densities. This can be summed across management units or the entire range to provide population estimates. If presence-absence data or presence-only data are used, the resulting output is a predicted probability of occurrence. For both Canada Warbler and Wood Thrush, we used geographically-weighted regression models (*hereafter*, 'GWR models'; (Fotheringham et al. 2003) as our SDMs. Using GWR models enabled us to partition species' ranges into regions with distinct habitat associations.

We fit GWR models using point count data mostly from the North American Breeding Bird Survey (https://www.pwrc.usgs.gov/bbs/), the Boreal Avian Modelling Project (http://www.borealbirds.ca), and a few other minor sources (Table S1.1). The ranges of both species extend into the United States (BirdLife International and NatureServe 2018). To minimize points within Canada on the Canada/United States border becoming outliers with inordinate influence, we included point-count data from both Canada and from adjacent or near-adjacent states with similar forest types within the delineated breeding ranges. We ran a separate GWR analysis for each species, assembling data from 403,005 point-count surveys for Canada Warbler (62% from BBS; 2% with one or more detections) and 399,016 point count surveys for Wood Thrush (72% from BBS; 4% of all surveys with one or more detections). To correct for variations in sampling protocol and other factors affecting detectability, we calculated point-count specific offsets using the QPAD method (Sólymos et al. 2013). To control for variation in sampling effort between states and provinces, and to improve model performance, we generated $n = 10$ spatially balanced random subsamples of the data. This was also done to help us look for and find patterns in the output—like how consistently certain points clustered together across samples. To do this, we overlaid the breeding ranges of each species used within GWR modeling with a grid (100 x-intervals by 60 y-intervals; see Appendix S1 for further details) and randomly sampled an equal number of point counts from each cell. This procedure was replicated 10 times, and a GWR model was fit to each replicate.

For each covariate (Table S1.2) in each GWR analysis, separate model coefficients were estimated at each point-count location, allowing spatially varying relationships between the species densities and habitat covariates and thereby allowing for differential habitat selection to be detected across each species' range. We used multivariate cluster analysis of the location-specific model coefficients to identify regions with similar habitat associations (based on coefficient similarity among different sites; Fotheringham et al. 2003; Fig. S1.1). Finally, we identified management units by intersecting habitat association regions with jurisdictional and/or other relevant management boundaries and/or expert opinion as necessary (Environment and Climate Change Canada 2014). This process may result in multiple alternate delineations for a particular species. These delineations were evaluated by a separate advisory committee for each species. Each committee chose the option having the fewest management units consistent with their understanding of a particular species' biology and distribution. Steps 3, 4, and 5 are then conducted for or within each management unit (Appendix S1).

Step 3 Predict current distributions and abundance

Like Step 2, Step 3 relies on SDMs, but with the aim of spatial prediction of distribution within management units. We fit boosted regression tree models (*hereafter,* 'BRTs'; Elith and Leathwick 2009; Stralberg et al. 2015a; Micheletti et al. 2021) due to their predictive accuracy and ability to account for nonlinear responses, interactions, and large numbers of

covariates. We modeled the point-count data assuming a Poisson error distribution, with detectability offsets as above. These models predicted expected densities in units of singing males per hectare (Sólymos et al. 2013).

For each species, we ran BRT models for each management unit identified in Step 2. Covariates used for each species were chosen based on published literature from Step 1, and in consultation with advisory teams. When SDMs are used in Step 3 to make spatial predictions over a management unit, it may be possible to use available covariates with a finer cell size, which may influence the choice of habitat covariates. For Canada Warbler, covariates included forest stand age, biomass, proportional cover of individual tree species (Beaudoin et al. 2014), proportional cover of urban/agricultural footprint, and compound topographic index. For Wood Thrush, covariates included forest age and biomass, elevation, and proportional cover of different land cover types (AAFC 2021). There were multiple BRTs run for each species, each varying in the spatial scales at which predictors were assessed for importance: a "local" scale within a 250-m square cell containing each point count survey and one or more "landscape" scales (Canada Warbler: 250 and 750 m radii; Wood Thrush: 150, 250, 1000 and 2000 m radii), in which environmental variables were summarized by assigning greater weights to values in cells closer to each point count (i. e., Gaussian filtering; Chandler and Hepinstall-Cymerman 2016) (Appendix S2: full predictor lists in Tables S2.1, S2.2). Weights followed a normal distribution and the landscape scale for summarizing variables was specified by a sigma value ($=1$ standard deviation), with larger sigma values for larger landscape scales. We then ran and evaluated the predictive accuracy of several BRT models varying in predictors for each species and unit. To assess uncertainties in predicted density, we fit BRTs to $n=250$ bootstrap samples of the data. From each bootstrapped model, we generated a raster of predicted densities at a resolution of 250 m. From these, we calculated rasters of mean predicted density and variance measures to represent uncertainty (the upper and lower 90% CIs). We also calculated the mean and variance of population size and estimated population size for each management unit (Appendix S2).

Step 4 Forecasting future distributions and population sizes

Here, the models of Step 3 are used for spatial prediction on simulated future landscapes (details in Appendix S3), where habitats change over time according to coupled models of vegetation dynamics, natural disturbances such as wildfire and anthropogenic disturbances such as forest harvesting, often with exogenous climate projections. Ecological forecasting is a rapidly developing field (Bodner et al. 2021; Lewis et al. 2022), but doing it to address a specific question on a specific region remains a highly non-trivial and specialised task. Here, we take advantage of pre-existing studies wherever possible. For this reason, study areas for Step 4 were located within the management units identified in Step 2 and used for modeling in Step 3 but did not necessarily correspond exactly with the designated management units.

In brief, we mostly used applied land-use and climate-change simulations from pre-existing studies by other research groups for northeastern Alberta (Cadieux et al. 2020) and Quebec, New Brunswick, and Nova Scotia (unpublished), run using the simulator LANDIS-II (Scheller et al. 2007). In these simulation studies, forest disturbance rates resulted from different combinations of forest harvest regimes (ranging from no harvest to high-intensity clear-cutting) and natural disturbance (e. g., tree mortality from forest fires, drought, insect outbreaks) influenced by climate change between now and 2100. The

amount of climate change varied among scenarios as described by Representative Concentration Pathway (RCP) values (e.g., 2.6, 4.5 and 8.5), with higher RCP values associated with larger increases in atmospheric CO_2 and greater rates of warming (van Vuuren et al. 2011). LANDIS-II simulations of forest succession were not available for parts of Ontario within the Wood Thrush range; instead, we ran a land-use scenario without climate change for those regions with another simulator, ALCES Online (Carlson et al. 2014). Further details about both simulators and their scenarios are described in Appendix S3 and in Leston (2022).

Step 5 Candidate critical habitat identification by spatial prioritization

The final step in our framework identifies areas likely to support current and future species populations, which can then be considered as candidates for designation as critical habitat. We used the spatial prioritization software Zonation 4.0 (Moilanen et al. 2014). Zonation ranks each raster cell by its contribution to meeting objectives for species population and connectivity that the user defines. As input features to Zonation, we used the current predicted densities (Step 3) and future predicted densities across scenarios (Step 4) for each species. For example, we determined and mapped the amount of land area required to represent 50, 75, 90 and 100% of the current (2020) population in each management unit based on predicted density rasters. To gauge potential population sustainability, we assessed these same land base requirements with respect to current and future distribution maps simultaneously, weighting future maps at 0.75 to account for the greater uncertainty in the predictions. In cases with multiple scenarios, we reported the best, intermediate, and worst cases (specifications in Appendix S4).

Results

Using our case studies, we demonstrate how findings from each step of the framework are used to better understand species-habitat relationships as well as inform delineation of critical habitat.

Step 1 Review distribution and life history characteristics

Based on our desktop review of current distribution and life history characteristics, we determined key features that informed (1) covariate selection for modeling and (2) designation of management units. The Canada Warbler breeds across boreal and hemiboreal forests in Canada (Reitsma et al. 2020). Previous studies suggest that Canada Warbler uses different forest types and topographic features as breeding habitat in Maritime Canada (lowland and disturbed coniferous forests), Ontario and Quebec (upland disturbed mixed-wood forest with a dense shrub understory) and western Canada (older upland deciduous forests) (Chace et al. 2009; Goodnow and Reitsma 2011; Ball et al. 2016; Crosby et al. 2019). Canada Warbler preferences for different forest types, climates, and topography at opposite ends of its range, along with the vulnerability of these forest types to climate change led us to include forest and non-forest land cover, information associated with forest age (i.e., height, canopy cover), topography, and climate variables in the GWR models (Appendix S1: full predictor list in Table Appendix S1.2).

In contrast, Wood Thrush is limited to Eastern Canada where it mainly nests in mature deciduous forests, but also uses swamps, shrubland and younger forests (Evans et al. 2020). For these reasons, we included land cover types, forest height and canopy cover and topography variables. Due to its smaller range in Canada, we did not have strong a priori reasons to include climate variables in Wood Thrush GWR models (Appendix S1: full predictor list in Table Appendix S1.2).

Step 2 Delineation of management units

For the Canada Warbler, cluster analyses derived from GWR models indicated evidence of three clusters based on differential habitat associations across the range: (1) western Canada (from the Yukon Territory and British Columbia to mid-Manitoba), (2) central Canada (from mid-Manitoba to 90W in Ontario) and (3) eastern Canada (Fig. 2). Based on desktop information synthesized in Step 1 suggesting different habitat use in Ontario and Quebec versus Maritime Canada, we performed a secondary cluster analysis using only data from eastern Canada (Figs. Appendix S1.2–S1.3). We identified the northern 60% of Nova Scotia as distinct within eastern Canada (Figs. 3, Appendix S1.2). Of the four clusters identified for Canada Warbler, we focused on further examining the two clusters at the ends of the range (western Canada and northern Nova Scotia) for demonstrating Steps 3–5 of the framework (Fig. 2), based in part on available forecasting scenario data (Methods, Step 4). We overlaid jurisdictional boundaries over the western Canada cluster, identifying the province of Alberta as a distinct management unit, and excluded the Yukon and British Columbia, because (1) land management is generally a provincial responsibility; (2) there were some land uses within Canada Warbler's range in Alberta that were not present elsewhere and (3) we had access to detailed footprint data in Alberta but not elsewhere.

Cluster analysis on GWR results found no spatial variation in habitat selection by Wood Thrush in Canada (Figs. 2B, Appendix S1.2–S1.3), which allowed for species distribution modeling in Step 3 to be performed across the specie's entire eastern Canadian range, rather than by management unit. Four management units were delineated based on provincial boundaries and used for Steps 4 and 5, as each province has its own responsibility to manage forest lands within its borders.

Step 3 Predict current distributions and abundance

For Canada Warbler, BRT model results corroborated GWR model results, indicating different habitat preferences in northern Nova Scotia and Alberta. Canada Warbler densities in Nova Scotia were higher at sites with more balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), and red spruce (*Picea rubens*) and higher compound topographic index (CTI) values (larger catchment areas with shallow slopes) within the surrounding landscape, and lower above ground biomass, eastern hemlock, white spruce (*Picea glauca*), and deciduous trees within the surrounding landscape. In Alberta, Canada Warbler densities were higher at sites with lower CTI values (smaller catchment areas with steep slopes) and higher at sites with more above ground biomass and deciduous trees (Table 1; Appendix S2). From the mean predicted density maps, we estimated a current population of 38,282 (90%CI 21,198–55,367) Canada Warbler males in northern Nova Scotia and 274,176 (90%CI 165,447−442,813) in Alberta.

Wood Thrush abundance in eastern Canada increased when up to 80% of land within 150 m consisted of swamps, when shrublands or coniferous forests comprised no more
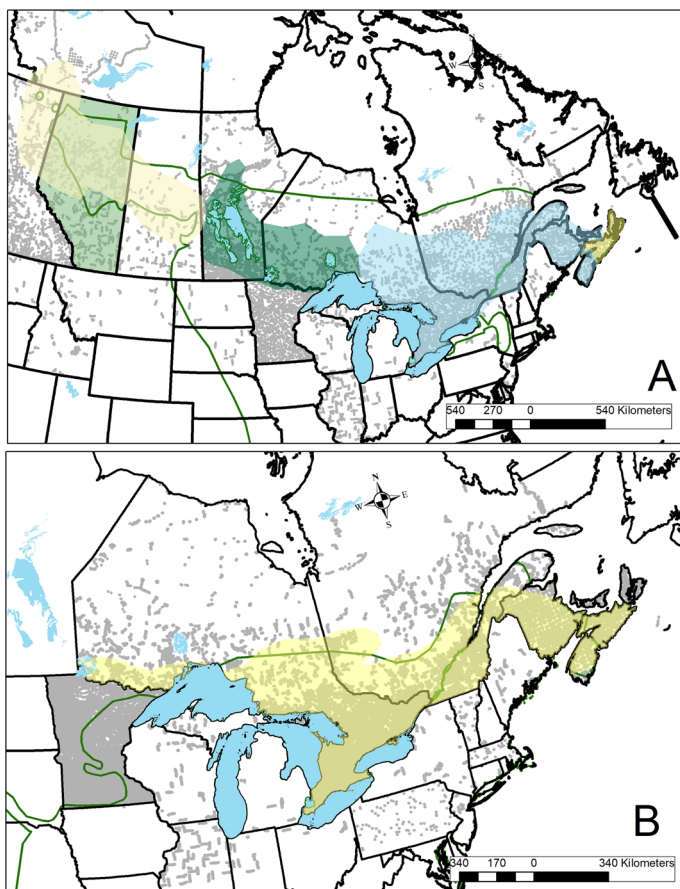
Fig. 2 Study areas and data used in the geographically weighted (GWR) models to identify management units for Canada Warbler (**A**) and Wood Thrush (**B**) in Canada. Grey points = point count locations available for GWR models. Yellow, dark blue, and light blue polygons **A** regional boundaries of point count locations with Canada Warbler detections identified as belonging to separate clusters after GWR models, with points in northern Nova Scotia (nNS) being assigned to a separate cluster (yellow) from the rest of eastern Canada (light blue) after more GWR models. Yellow polygon **B** regional boundary of point count locations with Wood Thrush detections, all identified as belonging to a single cluster after GWR models. We delineated and selected management units for Canada Warbler in Alberta and nNS and used a single region for Wood Thrush after cluster analysis for further study. Dark green lines: species range limits according to NatureServe (BirdLife International and NatureServe 2018)

than 20% of land within 2000 m, and with increasing deciduous forest cover within 150 m (Table 1; Appendix S2). From the mean predicted density maps, we estimated a current population of 1,377,629 (90%CI 1,115,256–1,640,314) Wood Thrush males in eastern Canada.

Step 4 Forecast future distributions and population sizes

For Canada Warbler, we chose two management units identified from GWR models: (1) the Alberta-Pacific Forest Industries Inc. Forest Management Agreement Area (Al-Pac

Table 1 The relative importance, range and direction of effect of the six most important variables predicting density of each species in a management unit

Species	Management unit	Predictor	Relative importance	Spatial scale	Predictor value range	Direction of effect
Canada Warbler	Alberta	CTI	27	250 m	0–15	(−)
		Land occupied by birch*	11	750 m	0–100%	(+)
		Land occupied by aspen*	10	250 m	0–100%	(+)
		Land occupied by tamarack*	9	250 m	0–100%	(+)
		Land occupied by seismic lines	9	Local	0–100%	(+)
		Land occupied by power lines	7	Local	0–100%	(−)
Canada Warbler	Northern Nova Scotia	Land occupied by red pine*	21	750 m	0–100%	(+)
		Land occupied by red maple*	10	750 m	0–100%	(−)
		CTI	8	750 m	0—10	(+)
		Land occupied by birch*	8	750 m	0–100%	(−)
		Land occupied by balsam fir*	7	750 m	0–100%	(+)
		Land occupied by red spruce*	6	750 m	0–100%	(+)
Wood Thrush	Eastern Canada	Land occupied by swamp	22	150 m	0–100%	(+)
		Land occupied by shrubland*	18	2000 m	0–100%	(−)
		Land occupied by deciduous forest*	10	150 m	0–100%	(+)
		Within 125 m of major road	10	Local	Yes=1/no=0	(+)
		Within 125 m of any road	8	Local	Yes=1/no=0	(−)

Relative importance of predictors is a percentage (number of times each predictor is selected in the BRT's trees, rescaled so that the importance of all predictors adds up to 100) and spatial scale denotes the distance within which effect of the predictor had the strongest influence on density (local=pixel)

CTI compound topographic index

* Predictors whose values were allowed to vary within climate change and land use scenarios in Step 4

FMA) in the northeast of the Alberta management unit (Fig. Appendix S3.1) and (2) the northern Nova Scotia (nNS) management unit that we used for BRTs in Step 3 (Figs. 3, Appendix S3.2). These are data-rich areas with strongly contrasting habitats and land uses. We used results of published simulations of land cover change resulting from forest harvesting and climate change for the Al-Pac FMA (Cadieux et al. 2020) and equivalent unpublished simulations for nNS (details in Appendix S3). Scenarios in both management units were run using LANDIS-II (Scheller and Mladenoff 2004; Scheller et al. 2007). From each simulation, we generated forecasting scenarios based on combinations of climate change intensity (no change, moderate, and high levels of climate warming) and varying levels of tree biomass removal from forest harvesting (Tables Appendix S3.1, S3.2). A total of 9 simulation scenarios were developed for Canada Warbler in the Al-Pac FMA and 18 in nNS.

In the Canada Warbler scenarios, climate change had stronger, more negative effects than harvest on coniferous forest biomass in Alberta; however, deciduous forest biomass also declined over time with a warming climate in Alberta (Appendix S3; Fig. Appendix S3.1). In contrast in Nova Scotia, negative impacts of climate change were stronger for balsam fir (*Abies balsamea*) than other conifers and deciduous forest was predicted to expand at the expense of coniferous forest with a warming climate in eastern Canada (Appendix S3; Fig. Appendix S3.2) (Taylor et al. 2017; Boulanger and Pascual Puigdevall 2021).

Large declines in habitat for Canada Warbler were projected for the Alberta study area. We estimated the 2019 population size (based on the assumption that habitat is limiting, and on estimated carrying capacity of habitat) for the LANDIS-simulated area in northeastern Alberta to be 38,466 Canada Warblers (90%CI 24,597–59,886). In Alberta, population sizes in 2100 varied from 61% less (best-case: baseline climate scenario, no harvest) to 73% less (worst-case: RCP 4.5 with 0.6% annual harvest rate) than the 2019 population. Canada Warbler habitat declined with both increasing harvest rate and a warming climate (Table Appendix S3.3).

An increase in Canada Warbler habitat was projected for 17 of 18 future scenarios in Nova Scotia between 2019 and 2100; however, the degree of projected, habitat-mediated population growth was smaller under the RCP 4.5 and RCP 8.5 climate scenarios than under baseline climate conditions (Appendix S3). For Canada Warbler, we estimated the 2019 population size for the LANDIS-simulated area in northern Nova Scotia to be 38,282 males based on the mean predicted values across bootstrap replicates (90%CI 21,198–55,367). Projected potential population sizes in 2100 ranged from 1% less (worst-case: RCP 8.5 scenario with ecosystem-based forest management) to 73% more (baseline climate scenario, i.e., no increase in CO_2 emissions, at historic harvesting rates). Canada Warbler showed a mixed response to harvest in these scenarios (Table Appendix S3.3).

While the advisory team for Wood Thrush identified a single management unit across provinces in Step 2 and while we ran models within this management unit in Step 3, we used output from pre-existing, unpublished land cover forecasting scenarios run separately in each of southern Quebec, southern New Brunswick and southern Nova Scotia to project future density and distribution of Wood Thrush in each of those provinces separately (based on LANDIS-II simulations; Appendix S3, Table Appendix S3.1; Leston 2022). No pre-existing LANDIS-II simulation results were available for southern Ontario, so we used the ALCES Online simulator (Carlson et al. 2014; https://www.online.alces.ca/) to project forest composition and age from 2020 to 2070 under forest harvesting and other disturbances with baseline climate, without projecting changes in climate or succession and spread of individual tree species. As for Canada Warbler in the Al-Pac FMA and nNS, there were multiple available LANDIS-II simulations available for Wood Thrush in
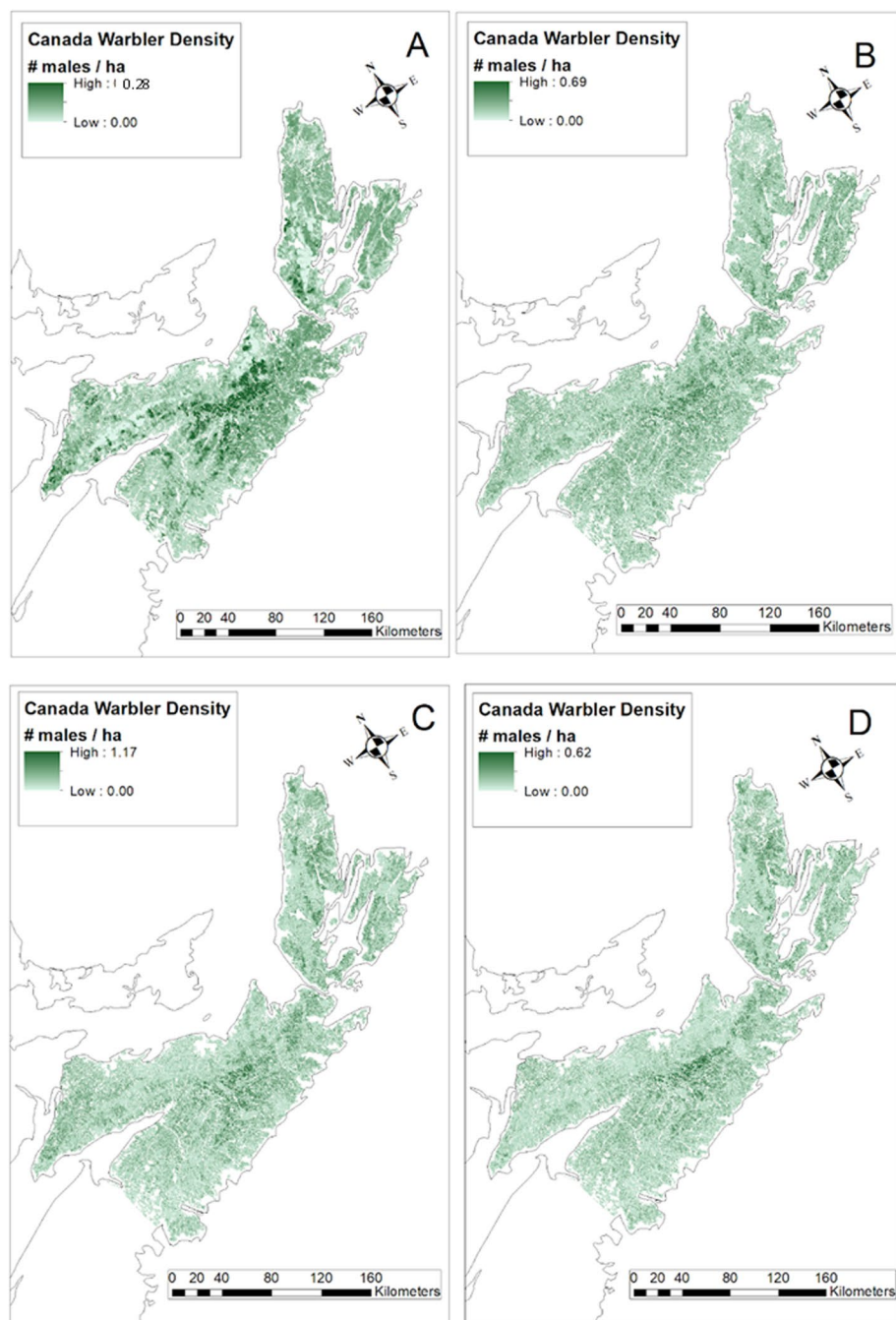
Fig. 3 Predicted distribution of Canada Warbler within the LANDIS-II scenarios in the northern Nova Scotia management unit used in regional modeling, Canada. **A** current distribution, as of 2019. **B** Distribution in 2100 under the best-case scenario. **C** Distribution in 2100 under the medium-case scenario. **D** Distribution in 2100 under the worst-case scenario

Quebec, New Brunswick, and Nova Scotia, but there was only a single available ALCES Online scenario to use for Wood Thrush in Ontario (Appendix S3).

In the Wood Thrush scenarios, as in the Canada Warbler scenarios run in northern Nova Scotia, there were larger negative impacts of climate change than harvest on biomass of coniferous tree species, primarily balsam fir, while biomass of deciduous tree species generally increased with a warming climate (Appendix S3; Figs. Appendix S3.3, S3.4).

We estimated a current population of 510,438 (90%CI 299,868–721,010) Wood Thrush males in Ontario, 612,380 (90%CI 577,207–647,552) in Quebec, 169,926 (159,611–180,242) in New Brunswick, and 71,533 (66,106–76,960) in Nova Scotia (Appendix S2; Table Appendix S3.1). We projected Wood Thrush increases under all land-use and climate change scenarios run in Quebec (91–109%), New Brunswick (54–171%), and Nova Scotia (179–276%) (Appendix S3; Table Appendix S3.3). There were smaller increases in Wood Thrush habitat with harvest and larger increases with warming climate in Quebec and larger increases in Wood Thrush habitat with both harvest and warming climate in Nova Scotia. We also projected a 22% increase—albeit non-significant with high uncertainty—within the single ALCES Online scenario run in Ontario (Appendix S3; Table Appendix S3.3).

Step 5 Candidate critical habitat identification by spatial prioritization

In northern Nova Scotia, 7, 19, 35 and 84% of the total study area (2,610,300 ha) would be required to maintain 50, 75, 90 and 100% of the current Canada Warbler population (32,283 males), respectively, assuming that habitats are at carrying capacity (Fig. 4; Appendix S4; Fig. Appendix S4.1). The best- and medium-case scenarios projected an increase in the Canada Warbler population by 2100 (73% and 20% increases, respectively), while the worst-case scenario predicted a negligible decrease (< 1% of current population). The corresponding Zonation prioritization scenarios—which rank locations based on both current density and predicted density in a particular future scenario—estimated that less land would need to be conserved to maintain 50, 75, 90 and 100% of the current Canada Warbler population (best-case: 2, 4, 8, and 64% of the study area; medium-case: 2, 4, 9 and 54%; worst-case: 2, 4, 9 and 66%, respectively) (Appendix S4; Fig. Appendix S4.1). Areas with the highest projected densities and the top 50% of the priority areas were mostly inland and south of Cape Breton Island (Fig. 5; Appendix S4).

In northeastern Alberta, 9, 19, 32 and 77% of the total study area (5,103,581 ha) would be required to maintain 50, 75, 90 and 100% of the current Canada Warbler population (35,592 males) under current climate conditions (Appendix S4; Fig. Appendix S4.2). However, as Canada Warbler was projected to decline to under 50% of its current population in all Alberta scenarios, at best, 41.5% of the current population could be maintained by habitat protected in 1.7% of the landscape (the best-case scenario). Areas with the highest predicted densities and the top 50% of the priority areas were mostly concentrated along the Athabasca River in north-eastern Alberta (Appendix S4; Fig. Appendix S4.3).

Considering only current Wood Thrush habitat, maintaining 50, 75, 90 and 100% of the current Wood Thrush population required 15, 39, 66, and > 99% of the Quebec study area; 18, 42, 68 and > 99% of the New Brunswick study area; and 18, 43, 67 and > 99% of the Nova Scotia study area. When Zonation scenarios considered both current habitat and future (2100) habitat in each province's LANDIS-II scenarios, less land was required (Appendix S4; Fig. AppendixS4.4–12).
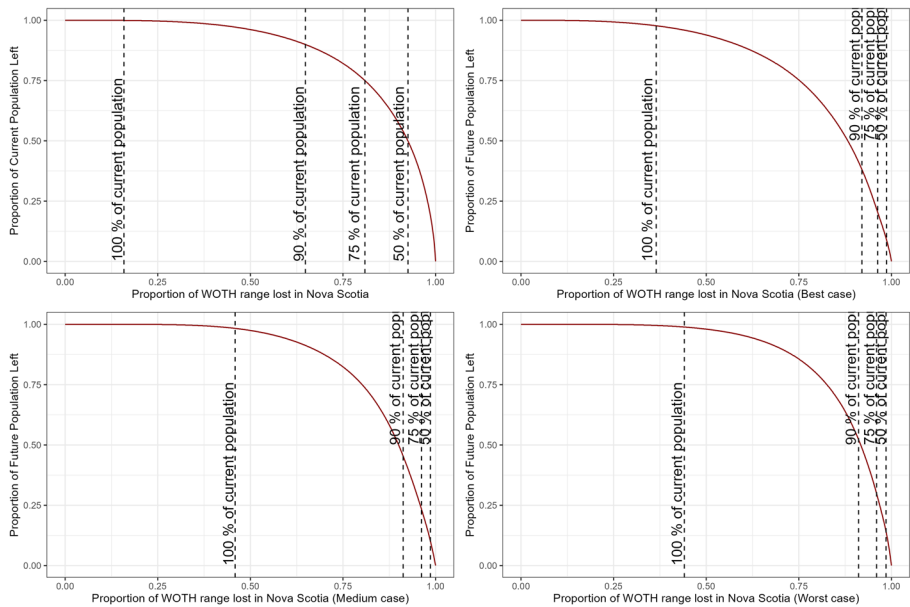
Fig. 4 Runtime plots showing the proportion of the current and future Canada Warbler population remaining in its current range in northern Nova Scotia as lands (250 m cells) are removed from consideration for conservation or management as important Canada Warbler habitat, under four Zonation scenarios. Zonation scenarios: Current = based on current population density alone; Best = based on current density + 2100 population from the best-case LANDIS-II scenario; Medium = based on current density + 2100 population from the medium-case LANDIS-II scenario; Worst = based on current density + 2100 population from the worst-case LANDIS-II scenario. As the 2100 population was projected to be higher than the current population in northern Nova Scotia, less land was required to maintain various percentages of the current population levels, when future distribution of the Canada Warbler was also used to prioritize lands as important habitat. Since population projections were similar across different LANDIS-II scenarios, the amount of land that can be removed barely differed in Zonation scenarios based on the best, medium, and worst-case scenarios

Combining results from separate Zonation exercises run in western and eastern Ontario (29,726,350 ha), when only current Wood Thrush habitat was considered, 22, 46, 70 and > 99% of land within the Wood Thrush range in Ontario would have to be prioritized for protection or management to maintain 50, 75, 90 and 100% of the current Wood Thrush population (510,438 males). When both current and future habitat in the single ALCES Online scenario was also considered, the Zonation analysis suggested that 8, 19, 32 and 69% of the Wood Thrush range in Ontario would have to be prioritized to maintain 50, 75, 90 and 100% of the current Wood Thrush population circa 2070 (Appendix S4; Figs. Appendix S4.13, S4.14).

Discussion

There are many challenges limiting our ability to effectively identify a species' current and future critical habitat. Wide-ranging species pose unique challenges for critical habitat identification given variation in data availability and habitat relationships over large areas. These challenges are exacerbated in dynamic landscapes, and under a changing climate.
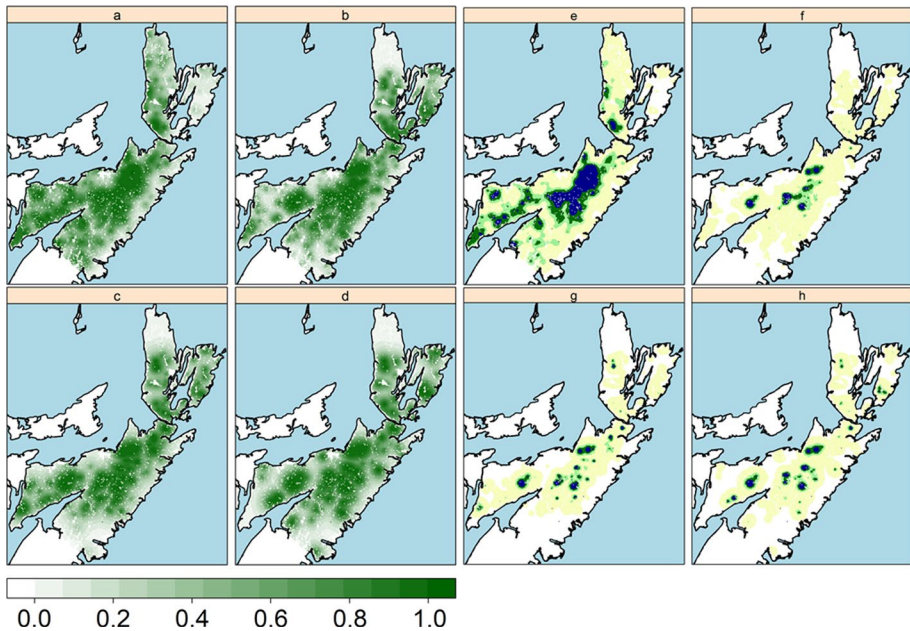
Fig. 5 Priority areas for conservation of Canada Warbler in northern Nova Scotia under four scenarios. Maps a-d indicate priority rankings (0 = lowest priority and 1 = highest priority) based on **a** current distribution, **b** current + best-case 2100 distribution, **c** current + medium-case 2100 distribution and **d** current + worst-case distribution in LANDIS-II scenarios, whereas colors in e–h indicate the area necessary to maintain specified percentages of the 2019 population under the **e** current, **f** best-case, **g** medium-case and **h** worst-case scenarios. In panels e–h, areas colored in blue, blue + dark green, blue + dark green + light green, and blue + dark green + light green + yellow indicate the cumulative areas necessary to maintain up to 50, 75%, 90%, and 100% of the current population, respectively. White areas do not contribute meaningfully to maintenance of the current population (i. e., removal of these pixels removes habitat for ~0% of current population)

We presented an approach that addresses these challenges. Although we applied this framework to two wide-ranging species in Canada, our framework can be adapted to focus on other wide-ranging species around the world. We discuss the application of the framework below using the results of our case studies.

Our GWR models in Step 2 showed that Canada Warbler demonstrated spatial variation in habitat associations across Canada, consistent with Crosby et al. (2019), but that Wood Thrush did not, possibly due to its smaller distribution in Canada. Our BRT models in Step 3 corroborated previous findings that Canada Warbler used older deciduous forests within varied terrain in Alberta and wet coniferous forests in Nova Scotia, whereas Wood Thrush used older deciduous forest with some swamp and shrublands in eastern Canada. Coniferous forests used by Canada Warbler in the Maritimes, along with mixedwood forest types used by this species elsewhere in eastern Canada may decline with global warming (Taylor et al. 2017; St-Laurent et al. 2022). Deciduous forests used by Canada Warbler in western Canada and by Wood Thrush in eastern Canada may increase with warming (Taylor et al. 2017), although older deciduous forests may increase more in the absence of harvest (Cadieux et al. 2020). Suitable habitat for Canada Warbler may expand with anthropogenic disturbances (e.g., wood harvest) when

they create and or maintain regenerating stands with dense shrub understory (COSE-WIC 2008). Beyond supporting identification of critical habitat, spatial outputs from density models and prioritization exercises may be useful in forest management or other forms of land-use planning.

Our framework can be used to evaluate not only current habitat needs, but also future changes to habitat resulting from natural or human disturbance with or without climate change. Land-use scenarios projected that populations of Canada Warbler would respond differently to timber harvest across its range: negatively in Alberta and generally positively in Nova Scotia, although we note that: (1) in the Alberta scenarios, habitat restoration and alternative harvest strategies to clear-cutting were not considered; (2) in Nova Scotia, the forested wetlands used by Canada Warbler are not generally targeted for harvest, but are not properly captured in the wetland inventory that would otherwise provide protective measures afforded to other wetlands (Nova Scotia Wetland Conservation Policy 2019). The same scenarios projected less habitat for Canada Warbler in both regions under a warming climate, consistent with projected decreases in coniferous habitats in eastern (Taylor et al. 2017; Tremblay et al. 2018; Boulanger and Puigdevall 2021) and average forest stand age in western Canada (Cadieux et al. 2020). LANDIS-II scenarios run in Quebec, New Brunswick and Nova Scotia projected that Wood Thrush would increase in those provinces, particularly with moderate climate warming (Leston 2022; Appendix S3). The latter results are consistent with projected increases in deciduous forest growth rates along with declines in coniferous forests (Taylor et al. 2017; Boulanger and Puigdevall 2021). Our single Ontario land-use scenario in ALCES Online suggested a negligible increase in Wood Thrush abundance would occur between 2020 and 2070. Although analyses in Steps 4 and 5 suggested that long-term protection of sufficient habitat for current populations is feasible for Canada Warbler and Wood Thrush in eastern Canada (but will be difficult for Canada Warbler in Alberta), further scenarios involving alternative harvest and restoration strategies should be considered. The incorporation of future distributions into conservation planning exercises also could enable critical habitat to be dynamically identified, allowing for the movement of critical habitat locations over time. Our framework allows the dynamic nature of habitat/climate change to be considered beforehand in areas that are selected as critical habitat. Areas that are predicted to support species now and over time would be ranked as particularly important to protect as refugia.

Locations that receive higher ranks in Step 5 of the framework would have stronger support for designation as critical habitat required for species' recovery. Not only do sites with higher ranks generally support higher current (and optionally, future) densities or occupancy of species, but locations can optionally be ranked higher if they are closer to or clustered with other optimal habitat for species at risk. Ranking locations this way minimizes fragmentation of the best-ranked habitats, which could reduce negative effects of fragmentation on habitat quality, reproductive success, and survival of species in critical habitat designated from these locations, further improving the odds of species' recovery.

Given limits on resources for habitat protection of multiple species (Martin et al. 2018), useful outputs from Step 5 of the framework include runtime plots showing how much additional land is required to achieve a certain conservation target. Runtime plots from our Zonation exercises suggested a point of diminishing returns beyond which the amount of land required to protect or manage for 90% of a population target sharply increases. Although we have not done so in this paper, Zonation exercises can be configured to calculate the financial cost of achieving a specific conservation target. Where multiple species at risk co-occur, Zonation can be used to optimize protection for more species at risk (Moilanen et al. 2014).

Our framework was designed to support critical habitat identification for wide-ranging species that may use habitats differently across their ranges, although steps 1 and 3–5 may be applied to species with small ranges and little or no a priori evidence of differential habitat selection. Spatial patterns of habitat use for some species may be poorly known due to poor survey coverage in parts of the species' range that are relatively remote and inaccessible to humans. BBS data is one of the few comprehensive avian monitoring datasets with extents approximating the national ranges of species. However, habitat representation in the BBS data is biased towards roadside habitats and against roadless areas (Sólymos et al. 2020). We addressed this challenge by integrating data from dozens of independent studies conducted away from major roads and population centers, along with methods that facilitate the integration of survey data collected from different survey methods (Sólymos et al. 2013), including data from autonomous recording units (Van Wilgenburg et al. 2017; Shonfield and Bayne 2017). These disparate datasets made up 30–40% of the data assembled for each species. We anticipate our framework can be effectively applied to other species and systems using this integration method with readily available data sources (e.g., eBird for birds, GBIF for other taxa). For birds at least, if abundance data are available then detectability offsets are newly available for North American species (Edwards et al. 2023).

The analytical framework presented here was designed to be flexible and to complement other sources of information available to identify critical habitat (Environment and Climate Change Canada 2014). The models used within this framework can be replaced or adapted to the species, available survey and covariate data, and ecological objectives (Guisan and Zimmermann 2000; Phillips et al. 2006; Elith and Leathwick 2009). Other forest landscape models or land use and climate change simulators other than LANDIS-II and ALCES Online (e.g., Patchworks: Leston et al. 2020; LandR: Micheletti et al. 2021; SyncroSim: Daniel et al. 2016; Norris et al. 2021; Provencher et al. 2021; Lucet and Gonzalez 2022) can also be used, depending on the species of interest, the types of disturbance affecting the species' habitat, and the type of habitat. Conservation planning tools like Zonation can be used to evaluate multiple land-use planning objectives, including specific occurrence locations (e.g., Westwood et al. 2020) or other species of conservation interest (Stralberg et al. 2018). Although critical habitat is identified in Canada from ecological needs and not socioeconomic factors (Rosenfeld and Hatfield 2006), socioeconomic factors and stakeholder objectives may also be considered as criteria within conservation planning exercises in separate initiatives by conservation partners (e.g., Canada Warbler; Westwood et al. 2020).

Our framework could also be extended by including a population growth modeling step, as our population projections were based on the amount of suitable habitat rather than population dynamics. This step would occur in tandem with or after development of GWRs (Step 2) or regional SDMs (Step 3), using locations with multiple years of surveys and marking individuals within habitats identified in the SDMs. For birds, this step could involve migratory connectivity information and full annual cycle models (Hostetler et al. 2015) to connect areas of higher threat in wintering ranges to their respective areas in the breeding range, potentially informing a prioritization of breeding range critical habitat according to "wintering ground threat". Where repeated yearly population counts, capture-recapture histories of marked individuals, and reproductive success data coincide, integrated population models (Schaub and Abadi 2011) or agent-based or individual-based models (DeAngelis and Diaz 2019) may be used to estimate population growth.

Limitations of our framework include the assumption that predicted density of species reflects the fitness and population viability of that species in the same habitats (Rosenfeld and Hatfield 2006). In studies from Alberta, higher Canada Warbler densities have been negatively associated with pairing or nesting success (Flockhart et al. 2016; Hunt et al.

2017). Density estimation in our SDMs also did not consider spatial pattern in critical habitat (e.g., patch size, distance to patches, fragmentation) and its influence on metapopulation dynamics, although our landscape-scale forest composition metrics likely reflect landscape pattern. In eastern Canada, however, Wood Thrush pairing and nesting may be successful in urbanizing forest landscapes (Phillips et al. 2005; Friesen et al. 2013). Apart from a few species, like caribou (Environment Canada 2011), data for evaluating habitat connectivity and demographic parameters throughout the life cycle is still unavailable or limited for most species at risk (Camaclang et al. 2015; Lemieux Lefebvre et al. 2018; DeAngelis and Diaz 2019). While our land-use simulations are robust, projected results are only meaningful within the limits of the scenarios. For example, the single ALCES Online scenario we ran for Wood Thrush did not consider effects of climate change on forest succession, nor did it consider non-harvest footprint. The LANDIS-II scenarios for Canada Warbler in Alberta only considered different rates of clear-cutting (Cadieux et al. 2020) but did not consider other harvest strategies or habitat restoration techniques (Leston et al. 2020). We acknowledge that limiting harvest scenarios to clear-cutting may have emphasized negative harvest effects on Canada Warbler in Alberta compared to Nova Scotia. Despite these limitations, the publicly available reproducible code to apply our framework can facilitate future re-analyses and refinements should key elements of the model need revision or should new or improved data become available.

We acknowledge that we only obtained information supporting critical habitat for Canada Warbler and Wood Thrush on their breeding grounds in Canada, because critical habitat identified under the Species at Risk Act can only be legally identified in Canada. However, Steps 3–5 can also be applied to other habitats throughout the life cycle of a species, whether or not those habitats are within a country's jurisdiction, and these habitats can be protected or managed by other means. While declines may still occur due to habitat loss and mortality on migration and wintering grounds (Céspedes and Bayly 2019; González et al. 2020), these results should assist recovery actions and habitat protection within breeding grounds in Canada, which meets the requirements of the Species at Risk Act for Canada.

Conclusion

Our framework provides a new approach for supporting critical habitat identification in an increasingly reproducible and transparent manner and may be used as a roadmap to identify concrete species' recovery measures that are robust to changes in climate and land use. Although this framework was developed in a Canadian context, it may be applied to wideranging species globally, and to conservation and ecosystem management applications beyond the identification of critical habitat.

Code availability Analysis scripts used in running and processing results from GWR models are in the repositories *GWmodel-CanadaWarbler* and *GWmodel-WoodThrush* at https://github.com/LionelLeston/. Analysis scripts used in modeling current and future distributions from LANDIS scenarios, and processing results from those LANDIS scenarios and Zonation conservation planning exercises are in repositories *SDM-riskAssessment-CanadaWarbler-Alberta*, *SDM-riskAssessment-CanadaWarbler-Alberta*, and *riskAssessment-WoodThrush-LANDIS* at https://github.com/LionelLeston/. Analysis scripts used in modeling current and future Wood Thrush distribution from ALCES Online scenarios are in *riskAssessment-WoodThrush-ALCESOnline* at https://github.com/LionelLeston/. Data used in all models is either available from the Boreal Avian Modelling Project or via links to the original data sources, provided within the folder structure of the R project in each repository.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Agriculture and Agri-Food Canada (AAFC) (2021) Annual crop inventory. https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9. Accessed 1 Jan 2021

Adve N (2014) Moving home: global warming and the shifts in species' range in India. Econ Pol Weekly 49:34–38

Ball J, Sólymos P, Schmiegelow F et al (2016) Regional habitat needs of a nationally listed species, Canada Warbler (*Cardellina canadensis*), in Alberta. Avian Conserv Ecol, Canada. https://doi.org/10.5751/ACE-00916-110210

Beaudoin A, Bernier PY, Guindon L et al (2014) Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Can J Res 44:521–532. https://doi.org/10.1139/cjfr-2013-0401

BirdLife International and Handbook of the Birds of the World (2018) Bird species distribution maps of the world. Version 7.0. http://datazone.birdlife.org/species/requestdis

Bodner K, Rauen Firkowski C, Bennett JR et al (2021) Bridging the divide between ecological forecasts and environmental decision making. Ecosphere 12:e03869. https://doi.org/10.1002/ecs2.3869

Boulanger Y, Pascual Puigdevall J (2021) Boreal forests will be more severely affected by projected anthropogenic climate forcing than mixedwood and northern hardwood forests in eastern Canada. Landsc Ecol 36:1725–1740. https://doi.org/10.1007/s10980-021-01241-7

Cadieux P, Boulanger Y, Cyr D et al (2020) Projected effects of climate change on boreal bird community accentuated by anthropogenic disturbances in western boreal forest, Canada. Divers Distrib 26:668–682. https://doi.org/10.1111/ddi.13057

Camaclang AE, Maron M, Martin TG, Possingham HP (2015) Current practices in the identification of critical habitat for threatened species. Conserv Biol 29:482–492. https://doi.org/10.1111/cobi.12428

Carlson M, Stelfox B, Purves-Smith N, Straker J, Berryman S, Barker T, Wilson B (2014) ALCES online: web-delivered scenario analysis to inform sustainable land-use decisions. In: Ames DP, Quinn NWT, Rizzoli AE (eds) Proceedings of the international congress on environmental modelling and software. International Environmental Modelling and Software Society, San Diego, pp 1–8

Carfagno GL, Weatherhead PJ (2006) Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Can J Zool 84:1440–1452. https://doi.org/10.1139/z06-124

Céspedes LN, Bayly NJ (2019) Over-winter ecology and relative density of Canada Warbler *Cardellina canadensis* in Colombia: the basis for defining conservation priorities for a sharply declining long-distance migrant. Bird Conserv Int 29:232–248. https://doi.org/10.1017/S0959270918000229

Chace JF, Faccio SD, Chacko A (2009) Canada Warbler habitat use of northern hardwoods in Vermont. Northeast Nat 16:491–500. https://doi.org/10.1656/045.016.n401

Chandler R, Hepinstall-Cymerman J (2016) Estimating the spatial scales of landscape effects on abundance. Landsc Ecol 31:1383–1394. https://doi.org/10.1007/s10980-016-0380-z

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Sci 333:1024–1026. https://doi.org/10.1126/science.12064

COSEWIC (2008) COSEWIC assessment and status report on the Canada Warbler *Wilsonia canadensis* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

COSEWIC (2012) COSEWIC assessment and status report on the Wood Thrush *Hylocichla mustelina* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

COSEWIC (2020a) COSEWIC guidelines for recognizing designatable units. https://cosewic.ca/index.php/en-ca/reports/preparing-status-reports/guidelines-recognizing-designatable-units.html

COSEWIC (2020b) COSEWIC assessment and status report on the Canada Warbler *Cardellina canadensis* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK (2000) Considering evolutionary processes in conservation biology. Trends Ecol Evol 15:290–295. https://doi.org/10.1016/S0169-5347(00)01876-0

Crosby AD, Bayne EM, Cumming SG et al (2019) Differential habitat selection in boreal songbirds influences estimates of population size and distribution. Divers Distrib 25:1941–1953. https://doi.org/10.1111/ddi.12991

Daniel CJ, Frid L, Sleeter BM, Fortin MJ (2016) State-and-transition simulation models: a framework for forecasting landscape change. Methods Ecol Evol 7:1413–1423. https://doi.org/10.1111/2041-210X.12597

DeAngelis DL, Diaz SG (2019) Decision-making in agent-based modeling: a current review and future prospectus. Front Ecol Evol 6:237. https://doi.org/10.3389/fevo.2018.00237

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Nat Acad Sci 105:6668–6672. https://doi.org/10.1073/pnas.0709472105

Dénes FV, Silveira LF, Beissinger SR (2015) Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods Ecol Evol 6:543–556. https://doi.org/10.1111/2041-210X.12333

Edwards BPM, Smith AC, Docherty TDS et al (2023) Point count offsets for estimating population sizes of North American landbirds. Ibis 165:482–503. https://doi.org/10.1111/ibi.13169

Elith J, Leathwick JR (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

Endangered Species Act (1973) https://www.govinfo.gov/app/details/COMPS-3002. Accessed 20 Feb 2023

Environment Canada (2011) Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices

Environment and Climate Change Canada (2014) Critical habitat identification toolbox: species at risk act guidance. https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/critical-habitat-descriptions/identification-toolbox-guidance.html. Accessed 20 Feb 2023

Environment Protection and Biodiversity Conservation Act (1999) https://www.legislation.gov.au/Details/C2016C00777. Accessed 20 Feb 2023

Evans M, Gow E, Roth RR, Johnson MS, Underwood TJ (2020) Wood Thrush (*Hylocichla mustelina*), version 1.0. In: Poole AF (ed) Birds of the world. Cornell Lab of Ornithology, Ithaca

Flockhart DTT, Mitchell G, Krikun R, Bayne E (2016) Factors driving territory size and breeding success in a threatened migratory songbird, the Canada Warbler. Avian Conserv Ecol 11:4. https://doi.org/10.5751/ACE-00876-110204

Fois M, Cuena-Lombraña A, Fenu G, Bacchetta G (2018) Using species distribution models at local scale to guide the search of poorly known species: review, methodological issues and future directions. Ecol Model 385:124–132. https://doi.org/10.1016/j.ecolmodel.2018.07.018

Fotheringham AS, Brunsdon C, Charlton M (2003) Geographically weighted regression: the analysis of spatially varying relationships. Wiley, Hoboken

Freeman BG, Freeman AMC (2014) Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. Proc Nat Acad Sci 111:4490–4494. https://doi.org/10.1073/pnas.1318190111

Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proc Nat Acad Sci 115:11982–11987. https://doi.org/10.1073/pnas.1804224115

Friesen LE, Casbourn G, Martin V, Mackay RJ (2013) Nest predation in an anthropogenic landscape. Wilson J Ornithol 125:562–569. https://doi.org/10.1676/12-169.1

Geldmann J, Barnes M, Coad L, Craigie ID, Hockings M, Burgess ND (2013) Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol Conserv 161:230–238. https://doi.org/10.1016/j.biocon.2013.02.018

González AM, Wilson S, Bayly NJ, Hobson KA (2020) Contrasting the suitability of shade coffee agriculture and native forest as overwinter habitat for Canada Warbler (*Cardellina canadensis*) in the Colombian Andes. Condor 122:duaa011. https://doi.org/10.1093/condor/duaa011

Goodnow ML, Reitsma LR (2011) Nest-site selection in the Canada Warbler (*Wilsonia canadensis*) in central New Hampshire. Can J Zool 89:1172–1177. https://doi.org/10.1139/z11-094

Green DM (2005) Designatable units for status assessment of endangered species. Conserv Biol 19:1813–1820. https://doi.org/10.1111/j.1523-1739.2005.00284.x

Grinder RM, Wiens JJ (2023) Niche width predicts extinction from climate change and vulnerability of tropical species. Global Change Biol 29:618–630. https://doi.org/10.1111/gcb.16486

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Habitats Directive (1992) EU measures to conserve Europe's wild flora and fauna. https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive_en. Accessed 11 Oct 2023

Hessami MA, Bowles E, Popp JN, Ford AT (2021) Indigenizing the North American model of wildlife conservation. FACETS 6:1285–1306. https://doi.org/10.1139/facets-2020-0088

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biol 12:450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hostetler JA, Sillett TS, Marra PP (2015) Full-annual-cycle population models for migratory birds. Auk 132:433–449. https://doi.org/10.1642/AUK-14-211.1

Hunt AR, Bayne EM, Haché S (2017) Forestry and conspecifics influence Canada Warbler (*Cardellina canadensis*) habitat use and reproductive activity in boreal Alberta, Canada. Condor 119:832–847. https://doi.org/10.1650/CONDOR-17-35.1

Jetz W, Sekercioglu CH, Watson JE (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. Conserv Biol 22:110–119. https://doi.org/10.1111/j.1523-1739.2007.00847.x

Langpap C, Kirkvliet J (2012) Endangered species conservation on private land: assessing the effectiveness of habitat conservation plans. J Environ Econ Man 64:1–15. https://doi.org/10.1016/j.jeem.2012.02.002

Leblond M, Boulanger Y, Pascual Puigdevall J, St-Laurent MH (2022) There is still time to reconcile forest management with climate-driven declines in habitat suitability for boreal caribou. Glob Ecol Conserv 39:e02294. https://doi.org/10.1016/j.gecco.2022.e02294

Lemieux Lefebvre S, Landry-Cuerrier M, Humphries MM (2018) Identifying the critical habitat of Canadian vertebrate species at risk. Can J Zool 96:297–304. https://doi.org/10.1139/cjz-2016-0304

Leston L, Bayne E, Dzus E et al (2020) Quantifying long-term bird population responses to simulated harvest plans and cumulative effects of disturbance. Front Ecol Evol 8:252. https://doi.org/10.3389/fevo.2020.00252

Leston L (2022) Modeling framework to support critical habitat identification for the Wood Thrush in Canada. Zenodo. https://doi.org/10.5281/zenodo.7153499

Lewis ASL, Rollinson CR, Allyn AJ et al (2022) The power of forecasts to advance ecological theory. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.13955

Lucet V, Gonzalez A (2022) Integrating land use and climate change models with stakeholder priorities to evaluate habitat connectivity change: a case study in southern Québec. Landsc Ecol 37:2895–2913. https://doi.org/10.1007/s10980-022-01516-7

Martin TG, Kehoe L, Mantyka-Pringle C et al (2018) Prioritizing recovery funding to maximize conservation of endangered species. Conserv Lett 11:e12604. https://doi.org/10.1111/conl.12604

Maxwell S, Fuller R, Brooks T et al (2016) Biodiversity: the ravages of guns, nets and bulldozers. Nature 536:143–145. https://doi.org/10.1038/536143a

Micheletti T, Stewart FEC, Cumming SG et al (2021) Assessing pathways of climate change effects in SpaDES: an application to boreal landbirds of Northwest Territories Canada. Front Ecol Evol 9:679673. https://doi.org/10.3389/fevo.2021.679673

Miller AH (1942) Habitat selection among higher vertebrates and its relation to intraspecific variation. Am Nat 76:25–35

Moilanen AJ, Pouzols FM, Meller L, Veach V, Arponen A, Leppänen J, Kujala H (2014) Spatial conservation planning methods and software: ZONATION 4.0 User Manual; Version 4; Conservation Biology Informatics Group, Helsinki, Finland, University of Helsinki

Norris AR, Frid L, Debyser C et al (2021) Forecasting the cumulative effects of multiple stressors on breeding habitat for a steeply declining aerial insectivorous songbird, the Olive-sided Flycatcher (*Contopus cooperi*). Front Ecol Evol 9:635872. https://doi.org/10.3389/fevo.2021.635872

Nova Scotia Wetland Conservation Policy (2019). https://novascotia.ca/nse/wetland.conservation.policy.asp. Accessed 20 Feb 2023

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. https://doi.org/10.1038/nature01286

Phillips J, Nol E, Burke D, Dunford W (2005) Impacts of housing developments on Wood Thrush nesting success in hardwood forest fragments. Condor 107:97–106. https://doi.org/10.1093/condor/107.1.97

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pounds AJ, Bustamante M, Coloma L et al (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161–167. https://doi.org/10.1038/nature04246

Powers RP, Jetz W (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nat Clim Change 9:323–329. https://doi.org/10.1038/s41558-019-0406-z

Provencher L, Badik K, Anderson T et al (2021) Landscape conservation forecasting for data-poor at-risk species on Western public lands, United States. Climate 9:79. https://doi.org/10.3390/cli905007

Reitsma LR, Hallworth MT, McMahon M, Conway CJ (2020) Canada Warbler (*Cardellina canadensis*), version 2.0. In: Rodewald PG, Keeney BK (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.canwar.02

Rosenberg KV, Dokter AM, Blancher PJ et al (2019) Decline of the North American avifauna. Science 366:120–124. https://doi.org/10.1126/science.aaw1313

Rosenfeld J, Hatfield T (2006) Information needs for assessing critical habitat of freshwater fish. Can J Fish Aquat Sci 63:683–698. https://doi.org/10.1139/f05-242

Species at Risk Act (SARA) (2002) https://laws.justice.gc.ca/eng/acts/s-15.3/. Accessed 20 Feb 2023

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. J Ornithol 152:227–237. https://doi.org/10.1007/s10336-010-0632-7

Scheller RM, Domingo JB, Sturtevant BR et al (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Model 201:409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation and application. Ecol Model 180:211–229. https://doi.org/10.1016/j.ecolmodel.2004.01.022

Shonfield J, Bayne E (2017) Autonomous recording units in avian ecological research: current use and future applications. Avian Conserv Ecol 12:14. https://doi.org/10.5751/ACE-00974-120114

Shoo LP, Williams SE, Hero JM (2005) Climate warming and the rainforest birds of the Australian wet tropics: using abundance data as a sensitive predictor of change in total population size. Biol Conserv 125:335–343. https://doi.org/10.1016/j.biocon.2005.04.003

Sólymos P, Matsuoka SM, Bayne EM et al (2013) Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. Methods Ecol Evol 4:1047–1058. https://doi.org/10.1111/2041-210X.12106

Sólymos P, Toms JD, Matsuoka SM et al (2020) Lessons learned from comparing spatially explicit models and the partners in flight approach to estimate population sizes of boreal birds in Alberta, Canada. Condor 122:duaa007. https://doi.org/10.1093/condor/duaa007

St-Laurent MH, Boulanger Y, Cyr D et al (2022) Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. Sci Total Environ 838:156244. https://doi.org/10.1016/j.scitotenv.2022.156244

Stralberg D, Bayne EM, Cumming SG et al (2015a) Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: a modified refugia approach. Divers Distrib 21:1112–1128. https://doi.org/10.1111/ddi.12356

Stralberg D, Matsuoka SM, Hamann A et al (2015b) Projecting boreal bird responses to climate change: the signal exceeds the noise. Ecol Appl 25:52–69. https://doi.org/10.1890/13-2289.1

Stralberg D, Wang X, Parisien MA et al (2018) Wildfire-mediated vegetation change in boreal forests of Alberta. Canada Ecosphere 9:e02156. https://doi.org/10.1002/ecs2.2156

Taylor AR, Boulanger Y, Price DT et al (2017) Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. For Ecol Manag 405:284–294. https://doi.org/10.1016/j.foreco.2017.07.033

Taylor MFJ, Sattler PS, Evans M et al (2011) What works for threatened species recovery? An empirical evaluation for Australia. Biodivers Conserv 20:767–777. https://doi.org/10.1007/s10531-010-9977-8

Thinley P, Rajaratnam R, Morreale SJ, Lassoie JP (2021) Assessing the adequacy of a protected area network in conserving a wide-ranging apex predator: the case for tiger (*Panthera tigris*) conservation in Bhutan. Conserv Sci Practice 3:e318. https://doi.org/10.1111/csp2.318

Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68:647–657. https://doi.org/10.1046/j.1365-2656.1999.00330.x

Tremblay JA, Boulanger Y, Cyr D et al (2018) Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. PLoS ONE 13:e0191645. https://doi.org/10.1371/journal.pone.0191645

van Vuuren DP, Edmonds JA, Kainuma M et al (2011) A special issue on the RCPs. Clim Change 109:1. https://doi.org/10.1007/s10584-011-0157-y

Van Wilgenburg S, Sólymos P, Kardynal K, Frey M (2017) Paired sampling standardizes point count data from humans and acoustic recorders. Avian Conserv Ecol 12:13. https://doi.org/10.5751/ACE-00975-120113

Waples RS (1991) Definition of "species" under the endangered species Act. Application to Pacific Salmon. NOAA technical memorandum NMFS F/NWC–194. p 19

Ward MS, Simmonds JS, Reside AE, Watson JE, Rhodes JR, Possingham HP, Trezise JA, Fletcher R, File L, Taylor M (2019) Lots of loss with little scrutiny: the attrition of habitat critical for threatened species in Australia. Conserv Sci Pract: e117. https://doi.org/10.1111/csp2.117

Webber QMR, Ferraro KM, Hendrix JG, Vander Wal E (2022) What do caribou eat? A review of the literature on caribou diet. Can J Zool 100:197–207. https://doi.org/10.1139/cjz-2021-0162

Wesolowski T, Fuller RJ (2012) Chapter 3 Spatial variation and temporal shifts in habitat use by birds at the European scale. In: Fuller RJ (ed) Birds and habitat: relationships in changing landscapes. Cambridge University Press, New York, pp 63–92

Westwood AR, Lambert JD, Reitsma LR, Stralberg D (2020) Prioritizing areas for land conservation and forest management planning for the threatened Canada Warbler (*Cardellina canadensis*) in the Atlantic Northern Forest of Canada. Divers 12:61. https://doi.org/10.3390/d12020061

Whitehead H, Ford JKB, Horn AG (2023) Using culturally transmitted behavior to help delineate conservation units for species at risk. Biol Conserv 285:110239. https://doi.org/10.1016/j.biocon.2023.110239

Wilcove DS, Rothstein D, Dubow J et al (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615. https://doi.org/10.2307/1313420

Wilgenburg SLV, Mahon CL, Campbell G et al (2020) A cost efficient spatially balanced hierarchical sampling design for monitoring boreal birds incorporating access costs and habitat stratification. PLoS ONE 15:e0234494. https://doi.org/10.1371/journal.pone.0234494

Winkler K, Fuchs R, Rounsevell M, Herold M (2021) Global land use changes are four times greater than previously estimated. Nat Commun 12:2501. https://doi.org/10.1038/s41467-021-22702-2

Woo-Durand C, Matte J-M, Cuddihy G et al (2020) Increasing importance of climate change and other threats to at-risk species in Canada. Environ Rev 28:449–456

Wright SJ, Muller-Landau HC, Schipper JAN (2009) The future of tropical species on a warmer planet. Conserv Biol 23:1418–1426. https://doi.org/10.1111/j.1523-1739.2009.01337

Yannic G, St-Laurent MH, Ortego J et al (2016) Integrating ecological and genetic structure to define management units for caribou in Eastern Canada. Conserv Genet 17:437–453. https://doi.org/10.1007/s10592-015-0795-0

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