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ARTICLE

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A generalized modeling framework for spatially extensive species abundance prediction and population estimation

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Abstract

Spatially explicit estimates of species abundance and distribution are increasingly needed to support conservation planning and management across multiple spatial scales. We present a generalized modeling framework that bridges the gap between local studies and regional to national planning by compiling and harmonizing diverse datasets to predict avian abundance at fine resolution and broad extent. We applied detectability offsets to integrate point-count data from over 250,000 locations across subarctic Canada. Data were subsampled by two time periods and 16 geographic regions, and we used boosted regression trees to model the density of 143 boreal landbird species as a function of climate, vegetation composition (local [250 m] and landscape [~1.5 km]), land cover, and topography. Bootstrapped regional predictions were combined to generate density maps, region- and habitat-specific estimates, and Canada-wide population totals. We estimated ~3.56 billion breeding males (7.13 billion individuals),

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with most occurring in boreal and hemi-boreal regions. Forest generalists accounted for nearly half the total (1.57 billion males), followed by boreal specialists (1.05 billion), habitat generalists (350 million), and species associated with eastern forests (274 million), grasslands (124 million), western forests (74.7 million), wetlands (63.5 million), and Arctic tundra (17.7 million). Introduced species totaled 48.9 million breeding males. Across species, landscape-level vegetation composition explained most variation in abundance, indicating that climate effects are primarily indirect, operating through vegetation. Landscape-scale variables were critical to capturing this variation. Model classification accuracy was highest for forest- and grassland-associated species (lowest for mountain and urban species), and for the families Regulidae and Phasianidae (lowest for Bombycillidae and Paridae). This work provides a standardized, updatable, and reproducible workflow for generating spatially explicit bird abundance estimates. These products can be revised as new data become available and used to support ongoing conservation and land-use decisions.

KEYWORDS
avian density and distribution, boosted regression trees, boreal birds, data integration, species abundance models

INTRODUCTION

Human activities are causing rapid changes in the abundance and distribution of many species, creating a high degree of uncertainty around management decisions and long-term conservation planning (Polasky et al., 2011). Many countries have set ambitious conservation targets designed to reduce or prevent biodiversity loss, as outlined by the Kunming-Montreal Global Biodiversity Framework (GBF, https://www.cbd.int/gbf). To achieve these targets, certain key information needs have been identified (Buxton et al., 2021). Among these are estimates of species' population sizes and distributions at a range of extents, from local to continental. Predictive species density and distribution maps play an important role in conservation and land-use planning (e.g., Eken et al., 2004; Leston et al., 2020; Stralberg et al., 2018), in priority species identification (e.g., Carter et al., 2000), and in species recovery planning (e.g., Foin et al., 1998; Leston et al., 2024). However, a primary scientific challenge is generating these estimates at a spatial extent large enough to address national priorities and at a resolution high enough to support regional land-use and resource management planning (Carroll et al., 2022).

Abundance-based species distribution models (SDMs) (Waldock et al., 2022) offer an obvious pathway to creating spatially explicit population estimates across broad extents. SDMs have been used extensively to predict the spatial distribution of species at a range of scales (Elith & Leathwick, 2009; Engler et al., 2017), typically using probability of occurrence as the response variable. While there is a strong link between regional occupancy (occurrence extent) and abundance (Zuckerberg et al., 2009), the relationship can vary substantially among species, population sizes, and spatial extents of sampling and analysis (Freckleton et al., 2005). Therefore, occurrence may not always be a reliable surrogate for abundance (Johnston et al., 2015), especially when estimated from spatially aggregated data (e.g., counts along routes and transects rather than at point locations). Furthermore, distributions of occurrence may remain relatively stable during periods of population decline (Johnston et al., 2015; Waldock et al., 2022).

Abundance-based SDMs have significant advantages over probability of occurrence models for conservation planning (Veloz et al., 2015), including the ability to estimate population sizes (Callaghan et al., 2021; Rosenberg et al., 2019; Woodward et al., 2020); yet they have generally seen little use. Broad implementation of abundance-based SDMs is hindered by a number of challenges, especially in remote and sparsely sampled regions within heterogeneous biomes, where extrapolation may be inappropriate. In this paper, we identify five major challenges, present a generalized framework for overcoming them, and offer directions for future progress. To meet the needs of ecologists, managers, and policy-makers, we maintain that a generalized abundance modeling framework should: (1) integrate disparate data sources and survey methods to maximize the amount of information incorporated into spatial predictions (Miller et al., 2019; Pacifici et al., 2017; Sólymos et al., 2020); (2) provide reliable estimates at spatial extents and resolutions relevant to conservation planning and management decision-making (Van Wilgenburg et al., 2020); (3) be reproducible and easily updated, with a system for quickly incorporating new data and regenerating outputs (Barros et al., 2023; McIntire et al., 2022); and (4) be open-source (Barros et al., 2023) so that the methods and results can be critically evaluated and easily applied to new contexts. We use our framework to generate spatially explicit density predictions and population estimates for landbirds—that is, bird species associated with terrestrial habitats—across the subarctic Canada, with the intent that models and predictions be regularly updated. However, our framework is applicable to other taxa such as waterfowl (Adde et al., 2020, 2021; Barker et al., 2014) and to regions where extensive, coordinated monitoring programs do not exist (Moussy et al., 2022).

CHALLENGES AND OPPORTUNITIES

Developing a generalized abundance modeling framework poses several challenges, especially in remote and sparsely sampled regions. Here, we discuss recent advancements in statistics, computing, and remote sensing that have presented opportunities to overcome these challenges.

Challenge 1: Data availability

The expansion of community science programs (e.g., Cadman et al., 2007; Sauer et al., 2017; Sullivan et al., 2014) combined with an increase in open data platforms has led to a rapidly increasing volume of data available for modeling species abundance, occurrence, and distribution (La Sorte et al., 2018; Milanesi et al., 2020). In addition, technological improvements have made the use of tools for remote data collection like camera traps (Burton et al., 2015; Gilbert et al., 2021) and autonomous recording units (hereafter ARU; Gibb et al., 2019; Shonfield & Bayne, 2017; Sugai et al., 2019) increasingly affordable.

Despite increasing data availability, biases persist in spatial coverage, survey effort, and species reporting (Johnston et al., 2021), affecting the accuracy and precision of abundance and distribution estimates (Hughes et al., 2021; Sólymos et al., 2020; Van Wilgenburg et al., 2020). Within Canada, many of these sampling biases are associated with the road network. The road-based breeding bird survey (BBS, Sauer et al., 2017), for example, has limited coverage in many remote areas of the boreal forest (Machtans et al., 2014), overrepresenting upland versus wetland habitats (Van Wilgenburg et al., 2020), and underrepresenting naturally disturbed areas (Van Wilgenburg et al., 2015). In addition to habitat biases associated with the road network, data from roadless areas are important because roads directly affect the distributions of many bird species (Pankratz et al., 2017; Sólymos et al., 2020). Further, roadless areas may sustain important, landscape-level ecological processes, thereby supporting healthier populations in comparison with more degraded landscapes (Betts et al., 2022; Venier et al., 2014; Watson et al., 2018).

Even relatively well-studied taxa like birds suffer from the biases enumerated above. There is therefore a need to harmonize and integrate data from multiple data sources (Miller et al., 2019). Most landbird studies use point-count surveys (Ralph et al., 1993), a method that involves having a trained observer stand at a location and record all the birds that are detected during a set amount of time within a fixed or unlimited distance away from the count station; specific protocols differ depending on study objectives (Matsuoka et al., 2014). Given biases and gaps in existing continental-scale monitoring programs such as BBS and provincial breeding bird atlas programs, data from localized studies may be used to fill gaps in coverage and create more accurate national-level population estimates (Sólymos et al., 2020). To this end, the Boreal Avian Modeling (BAM) project, a partnership among university, government, private, and nonprofit organizations, compiled avian point count data from multiple monitoring programs and independent studies across subarctic Canada (and the northern United States) into a single repository with a common data structure (Barker et al., 2015; Cumming et al., 2010; partners and data providers listed at https://borealbirds.ca/about-us/partners-sponsors/). The BAM project was initiated to develop predictive models of the distribution of avian populations and to improve understanding of the environmental drivers of boreal birds (Cumming et al., 2010). The database has since been expanded to include analogous ARU data processed by expert human listeners via the WildTrax platform (Alberta Biodiversity Monitoring Institute, 2022).

Challenge 2: Heterogeneity in data collection protocols

When creating a harmonized database, variability in survey protocols among projects makes detectability adjustments for density estimation challenging (Matsuoka et al., 2014). Differences among datasets in survey protocols (sampling radius and count duration) and conditions (time of day, day of year, land-cover type) lead to differences in detection rates. The key components of avian detectability are considered to be availability (p), the probability that an individual bird present at the time of the survey was available for detection, either through visual or auditory cues; and perceptibility (q), the conditional probability that available birds were detected. By estimating p and q via removal models and distance sampling, respectively, Sólymos et al. (2013) developed the so-called QPAD approach to estimate survey-level statistical offsets for density (d) as a function of p, q, and survey area (a). When including these offsets in abundance models, predictions are produced in common units (i.e., in number of singing males per hectare) that can be summed across prediction areas to produce regional population estimates.

The advent of ARUs and camera traps provides the opportunity to apply similarly standardized methods to a much larger group of taxa (Cameron et al., 2020; Garland et al., 2020; Wearn & Glover-Kapfer, 2019). As with point-count and ARU data, camera traps provide the opportunity to create precalculated offsets based on site-specific survey conditions (Becker et al., 2022). Increasingly, methods are being developed to integrate information from multiple datasets by combining estimators for different data types while accommodating strengths and weaknesses of each (Miller et al., 2019; Pacifici et al., 2017, 2019).

Challenge 3: Complex population responses to environmental factors

Species distribution and abundance are determined by a complex suite of ecological processes interacting across multiple scales of space and time (Johnson, 1980; Mayor et al., 2009; Wiens, 1989). Quantifying the relationship between species distributions and environmental factors is complicated by considerations such as differing scales of effects (Crosby et al., 2023; Wiens, 1989), nonlinear responses, spatial variation in population-limiting factors (Austin, 2007; Elith et al., 2010), and cross-scale interactions among variables (Schooley & Branch, 2007). Dealing with this complexity using generalized linear models (sensu Ball et al., 2016; Sólymos et al., 2020; Westwood et al., 2019) can be time consuming and difficult to apply across species and regions. A machine learning approach utilizing boosted regression trees (BRT, Elith et al., 2008) can overcome these hurdles because it is an ensemble approach, where multiple regression trees are fit sequentially so that each tree focuses on capturing the unexplained variability from the previous trees (Elith et al., 2008). The major advantages of BRT models are that they can accept large numbers of variables, automatically handle interactions, and fit complex nonlinear relationships (De'ath, 2007). BRTs can reliably identify important predictor variables, safeguard against extreme overprediction (a common shortcoming of parametric models), and exhibit better predictive performance than many traditional modeling methods (Elith et al., 2008). This BRT approach, combined with QPAD offsets, has been used to develop bioclimatic models and predict bird distribution and abundance responses to climate change (Micheletti et al., 2021; Raymundo et al., 2024; Stralberg, Matsuoka, et al., 2015).

Challenge 4: Temporally variable landscape conditions

Another aspect of spatially explicit abundance modeling with temporally heterogeneous data is that landscape change can be rapid and widespread, especially in regions prone to extensive disturbance processes like fire and insect outbreaks (Brandt et al., 2013; Venier et al., 2014). The primary challenge in such a context is accurately linking sampling data to relevant predictor variables. The development of remotely sensed time-series data giving consistent estimates of environmental conditions across large spatio-temporal extents has helped to alleviate this issue (e.g., Beaudoin et al., 2014, 2017). With increased computer storage and processing capacity (Gorelick et al., 2017), high-resolution (30-m), LANDSAT-based vegetation data products have since become more readily available at sub-decadal time intervals and over large spatial extents (e.g., Guindon et al., 2024; Hermosilla et al., 2022; White et al., 2022).

Challenge 5: Differential habitat selection

A major and often unrecognized difficulty in modeling species distributions across large spatial extents is that a single species can display high variability in habitat relationships across its geographic range (i.e., differential habitat selection). Crosby et al. (2019) showed that regionally specific models for six migratory bird species in Canada had little predictive ability in other regions, and that failure to account for that regional variability strongly affected estimates of density and distribution. Differential habitat relationships could result from genetic differences among sub-populations, variation in biotic interactions, or changing habitat preferences with availability (Jankowski et al., 2010; Matthiopoulos et al., 2015; Peterson & Holt, 2003). It may also stem from inadequate nuance in the environmental variables that drive species abundance patterns (e.g., seasonal climate extremes vs. annual means). To account for differential habitat selection among regions, models may be developed for separate, overlapping geographic units, and then combined for mapping and population estimation purposes (sensu Fink et al., 2010). Hierarchical modeling approaches can also be used to address the different spatial scales at which environmental predictors operate (Mateo et al., 2024).

METHODS

Our generalized modeling framework is illustrated conceptually in Figure 1. We integrated avian point-count data from research and monitoring projects conducted between 1991 and 2018 across subarctic Canada (~296,000 surveys). Using regional subsamples and applying detectability offsets, we developed 32 boosted regression trees per region to model the density of 143 boreal landbird species as a function of 216 environmental covariates representing climate, local- and landscape-level vegetation composition, land cover, topography, and survey year. Average model predictions for each region were then combined to generate predictive density maps, habitat- and region-specific density estimates, and Canada-wide population estimates. We also evaluated variable importance by predictor category and evaluated model performance by taxonomic group, habitat, and region.

Study area

Our study area was the subarctic portion of Canada (Figure 2), which represents large spatial gradients of climate, landforms, soils, and land-use patterns. The boreal biome is predominant, covering approximately 552 million ha of the ~1 billion ha considered (Brandt et al., 2013). Northern boundaries were determined by mapped bird conservation regions (BCRs; Bird Studies Canada & NABCI, 2014). In our study area, where national survey grids are lacking, bird population estimates are primarily based on roadside counts from the North American Breeding Bird Survey (BBS, Sauer et al., 2017). The reliance of the BBS on roadside surveys means large parts of northern Canada and Alaska lack sufficient survey effort for reliable regional-scale

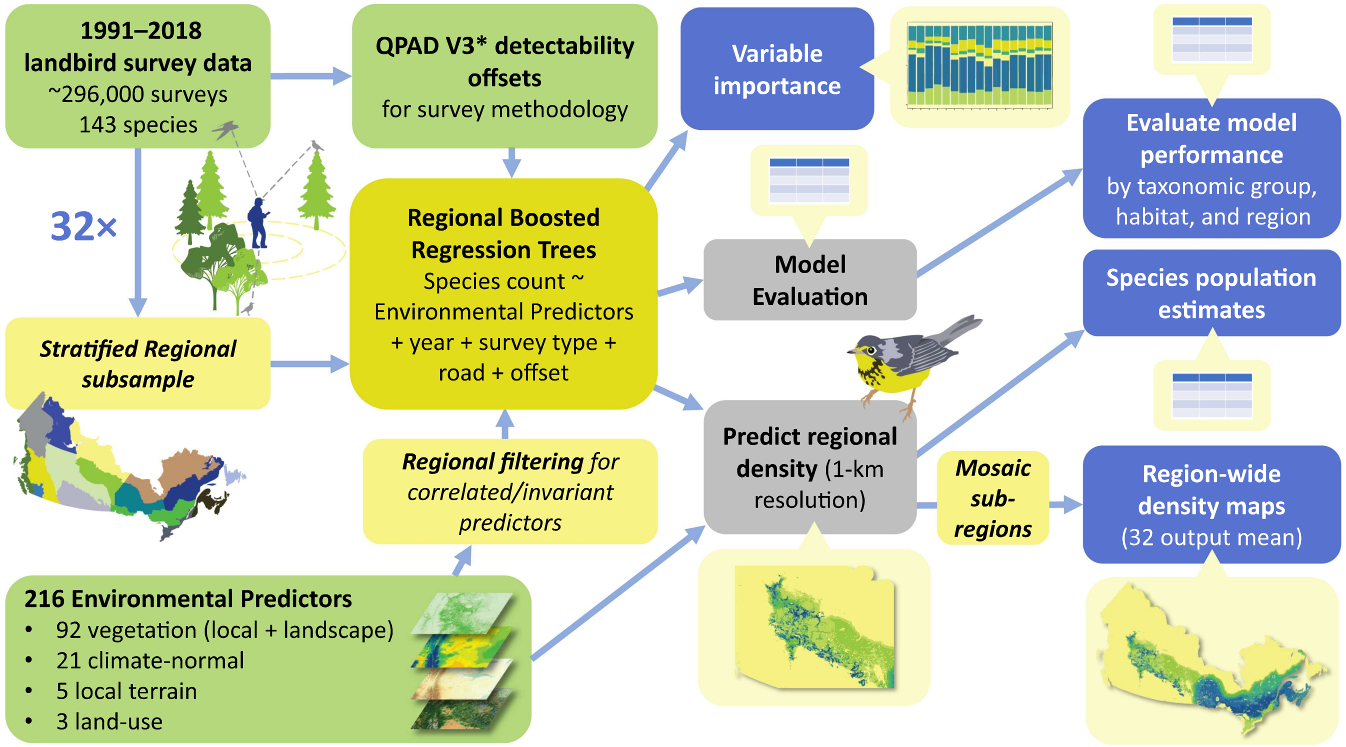

FIGURE 1 Flowchart overview of generalized modeling framework for spatially extensive species abundance prediction and population estimation. Green boxes indicate data inputs; light yellow indicates data filtering or compiling; dark yellow indicates model building; gray indicates model processing; blue indicates final products. Illustration credit: Sarah Nason.

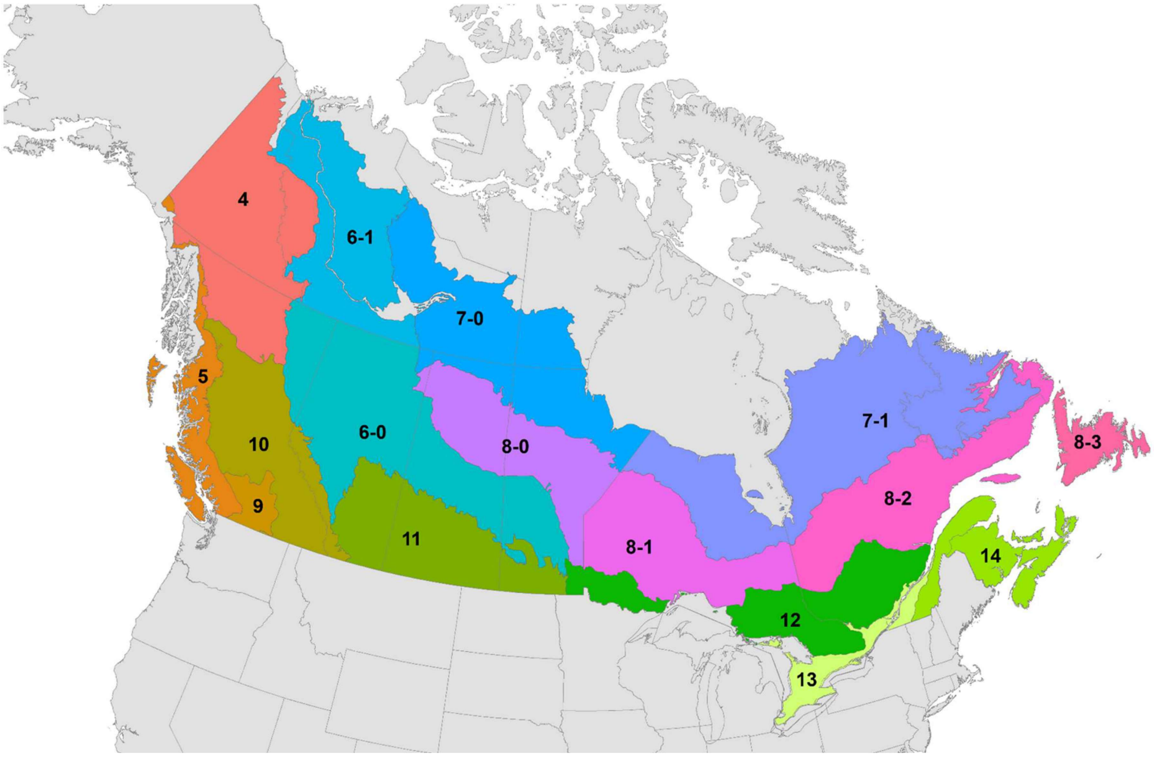

FIGURE 2 Canadian subarctic study area showing model-building regions based on a combination of bird conservation regions (BCRs) and Canadian provincial boundaries (Bird Studies Canada and NABCI, 2014). BCRs included were 4 (Northwestern Interior Forest), 5 (Northern Pacific Rainforest), 6 (Boreal/Taiga Plains), 7 (Taiga Shield and Hudson Plain), 8 (Boreal Softwood Shield), 9 (Great Basin), 10 (Northern Rockies), 11 (Prairie Potholes), 12 (Boreal Hardwood Transition), 13 (Lower Great Lakes/St. Lawrence Plain), and 14 (Atlantic Northern Forests). Hyphenated regions represent BCRs that were split for modeling purposes.

population estimates (Van Wilgenburg et al., 2020). Several initiatives have developed broad-scale sampling designs for these northern regions (e.g., Cadman et al., 2007; Handel et al., 2021; Van Wilgenburg et al., 2020), but large areas remain un-surveyed. Efforts to analyze and predict spatio-temporal density patterns at national and continental scales have therefore relied on ad hoc data assemblages. Reliable spatial prediction from ad hoc data is challenged by several factors (Cumming et al., 2010; Sólymos et al., 2013), leading to the need for application-specific data integration methods and frameworks (Fletcher et al., 2019; Isaac et al., 2020; Pacifici et al., 2017).

Avian data and subsampling

We extracted avian point-count data within our study area from version 4.0 of the BAM database, which is focused on forested regions of Canada. We supplemented this point-count database with BBS and Breeding Bird Atlas (BBA) data, as well as ARU data from the WildTrax database (Alberta Biodiversity Monitoring Institute, 2022). Point counts in our database were conducted between 1991 and 2018, with 97% done between 1997 and 2014. The database used for modeling included 256,316 sampling locations across 175 different projects, and a total of 296,061 point counts (Sólymos et al., 2025). ARU, BBS, and BBA data constituted 2.3%, 30%, and 53% of point counts, respectively.

The data were not evenly distributed either spatially or temporally, with most samples and environmental representation coming from the southern portion of the study area (Figure 3). To account for this spatial and temporal imbalance in our analysis, we stratified samples by geography and year, using a 2.5 km × 2.5 km grid to define spatial clusters of data. We then created subsamples of the data by randomly selecting a single point count from each cluster in each year (130,424 grid cell × year combinations). This subsampling routine ensured that the data would not include multiple surveys from a single location in the same year.

We subdivided point-count locations into 16 BCR × province units (Figure 2; hereafter regions). Very small regions were merged as needed to maintain areas of adequate size for modeling (i.e., as an a priori GIS exercise). We developed species abundance models for the 143 landbird species for which we were able to calculate

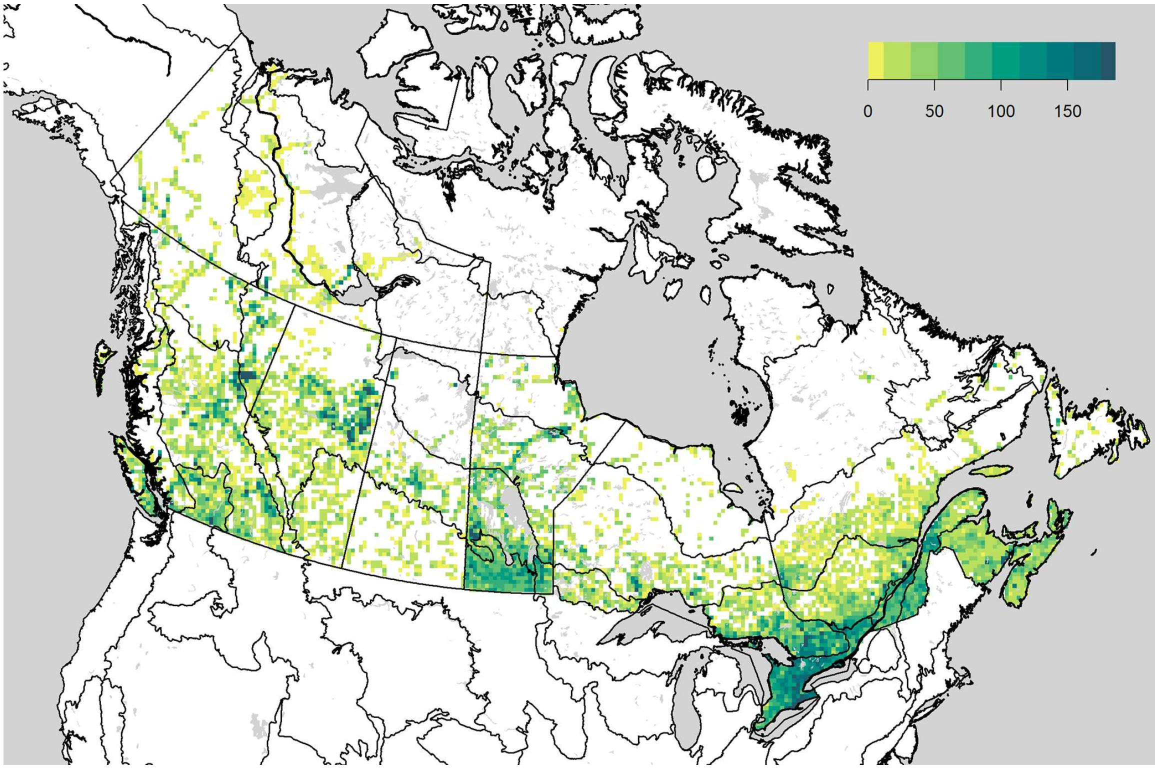

FIGURE 3 Sample point density (in number of sites surveyed per 20-km pixel). Black lines represent Bird Conservation regions in North America and provincial and territorial boundaries in Canada.

detectability offsets (sensu Sólymos et al., 2013; see https://doi.org/10.5281/zenodo.14854040; Sólymos et al., 2025). Species with insufficient point-count data for offset estimation (detected on <25 point counts; Sólymos et al., 2018) included nocturnal and crepuscular species such as owls and nightjars, which are generally not well detected with morning point-count surveys, as well as species associated primarily with aquatic rather than terrestrial habitats (e.g., waterfowl).

Environmental covariates

We assessed the influence of environmental conditions on avian density by spatio-temporally matching environmental variables (Table 1) to point counts. To account for differing landscape conditions among years, we used consistently derived vegetation data from 2001 and 2011 (Beaudoin et al., 2014, 2017). Vegetation variables were derived at a 250-m spatial resolution from *k*-nearest neighbor (*k*NN) models that were derived from forest sample plots from Canada's National Forest Inventory combined with MODIS satellite imagery, climate, and terrain data (Beaudoin et al., 2014, 2017). We matched survey data to the vegetation data closest to the survey year, so that surveys conducted in 2005 or earlier were associated with the 2001 dataset, while surveys from 2006 and later were associated with the 2011 dataset. Our vegetation variables included pixel-level (250-m scale) and landscape-level biomass of individual tree species and stand age. We calculated landscape-level variables based on a moving-window average over the Beaudoin et al. (2017) data, using a Gaussian weighting of surrounding pixels with the *focal()* function from the *raster* package (Hijmans & van Etten, 2014) in program R v. 3.4.3 (R Core Development Team, 2017), with a SD of 750 m (i.e., 68% of values within a 750-m radius; 95% of values within a 1.5-km radius).

To capture other sources of environmental variation not represented in vegetation data, we used terrain, land-use, and climate-normal variables (i.e., 30-year climate means) (Table 1). Terrain metrics, calculated using the *terrain()* function in the *raster* package for program R, were based on a 100-m digital elevation model for North America obtained from the AdaptWest project (https://adaptwest.databasin.org; Michalak et al., 2015). Elevation was derived from SRTM v4.1 data below 60° N, and ASTER GDEM v2 data above 60° N. Land-use and land-cover variables were based on the 2005 MODIS-based 250-m North American land-cover map (Commission for Environmental Cooperation, 2013). We used a binary indicator of road presence within 1 km of the point derived from global human footprint maps (Venter et al., 2016) to account for the influence

TABLE 1 List of candidate variables included in boosted regression tree models of bird abundance, grouped by variable class.

Variable class	Variable	Resolution	Reference
Time	Year of survey	N/A	N/A
Survey method	ARU (1) or human point count (0)	N/A	N/A
Climate	Annual heat: moisture	1 km	Wang et al. (2016)
Climate	Beginning of the frost free period	1 km	Wang et al. (2016)
Climate	Climatic moisture deficit	1 km	Wang et al. (2016)
Climate	Degree days (<0)	1 km	Wang et al. (2016)
Climate	Degree days (<18)	1 km	Wang et al. (2016)
Climate	Degree days (>18)	1 km	Wang et al. (2016)
Climate	Degree days (>5)	1 km	Wang et al. (2016)
Climate	End of the frost-free period	1 km	Wang et al. (2016)
Climate	Extreme minimum temperature	1 km	Wang et al. (2016)
Climate	Extreme maximum temperature	1 km	Wang et al. (2016)
Climate	Frost-free period	1 km	Wang et al. (2016)
Climate	Mean annual precipitation	1 km	Wang et al. (2016)
Climate	Mean annual temperature	1 km	Wang et al. (2016)
Climate	Mean cold month temperature	1 km	Wang et al. (2016)
Climate	Mean summer precipitation	1 km	Wang et al. (2016)
Climate	Mean warm month temperature	1 km	Wang et al. (2016)
Climate	Number of frost-free days	1 km	Wang et al. (2016)
Climate	Summer precipitation	1 km	Wang et al. (2016)
Climate	Winter precipitation	1 km	Wang et al. (2016)
Climate	Summer heat: moisture	1 km	Wang et al. (2016)
Climate	Average summer temperature	1 km	Wang et al. (2016)
Climate	Average winter temperature	1 km	Wang et al. (2016)
Climate	Temperature difference	1 km	Wang et al. (2016)
Vegetation	*Abies amabalis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Abies balsamea* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Abies lasiocarpa* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Abies* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer macrocarpa* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer negundo* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer pensylvanicum* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer rubrum* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer saccharum* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer saccharinum* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer spicatum* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Acer* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Alnus rubra* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Alnus* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Arbutus menziesii* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Betula alleghaniensis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Betula papyrifera* biomass	250 m	Beaudoin et al. (2017)

TABLE 1 (Continued)

Variable class	Variable	Resolution	Reference
Vegetation	*Betula populifolia* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Betula* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Carpinus caroliniana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Carya cordiformis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Chamaecyparis nootkatensis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Fagus grandifolia* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Fraxinus americana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Fraxinus nigra* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Fraxinus pennsylvanica* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Generic broadleaf* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Generic needleleaf* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Juglans cinerea* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Juglans nigra* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Juniperus virginiana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Larix laricina* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Larix lyallii* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Larix occidentalis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Larix* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Malus* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Ostrya virginiana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea abies* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea engelmannii* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea glauca* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea mariana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea rubra* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea sitchensis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Picea* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus albicaulis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus banksiana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus contorta* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus monticola* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus ponderosa* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus resinosa* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus strobus* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Pinus sylvestris* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Populus balsamifera* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Populus grandidentata* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Populus* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Populus tremuloides* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Populus tridentata* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Abies amabalis* biomass	250 m	Beaudoin et al. (2017)

(Continues)

TABLE 1 (Continued)

Variable class	Variable	Resolution	Reference
Vegetation	*Pseudotsuga menziesii* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Prunus serotina* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Quercus alba* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Quercus macrocarpa* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Quercus rubra* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Quercus* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Salix* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Sorbus americana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Thuja occidentalis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Thuja plicata* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Tilia americana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Tsuga canadensis* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Tsuga heterophylla* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Tsuga mertensiana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Tsuga* spp. biomass	250 m	Beaudoin et al. (2017)
Vegetation	*Ulmus americana* biomass	250 m	Beaudoin et al. (2017)
Vegetation	Broadleaf biomass	250 m	Beaudoin et al. (2017)
Vegetation	Needleleaf biomass	250 m	Beaudoin et al. (2017)
Vegetation	Unknown biomass	250 m	Beaudoin et al. (2017)
Vegetation	Branch biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Foliage biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Stem bark biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Stem wood biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Total dead biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Total live aboveground biomass (t/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Stand age (m)	250 m	Beaudoin et al. (2017)
Vegetation	Crown closure (%)	250 m	Beaudoin et al. (2017)
Vegetation	Stand height (m)	250 m	Beaudoin et al. (2017)
Vegetation	Merchantable volume (m^3/ha)	250 m	Beaudoin et al. (2017)
Vegetation	Total volume (m^3/ha)	250 m	Beaudoin et al. (2017)
Land cover	% nonvegetated	250 m	Beaudoin et al. (2017)
Land cover	% vegetated	250 m	Beaudoin et al. (2017)
Land cover	% nontreed vegetation	250 m	Beaudoin et al. (2017)
Land cover	% treed vegetation	250 m	Beaudoin et al. (2017)
Land cover	Road (yes/no)	1 km	Venter et al. (2016)
Land cover	2005 development % (landscape)	250 m	CEC (2013)
Land cover	2005 open water % (landscape)	250 m	CEC (2013)
Land cover	2005 Land-cover class	250 m	CEC (2013)
Topography	Terrain position index	100 m	Michalak et al. (2015)
Topography	Terrain ruggedness index	100 m	Michalak et al. (2015)
Topography	Slope	100 m	Michalak et al. (2015)

TABLE 1 (Continued)

Variable class	Variable	Resolution	Reference
Topography	Roughness index	100 m	Michalak et al. (2015)
Topography	Landform class	100 m	Michalak et al. (2015)

Note: Vegetation biomass variable units are (tons/ha) × 100. Vegetation variables were developed at both the local and landscape levels, for a total of 178 vegetation variables (79 × 2). Landscape-level vegetation variables were based on a Gaussian weighting of surrounding pixels, with a SD of 750 m (i.e., 68% of values within a 750-m radius; 95% of values within a 1.5-km radius).

Abbreviations: ARU, autonomous recording units; N/A, not applicable.

of roads at a landscape level. Climate-normal variables were based on 30-year mean conditions from 1981 to 2010 weather station data interpolated to a 1-km^2 resolution (https://adaptwest.databasin.org; Wang et al., 2016). In all, we considered 216 variables: 92 vegetation variables (at the pixel and landscape levels); 21 climate-normal variables; 5 local terrain variables; 3 land-use variables; survey year; roads; and survey type (human point count or ARU-based count). Prior to modeling, we screened the environmental predictor variables to eliminate constant (no variation within a region, usually due to zero values) or highly correlated (Pearson's correlation >0.9) variables to improve processing time.

Model development

We estimated species density (in number of singing males per hectare) by fitting BRT models to the point-count and environmental predictor data, using statistical offsets to account for detectability differences caused by heterogeneity in survey protocols and environmental conditions (QPAD, sensu Sólymos et al., 2013). In this approach:

$$E[Y] = \lambda = DAp(t_J)q(r_K),$$

where $E[Y] = \lambda$ is the expected count of a species during a survey, D is point-level species density, A is area sampled, $p(t_J)$ is the probability of an individual singing during the cumulative time interval t_J, given presence (availability), and $q(r_K)$ is the probability of an individual being detected, given singing, within point count radius r_K (detectability) (Sólymos et al., 2013). Thus, "QPAD" refers to different elements (q, p, A, D) of the expected count model, which can be modified according to different methodological, temporal, and environmental covariates present during a survey. The approach estimates a correction factor ($C = Apq$) for heterogeneous count data, so that $D = \lambda/C$. In our implementation, C was calculated using time-removal models to estimate p (Sólymos et al., 2018) and distance sampling models to estimate q (Buckland et al., 2001), as described in Sólymos (2016) and Sólymos et al. (2013). For point counts that used a limited radius protocol (3% of dataset, e.g., a 150-m radius), A was defined as the area of a circle with the specified radius. For point counts that used an unlimited radius protocol (97% of dataset), A was set to the effective detection radius (EDR) derived from the half normal parameter of the distance sampling model. EDR is the distance from an observer where the number of individuals missed within equals the number of individuals detected beyond, and therefore allows q to be set to 1 (Buckland et al., 2009). C was then specified as a statistical offset ($o = \log(C)$) when modeling count data: $\log(\lambda) = \log(D) + o$, where density $D =$ singing males per hectare. We used the Poisson likelihood as the loss function for count outcomes in the boosted regression trees.

In calculating offsets, we identified the best model, considering the effects of time of day (time since local sunrise) and day of year (ordinal day and days since start of local spring) on the probability of availability given presence, and the effects of tree cover (Hansen et al., 2003) and land-cover class (CEC, 2013) on the probability of detection given availability (Sólymos, 2016). Using these offsets, we then modeled D in a BRT framework as a function of multiple covariates relating to species density. We assumed that ARU detectability is similar to detectability by human observers (Yip et al., 2017). Nevertheless, we used an indicator variable to account for possible differences in effective area sampled between human counts and ARUs following Van Wilgenburg et al. (2017).

We built separate BRT models for each region (BCR × province), including overlapping 100-km buffers (within Canada only, due to the limited extent of the Beaudoin et al. (2017) vegetation data) to reduce the influence of arbitrary regional boundaries. We chose to use predefined model regions rather than systematic moving windows (e.g., Fink et al., 2010) primarily because it represents a modular approach that may be easily updated with the best available regional datasets. Moving windows were also difficult to implement given the regional variation in amounts of point count data.

We conducted the modeling as a two-step process. In the first step, we fit a 10-fold cross-validated BRT model to a single subsample from the regional dataset using the *gbm.step()* function from the *dismo* package (Hijmans et al., 2020) in program R. The purpose of this initial step was to establish the optimal number of trees without overfitting the model and to eliminate uninformative variables. We capped the number of trees at 10,000 and used a learning rate of 0.001, bag fraction of 0.5, and interaction depth of 3, as recommended by Elith et al. (2008) and consistent with Micheletti et al. (2021) and Stralberg, Matsuoka, et al. (2015). In the second step, we fit BRT models to 32 bootstrapped subsamples (the number of processors available) of the regional data using the maximum number of trees and the subset of variables determined from the first step. Post hoc analysis indicated that the bootstrap SE for most species (73% of species × region combinations) converged to a 95% asymptote before 32 replicates (mean = 26; Appendix S1: Figure S1). Code and data for ongoing model development are available, with frequent updates, at https://github.com/borealbirds/LandbirdModelsV5.

Model evaluation

We calculated validation metrics by making predictions from each of the 32 bootstrap-based BRT models for each region. Variation across bootstrapped predictions was evaluated by the overall concordance correlation coefficient (OCCC; Barnhart et al., 2002; Lin, 1989). OCCC is the product of measures of the overall precision (how far each observation deviates from the best fit line) and the overall accuracy (how far the best-fit line deviates from the 1:1 line). High values represent better combined accuracy and precision.

We used the bootstrap-averaged predictions to calculate expected counts at each survey under the null model $[\lambda = \exp(\text{initial intercept estimate of the BRT}) \times C]$ and the final BRT $[\lambda = \text{estimate from all trees combined} \times C]$. These initial and final predictions were used to calculate the area under the receiver operating characteristic curve (ROC AUC, Zipkin et al., 2012) to assess classification accuracy (counts treated as detection/nondetection). We also calculated the pseudo R^2 to quantify the proportion of variance explained using a Poisson density, comparing deviance relative to the null and saturated models.

We examined factors influencing the predictive ability of our models by post hoc analyses on AUC statistics saved from each model. Prior to analysis, we converted the AUC score for each species nested within each region to a binary variable indicating whether the AUC was <0.7 (1) or exceeded 0.7 (0) based on a value of 0.7, as values above this threshold are generally seen as providing at least fair predictive ability (Carter et al., 2016). Within each region, we identified and mapped the proportion of modeled species that did not achieve AUC ≥0.7 to interpret cross-species spatial patterns in model predictive ability. In addition, we modeled the probability that models did not achieve AUC ≥0.7 using generalized linear mixed models, including model region as a random intercept and habitat affinity (Sólymos et al., 2018) and species taxonomic families (Jetz et al., 2012) as fixed effects. We fit seven competing models, including all combinations of main effects but no interactions, and selected the most parsimonious model based on corrected Akaike information criterion for sample size (AIC_c). To determine the habitat guilds and taxonomic groups that were most likely to not achieve adequate model fit, we used contrasts against the factor level for which the estimated marginal means suggested the lowest probability of not achieving the AUC threshold of 0.7.

Variable importance

Variable importance was assessed by summing percent relative influence values (Friedman & Meulman, 2003) across species and variables by thematic group and region. Thematic groups evaluated were climate normals, land cover, local vegetation, landscape vegetation, topography, time (year effect), and survey method (Table 1).

Density and population estimates

We used the resulting BRT models to make species- and region-specific density predictions to a 1-km^2 resolution raster, using recent (2011) vegetation layers. Although point-count surveys best represent hectare-scale processes and patterns, we deemed such a fine resolution unnecessary for continental-scale predictions, especially given that many key predictors had a coarser native resolution (up to 1 km^2). Thus, we applied a hundredfold scaling of model predictions with the assumption that mean densities would be maintained. To achieve this scaling, continuous inputs were resampled with bilinear interpolation to take the mean value of pixels for each variable; categorical inputs were resampled using a nearest neighbor algorithm. We set the ARU variable to 0, the year variable to 2011, and the road variable to 0, such that our predictions represented the expected number of males per ha based on a point count conducted in 2011 in off-road habitat. That is, we accounted for roadside bias through the inclusion of the road variable in our models, but we treated every pixel in the predictive process as nonroad habitat, given the 1-km^2 resolution. In this respect, we assumed that road effects are primarily a function of detectability. To the extent that roadside biases reflect real differences in abundance, our approach may result in a small over- or underestimation of total population sizes.

We generated 32 prediction rasters (1-km^2 resolution) for each species-by-region combination. When the actual bootstrap sample for a region did not contain any detections of the species, we predicted zero for that region. For each bootstrap replicate, we converted predicted density (in number of males per hectare) to abundance within each 1-km^2 cell (using $N = 100 \times D$ to scale from hectares to square kilometers) and summed over all cells in each region. Within each region, we estimated the median density by land-cover class and estimated lower and upper bounds as the 5th and 95th percentiles, respectively. Our population estimate for the total number of males was the median of the bootstrap distribution, and uncertainty bounds were estimated as the 5th and 95th percentiles. We estimated the total number of breeding males by species, by region, and for groups of species associated with the same primary breeding habitat (as defined by Rosenberg et al., 2019).

Density maps

We developed national density maps for each species (in number of males per hectare) by mosaicking regional predictions (including 100-km buffer zones) for each bootstrap replicate of the full study extent. We used overlapping buffer zones to create a smooth transition between the predictions of neighboring regions. This was done by producing a weighting raster for each region, the values of which increased as a function of proximity to the region's core (pixel weight = distance of focal pixel to nearest edge/maximum pixel distance to edge; 0-1). Combined predictions were then produced as the mosaicked, weighted sum of each regional prediction divided by the mosaicked sum of each regional weighting raster. We note that calculating mean density and abundance from these distribution maps leads to slightly different population estimates than those using the bootstrap-based aggregation approach described above.

In some cases, mosaics of the expected values created sharp transitions in predicted density across some boundaries coinciding with large regional differences in density. This variation in density across a large study area presented challenges for mapping, and so we balanced mapping detail with aesthetics to create smoother transitions across boundaries. To make national scale maps, we began by using expected density within the model-building area as a presence/absence threshold (Stralberg, Bayne, et al., 2015), with areas of density below this mean density ("absence") represented in light yellow. However, we found that this approach did not adequately describe the abundance patterns of all species, especially those that are widely distributed. So we adjusted the minimum thresholds according to visual alignment with known range limits. If maps based on these mean density thresholds resulted in a nontrivial number of occurrence locations mapped as absence, we sequentially adjusted these thresholds downward until that was no longer the case (starting with 0.05, then 0.01, then finally 0.001). Equal-interval legends, capped at the 99th percentile of predictions, were used to classify remaining density predictions for mapping. We note that these manipulations altered the appearance of the maps, but did not change the predicted densities. We emphasize that categorical map legends necessarily introduce subjectivity into the interpretation of species' distribution and abundance patterns and note that the legend breaks we used may not be the best ones for all mapping needs. Maps and model results are available at https://doi.org/10.5281/zenodo.14854040 (Sólymos et al., 2025).

RESULTS

We considered 143 species and 16 regions, for a total of 2288 potential species × region combinations. Boosted

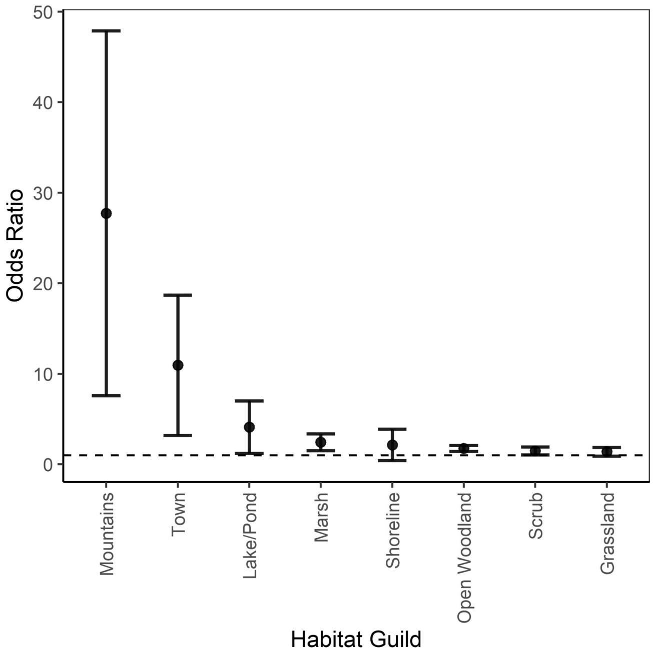

FIGURE 4 Contrast in the odds (mean odds ratio ± SE) that models for the given habitat guild would show poor predictive ability based on area-under-the-receiver-operating-characteristic-curve (AUC) values <0.7. Dashed reference line at unit odds ratio represents no difference in estimated probabilities of poor model performance, with values >1 indicating a higher probability of showing poor model performance compared to the forest-inhabiting reference group.

regression-tree models were not run for 420 (18%) combinations with no detections. Models could not be fit due to insufficient data for an additional 291 (13%) combinations of species and regions. Abundance estimates were assigned 0 values for all 711 (31%) of these combinations. For the remaining 1577 (69%) species-region models that were successfully run over 32 bootstrap replicates, species prevalence rates (proportion of surveys with species detections) ranged from <0.0001 to 0.37.

Model evaluation

Models varied widely with respect to validation metrics. Pseudo-R^2 values ranged from <0 (due in part to influential density offsets) to 0.810 (median = 0.14). OCCC values ranged from 0.08 (worst) to 0.996 (best), with a median of 0.91; and AUC values ranged from 0.43 (worst) to 0.98 (best) with a median of 0.79 (https://doi.org/10.5281/zenodo.14854040; Sólymos et al., 2025).

Our most parsimonious model for the probability of achieving at least fair predictive ability (AUC ≥ 0.7) included migratory guild, habitat guild, and taxonomic family. Neotropical migrants were the migratory guild least likely to have poor predictive ability (estimated marginal mean [hereafter EMM] = 0.30, SE = 0.06), followed by residents (EMM = 0.34, SE = 0.09), short-distance migrants (EMM = 0.46, SE = 0.06) and nomadic species (EMM = 0.58, SE = 0.11). Predictive ability did not differ between residents and neotropical migrants (odds = 1.18, SE =0.54). In contrast, nomadic species were 3.2 (SE = 1.4) and short-distance migrants were 1.9 times (SE = 0.4) more likely than neotropical migrants to have poor predictive ability. Forest-dwelling species were the least likely to have poor predictive ability (EMM = 0.19, SE = 0.03) and most habitat guilds did not differ substantially from forest birds (Figure 4). Three habitat guilds that were more likely to have poor predictive ability than forest birds were species inhabiting lakes/ponds, which were 4.1 times (SE = 2.9) more likely to have poor

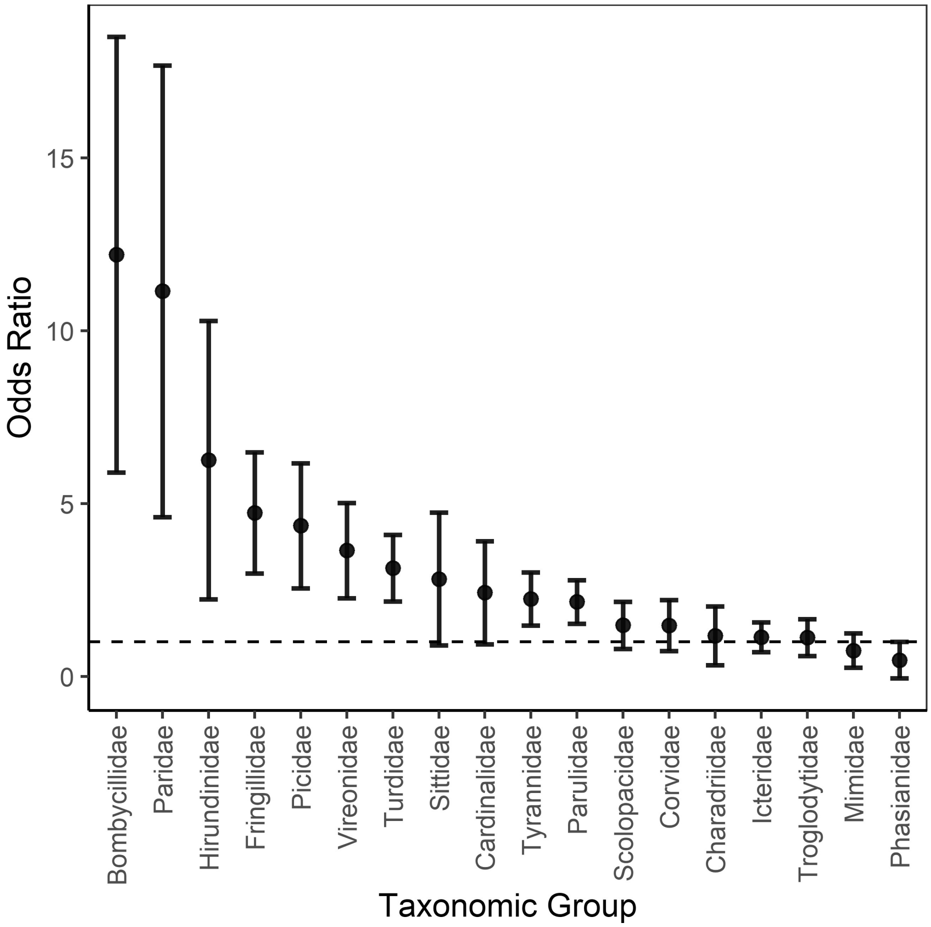

FIGURE 5 Contrast in the odds (mean odds ratio ± SE) that models for the given taxonomic group would show poor predictive ability based on area under the receiver operating characteristic curve (AUC) values <0.7. Dashed reference line at unit odds ratio represents no difference in estimated probabilities of poor model performance, with values >1 indicating a higher probability of showing poor model performance compared to the Regulidae (kinglets) reference taxonomic group.

predictive ability; species inhabiting towns, which were 10.9 times (SE = 7.8) more likely; and species inhabiting mountains, which were 27.7 times (SE = 20.2) more likely to have models with poor predictive ability compared to forest birds. Taxonomically, species in the kinglet family (Regulidae) were the least likely to have models with poor predictive accuracy (EMM = 0.13, SE = 0.09). Model performance differed among taxonomic groups (Figure 5). In particular, waxwings (Bombycillidae) were 26.3 (SE = 23.4) times, tits (Paridae) were 24.3 (SE = 22.4) times, and finches (Fringillidae) were 10.3 (SE = 8.3) times more likely than the kinglets to have models with poor predictive performances based on AUC. Overall, poor model fit tended to be most prevalent in species and region combinations in the northwestern and northeastern extremes of the study area (Figure 6).

Variable importance

Across species and regions, landscape-level (up to ~1.5 km) vegetation metrics comprised the most influential set of predictors, followed by either local vegetation (250 m) or climate normals (1 km), depending on the region (Figure 7; https://doi.org/10.5281/zenodo.14854040; Sólymos et al., 2025). Land cover, topography, time, and survey method, in that order, were consistently the next most influential groups of predictors across regions. The influence of landscape-level vegetation metrics was highest relative to the influence of climate variables in region 12 (Boreal Hardwood Transition, Figure 7). The influence of climate variables was highest relative to landscape-level vegetation metrics in region 7-0 (Taiga Shield and Hudson Plains, West). Compared to other regions, land cover had the largest relative influence in region 5 (Northern Pacific Rainforest). Survey method had low relative importance across regions, but had non-negligible importance in the regions for which ARU data were used (regions 6-0, 8-0, and 8-1).

In terms of individual variables, the most important variable overall was survey year, followed by average summer and winter temperature, respectively. Least important overall was the binary road variable.

Population estimates

Population estimates for all of subarctic Canada indicated that the 10 most abundant species made up 35.6% of the total landbird population, and were, in descending order,

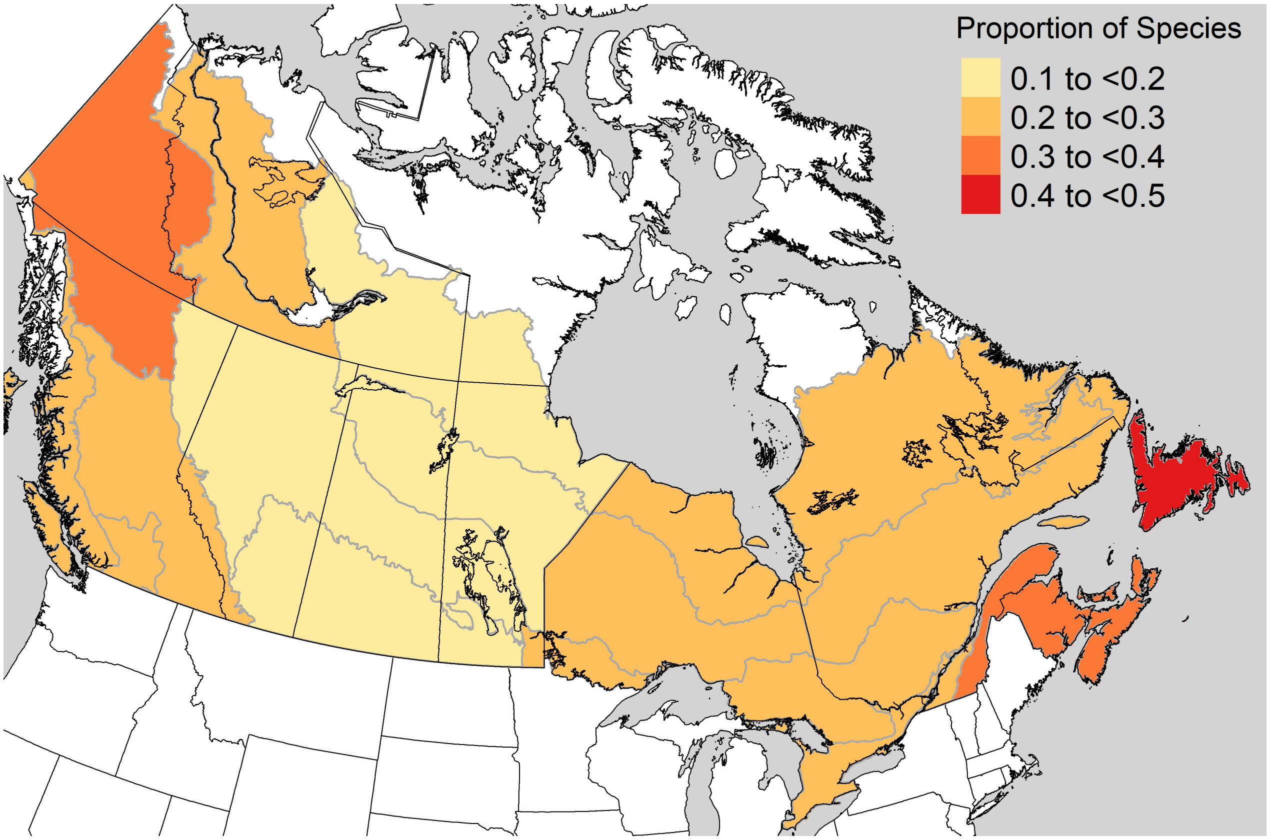

FIGURE 6 Proportion of modeled species with poor model fit (area under the receiver operating characteristic curve [AUC] < 0.7) by model region (gray lines, see also Figure 1).

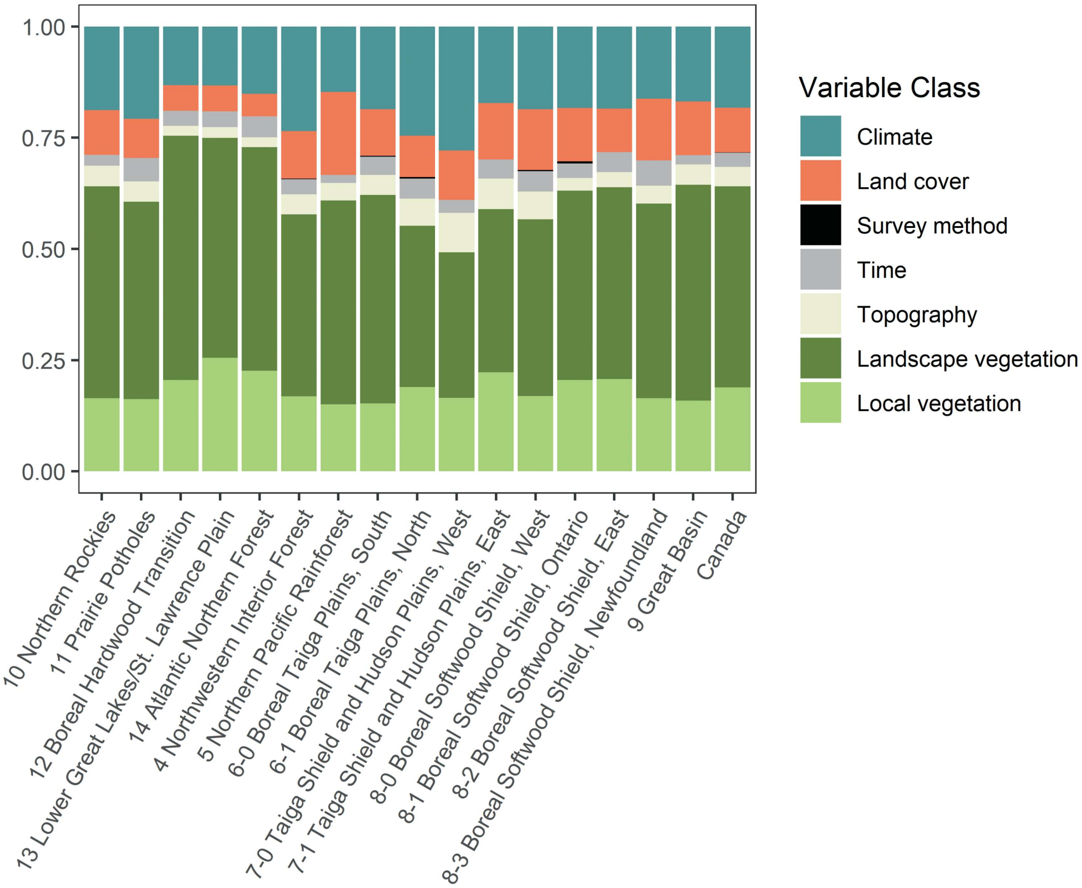

FIGURE 7 Relative importance of variable classes for explaining variation in 143 landbird densities in 16 regions, and all of Canada, from boosted regression tree models. See Table 1 for specific variables included in each group.

Yellow-rumped Warbler (*Setophaga coronata*), Dark-eyed Junco (*Junco hyemalis*), American Robin (*Turdus migratorius*), White-throated Sparrow (*Zonotrichia albicollis*), Swainson's Thrush (*Catharus ustulatus*), Tennessee Warbler (*Leiothlypis peregrina*), Pine Siskin (*Spinus pinus*), Ruby-crowned Kinglet (*Regulus calendula*), Chipping Sparrow (*Spizella passerina*), and Magnolia Warbler (*Setophaga magnolia*) (Table 2). The Yellow-rumped Warbler population was estimated at 203 million breeding males (5.7% of total landbird population), based on the mean of the bootstrap distribution (5th percentile = 199 million, 95th percentile = 209 million) (Table 2; https://doi.org/10.5281/zenodo.14854040; Sólymos et al., 2025). The total number of breeding males, across 143 species, was estimated at 3.56 billion (3.42 lower bound, 3.76 upper bound). Applying a simple pair adjustment of two would result in an estimate of 7.13 billion landbirds (6.84 lower bound, 7.51 upper bound). There is some potential for estimation bias due to our setting of the road variable to 0 for prediction. However, given the very low influence of this coarse-resolution variable, the effect does not appear to be meaningful.

Most landbirds (2.29 billion breeding males or 64%) were estimated to occur in the Boreal region, 1.01 billion breeding males in the Western Boreal region, and 1.28 billion in the Eastern Boreal and Hemiboreal regions (Figure 8). Densities in these regions were generally low, however (Figure 9). Combined densities across species were highest in the Atlantic and Great Lakes regions (Figure 9), which were estimated to contain 5% (174 million) and 3% (92 million), respectively, of the total estimated population of breeding males (Figure 8).

With respect to breeding habitat groups, forest generalists (1.57 billion breeding males) and boreal forest-associated species (1.05 billion males) had the highest predicted population sizes (Figure 8). Our predictions for the remaining habitat categories were 350 million habitat generalists, 274 million eastern forest-associated, 124 million grassland-associated, 74.7 million western forest-associated, 63.5 million wetland-associated, 48.9 million introduced, and 17.7 million Arctic tundra-associated breeding males.

Density maps

Density estimates (in number of males per hectare) often varied widely across regions and land-cover types within

TABLE 2 Estimated Canada-wide abundance (million breeding males) for all species.

Common name (scientific name)	Abundance (M males)
Yellow-rumped Warbler (*Setophaga coronata*)	203.2 (199.2, 209.4)
Dark-eyed Junco (*Junco hyemalis*)	151.1 (147.9, 155.3)
American Robin (*Turdus migratorius*)	136.6 (134.8, 139.3)
White-throated Sparrow (*Zonotrichia albicollis*)	128.1 (125.4, 130.4)
Swainson's Thrush (*Catharus ustulatus*)	122.4 (120.4, 124.2)
Tennessee Warbler (*Oreothlypis peregrina*)	115 (113, 117.6)
Pine Siskin (*Spinus pinus*)	114 (109.6, 120.5)
Ruby-crowned Kinglet (*Regulus calendula*)	113.1 (110.2, 116.4)
Chipping Sparrow (*Spizella passerina*)	108.5 (105.4, 110.4)
Magnolia Warbler (*Setophaga magnolia*)	78.05 (76.28, 80.2)
Golden-crowned Kinglet (*Regulus satrapa*)	77.92 (75.47, 80.04)
Cedar Waxwing (*Bombycilla cedrorum*)	69.59 (67.17, 72.25)
Red-eyed Vireo (*Vireo olivaceus*)	68.52 (67.58, 69.85)
Gray Jay (*Perisoreus canadensis*)	62.48 (58.57, 66.07)
Yellow Warbler (*Setophaga petechia*)	62.44 (60.72, 65)
Alder Flycatcher (*Empidonax alnorum*)	60.73 (59.22, 62.51)
Lincoln's Sparrow (*Melospiza lincolnii*)	58.66 (55.72, 60.7)
Red-winged Blackbird (*Agelaius phoeniceus*)	54.2 (53.32, 55.65)
Wilson's Warbler (*Cardellina pusilla*)	53.56 (52.08, 56.52)
American Redstart (*Setophaga ruticilla*)	52.01 (50.46, 53.5)
Orange-crowned Warbler (*Oreothlypis celata*)	51.6 (50.2, 54.1)
Hermit Thrush (*Catharus guttatus*)	51.23 (50.2, 53.15)
Savannah Sparrow (*Passerculus sandwichensis*)	46.27 (44.2, 48.63)
Least Flycatcher (*Empidonax minimus*)	45.93 (44.65, 47.04)
American Goldfinch (*Spinus tristis*)	45.76 (44.84, 46.83)
Nashville Warbler (*Oreothlypis ruficapilla*)	45.21 (44.04, 46.62)
Blackpoll Warbler (*Setophaga striata*)	42.87 (40.92, 47.28)
Black-capped Chickadee (*Poecile atricapillus*)	41.21 (40.29, 42.21)
Brown-headed Cowbird (*Molothrus ater*)	40.78 (39.87, 41.87)
Warbling Vireo (*Vireo gilvus*)	39.14 (38.43, 39.95)
Ovenbird (*Seiurus aurocapilla*)	38.82 (37.97, 39.59)
Common Yellowthroat (*Geothlypis trichas*)	38.44 (37.54, 39.58)
Song Sparrow (*Melospiza melodia*)	38.3 (37.74, 38.81)
White-winged Crossbill (*Loxia leucoptera*)	37.5 (31.89, 43.15)
Boreal Chickadee (*Poecile hudsonicus*)	36.87 (33.82, 39.52)
Clay-colored Sparrow (*Spizella pallida*)	34.37 (33.56, 35.03)
Eastern Bluebird (*Sialia sialis*)	31.83 (24.25, 69.3)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	30.31 (28.63, 32.19)
Northern Waterthrush (*Parkesia noveboracensis*)	29.06 (27.79, 29.78)
Red-breasted Nuthatch (*Sitta canadensis*)	28.54 (27.75, 29.31)
Palm Warbler (*Setophaga palmarum*)	27.71 (25.14, 28.95)
White-crowned Sparrow (*Zonotrichia leucophrys*)	27.35 (25.48, 29.22)
Fox Sparrow (*Passerella iliaca*)	27.06 (25.6, 28.09)
Red-breasted Nuthatch (*Sitta canadensis*)	28.54 (27.75, 29.31)
European Starling (*Sturnus vulgaris*)	25.64 (24.03, 27.03)
Black-and-white Warbler (*Mniotilta varia*)	25.08 (24.19, 26.14)
Brewer's Blackbird (*Euphagus cyanocephalus*)	23.11 (22.08, 24.25)
Bay-breasted Warbler (*Setophaga castanea*)	23.05 (21.32, 23.88)
Common Grackle (*Quiscalus quiscula*)	23.02 (21.84, 23.72)
Swamp Sparrow (*Melospiza georgiana*)	22.81 (22.09, 24.31)
Northern Flicker (*Colaptes auratus*)	20.94 (19.97, 21.52)
Barn Swallow (*Hirundo rustica*)	20.41 (19.57, 21.29)
Bohemian Waxwing (*Bombycilla garrulus*)	19.96 (14.6, 31.45)
Townsend's Warbler (*Setophaga townsendi*)	19.3 (18.01, 20.01)
Blue-headed Vireo (*Vireo solitarius*)	18.98 (18.04, 19.63)
House Sparrow (*Passer domesticus*)	18.16 (17.29, 19.15)
Red Crossbill (*Loxia curvirostra*)	18.14 (16.23, 20.68)
Winter Wren (*Troglodytes hiemalis*)	17.82 (16.9, 18.73)
Chestnut-sided Warbler (*Setophaga pensylvanica*)	17.18 (16.75, 17.56)
Cliff Swallow (*Petrochelidon pyrrhonota*)	16.64 (12.88, 21.13)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	16.58 (16.04, 17.12)

(Continues)

TABLE 2 (Continued)

Common name (scientific name)	Abundance (M males)
Wilson's Snipe (*Gallinago delicata*)	16.12 (15.14, 16.61)
Mourning Warbler (*Geothlypis philadelphia*)	15.95 (15.23, 16.48)
Tree Swallow (Tachycineta bicolor)	15.85 (15.02, 16.44)
Hammond's Flycatcher (*Empidonax hammondii*)	15.82 (15.12, 16.65)
Common Raven (*Corvus corax*)	15.13 (14.33, 15.53)
Bobolink (*Dolichonyx oryzivorus*)	14.48 (13.83, 15.2)
Black-throated Green Warbler (*Setophaga virens*)	14.18 (13.55, 14.54)
American Crow (*Corvus brachyrhynchos*)	14.02 (13.8, 14.37)
Philadelphia Vireo (*Vireo philadelphicus*)	13.46 (12.78, 14.21)
Cape May Warbler (*Setophaga tigrina*)	11.9 (10.93, 13.47)
Blackburnian Warbler (*Setophaga fusca*)	11.75 (11.47, 12.33)
Veery (*Catharus fuscescens*)	10.68 (10.33, 10.93)
Hairy Woodpecker (*Picoides villosus*)	10.54 (9.97, 11.15)
Western Tanager (*Piranga ludoviciana*)	10.53 (10.16, 10.94)
Brown Creeper (*Certhia americana*)	9.87 (8.76, 10.96)
Mourning Dove (*Zenaida macroura*)	9.42 (9.17, 9.6)
Varied Thrush (*Ixoreus naevius*)	9.22 (8.79, 9.49)
Blue Jay (*Cyanocitta cristata*)	9.21 (9.02, 9.33)
Ruby-throated Hummingbird (*Archilochus colubris*)	8.91 (8.34, 10.02)
American Tree Sparrow (*Spizella arborea*)	8.4 (6.89, 9.52)
Horned Lark (*Eremophila alpestris*)	8.21 (6.97, 9.11)
Vesper Sparrow (*Pooecetes gramineus*)	7.77 (7.59, 7.83)
House Wren (*Troglodytes aedon*)	7.74 (7.57, 7.9)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	7.61 (7.32, 7.81)
Dusky Flycatcher (*Empidonax oberholseri*)	7.24 (6.89, 7.54)
Mountain Bluebird (*Sialia currucoides*)	6.83 (6.41, 7.31)
Purple Finch (*Carpodacus purpureus*)	6.77 (6.14, 7.15)
Killdeer (*Charadrius vociferus*)	6.42 (6.13, 6.66)
Black-throated Blue Warbler (*Setophaga caerulescens*)	6.14 (5.94, 6.4)
Lapland Longspur (*Calcarius lapponicus*)	6.1 (4.9, 7.28)
Downy Woodpecker (*Picoides pubescens*)	6.1 (5.84, 6.51)
Rusty Blackbird (*Euphagus carolinus*)	6.06 (4.65, 7.46)
Gray-cheeked Thrush (*Catharus minimus*)	6.01 (5.1, 6.79)
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	6 (5.47, 6.41)
Northern Parula (*Setophaga americana*)	5.88 (5.72, 6.09)
Rock Pigeon (*Columba livia*)	5.76 (5.38, 6.08)
Eastern Kingbird (*Tyrannus tyrannus*)	5.53 (5.34, 5.82)
Olive-sided Flycatcher (*Contopus cooperi*)	5.25 (4.89, 5.55)
Gray Catbird (*Dumetella carolinensis*)	5.19 (4.98, 5.4)
Canada Warbler (*Cardellina canadensis*)	4.67 (4.41, 5)
Le Conte's Sparrow (*Ammodramus leconteii*)	4.51 (4.28, 4.84)
Evening Grosbeak (*Coccothraustes vespertinus*)	4.29 (4.05, 4.6)
Spotted Sandpiper (*Actitis macularius*)	3.89 (3.42, 4.38)
Baltimore Oriole (*Icterus galbula*)	3.87 (3.77, 4)
Pine Grosbeak (*Pinicola enucleator*)	3.82 (2.97, 5.68)
Ruffed Grouse (*Bonasa umbellus*)	3.75 (3.56, 4.01)
Greater Yellowlegs (*Tringa melanoleuca*)	3.56 (3.13, 4.13)
Bank Swallow (*Riparia riparia*)	3.55 (2.96, 4.4)
Lesser Yellowlegs (*Tringa flavipes*)	3.22 (2.95, 3.57)
Belted Kingfisher (*Megaceryle alcyon*)	3.01 (2.69, 3.42)
Western Wood-Pewee (*Contopus sordidulus*)	2.99 (2.73, 3.34)
Solitary Sandpiper (*Tringa solitaria*)	2.85 (2.23, 3.5)
Eastern Phoebe (*Sayornis phoebe*)	2.79 (2.66, 2.98)
Black-backed Woodpecker (*Picoides arcticus*)	2.59 (2.33, 2.99)
Connecticut Warbler (*Oporornis agilis*)	2.4 (2.3, 2.58)
Pileated Woodpecker (*Dryocopus pileatus*)	2.37 (2.29, 2.48)
Townsend's Solitaire (*Myadestes townsendi*)	2.3 (2.04, 2.58)
Black-billed Magpie (*Pica hudsonia*)	2.16 (2.07, 2.21)
Great Crested Flycatcher (*Myiarchus crinitus*)	1.97 (1.87, 2.05)
White-breasted Nuthatch (*Sitta carolinensis*)	1.95 (1.88, 2.07)
American Three-toed Woodpecker (*Picoides dorsalis*)	1.7 (1.52, 2.08)
Willow Ptarmigan (*Lagopus lagopus*)	1.49 (1.06, 1.84)

(Continues)

TABLE 2 (Continued)

Common name (scientific name)	Abundance (M males)
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	1.49 (0.88, 2.46)
Sedge Wren (*Cistothorus platensis*)	1.48 (1.35, 1.59)
Marsh Wren (*Cistothorus palustris*)	1.4 (1.26, 1.56)
Indigo Bunting (*Passerina cyanea*)	1.27 (1.21, 1.33)
Eastern Wood-Pewee (*Contopus virens*)	1.16 (1.1, 1.23)
Brown Thrasher (*Toxostoma rufum*)	0.679 (0.646, 0.713)
Scarlet Tanager (*Piranga olivacea*)	0.667 (0.627, 0.709)
Nelson's Sparrow (*Ammodramus nelsoni*)	0.586 (0.439, 0.768)
Pine Warbler (*Setophaga pinus*)	0.56 (0.531, 0.605)
Upland Sandpiper (*Bartramia longicauda*)	0.538 (0.509, 0.583)
Northern Cardinal (*Cardinalis cardinalis*)	0.532 (0.514, 0.553)
Wood Thrush (*Hylocichla mustelina*)	0.51 (0.487, 0.53)
American Pipit (*Anthus rubescens*)	0.347 (0.123, 0.606)
Sooty Grouse (*Dendragapus fuliginosus*)	0.316 (0.263, 0.353)
Grasshopper Sparrow (*Ammodramus savannarum*)	0.299 (0.252, 0.349)
Yellow-throated Vireo (*Vireo flavifrons*)	0.297 (0.219, 0.4)
Eastern Towhee (*Pipilo erythrophthalmus*)	0.249 (0.224, 0.284)
Field Sparrow (*Spizella pusilla*)	0.208 (0.194, 0.224)
Golden-winged Warbler (*Vermivora chrysoptera*)	0.133 (0.107, 0.163)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	0.032 (0.023, 0.045)

Note: Values in parentheses are the 5th and 95th percentile of the bootstrap distribution.

a given species range (https://doi.org/10.5281/zenodo.14854040; Sólymos et al., 2025). For two example species, Canada Warbler (*Cardellina canadensis*, Figure 10) and Connecticut Warbler (*Oporornis agilis*, Figure 11), both of which have experienced recent population declines (Rosenberg et al., 2019), density patterns varied across the Canadian portions of their breeding ranges. In the Boreal Plains (6-0) region, Canada Warbler median predicted densities were 0.0182 and 0.0089 males/ha in deciduous and conifer land-cover types, respectively. In the Boreal Hardwood Transition (12) region, median predicted densities were similar to those for region 6-0 in deciduous land-cover types (0.026 pairs/ha), but over twice as high in conifer land-cover types (0.024 males/ha). The Connecticut Warbler had higher median predicted densities in the west compared to the east in all land-cover types. Very few Connecticut Warbler were predicted in the Boreal Hardwood Transition region (12), with median densities of 0.0019 males/ha in deciduous land-cover types and 0.0021 males/ha in conifer land-cover types. In the Boreal Plains region (6-0), density predictions for Connecticut Warbler were nearly 10 times higher: 0.0166 males/ha in deciduous and 0.0145 males/ha in conifer land-cover types. Densities were somewhat lower in the Boreal Softwood Shield region of Ontario (8-1): 0.0087 males/ha in deciduous and 0.0096 males/ha in conifer land-cover types.

Population summaries, maps, variable importance, and validation metrics for all species are available for download at https://doi.org/10.5281/zenodo.14854040 (Sólymos et al., 2025). Additional variable importance details for example species and regions, including the top 20 variables (Appendix S2: Tables S1–S4), partial dependence plots (Appendix S2: Figures S1–S4) and two-way covariate interaction strengths (Appendix S2: Tables S5–S8) can be found in Appendix S2.

DISCUSSION

Here we have demonstrated the application of a comprehensive framework for developing fine-grained, spatially explicit population estimates for terrestrial bird species over large extents. Our framework integrates an approach for harmonizing data from across different surveys; a process for converting raw counts collected using nonstandardized methods to generate standardized density estimates; and the development of systematic, hierarchically structured models that can account for many complex factors affecting species distributions. On average, these models estimated a total of approximately 7.13 billion breeding landbirds (3.56 billion breeding males) representing 143 species across subarctic Canada, with most individuals breeding within boreal and hemi-boreal regions. Given Canada's forest-dominated land base, forest generalist species made up the largest part of this total estimate, followed by boreal forest specialist species. Although included here when available, grassland-specific surveys were not targeted in the data compilation process, and thus population estimates of grassland-associated species are likely better quantified by grassland-targeted studies (Prairie Habitat Joint Venture, 2021). By standardizing and combining many individual studies to fill the gaps remaining from larger coordinated survey programs, we provide scalable and spatially explicit landbird population estimates at an extent and resolution not previously available. With new avian data and improved covariate data, our modular framework may be easily updated to yield

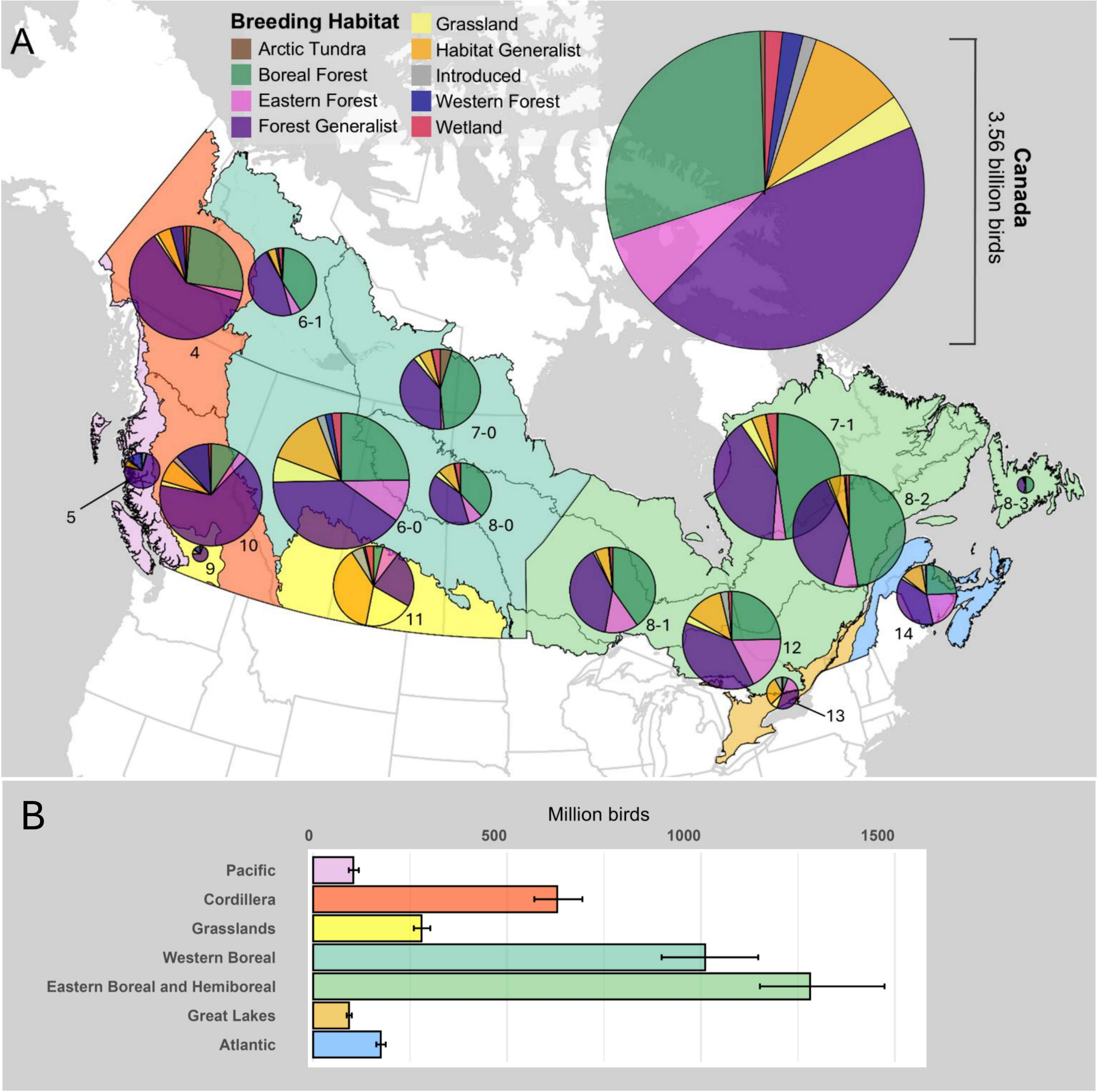

FIGURE 8 (A) Summary of Canada-wide and regional population estimates for species groups based on primary breeding habitat (as defined by Rosenberg et al., 2019). Pie chart radii are scaled based on a region's proportion of the total population. (B) Estimated abundance by geographic zone. Error bars show the 5th and 95th percentiles of the bootstrap distribution.

population and density estimates of increasing accuracy and precision. It also has the potential to be adapted to other taxa in other regions, thus laying the foundation to advance decision making and action at regional, national, and continental scales.

We applied a national-scale, ad hoc point-count database, which offers a unique integration of structured and semistructured data (sensu La Sorte et al., 2018), to the problem of generating spatially explicit population estimates for subarctic Canada. Previous efforts to estimate North American bird populations at large extents, such as those relying heavily on BBS data, are complicated by issues of roadside survey bias, lack of adequate habitat representation, and species detectability assumptions (Sólymos et al., 2020; Thogmartin et al., 2006). Although the Boreal Avian Modeling Project database that we used still has gaps in habitat representation, particularly in northern areas (Van Wilgenburg et al., 2020), the

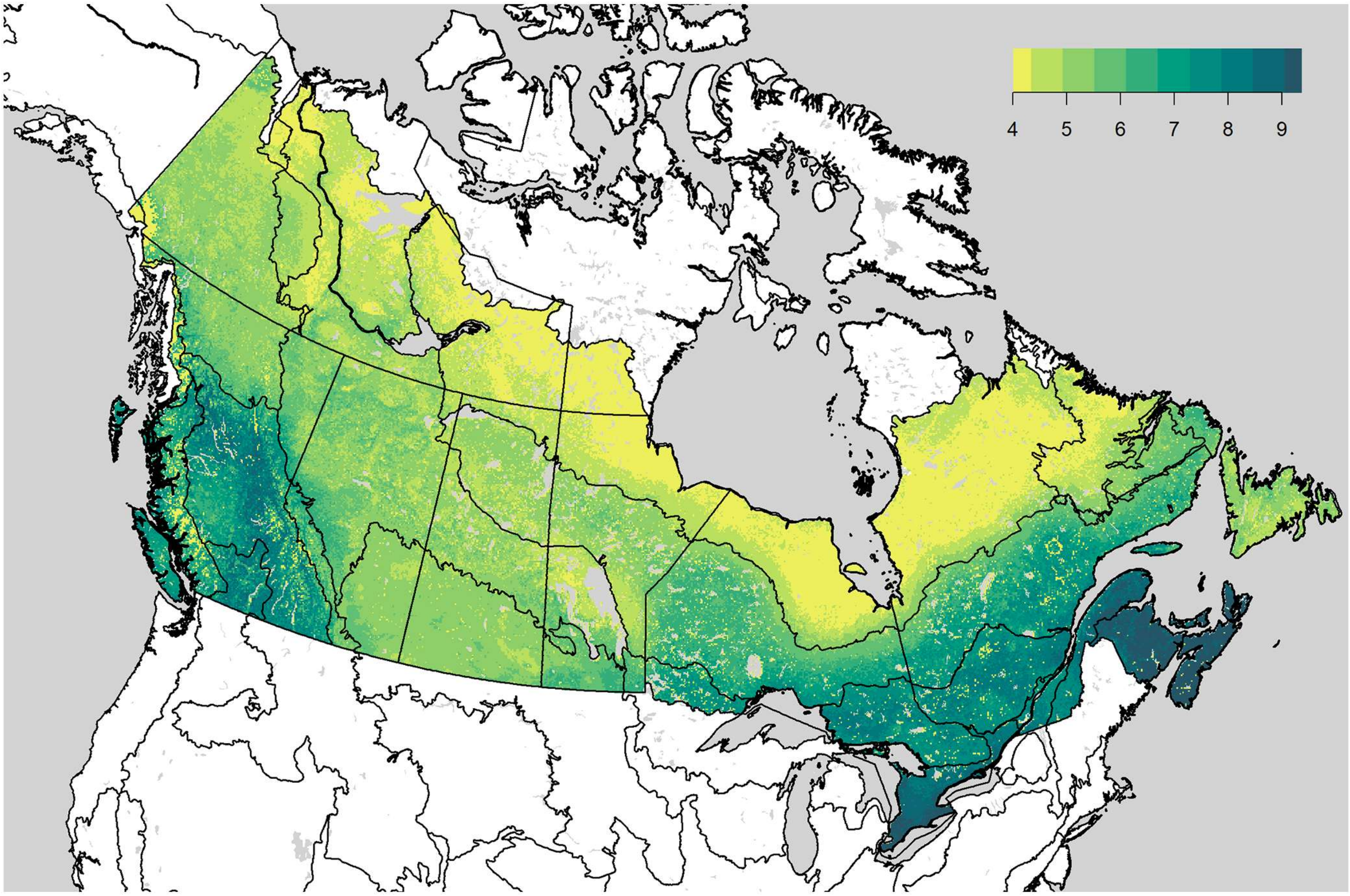

FIGURE 9 Predicted avian density (in number of males per hectare) for subarctic Canada summed over 143 species.

inclusion of large numbers of off-road surveys significantly reduces the roadside bias and habitat representation issues plaguing other databases (Sólymos et al., 2020). Moreover, even in areas with high BBS route coverage, populations have thus far been estimated over broad geographic regions (Partners in Flight, 2020; Stanton et al., 2019). In contrast, our predictive modeling framework allows for spatially explicit estimates at a much higher spatial resolution, thus facilitating greater precision in regional conservation planning (Leston et al., 2024). Future model iterations (in progress) will incorporate data from neighboring (United States) jurisdictions to improve cross-border coordination of conservation and management activities.

The ability to harmonize species abundance data collected with different sampling protocols and detectability—albeit with the same general survey method (i.e., point counts) and parameters—was a key factor in translating a heterogeneous database into population estimates. This standardization was enabled by the QPAD method, which considers the probability of detection (q) and availability (p) of birds in relation to area (a) and density (d) (Sólymos et al., 2013). Although we used custom offsets developed from a subset of our dataset, general offsets have been developed for a large number of North American landbird species and are available to be applied to density models for additional species over larger areas (NA-POPS initiative, Edwards et al., 2023). With the QPAD method, relative abundance estimates are most sensitive to the representativeness of habitat strata, while absolute numbers are most sensitive to estimates of detection distances (Sólymos et al., 2020). Therefore, as the latter is an active area of bioacoustic research, total population numbers may be revised as bioacoustic methods and recording equipment improve. As well, relative abundance estimates may become more precise as new data collection improves coverage of covariate space, particularly given new efforts to collect data in known data gaps using stratified sampling with hierarchically structured surveys (Pavlacky et al., 2017; Van Wilgenburg et al., 2020). Incorporation of data from randomized sampling will also allow formal assessment of the risk of bias in species distribution models created with data derived largely from nonprobability-based sampling (Boyd et al., 2023).

Our machine learning approach to model-building, and the large number of covariates considered, allowed us to account for variable interactions and nonlinearities

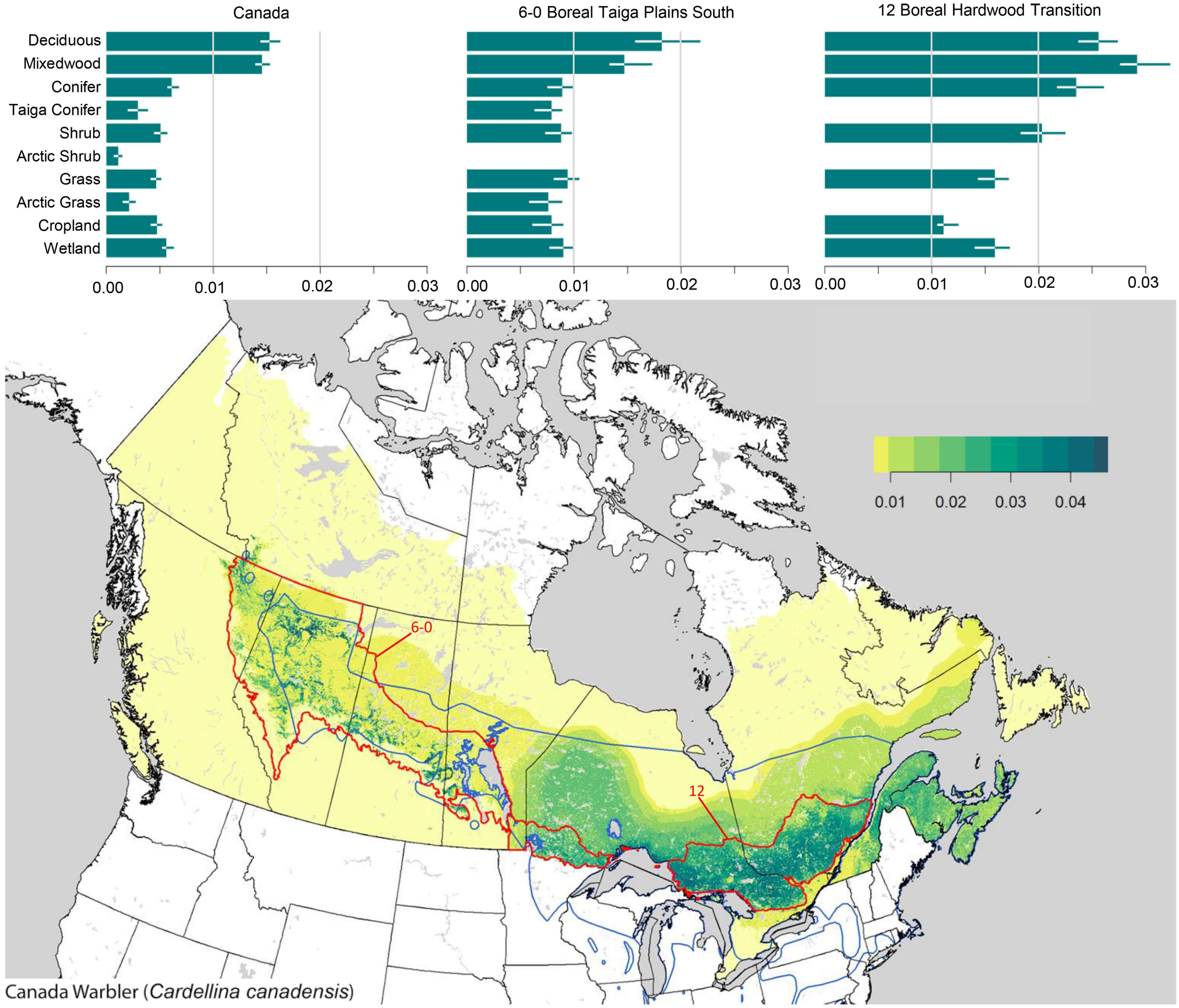

FIGURE 10 Example of species' density (in number of males per hectare) maps and habitat-specific density estimates for Canada and two regions for Canada Warbler (*Cardellina canadensis*). Model regions and NatureServe species' ranges are outlined in red and dark blue, respectively.

in an automated fashion over large areas, thereby representing the complexity of species abundance patterns better than simpler linear models. When looking across the entirety of Canada, environmental gradients are much more evident in climate variables than in vegetation patterns, despite clear climatic controls on individual plant species (McKenney et al., 2007). Consequently, avian SDMs fit at the national scale have generally been dominated by climate variables, some combination of which readily explains gradients in species distribution, whether those influences are direct or indirect (Cumming et al., 2014; Stralberg, Matsuoka, et al., 2015). By partitioning models into ecoregional units with relatively homogeneous climate regimes, we aimed to remove the influence of continental scale climatic gradients and emphasize local and landscape-level predictors such as vegetation, land cover, and topography. Although climate variables were still important predictors of abundance for most species, most of the explainable variation in bird density was attributed to vegetation characteristics, in particular landscape-level proportions of individual tree species and forest structural characteristics, as mapped by Beaudoin et al. (2014). This represents a refinement in comparison with purely bioclimatic models, especially in human-modified landscapes with vegetation patterns that are decoupled from climate drivers. However, the combined influence of climate and

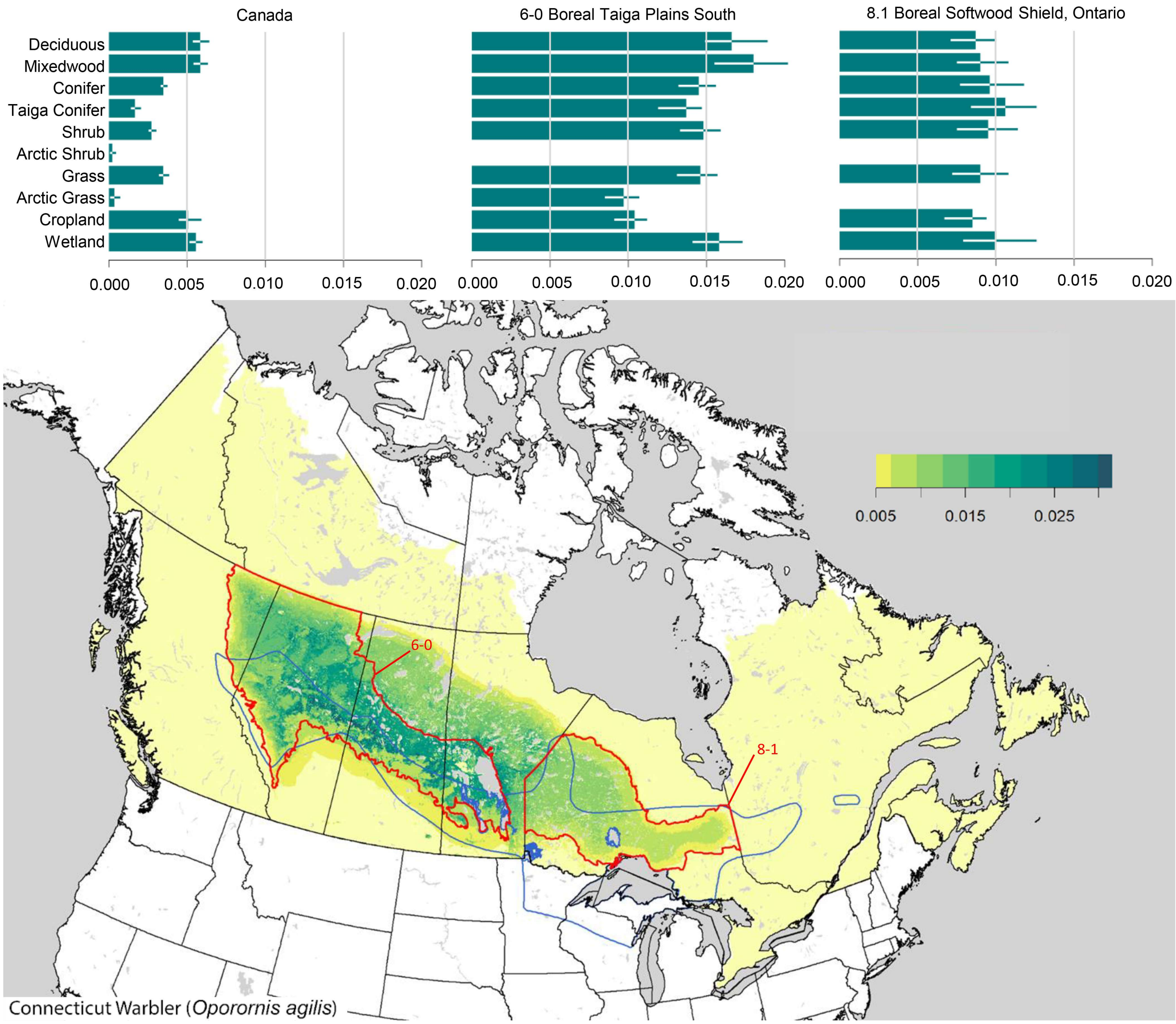

FIGURE 11 Example of species' density (in number of males per hectare) map and habitat-specific density estimates for Canada and two regions for Connecticut Warbler (*Oporornis agilis*). Model regions and NatureServe species' ranges are outlined in red and dark blue, respectively.

landscape-level vegetation variables in our models resulted in spatial predictions that were generally driven by broad physical gradients more than local habitat heterogeneity. A large portion of the variance remained unexplained, indicating that unmapped habitat conditions, as well as population and community dynamics, may also play an important role.

The dominance of these broad-scale gradients in our predicted density maps is partly due to the ecoregional scale at which these models were constructed, as well as population and community dynamics that result in unsaturated habitats, reducing our ability to explain local patterns. As spatio-temporal accuracy and precision of remotely sensed predictors improve, the influence of local habitat variation in the models should increase, improving their value for local and regional management purposes. However, in areas with good avian data coverage, the full influence of local habitat variability may be better captured by developing regionally specific models incorporating additional hierarchical structure and population dynamics.

Model performance and biases

We leveraged spatially extensive datasets, covariates, and a generalized modeling framework to reduce the risk of model bias (Boyd et al., 2023; Fourcade et al., 2018).

Although our models generally performed well, post hoc analyses suggested that they experienced a few biases related to geography, habitat affinity, and taxonomy. This result supports recent work by Morelli et al. (2024), who found that model performance was better for specialist species than generalist species. Thus, applying metrics of niche specialization might be a fruitful future refinement. Historic underrepresentation of sampling in the far north, mountains, and lakeshores likely contributed to reduced model performance in those areas. Ongoing efforts to employ spatially balanced sampling across the boreal forest biome of Canada using a hierarchically stratified sampling design (Van Wilgenburg et al., 2020) should improve the performance of future models. Some of the taxonomic groups that were more likely to show poor model performance (waxwings and finches) have generally been less well surveyed using point count methods due to their nomadic habits and poor timing of surveys. The inclusion of data from ARUs and/or carefully standardized checklist data (Robinson et al., 2020) could improve the predictive ability of future models.

Conservation applications

The framework presented here represents a model-based approach to improving continental-scale estimates of population size and distribution, which is fundamental to conservation and management. This type of information is required to evaluate species' status (e.g., Species At Risk Act, Government of Canada, 2019), identify stewardship and management responsibilities under the Migratory Birds Convention Act (Government of Canada, 1994), and prioritize conservation resources (Stralberg et al., 2018; Veloz et al., 2015). By improving our understanding of spatial population patterns, we can better quantify losses, gains, and distributional shifts in bird populations, ultimately facilitating more targeted conservation measures.

The documentation of avian population declines by Rosenberg et al. (2019) was enabled by continental-scale population estimates that can be refined with model-based approaches such as those presented herein. As it incorporates temporally varying model covariates, as well as a year term, our modeling approach can ultimately be used to move beyond current snapshots and refine estimates of population changes over time based on changes in habitat. This version of our models was limited by the availability of temporally specific spatial data on forest composition and structure (2001 and 2011; Beaudoin et al., 2014). We also limited our covariate selection to mostly static or long-term (i.e., climate-normal) variables. However, future model iterations, fueled by rapidly increasing volumes of remotely sensed land-cover data (e.g., Guindon et al., 2024; Hermosilla et al., 2022) and processing capacity (Campos et al., 2023; Crego et al., 2022), can incorporate a broader range of annual vegetation, disturbance, and climate indices. The resulting spatially refined population trends—which may be partitioned into habitat-driven versus unexplained trends—can be used to inform species status assessments on a more frequent basis as climate and vegetation change continue to alter Canada's forest landscapes and bird habitats. The easily updatable framework presented here makes such frequent assessments possible.

Although spatially explicit population trends require more focused attention (e.g., Ball et al., 2016), current estimates of species population size and distribution are relatively easy to produce and update as new data become available. Our modular, ecosystem-based approach is flexible enough to accommodate the incorporation of regional mapping products that may better capture important habitat differences than national and continental-scale products. Because national estimates are based on combined bootstrapped mean projections for separate regions, individual regional models can be updated independently and with distinct individual variables.

CONCLUSION

Given human pressures on biodiversity and ongoing species declines (Robbins et al., 1989; Rosenberg et al., 2019), the optimization of conservation and land management outcomes for biodiversity is increasingly important. Spatially explicit density estimates, as we have presented here, provide opportunities to make conservation investments and management actions more efficient. We have integrated a wide range of remotely sensed spatial datasets and survey methods, leveraging those important individual contributions to provide the best possible species-specific abundance estimates at a range of spatial scales relevant to conservation planning and land management. In doing so, we developed an open, modular, and reproducible approach to allow for regular updates to models and data products (available at https://github.com/borealbirds/LandbirdModelsV5; Sólymos et al., 2025). Although population and density estimates will continue to improve, current and future iterations of the models presented here constitute a significant improvement over aggregated regional estimates and an asset to conservation decision-making.

AUTHOR CONTRIBUTIONS

Péter Sólymos and Diana Stralberg conceived and executed the research. Diana Stralberg, Teegan D. S. Docherty, Andrew D. Crosby, Steven L. Van Wilgenburg, and Péter

Sólymos wrote the paper. Elly C. Knight, Anna Drake, and Mannfred M. A. Boehm assisted with analysis and development of figures and tables, Lionel Leston, Judith D. Toms, and Samuel Haché contributed statistical and ornithological expertise. Jeffrey R. Ball, Samantha J. Song, Fiona K. A. Schmiegelow, Steven G. Cumming, and Erin M. Bayne provided financial support and project guidance. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Most of the data used to develop these models are either publicly available or visible by request via the https://wildtrax.ca data repository. R code and the specific set of bird data and environmental covariates used in the models (Sólymos et al., 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.14854040. Spatial coordinates were removed to anonymize the data, since not all datasets are publicly available.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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