Projected effects of climate change on boreal bird community accentuated by anthropogenic disturbances in western boreal forest, Canada

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Abstract

Aim: Climate change is expected to influence boreal bird communities significantly, notably through changes in forest habitat (composition and age structure), in the coming decades. How these changes will accumulate and interact with anthropogenic disturbances remains an open question for most species.

Location: Northeastern Alberta, Canada.

Methods: We used the LANDIS-II forest landscape model to project changes in forest landscapes, and associated bird populations (72 passerine species), according to three climatic scenarios (baseline, RCP 4.5 and RCP 8.5) and three forest harvesting scenarios of differing intensity.

Results: Both forest harvesting and climate-related drivers were projected to have large impacts on bird communities in this region. As a result of climate-induced increases in fire activity as well as decreased conifer productivity, our simulations projected that an important proportion of Alberta's boreal forests would transition to treeless habitat (i.e. grass- or shrub-dominated vegetation) while many conifer-dominated stands would likely be replaced by broadleaf tree cover. Consequently, the abundance of bird species associated with open and deciduous habitats were projected to increase. With a strong anthropogenic climate-forcing scenario (RCP 8.5), sharp declines in abundance of coniferous trees were also projected, particularly in mature and old forest stands, triggering major declines for bird species associated with coniferous and mixedwood forest types.

Main conclusions: As the most comprehensive simulation of climate change and harvesting impacts on avian habitats in the North American boreal region to date, our study stresses the importance of considering key habitat characteristics like forest age structure and composition through forest landscape modelling and identifies 18 bird species particularly sensitive to climate change. Our simulations suggest that a change in forest management practices could play an important role in the...
1 | INTRODUCTION

The North American boreal forest region, referred to as North America’s bird nursery with over 300 nesting bird species (Wells & Blancher, 2011), is currently warming more than twice as fast as the rest of the world (Environment & Climate Change Canada, 2019). Combined with increasing anthropogenic pressures (forestry, energy and mineral resource extraction), the boreal forest is predicted to experience profound changes in forest composition and age structure over the 21st century (e.g. Boulanger, Taylor, et al., 2016; Gauthier, Bernier, Kuuluvainen, Shvidenko, & Scheepaschenko, 2015; Price et al., 2013; Rehfelt, Crookston, Sáenz-Romero, & Campbell, 2012), and these important changes would likely impact bird habitats. Indeed, boreal climate conditions are expected to shift northward and upward with warming temperatures, with an expected contraction of the boreal biome of up to 42% by the end of this century (Rehfelt et al., 2012; Stralberg et al., 2019). As many boreal bird species are dependent on specific habitats to complete their life cycles, shifts in the extent and distribution of boreal vegetation are likely to strongly influence bird communities over the coming decades (Cadieux et al., 2019; Rodenhouse et al., 2008; Stralberg et al., 2019; Stralberg, Matsuoka, et al., 2015; Tremblay et al., 2018). Indeed, large declines of climatically suitable boreal bird habitat have been projected for both North American (Stralberg, Bayne, et al., 2015) and Scandinavian species (Virkkala, Heikkinen, Leikola, & Luoto, 2008).

Under climate change, multiple agents operating at various spatio-temporal scales are likely to drive changes in the extent and attributes of the boreal forest, and hence affect bird habitat. At the stand scale, changes in temperature and precipitation will shift forest productivity and composition by directly influencing rates of mortality, regeneration and growth of tree species (Boulanger, Taylor, et al., 2016; Chen, Luo, Reich, Searle, & Biswas, 2016; Girardin et al., 2016; Searle & Chen, 2017). At the forest landscape scale, climate-induced changes in natural disturbance frequency and severity, such as greater recurrence of drought events (Allen et al., 2010; Michaelian, Hogg, Hall, & Arsenault, 2011) or more area burned (Boulanger, Gauthier, & Burton, 2014; Boulanger, Gray, Cooke, & Grandpré, 2016; Stralberg, Wang, et al., 2018), are expected to have strong impacts on forest composition and structure. Consequently, young forests dominated by pioneer deciduous tree species (e.g. Populus tremuloides Michx.) are projected to increase in relative abundance, while the proportion of old, conifer-dominated boreal forest is expected to decrease significantly (Boulanger, Taylor, et al., 2016; Mahon et al., 2014; Mekonnen, Riley, Randerson, Grant, & Rogers, 2019). Rising carbon dioxide concentrations coupled with warming also increases the proportions of broadleaf and early-successional conifers at the expense of late-successional conifers (Searle & Chen, 2017). In Western Canada, increases in droughts and fires at the southern edge of the boreal forest will likely drive a transition from this ecosystem to a prairie one (Stralberg, Wang, et al., 2018), representing a large loss of forest habitat for boreal birds.

Coupled with climate change and natural disturbances, the rapid expansion of industrial development in the boreal forest, including forestry, energy and mineral resource extraction (Gauthier et al., 2015), is expected to further transform boreal bird habitats. Forest harvesting, in particular, causes changes in forest structure, composition and age (Boucher, Grondin, & Auger, 2014; Cyr, Gauthier, Bergeron, & Carcaillot, 2009) and influences the composition and abundance of bird communities (Drapeau et al., 2000; Schieck & Song, 2006). Furthermore, birds associated with old boreal mixed-wood and coniferous forests have been identified as particularly vulnerable to short-rotation even-aged management, which reduces the availability of old forests on the landscape and promotes the conversion of mixed and coniferous dominated landscapes to broadleaf dominance (Drapeau et al., 2000; Hobson & Bayne, 2000; Imbeau, Mönkkönen, & Desrochers, 2001; Niemi et al., 1998; Schieck & Song, 2006).

More specific estimates of how the boreal forest is expected to change in future decades are of great importance for bird conservation planning (Jetz, Wilcove, & Dobson, 2007), especially for birds with specific habitat requirements (Cadieux et al., 2019; Mahon et al., 2016; Stralberg, Bayne, et al., 2015). However, spatio-temporally explicit bird habitat projections are complex and require the integration of anthropogenic climate scenarios, as well as natural and anthropogenic disturbances. To date, the majority of studies of climate change impacts on birds have relied on bioclimatic niche models. These models use associations between observed geographical distributions and climatic variables to project future occurrences of species (Araújo & Peterson, 2012). Therefore, bioclimatic niche models do not explicitly capture any of the processes driving changes in forest ecosystems and hence on habitat, including effects of harvesting and natural disturbances at both the stand and landscape scales. Other models such as dynamic global vegetation models (DGVMs) are frequently run at a scale that is too broad to assess the cumulative and interactive
impacts of climate and harvesting at the stand level. These limitations greatly compromise their use for assessment of near-future impacts on wildlife habitat. Forest landscape models (FLMs) dynamically integrate natural and anthropogenic disturbances, leading to more realistic projections of short-term changes in habitat—which niche-based projections cannot provide. FLMs can project climate-induced vegetation changes while taking into account migration lags in forest vegetation distribution relative to the projected shifts in climatic zones. Moreover, these models, such as LANDIS-II (Scheller et al., 2007), can simultaneously test different forest management scenarios at stand and landscape scales that are relevant to bird habitat projections (Boulanger, Taylor, et al., 2016; Cadieux et al., 2019; Tremblay et al., 2018). Furthermore, FLMs can be used to quantify the relative contributions of different drivers of change in a changing climate—for example fire, growth and productivity, and forest harvesting (Boulanger, Taylor, Price, Cyr, & Sainte-Marie, 2018).

In this study, we used an FLM (i.e. LANDIS-II) combined with vegetation-based bird density models to project future distributions and abundances of 72 passerine species, hereafter songbirds, in the western North American boreal forest for the coming decades (up to 2100). We aimed to project the evolution of forest landscapes according to three climatic scenarios and three forest harvesting scenarios, to project changes in the boreal bird community and to assess the relative impacts of climate change (realized through changes in wildfire and tree growth) and forest harvesting on future bird abundance.

2 | METHODS

A schematic representation of the methods can be found in Figure 1, and more details about the model parameters can be found in previous publications (Boulanger, Taylor, et al., 2016; Taylor et al., 2017; Tremblay et al., 2018) as well as in the Supplementary Material.

2.1 | Study region

The 6.37 million ha study region is located in the Boreal Plains ecozone of northeastern Alberta, Canada (Figure 2) and contains coniferous and broadleaved trees, primarily as mixedwood forests. It overlaps three of Alberta’s natural subregions, namely the Central Mixedwood, Dry Mixedwood and Boreal Highlands (Beckingham & Archibald, 1996). In upland areas (ca. 60% of the area), mesic sites tend to be dominated by trembling aspen, white spruce [Picea glauca (Moench) Voss], balsam poplar [Populus balsamifera L.], balsam fir [Abies balsamea (L.) P. Mill.] and white birch [Betula papyrifera Marsh.], while xeric sites tend to be dominated by jack pine (Pinus banksiana Lamb.). Lowland sites (ca. 40% of the area) are mainly forested wetlands and bogs dominated by black spruce [Picea mariana (P. Mill.) B. S. P.] and tamarack (Larix laricina (Du Roi) K. Koch). The topography is generally flat and elevation ranges from ca. 400 m to over 900 m.

Large and relatively frequent stand-replacing fires are the most common disturbance agent in the study region (Tymstra, Wang, & Rogeau, 2005). However, anthropogenic disturbances occur on approximately two million ha of the study region in the form of forest harvesting, while 4.8 million ha, much of which lies in lowland areas, are not considered commercially productive (Alberta-Pacific Forest Industries Inc., 2020).

2.2 | Climate data

Monthly time series of current climate were interpolated from climate station records using the data of McKenney et al. (2013). We created climate scenarios by merging 30-year monthly climate normals for 1961–1990, interpolated from climate station records (McKenney et al., 2013) with projections of future monthly changes derived from the Canadian Earth System Model version 2 up to 2100 (CanESM2; Arora et al., 2011). Two different radiative forcing scenarios, known as Representative Concentration Pathways (RCP; e.g. Van Vuuren et al., 2011), namely RCP 4.5 and RCP 8.5, were downloaded from the World Climate Research Program (WCRP) Climate Model Intercomparison Project Phase 5 (CMIP5) archive. The CanESM2 projections indicate that mean annual temperature will increase by about 3.5°C (RCP 2.6) to 7.5°C (RCP 8.5) throughout the southern boreal region by 2100 (compared with c. 2000), while average precipitation is projected to increase by 10 to 25%. Data from CanESM2 for the 1961–2100 period were bias-corrected by expressing them as differences from (temperature) or ratios of (precipitation) the CanESM2 simulated monthly means for 1961–1990.

2.3 | The models

2.3.1 | Simulation setup

We used LANDIS-II (Scheller & Mladenoff, 2004) to project future forest attributes within our study area. In LANDIS-II, the forest landscape is represented by a grid of interacting cells within which stand-level forest processes (tree establishment, growth, competition and mortality) occur while landscape-level processes, such as tree seed dispersal and forest disturbances including fire and harvesting, generally affect multiple cells in a spatially, interactive manner. In our experiment, we set cell resolution to 250 m (6.25 ha) and simulations were run at 10-year time steps across all activated extensions. Forest composition and structure in each cell were initialized using forest properties derived from the Alberta Biodiversity Monitoring Institute (ABMI) cover products (as of the year 2010; ABMI, 2012) and the Canadian National Forest Inventory (NFI; nfi.nfis.org) and combined with stand age cohort data derived from provincial forest inventory plots. Each of these cells was then assigned to a “landtype” with homogeneous soil (Mansuy et al., 2014) and climate conditions.

A modified version of the LANDIS-II Biomass Succession extension v 3.1 (Scheller, 2013) was used to simulate forest succession.
The Biomass Succession extension emulates succession at the stand (cell) level by simulating the recruitment and growth of tree cohorts (not individual trees). It permits multiple cohorts of tree species to establish and interact within a cell through resource (i.e. “growing space” sensu Scheller & Mladenoff, 2004) limitations based on species-specific traits. The succession of each cell is driven by these stand-level interactions, in addition to disturbance history and seed source availability. Specific parameters that define basic life history traits are assigned to all species (see Table 1 for a full listing). To account for the effects of climate change, the forest gap model PICUS (version 1.5; http://picus.boku.ac.at) was used to develop the dynamic tree species- and landtype-specific parameters required to operate LANDIS-II. PICUS is an individual tree-based, spatially explicit forest ecosystem model that simulates germination, establishment, growth and mortality of individual trees on 100 m² patches of forest area (see Boulanger, Taylor, et al. (2016) and Taylor et al. (2017) for more details). Hence, three dynamic inputs of the Biomass Succession extension, namely maximum biomass (maxAGB; g/m²), maximum aboveground net primary productivity (maxANPP; g m⁻² year⁻¹) and species establishment probability (SEP), were derived from PICUS by running monospecific stand simulations for each combination of species, climate conditions and landtype. Those parameters were allowed to change during the course of the subsequent LANDIS simulations to represent the effect of climate change on each species’ potential growth. For a complete description of the calibration, the validation procedures regarding these parameters,
and a description of how these dynamic inputs were derived from the outputs of PICUS, refer to Tremblay et al. (2018).

We considered two natural disturbance agents, namely wildfires and drought. Wildfire accounts for the majority of areas naturally disturbed in the study area (Tymstra et al., 2005) and is widely recognized to have major impacts on Canada’s forest landscapes (Price et al., 2013; Volney & Hirsch, 2005). Fire simulations were carried out using the LANDIS-II Base Fire extension (He & Mladenoff, 1999), which simulates stochastic fire events dependent upon fire ignition, initiation and spread. Fire regime data (annual area burned, fire occurrence, and mean fire size) were first compiled into “fire regions” corresponding to the Canadian Homogeneous Fire Regime (HFR) zones (Boulanger et al., 2014). Baseline and future fire regime parameters within each fire region were calibrated with models developed by Boulanger et al. (2014), and they were updated to account for changing climate conditions under the different RCP scenarios (Gauthier et al., 2015).

Drought-induced mortality was simulated by first modelling species-specific mortality curves according to the climate moisture index (CMI), calculated as the difference between annual precipitation and potential evapotranspiration (see Brecka, 2018 for more details). Species-specific mortality was retrieved from undisturbed permanent sample plots located within the Boreal Plains ecozone. This was used to construct generalized linear models predicting the 10-year proportion of species biomass killed according to decadal CMI values (Chen et al., 2016). Using the same climate datasets described above, we projected future CMI values under all landtypes under each climate scenario and each 30-year period (i.e. 2011–2040, 2041–2070; 2071–2100). Future species-specific drought-related mortality was then projected using future CMI values and drought-related mortality models. Projected drought-related species-specific mortality was then included in the LANDIS-II simulations by removing biomass accordingly using the Biomass Harvest extension (v3.0; Gustafson, Shifley, Mladenoff, Nimerfro, & He, 2000). Drought-induced mortality was applied equally to all tree age cohorts.

Forest harvesting was simulated using the Biomass Harvest extension. Only clearcut harvesting was simulated as this logging strategy is most frequently used in the study area (https://alpac.ca/index.php/forest-sustainability/forest-planning). Only stands in upland areas and that comprised cohorts older than 60 years old were allowed to be harvested. When harvested, clearcutting was simulated to remove of all age cohorts present except for the 0- to 10-year age cohort. Mean harvested patch size and total harvested area were summarized by forest management units. Harvesting parameters were held constant throughout the simulations. Three harvesting scenarios were simulated according to a gradient of harvesting pressure, from no harvesting (no harvesting), to clearcutting with intensity similar to current management practices (baseline harvesting—applied to 0.3% of the harvestable upland area per year; ABMI, 2017), to high-intensity clearcutting (high harvesting—applied to 0.6% of the harvestable upland area per year).

Simulations were run for three climate scenarios (baseline, RCP 4.5 and RCP 8.5) as well as under the three harvesting scenarios.
Five replicate simulations were run for 200 years, starting in the year 2000, with 10-year time steps. Except for scenarios involving the baseline climate, fire regime parameters were allowed to change in 2010, 2040 and 2070 according to the average climate corresponding to each forcing scenario. Dynamic growth and establishment parameters (SEP, maxANPP and maxAGB) as well as drought mortality were allowed to change according to climate scenarios following the same schedule but only for upland areas. Indeed, our current understanding of the vulnerability of peatland systems to climate change is very limited (e.g. Schneider, Devito, Kettridge, & Bayne, 2016). As such, lowland pixels were kept as “active” to allow fire spread and seed dispersal, but growth parameters were kept constant. A similar simulation strategy was used by Stralberg, Wang, et al. (2018) in this area. As a result, future forest landscape, as well as bird community results, was reported for uplands only.

### 2.3.2 Boreal songbird community

To represent the boreal bird community, we selected passerines with breeding ranges that overlapped with the study region. We further limited this selection to 72 songbirds that were adequately modelled within Northern Alberta by excluding species that were too rare (number of detections <5 x degrees of freedom in models) or for which model goodness-of-fit was low (AUC < 0.6). These predictive models were based on point count data, including surveys from the North American Breeding Bird Survey (BBS; pwrcc.usgs.gov/bbs/), Boreal Avian Modelling Project (BAM; borealbirds.ulaberta.ca) and the ABMI (abmi.ca). The models were built following the methodology outlined in Ball et al. (2016) and Sólymos et al. (2020). Land cover associations were based on the dominant land cover (native vegetation and human footprint) type within a 150-m radius buffer around the points. Native vegetation classes included deciduous, mixedwood, white spruce, pine, black spruce forest stands, treeted fen, shrub, grass/herb, graminoid fen, marsh and swamp cover types. Ages of forest stands (area-weighted average age at the year of the survey) originating from natural disturbances or forest harvesting were also assessed within the 150-m radius buffers. Survey counts were modelled by Poisson generalized linear models with a logarithmic link. We used the QPAD approach (\(E[Y] = Q \times P \times A \times D\)) where perceptibility \(Q\), availability \(P\), area \(A\) and density \(D\); Sólymos et al., 2013) to account for differences in sampling protocol and covariate effects on detectability via offsets in the generalized linear models. This approach standardizes the estimates to reflect density (number of singing individuals per ha) within the different land cover type and stand age categories.

As a result of these models, ABMI provides expected density for the selected bird species for each cover type, and data are available via the "cure4insect" R extension package (Sólymos, Allen, Azeria, White, ABMI, & BAM, 2018; see model summaries at abmi.ca/data). We used expected density per species in conjunction with projected forest cover types to estimate expected bird abundance. Aboveground biomass density (t/ha) for each tree species as well as stand age and stand origin as projected by LANDIS-II was used to derive habitat types (forest cover types) using the same classification scheme used to define ABMI forest cover types (see above). Stand-scale (250 m) forest cover information was derived for each LANDIS-II simulation run at a 10-year time step. We also regrouped bird species based on their main habitat associated with the following habitat types (deciduous, mixedwood, coniferous and treeless) and stand age classes (<30 years [young]; 30–60 years [closed]; 60–80 years [mature]; >80 years [old]).

### 2.4 Analyses

Cumulative impacts of harvesting and climate change were assessed by comparing temporal trends of tree species aboveground biomass and songbird abundance under each climate and harvesting scenario over time. Outputs from the five simulation replicates were averaged. Trends were assessed using simulations where all disturbances (fire, drought and harvesting) were considered. The impact of climate change and harvesting on simulated songbird abundance was calculated as the percentage of change in simulated songbird abundance relative to the proportion obtained under the baseline harvesting and baseline climate scenario (hereafter referred to the “reference scenario”) following:

\[
\left( \frac{(\text{ProjAbund}_t / \text{RefAbund}_t) - 1}{\text{RefAbund}_t} \right) \times 100
\]

where \(\text{RefAbund}_t\) is the abundance of a bird species under the reference scenario (baseline climate and baseline harvesting), \(\text{ProjAbund}_t\) is the projected abundance of the same species for the given future time period, and \(t\) is time in years (Cadieux et al., 2019). This method was used to get a direct assessment of the effects of climate change and harvesting while controlling for forest succession.

Additional simulations were conducted to assess the importance of a selected driver of change on bird abundance. Simulations were conducted following a three-way factorial design according to harvesting (no harvesting, 0.3% and 0.6%), fire (baseline fire, projected fire) and climate change effects on dynamic biomass succession inputs and drought. The relative contribution of each factor was assessed by estimating the variance of songbird abundance that it explained using omega-squared values (\(\omega^2\)) calculated following a 3-way factorial ANOVA. We calculated \(\omega^2\) for each driver of change, at each time step, as:

\[
\omega^2 = \frac{\text{SSeffect} - (df_{\text{effect}} \times (MS_{\text{error}}))}{\text{MS}_{\text{error}} + \text{SS}_{\text{tot}}} \tag{2}
\]

where \(\text{SS}_{\text{effect}}\) is the sum of squares related to the driver of change (the effect), \(df_{\text{effect}}\) is the degree of freedom of the effect, \(MS_{\text{error}}\) is the mean square of the error and \(SS_{\text{tot}}\) is the total sum of squares. ANOVA and \(\omega^2\) calculations were performed separately for each RCP scenario. Based on the relative importance of drivers on bird species, we defined species sensitive to climate change as those declining more than 25% according to climate-sensitive drivers (either fire or tree growth) under RCP 8.5 and the current harvest scenario at 2100.
3 | RESULTS

3.1 | Cumulative impacts of climate change and harvesting on boreal forest landscapes

Climate change and forest harvesting were projected to have a strong influence on tree species biomass as well as on forest cover types and age. Under the RCP 8.5 scenario, annual area burned increased from ca. 0.5% in 2000 to 2.0% in 2100 and biomass killed by drought increased from ca. 15% in 2010 to 18% in 2100. Mean aboveground biomass was projected to decline significantly with increasing anthropogenic forcing, with RCP 8.5 scenario projected to result in the largest losses (from 86 to 39 t/ha in 2100 under baseline harvesting; Figure 3). Forest cover was projected to decrease under all climate scenarios (Figure 4) with the largest proportions of treeless land occurring under RCP 8.5 (from 0% in 2000 to 25% in 2100 under the baseline harvesting scenario).

Upland mixedwood and conifer-dominated stands were projected to decrease with increasing anthropogenic climate forcing, falling to the lowest proportions in the simulated landscapes under RCP 8.5 (Figure 4). The combined proportion of aboveground biomass for jack pine and white spruce decreased from 41% to 23% in 2100 under RCP 8.5 and the baseline harvesting scenario (Figure 3). On the other hand, the proportion of aboveground biomass of the broadleaved species was projected to increase (Figures 3 and 4). For example, the proportion of poplar biomass increased from 50% to 67% in 2100 under RCP 8.5 and baseline harvesting scenario (Figure 3).

Increased forest harvesting accelerated the loss of upland mixedwood and coniferous stands. The largest decreases in such stands were simulated with high harvesting by 2100 under all climate conditions.
scenarios (Figure 4). Under RCP 8.5, mixedwood and coniferous stands declined from 62% of upland cover at the beginning of simulations to 39% under no harvesting and to 23% under high harvesting by 2100 (Figure 4).

Forest stand age was heavily influenced by climate and forest harvesting scenarios, regardless of forest cover type. Under the no harvesting and the baseline climate scenario, 72% of upland forest stands were projected to be at least 80 years old by 2100, but this decreased to only 40% under RCP 8.5 (Figure 5). This proportion was further reduced, to ca. 30%, under high harvesting (Figure 5).

3.2 Projected changes in the boreal bird community structure

3.2.1 General trends of bird abundance under climate change

Important changes were projected for the boreal bird community in the study area in response to both climate change and harvesting scenarios. Changes in bird abundance varied greatly among species and habitat type associations (Table 2). Compared to the reference scenario, an average 13% increase in abundance across all species by 2100 was projected for the most severe climate change scenario (RCP 8.5) under baseline harvesting. This increase was largely attributed to major increases in the abundances of treeless-associated bird species (an average of 83% for fifteen species; Figure 6a), but also to bird species associated with early and closed forest habitats (average increase of 12% for 23 species; Figure 6a). Conversely, species associated with mature coniferous stands showed declines with an average of 27% for six species under the RCP 8.5 and baseline harvesting by 2100 (Figure 6b). Our simulations projected large declines in the abundance of 16 species associated with old mixed and coniferous forests (Figure 6b); the average decrease was 30% with the Brown Creeper (Certhia americana), a sensitive species to forest harvesting, declining by 29% under RCP 8.5 and baseline harvesting by 2100 (Table 2).

3.2.2 Importance of change components

The climate-driven ecological processes (i.e. forest growth, mortality caused by drought and wildfire occurrence) as well as the climate-independent driver, forest harvesting, all had important projected influences on boreal bird communities. Increases in fire activity had the largest overall impact on boreal bird communities, ranging from strongly beneficial to profoundly detrimental (Tables 2 and S2.1). Wildfire was beneficial for species associated with treeless habitats (Table 2). Alternatively, it was detrimental to birds associated with old and mature mixedwood and coniferous forests, explaining close to 50% of the decline in these bird species’ abundances by 2100 (Table 2).

Forest harvesting had the second most important influence on bird abundance (Tables 2 and S2.1). This driver of forest change was most detrimental for birds associated with mature and old habitat and especially for those in old deciduous and mixedwood forests (Figure 6a,b). For ten species, harvesting explained >40% of the projected bird abundance declines by 2100 (Table S2.1). Under RCP 8.5 and high harvesting, the Canada Warbler (Cardellina canadensis), a threatened species in Canada and in Alberta, was projected to decline by 17%, compared to a 39% increase under the no harvesting scenario (Table S2.1). On the other hand, baseline and high harvesting scenarios benefited other species associated with mature deciduous-dominated forests such as Connecticut Warbler (Oporornis agilis; from −41% under no harvesting to +20% under high harvest), because of the increase in deciduous-dominated forests (Table 2) under RCP 8.5 by 2100 (Table S2.1).
### Table 2: Projections of changes in bird population abundances for three harvesting scenarios under RCP 8.5 by 2100 (mean ± SD). The relative contributions of key components of change (wildfire, forest growth rate and harvesting) are also presented as values of $\omega^2$ (see section "Analyses" for details). Only species with a projected change in abundance of more than 25% from the baseline harvesting scenario are reported here (see Table S2.1 in Supporting Information for projections for all species).

| Species                      | Sensitive to climate change | Cover type and forest age | Percentage change under harvesting scenarios (%) | Key drivers of change relative contributions ($\omega^2$) |
|------------------------------|----------------------------|---------------------------|-------------------------------------------------|------------------------------------------------------|
|                              |                            |                           | No harvesting | Baseline harvest | High harvesting | Fire | Growth | Harvesting |
| American Crow                |                            | Treeless                   | 70 ± 3        | 74 ± 6          | 82 ± 4         | 97   | 0      | 1          |
| American Goldfinch           |                            | Treeless                   | 83 ± 3        | 86 ± 7          | 89 ± 4         | 96   | 2      | 1          |
| Baltimore Oriole             |                            | Treeless                   | 100 ± 7       | 109 ± 11        | 119 ± 8        | 92   | 2      | 4          |
| Black-billed Magpie          |                            | Treeless                   | 84 ± 6        | 104 ± 10        | 129 ± 10       | 84   | 0      | 14         |
| Brown-headed Cowbird         |                            | Treeless                   | 24 ± 2        | 27 ± 3          | 32 ± 4         | 70   | 14     | 12         |
| Clay-colored Sparrow         |                            | Treeless                   | 80 ± 3        | 103 ± 8         | 126 ± 6        | 85   | 0      | 14         |
| Eastern Kingbird             |                            | Treeless                   | 146 ± 15      | 149 ± 21        | 149 ± 20       | 96   | 3      | 0          |
| House Wren                   |                            | Treeless                   | 108 ± 5       | 111 ± 10        | 118 ± 7        | 97   | 1      | 1          |
| Nelson's Sparrow             |                            | Treeless                   | 262 ± 23      | 254 ± 29        | 258 ± 24       | 99   | 0      | 0          |
| Savannah Sparrow             |                            | Treeless                   | 188 ± 12      | 193 ± 15        | 208 ± 13       | 99   | 0      | 0          |
| Song Sparrow                 |                            | Treeless                   | 30 ± 5        | 40 ± 5          | 47 ± 3         | 69   | 4      | 21         |
| Black-and-white Warbler      |                            | Young deciduous            | -5 ± 4        | 26 ± 3          | 48 ± 7         | 0    | 16     | 80         |
| Least Flycatcher             |                            | Young deciduous            | 52 ± 3        | 57 ± 5          | 61 ± 4         | 38   | 46     | 13         |
| Yellow-bellied Flycatcher    |                            | Young deciduous            | 67 ± 11       | 53 ± 15         | 36 ± 28        | 78   | 1      | 6          |
| Tree Swallow                 |                            | Young mixedwood            | 44 ± 2        | 52 ± 4          | 61 ± 3         | 91   | 0      | 6          |
| American Redstart            |                            | Closed deciduous           | 11 ± 3        | 42 ± 4          | 63 ± 9         | 3    | 29     | 65         |
| Red-eyed Vireo               |                            | Closed deciduous           | 1 ± 3         | 27 ± 3          | 46 ± 5         | 1    | 20     | 75         |
| Veery                        |                            | Closed deciduous           | 53 ± 8        | 72 ± 10         | 89 ± 9         | 71   | 3      | 20         |
| Dark-eyed Junco              | Yes                        | Closed coniferous          | -42 ± 1       | -43 ± 1         | -47 ± 1        | 38   | 57     | 2          |
| Wilson's Warbler             | Yes                        | Closed coniferous          | -37 ± 1       | -39 ± 1         | -45 ± 0        | 29   | 47     | 18         |
| Philadelphia Vireo            |                            | Mature deciduous           | 16 ± 2        | 26 ± 2          | 34 ± 2         | 4    | 64     | 28         |
| Canada Jay                   | Yes                        | Mature coniferous          | -29 ± 0       | -35 ± 1         | -41 ± 1        | 59   | 19     | 21         |
| Pine Grosbeak                | Yes                        | Mature coniferous          | -47 ± 1       | -47 ± 3         | -52 ± 2        | 73   | 9      | 10         |
| Red Crossbill                | Yes                        | Mature coniferous          | -27 ± 7       | -30 ± 5         | -42 ± 6        | 66   | 5      | 18         |
| Yellow-rumped Warbler        | Yes                        | Mature coniferous          | -30 ± 1       | -34 ± 2         | -37 ± 1        | 86   | 8      | 4          |
| Yellow Warbler               | Old deciduous              | 57 ± 2                    | 55 ± 3        | 57 ± 2          | 32   | 61     | 4          |
| Bay-breasted Warbler         | Yes                        | Old mixedwood              | -22 ± 1       | -32 ± 3         | -39 ± 3        | 71   | 4      | 23         |
| Blue-headed Vireo            | Yes                        | Old mixedwood              | -17 ± 1       | -29 ± 2         | -37 ± 2        | 64   | 2      | 32         |
### TABLE 2
(Continued)

| Species                 | Sensitive to climate change | Cover type and forest age | Percentage change under harvesting scenarios (%) | Key drivers of change relative contributions ($\omega^2$) |
|-------------------------|-----------------------------|---------------------------|-----------------------------------------------|-----------------------------------------------|
|                         |                             |                           | No harvesting | Baseline harvest | High harvesting | Fire | Growth | Harvesting |
| Brown Creeper           | Yes                         | Old mixedwood             | 2 ± 3         | -29 ± 4         | -51 ± 3         | 34   | 1      | 62         |
| Cape May Warbler        | Yes                         | Old mixedwood             | -25 ± 1       | -37 ± 2         | -48 ± 2         | 38   | 15     | 44         |
| Purple Finch            | Yes                         | Old mixedwood             | -30 ± 1       | -37 ± 2         | -41 ± 1         | 58   | 32     | 5          |
| Red-breasted Nuthatch   | Yes                         | Old mixedwood             | -9 ± 2        | -28 ± 3         | -42 ± 3         | 46   | 0      | 51         |
| Western Tanager         | Yes                         | Old mixedwood             | -4 ± 2        | -29 ± 3         | -47 ± 2         | 31   | 0      | 66         |
| Boreal Chickadee        | Yes                         | Old coniferous            | -34 ± 0       | -42 ± 2         | -49 ± 2         | 55   | 19     | 24         |
| Golden-crowned Kinglet  | Yes                         | Old coniferous            | -27 ± 3       | -45 ± 3         | -61 ± 2         | 40   | 7      | 50         |
| Pine Siskin             | Yes                         | Old coniferous            | -30 ± 1       | -31 ± 2         | -33 ± 2         | 42   | 50     | 3          |
| Ruby-crowned Kinglet    | Yes                         | Old coniferous            | -42 ± 1       | -44 ± 2         | -47 ± 1         | 53   | 40     | 5          |
| White-winged Crossbill  | Yes                         | Old coniferous            | -35 ± 1       | -41 ± 2         | -49 ± 1         | 59   | 17     | 22         |

*Scientific names for all species are found in Table S2.1 in Supporting Information.

*A species sensitive to climate change was defined as a bird species that was projected to experience a population abundance decline of >25% by 2100 due to alterations in habitats caused by climate change (fire and growth) under the RCP 8.5 climate projection (as simulated by the CanESM2 global climate model) and the baseline harvesting scenario.

*CRefers to the impacts of changes in dynamic biomass succession inputs and in drought.
Stand-scale drivers of forest change directly influenced by climate change (i.e. productivity and drought-related mortality) were projected to cause significant changes in bird population abundance for relatively few species (Table 2). For example, the Ruby-crowned Kinglet (Regulus calendula) was projected to experience a 44% decline in population abundance by 2100, under RCP 8.5 and baseline harvesting; changes in forest growth were estimated to contribute approximately 40% of this decline (Table 2).

3.2.3 Identification of bird species sensitive to climate change

Of the 72 passerine species, we identified 18 forest-associated species that were projected to decline in population abundance by more than 25% by 2100 under the RCP 8.5 with baseline harvesting (Table 2). The majority (89%) of these species are associated with mature and old forest habitats with mixedwood or coniferous dominated cover. For example, the Canada Jay (Perisoreus canadensis), the Ruby-crowned Kinglet and the Boreal Chickadee (Poecile hudsonicus), all mature and old conifer-associated species, were projected to decline by 35%, 44% and 42%, respectively, by 2100 under RCP8.5 and the baseline harvesting. Further, old mixedwood-associated species like the Bay-breasted Warbler (Setophaga castanea), Cape May Warbler (Setophaga tigrina) and the Western Tanager (Piranga ludoviciana) were projected to decline by 32%, 37% and 29% respectively by 2100 under the same climatic and forest harvesting scenarios. Furthermore, many species with strong climate change-induced declines were also identified as species for which a reduction in the intensity of forest harvesting could lessen the adverse effects of climate change (Table 2). For example, the Golden-crowned Kinglet was projected to decline more severely (by 61%) under high harvesting by 2100 and by 45% and 27% under the baseline harvesting and no harvesting scenarios, respectively, under RCP 8.5 (Table 2).

4 DISCUSSION

This study improves our understanding of how the avian community in the western boreal region of North America is likely to be influenced by changes in suitable habitats resulting from climate change combined with natural and anthropogenic disturbances. The use of forest landscape models (FLM) permitted us to simulate changes in forest stand composition and age structure, two important drivers of bird abundance, at temporal and spatial scales suitable for conservation planning (Cadieux et al., 2019). These simulations suggest there will be large, future shifts in the composition and abundance of the boreal bird community caused by significant declines in overall forested area, particularly in coniferous and old-growth stands. As a result, boreal forest bird species that are specialists of those habitats are likely to suffer substantial declines.

4.1 Wildfire and climate change as important drivers of shifts in the boreal bird community

Projected increases in fire activity, due to climate change, was the most important driver of change for the boreal bird community. This is in agreement with other studies (Boulanger, Taylor, et al., 2016; Stralberg, Wang, et al., 2018), which identified wildfire as the most important driver of change for southern boreal forest landscapes. In
our simulations, a significant proportion of coniferous and mixed-wood boreal forest transitioned to deciduous-dominated stands (from ca. 38% to 46% in area) or to treeless land (from ca. 0% to 23% in area) by 2100 under the most severe climate scenario. This represents not only a large change in forest composition but also a major net loss of forested bird habitat. Our simulations agree with recent findings suggesting that wildfire will act as a catalyst for forest change in a changing climate (Stralberg, Wang, et al., 2018). More specifically, our results predict significant effects on the boreal bird community through habitat alterations. First, it will likely lower the mean age of forest on the landscape by reducing the availability of old-growth stands. Second, it will generally promote the recruitment of pioneer deciduous species at the expense of conifers (Boulanger et al., 2019) or cause a transition from forest cover to treeless habitat, likely grass- or shrub-dominated vegetation (Stralberg, Wang, et al., 2018). As projected by other studies (Boulanger, Taylor, et al., 2016; Boulanger et al., 2018; Stralberg, Wang, et al., 2018; Tremblay et al., 2018), deciduous-dominated stands were projected to increase at the expense of mixedwood and conifer-dominated stands. Similarly, Stralberg, Wang, et al. (2018) found that wildfires across all of Alberta’s boreal forests could be responsible for conversion of approximately half of the coniferous and mixedwood forest cover to deciduous cover and grasslands by 2100.

Our results also suggest that the proportion of old forest (>80 years) will decline significantly with climate change (loss of ca. 30% of old forests by 2100, compared to the reference scenario). These critical changes may unfold within a few decades, causing profound impacts on several bird species. Birds associated with mature to old coniferous and mixedwood forests were projected to experience the highest declines in abundance. Hence, we classified 18 bird species as species sensitive to climate change, and for which special attention is needed. These results corroborate projections of Stralberg, Bayne, et al. (2015) in which boreal-associated late-seral birds were projected to suffer large reductions in suitable habitats due to climate change using a seral stage-adjusted bioclimatic envelope approach. Similarly, the Black-backed Woodpecker (Picoides arcticus), an old coniferous forest-associated species, was projected to dramatically decline in breeding productivity with climate change and forest harvesting in eastern Canada (Tremblay et al., 2018). Also working in the northern Alberta, Mahon et al. (2014) found that mature and old forest birds were projected to decline significantly over a 100-year simulation period. However, we found key subtle differences between our results and results coming from bioclimatic envelope approach that do not explicitly simulate vegetation-based processes (Stralberg, Bayne, et al., 2015). Our simulations showed smaller declines of species associated with young and mature coniferous forests and greater declines for species associated with old forests (Appendix S3), emphasizing the role of forest age structure over composition. These differences are likely caused by the use of a FLM in our study, which dynamically integrates natural and anthropogenic disturbances along with stand-scale processes (e.g. growth and succession) offering then to consider the lag in forest vegetation distribution relative to the projected shifts in climatic zones, and explicitly capture changes in the forest age structure.

The large projected increase in treeless land in our simulated area was beneficial for many bird species, with an average population increase of 83% for species associated with treeless habitats and with some species’ abundance projected to more than double (e.g. Savannah Sparrow—Passerculus sandwichensis and House Wren—Troglodytes aedon). The northward migration of grasslands into the boreal forest biome could represent a northern expansion of the breeding range for other range-limited species like the Sprague’s Pipit (Anthus spragueii), a threatened species in Canada (Government of Canada, 2020). Northward expansion of suitable breeding climate was projected for half of Alberta’s grassland songbirds by 2100 in a study by Nixon, Fisher, Stralberg, Bayne, and Farr (2016). However, these authors underline that grassland specialists like A. spragueii would probably be limited by a lag in soil development and vegetation establishment. To this end, our simulations do suggest that wildfire would act as a catalyst, likely increasing the speed of vegetation transition from forests to treeless land (likely grassland), as repeated fires impede the development of forest regeneration. Our results suggest that the general increase in grassland-associated species at the expense of species associated with old-growth coniferous forests can be interpreted partly as a northward expansion of grassland habitats into the boreal forest biome.

### 4.2 Effects of climate change accentuated by forest harvesting

For most boreal forest birds, the effects of climate change, positive or negative, were amplified by forest harvesting in our simulations. As such, our study highlights the important role of forest management when projecting climate-driven changes in future bird populations. Intensive or short-rotation forestry can have critical effects on boreal bird communities by lowering the availability of overmature forest, which many bird species are associated with (Hobson & Bayne, 2000; Schieck & Song, 2006). Boulanger et al. (2019) found forest harvesting in a warming climate will likely greatly accelerate discrepancies between pre-settlement and future forest composition by favouring pioneer and temperate deciduous tree species at the expense of shade-tolerant conifers. These results are consistent with Mahon et al. (2014), Roberge et al. (2018) and Tremblay et al. (2018) which conclude that boreal birds will likely benefit from a higher proportion of protected areas and reduced anthropogenic disturbances. Conversely, higher intensity of forest harvesting was projected to benefit many species, most of which were associated with young and open forests and mature mixed or deciduous forests.

### 4.3 Limitations of the simulations

Our results may be useful in identifying future threats for western North American boreal bird communities, but there are some
important caveats. First, our simulations focused on bird habitat, not population density per se. As such, our simulations may have underestimated the negative impact of climate change for some songbirds as we did not account for other climate-driven changes that may affect bird populations, such as variations in prey or food availability or for species-specific tolerances to temperature changes. Also, our simulations did not account for the potential for new species to migrate into the study region from the south. These species could have significant impacts on some boreal birds through interspecific interactions, including predation and competition for nesting or foraging resources.

4.4 | Conservation implications

Our study sheds much-needed light on passerines associated with old boreal forest habitats (see details in Table 2). For the majority of these species, the adverse effects of climate change were strongly accentuated by forest harvesting. As suggested by Mahon et al. (2014), an effective solution could be to reduce the intensity of harvesting and to retain a higher proportion of protected areas to maintain greater representation of old mixed and coniferous boreal forests on the landscape. For instance, we showed that the negative effects of forest harvesting were particularly important for old forest-associated species such as the Black-throated Green Warbler (Setophaga virens—sensitive species in Alberta), the Brown creeper (sensitive species in Alberta) and the Canada Warbler (At Risk in Alberta and in Canada; see Table S2.1 for species with special status). These three species are examples of birds associated with old deciduous and mixedwood habitats that would benefit from a lower intensity of forest harvesting under a changing climate. Such extensive measures could benefit threatened and sensitive species but also the bird community in general. Furthermore, conservation measures could be implemented in specific areas of the boreal forest most likely to act as refugia from wildfire (Krawchuk et al., 2016; Nielsen, DeLancey, Reinhardt, & Parisien, 2016) or from changes in climate (Stralberg, Carroll, et al., 2018) to be most effective. In any case, our results show there is urgent need to consider future climate threats for boreal bird species; however, threat evaluation while assessing status of species at risk in Canada is based on a 10 years horizon (following IUCN Standards and Petitions Committee (2019) guidelines), which is inappropriate for climate change impacts as impacts will be occurring on a longer horizon. Hence, we recommend the use of a vulnerability-adaptation framework to guide bird conservation based on species’ individual sensitivity and exposure to climate change (Stralberg et al., 2019). This adaptation framework would assess different species’ vulnerabilities and provide a suite of strategies to pursue, varying from classical conservation (i.e. in situ management) to more drastic strategies (i.e. such as habitat manipulation or even species translocation). For species with high exposure to climate change, such as the 18 species we identified as species sensitive to climate change, long-term investments in protecting refugia and “stepping stones” (sensu Stralberg et al., 2019) will likely be most effective, favouring natural corridors to help bird species connect with the future range of their habitat in a more fragmented landscape (Stralberg et al., 2019). Future work in this regard using our spatially explicit simulation approach may help identify areas where conservation of old forest stands will be most effective.

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DATA AVAILABILITY STATEMENT

Bird dataset and related scripts are available at https://doi.org/10.5061/dryad.mkkh70w2

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**BIOSKETCH**

The main objective of our team is to estimate the potential impacts of climate change on boreal forest landscapes and biodiversity considering harvesting and natural disturbances (such as wildfire, spruce budworm outbreaks and drought). We have used the LANDIS-II forest landscape model to simulate forest change under several future scenarios. Ultimately, our simulations produced useful information for incorporating the context of climate change into decision-making for forest management, biodiversity conservation and recovery of species at risk.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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