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# Projecting bird assemblage responses to climate-driven changes in managed boreal forest landscapes of Québec

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## ABSTRACT

Climate change presents a major threat to biodiversity, particularly in northern ecosystems. This study investigates the impacts of climate change and forest management on bird species assemblages in the boreal forests of Québec over the 2020–2100 horizon. Using spatially explicit simulations of forest landscapes and empirical abundance models for 73 bird species, we examined shifts in bird species distributions and habitat changes under various climate scenarios. Our findings highlight a range of sensitivity among bird assemblages across latitude. Results indicate that species associated with boreal coniferous and mixed forests are at greater risk of population decline, especially in southern regions, compared to more generalist species, which showed greater adaptability to changing conditions. The study incorporated the effects of wildfire, demonstrating its significant influence on bird distribution shifts along an east-west axis. Notably, increases in wildfires, especially in the northwest of the study area, may drive northwestward shifts of species associated with human-temperate forests, which can benefit from landscapes dominated by younger stands and pioneer tree species. Additionally, results show that climate change, directly and indirectly via increased wildfires, is the primary driver of habitat shifts for bird species, with its relative contribution projected to exceed forest management impacts by 2100. This research underscores the necessity of integrating disturbance regimes and comprehensive habitat modeling to better predict and manage climate change impacts on avian biodiversity in boreal ecosystems. Our results suggest that targeted conservation actions will be crucial for mitigating future climate-driven distribution shifts and population declines of boreal birds.

## 1. Introduction

Boreal forests are increasingly affected by warming temperatures, changing precipitation patterns, and extreme weather events associated with climate change (Gauthier et al., 2015). The fact that these forests are intimately linked to cold and humid climates makes them particularly vulnerable to increasing temperatures (Price et al., 2013). These changes are likely to alter species habitat distribution and availability (IPCC, 2021; Price et al., 2013; Régnière et al., 2012). Moreover, such changes may be cumulative, considering that forest management practices in boreal regions have increasingly shifted natural forests towards production forestry, which involves structural changes, including shifts in age-class distribution, corresponding to a loss of older forests to the expanse in early-successional and young forest stands, (Bürgi et al., 2017; Drapeau et al., 2009a; Mackey et al., 2023). These changes can affect habitat quality and availability for wildlife, especially species that rely on older forest structures (Blois et al., 2013; Drapeau et al., 2009b; Mantyka-Pringle et al., 2012; Oliver and Morecroft, 2014).

Birds are a key element of boreal forest ecosystems and are essential for maintaining ecosystem functions and services (Blancher and Wells, 2005; Cadieux et al., 2023; Martin et al., 2004). However, forest management practices have led to changes in forest cover, notably through a

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shift in forest age classes. The overall extent of older forests has decreased considerably, balanced by increases in regenerating and early-successional stands (Drapeau et al., 2009a; Gauthier et al., 2009; Mackey et al., 2023), and resulting in changes in bird density and distribution (Betts et al., 2022; Drapeau et al., 2016, 2000). At the same time, many species' ranges are projected to shift in size, latitude, and elevation under future climates (Virkkala and Lehikoinen, 2014). While global climate and land-use changes may ultimately lead to species extinction, community reorganization, and biotic homogenization, understanding the complex interactions between these two dominant drivers of global environmental change and their impacts on species and communities remains a dynamic area of research. In the boreal region, future projections based on bioclimatic models have suggested the potential for dramatic species range shifts, depending on disturbance dynamics and the rate of forest change (Bateman et al., 2020; Berteaux et al., 2018; Stralberg et al., 2015a, 2015b). Given extensive forest management and industrial development activities, it is important to be able to consider climate change and forest management simultaneously (Bouderbala et al., 2023; Cadieux et al., 2020; Labadie et al., 2024b; Raymundo et al., 2024).

Understanding the potential effects of global change on bird assemblages requires an understanding of spatial heterogeneity in landscape changes. The boreal forest is characterized by relatively low productivity and is dominated by few broadly distributed tree species within the *Picea*, *Abies*, *Pinus*, *Populus*, *Betula* and *Larix* genera (Lenihan, 1993; McKenney et al., 2007). Despite relatively low tree species richness, boreal forest stands exhibit high habitat heterogeneity, shaped by active natural disturbance regimes, and a diversity of physical setting (i.e., topography and soil characteristics) (Price et al., 2013). In the context of a warming climate, the boreal forest is expected to have a higher proportion of deciduous vegetation (Boulanger and Pascual Puigdevall, 2021). This, combined with a progressive decrease in the extent of older forests because of increased disturbances, both from forest harvesting and natural origins, may be one of the major threats to the integrity of boreal communities (Cadieux et al., 2020; Cadieux and Drapeau, 2017; Carroll, 2007; Drapeau et al., 2000; Janssen et al., 2009; Labadie et al., 2024a). Yet, there has been little focus on the variability among birds in their responses to these interacting environmental pressures. To fill this research gap, we combined LANDIS-II, a spatially explicit simulation model of forest landscapes (Scheller et al., 2007) with empirical machine-learning models of bird abundance and distribution (Labadie et al., 2024b), developed from point-count data compiled by the Boreal Avian Modeling Project (BAM; Barker et al., 2015). From these spatially explicit models, we projected the impacts of climate change and forest management scenarios on bird populations over a large portion of the eastern North American boreal forest. The diverse regional characteristics pertaining to the vast commercial forest (~423,000 km$^2$) of Québec offer a unique opportunity to examine the spatial heterogeneity of future boreal forest ecosystems induced by climate- and forest management-changes. While recent studies have examined the effects of climate and forest management in specific regions of Québec (e.g., Bouderbala et al., 2023; Labadie et al., 2024b), our study extends this approach across all commercial forests in Québec. This comprehensive spatial coverage enables a detailed analysis of how drivers of change impact bird assemblages and bioclimatic subdomains across a much larger and more heterogeneous landscape.

We conducted spatially explicit simulations of forest landscapes to estimate how changes in forest composition and structure would alter individual bird densities, habitat suitability and distribution based on BAM empirical models of distribution and abundance for 73 bird species. We synthesized the results at the level of species assemblages associated with specific forest habitats rather than focusing on individual species trends. This approach allowed us to examine broader habitat-based trends, which align more closely with the study's objectives. Indeed, our research specifically focused on understanding how the impacts of forest management and climate change vary across different assemblages of species associated with specific forest habitats, how the responses of these bird species assemblages differ spatially, and how the drivers of change vary across bird assemblages and bioclimatic subdomains.

## 2. Methods

### 2.1. Study areas

Our study area includes the hemiboreal and boreal zones of the commercial forests of Québec (Canada) (Fig. 1). The boreal zone in the north is mainly composed of coniferous species, described as the black spruce-feathermoss bioclimatic domain, whereas the southern fringe is represented by the mixedwood balsam fir-white birch bioclimatic domain (Fig. 1, Saucier et al. (1998); Talbot (2008). The hemiboreal zone is in the mixed forest subzone and is represented by the balsam fir-yellow birch bioclimatic domain (Fig. 1). Forest stands established in different topographic, geological, and geomorphologic contexts were represented in this extensive study area, which covered most of the contiguous commercial forests of Québec.

### 2.2. Model overview

This research features the projection of population densities for multiple bird species within projected forest landscapes, considering different scenarios of climate change and forest management (Fig. 2). The forest landscape simulations used in this study were obtained from Boulanger and Pascual Puigdevall (2021). Our investigation integrates models of bird species densities derived from avian point count data spanning from 1996 to 2022, originating from the Boreal Avian Modeling (BAM) project (Barker et al., 2015). Point-count data were used to develop predictive models linking bird densities with forest characteristics (see Labadie et al., 2024b and below for details). From these models, we projected expected density for individual bird species within future simulated forest landscapes subjected to two levels of forest harvesting (No harvest and Harvest) and encompassing three CMIP5 (Taylor et al., 2012) climate change scenarios. The first climate scenario, referred to as the baseline scenario, and the other two scenarios, namely Representative Concentration Pathway (RCP) 4.5 and RCP 8.5, were used to project future climate conditions (Van Vuuren et al., 2011). RCP 4.5 represents a moderate warming scenario with stabilized emissions at year 2100, whereas RCP 8.5 is a high-emissions scenario with more severe projected warming and no stabilization of the emissions. We synthesized the results at the level of species assemblages associated with specific forest habitats rather than by individual species (see section 5b). Bird assemblages were determined with a redundancy analysis (RDA) coupled with a hierarchical cluster analysis. We used predicted species densities and environmental variables from the reference year as inputs for the RDA. Species scores from the RDA were then used to group species into assemblages based on habitat associations.

### 2.3. Spatially explicit forest simulation model

Below, we provide an overview of the main components of the different models and forest landscape details (detailed in Appendix S1 Section S1). Readers interested in obtaining additional information regarding these aspects can consult Appendix S1 Section S1 and other studies, such as Boulanger and Pascual Puigdevall (2021) for details on the forest simulation model.

In this study, future forest landscape projections were generated based on three different global warming trajectories (Van Vuuren et al., 2011). To project future climate conditions, we used results obtained from the Canadian Earth System Model version 2 (CanESM2). The first scenario, referred to as the baseline scenario, assumed no climate change and projected current (1981–2010) climate conditions

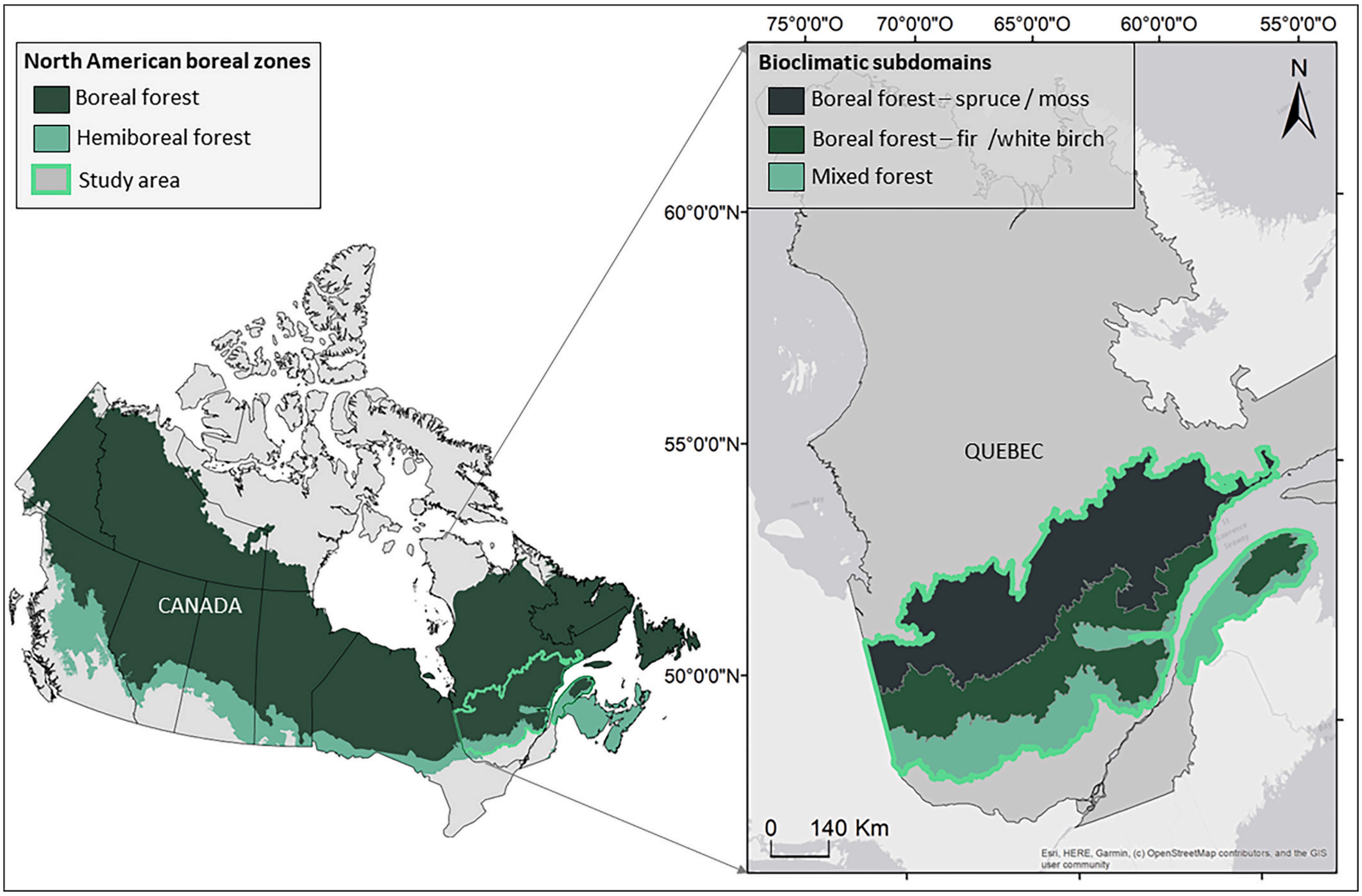

**Fig. 1.**. Location of the study area (in light green) in the province of Québec, Canada and the North American boreal zones in Canada (following Brandt, 2009). On the right, the three bioclimatic subdomains (Robitaille and Saucier, 1998) of Québec's commercial forests are shown. The study area represents 7% of the Canadian boreal and hemiboreal zones. Sources of the basemap: Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS User Community (ESRI).

throughout the simulation period. The other two scenarios, RCP 4.5 and RCP 8.5, were based on increased anthropogenic radiative forcing and were used to project future climate conditions. RCP 4.5 was considered more optimistic with an anticipated temperature increase of around 3 °C in the study area, while RCP 8.5 was viewed as more pessimistic, predicting an increase of 7.5 °C in the study area by 2100 compared to 2000.

LANDIS-II v6 (Scheller and Mladenoff, 2004) was used to conduct forest landscape simulations. LANDIS-II is a raster-based spatially-explicit forest landscape model that dynamically simulates ecological processes at both the stand- and landscape scales, accounting for disturbances, seed dispersal, and competition between tree cohorts (Scheller et al., 2007). Changes in temperature and precipitation resulting from climate change are considered, as they affect tree species' growth and establishment parameters (Lexer and Hönninger, 2001), as well as the natural disturbance regime. Forest succession emerges from interactions between tree cohorts, based on those growth and establishment parameters and fixed species traits (e.g., shade tolerance, longevity, seed dispersal, etc.), in addition to disturbance history and resulting mortality. The simulated area was the full extent of the commercial forests of Québec. Spruce budworm outbreaks, windthrow and climate-induced changes in wildfires were included as natural disturbances. Adjusting the growth and regeneration rates of various tree species at the individual stand level was conducted through the Biomass Succession v3.2 extension (Scheller and Mladenoff, 2004). Additionally, future fire dynamics were calibrated in line with Boulanger et al. (2014), treating them as probabilistic occurrences across the landscape using the Base Fire v3.0 extension. Recurrent spruce budworm infestations, occurring every 40 years, were modeled using the Biological Disturbance Agent extension (Sturtevant et al., 2004), which prioritized balsam fir, along with white and black spruce as primary hosts in descending order of susceptibility. Logging activities were represented through simulations conducted with the Biomass Harvest extension (v3.0; (Gustafson et al., 2000). We assessed the impact of a business-as-usual forest management scenario that emulates ecosystem-based forest management complying with Québec legislation on sustainable forest development (Québec, 2013). The prescriptions for each forest management unit (FMU) were defined based on various stand- (local soil and vegetation characteristics) and FMU-level parameters, including the proportion of biomass harvested during each harvest event, harvested patch size, minimum stand age for harvest, which cohort should be harvested, and the proportion of the FMU that should be harvested per timestep according to this prescription. Harvesting prescriptions details can be found in Boulanger and Pascual Puigdevall (2021). In summary, harvesting in the southern part of the study area was mainly simulated as small-patch partial harvest, notably in deciduous stands, whereas in the northernmost part of the study area, large patch clear-cutting was much more common. Harvest rates remained constant throughout the simulations, unless there were insufficient stands that met the criteria for harvest, in which case harvest proceeded until no more eligible stands were available.

Simulations were conducted using a 10-yr time step and a 250-m resolution for 130 years, beginning in 2020 for each of the three radiative forcing scenarios. Each scenario was replicated five times, to consider the effects of stochastic parameters (Boulanger and Pascual Puigdevall, 2021). For the purpose of this study, we cropped Boulanger and Pascual Puigdevall (2021) simulation results to the study area while constraining our interpretation of the results to the first 80 years

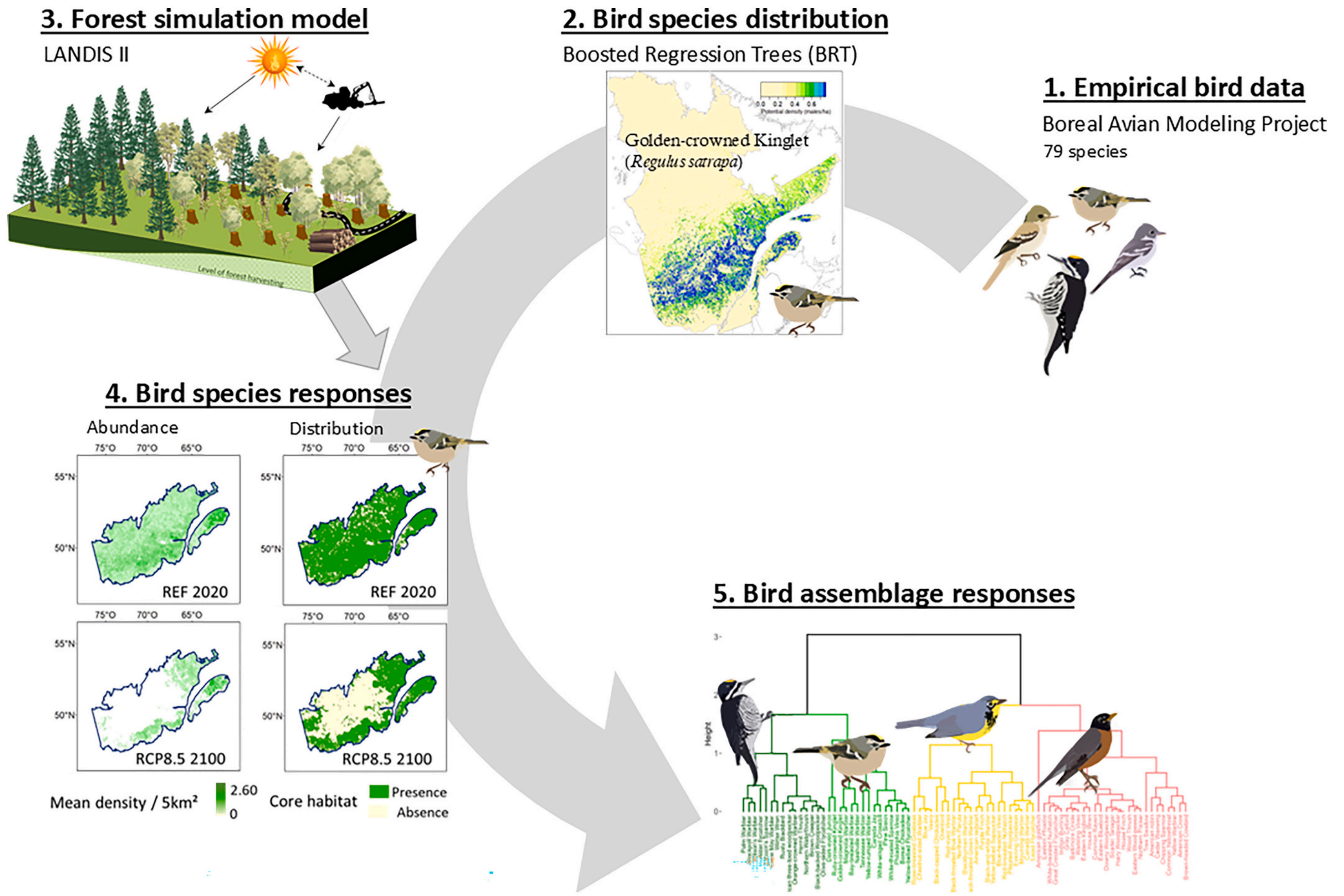

**Fig. 2.**. Schematic representation of the simulation design implemented in this study. (1-2) Data on bird observations were used to build species-specific predictive density models. (3) A forest landscape model, LANDIS-II, was used to simulate stand- (i.e., individual tree establishment, growth, and mortality) and landscape-scale dynamics (seed dispersal, natural, and anthropogenic disturbances), allowing climate change and land use to differentially impact forest landscapes. (4) LANDIS-II simulation outputs were used along with vegetation-based bird density models to project future distributions and densities of 73 bird species. (5) We then conducted analyses on bird assemblages that were determined with a redundancy analysis coupled with a hierarchical cluster analysis.

(2020–2100).

### 2.4. Bird species abundance models

Species abundance models were developed according to methods described in Labadie et al. (2024b) and summarized here. In summary, boosted regression tree models were built using an avian point-count dataset assembled by the Boreal Avian Modeling Project (BAM; borealbirds.ca) and standardized using detectability offsets described in Sólymos et al. (2013). The BAM dataset contains data from various sources, including the volunteer Breeding Bird Survey (BBS; pwrc.usgs.gov/bbs), the Québec 2nd breeding bird atlas (Robert et al., 2019), and institutional and individual contributors. Common forest landbird species were selected based on seasonal histograms of eBird sightings, resulting in 79 species (Table S1). We used a total of 64,107 surveys conducted at 33,674 unique locations (all of the observations contained within our study area). To develop the models, we randomly subsampled one survey per location (Table S1). For each of these species, we modeled density (males/ha) as a function of different vegetation and landscape variables using Boosted Regression Trees (BRT; Elith et al., 2008) with a Poisson distribution. 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 Stralberg et al. (2015b). We used 47 variables characterizing the forest structure and composition at local and landscape scales (Table S2). To ensure compatibility with LANDIS-II outputs, namely species-specific biomass and stand age, vegetation variables were based on predictive models derived from the Canadian National Forest Inventory and 250-m MODIS imagery, which provide similar variables (Beaudoin et al., 2018, 2014). Covariates used for bird model fitting were either assumed static (e.g., water bodies, wetland) or dynamic and allowed to change between simulations and time steps in LANDIS-II simulations (i.e., tree species biomass, age, and climate covariates). As suggested by Chandler and Hepinstall-Cymerman (2016), variables were quantified at two spatial extents: the original value assigned to each 250-m cell (6.25 ha "local effect") and mean values at the landscape scale based on a Gaussian filter with sigma = 750 m (*focalweight* function in the *raster* package, Hijmans and van Etten (2012)), which included information from an area up to ~700 ha (1500-m radius). The *gbm.step* function in the *dismo* package (Hijmans et al., 2022) was used to build and predict the models. Pseudo-$R^2$ (deviance explained) based on cross-validation mean deviance values was used as an indicator of model explanatory power (Table S1) and variable importance scores for vegetation and climate predictors were used to assess the relative contributions of individual predictors in each species' model (Table S3). This allowed projecting population distributions for each bird species at multiple time steps, as well as bird assemblages associated with each forest cover and age class (i.e., habitat), that we determined with a redundancy analysis coupled with a hierarchical cluster analysis (as detailed in 5.a. Bird assemblage analyses and in Table S1).

### 2.5. *Data analyses*

In this study, we examined the projected changes in bird abundance and core habitat size, categorized into distinct assemblages, with a particular emphasis on sensitive species (i.e., species projected to undergo substantial changes — either an increase or decrease of >25 % — in their population abundance or core habitat size). Our analysis primarily focused on the most severe climate change scenario, RCP 8.5, and its implications due to shifts in forest composition by the year 2100 (see Appendix S1 Section S1 for details). We initially included 79 bird species to determine assemblages based on their forest habitat preferences, ensuring a comprehensive representation of the ecosystem. However, for subsequent analyses, we removed 6 species as models describing their density exhibited very low pseudo-R-squared values, indicating insufficient predictive power. This approach allowed us to maintain the robustness of the assemblage determination while ensuring the reliability of the cumulative impact analyses.

### a. **Bird density estimates and core habitat**

We used the projected density estimates obtained from the BRT models applied to LANDIS-II outputs to estimate the pixel-level density (breeding males/ha) of each bird species at each time step. The outcomes from the five replicates were averaged for every climate scenario and time step. Each projected density map was rescaled at a 5-km resolution to smooth out variation associated with local heterogeneity, and summed up to obtain abundance estimates. The core habitat for a given bird species was then defined as the grid cells where the model-predicted density in 2020 exceeded the median reference predicted density for that species within the model-building area (as in (Stralberg et al., 2015a).

### b. **Bird assemblage analyses**

We conducted further analyses on bird assemblages (i.e., sets of species that share, at least partially, similar habitat requirements) rather than on individual species to understand cumulative impacts of climate change and forest management on bird assemblages and how their responses may differ spatially. To do so, we conducted a redundancy analysis coupled with a hierarchical cluster analysis to determine bird assemblages based on their forest habitat preferences.

#### 2.5.1. *Redundancy analysis*

A redundancy analysis (RDA) was performed to assess affinities of bird species with environmental explanatory variables and hence to define bird assemblages. Redundancy analysis, a method similar to multiple regression but for a matrix of dependent variables, combines ordination and regression components to identify patterns in response data that are best described by the particular subset of environmental or predictor factors used (Legendre and Legendre, 2012). The multivariate species variables were the predicted densities of birds smoothed at 5-km obtained from the BRT. We used the Hellinger-transform method to reduce the importance of rare species (Borcard et al., 2018; Legendre and Gallagher, 2001). This transformation is particularly suited to data with low counts and many zeros. The environmental variables ($n = 47$) were standardized before analyses (Borcard et al. (2018); more details in Table S2). Only significant environmental factors from the preliminary analysis were used in the final iteration ($n = 28$), and the final set of environmental variables was chosen in a preliminary RDA using forward selection ($\alpha = 0.001$), as recommended by Lepš and Šmilauer (2003) (Table S4). The RDA was performed with the *rda* function in the *vegan* package (Oksanen, 2017) in R version 4.2.2 (R Core Team, 2021). Variance inflation factors (VIF, threshold value of 10; (Borcard et al., 2018)) were calculated to ensure that multicollinearity among the predictor variables retained for analyses was avoided (Zuur et al., 2010). The global significance of the RDA was performed with a permutation test ($n = 999$).

#### 2.5.2. *Hierarchical cluster analysis*

The environmental variables explained 75.9 % of the variation in predicted densities of bird assemblages across sites. The first two axes of the RDA explained 60.3 % of the total variance, with the first axis alone explaining 45.8 %. The species-specific RDA scores from axes 1 and 2 were used in a hierarchical cluster analysis to determine bird assemblages based on their forest habitat preferences as characterized by the environmental variables. Species scores were proportionally scaled to both axes' eigenvalues. We then calculated a pairwise Euclidian distance matrix between species based on the scores of the two axes and ran a hierarchical cluster analysis on this matrix with complete linkage as the clustering method. Four clusters were determined by maximizing the *Silhouettes* index with the a*s.clustrange* function from the *WeightedCluster* package (Studer, 2013) in R.

#### 2.5.3. *Bird assemblage specificity*

We then assessed the main environmental variables associated with each bird assemblage. To do so, we selected point-count locations used in the BRT model where at least half of the bird species within a chosen assemblage were predicted to be present. From all those selected sites, the environmental characteristics used (e.g., the total tree biomass, mean stand age, urban development, proportion of water, proportion of boreal coniferous and deciduous stands and the proportion of thermophilous coniferous and deciduous stands) were summarized.

### c. **Bird species and assemblage's responses under the cumulative impact of climate change and forest management**

We have chosen to focus on the outcomes related to bird assemblage responses and have therefore provided a brief description of the landscape composition changes in the Appendix S1 Section S1.

#### 2.5.4. *Bird species abundance*

We evaluated changes in the abundance of each individual bird species within each of the three bioclimatic subdomains by calculating the difference of the simulated abundance predicted under the climate forcing scenarios at year 2050 and 2100 relative to the simulated abundance predicted under the reference period (i.e., in 2020). For each climate scenario and time step, the cumulative impact of forest management and climate change were considered important when a given bird species showed ≥25 % change in abundance (either decrease or increase) compared with the reference period (i.e., sensitive species) as in Cadieux et al. (2020). The rationale for using this percentage of change to identify sensitive species is in line with IUCN scores to consider species populations that show a moderate threat (changes between 10 and 30 % (Master et al., 2012). It also echoes Mahon et al. (2019) paper on boreal landbirds responses to stressors created by multiple resource industries to identify winners and losers where substantial changes in species densities correspond to increases or decreases >20 %. For each of the three bioclimatic subdomains, we then assessed the percentage of sensitive individual bird species within each assemblage.

#### 2.5.5. *Bird species core habitat size*

We evaluated changes in the size of the core habitat for a given individual bird species within the three bioclimatic subdomains by comparing core area in 2050 and 2100 under each cumulative climate change and forest management scenario with the core area predicted at initialization (2020). For each scenario and time step, the cumulative impact of forest management and climate change were considered important when the species core habitat either shrunk or expanded by >25 % compared with the reference period for each of the three bioclimatic subdomains. We then assessed the percentage of sensitive individual bird species within each assemblage for each of the three bioclimatic subdomains.

### 2.5.6. Bird assemblage distribution shifts

To understand how climate change and forest management are expected to impact the distribution of specific bird species assemblages at the subcontinental scale, we determined changes in the location of the weighted spatial centroid of each assemblage in 2050 and 2100 under each scenario. Bird assemblage centroids were first assessed by calculating the spatial centroid of each bird species pertaining to the given assemblage by using the projected bird abundance and the *wt.centroid* function from the package *spatialEco* (Evans et al., 2023) in R. Species-specific spatial centroids were calculated under each scenario in 2020, 2050 and 2100. Then, centroids for a given assemblage were determined by calculating the kernel of each bird assemblage from individual bird species centroids. We used these kernels to assess assemblage's centroids by calculating their spatial weighted mean. We then assessed shifts of each bird assemblage centroid by calculating the distance and the direction separating centroid locations between time steps under each scenario.

## d. Specific impact of the drivers of change

The relative contribution of each driver of change, i.e., climate change impacts on stand-level dynamic, forest management (harvesting rate), and the increase in wildfires due to climate change, was assessed by estimating the variance of individual bird abundance and the size of bird core habitat specifically explained by each driver using omega-squared values ($\omega^2$). In this analysis, to allow distinct assessment of its effects on forest composition and bird assemblages, we distinguished the stand-level effects of climate change (referred to "impacts of climate change"), including modifications in tree growth and regeneration rates, and induced-changes in wildfire due to climate change as a separate disturbance factor. Analyses were completed for each bioclimatic subdomain separately. To do so, we ran additional forest landscape simulations in which we controlled for forest management (by running additional simulations without harvesting) and climate-induced increase in fire activity (by running additional simulations keeping fire parameters as under the baseline scenario) according to a factorial design. Other simulations parameters were kept similar to those used for simulations assessing the cumulative effects of forest management and climate change). Specific bird densities were then computed for these simulations as described above. Following a three-way factorial ANOVA, where each driver of change was considered as a factor, we calculated $\omega^2$ for each driver of change, at each time step, as in Cadieux et al. (2020):

$$\omega^2 = \left(\mathrm{SS_{effect}} - \left(\mathrm{df_{effect}} \times \mathrm{MS_{error}}\right)\right) \Big/ \left(\mathrm{MS_{error}} + \mathrm{SS_{tot}}\right) \tag{1}$$

where $SS_{effect}$ is the sum of squares related to the driver of change (the effect), $df_{effect}$ is the degree of freedom of the effect, $MS_{error}$ is the mean square of the error, and $SS_{tot}$ is the total sum of squares. ANOVA and $\omega^2$ calculations were performed separately for each climate scenario.

The mean $\omega^2$ values for a given assemblage were determined by averaging the $\omega^2$ values of individual bird species within each specific assemblage. This allowed to discern variations in the relative contribution of each driver of change among the distinct bird assemblages.

## 3. Results

Overall, results indicated a progressive increase over time in sensitive species showing density gains in the more extreme climate scenarios (RCP 8.5), with the proportion of sensitive species increasing in density reaching 53 % under RCP 8.5 in 2100, compared to 46 % under the baseline scenario. Sensitive species with density decreases also tended to increase over time, from 17 % in the baseline scenario to 25 % under RCP 8.5 in 2100, indicating heightened vulnerability under more intense climate scenarios.

The proportion of sensitive species exhibiting core habitat gains or losses also varied with climate scenario and time. By 2100, under RCP 8.5, 18 % of sensitive species gained core habitat presence, compared to 3 % in 2050. Habitat vulnerability also increased under RCP 8.5, with 10 % of sensitive species showing significant loss of core habitat by 2100, up from 0.5 % in 2050.

Bird responses showed distinct patterns within bioclimatic subdomains. In the boreal fir-white birch and boreal spruce-moss bioclimatic subdomains, both located in the boreal forest, the proportion of species with increasing density was projected to rise by 10 % between the baseline scenario and RCP 8.5 in 2100. In contrast, the mixedwood bioclimatic subdomain showed stability, with little change in the proportion of species exhibiting density increases across scenarios. Similarly, for sensitive species experiencing density decreases, the proportion was expected to nearly double in the boreal fir-white birch and boreal spruce-moss subdomains between the baseline scenario and RCP 8.5 in 2100, while remaining stable in the mixedwood subdomain.

The hierarchical cluster analysis resulted in four distinguishable clusters, with a similar number of bird species within each assemblage (Fig. 3). Based on vegetation inputs, we described the four clusters (bird assemblages) as species associated with 1) boreal coniferous forests (Fig. S3a), 2) boreal mixedwood forests (Fig. S3b), 3) thermophilous mixedwood forests (Fig. S3c), and 4) human-temperate forests (Fig. S3d). Spatial centroids of each species assemblage corresponded well to the forest characteristics within which these birds were associated (Fig. S4).

Our results revealed latitudinal variations in bird species assemblage responses, with distinct latitudinal trends in the two response variables (i.e., changes in abundance and core habitat size). For bird abundance, it was observed that within the mixedwood, boreal fir-white birch, and boreal spruce-moss bioclimatic subdomains, 22 %, 33 %, and 19 % of all individual bird species, respectively, were anticipated to experience a large decline in abundance (≥25 %) (Fig. 4). The boreal fir-white birch subdomain had the highest number of sensitive species in each assemblage that are predicted to decline in abundance (Table S5). Within the same subdomains, 41 %, 55 %, and 64 % of species, respectively, were projected to see a large increase in abundance (Fig. 4, Table S5). A distinct pattern emerged among bird assemblages: the assemblages associated with human-temperate forests and with thermophilous mixed forests had the highest percentages of species projected to experience an increase in abundance (Fig. 4). Conversely, the assemblages of boreal mixed and boreal coniferous species had the greatest percentage of species projected to undergo a decrease in abundance (Fig. 4).

In terms of the size of their core habitat, 7 %, 15 %, and 8 % of bird species in the respective subdomains (i.e., mixedwood, boreal fir-white birch, and boreal spruce-moss bioclimatic subdomains) were projected to lose >25 % of their core habitat, while 5 %, 25 %, and 25 % of species within these subdomains were projected to gain >25 % in the size of their core habitat (Fig. 4, Table S5). Fewer species exhibited sensitivity when examining changes in the size of their core habitat compared to changes in population abundance (Fig. 4). Notably, bird species associated with boreal mixedwood stands were consistently identified as the most negatively affected within all three subdomains. In contrast, bird species associated with human-temperate forests were predicted to be the assemblage with an important increase in the size of their core habitat (Fig. 4).

Furthermore, 13 species associated with human-temperate forests and 7 species associated with thermophilous mixedwood forests were predicted to increase in abundance by 2100 under RCP 8.5 in each bioclimatic subdomain (Table S5). Conversely, 9 species associated with boreal forests (3 associated with boreal coniferous forests and 6 associated with boreal mixedwood forests) were predicted to decrease in abundance in each bioclimatic subdomain (Table S5).

Most assemblages were projected to shift to the northeast in response to the impact of climate change and forest management on forest

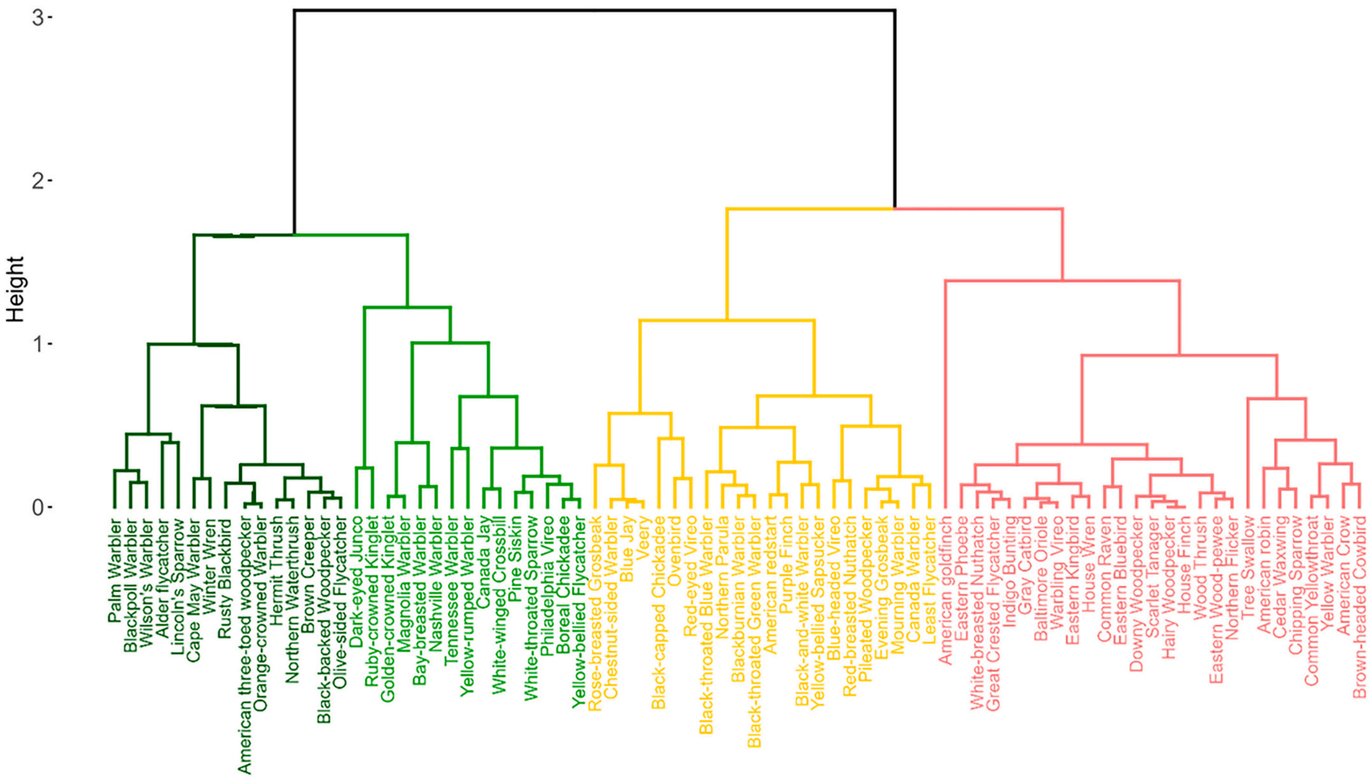

**Fig. 3..** Results of hierarchical clustering. The four clusters were identified by maximizing the Silhouettes index gained by cutting the tree at different levels and the ecological interpretability of the resulting clusters. 1) boreal coniferous forests (dark green; cluster 1), 2) human-temperate forests (red; cluster 2), 3) thermophilous mixedwood forests (yellow; cluster 3), and 4) boreal mixedwood forests (light green; cluster 4). Height (y-axis) represents the distances between clusters.

structure and composition (Figs. 5, S5), but species associated with human-temperate forests were predicted to shift westward (Figs. 5, S5). However, regardless of the shift in longitude, all bird assemblages were also projected to shift northward. Shifts were most severe under the most aggressive climate change scenario (RCP 8.5) for birds associated with boreal mixedwood and coniferous forests (Table S6). These bird assemblages were projected to shift almost twice as far in 80 years under RCP 8.5 compared to RCP 4.5 (Fig. 5). For the two other bird assemblages, projected range centroid shifts were rather similar between RCP 4.5 and RCP 8.5 (Fig. 5). Results showed rather large inter-specific variations in spatial centroids within a given assemblage (Figs. S8–S10).

By 2100 under RCP 8.5, climate change impacts on stand-level dynamics were projected to be the main drivers of changes in bird abundance and core habitat size for all bird species assemblages within the mixedwood bioclimatic subdomain (Fig. 6). Within the boreal fir-white birch bioclimatic subdomain, both climate-induced changes in stand-level dynamics and increases in wildfires were projected to mainly drive bird abundance changes (Fig. 6a). The increase in wildfires was projected to be the main driver of core habitat changes, except for the bird assemblage associated with boreal coniferous stands, which was mainly affected by climate-induced changes in stand-level dynamics (Fig. 6b). In the northernmost regions, within the boreal spruce-moss bioclimatic subdomain, abundance and core habitat size for bird species associated with human-temperate forests, as well as the birds associated with boreal mixed forests, were projected to be mostly impacted by changes in wildfires (Fig. 6). Bird species associated with thermophilous mixed stands were projected to be most impacted by both changes in forest management and wildfires (Fig. 6). The abundance and core habitat sizes of bird species associated with boreal coniferous stands were projected to be most impacted by both climate-induced changes in stand-level dynamics and the increase in wildfires (Fig. 6).

Under RCP 4.5 in 2100, the relative contribution of forest management was generally larger than under RCP 8.5. Within the boreal fir-white birch and the boreal spruce-moss bioclimatic subdomains, the relative contribution of climate change was projected to be smaller under RCP 4.5 compared with RCP 8.5. We also observed that the relative contribution of forest management in comparison to other sources of variation, decreased over time (Figs. S6–S7). Indeed, in 2050 under RCP 8.5, the relative contribution of forest management explained, on average, 30 % of abundance changes (Figs. S6), compared to 15 % by 2100 (Fig. 6a). Similarly, in 2050 under RCP 8.5, the relative contribution of forest management explained, on average, 27 % of the change in core habitat (Fig. S7), compared to 14 % by 2100 (Fig. 6b). The relative contribution of changes in wildfires was predicted to remain fairly constant over time, while the relative contribution of climate-induced changes in stand-level dynamics was predicted to increase by 8 % on average in 2100 compared to 2050 (Figs. 6, S6–S7).

## 4. Discussion

This study highlights the critical interplay between climate change and forest management in shaping future bird assemblages through changes in suitable habitats. Through forest landscape simulations, our study focused on the impacts of natural disturbance and forest harvesting on forest composition, and consequent effects on bird habitats. We underscore the significance of the potential for forest management practices and climate change, through the induced shifts in forest stand composition, to shape biodiversity within Québec's commercial forests over the coming decades. While species distribution models for this region have focused on the potential impacts of either climate change using a correlational approach (Bateman et al., 2020; Berteaux et al., 2018; Stralberg et al., 2015b) or land-use changes (Betts et al., 2022) on birds, our combined modeling approach provides a more in-depth analysis of the interaction between climate change and forest management effects. Importantly, our models did not directly link climate change to bird populations but instead accounted for the delayed

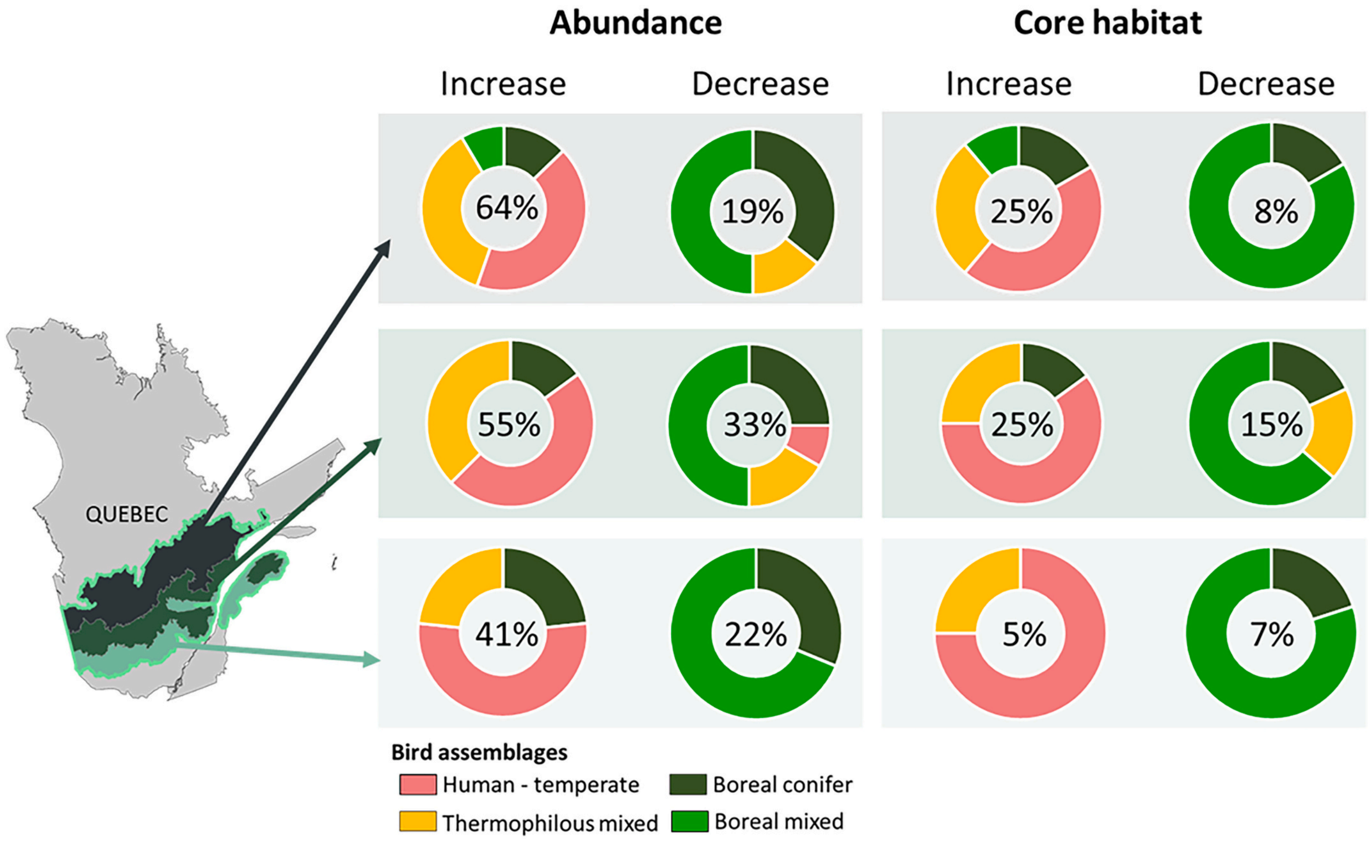

**Fig. 4..** Percent of bird species that are predicted to be sensitive to the cumulative impact of climate change and forest management under RCP 8.5 in 2100. The cumulative impact of forest management and climate change are considered important when bird species associated to a bird species assemblage show an increase or a decrease in their abundance or the size of their core habitat of more than 25% compared to the reference period (i.e., 2020). The three bioclimatic subdomains are indicated on the map: the mixedwood (light green), boreal fir-white birch (medium green), and boreal spruce-moss (dark green) bioclimatic subdomains.

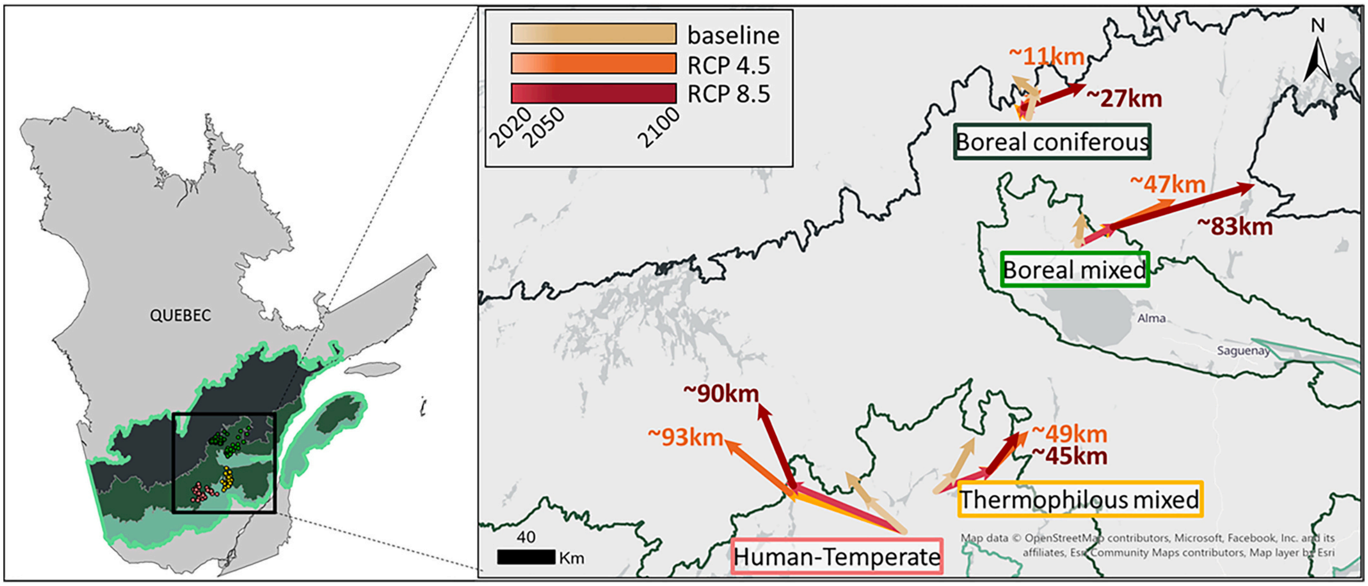

**Fig. 5..** Direction and distance of predicted range centroid shift of bird assemblages in 2050 (light color) and 2100 (dark color) under baseline, RCP 4.5 and RCP 8.5 climate scenarios. The origin of the arrows corresponded to the centroid in the reference period (2020) for each bird assemblage. Values in red and orange corresponded to the distance (in Km) between the centroid in 2020 and the centroid under RCP 8.5 and RCP 4.5, respectively, in 2100 for each bird assemblage.

response of forest vegetation to climate change. While conservative, this approach allowed us to simulate long-term responses to disturbances and assess the sensitivity of the avifauna at both the species and assemblage levels.

On average, across all scenarios and bioclimatic domains, our projections indicated that 15 % of bird species may see a decline in

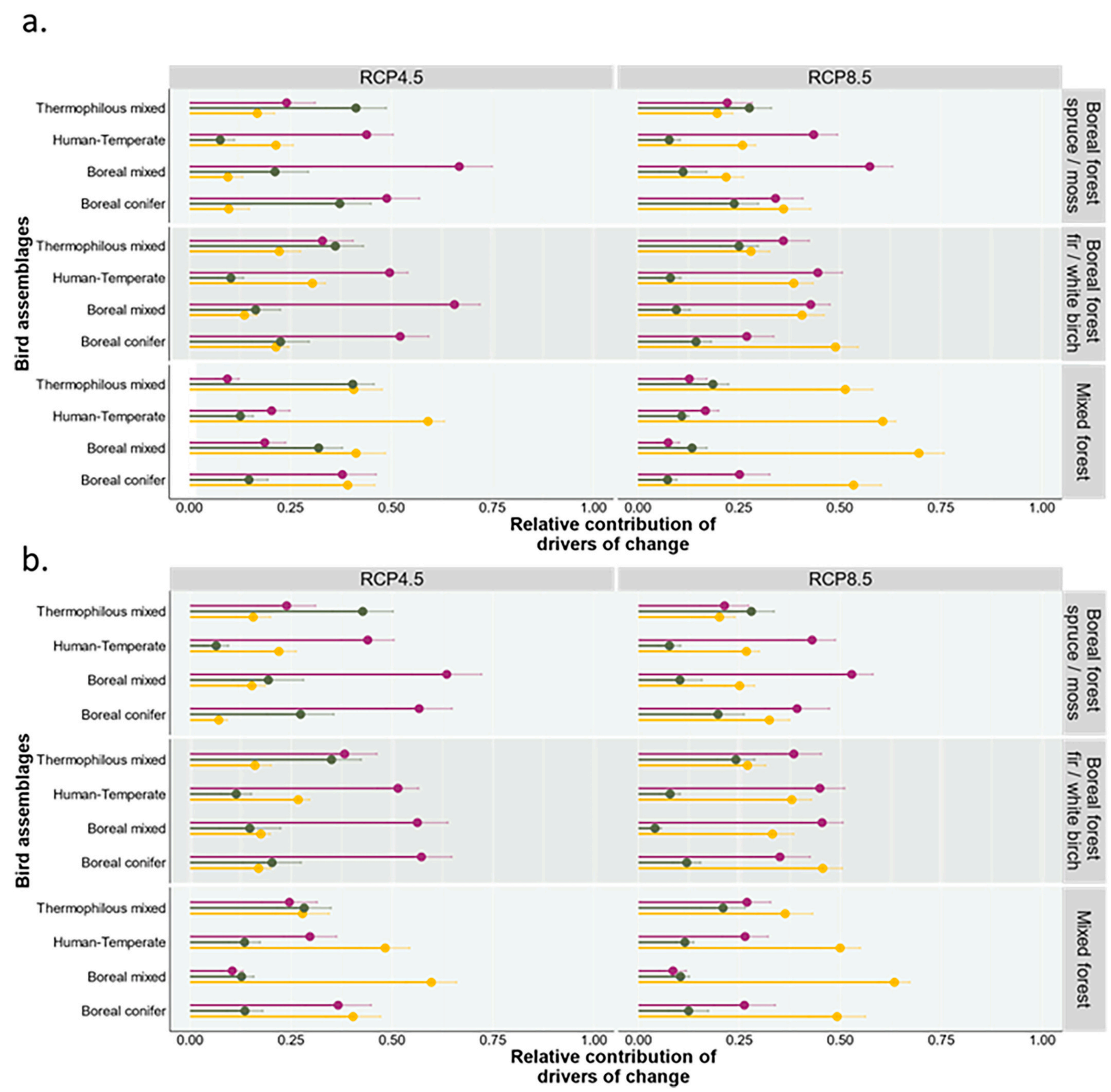

**Fig. 6..** The mean relative contribution of drivers of change (climate change (yellow), wildfires (purple) and forest management (green)) on a) bird abundance and b) core area as values of ω2 (mean) for each bird assemblage, under RCP 4.5 and RCP 8.5 at year 2100 relative to the change simulated in 2020. Error bars are represented in lighter shades of the same colors.

abundance, and 3 % of species may experience a reduction in their core habitat by >25 % by 2100. Our results based on forest landscape changes are less dramatic than those reported by Stralberg et al. (2015a, 2015b), who projected abundance declines for approximately 50 % of boreal bird species, or Bateman et al. (2020), who predicted significant range losses for over 90 % of boreal species. However, our study identifies a few species (Table S5), such as the Golden-crowned Kinglet (*Regulus satrapa*) and the Cape May Warbler (*Setophaga tigrina*), that are projected to decline in abundance by >70 % and lose approximately 50 % of their core habitat. As emphasized by Raymundo et al. (2024), a forest landscape simulation approach allows for the identification of climate-vulnerable species, including both currently at-risk species such as Blackpoll Warbler (*Setophaga striata*) and Rusty Blackbird (*Euphagus carolinus*), and common species that are not currently listed as a conservation concern. Furthermore, our findings emphasize the varying degrees of vulnerability among bird assemblages. Species associated with boreal coniferous and mixed forests were projected to be at a higher risk of decline, particularly in the forest’s southern regions, compared to more generalist species, better suited to the conditions of temperate or human-altered habitats. Notably, under a scenario with mitigated emissions (RCP 4.5), the projected changes were less severe compared to a scenario where emissions persistently increase throughout the century (RCP 8.5). This highlights the critical role of climate-change mitigation for bird conservation (Bateman et al., 2020).

We found that the long-term projected effects of climate change are likely to lead to a shift in forest structure and composition characterized by younger forests with an increase in deciduous cover (Boulanger and Pascual Puigdevall, 2021; Drapeau et al., 2000; Nitschke, 2008). The projected influence of climate change at the stand level decreased with latitude, while the influence of wildfires, which are expected to reduce the occurrence of old-growth stands (Bergeron et al., 2017; Boulanger et al., 2016; Tremblay et al., 2018), increased with latitude. The decrease in old-growth forest is likely to be exacerbated by the legacy of ongoing even-aged forest management, which has already shifted the age structure of the forest towards young stands (Cyr et al., 2009; Drapeau et al., 2009a; Mackey et al., 2023; Tremblay et al., 2018). Increases in the frequency of wildfires are also generally anticipated to facilitate the establishment of pioneer deciduous species at the expense of conifers, especially in the western part of the study area (Boulanger and Pascual Puigdevall, 2021). In contrast with northern regions, climate-change impacts at the stand level would be the dominant driver of landscape and bird changes in the southern boreal mixedwood region, through increased tree competition and mortality caused by warmer climate and drought (Boulanger and Pascual Puigdevall, 2021). The dominant relative contribution of wildfires on birds is consistent with other recent predictions in western (Cadieux et al., 2020) and eastern Canada (Tremblay et al., 2018). Our results thus suggest that birds occurring in northern boreal forest regions are expected to be more heavily impacted than those in southern mixedwood regions (Boulanger and Pascual Puigdevall, 2021), due to the cumulative influence of both direct (via increased drought and heat) and indirect (via increased wildfire frequency) effects of climate change on the forest cover.

Our analysis revealed temporal heterogeneity in the relative contributions of the different drivers on landscape compositional changes. Specifically, the relative contribution of climate change was projected to strengthen over time, while the relative contribution of forest management would slightly decrease, leading to a larger influence of climate change and an associated increase in wildfires, overshadowing the impact of forest management by 2100. As a result, forest management is likely to have a stronger impact in the short-term, while climate change will likely have a stronger impact on the long term (Parmesan et al., 2013, Labadie et al., 2024b). Therefore, forest management is playing a crucial role in altering forest conditions up to when climate-driven shifts in bird assemblages will occur, as forest management impacts persist and may exacerbate the consequences of climate change. The long-term influence of forest management on forest cover dynamics is significant (Bergeron et al., 2006; Mackey et al., 2023). Landscapes altered by even-aged management practices, characterized by a high ratio of young forests at the expense of mature and old growth, have lasting impacts on a forest's resilience to fire (Boucher et al., 2017; Cyr et al., 2009). Heavily harvested landscapes under climate-induced increases in fire activity are more prone to regeneration failures (Splawinski et al., 2019) while cumulative disturbances can exacerbate the “caducification”, i.e., the increase in deciduous biomass, of the boreal forest (Boulanger and Pascual Puigdevall, 2021). With climate change projected to increase wildfire frequency in the near term, these managed forests are increasingly challenged in their ability to regenerate effectively.

Current forest management practices in Québec's commercial forests predominantly rely on even-aged management (Cyr et al., 2009), which mainly include clear-cutting designed to meet industrial timber demands. This sylvicultural system, while efficient for wood production, often results in landscape homogenization and a significant reduction in the structural complexity of forest landscapes necessary for biodiversity (Gauthier et al., 2009; Venier et al., 2014). Furthermore, the short rotation cycles commonly applied in managed forests fail to allow sufficient recovery of older forest attributes, which are critical for maintaining birds associated with older forests, habitat diversity and forest resilience (Boucher et al., 2017; Drapeau et al., 2016; Gauthier et al., 2009). Addressing these limitations would benefit from a shift towards ecosystem-oriented management strategies that incorporate longer rotation cycles, more retention harvesting, and mixed-species planting (Boulanger et al., 2023; Cyr et al., 2022; Splawinski et al., 2019). These practices would also align with goals for carbon storage, ecosystem services, and biodiversity conservation, thus helping to bridge current gaps in management (Gauthier et al., 2009; Labadie et al., 2024b). While some of these methods may already be recognized, barriers to their widespread implementation include economic constraints, policy rigidity, and a limited integration of recent scientific insights on ecosystem dynamics into practical guidelines.

As a function of projected vegetation changes, we observed substantial latitudinal variation in the proportions of individual bird species within each assemblage that were sensitive to the cumulative impact of climate change and forest management. In the northern portion of the study area, the proportion of species that was projected to increase in abundance under RCP 8.5 by 2100 was 3.4 times higher than the proportion that was anticipated to decrease. Conversely, in the southern portion of the study area, where fewer species were projected to increase in abundance, the proportion of increasing species was projected to be 1.9 times higher. We observed the same pattern for projected core habitat changes. Indeed, the number of species that were projected to increase in the boreal regions was five times higher than the number projected to increase in the southern region, and mostly consisted of species associated with human-temperate forests. This projected northward shift in abundance is consistent with modeling results for many North American and European regions and bird species (Barbet-Massin et al., 2012; Berteaux et al., 2018; McCaslin and Heath, 2020). However, our study may underestimate the changes in bird communities in the southern regions, as the colonization of more southern species within the mixedwood bioclimatic subdomain was not considered. Studies by Berteaux et al. (2010, 2014) suggest a potential increase in biodiversity across Québec within this century, as climate change may lead to population increases for species currently limited by cold temperatures (Berteaux et al., 2018, 2014).

Projected concurrent changes in landscape composition and climate combined will likely lead to asynchronous shifts in community structure (Folke et al., 2004). While the inertia in current forests may allow some bird species to persist, others may be more vulnerable to vegetation changes initiated by harvest and wildfire. The nature of community change may thus be largely dependent on future fire regimes and the rate of forest harvesting.

The projected change in landscape composition translated into projected shifts of bird distribution centroïds by approximately 0.14 to 1.16 km per year, depending on the climate scenario. This rate aligns with studies that have estimated actual observed rates of range shift in response to contemporary climate change (1.03 km/y La Sorte and Thompson III, 2007; 1.5 km/y Martins et al., 2024; 0.63 km/y Parmesan and Yohe, 2003). However, our findings suggest a much more moderate pace than what is suggested by correlative bioclimatic models, i.e., two to ten times slower than the shifts reported in Bateman et al. (2016), Chen et al. (2011) and McCaslin and Heath (2020). This discrepancy underscores the possibility for factors beyond climate change alone to influence shifts in abundance (Lehikoinen and Virkkala, 2016). Indeed, climate and land-use changes act synergistically (Northrup et al., 2019), and lags in vegetation responses are expected. Subsequently, shifts of bird distribution will depend on the velocity of vegetation changes, and the level of disturbance affecting bird habitats.

By including the impact of natural disturbances on forest composition, and subsequently on bird habitats, we also showed that wildfires are expected to influence bird distribution shifts along an east-west gradient. For one, we found that increases in wildfire may explain northwestward shifts of bird species associated with human-temperate forests that benefit from landscapes dominated by younger stands and pioneer tree species. Conversely, boreal bird assemblages are likely to seek landscapes less prone to fire, a shift that may not be explained or predicted with bioclimatic envelope models. Understanding the nuances of species-specific movement directions and the velocity of these changes is crucial for accurate predictions of species distributions and for informing conservation efforts.

The projected increase in deciduous vegetation induced by climate change and forest management was associated with a projected increase in generalist species and those favoring disturbed habitats, at the expense of disturbance-sensitive species (Betts et al., 2022; Nitschke, 2008). Accordingly, our results highlight that bird species composition within Québec is projected to shift towards species associated with human-temperate forests and thermophilous mixed forests at the expense of birds associated with boreal forests. Across bioclimatic domains, 12 boreal mixedwood forest species (i.e., 80 % of the 15 species within this assemblage) were predicted to be sensitive under the most severe anthropogenic climate change. These findings align with prior studies on the cumulative effects of land-use change and wildfire (Regos et al., 2018), as well as insights from Drapeau et al. (2016). In contrast, 48 % of bird species associated with human-temperate forests were anticipated to increase in abundance by >25 % within the three bioclimatic subdomains. Given the different rates of change across assemblages, there is a possibility for novel species communities to form, revealing previously unobserved species interactions. These new interactions could influence population dynamics in unforeseen ways, potentially leading to localized extinctions if species cannot rapidly adapt to the changing patterns of co-occurrence (Stralberg et al., 2009).

## 5. Limitations

It is important to acknowledge several factors that were not fully considered in the study. Firstly, we did not explicitly account for the potential impacts of forest fragmentation and spatial habitat patterns on habitat quality. While our research demonstrated significant changes in forest composition by 2050, particularly in response to forest management practices, the subsequent alterations in forest structure, which often result in increased fragmentation, were not comprehensively addressed (Villard and Metzger, 2014). However, we did include landscape-scale forest composition in our models, which Drapeau et al. (2000) found to have a more important influence on bird community composition varied than landscape structure. Furthermore, we did not include climate directly in our bird models, but rather focused on changes in bird habitat. Thus, we did not investigate the complexities of thermal tolerance, prey availability, or other effects of climate not directly related to forest composition and structure. Also, we did not consider the impact of climate change and forest management on species interactions, and changes in predation and competition linked with the potential arrival of new species from the south. Lastly, for boreal species, our simulations did not extend beyond the northern limit for forest management activities, which may constrain the projected shifts in species centroids and potentially underrepresent the full extent of their northward movement.

## 6. Conclusion

Our study underscores the need for further research into the complex interplay between climate change, land use, and biodiversity in boreal ecosystems. Ultimately, our findings provide a valuable foundation for the development of effective conservation strategies in boreal forest ecosystems, ensuring the preservation of avian diversity during rapid environmental transformations. Future studies should aim to refine our understanding of how adaptive conservation strategies and specific forest management practices can mitigate the adverse effects of climate change on birds. For example, mitigation efforts could be coupled with selective logging and conservation of climate-change refugia, especially in the boreal zones that are predicted to experience intensifying pressure from forest harvesting and the increase in wildfires. A nuanced approach to forest management, recognizing its potential both as a threat and as a tool for conservation, is vital for informing policy decisions and management practices aimed at maintaining the boreal forest's resilience in the face of climate change.

## CRediT authorship contribution statement

**Guillemette Labadie:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Yan Boulanger:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Pierre Drapeau:** Writing – review & editing, Funding acquisition. **Diana Stralberg:** Writing – review & editing, Data curation. **Junior A. Tremblay:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110956.

## Data availability

The datasets generated during and analyzed during the current study will be made available in the Dryad repository, if the paper gets accepted for publication.

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