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Assessing Pathways of Climate Change Effects in SpaDES: An Application to Boreal Landbirds of Northwest Territories Canada

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Distributions of landbirds in Canadian northern forests are expected to be affected by climate change, but it remains unclear which pathways are responsible for projected climate effects. Determining whether climate change acts indirectly through changing fire regimes and/or vegetation dynamics, or directly through changes in climatic suitability may allow land managers to address negative trajectories via forest management. We used SpaDES, a novel toolkit built in R that facilitates the implementation of simulation models from different areas of knowledge to develop a simulation experiment for a study area comprising 50 million ha in the Northwest Territories, Canada. Our factorial experiment was designed to contrast climate effects pathways on 64 landbird species using climate-sensitive and non-climate sensitive models for tree growth and mortality, wildfire, and landbirds. Climate-change effects were predicted to increase suitable habitat for 73% of species, resulting in average net gain of 7.49 million ha across species. We observed higher species turnover in the northeastern, south-central (species loss), and western regions (species gain). Importantly, we found that most of the predicted differences in net area of occupancy across models were attributed to direct climate effects rather than simulated vegetation change, despite a similar relative importance of vegetation and climate variables in landbird models. Even with close to a doubling of annual area burned by 2100, and a 600 kg/ha increase in aboveground tree biomass predicted in this region, differences in landbird net occupancy across models attributed to climate-driven forest growth were very small, likely resulting from differences in the pace of vegetation and climate changes, or vegetation lags. The effect of vegetation lags (i.e., differences from climatic equilibrium) varied across species,

resulting in a wide range of changes in landbird distribution, and consequently predicted occupancy, due to climate effects. These findings suggest that hybrid approaches using statistical models and landscape simulation tools could improve wildlife forecasts when future uncoupling of vegetation and climate is anticipated. This study lays some of the methodological groundwork for ecological adaptive management using the new platform SpaDES, which allows for iterative forecasting, mixing of modeling paradigms, and tightening connections between data, parameterization, and simulation.

Keywords: landscape simulation, ecological forecasting, vegetation, fire, decision support, forest management, reproducibility, reusability

INTRODUCTION

The North American boreal forest represents approximately 48% of the continent's forests (Smith et al., 2018), and it provides breeding habitat for half of North American bird species (Wells and Blancher, 2011). In recent decades, the southern boreal forest has seen rapid economic development from forestry, agriculture, oil, bitumen and gas, with attendant consequences for the region's biodiversity (Hebblewhite, 2017; Mahon et al., 2019; Stewart et al., 2020). However, in the northern parts of the boreal forest, climate change is perhaps the greatest threat to biodiversity (Price et al., 2013). The region is warming at twice the global average rate (Masson-Delmotte et al., 2019), which is expected to increase the frequency, extent, and severity of droughts and wildfires (Boulanger et al., 2014; Gauthier et al., 2015; Masson-Delmotte et al., 2019). An overall decrease in tree productivity and total biomass may be expected in these northern regions (Boulanger et al., 2017), with projected shifts from mid- and late-successional conifers (*Picea* spp.) to fire-adapted pioneer species of genus *Populus* and *Pinus*. Major vegetation transitions of this nature have been documented (Wang et al., 2020), with a combination of frequent fire and drought (Whitman et al., 2019) as well as permafrost thaw (Helbig et al., 2016) potentially playing major roles. As a result, climate change may alter the diversity and abundance of many terrestrial taxa (Dawson et al., 2011), including landbirds (Stralberg et al., 2015a; Cadieux et al., 2020).

More than half of boreal landbird species have shown declines in abundance over the last five decades (Rosenberg et al., 2019) and climate change may exacerbate these trends. According to Stralberg et al. (2015a), projected changes in end-of-century breeding habitat for boreal landbirds range from an average 40% change based on bioclimatic models alone (with 45% of species decreasing), to a projected 20–60% contraction when considering vegetation lags due to climate change (70–100% of species decreasing). Similarly, Bateman et al. (2020a) estimated that 98% of 48 modeled boreal landbird species were at moderate to high risk of range size contraction due to climate change, based on bioclimatic niche models. Climate change may cause range and/or population changes through several mechanisms, with different implications for management. Climate change might act indirectly, through climate-induced changes to vegetation or wildfire and resulting change to habitat, or directly, through non-vegetation mediated climatic effects. The relative importance of these pathways has important implications for management. For

example, if climate-caused declines are indirect, land managers can use tree-planting, vegetation restoration, or fuel limitation as on-the-ground adaptation strategies to reduce the system's vulnerability to the effects of climate change (Bauduin et al., 2020), and consequently improve conservation. If climate-caused declines are direct, more drastic adaptation actions such as species translocation, as well as mitigation strategies that can change climate trajectories in the short-term may be needed to meet conservation objectives. Quantifying the relative importance of these alternate pathways is a matter of urgency given current and projected declines in boreal landbirds (Tremblay et al., 2018; Stralberg et al., 2019; Cadieux et al., 2020).

Separating direct from indirect pathways of climate effects poses a significant challenge for standard statistical modeling approaches to both predicting and forecasting wildlife distribution. Interactions and feedback loops (or simply "feedbacks") among different drivers of change are not yet fully understood, but have the potential to greatly influence outcomes (Bush and Lemmen, 2019; Wilcox et al., 2019; Turetsky et al., 2020). It has been shown, for example, that the forecasted direction of species' movements under climate change in some cases suggests northern retractions rather than the expected expansions (e.g., Clason et al., 2020). Our current ability to forecast how the various pathways of climate may affect landbird occupancy in boreal forests is limited. Landbird projections to date have been mostly based on statistical correlations between landbird abundance and climate and vegetation covariates, without including feedbacks between climate, habitat, and disturbance regimes (but see Tremblay et al., 2018; Cadieux et al., 2019, 2020). More realistic near-term forecasts can come from dynamic simulations where ecological elements can interact during the forecast period. Interactions and feedbacks could allow, for example, annual vegetation changes to affect annual wildfire forecasts, which in turn affect subsequent vegetation (Marchal et al., 2017a,b, 2019). Absent this, forecasts may diverge too greatly from the upcoming future, potentially resulting in ineffective management actions and misapplication of scarce conservation resources. To address such challenges in the field of predictive ecology (Peters, 1982; Clark, 2001; Dietze et al., 2018; Yates et al., 2018; Dietze and Lynch, 2019; White et al., 2019) and conservation biology (Travers et al., 2019), and improve both uncertainty assessment and conservation resource allocation, the ability to integrate dynamic simulation models such as of forest growth and mortality, wildfire, and wildlife distribution is

essential. Spatial Discrete Event Simulation (SpaDES) has been developed with such purposes in mind (Chubaty and McIntire, 2021; McIntire et al., 2021).

Spatial Discrete Event Simulation is a platform that facilitates the use of the PERFICT approach, which stands for Predictive Ecology that is built on the concepts of Reusability, Free availability, and Interoperability of models, which are built around a Continuous workflow, and Tested automatically (McIntire et al., 2021). In a nutshell, the SpaDES platform allows wrapping models (typically implemented in R scripts) into *modules* and schedules the execution of these modules, allowing for different models (e.g., from siloed areas of knowledge) to interact through their shared inputs and outputs. For example, both forest age and species composition influence the estimation of wildfire parameters (i.e., ignition, escape, and spread probabilities), which in turn, are used to simulate landscape burning modifying both the forest age and its composition (i.e., via serotiny). Continuing the simulation, the new forest composition and age modify the following year's fire parameter probabilities. Species distribution models are then influenced by the forest composition and potentially other parameters for each simulation year, and can eventually also play a role in modifying both forest growth and wildfire regimes if biological processes such as seed dispersal are modeled. Because SpaDES is implemented in R, it allows tight coupling of data import, processing, modeling, and analyses with simulation components.

Focusing on the Taiga Plains ecozone within the Northwest Territories, Canada, we used this novel and dynamic simulation platform to (i) begin teasing apart the individual effects of direct and indirect climate-change pathways, and (ii) forecast the combined direct and indirect effects of climate pathways, including their interactions and feedbacks, on landbirds. To answer such complex ecological forecasting questions, we developed a simulation experiment of climate sensitive/non-climate sensitive models for (i) forest growth, (ii) wildfire, and (iii) landbird densities. We used existing modules for forest growth and wildfire and wrapped the landbirds' statistical models into a module, as described below. Considering the large simulated effects of climate on both vegetation (Boulanger et al., 2017) and wildfire regime in several boreal regions (Boulanger et al., 2014; Gauthier et al., 2015; Masson-Delmotte et al., 2019; Cadieux et al., 2020), we anticipated that all pathways would contribute substantially to the effect of climate on landbird species forecasted occupancy. Using SpaDES allowed us to integrate statistical and geospatial simulations to generate tightly coupled data-simulation forecasts covering large spatial and temporal extents (McIntire et al., 2021) to begin investigating the pathways through which climate change will affect boreal landbird species.

MATERIALS AND METHODS

Study Area and Species

The Taiga Plains ecozone within the Northwest Territories is located in northwestern Canada, and encompasses approximately 50 million ha (**Supplementary Appendix I Figure A1**).

This vast area is primarily composed of upland (50%) and lowland (15%) boreal forests, intermixed with many lakes and small waterbodies (15%), with the remaining 20% land cover composed mostly of low vegetation (i.e., shrubs, herbs, barren ground), ice, and human development (Ecosystem Classification Group, 2007). The predominant tree species are black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and tamarack (*Larix laricina*) (Ecosystem Classification Group, 2007).

The Northwest Territories hosts nearly 300 breeding landbird species (Lepage, 2019), with twenty of these considered Species at Risk (SAR) at the federal and/or territorial government levels (GNWT, 2019). Our present analysis focused on 64 of these landbird species (**Table 1**), including two SAR. The species selected for modeling were chosen primarily based on the availability of survey data within the Northwest Territories and the availability of density offsets (Sólymos et al., 2013) to standardize point-count survey estimates (see section "Landbird Models").

Simulation Experiment

We developed statistical and simulation models for boreal landbirds, wildfire, and forest growth using the SpaDES modeling framework (Chubaty and McIntire, 2021; **Figure 1**), implemented as a suite of packages in R (R Core Team, 2019). Even though many of the drivers used in the geospatial simulation models (specifically LandR-Biomass and FireSense; see below) have been estimated using statistical approaches, we distinguish "simulation models" as iterative, dynamic models whose subsequent iteration depends on the previous state. This describes the vegetation and fire models, but not the "statistical" landbird models, for which predictions are derived solely from the covariates, which may or be dynamic or static, at the time of prediction (e.g., as "simulated" by the fire and vegetation models).

We developed or adapted three types of ecological models: (i) forest growth and succession (simulation model); (ii) wildfire (simulation model); and (iii) landbird species densities (statistical models). We developed pairs of each of these three model types: "climate-sensitive" (CS) variants in which climate covariates are explicit, and "non-climate-sensitive" (non-CS) variants where climate covariates are excluded (although climate may act implicitly, e.g., via vegetation covariates), for a total of six models: two forest growth succession models (CS and non-CS), two wildfire models (CS and non-CS), and two landbird density (CS and non-CS). To disentangle climate pathways, we developed a fully factorial simulation experiment involving the three model types with two levels each (CS and non-CS), resulting in $2 \times 2 \times 2 = 8$ treatment combinations (labeled I to VIII; **Table 2** and **Figure 2**). By developing six unique models, we are implementing a "best-in-type" approach to forecasting. Such a novel approach involves building two distinct models (CS and non-CS) for each model type (tree growth, wildfire, and landbird) rather than one "full" model of each type where the non-CS forecast is simply the full model with fixed climate covariates at their mean. The best-in-type

TABLE 1 | Landbird species code, common and scientific names, and the number of records (number of individuals detected in point count surveys) per species in the dataset used to build the landbird statistical models.

Species code	Common name	Scientific name	No. records
ALFL	Alder Flycatcher	<i>Empidonax alhorum</i>	21,766
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	25,672
AMRE	American Redstart	<i>Setophaga ruticilla</i>	17,689
AMRO	American Robin	<i>Turdus migratorius</i>	34,825
ATSP	American Tree Sparrow	<i>Spizella arborea</i>	354
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	5,963
BBWA	Bay-breasted Warbler	<i>Setophaga castanea</i>	4,048
BBWO	Black-backed Woodpecker	<i>Picoides arcticus</i>	421
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	8,258
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	9,092
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	6,358
BLPW	Blackpoll Warbler	<i>Setophaga striata</i>	1,132
BOCH	Boreal Chickadee	<i>Poecile hudsonicus</i>	2,567
BRBL	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	5,643
BRCR	Brown Creeper	<i>Certhia americana</i>	3,196
BTNW	Black throated Green Warbler	<i>Setophaga virens</i>	9,318
CAWA	Canada Warbler	<i>Cardellina canadensis</i>	3,715
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	41,075
CORA	Common Raven	<i>Corvus corax</i>	14,733
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	14,935
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	17,901
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	895
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	1,407
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	2,302
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>	9,999
HETH	Hermit Thrush	<i>Catharus guttatus</i>	25,251
HOLA	Horned Lark	<i>Eremophila alpestris</i>	300
LCSP	Le Conte's Sparrow	<i>Ammodramus leconteii</i>	6,727
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	26,990
LISP	Lincoln's Sparrow	<i>Melospiza lincolni</i>	23,225
MAWA	Magnolia Warbler	<i>Setophaga magnolia</i>	10,868
NOFL	Northern Flicker	<i>Colaptes auratus</i>	5,012
NOWA	Northern Waterthrush	<i>Parkesia noveboracensis</i>	4,675
OCWA	Orange-crowned Warbler	<i>Oreothlypis celata</i>	5,245
OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>	1,575
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	57,723
PAWA	Palm Warbler	<i>Setophaga palmarum</i>	4,709
PISI	Pine Siskin	<i>Spinus pinus</i>	12,022
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	1,757
PUFI	Purple Finch	<i>Haemorhous purpureus</i>	1,183
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	14,546
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	10,964
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	20,671
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	51,564
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>	4,214
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	28,540
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	19,748
SOSP	Song Sparrow	<i>Melospiza melodia</i>	16,415
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	5,945
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	48,944
TEWA	Tennessee Warbler	<i>Oreothlypis peregrina</i>	68,503
TRES	Tree Swallow	<i>Tachycineta bicolor</i>	6,375

(Continued)

TABLE 1 | (Continued)

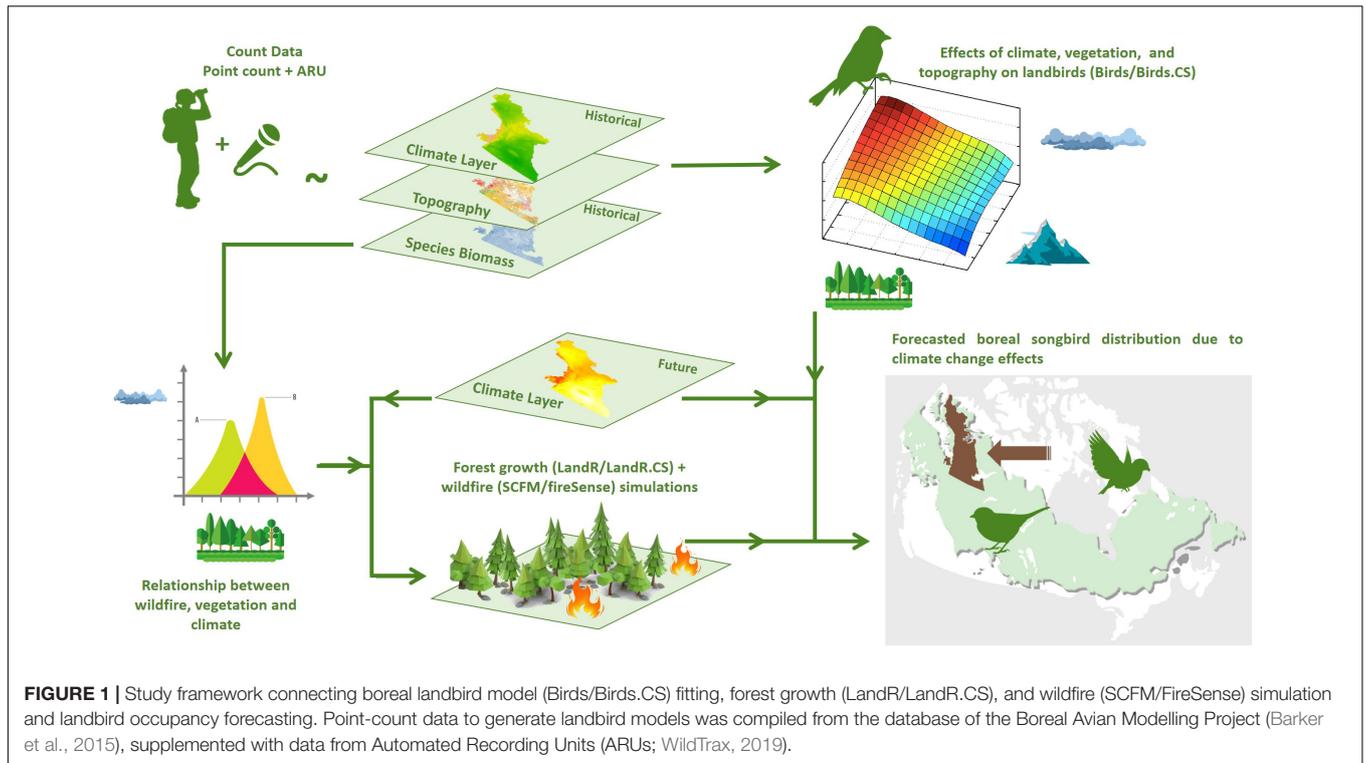
Species code	Common name	Scientific name	No. records
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	10,734
WCSP	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	1,965
WETA	Western Tanager	<i>Piranga ludoviciana</i>	9,671
WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>	2,657
WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>	1,324
WIWR	Winter Wren	<i>Troglodytes hiemalis</i>	9,391
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	86,333
WWCR	White-winged Crossbill	<i>Loxia leucoptera</i>	6,778
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	2,202
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	13,672
YEWA	Yellow Warbler	<i>Setophaga petechia</i>	24,564
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	59,281

approach proposed here partitions more of the variance to non-climate covariates in the non-CS model than it does in its climate-sensitive counterpart, since there is likely some degree of collinearity between these covariates. While some of the extra partitioned variance will be noise, some of it will be a signal incorrectly attributed to the climate covariates in the CS models. This results in a more informative non-CS model than a single “full” model type. A caveat to this approach is that the “control” model (in the present work, the non-CS) is not merely a simplified version of the “experimental” model (in the present work, the CS model with no climate covariates): they are alternative fits to data with different assumptions. As discussed below, we focused on assessing the pathways of climate change effects on landbirds (i.e., differences between models) rather than exploring forecasted climate-sensitive landbird occupancy (i.e., forecasts of one model). In this case, using a “full control model” that would only include factors that are not changing over time (i.e., our non-CS model I with included static climate variables) would result in mostly unchanging predictions, which are not relevant for the purpose of this study. Therefore, while our control model could include climate variables, it would not present different outcomes from the one used. Our used approach has the advantage of allowing researchers to reuse models from any arbitrary source, regardless of the area of research and method used, e.g., computer simulation or machine learning, in this case.

We ran 90-year simulations at an annual time step from 2011 through 2100. We used a common spatial resolution of 250 m across all models to align with the resolution of the input stand biomass layers. For each of the eight treatment combinations, we ran 10 replicate simulations to incorporate the inherent stochasticity of the wildfire and vegetation dynamics models. Finally, for each component of this study we have selected, to our knowledge, the best available models given the available data and process models, and our objectives.

Climate Data

We obtained historical climate normals (1981–2010) from ClimateNA (Wang et al., 2016) and <https://adaptwest.databasin.org/> to match as closely as possible the years of data in each



of the vegetation, fire and bird databases and used these for parameterizing each of the climate-sensitive components of the respective models. We obtained annual (2011–2100) climate projection layers, downscaled to a 1-km grid cell resolution using the ClimateNA software, from forecasts of the Community Climate System Model version 4 (CCSM4) general circulation model from the U.S. National Center for Climate Research. CCSM4 is a coupled climate model that simulates earth’s climate system. It was chosen due to its high spatial resolution (0.9424° latitude, 1.2500° longitude) and because it has shown good overall performance in other regions when compared to

other climate models with available annual forecasts (Ahmed et al., 2019) and its averaged precipitation and temperature changes are the closest to the ensemble model for our study region (Fajardo et al., 2020). We used climate forecasts under Representative Concentration Pathway (RCP) 8.5, which may be considered as a worst-case scenario of climate change for 2100 based on a continuation of current policies and economic incentives (Hausfather and Peters, 2020). We chose RCP 8.5 as evidence suggests that the average increase in temperature in the present century will likely exceed RCP 4.5 (Sherwood et al., 2020), supporting instead the use of RCP 8.5 for forecasts (Schwalm et al., 2020). We focus our current work on assessing uncertainty due to climate effect pathways, rather than other sources of uncertainty, such as choice of climate model or emissions scenario. The climate data was post-processed to match the resolution of the vegetation layers by applying a bilinear interpolation using the function *postProcess* from the reproducible R package (McIntire and Chubaty, 2021).

TABLE 2 | Wildfire, forest growth and landbird models used in a factorial simulation experiment to explore the pathways through which climate change might drive responses and forecast the net effect of climate change on different boreal landbird species.

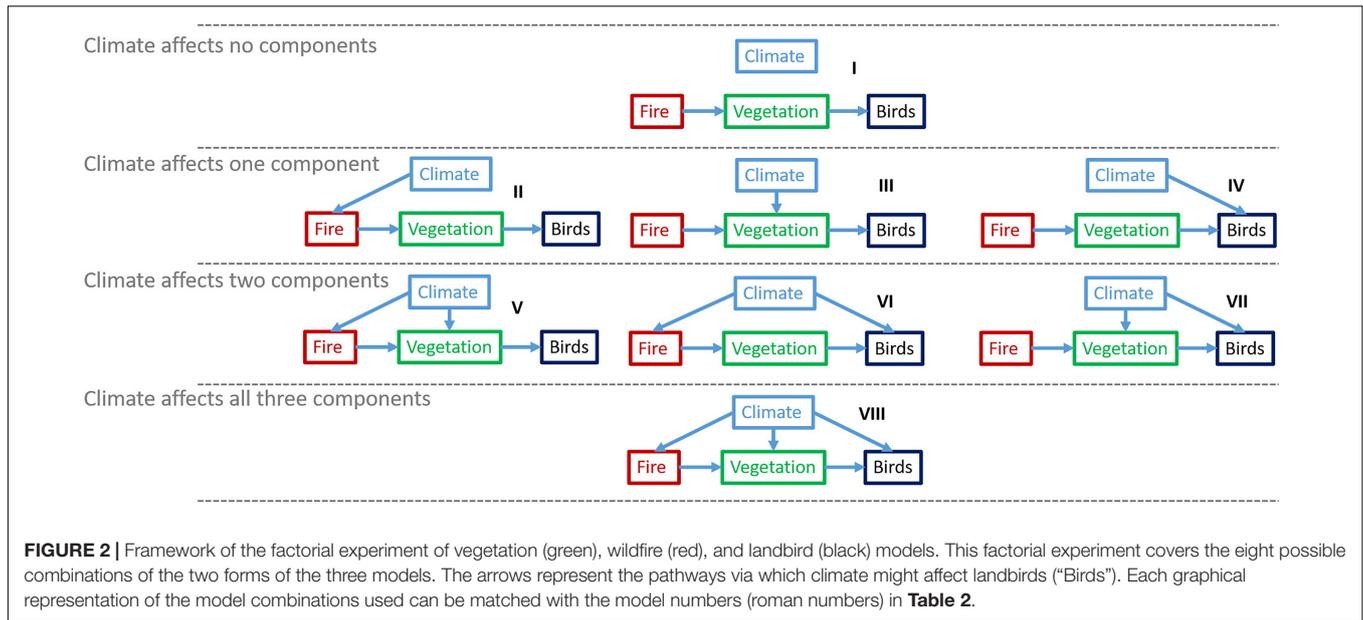
Short code	Wildfire model	Forest growth model	Landbird model
I	SCFM	LandR	Birds
II	FireSense	LandR	Birds
III	SCFM	LandR.CS	Birds
IV	SCFM	LandR	Birds.CS
V	FireSense	LandR.CS	Birds
VI	FireSense	LandR	Birds.CS
VII	SCFM	LandR.CS	Birds.CS
VIII	FireSense	LandR.CS	Birds.CS

Each model type ($n = 3$) presented two possible formulations ($n = 2$; climate-sensitive and non-climate-sensitive). The factorial experiment used all eight possible combinations of these models ($2^3 = 8$). Climate sensitive model variants are indicated in bold.

Models

Forest Growth and Succession Models

For non-CS and CS forest growth and succession models we used the LandR Biomass and LandR.CS model suites, respectively. The LandR Biomass (“LandR” hereafter) model (**Supplementary Appendix II**), is an implementation of the LANDIS-II biomass succession model (v3.2.1; Scheller and Mladenoff, 2004) in R. LandR has some minor model algorithm differences compared to LANDIS-II, notably simultaneous within-year growth across cohorts, rather than sequential. As with LANDIS-II, there are many tree species-level traits to parameterize. We parameterized



tree species’ *growth curve* and *mortality shape* based on permanent sample plot data (**Supplementary Appendix II** and Acknowledgments Section). For other species-level traits (*longevity*, *sexual maturity*, ability to *resprout*), we used the best available estimates from the literature and trait values used in LANDIS-II applications (**Supplementary Appendix II**). Briefly, during simulations using LandR, one or more cohorts (defined as the biomass of a given tree species with a given age in a pixel) is created and maintained as a non-linear function of growth and mortality equations (i.e., growth curves and within-pixel competition), dispersal dynamics, and responses to disturbances, such as wildfire (i.e., mortality, serotiny, and resprouting; more details in **Supplementary Appendix II**). The main output from LandR consists of annual tables and maps of the biomass and age of every tree species cohort in every pixel with at least one cohort.

To create the CS version of LandR, we modified cohort growth and mortality equations following the statistical approach developed in Luo et al. (2019). Rather than using their simultaneous multivariate approach, from which we could not correctly predict without developing our own custom statistical routines, we fit two separate univariate models for plot-level biomass growth increment (t/year) and biomass mortality (t/year) as functions of spatially explicit climate variables. Specifically, we first calculated the annual growth and mortality from permanent sample plots (**Supplementary Appendix II**) located in the Boreal and Taiga Plains ecozone. Even though there are permanent sample plots in the Northwest Territories, the (i) minimum three repeated measurements to fit a statistical model for growth and mortality are still lacking, (ii) there are not enough sampling plots to be modeled without supplementation from other portions of the ecoregion, and most importantly, (iii) there are concerns regarding the time disparity between repeated measures for these permanent sample plots and the reference years from other permanent sample plots. Therefore, we used data from across the southern part of the ecoregion in Alberta

and Saskatchewan to be able to model the climate effects on growth and mortality. This also allowed us to encompass some of the warmer future climates that might characterize our study area in the future. We then related plot-level biomass growth increment and mortality to annual temperature anomalies (ATA) and an annual Climate Moisture Index (CMI; Hogg, 1994), accounting for cohort age (*sensu* Chen et al., 2016). We used a Generalized Linear Mixed Model (GLMM) and a Generalized Additive Model specifying the Location, Scale, and Shape of the data distribution (GAMLSS; gamlss R package; Rigby and Stasinopoulos, 2005), for growth increment and mortality, respectively. We then calculated CMI and ATA using historical monthly temperature and precipitation for summer months (**Supplementary Appendix I Figure A2**). For each driver (tree growth or tree mortality), we calculated the annual “climate effect ratio” (CER), which is the ratio of the growth (or mortality) under each annual future climate and the growth (or mortality) under the averaged historic climate, for each pixel. We finally multiplied the LandR-derived growth and mortality by this CER. This gives, for example, no change in growth (or mortality) when a future year has the same climate as the historical average, because the ratio is 1. As future climate changes, this ratio can go above or below 1, resulting in deviations from the non-CS stand-level growth (or mortality). We did not apply the CER to cohorts under 20 years of age because they were not represented in the permanent sample plots, lacking information on their climate sensitivity. We, therefore, determined their growth and mortality using the default LANDIS-II equations. We also placed upper and lower limitations on this ratio (1.66 and $1/1.66 = 0.6$, respectively, which allows for up to a 66% increase or decrease in growth and mortality) in an attempt to balance two opposing sources of forecasting error: minimizing cases where we deemed that the extrapolation would be too great and not allowing for future climate to have unrealistically severe effects on growth and mortality. In other words, we used a percentile to estimate the

effect of climate on growth/mortality for climate sensitive forest growth models, where we divided the current climate effects by reference climate effects. We used these upper and lower limits to circumvent problems caused by very small denominators as well as constraining predictions outside the data range used to generate the model. We selected these thresholds to be slightly outside the range of the most extreme predictions made within the first few decades of projected climate values. We attempted to extract tree species-specific CER, but there were insufficient sample sizes for most species. As a result, we used plot-level growth increment and mortality.

We ran the above dynamic forest growth models for all “treed” pixels, including treed wetlands. Land cover classes modeled were the ones classified as “treed” by Latifovic and Pouliot (2005), i.e., 1–15, 20, 32, 34, 35, and 39. Even though 34 and 35 are classified as burned, we converted those to the nearest-neighbor’s forested class to allow for forest regeneration. We used Beaudoin et al. (2014) dataset as our starting layers for biomass (for details, please refer to **Supplementary Appendix II**). Data were not supplemented with the Northwest Territory’s forest inventory data due to the small spatial coverage of this dataset in comparison to the size of our study area. We did not simulate dynamic vegetation changes for non-treed locations: non-vegetated, non-treed wetlands, shrublands, herb dominated, grasslands, croplands, and lichen dominated land cover classes, which summed to 35% of the total landscape cover. These were held static during simulations as we did not have access to a sufficiently fine-grained dynamic forest growth model within the study area.

Wildfire Models

We used two landscape fire models, SCFM and FireSense to represent non-CS and CS fire models, respectively. SCFM is a three-stage landscape fire model (Cumming et al., 1998; Armstrong and Cumming, 2003). It simulates wildfire as a process of ignition (fires that ignited at a given time period), escape from ignition pixels to neighboring cells (the binary probability of escaping or extinguishing), and spread from escaped pixels across a rasterized landscape (if a fire escapes, what is the probability it will burn the neighboring cells). This approach is a variant of percolation models (Hargrove et al., 2000). Fires are extinguished when no further spreading occurs. Each of the three stages is probabilistic, and the probabilities were estimated from historical fire data between 1965 and 2016 (Canadian Forest Service, 2019). We considered lightning-caused fires only, as human-caused fires have been negligible within our study area (Canadian Forest Service, 2019). We estimated ignition rate (fires per 100 km² yr⁻¹ – translated to pixel-level probability of ignition) from all known fires of all sizes. We estimated the pixel-level escape probability as the ratio of fires > 1 pixel to the number of fires. We calculated the mean size of escaped (i.e., realized) fires (> 1 pixel area burned) from historic fire data obtained from the Canadian National Fire Database (Canadian Forest Service, 2019). We estimated the spread probability using a calibration approach whereby we simulated approximately 100,000 fires with different landscape-constant spread probabilities. We fitted a shape-constrained Generalized

Additive Model (Pya and Wood, 2015) to the scatterplot of spread probabilities simulated fire sizes. From this curve, we determined the landscape-specific, pixel-level spread probability that reproduces the historical mean fire size for the landscape. All pixels were either flammable with their given ignition, escape, and spread probabilities (not only treed land cover classes, but also lower vegetation ones) or non-flammable (water bodies, ice and snow, rocks and non-vegetated areas such as human development). The model simulates stand-replacing fires only, and the only influence of climate and vegetation on SCFM is indirect through their influence on the historical fire regime.

FireSense also simulates fires through percolation as described for SCFM, but with ignition, escape, and spread probabilities that vary spatially and temporally as a function of annual fire weather and vegetation. We developed statistical models to predict the simulation parameters from these covariates, using methods adapted from Marchal et al. (2017a,b, 2019). We used Monthly Drought Codes from annual Global Climate Model projections (*sensu* Bergeron et al., 2010) as annual fire weather covariates. For ignition and escape, we classified the historical and projected landscapes based on land cover classes (Latifovic and Pouliot, 2005), while for spread, the most complex model of the three, we classified the historical and projected landscapes into one of the four land cover classes, following this order: (i) **young** (< 15 years since disturbance), (ii) **deciduous** leading, (iii) **conifer** leading, and (iv) **other**; the pixel “leading” tree species or land cover class is that accounting the largest proportion of total species biomass.

Landbird Models

We used landbird density models fit by the Boreal Avian Modelling (BAM) project (Cumming et al., 2010; Barker et al., 2015) with avian point count data from the Boreal and Taiga Plains ecozone [as represented by Bird Conservation Region 6 (Bird Studies Canada and NABCI, 2014; **Supplementary Appendix I Figure A1**)]. Data were compiled as part of the BAM project and include data from both publicly available and independent projects within the boreal and hemi-boreal regions of North America. These human-based avian point-count surveys were conducted between 1993 and 2018. The BAM database was supplemented with point-count data from autonomous recording units (ARU) deployed in the Northwest Territories and Alberta between 2012 and 2018 by the Canadian Wildlife Service and the University of Alberta Bioacoustic Unit (WildTrax, 2019). The final database used to fit the bird models comprised 126,621 point-counts (5.5% of which were from ARUs), from a total of 42,612 sampling stations. This resulted in 975,527 individual bird records (**Table 1**) for the species modeled in this study. Of these point-counts, 63% took place in Alberta, 9% in British Columbia, 11% in Manitoba, 6% in Saskatchewan, and 11% in the Northwest Territories. Even though there is unbalanced spatial coverage due to the challenging nature of data collection in remote Northern forests, the data coming exclusively from the Northwest Territories still comprised almost 4,700 unique sampling stations. To minimize the influence of this spatial data imbalance on the landbird models, we weighted individual point-count observations (counts) according to the inverse of the number

of surveys conducted within a 5 km × 5 km window around the survey station (including repeat visits to the same station), thereby down-weighting the influence of individual surveys in heavily sampled areas.

For each landbird species ($n = 64$; **Table 1**), we developed two species density models: non-CS (vegetation and terrain covariates only) and CS (vegetation, terrain, and climate covariates). Even though we recognize that the non-CS model is not necessarily insensitive to climate, its effect would be mostly indirect, and we chose to use a consistent naming convention (CS vs. non-CS) for our factorial experiment. These count models were fit as boosted regression trees (BRT) with a Poisson distribution using the *gbm.step* function in the *dismo* package (Hijmans et al., 2011), following methods outlined in Stralberg et al. (2015b). We used ten-fold cross-validation to assess model robustness to sampling bias. The covariates (**Table 3**) used for the bird model fitting were either: (i) assumed static over the simulated period and not allowed to change, e.g., water bodies, wetland, urban/agriculture, water proportion, human development proportion (Latifovic and Pouliot, 2005); (ii) static, i.e., topographic ruggedness (Sappington et al., 2007); or (iii) dynamic and allowed to change, e.g., tree species, biomass, age, and climate covariates. Tree species biomass covariates for fitting the bird models were derived from predicted biomass layers for 2001 or 2011 (Beaudoin et al., 2014, 2017). Pre-2006 sampling events were associated with the 2001 biomass data, whereas events from 2006 and up were associated with the

2011 biomass data. Tree species used for biomass covariates included the main tree species present in the study area: paper birch, tamarack, white spruce, black spruce, jack pine, and trembling aspen.

To standardize the landbird density models, we accounted for differences in sampling protocol and covariate effects on landbird species detectability using statistical offsets. This included the effects of time of day and day of year on the probability of availability given presence, and the effects of tree cover and land-cover type on the probability of detection given availability (Sólymos et al., 2013). Offsets were calculated based on removal and distance-sampling models (Sólymos et al., 2018). The adjustments appeared as offsets in the BRTs so that expected values represented species density. We assumed that ARU detectability rates were similar to those of human observers (after Van Wilgenburg et al., 2017; Yip et al., 2017). We assessed potential correlation between predictors using Pearson correlation coefficients between climate, topographic, and vegetation covariates. We did not include covariates that presented stronger correlation than 0.9 with other covariates (*sensu* Stralberg et al., 2015b).

We also summed relative importance of vegetation and climate variables (i.e., predictors) to assess the combined relative importance of climate vs. vegetation (and assumed-static covariates) in each species' model. The summed relative importance for climate predictors was compared with the net effect on occupancy (see below) using linear regression.

TABLE 3 | Type of covariates, covariate acronyms, definitions, and range of possible values for the covariates used to build the landbird models.

Type	Covariate acronym	Definition	Possible values
Naturally dynamic, but held static	wat	Sample point is defined as water	Binary variable, 1 or 0
	wet	Sample point is defined as wetland	Binary variable, 1 or 0
	led25	Water proportion within 5 × 5 moving window	Continuous variable, from 0 to 0.04
	dev25	Development proportion within 5 × 5 moving window	Continuous variable, from 0 to 0.04
Naturally static	vrug	Topographic ruggedness	Continuous variable, between 0 and 0.165
Naturally dynamic and simulated	Species_Betu_Pap_v1	Total biomass of paper birch	Integer variable, from 0 to 5599
	Species_Lari_Lar_v1	Total biomass (t/ha × 100) of tamarack	Integer variable, from 0 to 4364
	Species_Pice_Gla_v1	Total biomass (t/ha × 100) of white spruce	Integer variable, from 0 to 12822
	Species_Pice_Mar_v1	Total biomass (t/ha × 100) of black spruce	Integer variable, from 0 to 11257
	Species_Pinu_Ban_v1	Total biomass (t/ha × 100) of jack pine	Integer variable, from 0 to 8476
	Species_Popu_Tre_v1	Total biomass (t/ha × 100) of trembling aspen	Integer variable, from 0 to 14572
	Structure_Stand_Age_v1	Stand Age	Integer variable, from 0 to 298
	AHM	Annual heat-moisture index (MAT+10)/(MAP/1000)	Continuous variable, between 5 and 33
	CMD	Hargreaves climatic moisture deficit (mm)	Continuous variable, between 0 and 311
	eFFP	The day of the year on which frost-free period ends	Continuous variable, between 224 and 266
	EMT	Extreme minimum temperature over 30 years	Continuous variable, between -54 and -39
	FFP	Frost-free period	Continuous variable, between 49 and 125
	MAP	Mean annual precipitation (mm)	Continuous variable, between 217 and 839
	MAT	Mean annual temperature (°C)	Continuous variable, between -9 and 3
	NFFD	The number of frost-free days	Continuous variable, between 75 and 162
	PPT_wt	Winter precipitation (mm)	Continuous variable, between 28 and 164
SHM	Summer heat-moisture index [(MWM)/ (MSP/1000)]	Continuous variable, between 18 and 111	
Tave_sm	Summer mean temperature (°C)	Continuous variable, between 8 and 18	
TD	Temperature difference between MWM and MCM, or continentality (°C)	Continuous variable, between 21 and 44	

Land cover model covariates were derived from the Commission for Environmental Cooperation (CEC) North American Land Cover 2005, vegetation biomass was derived from Beaudoin et al. (2014, 2017) and climate covariates representing the 1981–2010 normal period were derived from Wang et al. (2016).

Quantifying Direct and Indirect Climate Effects on Landbird Occupancy

Our analyses were based on changes in mapped predicted densities within the study region, over the course of a simulation. Predicted densities in 2011 included large areas of very low (effectively zero) densities, outside of species' known distributions (BirdLife International, 2021), as well as very small areas with very high densities (up to three orders of magnitude higher densities than average). This increased the complexity of the estimation of density changes between scenarios. To address this, we converted species' density maps into occupancy maps by applying species-specific density thresholds defined by historically identified high density areas, i.e., areas where predicted densities exceeded the mean predicted density within the model-building area (*sensu* Stralberg et al., 2015a). Although the thresholds used to define occupancy may affect pixel-level changes, the relative magnitudes of direct, indirect, and net climatic effects are likely insensitive to the choice of threshold. Changes in thresholds used to define occupancy would likely modify the magnitude of change in occupancy, but not the qualitative differences in change observed among the three pathways. We generated these occupancy maps for 2011 and 2100, for each species, treatment, and replicate resulting in 160 maps per species (2 years \times 8 treatments \times 10 replicates).

For each landbird species, treatment and replicate, we subtracted the 2011 occupancy map from the 2100 occupancy map. The resulting 80 maps representing the changes in occupancy for each of the 64 species had pixels coded 1, -1, or 0, depending whether a pixel changed from 0 to 1 (gain of the given species in that pixel), changed from 1 to 0 (loss of the given species in that pixel), or did not change, respectively. For each pathway effect (direct, indirect via vegetation, indirect via fire), we stacked the 80 maps into two groups (CS and non-CS), resulting in 40 maps per pathway effect of the CS model versions, and 40 per pathway effect of the non-CS versions (i.e., vegetation pathway - CS group = III, V, VII, VIII and non-CS group = I, II, IV, VI; fire pathway - CS group = II, V, VI, VIII and non-CS group = I, III, IV, VII; direct pathway - CS group = IV, VI, VII, VIII and non-CS group = I, II, III, V; see **Table 2** and **Figure 2**). For estimating the net effect of climate, i.e., cumulative and additive effects of climate change pathways, we only used the full CS (Scenario VIII) and the full non-CS (Scenario I) models, which resulted in two groups of 10 maps per species. We then estimated the per-pixel probabilities of gain and loss for each of these groups (two additional maps), separately:

$P_{\text{gain}} = \text{number of replicates with gain} / \text{total number of replicates}$
(i.e., either 40 if individual pathway effects, or 10 for the net effects)

$P_{\text{loss}} = \text{number of replicates with loss} / \text{total number of replicates}$

This resulted in 16 maps per species: one gain and one loss of occupied area maps for each of the two climate grouping, CS and non-CS, for each of the four pathway and net effects [(i) direct, (ii) indirect via vegetation, (iii) indirect via fire, and (iv) net effect, i.e., $2 \times 2 \times 4$]. For each species, we multiplied probabilities by pixel area to estimate the mean areas (in ha) of species gain and loss per pathway. Then, for each species we subtracted areas of species

loss from areas of species gain, to estimate the total climate effect on occupancy for each pathway. A schematic representation of this process is found in **Figure 3**. Information regarding code and data to reproduce the analysis can be found in a GitHub repository¹. Finally, we mapped the change in the number of species (i.e., species turnover) between 2100 and 2011 due to net climate effects by calculating the difference in occupancy between the full CS (VIII) and full non-CS (I) models across species (**Figure 2**).

RESULTS

Landbird Model Performance and Variable Importance

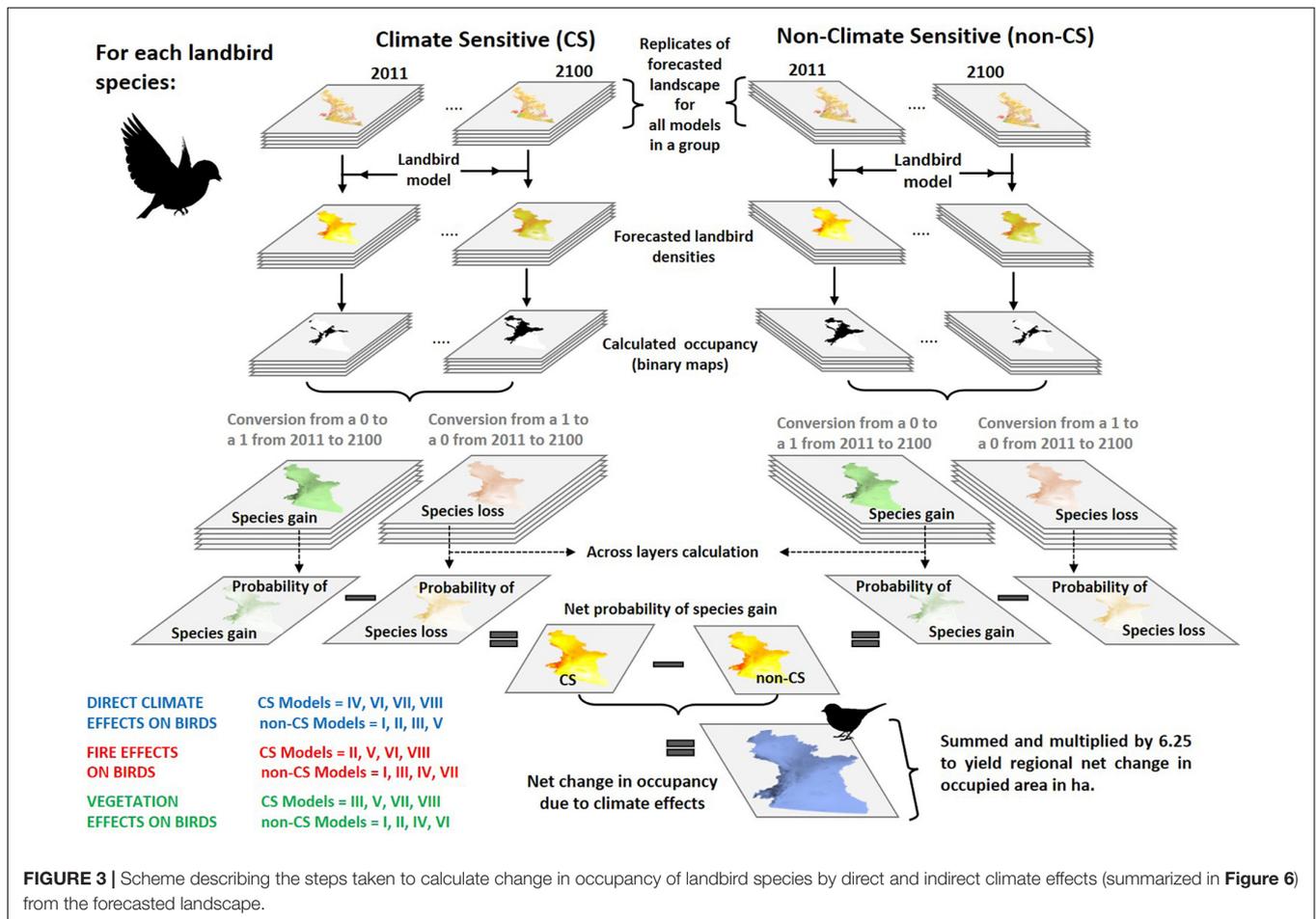
Model performance varied widely across landbird species and models. Pseudo- R^2 values ranged from 0.02 (WIWA) to 0.459 (SAVS) for non-climate sensitive models, and from 0.079 (NOFL) to 0.705 (ATSP) for climate-sensitive models (**Supplementary Appendix III**). The total relative importance of vegetation variables averaged 59% in non-climate-sensitive models (with a mean *pseudo- R^2* of 0.21) and 24% in climate-sensitive models (with a mean *pseudo- R^2* of 0.25; **Supplementary Appendix III**). Climate-sensitive landbird models showed widely varying relative importance of climatic variables, ranging from 19% (OVEN) to 91% (WCSP) across species (**Supplementary Appendix I Figure A3** and **Supplementary Appendix III**).

Climate Effects on Forest Growth and Mortality and Wildfire

The CS forest growth simulation model showed a net increase in tree biomass of 400 kg/ha (15.4%; **Figure 4**) compared to results from the non-CS simulation model. CS fire simulations alone resulted in a net increase in tree biomass of 100 kg/ha, representing a 13% increase across the whole study area compared to results from the non-CS fire simulations (**Figure 4**). Another 100 kg/ha increase can be accounted for by interactions between fire and vegetation in the combined CS models. Thus, the net climate effect on tree biomass was an increase of 600 kg/ha in 2100 (**Figure 4**). Net climate effects on biomass changes can be spatially seen in **Supplementary Appendix I Figure A4**. The distribution of pixel-level leading tree species showed fairly modest changes, with higher deciduous conversion in the southeastern portion and more conversion to conifer in the central and eastern portions (**Supplementary Appendix I Figure A5**), with small increases in black-spruce dominated mixed stands, and small decreases in mixed stands dominated by white spruce and trembling aspen (see **Supplementary Appendix I** for detailed results).

Comparing CS to non-CS fire simulations, mean annual area burned increased by 280 thousand ha in 2100 (**Figure 5**). This represents a climate-driven increase of almost 90% relative to historical conditions (1965–2016). Given the modest changes in

¹<https://github.com/tati-micheletti/NWT/tree/FEE>



fuel type abundances reported above, this increase is attributable to the direct effects of climate warming on fire activity.

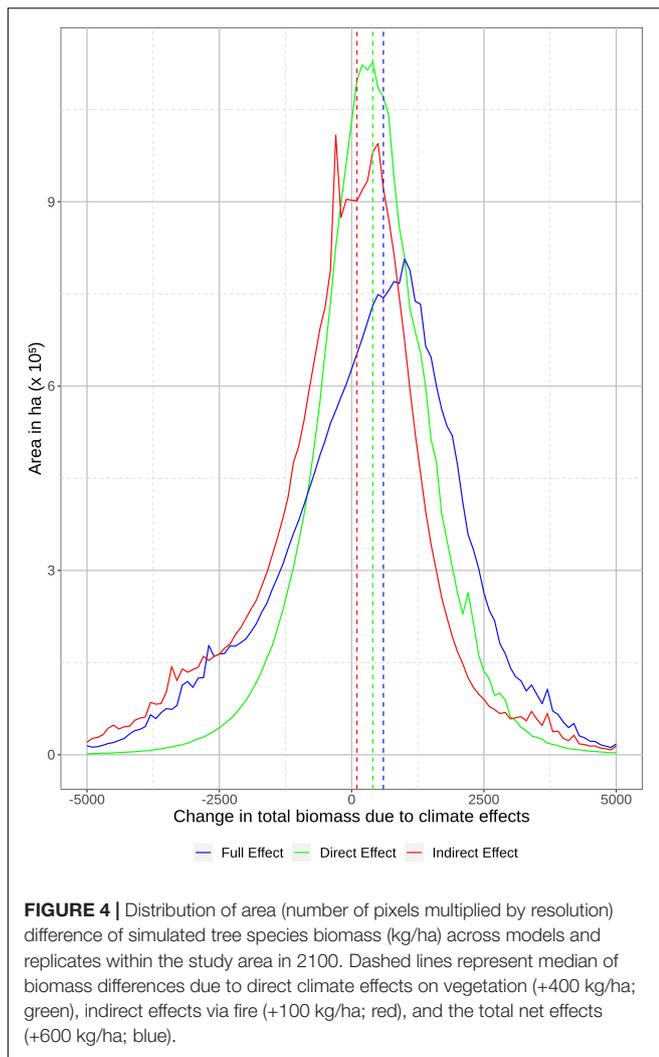
Climate Effects on Landbird Distributions

Climate change was projected to positively affect average landbird occupancy area in the Northwest Territories by about 7.39 million ha. This area represents approximately 15% of the Taiga Plains ecozone within the Northwest Territories (**Figure 6A** and **Supplementary Appendix IV**). Over all species, we forecasted a positive mean difference of 7.49 million ha exclusively due to the direct effects of climate change (dashed blue vertical line on **Figure 6B**), which were partially offset by a negative mean difference of 97 thousand ha due to indirect effects of climate via fire (dashed red vertical line on **Figure 6B**). Effects of climate via changes in forest growth and mortality were negligible (a positive mean difference of 4,250 ha; dashed green vertical line on **Figure 6B**). Overall, the direct effect of climate on landbirds was almost two orders of magnitude greater than the indirect effects, based on simulated changes in landbird distributions (**Figure 6**). We reiterate that results presented here are not simulated forecasts of future occupancy but instead represent the difference between forecasted occupancy with CS and non-CS models. Even though in some cases the present results might match forecasted occupancy (for example, if the

forecasts of non-CS models are unchanging through time) the present results (**Figure 6**) should not be interpreted as future distribution shifts or range expansions and contractions without careful consideration of the control model (model I).

Approximately 19% of the landbird species showed both positive and negative direct effects of climate as measured by the gained and lost areas (blue bars on **Figures 6A,B**). Most species (75%) showed a net area gain to direct effect of climate when comparing variants CS vs. non-CS (**Figure 6A**), while for 25% there was a net area loss due to direct effects of climate, when making the same comparison. The indirect effect of climate acting through fire or vegetation on landbird distribution varied considerably among species, generating important spatial variation in local gain and loss of occupied area (**Figures 6, 7**). The net climate effects across species were not correlated with the relative importance of climate variables in the CS models (**Figure 8**).

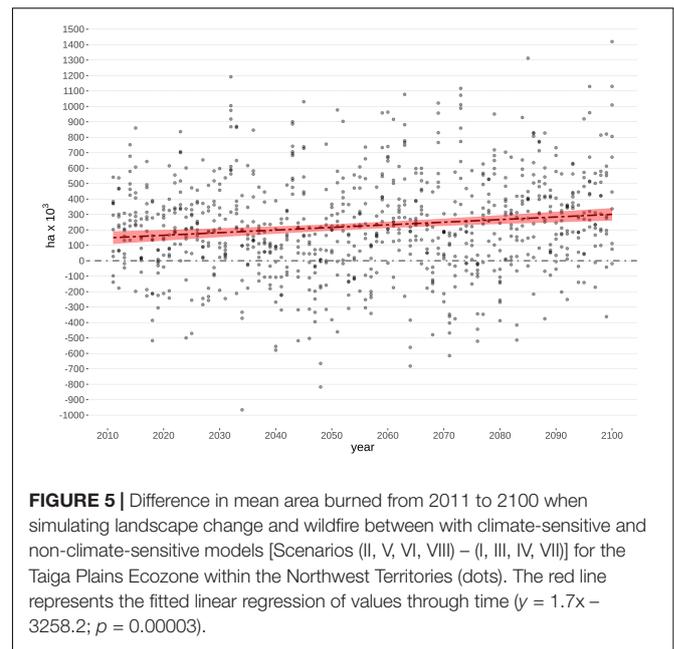
The forecasted effect of climate (CS vs. non-CS variants) suggested a net reduction in richness of up to 12 and seven species in the south-central and northeastern regions, respectively (**Figure 7**). In contrast, the western regions of the study area showed an increase of up to 20 species when comparing the CS vs. non-CS variants. Species turnover was highest in the



northeastern, south-central (higher species loss) and western regions (higher species gain) of the study area (Figure 7).

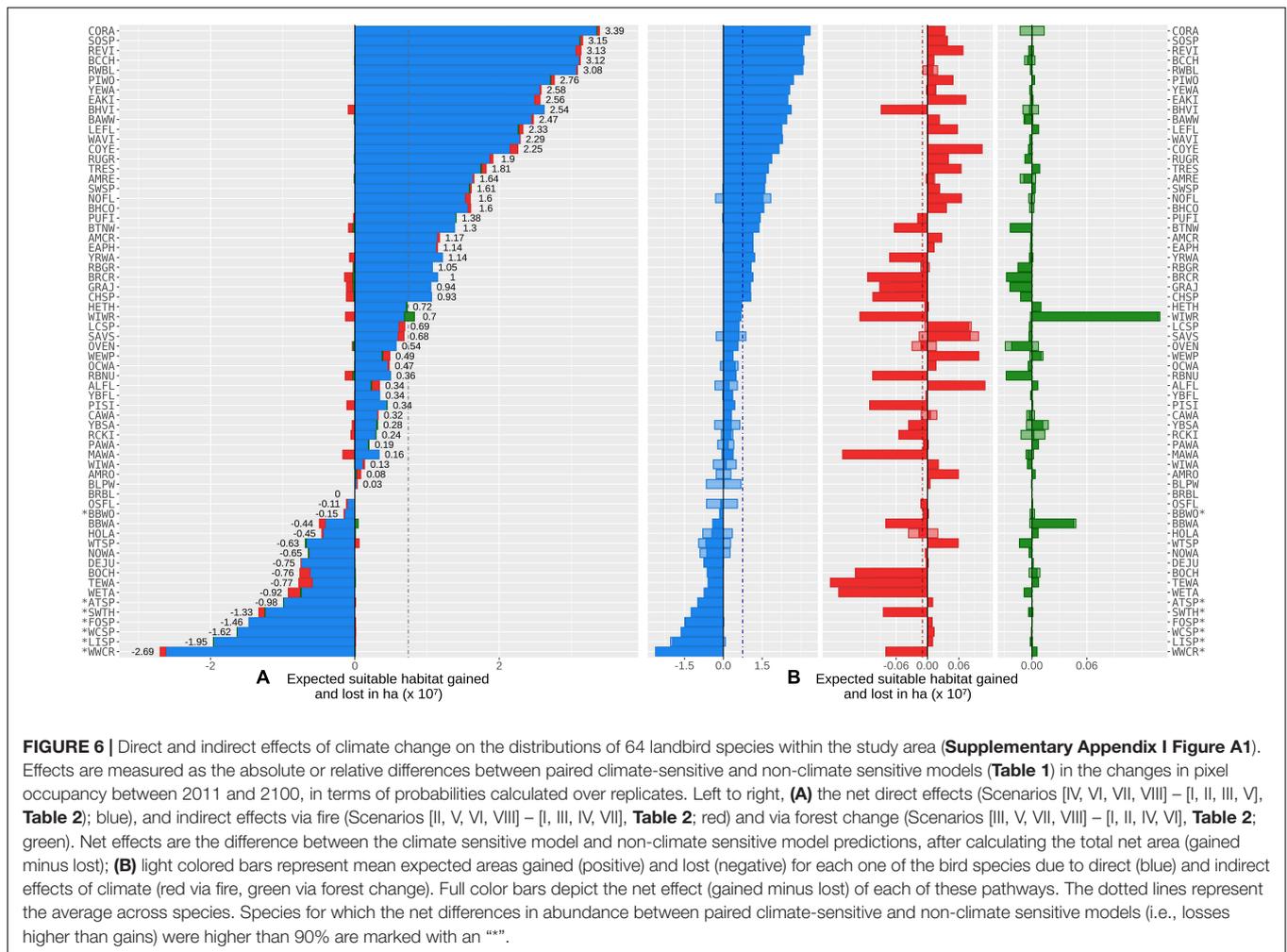
DISCUSSION

Understanding the relative importance of key pathways through which climate change affects ecosystems is important for informing potential adaptation and mitigation measures. The abundance and distribution of landbirds – and wildlife in general – are affected by climate change through the effects of climate on their habitat, more specifically on vegetation, i.e., indirect climate effects (Wiszniewski et al., 2013), but also directly through, e.g., physiological responses to temperature and precipitation (Riddell et al., 2021). Understanding the relative influence of direct and indirect effects enables wildlife managers to identify opportunities to address negative effects of changing climate on valued ecological indicators (Bauduin et al., 2020). We present a novel evaluation of the relative influences of three potential climate-change pathways (vegetation, wildfire, and climate) on future landbird distributions in Northwest Territories, Canada. Direct climate effects were approximately



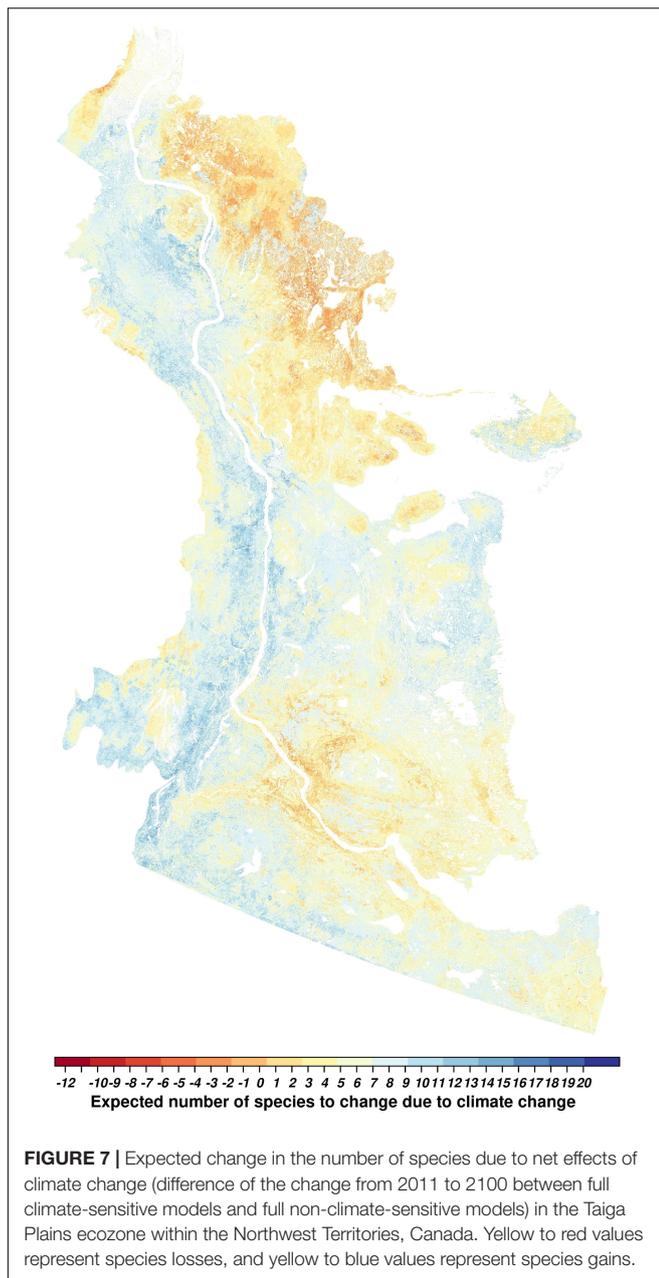
two orders of magnitude more important in explaining predicted changes in landbird occupancy than the indirect pathways. Despite a 90% simulated climate-driven increase in annual area burned by 2100, this did not translate into major vegetation changes across our large study area. Models simulated an average increase of 600 kg/ha in tree biomass, but with only modest changes in leading tree species due to climate change. These results suggest that actions directed at indirect pathways such as wildfire suppression or forest management may not be enough to effectively mitigate landbird species distributional changes under climate change.

In our models, climate drives both forest growth and mortality (i.e., via climate-affected modifiers to these parameters), as well as the probabilities of wildfire ignition, escape and spread. Yet, the indirect effects of climate change on species distribution were still marginal compared to direct effects. This might be explained by vegetation lags. Rapid climate change, accompanied by a relatively slow vegetation change, could result in a state of disequilibrium between climate and vegetation (Wu et al., 2015). Stralberg et al. (2015a) drew attention to the importance of considering lags in vegetation responses to changes in climate when evaluating the effects of climate change on the distributions of boreal landbirds. In theory, the more important the vegetation lag, the more landbird species are likely to experience important range contraction, due to reductions in suitable habitat (Stralberg et al., 2015a). Still, based on the simulated changes in forest growth, mortality, and wildfire regime, our results suggest that vegetation lags may be longer than the simulation time span used in this study, and that direct and/or indirect effects of climate will not necessarily impose important range contractions to most of the 64 species we studied, as previously proposed. Farther south, in Alberta, Cadieux et al.'s (2019) projections suggest larger changes in species composition, reflecting shorter lags in vegetation response to climate change.



Projected shifts in climate and habitat resulted in species distribution patterns with 47 of 64 (73%) of species projected to show an increase in the area they occupy and 16 of 64 (25%) of the species projected to show a decrease in the area occupied within the study area by 2100 when comparing CS vs. non-CS variants. Of the 47 species which net climate effects would increase the occupied area, 72% (34 species) currently have their range centroid south of our study area, supporting previous results projecting northward range shifts of migratory birds (Hitch and Leberg, 2007; Langham et al., 2015; Bateman et al., 2020b; McCaslin and Heath, 2020). Interestingly, these results might point to slower rates of change in mountain ranges, as well as the ability for species to move up slopes to suitable habitats. Species whose models project increases in its habitat extent generally have diverse habitat associations; however, species with the largest net gains (“winners”) are primarily associated with deciduous forests, e.g., Black-capped Chickadee (*Poecile atricapillus*), Yellow Warbler (*Setophaga petechia*), Black-and-white Warbler (*Mniotilta varia*), Least Flycatcher (*Empidonax minimus*), Warbling Vireo (*Vireo gilvus*), and Ruffed Grouse (*Bonasa umbellus*). Species whose models project the largest net losses (“losers”) are species associated

with: (1) conifer forest, such as White-winged Crossbill (*Loxia leucoptera*), Boreal Chickadee (*Poecile hudsonicus*); (2) non-forested habitats, such as Lincoln’s Sparrow (*Melospiza lincolni*), Fox Sparrow (*Passerella iliaca*); or (3) treeline-tundra habitats such as American Tree Sparrow (*Spizelloides arborea*), Horned Lark (*Eremophila alpestris*). These outcomes align with other simulation studies in the western boreal forests (Mahon et al., 2016; Cadieux et al., 2020), and highlight the importance of simulating landscape change with climate sensitive components when forecasting potential future species distributions. Still, two important caveats should be considered when interpreting these results. First, only forested habitats were simulated by the forest growth and mortality model which might influence expected changes in non-forested habitat, and consequently, on landbird species associated with these environments. Second, the extent of current range of landbird species could also influence expected gains and losses for species with narrow ranges within the data set, for example White-crowned Sparrow (*Zonotrichia leucophrys*). Although this species occurs within the Northwest Territories, it is uncommon across all of the northern region of Alberta, from which much of the data to fit the landbird statistical models was collected.



In light of the highly variable magnitudes of potential vegetation change in the North (e.g., Rehfeldt et al., 2012), further studies should aim to better understand temporal response of both forested and non-forested habitats, and wildfire regime to climate change, including lag responses of vegetation to climate change, and further assess the implications of climate and landscape change on landbird communities.

The lack of a relationship between importance of climate variables in the species distribution models and the net climate change effects in simulation (**Figure 8**) implies that our forecasted changes in landbird occupancy are not simply a consequence of the strength of climate variables in the CS models. It may be explained by the fact that the predicted densities

from a species distribution model are the *product* of the magnitude of the covariate effect (i.e., the importance of climate variables combined with the explanatory power of the model and the underlying simulated landscape covariates). This result (**Figure 8**) emphasizes the importance of actually *performing* forecasts (i.e., simulating landscape changes and forecasting species concurrent changes in occupancy) to understand plausible future outcomes (Dietze et al., 2018); it is not sufficient to infer possible futures directly from coefficients of species distribution models.

We recognize that there may be mismatches between the specific vegetation changes simulated and those captured by the landbird models, and that our results are a direct outcome of the particular forest growth and mortality, and wildfire models used. Our models also do not account for important ecological processes such as permafrost thaw or changes in surface hydrology (Helbig et al., 2016), nor do they capture or simulate extreme weather events (Tanner et al., 2017), that are likely to change with climate. We also could improve our models and obtain more refined landbird forecasts if including other explicit biological processes such as landbirds' dispersal capacity and potential changes in species interactions due to future climate change (i.e., mismatches in ecological networks). These processes could all alter avian habitat quantity and quality through direct and indirect mechanisms. Our choice of occupancy thresholds for landbirds may also have resulted in over- or under-estimation of species gains, losses, and turnover. However, this should not have influenced the overall patterns observed or our main finding, i.e., relatively small effects of indirect vs. direct climate pathways on landbird occupancy across our study area.

To our knowledge, this study represents the first example of a fully reproducible and reusable modeling workflow, covering every step from acquisition and assimilation of raw data, through the parameter estimation of all statistical models, the specification of simulation experiments, and their execution to generate the samples of forecasts. This study highlights the platform's ability to actually perform (i) yearly simulation of ecological processes (i.e., forest growth and wildfire) with (ii) existing feedbacks when forecasting species (i.e., landbird) distribution, in contrast to using a scenario based approach for forecasting, which neglects the effects ecological feedbacks among ecological processes, and (iii) on the same platform, as opposed to using one platform for the landscape simulation and another for wildlife modeling (*sensu* Regos et al., 2018), which improves both model reusability and nimbleness. This study also (iv) allowed us to account for direct effects of climate on both wildfire regimes and forest growth, and (v) represents both the vegetation component with a high level of details (i.e., several species cohorts per pixel), both of which have been previously identified as a limitation of other platforms and models (De Cáceres et al., 2013). Our workflow, using the SpaDES platform, allows for frequent updates and revisions, even to input datasets far upstream from the simulations. Further, at every step, we were able to include expertise of multiple subject experts to update and correct components of different models. We mixed numerous statistical modeling tools (e.g., BRTs, GAMLSS, GLM, GAMS, non-linear mixed effects models) and simulation paradigms

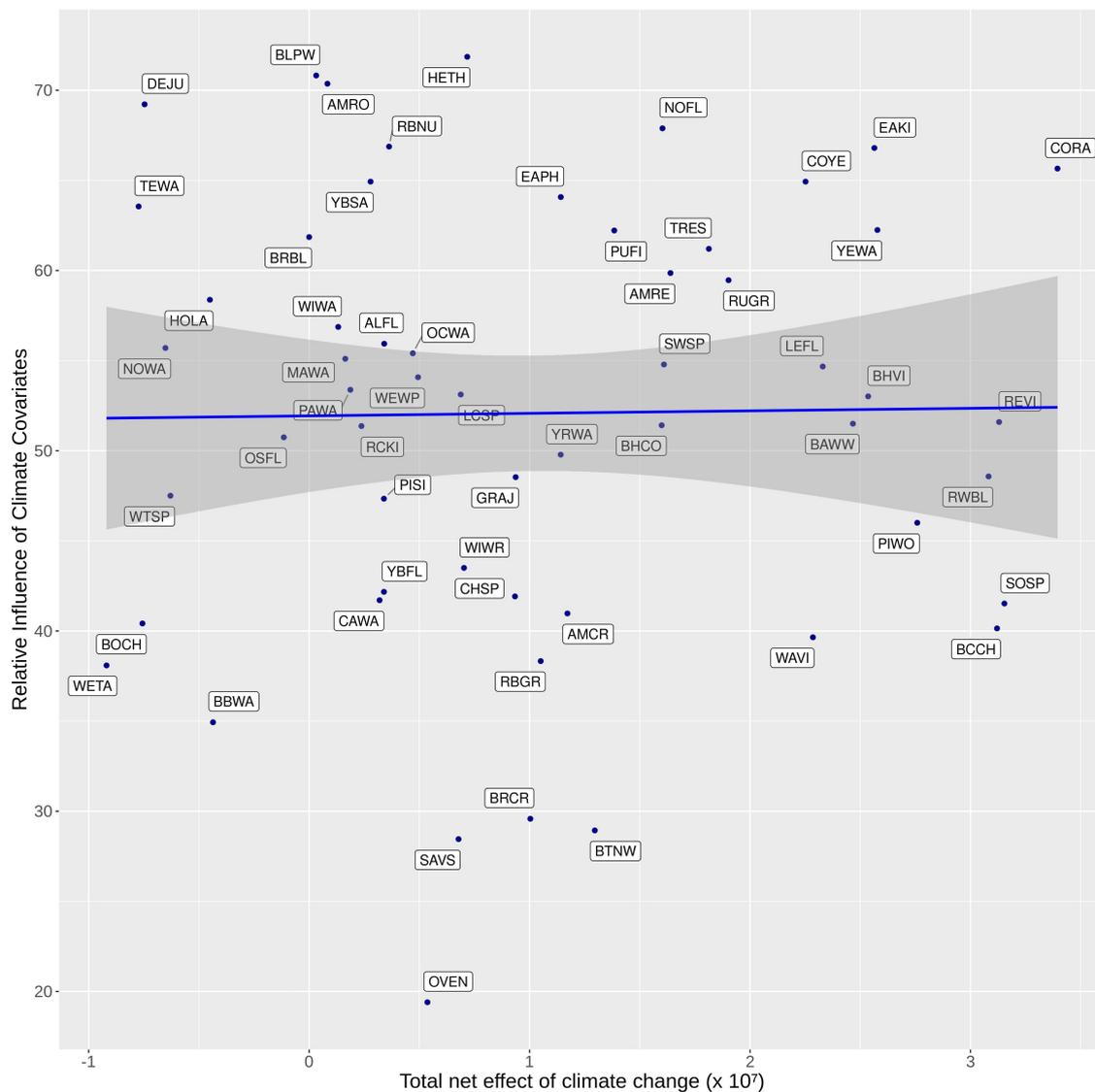


FIGURE 8 | Non-significant correlation (blue line) between relative importance of climate covariates in the climate-sensitive avian species distribution models and total net effect of climate change in terms of area – calculated as the difference of the area affected by climate change calculated between climate-sensitive and non-climate-sensitive predictions in 2100 – for 64 boreal landbird species within the Bird Conservation Region 6 within the Northwest Territories.

(e.g., percolation processes, continuous tree propagule dispersal, forest stand growth modeling), using the best science currently available from each discipline. The SpaDES platform allowed us to integrate these diverse tools in a single data-driven paradigm with reusable modular components (Chubaty and McIntire, 2021; McIntire et al., 2021). This platform is especially well suited to address the new generation of the ecological forecasting paradigm (Dietze et al., 2018; Stall et al., 2019; Bodner et al., 2020) and the implementation of the PERFICT approach (McIntire et al., 2021). This approach can, for example, help reduce model overfitting by enabling faster and iterative re-evaluation and updating of models and model fit. This can also be done, not only by the original model creators but also other researchers, when new data becomes available, speeding up scientific advances. This

nimble approach can improve science-based decision making processes, where increasingly complex ecological processes and management objectives can be addressed (McIntire et al., 2021).

This study, and the use of the SpaDES framework, sets the stage for continued testing and development of models and hypotheses to inform land management. The two avian model variants used for this experiment, although not necessarily state-of-the-art models, were appropriate for forecasting because they only required external climate inputs, and tree species composition and age. This made these models particularly well suited for integration with ecological process forecasting, as they did not include covariates for which forecasted data is not available. As with most forecasting studies, there were a large number of ecological processes that were held static or not

included in our simulations (e.g., wetland dynamics, permafrost change, extreme events, and anthropogenic disturbances), each of which may have impacts on our estimates of direct versus indirect climate effects on landbirds. A crucial element of our simulation system was the close connection between data and models, and between statistical data analysis and the parameterization of the ecological process models used in the simulation. SpaDES is the only platform, to our knowledge, that could handle our entire workflow. This study – and the models used and developed here – will become part of an iterative, continuously improving forecasting process (*sensu* Dietze et al., 2018; White et al., 2019). Future development will weave in forecast validation and integrate ecological processes (mentioned above), improving the capacity of these and other models to forecast likely impacts of climatic change and other processes of management concern.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

TM worked on the integration of models and development of the analysis. EM worked on the development of the analysis. DS, RP, SV, ML, CM, EB, SH, JT, and FSc worked on the development and assessment of the landbird-associated components. EM, SC, and IE worked on the development and assessment of wildfire-associated components. EM, CB, IE, and AC worked on the development and assessment of vegetation-associated components. All authors worked on the design, concept, and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.679673/full#supplementary-material>

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