



Original Research Article

Spatially explicit climate change projections for the recovery planning of threatened species: The Bicknell's Thrush (*Catharus Bicknelli*) as a case study

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ABSTRACT

With climate change, natural resource managers are faced with the challenging task of planning the conservation of habitat for threatened species. Classified as "threatened" under the Species at Risk Act in Canada, the Bicknell's Thrush (*Catharus Bicknelli* - BITH) is a migratory bird whose range is highly restricted. Bioclimatic models project more than 50% loss of suitable habitat - high elevation dense balsam fir (*Abies balsamea*) forests - in the northeastern USA by 2050 due to climate change. We used BITH as a case study to demonstrate the value of forest landscape models (e.g., LANDIS-II) to support decision-making on conservation of habitat of threatened species. We modeled the impacts of forest management and natural disturbances, as well as climate-induced changes, on forest stand and landscape structure. Under RCP climate forcing scenarios 2.6, 4.5 and 8.5, simulations projected significant changes in dominant tree species biomass, from coniferous to broadleaved deciduous, implying important losses of mature balsam fir forest. Climate change was projected to have severe effects with major changes projected to occur after 2080 and losses of more than half of BITH suitable habitat by 2100 for "worst-case" climate change scenarios. This contrasts with results from bioclimatic models which do not capture the expected lags in vegetation responses to changing climate. Our results also suggest that innovative forest management strategies could help maintain BITH habitat abundance under RCP 2.6 and RCP 4.5 climate forcing. Such results can provide guidance for considering effective long-term conservation of habitat for threatened species in a changing world.

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1. Introduction

Future changes in climate are expected to cause loss of global biodiversity with major impacts on bird species (Langham et al., 2015; Virkkala, 2016). These impacts are expected to be most dramatic for habitat specialist species due to their high

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dependence on specific habitat types which are often scarce and scattered in landscapes (Stralberg et al. in review). Among these, species critically dependent upon high-elevation boreal forest may experience some of the strongest effects of climate change. Indeed, this forest type is already sparse and isolated in northeastern North America and its area is expected to decrease dramatically as the climate zones it occupies shift to higher elevations. In some locations, this habitat will almost certainly disappear within decades to centuries (Iverson et al., 2008; Rodenhouse et al., 2008; Wang et al., 2014).

In this challenging context, natural resource managers and conservation authorities are faced with the difficult task of defining and planning the long-term conservation of habitats for species at risk (i.e., critical habitat - the habitat necessary for the survival or recovery of a listed species - Government of Canada, 2002). Natural disturbances and anthropogenic impacts are also expected to accumulate and interact with effects of climate change, making recovery plans even more challenging. However, forest management and habitat recovery plans have great potential to influence how future forest landscapes and species at risk will respond to changes in climate (Ravenscroft et al., 2010; Steenberg et al., 2013). For instance, specific forest management strategies can be proposed within critical habitats for their preservation or restoration (e.g., modified logging strategies). As such, there is a need to better understand the cumulative role of climate change and anthropogenic disturbances on species at risk, and their habitats, to develop sound and efficient recovery plans (Wiens et al., 2009).

The Bicknell's Thrush (*Catharus Bicknelli* -BITH) is a good example of habitat specialist species considered threatened in Canada (listed as Threatened under Canada's Species at Risk Act - Government of Canada, 2012), and for which climate change is considered a major threat to its survival (Rodenhouse et al., 2008). BITH has one of the most restricted breeding ranges in North America (Environment Canada, 2016), with approximately 95% of potential breeding habitat in Quebec, New Brunswick and Nova Scotia, and the remainder in northeastern US states (Maine, New Hampshire, Vermont and New York; COSEWIC, 2009). Its narrow breeding habitat niche is restricted to forests dominated by dense balsam fir (*Abies balsamea*) stands often found at high-elevation (Townsend et al., 2017). Balsam fir forests are projected to decline significantly in eastern Canada in coming decades as mean temperatures and drought stress increase (Boulanger et al., 2016a,b; 2017; Steenberg et al., 2013; Taylor et al., 2017). Other important threats to this species are the deforestation of its wintering grounds in the Greater Antilles and precommercial thinning in most of its Canadian breeding range (New Brunswick and Quebec), a common forest management technique to reduce stem density in young stands (Aubry et al., 2011; Chisholm and Leonard, 2008; McKinnon et al., 2014). As a result, climate change could add to existing anthropogenic disturbances to further reduce the Bicknell's Thrush habitat.

Although historically restricted to undisturbed dense balsam-fir forests, the BITH has also adapted to anthropogenic disturbances, notably clearcuts regenerating to dense balsam fir (Aubry et al., 2011, 2016; Chisholm and Leonard, 2008). These anthropologically disturbed stands are used by BITH within 10–20 years after logging when stand height reaches 3.5–5 m (Environment Canada, 2016). Approximately 90% of Canadian BITH breeding habitat is in managed forests (Environment Canada, 2016), so assessment of harvesting impacts on BITH habitat is a primary concern in the context of climate change. Careful planning of harvesting operations, notably within identified critical habitats, could help maintain or create suitable habitats for the BITH (Lambert et al., 2017). But to date, no studies have addressed possible interactions of specific harvesting strategies and climate change (Lloyd and McFarland, 2017).

Forest landscape models (FLM) can simulate natural and anthropogenic forest disturbances (e.g., forest harvesting, wildfire, insect outbreaks) and seed dispersal, along with stand-scale processes (e.g., growth and succession) under different climatic scenarios in a spatio-temporal manner (Scheller and Mladenoff, 2004). Such models have the potential to project climate-induced vegetation shifts, and provide the possibility to test different forest management scenarios at temporal and spatial scales suitable for conservation planning (Boulanger et al., 2016a,b; Tremblay et al., 2018). FLM model outputs (e.g., biomass by age cohort per tree species) can be interpreted as indicators for future bird habitat, allowing for the assessment of impacts of both specific forest management strategies and climate-induced changes on tree growth and natural disturbances (Tremblay et al., 2018).

We selected the BITH as a case study to demonstrate the utility of a FLM, namely LANDIS-II, to 1) simulate habitat dynamics in a spatiotemporal manner, and 2) test the effects of different management scenarios on habitat dynamics for different climatic scenarios. In addition, we evaluate the usefulness in a changing climate context, of conservation zones proposed by Environment and Climate Change Canada to support recovery of the species in Canada (Environment Canada, 2016) by assessing the abundance and spatiotemporal stability of high quality BITH habitat. We hypothesize that under long-term climate change scenarios, there will be a general decrease in coniferous species associated with BITH's breeding habitat and an increase in abundance and an upslope migration of temperate tree species reducing boreal-type habitats at high-elevation. This would cause a significant decline of BITH's habitat in parts of its Canadian range, and more specifically, in the conservation zones making them unsuitable for long-term conservation of the BITH breeding habitat. Nevertheless, we hypothesize that proper forest management strategies that enhance balsam fir regeneration will partially offset the loss of BITH habitat.

2. Material and methods

2.1. Studied regions

The simulated forest landscapes were located in two ecozones (Ecological Stratification Working Group, 1996), i.e., the Boreal Shield (BS) and the Atlantic Maritime (AM), estimated at 83,853 km² and 95,350 km², respectively (Fig. 1), which

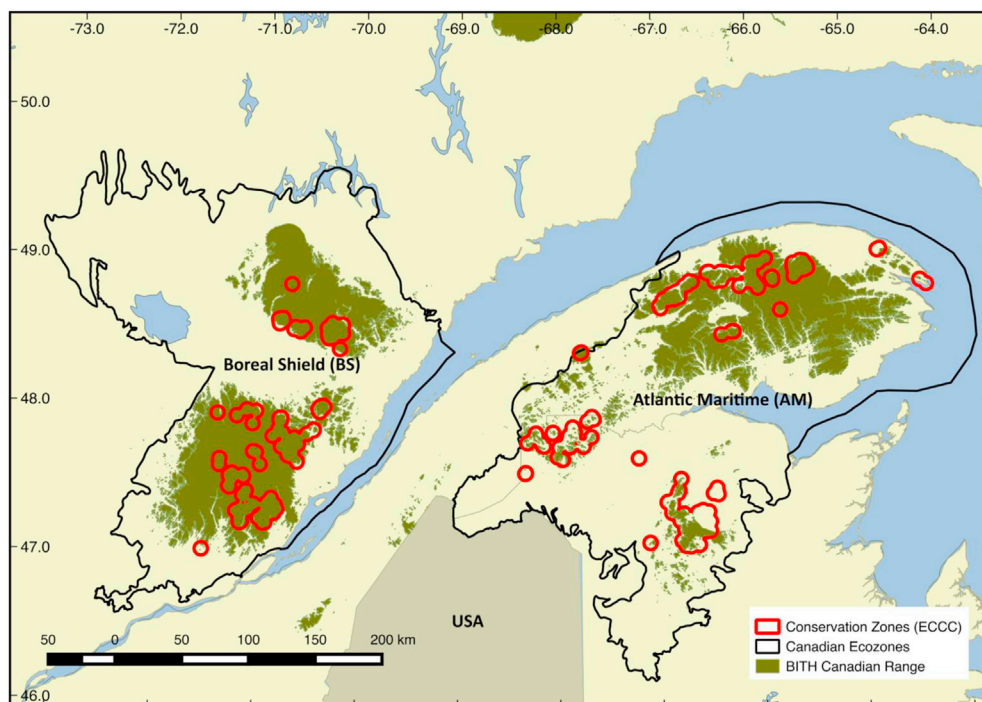


Fig. 1. Location of simulated areas in the Boreal Shield and the Atlantic Maritime ecozone in Eastern Canada. The BITH estimated *actual* range for the two regions is in green and conservation zone buffers are in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

contain the majority of identified critical BITH habitat in Canada (Environment Canada, 2016). The studied regions were located in central Quebec (between 46° and 49°N and 69°–72°W) and in eastern Quebec and New Brunswick (between 46° and 49°N and 69°–64°W). Vegetation in the BS ecozone is characterized by boreal mixedwood and coniferous forests, dominated on lower slopes by balsam fir and black spruce (*Picea mariana*) and on upper slopes by open black spruce forests with other co-occurring species: trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam fir and white spruce (*Picea glauca*). Mean annual temperature ranges from 0 to 1.5 °C and precipitation varies from 800 to 1600 mm (Robitaille and Saucier, 1998).

In the AM ecozone, where mean annual temperature ranges from 3 to 3.5 °C and mean annual precipitation is 900–1400 mm (Robitaille and Saucier, 1998), vegetation is characterized by mixed-wood forests composed of both cold-tolerant temperate and boreal tree species. Upland forests are mostly dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*), while forests in valleys are mostly composed of eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), balsam fir, and white spruce. At higher elevations, forests are mostly dominated by balsam fir and black spruce.

2.2. BITH's Canadian breeding range

The BITH's Canadian breeding range was defined using a model adapted from Lambert et al. (2005) and unpublished data of Environment and Climate Change Canada's (ECCC) Canadian Wildlife Service (CWS). The model identified an elevation threshold for BITH occurrence that co-varies with latitude and longitude ($elevation \sim latitude + longitude$), with breeding ranges of 13,351 km² in the BS and 12,139 km² in the AM (Fig. 1). Nevertheless, since this estimation is only based on elevation, latitude and longitude, the northern estimated range is imprecise due to the linear decrease of the relative importance of elevation in the model. For instance, the minimal elevation in the model at 49°N is 475m which covers a large part of the region.

2.3. Climate scenarios

Forest landscape changes were simulated for the 2000–2200 period using three different radiative forcing scenarios, known as Representative Concentration Pathways (RCP; Van Vuuren et al., 2011), namely RCP 2.6, RCP 4.5 and RCP 8.5. For the period 2000–2010, data interpolated from climate station records by McKenney et al. (2013) were used to produce monthly time series of “current climate”. Future climate projections for 2011–2100 for each RCP, as simulated by the Canadian Earth System Model version 2 (CanESM2; Arora et al., 2011), were downloaded from the World Climate Research Program (WCRP)

Climate Model Intercomparison Project Phase 5 (CMIP5) archive. A bias correction was performed on the data from CanESM2 for 1961–2100 by expressing them as differences from (temperature) or ratios of (precipitation) the CanESM2 monthly means for the 1961–1990 period (McKenney et al., 2013). The bias-corrected data were then merged with observed 30-year monthly climate normals for 1961–1990, interpolated from climate station records by McKenzie et al. (2013), to produce three RCP scenario climate projections for 2011–2100. The 2100–2200 period was an extension of 2100 conditions.

2.4. The models

To simulate forest landscape dynamics across our studied regions, we used LANDIS-II in combination with the forest gap model, PICUS (Lexer and Hönlninger, 2001; Seidl et al., 2014). PICUS was used to simulate fine-scale forest stand dynamics (i.e., individual tree establishment, growth and mortality in response to competition, climate and soil conditions). The results were then used to create dynamic input parameters for LANDIS-II, permitting it to simulate climate change effects on the forest landscape. Specific details on the coupling of LANDIS-II and PICUS are described in the methods of Tremblay et al. (2018) and in (Boulanger et al. 2016a,b), which include detailed supplementary documents. Here, we highlight only the major steps regarding the FLM simulations.

2.5. LANDIS-II, simulation setup and initial conditions

LANDIS-II is a spatially explicit forest landscape simulation model which integrates forest succession and disturbance (Scheller et al., 2007). A variety of model extensions managed by a core module allows it to simulate multiple stand- and landscape-level ecological processes (Scheller and Mladenoff, 2004). Forest landscapes in LANDIS-II are represented as a square grid of interacting cells for which the user defines the resolution and time step. Stand-level forest processes including tree establishment, growth, and mortality, occur within cells, while landscape-level processes such as tree seed dispersal and forest disturbances including fire, insect outbreaks and harvesting, involve multiple interacting cells. Each cell is assigned to a “landtype” (*sensu* Scheller and Mladenoff, 2004) which are assumed to have homogeneous soil and climate conditions; therefore, these landtypes may be used as spatial units in which various sub-models are parameterized. The landtypes we identified generally depict an altitudinal gradient in both the AM and BS ecozones. In this study, cell resolution was set to 250 m (6.25 ha) and simulations were run at a 10-year time step across all activated extensions. The seed dispersal algorithm described in Scheller et al. (2007) generates a two-part exponential probability (decaying) distribution which defines the farthest distance that 95% of seeds of a given species will travel in any direction, and the maximum distance that the remaining 5% of seeds will reach.

Forest structure and composition were initialized for every cell by combining 1) estimates of aboveground biomass for all tree species based on 2001 MODIS imagery (Beaudoin et al., 2014) available from the Canadian National Forest Inventory (NFI; <https://nfi.nfis.org>) and 2) cohort data from provincial permanent and temporary forest inventory plots (FIP). We performed nearest neighbor spectral analysis (NNSA) to associate each cell to the FIP with the shortest Euclidean distance using species-specific biomasses as well as mean annual temperature and total annual precipitation as variables. To ensure the shortest Euclidean distance between the FIP and the gridcell was mostly due to site productivity and not stand age, NNSA imputations were conducted separately for each age class group (20-yr age class bins). Cells containing less than 50% forest cover (by area, according to the inventory data) were excluded from the simulations. More details about this procedure can be found in Tremblay et al. (2018) and in Boulanger et al. (2016a,b).

2.6. The PICUS forest gap model

PICUS is a forest gap model that simulates germination, establishment, growth and mortality of individual trees in 10×10 m cells, emulating 100 m^2 patches of forest area. The model operates on annual time steps and cells interact spatially through a 3D canopy light module and seed dispersal, while assuming common effects of climate and soil properties on seed germination and tree growth. We used PICUS version 1.5 (<http://picus.boku.ac.at>), which has been calibrated for eastern Canadian forests (see Taylor et al., 2017) to develop species establishment probabilities [SEP], maximum annual net primary productivity [maxANPP] and maximum aboveground biomass [maxAGB] parameters for LANDIS-II which are described more fully below.

2.7. Forest succession and species growth potential

Simulation of forest succession was performed with a modified version of the LANDIS-II Biomass Succession extension v 3.1 (Scheller and Mladenoff, 2004) which includes the obligatory serotiny property of jack pine (*Pinus banksiana*). This extension simulates recruitment and growth of tree cohorts (not individual trees) in each grid cell, based on species-specific traits (cf Table 1 for a full listing). Cohorts of different tree species can co-exist within the cell and interact by competing for resources (i.e., growing space), leading to a simplistic representation of forest succession. Dynamic inputs, i.e., SEP, maxANPP, and maxAGB are derived from PICUS output.

More specifically, our calibrated version of PICUS was used to simulate mono-specific stands of each tree species on all landtypes using species parameters given in Table 2. Monthly time series of climate data for each time period (2000–2010,

Table 1

LANDIS-II input data for tree species simulated within the study regions.

Species	Species code	Longevity	Age at maturity	Shade tolerance ^a	Effective seed dispersal (m) ^b	Maximum seed dispersal (m)	Vegetative regeneration	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter
<i>Abies balsamea</i>	ABIE.BAL	150	30	5	25	160	No	None	0	25
<i>Acer rubrum</i>	ACER.RUB	150	10	3	100	200	Yes	Resprout	0	25
<i>Acer saccharum</i>	ACER.SAH	300	40	5	100	200	Yes	Resprout	1	15
<i>Betula alleghaniensis</i>	BETU.ALL	300	40	3	100	400	Yes	Resprout	1	15
<i>Betula papyrifera</i>	BETU.PAP	150	20	2	200	5000	Yes	Resprout	0	25
<i>Fagus grandifolia</i>	FAGU.GRA	250	40	5	30	3000	Yes	None	1	15
<i>Larix laricina</i>	LARI.LAR	150	40	1	50	200	No	None	0	25
<i>Picea glauca</i>	PICE.GLA	200	30	3	100	303	No	None	1	15
<i>Picea mariana</i>	PICE.MAR	200	30	4	80	200	No	Serotiny	1	15
<i>Picea rubens</i>	PICE.RUB	300	30	4	100	303	No	None	1	15
<i>Pinus banksiana</i>	PINU.BAN	150	20	1	30	100	No	Serotiny	0	25
<i>Pinus resinosa</i>	PINU.RES	200	40	2	12	275	No	None	1	15
<i>Pinus strobus</i>	PINU.STR	300	20	3	100	250	No	None	1	15
<i>Populus tremuloides</i>	POPU.TRE	150	20	1	1000	5000	Yes	Resprout	0	25
<i>Quercus rubra</i>	QUER.RUB	250	30	3	30	3000	Yes	Resprout	1	15
<i>Thuja occidentalis</i>	THUJ.OCC	300	30	5	45	60	No	None	1	15
<i>Tsuga canadensis</i>	TSUG.CAN	300	60	5	30	100	No	None	1	15

^a Index of the ability of species to establish under varying light levels where 1 is the least shade tolerant and 5 is the most shade tolerant.^b Distance within which 95% of seeds disperse.**Table 2**

Select input parameters specific to PICUS for species simulated within the study regions.

Species	Soil nitrogen ^a	Minimum soil pH ^b	Maximum soil pH ^b	Minimum GDD (Base temp 5 °C) ^c	Maximum GDD (Base temp 5 °C) ^c	Maximum SMI ^d	Optimum SMI ^d
ABIE.BAL	2	2	9	150	2723	0.3	0
ACER.RUB	2	2	9.5	500	6608	0.5	0.05
ACER.SAH	2	1.7	9.9	450	5093	0.3	0
BETU.ALL	2	2	10	500	4517	0.5	0.05
BETU.PAP	2	2.2	9.4	150	3081	0.5	0.05
FAGU.GRA	2	2.1	9	500	5602	0.7	0.1
LARI.LAR	1	3	9.6	150	2548	0.3	0
PICE.GLA	3	2	10.2	150	2495	0.5	0.05
PICE.MAR	2	2	8.5	150	2495	0.3	0
PICE.RUB	2	2	7.8	450	3239	0.3	0
PINU.BAN	1	2.5	10.2	300	3188	0.7	0.1
PINU.RES	1	2.5	8	500	3300	0.7	0.1
PINU.STR	2	2	9.3	500	4261	0.7	0.1
POPU.TRE	2	2.3	11	150	3024	0.5	0.05
QUER.RUB	1	2.3	9.3	500	5171	0.3	0
THUJ.OCC	2	3	10	500	3383	0.7	0.1
TSUG.CAN	2	2.2	9	500	4660	0.5	0.05

^a Nitrogen response curves: Three classes (1–3) with 1 being very tolerant.^b USDA plant fact sheets (USDA, NRCS 2016) and the Ontario Silvics Manual (OMNR, 2000) were used to derive the widest optimum pH range possible.^c Growing Degree Days (GDD). We used McKenney et al. (2011) growing season model, specifically the minimum GDD for the 0 °C and growing season window with degree days over 5 °C. For the maximum GDD, we used GDD Maximum from McKenney's previous growing season model (McKenney et al., 2007).^d Soil Moisture Index (SMI). Determines each species tolerance to drought (see Scheller and Mladenoff, 2004 pg. 52). HighTolerance (0.1–0.7), Med-Tolerance (0.05–0.5), LowTolerance (0–0.3).

2011–2040, 2041–2070, 2071–2100) and forcing scenario (baseline, RCP 2.6, RCP 4.5, RCP 8.5) were used to drive each simulation for 200 years, starting from bare-ground. In the LANDIS-II Biomass Succession extension, the maxAGB that a given tree species can sustain was set by averaging PICUS outputs for the total aboveground biomass of a stand after it had reached a stabilized state following the early, exponential growth phase of stand development. maxANPP can only be achieved in free growth conditions, i.e. in total absence of inter- or intraspecific competition. Therefore, maxANPP was derived from the PICUS outputs by calculating the maximum annual aboveground biomass increment ($\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) over the entire simulation period. Maximum values were typically observed during the early stages of stand development. SEP is defined as the probability of a given species cohort to successfully establish on a specific land type during one time step, under ideal conditions (i.e., when seeds are available and light conditions are adequate) and can range from 0 to 1. We considered the time (t) necessary for stems to reach > 1.3m height to accumulate aboveground biomass in PICUS as the average result of a random process associated with a constant annual probability of 1/t. We thus simulated the establishment of a cohort as a Bernoulli trial conducted every year during a 10-year period. As the time step used for the LANDIS-II simulations was 10 years (see below), we computed the probability of having at least one success in 10 consecutive trials based on the binomial distribution.

2.8. Bias correction of PICUS outputs and verification of emerging LANDIS-II successional patterns

Succession patterns under the baseline climate scenario were visualized and qualitatively verified against those reported in the literature (e.g. [Racey, 1996](#)). Accordingly, some adjustments were made to the species-specific static growth and mortality curve shape parameters ([Table 1](#)), which determine the acceleration of each species' growth rate and how soon mortality begins as each cohort of species reaches its maximum longevity. Finally, we conducted a validation and bias-correction procedure as in [Tremblay et al., \(2018\)](#) to adjust the dynamic inputs obtained from PICUS.

2.9. Natural disturbances

We considered two types of natural disturbance in our simulations, namely wildfire and spruce budworm outbreaks (SBW, *Choristoneura fumiferana* [Clem.]), which together are responsible for the majority of areas naturally disturbed in the study regions ([Guindon et al., 2014](#)).

SBW outbreaks were simulated using the Biological Disturbance Agent extension v3.0 ([Sturtevant et al. 2004, 2012](#)). This LANDIS-II extension is designed to simulate tree mortality following insect outbreaks and emulates outbreaks as a probabilistic event at the cell level. Probabilities are a function of regional outbreak status and of site and neighborhood resource dominance (e.g., host abundance within a 1-km radius of an affected cell). Host tree species were balsam fir, white spruce (*Picea glauca*), red spruce, and black spruce (listed in decreasing order of vulnerability). Host mortality is also dependent on age-specific susceptibility. We used parameters from different sources for the mixed boreal forest ([MacLean, 1980](#); [Sainte-Marie et al., 2014](#)). Calibration was performed using the maximum severity possible for regional outbreaks; outbreaks were assumed to last at most 10 years and to occur every 40 years, to be consistent with observed regional recurrence cycles ([Boulanger et al., 2012](#)).

Fire simulations were performed with the Base Fire extension ([He and Mladenoff, 1999](#)). This LANDIS-II extension is designed to simulate stochastic fire events dependent upon fire ignition, initiation and spread as a top-down process. In these simulations, fire is mainly influenced by climate. Fire regime data (annual area burned, fire occurrence, and mean fire size) were summarized into "fire regions" corresponding to the intersection of each region and the Canadian Homogeneous Fire Regime (HFR) zones ([Boulanger et al., 2014](#)). Baseline and future fire regime parameters within each fire region were calibrated according to models developed by [Boulanger et al. \(2014\)](#) and further updated for different RCP scenarios ([Gauthier et al., 2015](#)).

2.10. Forest harvesting

Forest harvesting was simulated using the Biomass Harvest extension (v3.0; [Gustafson et al., 2000](#)). Management areas were defined as either forest management units for public lands, or as ecodistricts ([Ecological Stratification Working Group, 1996](#)) for private lands. Three harvesting scenarios were simulated according to a gradient of harvesting pressure, from no harvesting (*Preserv*), to partial harvest (*PartHarv*), to clearcutting without precommercial thinning (*CCwoPT* – [Table 3](#)). These scenarios were based on best management practice guidelines for the province of Québec ([Gouvernement du Québec, 2014](#)) and for the northeastern USA ([Lambert et al., 2017](#)). Current harvesting practices in the simulated regions are generally clearcutting followed by pre-commercial thinning once the forest stands are ca. 15 years old. When a harvesting event occurred in a cell, all species were assumed to be harvested at the same rate, regardless of the harvesting scenario. Harvest was performed by management areas. Harvesting was not performed in protected areas (provincial and national parks). Maximum harvested patch size was set to 31.25 ha (i.e., six cells).

2.11. Simulation design

To estimate the cumulative impacts of harvesting and climate change on BITH habitat, we ran simulations in which successional dynamics as well as all disturbances (wildfire, spruce budworm and forest harvesting) were included. Five replicates were run for 200 years, each starting in the year 2000, for each climate forcing and harvesting scenario using a 10-year time step. Except for scenarios involving the baseline climate, climate-sensitive parameters (fire regime, maxANPP, maxAGB and SEP) were allowed to change in 2010, 2040, and 2070 according to the average climate corresponding to each forcing scenario. Climate conditions and hence dynamic parameters were held fixed at the 2071–2100 conditions for the 2100–2200 period.

Table 3
Harvesting scenarios used in the simulations.

Harvesting scenario	Abbreviation	Description
Clearcutting without precommercial thinning ^a	<i>CCwoPT</i>	Removes 100% biomass of cohorts older than 10 years old in stands >60 years old. Applied to 1% of area per year.
Partial harvesting ^a	<i>PartHarv</i>	Removes 100% biomass of cohorts older than 60 years old in stands >60 years old. Applied to 1% of area per year.
No harvest	<i>Preserv</i>	No harvesting was allowed in the breeding range as defined in section 2.2. <i>CCwoPT</i> was performed elsewhere as above

^a Was not simulated in the Atlantic Maritime at >900 m elevation as very few stands are subject to forest harvesting in this region at such an altitude.

2.12. Bicknell's Thrush habitat classification

LANDIS-II cell simulation outputs were classified into suitable BITH habitat at three different elevation ranges: 300–600 m, 600–900 m and >900 m as population densities generally increase with elevation in forest stands adequate for BITH (COSEWIC, 2009). A cell was considered as suitable habitat if it was dominated (>65%) by balsam fir biomass in the 20–50-year cohorts to best represent dense balsam fir regrowth. These suitable habitat characteristics were based on literature, field data and forest inventory maps (Aubry et al., 2018).

2.13. Analyses

Cumulative impacts of harvesting and climate change were assessed by comparing temporal trends in the following simulated variables for each climate and harvesting scenario: 1) Tree species-specific aboveground biomass; 2) proportion of BITH suitable habitat. Results for these variables were obtained by averaging the outputs of the five replicates of the simulations used to assess cumulative impact. We assessed trends among climate scenarios through quantitative measures of change and comparisons of the simulated mean values. Results were analyzed separately for the AM and BS regions. To better express the impact of climate change and harvesting on simulated habitat proportions, we calculated the percentage decrease or increase in simulated habitat relative to the proportion obtained under the *Preserv* harvest scenario and baseline climate (hereafter referred to the “reference scenario”) following:

$$\begin{cases} -\left(\frac{\text{RefBick}_t - \text{ProjBick}_t}{\text{ProjBick}_t}\right), & \text{RefBick}_t \geq \text{ProjBick}_t \\ \left(\frac{\text{ProjBick}_t - \text{RefBick}_t}{\text{RefBick}_t}\right), & \text{RefBick}_t < \text{ProjBick}_t \end{cases}$$

where RefBick_t is the proportion of critical Bicknell habitat values under the reference scenario (baseline climate and *Preserv* harvesting), while ProjBick_t is the projected proportion of critical Bicknell habitat for the given future period, and t is time in years. This allowed for a direct assessment of the effects of climate change and harvesting and controlling for forest succession.

2.14. Evaluation of conservation zones proposed

As part of the recovery strategy developed by Environment and Climate Change Canada for BITH, zones have been proposed as areas of suitable habitat, or that have the potential for suitable habitat, within a radius of 5 km of probable or confirmed BITH breeding activity. These zones are expected to act as areas that sustain BITH breeding populations, and, thus favor recovery (Environment Canada, 2016). For the purpose of this study, we referred to these zones as “conservation zones”. We evaluated the adequacy of the proposed conservation zones by comparing their extent with our projections of critical BITH habitat from the simulated climate and harvesting scenarios.

3. Results

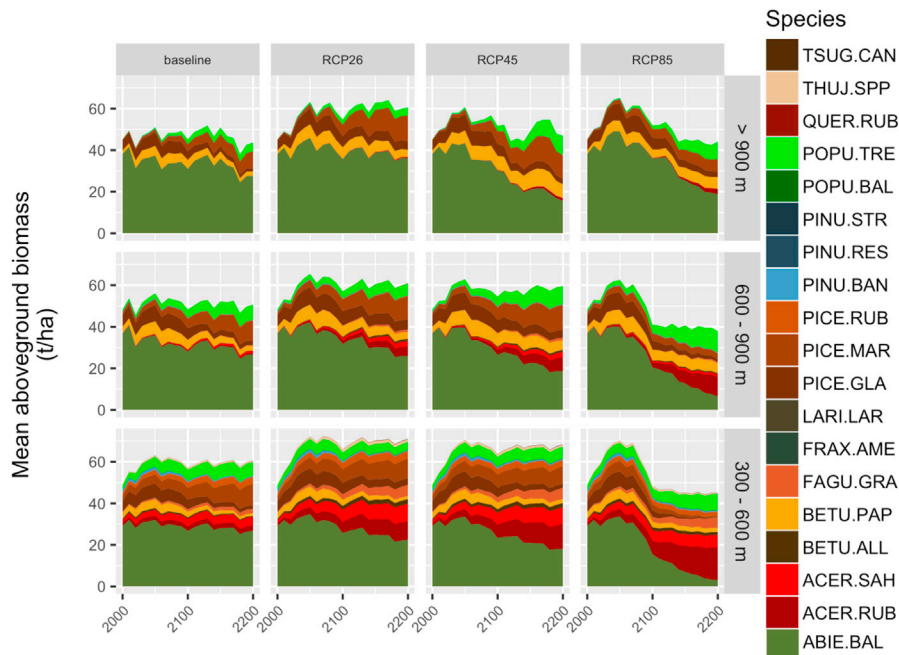
3.1. Impacts of climate change, natural disturbances and harvesting on tree species biomass for the two ecozones

Climate change had a strong impact on forest landscape structure within the study regions by enhancing biomass of deciduous and temperate species at the expense of boreal conifers, notably balsam fir (Figs. 2 and 3). The magnitude of change varied with elevation, climate forcing and forest management scenario; however, major changes in biomass were projected to occur mainly after 2080.

Our results projected a general increase in biomass and upslope migration of deciduous and temperate tree species, mostly trembling aspen, red maple (*Acer rubrum*), sugar maple, yellow birch and American beech (Fig. 2). The effects of climate change on forest composition were more noticeable at lower elevations (<600 m) where the proportion of coniferous tree species biomass declined by 50% after year 2100 in both ecozones, and more rapidly with stronger climate forcing (Fig. 3). The effect of climate change was less obvious at higher elevations (>600 m) but still evident. For example, when compared to values at 2000, losses up to 34% and 21% of balsam fir biomass were projected for 600–900 m and >900 m respectively for the year 2100 under RCP 2.6 and 4.5 for both regions (Fig. 2). Projected balsam fir biomass losses were greater under RCP 8.5 and entered a steep decline by approximately 2100 with a maximum loss of 45% at 600–900 m, and 22% at > 900 m compared to values at 2000 (Fig. 2). By 2200 and under the most severe climate forcing scenario these losses were very high, with balsam fir biomass being reduced by 83% in the AM at 600–900 m compared to values at 2000.

Projected tree species biomass differed only moderately among forest management scenarios. However, balsam fir biomass was generally greater at the end of the *CCwoPT* scenario, particularly in the BS region for all climate scenarios (Appendix A). For example, in the BS region, in 2100, under RCP 8.5, balsam fir biomass was projected as 40.1 t/ha for *CCwoPT* compared to 32.4 t/ha and 31.9 t/ha for the *Preserv* and *PartHarv* scenarios, respectively (Appendix A).

a. Atlantic Maritime (AM)



b. Boreal Shield (BS)

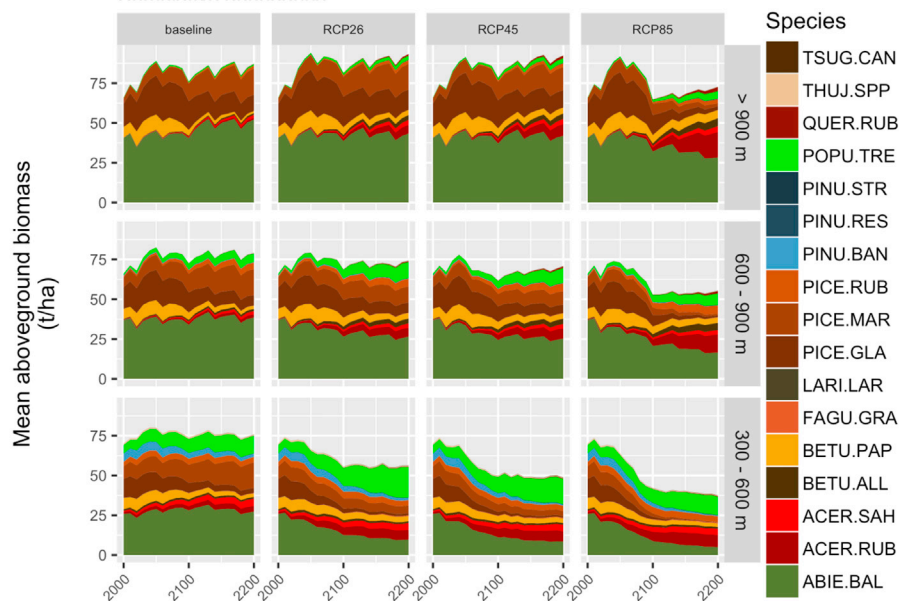


Fig. 2. Stacked species aboveground biomass for the two regions simulated under the baseline, RCP 2.6, RCP 4.5 and RCP 8.5 climate scenarios, for the *Preserv* forest harvest scenario and by elevation category (see [Appendix A](#) for other forest harvest scenario results). Species abbreviations are presented in [Table 1](#). The vertical colour sequences in the graphs follow the sequence shown in the legends. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Differences in biomass projections were also detected between ecozones. Total AGB was substantially reduced for stands at lower elevations (<600 m) in the BS region under the most severe climate forcing as the initial value of 70.1 t/ha decreased to 42.2 t/ha by 2100. ([Fig. 2b](#)). At low elevation (<600 m) there was a greater proportion of deciduous species (mostly aspen) in the BS under RCP 2.6 and RCP 4.5 compared to the AM, with these proportions generally increasing over time ([Figs. 2 and 3](#)).

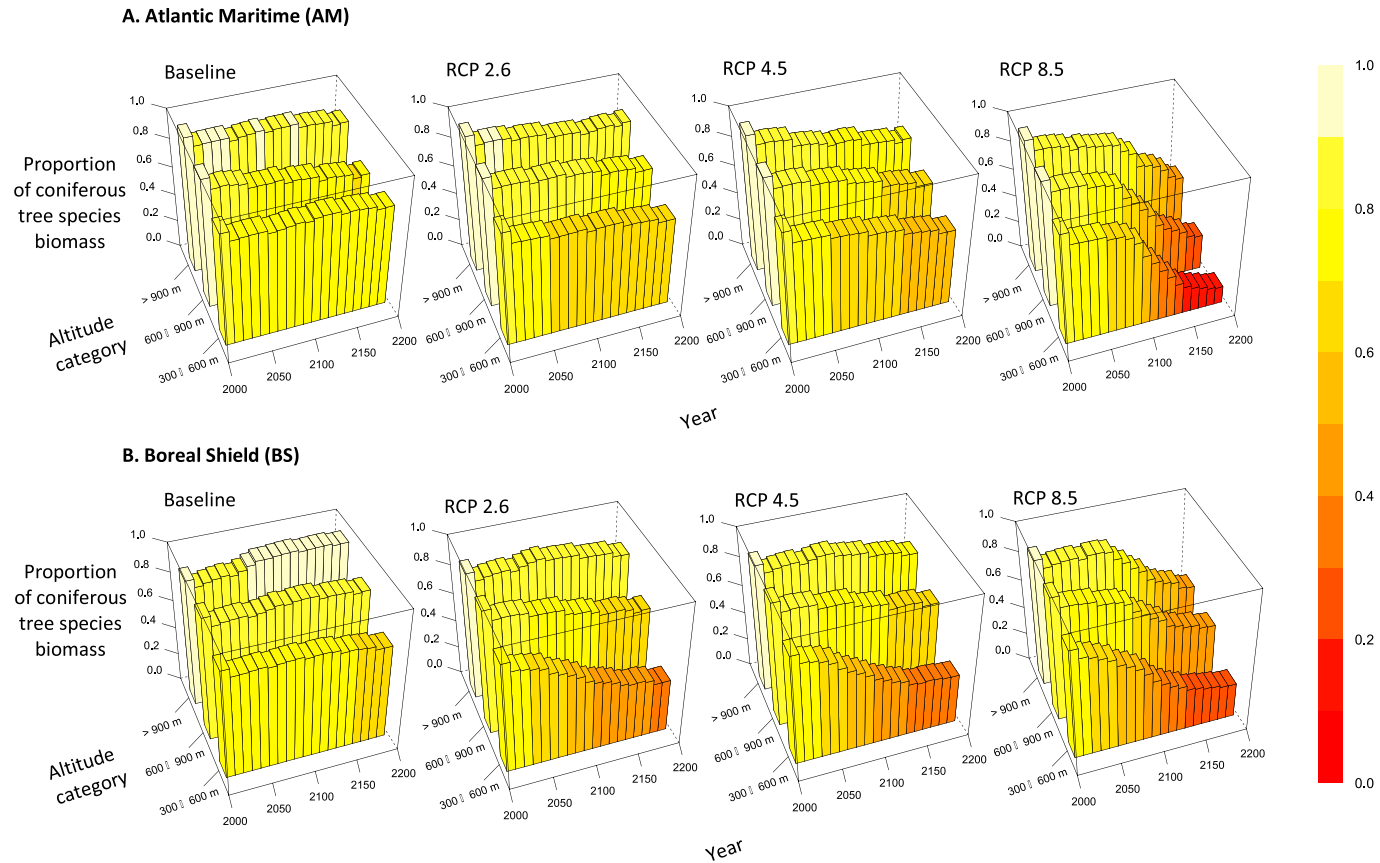


Fig. 3. Projected proportions of coniferous aboveground biomass for the two regions under the baseline, RCP 2.6, RCP 4.5 and RCP 8.5 climate scenarios, for the *Preserv* forest harvest scenario and by elevation category.

3.2. Cumulative impacts of climate change, natural disturbances and harvesting on Bicknell's Thrush's suitable habitat

Climate change was projected to cause strong declines in BITH suitable habitat in both ecozones. Under each climate forcing scenario and for the *Preserv* scenario, the simulations projected decreases in suitable habitat before 2100 compared to the reference scenario (Fig. 4). However, losses in suitable habitat were less severe at higher elevations and ranged from -10% to -34% above 900 m for the *Preserv* harvest scenario at 2100 in both ecozones (Fig. 4). For elevations in the 600–900 m range, important suitable habitat losses were projected for the *Preserv* harvest scenario: from -22% to -50% at 2100 (Fig. 4). At the lowest elevations considered, i.e., 300–600 m, suitable habitat decreased severely, from -55% to -85% for the *Preserv* scenario at 2100 (Fig. 4).

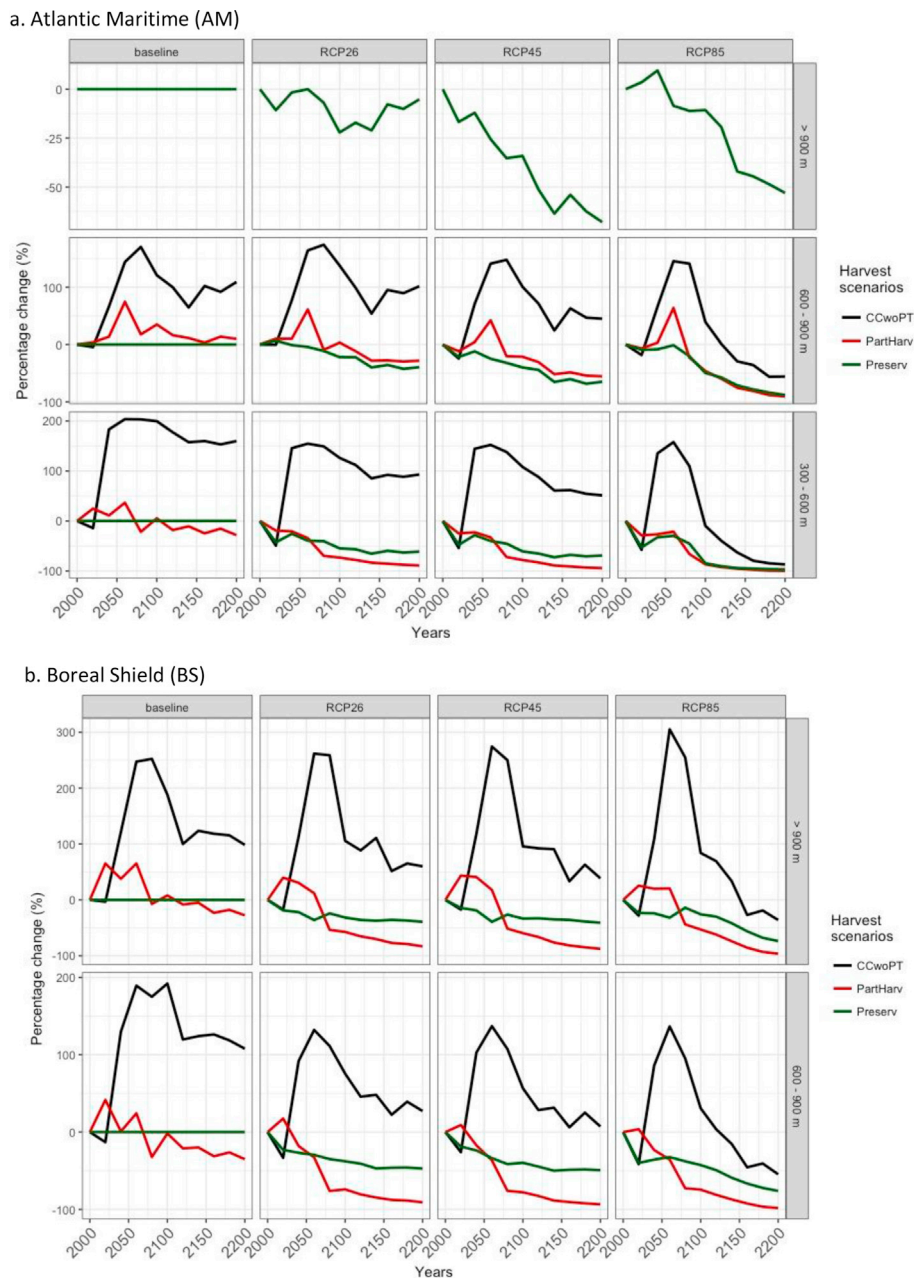


Fig. 4. Influence of climate change and harvest scenarios on BITH simulated habitat proportions in the study regions. The baseline scenario with the harvest treatment “*Preserv*” was used as the reference scenario to estimate simulated habitat percentage decrease or increase. In the AM region, only the *Preserv* scenario is illustrated for the elevation category >900 m since there are very few stands that are subject to forest management. In the BS region, stands at elevation 300–600 m are not considered suitable habitat for BITH and are thus not projected.

BITH habitat was strongly influenced by forest management. The harvesting strategy favoring young coniferous cohorts, the *CCwoPT*, was beneficial to BITH habitat, particularly under less severe climate forcing scenarios, since it had a direct impact on forest stand age and balsam fir abundance in stands. Increases in suitable habitat were projected under almost all simulations performed under the *CCwoPT* scenario at 2100, in both study regions. For example, in the BS under RCP 4.5, suitable habitat increased in the 600–900 m elevation category by approximately 50% by 2100 (Fig. 4).

3.3. Evaluation of suitable habitat in conservation zones

Conservation zones proposed by Environment and Climate Change Canada represented a relatively small portion of the study regions (8% of the BS and 9% of the AM), but encompassed an important proportion of all high elevation areas (>900 m) found in both regions (32% in the BS and 45% of all high elevation areas in the BS in the AM respectively). They included the majority of the BITH simulated habitats at the beginning of the simulation period (58% and 89% for the BS and AM respectively; Fig. 5). At year 2100, these proportions decreased to a minimum of 52% and 77% for the BS and AM respectively (Fig. 5), demonstrating relative spatiotemporal stability of conservation zones despite the projected general suitable habitat declines.

Suitable habitat in conservation zones were projected to strongly decrease under the *PartHarv* and *Preserv* harvest scenarios where habitat losses ranged from –38% to –73% at 600–900 m under the three RCP climate scenarios in the BS in 2100 (Fig. 6). The largest losses in suitable habitat were projected for the 300–600 m elevation range in the AM for *PartHarv* and *Preserv* harvest scenario under the most severe climate scenario where losses up to –86% were predicted (Fig. 6). However, suitable habitat was projected to increase substantially by 2100 under the *CCwoPT* scenario and under the climate scenarios RCP 2.6 and 4.5 as changes ranged from 81% to 158% among elevation classes, and from 69% to 106%, in the AM and the BS regions, respectively (Fig. 6). Under RCP 8.5 and under the same harvest scenario, changes in suitable habitat were smaller ranging from –7% to 18% in the AM and from 47% to 80% in the BS.

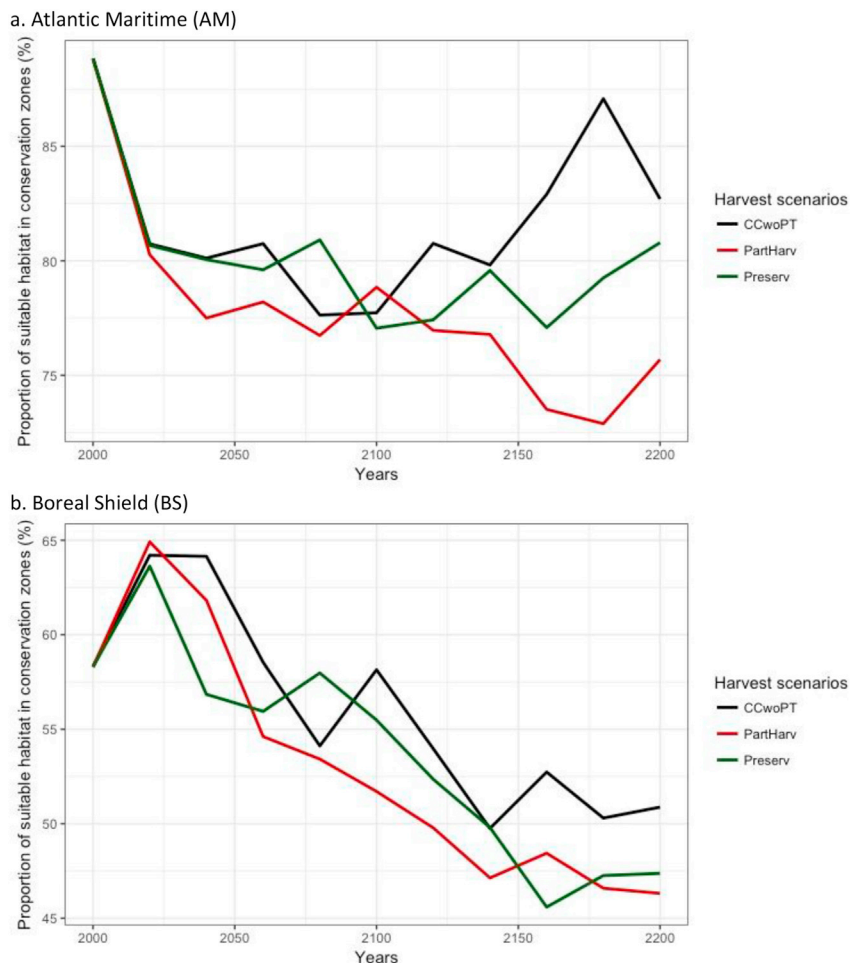


Fig. 5. Proportions of BITH suitable habitat within conservation zones for the two regions simulated under RCP 8.5 climate scenario.

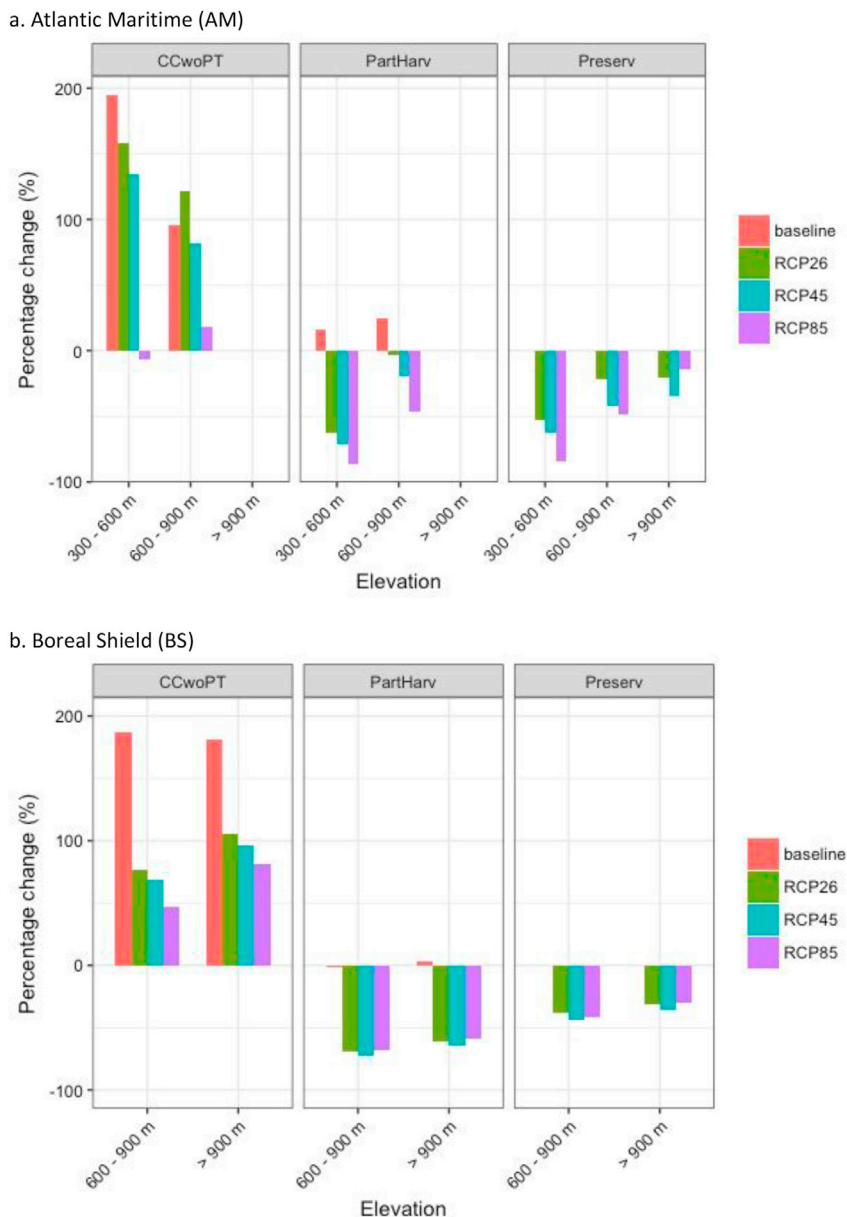


Fig. 6. Proportions of increase or decrease in suitable habitat at year 2100 in conservation zones. The baseline scenario with the harvest treatment “Preserv” at time = 2100 was used as a reference to estimate suitable habitat percentage change. Some values are missing for the AM in the >900 m category for the CCwoPT and the PartHarv scenario as very few stands are subject to forest harvesting in this region. Similarly, for the BS values are missing for the 300–600 m category since suitable habitat buffers covered only a small area in that region.

4. Discussion

Our simulations show climate change and conventional harvesting scenarios will have major impacts on the forest landscapes of central Quebec and New Brunswick, and hence on BITH habitat, leading to general decreases in BITH’s Canadian breeding range. However, changes to current harvesting practices could allow present-day habitat to be maintained or even increased.

4.1. Regional shifts in forest composition: from conifers to deciduous

A general trend of increasing biomass of temperate tree species was projected throughout the study regions along with a decrease in boreal tree species. Several studies in the southern boreal transition zone have projected increases in abundance of temperate tree species due to climate change (Boulanger et al., 2016a,b, Duveneck and Scheller, 2015; Scheller and Mladenoff,

2008; Steenberg et al., 2013). Modeling and field studies have shown that boreal species growing at the southern edge of their present-day distribution, notably including balsam fir, are likely to be vulnerable to warmer and drier climates, while temperate species at the northern edge of their ranges would thrive under these conditions (Reich et al., 2015; Girardin et al., 2015; Boulanger et al., 2016a,b). This has important implications since a northward and upward shift of the balsam fir distribution range could mean the loss of most BITH populations in the northern USA, Nova Scotia and New Brunswick.

Our projections also demonstrated the key role played by elevation, suggesting upslope migration of deciduous and temperate tree species will occur. Our results agree with studies by Rodenhouse et al. (2008) and Beckage et al. (2008) which predicted important climate-driven reductions in the area covered by high-elevation dense conifer-dominated stands in the northern USA, as the northern hardwood-boreal ecotone would shift upslope. However, our projections indicate major changes in species composition would occur around 2080–2100, compared to Rodenhouse et al. (2008) who projected >50% habitat loss by 2038, using bioclimatic models applied to the northeastern USA. Our results agree more closely with studies by Boulanger et al. (2017) who projected significant changes in species composition after 2080 for the Canadian boreal zone and Wang et al. (2016) who projected major changes in forest composition occurring after 2100 in the northeastern USA. Successional lags in vegetation responses to climate change are caused by several factors, including the average lifespans of competing tree species, the relative tolerances of different species changes in temperature and moisture stress, and seed dispersal distances (Wang et al., 2016). It is critically important to take such lags into account for habitat specialist species like the BITH, as they may provide greater insight with which to devise successful recovery strategies that are matched to specific regions (Stralberg et al., 2015; Wang et al., 2016).

4.2. BITH habitat dynamics: the importance of elevation

The combined effects of “worst-case” climate change and current harvesting practices will cause significant suitable habitat losses towards 2100 and beyond. However, projected loss of suitable habitat decreased substantially with increasing elevation. Hence, boreal forest stands at higher elevations (>900 m in our study) would likely act as climate refugia for the BITH and potentially for other species associated with boreal forests (*sensu* Stralberg et al., 2018). High elevation forest stands will likely be critical for the maintenance of BITH as about 70% of Canadian populations are located in suitable habitats above 800 m. These high-quality breeding sites for the BITH support the highest population densities (0.16–0.21 BITH per ha; COSEWIC, 2009), while population density is estimated to be much lower (0.017–0.035 BITH per ha; COSEWIC, 2009) at elevations below 800 m. Accordingly, conservation zones proposed by Environment and Climate Change Canada encompassed a large amount of high elevation areas found in both regions. And, even though suitable habitat was predicted to decline significantly in many simulations, more than half of suitable habitat left in the study regions are expected to be located in these zones in 2100 demonstrating relatively high spatiotemporal stability of these areas. However, our results highlight the importance of considering different conservation strategies depending on elevation and climate scenarios. Hence, in order to better adapt conservation zones to changing climate, we suggest that future conservation zones should target more specifically high elevation areas with potential for supporting BITH suitable habitats. Forest landscape model (FLM) simulations, as those presented in this study, can be useful tool to support such decision processes (prediction maps are available on the data basin portal - databasin.org/groups/c52c7d29d3e14230bc95c71af00b2595).

4.3. Forest harvesting as a suitable habitat management tool

Even though clearcuts can have an initial direct effect of habitat loss for BITH, the clearcutting scenario (CCwoPT) led to an increase in balsam fir biomass, with an increase in the proportion of relatively young dense stands that favour BITH breeding success (see also: Chisholm and Leonard, 2008; Aubry et al., 2011, 2016; Townsend et al., 2017). BITH habitat was projected to increase substantially with the CCwoPT scenario under RCP 2.6 and RCP 4.5. These results suggest that forest harvesting could play an important role as a management tool in the BITH recovery strategy. Although promising, we recommend that this harvesting strategy should only be used under specific situations as suggested by recently developed best-management practices (Gouvernement du Québec, 2014; Lambert et al., 2017). We suggest that the balance between 1) the conservation of sites that are suitable and occupied, or that have a good potential of becoming suitable and; 2) the use of clearcutting *without* precommercial thinning in non-occupied mature sites that have <15 000 stems/ha of balsam fir could be adjusted depending on the elevation. For example, the clearcut strategy could be used more generally at lower elevation where road networks are already developed and where intensive management is warranted due to higher forest productivity and a lower tolerance of BITH-suitable forest stands to climate change. In any event, local and periodic evaluations should be done to assess the need and feasibility of these treatments. Furthermore, we want to emphasize that our simulations did not consider precommercial thinning which is considered an important threat for the BITH and is a common practice after clearcutting in Québec and New Brunswick (Chisholm and Leonard, 2008; Aubry et al., 2011; McKinnon et al., 2014). At least for the province of Québec, up to 80% of naturally regenerating stands is treated with precommercial thinning (Cimon and Labbé, 2006); but this treatment is restricted in stands occupied by the BITH as long as stem density remains >11,000 stems/ha on total area disturbed in <33% (Gouvernement du Québec, 2014).

Stands suitable for BITH created by forest harvesting may differ markedly from naturally disturbed montane balsam fir forests. Clearcut logging generally creates large patches of similar aged trees and, with sustained yield management objectives, tends to normalize the age and vertical structure of forest landscapes. On the other hand, natural disturbances,

particularly on high elevation sites, tend to create small and scattered patches of forest regrowth, creating lots of variability in forest structure at small scale (<4 ha; Lambert et al., 2017; Sprugel, 1976; Reiners and Lang, 1979). This can provide a greater availability of smaller patches of suitable habitat (COSEWIC, 2009). Since BITH occupancy at breeding sites is influenced by both local- and landscape-scale factors (Frey et al., 2011), stability in availability of suitable habitat at local and landscape scales might be an important feature to maintain occupancy of breeding habitat by the BITH (COSEWIC, 2009). However, more studies are needed to properly evaluate the impacts of forest harvest strategies like clearcutting on BITH occupancy, reproductive success and population dynamics in its Canadian breeding range.

5. Limitations of the simulations

Our results may be used in the planning of recovery and conservation strategies of BITH populations, but there are some important caveats. First, we modeled the forest dynamics of BITH breeding habitat rather than the dynamics of the BITH populations themselves. It is unlikely that all habitats are fully occupied by BITH due to other ecological factors (Aubry et al., 2018). Given uncertainties about how BITH will colonize new habitat, a projected increase in the amount of simulated breeding habitat does not necessarily imply a direct corresponding increase in BITH populations. Second, we did not simulate tree stem density in our projections, which is an important variable in BITH habitat selection (Townsend et al., 2017; Lloyd and McFarland, 2017). Rather, we used stand structure (specifically, tree species age cohorts ranging between 20 and 50 years old) and forest composition (based on the proportion of balsam fir) to identify suitable BITH habitat. At high elevation sites, this might have excluded older forest stands with high stem density, due to harsh climate and small-size natural disturbances, which could provide additional habitat suitable for BITH (Ruel, 2000). Third, we may have underestimated the impacts of natural disturbances related to wind such as windthrow and fir waves (*sensu* Sprugel, 1976) which can also favor the creation of suitable BITH habitat. Finally, SBW outbreaks were simulated at their highest severity; this might have contributed to create more regenerating balsam fir stands, and hence potential BITH habitat, then would be expected under a less severe SBW outbreak regime. This likely explains much of the long-term increase in BITH habitat relative to the initial conditions under most climate scenarios, including the baseline climate conditions. Severe SBW outbreaks are projected to decrease in duration with climate change over the study area in the next decades because higher temperatures will likely limit SBW activity (Boulanger et al., 2016b).

6. Conclusion

Forest landscape models (FLM), which integrate landscape scale and stand scale processes, can be useful tools to evaluate the spatial and temporal dynamics of habitat for species at risk in forest environments. Simulation results for alternative future scenarios can inform designation and implementation of recovery strategies for threatened species. Our simulations projected a regional decrease in the availability of habitat for Bicknell's Thrush (BITH) in conifer-dominated stands in eastern Canada, due to an increase in the proportions of temperate and deciduous species. Forest harvesting involving clearcutting without pre-commercial thinning proved to be a promising management tool as it was projected to partially offset the loss of BITH habitat. Results from the study reported here could help guide conservation and restoration of breeding habitat for BITH and provide a concrete example of the usefulness of FLMs as a planning tool for the recovery planning for other threatened species.

As climate change is projected to bring major changes to the boreal forest in the long term, there is an urgent need to identify where and when potential new habitats for BITH and other threatened species could be created north of their current distributions, or at higher elevations in suitable terrain. FLMs could be an important tool in such an effort, with the important caveat that the capacities of populations of threatened species to colonize these future suitable habitats would also need to be determined.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00530>.

Appendix A

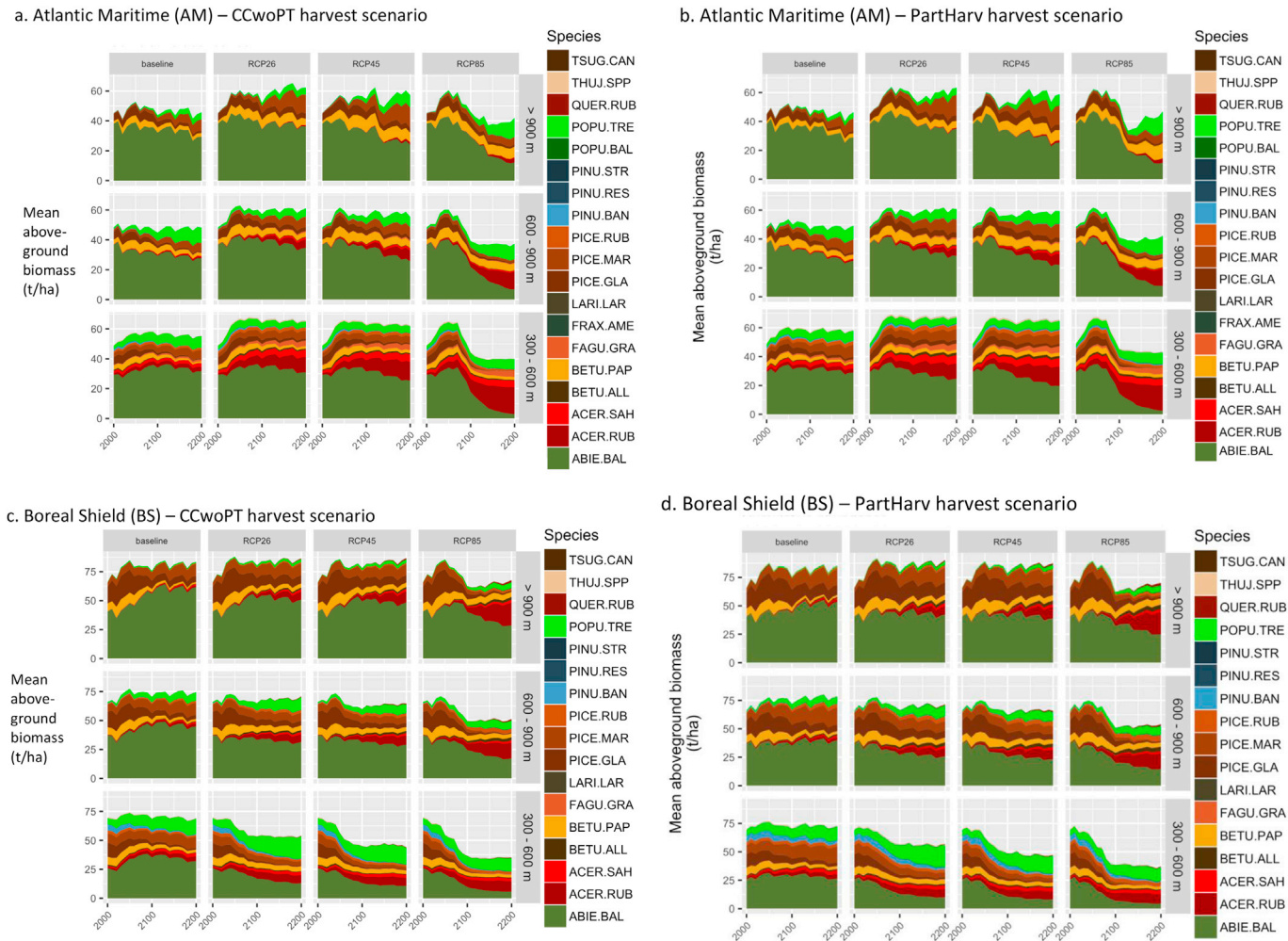


Fig. A1. Stacked species aboveground biomass for the two regions simulated under the baseline, RCP 2.6, RCP 4.5 and RCP 8.5 climate scenarios and by elevation category for the harvest scenario CCwoPT and PartHarv. Species abbreviations are presented in Table 1. The vertical colour sequences in the graphs follow the sequence shown in the legends.

a. Atlantic Maritime (AM) – CCwoPT harvest scenario

b. Atlantic Maritime (AM) – PartHarv harvest scenario

c. Boreal Shield (BS) – CCwoPT harvest scenario

d. Boreal Shield (BS) – PartHarv harvest scenario

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