CrossMark

RESEARCH ARTICLE

Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone

Yan Boulanger · Anthony R. Taylor · David T. Price ·
Dominic Cyr · Elizabeth McGarrigle · Werner Rammer ·
Guillaume Sainte-Marie · André Beaudoin · Luc Guindon ·
Nicolas Mansuy

Abstract

Context Forest landscapes at the southern boreal forest transition zone are likely to undergo great alterations due to projected changes in regional climate.

Objectives We projected changes in forest landscapes resulting from four climate scenarios (baseline, RCP 2.6, RCP 4.5 and RCP 8.5), by simulating changes in tree growth and disturbances at the southern edge of Canada's boreal zone.

Methods Projections were performed for four regions located on an east–west gradient using a forest landscape model (LANDIS-II) parameterized using a forest patch model (PICUS).

Results Climate-induced changes in the competitiveness of dominant tree species due to changes in potential growth, and substantial intensification of the fire regime, appear likely to combine in driving major changes in boreal forest landscapes. Resulting cumulative impacts on forest ecosystems would be manifold but key changes would include (i) a strong decrease in the biomass of the dominant boreal species, especially mid- to late-successional conifers; (ii) increases in abundance of some temperate species able to colonize disturbed areas in a warmer climate; (iii) increases in the proportions of pioneer and fire-adapted species in these landscapes and (iv) an overall decrease in productivity and total biomass. The greatest changes

Y. Boulanger (✉) · D. Cyr · A. Beaudoin ·
L. Guindon · N. Mansuy
Natural Resources Canada, Canadian Forest Service,
Laurentian Forestry Centre, 1055 du P.E.P.S, Stn. Sainte-Foy, P.O. Box 10380, Québec, QC G1V 4C7, Canada
e-mail: yan.boulanger@canada.ca

A. R. Taylor · E. McGarrigle
Natural Resources Canada, Canadian Forest Service,
Atlantic Forestry Centre, 1350 Regent Street South,
P.O. Box 4000, Fredericton, NB E3B 5P7, Canada

D. T. Price
Natural Resources Canada, Canadian Forest Service,
Northern Forestry Centre, 5320 122nd Street NW,
Edmonton, AB T6H 3S5, Canada

W. Rammer
Department of Forest and Soil Sciences, BOKU, Institute
of Silviculture (Institut für Waldbau), University of
Natural Resources and Life Sciences, Peter Jordanstr. 82,
1190 Vienna, Austria

G. Sainte-Marie
Département des Sciences Biologiques, Université du
Québec à Montréal, C.P. 8888 Succ. Centre-Ville,
Montréal, QC H3C 3P8, Canada

would occur under the RCP 8.5 radiative forcing scenario, but some impacts can be expected even with RCP 2.6.

Conclusions   Western boreal forests, i.e., those bordering the prairies, are the most vulnerable because of a lack of species adapted to warmer climates and major increases in areas burned. Conservation and forest management planning within the southern boreal transition zone should consider both disturbance- and climate-induced changes in forest communities.

Keywords   Climate change · LANDIS-II · PICUS · Boreal forest · Canada

Introduction

Recent climate change projections indicate that annual mean temperatures could increase by 4–5 °C by the end of the twenty-first century across Canada's boreal zone, if there is little progress on controlling global anthropogenic greenhouse gas emissions (Price et al. 2013). Such temperature increases will significantly impact the structure and function of the forest landscape (Gauthier et al. 2015a). Changes in temperature and precipitation regimes are expected to shift the optimal climate zones of many boreal tree species northwards by hundreds of kilometers (McKenney et al. 2007; Prasad et al. 2013), altering forest composition and diversity (Heyder et al. 2011; Reich et al. 2015) and the goods and services derived from these forests (Lovejoy and Hannah 2005; Price et al. 2013; Gauthier et al. 2015a).

In particular, the transition zone between the southern boreal and northern temperate forests may be particularly sensitive to changes in climate and could experience major changes in species composition (Heyder et al. 2011; Reich et al. 2015) resulting in shifts in the geographic distribution of trees and hence regional biomes (Beck et al. 2011). However, projecting such shifts is not trivial as there are many agents of change affecting forest landscapes. Firstly, changes in temperature and precipitation will have direct effects on individual tree species performance, e.g., growth, mortality, productivity, and recruitment (Luo and Chen 2013; Girardin et al. 2015), which lead to changes in inter-

specific competition and succession (Luo and Chen 2015; Price et al. 2015; Reich et al. 2015). Moreover, climate-induced changes in regional natural disturbance regimes may trigger more rapid alterations in forest communities (e.g., Keane et al. 2013). An increase in forest fire activity (Boulanger et al. 2014) or shifts in pest outbreaks (Boulanger et al. 2016) will likely change the prevalence of young forests dominated by early successional species (e.g., aspen, birch and jack pine), and trigger changes in net ecosystem productivity (Girardin et al. 2011; Chen and Luo 2015), while also facilitating northward range expansion of temperate tree species able to take advantage of canopy openings (Matthews et al. 2011; Woodall et al. 2013).

As shifts in climate and their effects on disturbances are likely to be spatially and temporally heterogeneous throughout the Canadian southern boreal region (Price et al. 2013), one can expect varying responses of the forest vegetation (Bergeron et al. 2014). For instance, annual area burned could increase by more than 300 % to reach values of 2 % or more per year in central Canada, which is much higher than in eastern Canada (Boulanger et al. 2014). Central and western boreal regions are more likely to suffer from ecologically significant water deficits, causing serious impacts on drought-sensitive tree species (Hogg and Bernier 2005; Price et al. 2013; Wang et al. 2014; Ireson et al. 2015). Regional variations in the current distribution of vegetation, and in functional traits of the constituent species, e.g., dispersal ability, post-disturbance reproductive ability and climate-related productivity, could also shape a spatially heterogeneous response in the changes to forest landscapes (Matthews et al. 2011). Physiognomic (e.g., geographic barriers, soil characteristics, Gewehr et al. 2014) and anthropogenic factors (e.g., harvesting, fragmentation; Scheller and Mladenoff 2008), may also interact strongly with climate change-related impacts. Therefore, some regions will likely be at greater risk than others. As such, a broad holistic and spatially explicit assessment is essential when assessing the range of potential future changes in southern boreal forest landscapes. Such an assessment should be of great benefit to managers and policymakers for developing and implementing successful adaptations of present-day forest management practices.

Large-scale impacts of global climate change on forest ecosystems are commonly assessed using correlative species distribution models (SDM) (e.g., Iverson and Prasad 2002; McKenney et al. 2007). SDM models are simplistic but can provide useful ways to incorporate future conditions easily into conservation and management planning and decision-making (Pearson and Dawson 2003; Wiens et al. 2009). However, they have well-known limitations (e.g., Thuiller et al. 2008) including the inability to account for community-level interactions (Franklin et al. 2016), dispersal, and landscape-scale disturbances (but see Engler and Guisan 2009; Prasad et al. 2013). Many of these limitations may be overcome through the use of more mechanistic forest landscape models (FLM; e.g., Scheller and Mladenoff 2005). These models allow for succession to emerge from stand-level processes and landscape-level disturbances, which are key to projecting plausible impacts of climate change (Gustafson 2013). FLM may be linked to finer-scale patch models (e.g., Linkages, JABOWA) within which fine-scale ecological processes that integrate important tree responses to climate change (e.g., differential seed germination rates, tree–tree interactions, etc.) are modeled (Taylor and Chen 2009).

In this paper, we aimed to integrate a well-established gap-model (PICUS) and a well-known FLM (LANDIS-II) to explore and assess the impacts of natural and anthropogenic disturbances as well as climate-induced changes on forest landscapes along a longitudinal gradient across Canada's southern boreal forest. Specifically, we assessed how these agents of change, when combined, will modify the total live aboveground biomass (AGB, t ha^{-1}) and annual aboveground net primary productivity (ANPP, kg m^{-2} year^{-1} as well as forest communities from changes in species-level AGB (t ha^{-1}). We hypothesized that the effects of a generally warmer and drier climate on growth, combined with sharp increases in disturbance frequency, will decrease total AGB and productivity in most regions. Concurrently, the increase in disturbances should promote increasing dominance of pioneer species over late-successional species and a warmer climate should favor warm-adapted mesophytic species at the expense of typical boreal species. We expected that western regions would be most at risk from these combined effects.

Methods

Study regions

Forest landscapes were simulated within four study regions located at the transitions between boreal and hemiboreal zones in each of four forested ecozones in Canada. These are, from west to east, the Boreal Plains (BP), the Boreal Shield West (BSW), the Boreal Shield East (BSE) and the Atlantic Maritimes (AM) (Fig. 1). Ecozones are the largest units of the National Ecological Framework of Canada (NEFC; Ecological Stratification Working Group 1996). The eastern and western parts of the Boreal Shield ecozone differ substantially in climate, however, and were split following Kurz et al. (2013) and Price et al. (2013). Each study region covers a transition zone between the southern edge of the boreal and the northern edge of the hemiboreal except for the AM which, because of its ocean proximity, lies entirely within the hemiboreal zone (Brandt et al. 2013). The area of each study region was set to span approximately 10 % of the "parent" ecozone. Each study region encompasses a wide variety of forest types, soils, and local climates, as well as anthropogenic and natural disturbance conditions (Supplementary Material S1 and S2).

Climate data

Monthly time series of current climate were interpolated from climate station records using the data of McKenney et al. (2013). Future climate projections were obtained for the Canadian Earth System Model version 2 (CanESM2) using data downloaded from the World Climate Research Program (WCRP) Climate Model Intercomparison Project Phase 5 (CMIP5) archive for each of three different radiative forcing scenarios, known as Representative Concentration Pathways (RCP, e.g., van Vuuren et al. 2011), namely RCP 2.6, RCP 4.5 and RCP 8.5. The RCP 2.6 scenario represents a situation where radiative forcing peaks at $\sim$3 W m^{-2} before 2100 and then declines to reach 2.6 W m^{-2} by 2100. In the RCP 4.5 scenario, radiative forcing is assumed to stabilize at 4.5 W m^{-2} after 2100 without an "overshoot" pathway. Conversely, in the RCP 8.5 scenario, the forcing reaches 8.5 W m^{-2} in 2100 and continues to increase for some time afterwards. According to these scenarios, mean annual temperature would increase by about 3.5 °C (RCP 2.6)

Fig. 1 Locations of the four regions where forest landscapes were simulated (delineated in *red*). There is one region for each of the following ecozones (delineated in *black*). *AM* Atlantic maritime, *BSE* boreal shield east, *BSW* boreal shield west, *BP* boreal plains. The boreal (*light gray*) and hemiboreal (*dark gray*) forest (sensu Brandt 2013) are also shown. (Color figure online)
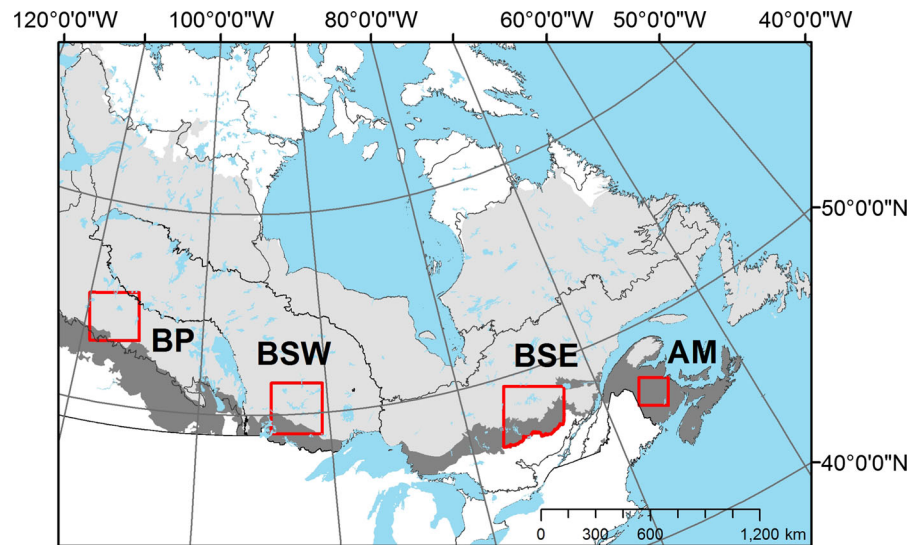
to 7.5 °C (RCP 8.5) throughout the southern boreal region by 2100 (compared with circa 2000), while average precipitation is projected to increase by 10–25 % regionally with very small differences among forcing scenarios (Supplementary Material S2). Data from CanESM2 for the 1900–2100 period were bias-corrected by expressing them as differences from (temperature) or ratios of (precipitation) the CanESM2 monthly means for the 1961–1990 period.

The forest landscape model LANDIS-II

LANDIS-II is a spatially-explicit raster-based forest landscape model that simulates disturbances, seed dispersal, and forest succession (Scheller et al. 2007). Species are defined using unique life-history attributes and are represented in each grid cell as 10-year age-cohorts. Cell resolution was set to 250 m (6.25 ha). Forest composition and structure in each cell were initialized using forest properties data derived from the Canadian National Forest Inventory (NFI) and cohort data from provincial permanent and temporary forest inventory plots (FIP). Using species biomass as well as mean annual temperature and total annual precipitation as variables, we performed a nearest neighbour spectral analysis to attribute the FIP showing the smallest Euclidean distance to each 250 m cell. This imputation was conducted on a 20-year age class basis to ensure that the Euclidean distance between FIP and the 250 m cell was mostly due to site

productivity and not stand age. Each of these cells was then assigned to a spatial unit (i.e., "landtype") with soil (Mansuy et al. 2014) and climate conditions considered homogeneous. Grid cells with more than 50 % of their area covered with non-forest cover types were classified as inactive.

Forest succession and species growth potential

Forest succession in each grid cell was then simulated using the LANDIS-II Biomass Succession extension v 3.1 (Scheller and Mladenoff 2004). This extension takes into account tree species cohort age, life history traits, and species-specific landtype responses, and simulates changes in cohort biomass over time as each cohort regenerates, ages and dies. Species life-history traits information was collected using various sources (e.g., Burns and Honkala 1990 and previous LANDIS-II publications) including several previous studies involving LANDIS-II for North American forest landscapes (Table 1).

To upscale physiological and demographic responses of tree species through time under different climate change scenarios, we parameterized our LANDIS-II simulation experiment with the individual tree-based, forest patch model PICUS, version 1.5 (Lexer and Hönninger 2001). PICUS simulates the dynamics of individual trees on 10 × 10 m patches across forest stand areas (generally 100–1000 patches, corresponding to total areas of 1–10 ha). It accounts

Table 1 LANDIS-II input data for tree species simulated within the four study regions

Species	Species code	Study region[a]	Longevity	Age at maturity	Shade tolerance[b]	Effective seed dispersal (m)[c]	Maximum seed dispersal (m)	Vegetative reproduction	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter
Abies balsamea	ABIE.BAL	AM, BSE, BSW	150	30	5	25	160	No	None	0	25
Acer rubrum	ACER.RUB	AM, BSE	150	10	3	100	200	Yes	Resprout	0	25
Acer saccharum	ACER.SAH	AM, BSE	300	40	5	100	200	Yes	Resprout	1	15
Betula alleghaniensis	BETU.ALL	AM, BSE	300	40	3	100	400	Yes	Resprout	1	15
Betula papyrifera	BETU.PAP	All	150	20	2	200	5000	Yes	Resprout	0	25
Fagus grandifolia	FAGU.GRA	AM, BSE	250	40	5	30	3000	Yes	None	1	15
Larix laricina	LARI.LAR	All	150	40	1	50	200	No	None	0	25
Picea glauca	PICE.GLA	All	200	30	3	100	303	No	None	1	15
Picea mariana	PICE.MAR	All	200	30	4	80	200	No	Serotiny	1	15
Picea rubens	PICE.RUB	AM, BSE	300	30	4	100	303	No	None	1	15
Pinus banksiana	PINU.BAN	All	150	20	1	30	100	No	Serotiny	0	25
Pinus resinosa	PINU.RES	AM, BSE, BSW	200	40	2	12	275	No	None	1	15
Pinus strobus	PINU.STR	AM, BSE, BSW	300	20	3	100	250	No	None	1	15
Populus balsamifera	POPU.BAL	AM, BSW, BP	130	20	1	1000	5000	Yes	Resprout	0	25
Populus tremuloides	POPU.TRE	All	150	20	1	1000	5000	Yes	Resprout	0	25

Table 1 continued

Species	Species code	Study region[a]	Longevity	Age at maturity	Shade tolerance[b]	Effective seed dispersal (m)[c]	Maximum seed dispersal (m)	Vegetative reproduction	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter
Thuja occidentalis	THUJ.OCC	AM, BSE, BSW	300	30	5	45	60	No	None	1	15
Tsuga canadensis	TSUG.CAN	AM, BSE	300	60	5	30	100	No	None	1	15

[a] See Fig. 1 for study region names

[b] 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

[c] Distance within which 95 % of seeds disperse

for spatially explicit interactions among patches via a 3D light module, and simulates seed dispersal explicitly, as well as the effects of climate and soil properties on tree population dynamics (Lexer and Hönninger 2001; Seidl et al. 2005). Selected species-specific parameters used in PICUS may be found in Table 2. Complete description of the model and how it was parameterized and validated can be found in Supplementary Material S3. PICUS was used to derive three sets of species-, climate-, and landtype-specific dynamics inputs used in Biomass succession extension in LANDIS-II, i.e., (i) species establishment probabilities (*SEP*), (ii) maximum possible aboveground net primary productivity (*maxANPP*), and (iii) maximum AGB (*maxAGB*). Using individual tree information from the NFI and selected Canadian provincial inventory plots, we parameterized PICUS for 17 tree species occurring in the study regions (Table 1). To be included, these had to represent at least 0.3 % of total AGB of a given study region according to the 2001 NFI forest properties maps at 250 m resolution (Beaudoin et al. 2014).

Using the PICUS model, we simulated mono-specific 1-ha stands for each of the leading tree species. A factorial simulation design was used to simulate all mono-specific stands for each study region, tree species and landtype under climate conditions for specific periods (2000–2010, 2011–2040, 2041–2070, 2071–2300) and forcing scenarios (baseline, RCP 2.6, RCP 4.5, RCP 8.5). All stands were simulated for 300 years from bare-ground and used the local soil (Mansuy et al. 2014) and climate time-series data. Values for *SEP*, *maxANPP* and *maxAGB* were then derived from these simulations (see Supplementary Material S4 for computational details).

Validation of dynamic growth parameters, as well as static growth- and mortality curve shape parameters, were assessed under baseline climate conditions by (i) assessing the realism of emerging successional pathways using pixel-level simulations as well as (ii) comparing species-specific biomasses at time $t = 0$ with the actual biomass estimated from the NFI forest cover maps (Beaudoin et al. 2014). Pixel-level simulations were conducted for one specific landtype chosen subjectively from the most common landtypes in a given study region to represent one general type of ecosystem (e.g., softwood boreal forest, mixedwood temperate forests, etc.). The successional pathways resulting from 1000-year simulations (Supplementary

Table 2 Select input parameters specific to PICUS for species simulated within the four study areas

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.BAL	2	2.3	11	150	3024	0.5	0.05
POPU.TRE	2	2.3	11	150	3024	0.5	0.05
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 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 (Lexer and Hönninger 2001) p. 52). High tolerance (0.1–0.7), MedTolerance (0.05–0.5), low tolerance (0–0.3)

Material S5) showed good agreement with those reported in the literature (e.g., Racey et al. 1996; McLaughlan et al. 2010; Cyr 2014). The initial biomass for most species showed little discrepancy with NFI forest cover maps (Supplementary Material S6). However, balsam fir biomass was underestimated in AM, and the biomasses of jack pine and maples species were overestimated in most study regions. Despite these small discrepancies, we decided the overall calibration results were satisfactory given that the pixel-level simulations generally followed the known successional trajectories for these latter species.

Natural disturbances

Two natural disturbance agents, namely fire and spruce budworm (SBW, *Choristoneura fumiferana* [Clem.]) outbreaks, were considered in the LANDIS-II simulations. Together, these accounted for the majority of area disturbed by fire and insects in the study regions and both are recognized to have major impacts on Canada's forest landscapes (e.g., Volney and Hirsch 2005). Fire simulations were conducted using the LANDIS-II Base Fire extension, which simulates stochastic fire events dependent upon fire ignition, initiation and spread. Fire regime data (annual area burned, fire occurrence, and mean fire size) were summarized into "fire regions" corresponding to the intersection of each region and the Canadian Homogeneous Fire Regime (HFR) zones of Boulanger et al. (2014). As we wished to constrain fire regime to known values for better traceability and reproducibility, fire simulations were not parameterized as a process emerging from dynamic changes in vegetation as well as from changes in climate. 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. 2015b, see also Supplementary Material S2).

Outbreaks of SBW were simulated using the Biological Disturbance Agent (BDA) extension v3.0 (Sturtevant et al. 2004), which is specifically designed to simulate host tree mortality following insect outbreaks. Host tree species for SBW included, from the most to least vulnerable, balsam fir (*Abies balsamea*), and white (*Picea glauca*), red (*P. rubens*) and black (*P. mariana*) spruce. Outbreaks are simulated as probabilistic events at the cell level with probabilities being a function of site and neighborhood resource dominance (e.g., host abundance within a 1-km radius) as well as regional outbreak status. Outbreak impacts (tree mortality) are contingent on these probabilities as well as on host species- and age-specific susceptibility. Parameters used in this study were calibrated and validated using various sources for the mixed boreal forest (e.g., MacLean 1980; Hennigar et al. 2008). Regional outbreaks were calibrated at highest severity level possible using this extension and were set to last at most one timestep (10 years) and to occur every 35 years in accordance with typical observed regional recurrence cycles (e.g., Boulanger et al. 2012).

Harvesting

Forest harvesting was simulated using the Biomass Harvest extension (v3.0; Gustafson et al. 2000). Historical harvest data (harvested AGB) were retrieved from MODIS-based annual (2001–2011) forest disturbance maps (Guindon et al. 2014) combined with the 2001 NFI forest properties maps, both at 250 m resolution to create estimates of cumulative AGB harvested during 2002–2011 at the 250-m grid cell scale. In this time period, grid cells where harvesting occurred along with estimated change proportion (%) were classified according to three levels of cumulative biomass removed (1–40, 40–80 and >80 %), hereafter considered as three harvesting prescriptions (Supplementary Material S1a). Mean harvested patch size, mean AGB harvested per prescription, and total harvested area, were summarized by "management areas" (i.e., either by forest management units for public lands or by ecodistricts for private lands). Older stands and those with the highest conifer proportion (according to species-level AGB) were given precedence for harvesting.

Simulation design

For each study region and climate forcing scenario, we ran five replicated LANDIS-II simulations for 300 years at 10-year time steps starting in the year 2000. SBW disturbance was not included in the BP region simulations because it is projected to remain a very minor disturbance factor in that region (Boulanger et al. 2016). Baseline parameters were used for the 2000–2010 period for all simulations as well as for the spin-up phase where the initial biomass of each species' cohort is grown according to cohort presence-absence. Except for simulations forced by the baseline climate, only the climate-sensitive parameters (fire regime, *maxANPP*, *maxAGB* and *SEP*) were allowed to change in 2010, 2040, and 2070 according to the specific anthropogenic forcing scenario, but were held fixed thereafter up to the year 2300.

Analyses

For each region, we compared temporal trends in total and species-level AGB and ANPP, for each forcing scenario with those obtained for the baseline scenario. We also assessed the magnitude of regional-level changes in forest communities by calculating Bray-Curtis dissimilarity indices for species-level AGB data obtained from the baseline simulations compared to those from each of the future climate scenarios.

As frequently performed in similar studies involving LANDIS-II, total and species-level AGB, ANPP and community dissimilarity are reported here as mean values as stochastic variation among replicates was small. No formal statistical tests were performed; rather we assessed trends among areas and RCPs through visual inspection of graphs and comparisons of mean values reported.

Results

Projections of potential species growth using PICUS

Strong variations in growth pattern among time periods and forcing scenarios revealed important climatic constraints for individual species as simulated by PICUS, shown by strong variation in

maxANPP, *SEP* and *maxAGB* (Supplementary Material S7). For several boreal species, climate-related potential growth was projected to decline with increasing forcing, but most markedly under the RCP 8.5 (Supplementary Material S7). The decline was particularly dramatic for balsam fir, black and white spruces and larch where growth was virtually nil for most landtypes under RCP 8.5 climatic conditions simulated for 2071–2100 (Supplementary Material S7). A few species (yellow birch, white pine, eastern hemlock, red and sugar maple, red oak and American beech) exhibited increased potential growth under most future climates, with the exception of RCP 8.5 for the 2071–2100 period, when potential growth was rather similar or even lower than estimated using baseline climate (Supplementary Material S7).

Projections of disturbance regime

Under baseline climate, annual area burned varied between 0.2 and 0.5 %, in the AM and BSW, respectively. As calibrated from the projections of Boulanger et al. (2014), annual area burned was projected to increase in all study regions, particularly under the RCP 8.5 climate scenario (240–610 % increase) and in the BSW where it reached 3.7 % year⁻¹ by the end of the twenty-first century (Supplementary Material S8). Increases in area burned were substantially smaller under RCP 2.6 and RCP 4.5. The area affected by SBW outbreaks gradually decreased under all future climate forcings, but most markedly under RCP 8.5, most notably in the AM where it shifted from 35 % in 2020 to less than 5 % in 2300. Elsewhere, areas projected to be affected by SBM diminished almost to zero by 2300 under RCP 8.5. Much smaller declines in area affected by SBW were projected under RCP 2.6 and 4.5 in the BSE and BSW while they remained similar to those projected for the baseline climate in AM (Supplementary Material S8).

Total biomass harvested under RCP 2.6 and RCP 4.5 remained similar to that simulated under baseline climate (Suppl. Mat S8). However, for the RCP 8.5 climate scenario, total biomass harvested declined by 25–50 % relative to baseline by 2300, even though harvesting prescriptions were kept similar throughout the simulations.

Projections of ANPP and total AGB

A clear west-to-east gradient in overall changes in ANPP (Fig. 2) and total aboveground biomass (Fig. 3) occurred, with the largest decreases in both indicators projected for the western-most regions (BP and BSW). In all regions, projected decreases in ANPP (Fig. 2) and total aboveground biomass (Fig. 3) were inversely related to the radiative forcing. Compared with baseline, aboveground biomass and ANPP were projected to decrease by more than 80 % by 2300 in the BSW, and by 25–45 % elsewhere, under the RCP 8.5 forcing scenario, whereas both parameters remained unchanged or only slightly decreased under RCP 2.6 and RCP 4.5. Exceptions were for the AM where productivity was projected to increase by ∼10 % between 2100 and 2150 under RCP 4.5. Changes relative to baseline occurred rather fast, with the largest changes occurring between ca. 2070 and ca. 2150 for most regions.

Regional-level changes in forest composition

Projected changes in forest species composition relative to baseline climate were highly variable among forcing scenarios and study regions (Fig. 4), with the most dramatic (Bray-Curtis Index > 0.5) occurring in the BP and BSW under RCP 8.5. The eastern study regions appeared to be as vulnerable as the western regions to changes in composition under the RCP 2.6 and RCP 4.5 scenarios. For all regions, overall changes in species composition were largest under RCP 8.5.

Regional trends in dissimilarities between communities experiencing baseline and future climate did not necessarily translate into similar regional changes in species-level biomass. Notably, changes in species communities in western regions (BP and BSW) were strongly driven by a shift in dominance to pioneer, disturbance-adapted species, especially under RCP 8.5 (Fig. 5). The net effect was to create generally younger forests composed of fewer species. In the eastern regions, however, the shift in forest composition resulted partially from an increase in the biomass of temperate, warm-adapted species (e.g., American beech, hemlock), and particularly of early to mid-successional species (e.g., red maple, white pine). These changes were rather small under the RCP 2.6 and RCP 4.5 but became more pronounced under RCP 8.5 (Fig. 5).

Other important changes in forest communities were projected to be widespread in all regions. Generally, biomass of most boreal conifer species decreased relative to baseline under all RCP scenarios for all regions, although the decrease was particularly swift and large under RCP 8.5 (Fig. 5). These changes were rather abrupt, with larch, balsam fir, and black and white spruces projected to disappear under RCP 8.5 sometime after ca. 2100, except in BP where these species were projected to survive but with greatly reduced AGB (Fig. 5). Biomass of these species was projected to decrease less strongly for all study regions under the RCP 2.6 and RCP 4.5 scenarios. In general, forest composition was projected to become impoverished, leaving drought-tolerant jack pine and aspen as the dominant species. Red spruce and red pine also declined throughout all regions within their current range although the decline was much smaller under the RCP 2.6 and RCP 4.5 scenarios. For a few species (notably, sugar maple, yellow birch, balsam poplar, trembling aspen and white cedar), aboveground biomass remained rather similar relative to baseline under RCP 2.6 and RCP 4.5 although small to major decreases were projected under RCP 8.5 (Fig. 5).

Discussion and conclusions

To our knowledge, this is the first study to project the impact of climate change on several southern boreal forest landscapes by integrating a stand-level model, PICUS, with a spatially explicit forest landscape model, LANDIS-II, to improve the precision of projected ecological changes in Canada. Our study demonstrates that impacts of global warming are likely to prove very significant throughout the southern boreal transition zone, but they are subject to major differences between east and west.

Our models projected a swift and widespread decline of mid- to late-successional boreal species along the southern boreal transition zone with some abrupt changes projected for as soon as the next 50–100 years. Such a decline can be explained by both climate changed-induced decreases in potential growth and by rapid increases in area burned. Both modeling and field studies have shown that boreal species growing at the southern edge of their present-day distribution are likely to be vulnerable to warmer temperatures (Huang et al. 2013; Fisichelli et al. 2014). Along with consequential increases in water stress, warmer temperatures increase the occurrence of hot days which reduce tree's photosynthetic capacity (e.g., Reich et al. 2015) while increasing metabolic respiration, hence inducing greater metabolic costs (Bond-Lamberty et al. 2014; Girardin et al. 2015). In this study, the PICUS model suggested that significant warming will impose strong constraints on the growth of several boreal species (notably balsam fir, white and black spruces and larch), sufficient to restrict survival by the end of the twenty-first century under RCP 8.5 (see Supplementary Material S7). Evidence for declining growth and increased tree mortality in recent decades within the southern boreal forest has been documented for black spruce (Girardin et al. 2015), jack pine (Luo and Chen 2015) and trembling aspen (e.g., Lapointe-Garant et al. 2010; Michaelian et al. 2011; Luo and Chen 2015). These declines were all partially linked to recent warming trends (but see also Price et al. 2015; Zhang et al. 2015). Important decline in growth and survival of boreal species has also been
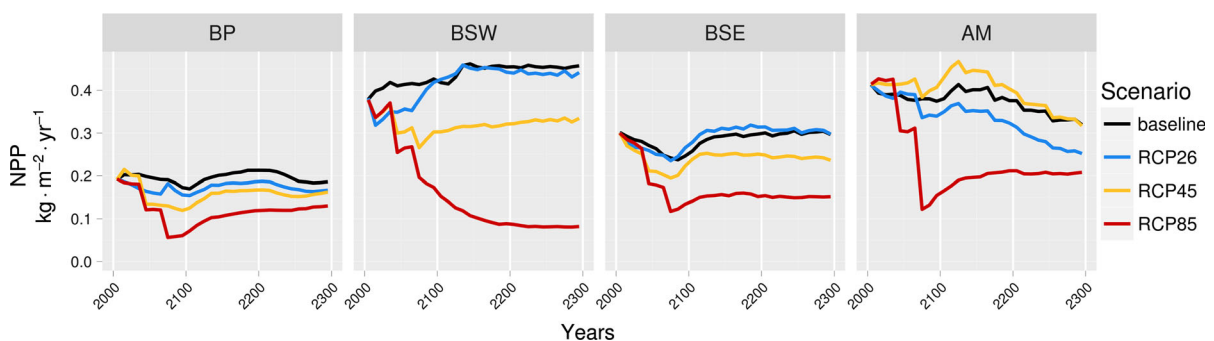

Fig. 2 Trends in aboveground net primary productivity (ANPP) for each of the four regions simulated under baseline, RCP 2.6, RCP 4.5 or RCP 8.5 climate scenarios
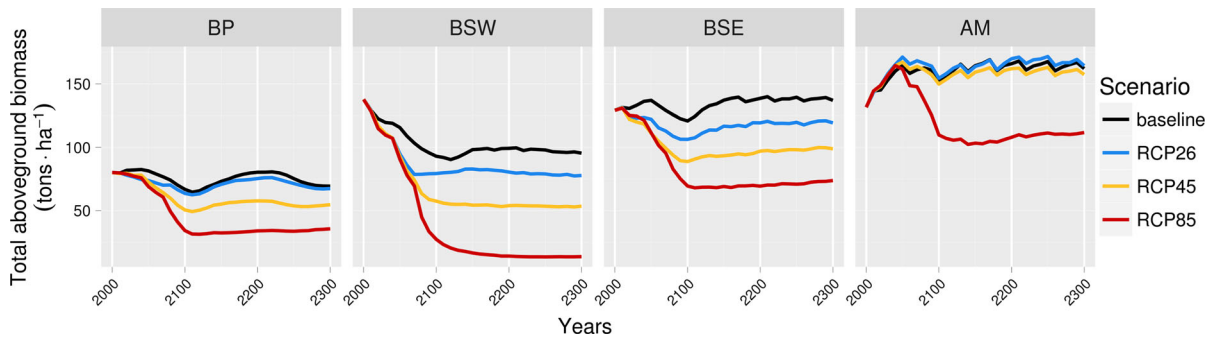
Fig. 3 Trends in total aboveground biomass (AGB) for each of the four regions simulated under baseline, RCP 2.6, RCP 4.5 or RCP 8.5 climate scenarios
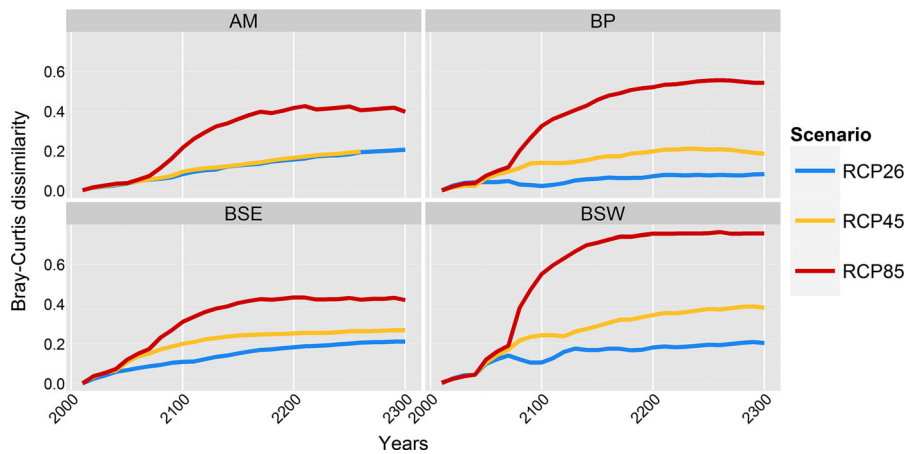

Fig. 4 Bray-Curtis dissimilarity indices for simulated forest communities projected under RCP 2.6, RCP 4.5 or RCP 8.5 climate scenarios compared with those simulated under baseline climate at the same timestep for each of the four study regions

projected under severe radiative forcing scenarios using other modeling approaches (Girardin et al. 2015). Very short fire return intervals (<50 years) as projected for the RCP 8.5 radiative forcing, in at least parts of the BSE, BSW and BP, could also trigger the widespread decline of boreal late-successional fire-avoiders such as balsam fir (De Groot et al. 2003) and white spruce. Black spruce could also be affected by repeated fires, especially if the return interval becomes shorter than typical seed-bearing age (ca 30 years), curtailing post-fire regeneration (Brown and Johnstone 2012). Such a decline for these widespread species within the broad Canadian southern boreal transition zone could contribute to rapid modifications of forest communities over very large areas.

As a corollary, increased growth rates of co-occurring temperate species under most radiative forcing scenarios would also strongly reduce the competitive ability of boreal species at the temperate-boreal forest interface (Reich et al. 2015), favoring the northward expansion of warm-adapted species in Eastern Canada (i.e., in the AM and BSE). Many studies have already projected a general increase in temperate species in this transition zone (e.g., Scheller and Mladenoff 2008; Steenberg et al. 2013; Duveneck and Scheller 2015). Our simulations show the abundance of temperate species would increase primarily in eastern regions, where these species are already a significant component of the current species pool, where annual precipitation amounts are generally non-limiting, and northward colonization is more likely. In fact, recent warming may already have contributed to the recent expansion of these species in adjacent boreal patches (e.g., Boisvert-Marsh et al. 2014;
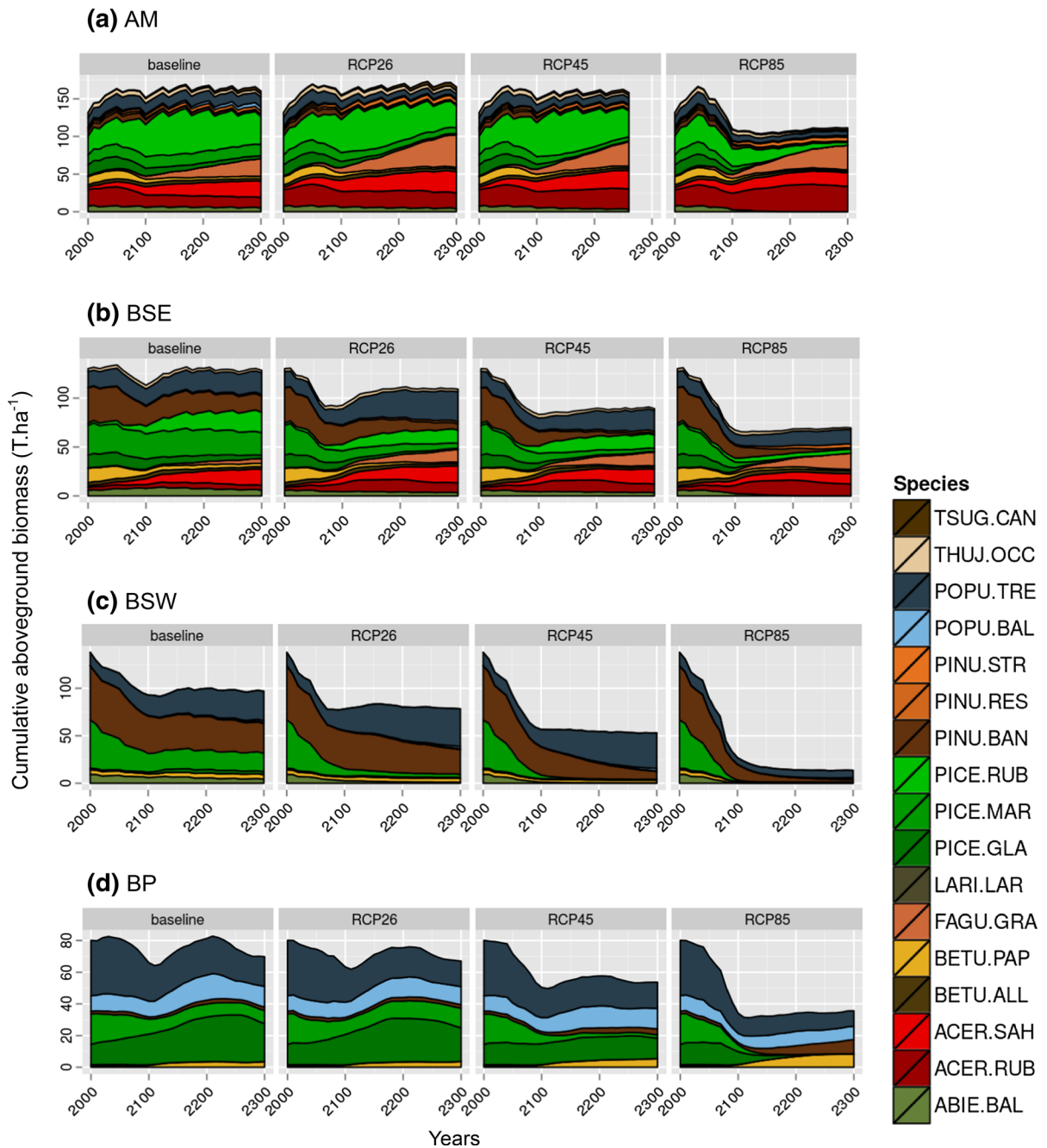
Fig. 5 Stacked species aboveground biomass for each of the four regions simulated under baseline, RCP 2.6, RCP 4.5 and RCP 8.5 climate scenarios. See Table 1 for species abbreviations. Stacked species biomasses in the graphs are in the same order as in the legend

Fisichelli et al. 2014). Although co-occurring temperate species might show a competitive advantage over boreal species in a warmer climate, excessive warming might impose further climatic constraints on temperate species even at their current northern cooler range

limit as significant declines in growth potential were projected in our simulations for these species under RCP 8.5 beyond 2070.

Projected increases in biomass of pioneer and fire-adapted boreal species, especially under RCP 8.5,

would result from projected increase in disturbed areas, particularly those burned throughout the southern boreal transition zone, and particularly in western regions. These species would comprise most of the surviving tree species in the BSW and BP where area burned is projected to increase by over 600 and 350 % under RCP 8.5, respectively (Supplementary Material S2). Furthermore, increased fire activity would likely enhance the northward expansion of some temperate species able to take advantage of canopy openings, including red maple (Zhang et al. 2014) and to a lesser extent white pine. Both species along with other temperate early-successional species were shown to have expanded their northward ranges recently (Boisvert-Marsh et al. 2014), notably by establishing more often in large gaps at the temperate-boreal transition zone (Leithead et al. 2010; Zhang et al. 2014). For instance, red maple regeneration at the northern edge of its range was shown to be highly contingent upon stand-replacing fires which would provide a favorable light environment (Zhang et al. 2014). These life-history traits evidently improve the capacity of temperate deciduous species to use opportunities for range expansion (Matthews et al. 2011). Increased fire activity could therefore be an indirect climate change trigger for invasion by temperate pioneer species by providing more suitable regeneration sites (Drobyshev et al. 2013; Boisvert-Marsh et al. 2014) and provide a significant competitive advantage (Reich et al. 2015) over boreal pioneers (e.g., jack pine, trembling aspen, and white birch) for which warmer climates impose strong constraints on potential growth (Supplementary Material S7).

The latter results emphasize the overwhelming impacts of disturbances, mainly fire, on future forest landscapes. Disturbances have been found to play a key role in defining how landscapes will respond to climate change (e.g., Keane et al. 2013; Seidl et al. 2014). Recent climate-induced shifts in fire regime mediated through changes in fire severity, fire seasonality and overall fire frequency have already contributed to changes in landscape patterns in Alaska (e.g., Kasischke and Turetsky 2006) and the southern Yukon (Hogg and Wien 2005). Other disturbances may yet play a minor role in such a shift. Indeed, the area affected by SBW outbreaks would actually decrease through the rapid climate- and fire-induced decline of main host species (e.g., balsam fir and white spruce). Harvested biomass would also decrease due to climate-induced declines in productivity. In this respect, changes in fire regime might represent one of the most important drivers in the successional dynamics of future boreal forest landscapes (De Groot et al. 2003; Keane et al. 2013).

Our projections strongly suggest that productivity and total biomass would decline rapidly, yet heterogeneously, along the southern boreal transition zone. One exception is for the AM region where total biomass would slightly increase from years 2000 to ca 2050 regardless of the climate scenario. The explanation for this could be that many of the landscapes in this region are relatively young as a result of past intensive harvesting (Supplementary Material S9). Otherwise, increased climate-induced growth potential for temperate species may barely compensate for the concomitant decrease of boreal species' productivity at the regional level (Scheller and Mladenoff 2005; Corlett and Westcott 2013). The primary reason for this is that northward colonization by temperate species would occur at a much slower rate (Boisvert-Marsh et al. 2014) than the projected shifts in their climate envelopes (Iverson and Prasad 2002; McKenney et al. 2007). Such "migration lag" implies that markedly less productive forests will appear along the temperate-boreal transition zone, especially under RCP 8.5. Modified disturbance regimes would also be accountable for some decrease in productivity. In the present case, the increase in area burned would be so important that it would hasten the persistent establishment of many more young stands with low biomass and relatively poor regeneration, to a point that regional-level productivity would strongly decrease in the long term. In this context, significant increases in net carbon emissions from widespread climate- or fire-induced mortality should be expected (Kurz et al. 2013) in the short term. In the longer term, declines in forest productivity would greatly reduce the C sequestration capabilities of the southern boreal transition zone (Bond-Lamberty et al. 2007; Kurz et al. 2008).

Considering sharp changes in productivity and species communities, our results strongly suggest that western regions are at much greater risk than those located in the eastern part of the transition zone. Western regions have been shown to be highly sensitive to changes in climate and disturbance rates during the Holocene (Williams et al. 2009) and are projected to remain so in the upcoming decades with

global warming (Hogg and Bernier 2005; Price et al. 2013; Ireson et al. 2015). Low-diversity forests, the scarcity of warmer-adapted species in present-day landscapes (Duveneck and Scheller 2015) and the potential for considerable climate-induced increases in fire activity suggest a strong decrease in forest productivity and density (De Groot et al. 2003; Frelich and Reich 2010), meaning a transition to forest conditions closer to those that prevailed during the Holocene ($\sim$4500–8000 cal year BP) in this area (Williams et al. 2009; Moos and Cumming 2011). Such a state shift from forest to parkland ecosystem can be expected to have profound impacts on ecosystem resilience, biodiversity and timber supply (Gauthier et al. 2015a).

Several limitations to this study are worth mentioning. Fire effects on forest communities are most probably overestimated as these were directly calibrated from HFR-based model projections (Boulanger et al. 2014) that do not take vegetation feedbacks into account. Such feedbacks are likely to be negative (Terrier et al. 2013), with recurrent fires promoting less flammable fuel (notably increased occurrence of young, predominantly deciduous stands). We did not include any impact of climate change per se on SBW population dynamics and hence on the vulnerability of SBW host species. SBW impacts are likely to be even lower than those simulated here as the climate envelope suitable for high SBW population growth rate would strongly shift northward with increasing climate forcing (Régnière et al. 2012). Also, possible CO_2 fertilization effects on tree growth were not considered. The potential interaction of higher CO_2 with significantly longer growing seasons adds uncertainty to predictions of reduced forest growth (e.g., Silva et al. 2010; Price et al. 2013; Arora et al. 2016). Given that productivity patterns were calibrated on 30-year averages of a future drier climate, our results may overestimate survival and forest productivity along the Prairie—boreal transition zone since potential widespread "pulses" of drought-induced dieback (e.g., Hogg and Bernier 2005; Peng et al. 2011) were not considered.

Changes in forest landscapes are likely to occur despite the fact that most boreal species have a rather high adaptive capacity through large environmental tolerance and population-level genetic diversity, and despite mechanisms (such as serotinous cones) evolved to cope with frequent disturbance (e.g.,

Aitken et al. 2008; Gauthier et al. 2015a). This demonstrates the high vulnerability of the southern edge of the boreal forest when facing a generally warmer and drier future regional climate. Anticipated consequences for forest goods and services would therefore be manifold and potentially severe (Gauthier et al. 2015a). The greatest uncertainty for the future of forest landscapes in Canada's southern boreal transition zone results from the considerable variations among radiative forcing scenarios. This in turn reflects the dependence of future forest dynamics on global and national efforts to mitigate climate change. As such, we stress that conservation and forest management planning within the southern boreal transition zone must consider the impact of climate on both natural disturbances and growth-driven changes in vegetation communities: adaptation of these management practices will be crucial.

References

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol Appl 1:95–111

Arora VK, Peng Y, Kurz WA, Fyfe JC, Hawkins B, Werner AT (2016) Potential near-future carbon uptake overcomes losses from a large insect outbreak in British Columbia, Canada. Geophys Res Lett 43:2590–2598

Beaudoin A, Bernier PY, Guindon L, Villemaire P, Guo XJ, Stinson G, Bergeron T, Magnussen S, Hall RJ (2014) Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Can J For Res 44:521–532

Beck PSA, Juday GP, Alix C, Barber VA, Winslow SE, Sousa EE, Heiser P, Herriges JD, Goetz SJ (2011) Changes in forest productivity across Alaska consistent with biome shift. Ecol Lett 14:373–379

Bergeron Y, Chen HYH, Kenkel NC, Leduc AL, Macdonald SE (2014) Boreal mixedwood stand dynamics: ecological processes underlying multiple pathways. For Chron 90:202–213

Boisvert-Marsh L, Périé C, De Blois S (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere 5:83

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89–92

Bond-Lamberty B, Rocha AV, Calvin K, Holmes B, Wang C, Goulden ML (2014) Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. Global Change Biol 20:216–227

Boulanger Y, Arseneault D, Morin H, Jardon Y, Bertrand P, Dagneau C (2012) Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks in southern Québec for the last 400 years. Can J For Res 42:1264–1276

Boulanger Y, Cooke BJ, Gray DR, De Grandpré L (2016) Model-specification uncertainty in future forest pest outbreak. Global Change Biol 25:1595–1607

Boulanger Y, Gauthier S, Burton PJ (2014) A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Can J For Res 44:365–376

Brandt JP, Flannigan MD, Maynard DG, Thompson ID, Volney WJA (2013) An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ Rev 21:207–226

Brown CD, Johnstone JF (2012) Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. For Ecol Manag 266:34–41

Burns RM, Honkala BH (1990) Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture handbook 654, vol. 2. U.S. Department of Agriculture, Forest Service, Washington, DC

Chen HYH, Luo Y (2015) Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. Global Change Biol 21:3675–3684

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends Ecol Evol 28:482–488

Cyr G (2014) Guide des stations forestières de la région écologique 3c—Hautes collines du Bas-SaintMaurice, 2e édition. Ministère des Ressources naturelles, Direction des inventaires forestiers, Division de la classification écologique et productivité des stations

De Groot WJ, Bothwell PM, Carlsson DH, Logan KA (2003) Simulating the effects of future fire regimes on western Canadian boreal forests. J Veg Sci 14:355–364

Drobyshev I, Guitard MA, Asselin H, Genries A, Bergeron Y (2013) Environmental controls of the northern distribution limit of the yellow birch in eastern Canada. Can J For Res 44:720–731

Duveneck MJ, Scheller RM (2015) Measuring and managing resistance and resilience under climate change in northern Great Lake forests (USA). Landscape Ecol 31:669–686

Ecological Stratification Working Group (1996) A national ecological framework for Canada. Agriculture and Agri-Food Canada and Environment Canada, Ottawa

Engler R, Guisan A (2009) MigClim: predicting plant distribution and dispersal in a changing climate. Divers Distrib 15:590–601

Fisichelli NA, Frelich LE, Reich PB (2014) Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography 37:152–161

Franklin J, Serra-Diaz JM, Syphard AD, Regan HM (2016) Global change and terrestrial plant community dynamics. Proc Natl Acad Sci USA 113:3725–3734

Frelich LE, Reich PB (2010) Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? Front Ecol Environ 8:371–378

Gauthier S, Bernier PY, Boulanger Y, Guo J, Guindon L, Beaudoin A, Boucher D (2015a) Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can J For Res 45:1439–1447

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015b) Boreal forest health and global change. Science 349:819–822

Gewehr S, Drobyshev I, Berninger F, Bergeron Y (2014) Soil characteristics mediate the distribution and response of boreal trees to climatic variability. Can J For Res 44:487–498

Girardin MP, Bernier PY, Gauthier S (2011) Increasing potential NEP of eastern boreal North American forests constrained by decreasing wildfire activity. Ecosphere 2, Article 25

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo X, Cyr G (2015) Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Global Change Biol 22:627–643

Guindon L, Bernier PY, Beaudoin A, Pouliot D, Villemaire P, Hall RJ, Latifovic R, St-Amant R (2014) Annual mapping of large forest disturbances across Canada's forests using 250 m MODIS imagery from 2000 to 2011. Can J For Res 44:1545–1554

Gustafson EJ (2013) When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landscape Ecol 28:1429–1437

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30:32–43

Hennigar CR, MacLean DA, Quiring DT, Kershaw JA Jr (2008) Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. For Sci 54:158–166

Heyder U, Schaphoff S, Gerten D, Lucht W (2011) Risk of severe climate change impact on the terrestrial biosphere. Environ Res Lett 6:034036

Hogg EH, Bernier PY (2005) Climate change impacts on drought-prone forests in western Canada. For Chron 81:675–682

Hogg EH, Wien RW (2005) Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can J For Res 35:2141–2150

Huang JG, Bergeron Y, Berninger F, Zhai L, Tardif JC, Denneler B (2013) Impact of future climate on radial growth of four major boreal tree species in the eastern Canadian boreal forest. PLoS ONE 8:e56758

Ireson AM, Barr AG, Johnstone JF, Mamet SD, van der Kamp G, Whitfield CJ, Michel NL, North RL, Westbrook CJ, DeBeer C, Chun KP, Nazemi A, Sagin J (2015) The changing water cycle: the Boreal Plains ecozone of western Canada. WIREs Water 2:505–521

Iverson LR, Prasad AM (2002) Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. For Ecol Manag 155:205–222

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33:L09703

Keane RW, Cary GJ, Flannigan MD, Parsons RA, Davies ID, King KJ, Li C, Bradstock RA, Gill M (2013) Exploring the role of fire, succession, climate, and weather on landscape dynamics using a comparative modeling. Ecol Model 266:172–186

Kurz WA, Shaw CH, Boisvenue C, Stinson G, Metsarata J, Leckie D, Dyk A, Smyth C, Neilson ET (2013) Carbon in Canada's boreal forest—a synthesis. Environ Rev 21:260–292

Kurz WA, Stinson G, Rampley GJ, Dymon CC, Neilson ET (2008) Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. Proc Natl Acad Sci USA 105:1551–1555

Lapointe-Garant MP, Huang JG, Gea-Izquierdo G, Raulier F, Bernier P, Berninger F (2010) Use of tree rings to study the effect of climate change on trembling aspen in Québec. Global Change Biol 16:2039–2051

Leithead MD, Anand M, Silva LCR (2010) Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal transition zone, Ontario, Canada. Oecologia 164:1095–1106

Lexer MJ, Hönninger K (2001) A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For Ecol Manag 144:43–65

Lovejoy TE, Hannah L (2005) Climate change and biodiversity. Yale University Press, New Haven

Luo Y, Chen HYH (2013) Observations from old forests underestimate climate change effects on tree mortality. Nat Commun 4:1655

Luo Y, Chen HYH (2015) Climate change-associated tree mortality increases without decreasing water availability. Ecol Lett 18:1207–1215

MacLean DA (1980) Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For Chron 56:213–221

Mansuy N, Thiffault E, Paré D, Bernier P, Guindon L, Villemaire P, Poirier V, Beaudoin A (2014) Digital mapping of soil properties in Canadian managed forests at 250 m of resolution using the k-nearest neighbor method. Geoderma 235–236:59–73

Matthews SN, Iverson LR, Prasad AM, Peters MP, Rodewald PG (2011) Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. For Ecol Manag 262:1460–1472

McKenney D, Pedlar J, Hutchinson M, Papadopol P, Lawrence K, Campbell K, Milewska E, Hopkinson RF, Price D (2013) Spatial climate models for Canada's forestry community. For Chron 89:659–663

McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. BioScience 57:939–948

McKenney DW, Pedlar JH, Rood RB, Price DT (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biol 17:2720–2730

McLaughlan MS, Wright RA, Jiricka RD (2010) Field guide to the ecosites of Saskatchewan's provincial forests. Saskatchewan Ministry of Environment, Forest Service, Prince Albert

Michaelian M, Hogg EH, Hall RJ, Arseanault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biol 17:2084–2094

Moos MT, Cumming BF (2011) Changes in the parkland-boreal forest boundary in northwestern Ontario over the Holocene. Quat Sci Rev 30:1232–1242

OMNR (2000) A silvicultural guide to managing southern Ontario forests. Version 1.1. Ontario Ministry of Natural Resources. Queen's Printer for Ontario, Toronto

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecol Biogeogr 12:361–371

Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat Clim Change 1:467–471

Prasad AM, Gardiner JD, Iverson LR, Matthews SN, Peters M (2013) Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. Global Change Biol 19:2196–2208

Price DT, Alfaro RI, Brown KJ, Flannigan MD, Fleming RA, Hogg EH, Girardin MP, Lakusta T, Johnson M, McKenney DM, Pedlar JH, Stratton T, Sturrock RN, Thompson ID, Trofymow JA, Venier LA (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ Rev 21:322–365

Price DT, Cooke BJ, Metsaranta JM, Kurz WA (2015) If forest dynamics in Canada's west are driven mainly by competition, why did they change? Half-century evidence says: climate change. Proc Natl Acad Sci USA 112:E4340

Racey GD, Harris AG, Jeglum JK, Foster RF, Wickware GM (1996) Terrestrial and wetland ecosites of northwestern Ontario. Ontario Ministry of Natural Resources, Northwest Science and Technology Field Guide FG-02

Régnière J, St-Amant R, Duval P (2012) Predicting insect distributions under climate change from ecophysiological responses: spruce budworm as an example. Biol Invasions 14:1571–1586

Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, Montgomery RA (2015) Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nat Clim Change 5:148–152

Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, Mladenoff DJ (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible spatial and temporal resolution. Ecol Model 201:409–419

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol Model 180:211–229

Scheller RM, Mladenoff DJ (2005) A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biol 11:307–321

Scheller RM, Mladenoff DJ (2008) Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. Clim Res 36:191–202

Seidl R, Lexer MJ, Jäger D, Hönninger K (2005) Evaluating the accuracy and generality of a hybrid patch model. Tree Physiol 25:939–951

Seidl R, Rammer W, Spies TA (2014) Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol Appl 24:2063–2077

Silva LCR, Anand M, Leithead MD (2010) Recent widespread tree growth decline despite increasing atmospheric CO_2. PLoS ONE 5:e11543

Steenberg JWN, Duinker PN, Bush PG (2013) Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. Ann For Sci 70:61–73

Sturtevant BR, Gustafson EJ, Li W, He HS (2004) Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecol Model 180:153–174

Taylor AR, Chen HYH (2009) A review of forest succession models and their application to forest management. For Sci 55:14

Terrier A, Girardin MP, Périé C, Legendre P, Bergeron Y (2013) Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecol Appl 23:21–35

Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgely GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152

USDA, NRCS (2016) The PLANTS Database (http://plants.usda.gov, 22 June 2016). National Plant Data Team, Greensboro, NC 27401-4901, USA

van Vuuren DP, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K, Hurtt GC, Kram T, Krey V, Lamarque JF, Masui T, Meinhausen M, Nakicenovic N, Smith SJ, Rose SK (2011) The representative concentration pathways: an overview. Clim Change 109:5–31

Volney WJA, Hirsch KG (2005) Disturbing forest disturbances. For Chron 81:662–668

Wang Y, Hogg EH, Price DT, Edwards J, Williamson T (2014) Past and projected future changes in moisture conditions in the Canadian boreal forest. For Chron 90:678–691

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci USA 106(S2):19729–19736

Williams JW, Shuman B, Bartlein PJ (2009) Rapid responses of the prairie-forest transition zone to early Holocene aridity in mid-continental North America. Global Plan Change 66:195–207

Woodall CW, Zhu K, Westfall JA, Oswalt CM, D'Amato AW, Walters BF, Lintz HE (2013) Assessing the stability of tree ranges and influence of disturbance in eastern US forests. For Ecol Manag 291:172–180

Zhang J, Huang S, He F (2015) Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. Proc Natl Acad Sci USA 112:4009–4014

Zhang Y, Bergeron Y, Zhao X-H, Drobyshev I (2014) Stand history is more important than climate in controlling red maple (*Acer rubrum* L.) growth at its northern distribution limit in western Quebec, Canada. J Plant Ecol 8:368–379