



Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region



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ABSTRACT

The impact of climate change on forests is expected to vary globally and regionally. Canada's Acadian Forest Region lies in the transition between the North American boreal and temperate forest biomes and may be particularly sensitive to changes in climate because many of its component species are currently at their southern or northern climatic range limits. Although some species may be lost, others may exhibit major productivity boosts—affecting the goods and services we derive from them. In this study, we use a well-established forest ecosystem simulation model, PICUS, to provide the first exploration of the impact of climate change on the composition and growth of the Acadian Forest Region for the period 2011 to 2100 under two radiative forcing scenarios, RCP 2.6 and RCP 8.5.

In the short term (2011–2040), little to no changes in forest composition or growth were projected under either forcing scenario compared with current forest conditions (simulated for 1981–2010 baseline climate); however, by mid-century, PICUS projected increasing departures from the baseline simulations in both composition and growth, with the greatest changes occurring under RCP 8.5 during the late 21st century (2071–2100). Our study indicates that under rapid 21st century warming, Canada's Acadian Forest Region will begin to lose its boreal character (i.e., “deborealize”) as key tree species fail to regenerate and survive. Furthermore, increased growth and establishment by warm-adapted, temperate tree species may be unable to keep pace with the rapid loss of boreal species. This potential “lag effect” may lead to a temporary decrease in forest growth and wood supply during the late 21st century.

1. Introduction

Global temperatures have warmed significantly since the beginning of the industrial revolution, with 2016 being the warmest year to date (NOAA, 2017). Already, some North American forests are showing signs of climate-induced changes, including alteration to physiological processes and natural disturbance regimes (e.g., Michaelian et al., 2011; Girardin et al., 2014). Future impacts are expected to vary regionally across North America with some areas facing decreases in forest productivity, due to increased drought and insect outbreaks, while other areas may experience boosts in growth and diversity (Vose et al., 2012;

Charney et al., 2016; D'Orangeville et al., 2016), implying that successful adaptation of forest management practices will require local-scale knowledge of the responses of forest structure and function to changes in climate (Price et al., 2013; Franklin et al., 2016).

Eastern Canada's Acadian Forest Region (Rowe, 1972; Loo and Ives, 2003) is part of an ecological transition zone occurring along the United States–Canada border area that links conifer-dominated boreal forest to the north with temperate deciduous forests to the south. Such transition zones are considered particularly susceptible to changes in tree species growth and other drivers of stand-level competition because many species that coexist in these ecosystems are close to their extreme

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southern or northern climatic limits (Heyder et al., 2011; Fisichelli et al., 2014). Climate-driven influences on competitive interactions are expected to cause changes in forest composition (Adler et al., 2012; Price et al., 2015; Reich et al., 2015); for example, cold-adapted boreal conifers, such as balsam fir (*Abies balsamea* L.) and black spruce (*Picea mariana* (Mill.) B.S.P.), which are currently at their southern limit in the Acadian Forest, are likely to compete poorly under a warming climate, decreasing in both growth and abundance (Bourque and Hassan, 2008; Girardin et al., 2015; Pedlar and Mckenney, 2017). Conversely, temperate species, such as red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.), are expected to benefit from warming, allowing them to compete more successfully (Iverson et al., 2008; Rogers et al., 2016). This could potentially cause a shift in the overall composition of the Acadian Forest toward dominance by temperate species. Even though temperate species can be expected to perform better in a warmer regional climate, the overall growth of the Acadian Forest may still decrease for some period because the rate of climate change projected for the 21st century will likely outpace the ability of southern species to colonize newly available sites and offset decreases in growth from the loss of cold-adapted boreal species (Zhu et al., 2012; Corlett and Westcott, 2013).

Projecting the effects of climate change on forest ecosystems has become a central challenge for global change ecology (McMahon et al., 2011; Franklin et al., 2016). Correlative species distribution models (niche models) are most commonly used to assess species vulnerability to climate change. These models usually project rapid poleward migration of species' suitable habitat under the most aggressive anthropogenic climate forcing scenarios (e.g., Iverson et al., 2008; McKenney et al., 2011b; Rogers et al., 2016). However, these models have well-known limitations that impede their capacity to project future forest conditions, including the inability to account for species population dynamics and community-level interactions (Thuiller et al., 2008; Araújo and Peterson, 2012). Furthermore, known constraints on species dispersal will likely limit the average rate of tree migration (depending also on local terrain and microclimatic conditions) to less than 10–20 km over the next 100 years (Hampe, 2011; Iverson et al., 2011; Corlett and Westcott, 2013). Therefore, understanding how climate change will directly affect the demographics and competitiveness of tree species already present in the Acadian Forest is likely most important for projecting near-term (50–100 years) forest conditions and their implications for forest management (Adler et al., 2012; Zhu et al., 2014; Searle and Chen, 2016).

Several of the limitations of species distribution models may be overcome through the use of process-based forest simulation models (Thuiller et al., 2008; Urban et al., 2016). Landscape-scale forest simulation models (e.g., LANDIS-II, Gustafson et al., 2014) are capable of simulating large areas (10^3 – 10^7 ha), including spatially explicit simulation of disturbances and tree seed dispersal, but they do so at the cost of simplifying or omitting tree-level details, notably the dynamics and interactions of individual trees which are undoubtedly important in assessing forest responses to climate change (McMahon et al., 2011; Shugart et al., 2015). Alternatively, individual tree-based “forest gap” models (e.g., FORSKA, FAREAST) that simulate the establishment, growth, and mortality of individual trees on a defined unit of forest area (i.e., a forest gap), usually the size of a forest inventory plot (100–1000 m²) permit simulating the direct effects of climate change on individual species' demographic processes, biotic interactions, and community dynamics (e.g., Price et al., 1999; Shuman et al., 2011).

In this paper, we provide an assessment of the impact of climate change on Canada's Acadian Forest Region using the well-established forest gap model, PICUS (<http://picus.boku.ac.at>). We used PICUS to explore the impacts of climate change on the composition and growth of the Acadian Forest Region using the “census” technique, whereby regional-level trends may be inferred from a detailed forest gap model by simulating a large number of forest sample plots across the region of interest (Shuman et al., 2011; Shugart et al., 2015).

More specifically, we investigated how two radiative forcing scenarios, known as Representative Concentration Pathways (RCP; van Vuuren et al., 2011), namely RCP 2.6 and RCP 8.5, would affect forest composition and growth. We hypothesized that under the “business-as-usual” high radiative forcing scenario (RCP 8.5), the Acadian Forest would undergo significant change in species composition and corresponding decreases in average growth (current annual increment, m³·ha⁻¹·yr⁻¹) by the end of the 21st century as the climate becomes increasingly unsuitable for cold-adapted, boreal tree species and outpaces the ability of temperate species to replace them. Conversely, we would expect little to no change in composition or growth due to climate change under RCP 2.6 (the low forcing scenario) as the projected moderate warming is unlikely to perturb the current forest beyond the limits of its natural variability.

2. Material and methods

2.1. Study area

Our study area includes the three Canadian Maritime Provinces: New Brunswick, Prince Edward Island, and Nova Scotia, totaling approximately 10.5 million ha (Fig. 1). The climate is largely determined by prevailing continental westerly winds, but moderated by the Atlantic Ocean, resulting in high humidity, frequently fluctuating weather conditions, mild winters, and cool summers. Mean January and July temperature are −8.2 °C and 17.5 °C, respectively, while mean annual temperature is 5.0 °C with an average annual frost-free period of 150 days. Mean annual precipitation is 1275 mm with approximately 20% of this occurring as snowfall (Environment Canada, 2016). Elevations vary from sea level to roughly 820 m further inland, as much of the study area lies within the northern extent of the Appalachian Mountain range. The high average annual precipitation, combined with cool, humid summers, encourages soil podzolization, resulting in relatively infertile, acidic surface soils in coastal areas. However, soil conditions vary substantially, and many upland ridges and rich river flood plains are well-drained and fertile, supporting high tree species diversity (Loo and Ives, 2003).

The Acadian Forest Region is a unique assemblage of approximately 32 tree species (Rowe, 1972; Loo and Ives, 2003). Red spruce is considered the forest's defining tree species, but other common species include sugar maple (*Acer saccharum* Marsh.), red maple, yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), red oak, eastern hemlock (*Tsuga canadensis* (L.) Carrière), red pine (*Pinus resinosa* Ait.), and eastern white pine (*Pinus strobus* L.), which are characteristic of the more southern, temperate forest types. Conversely, white birch (*Betula papyrifera* Marshall), trembling aspen (*Populus tremuloides* Michx.), tamarack (*Larix laricina* K. Koch), jack pine (*Pinus banksiana* Lamb.), eastern cedar (*Thuja occidentalis* L.), balsam fir, black spruce (*Picea mariana* (Mill.) B.S.P.), and white spruce (*Picea glauca* (Moench) Voss), are typically found in the more northerly and cooler boreal forest types.

Large-scale, stand-replacing natural disturbances, such as wildfire, are rare in the Acadian Forest (Seymour et al., 2002). Historical analyses suggest fire played a minor role in the pre-European settlement Acadian Forest, with return intervals of 800 years and longer (Wein and Moore, 1977, 1979). The predominant form of natural disturbance is small, gap-forming perturbations, in which individual trees or small groups of trees succumb to minor blow down, localized insect infestation (mainly spruce budworm outbreaks) and disease, or natural senescence. Because of long intervals between stand replacing disturbances, the historic, pre-European Acadian Forest is estimated to have been > 50% old (> 100 years) forest (Betts and Loo, 2002; Lorimer, 1977). Today, old forests have been reduced to < 5% of the landscape due to colonization, the introduction of non-indigenous pests and diseases, and forest management history (Loo and Ives, 2003).

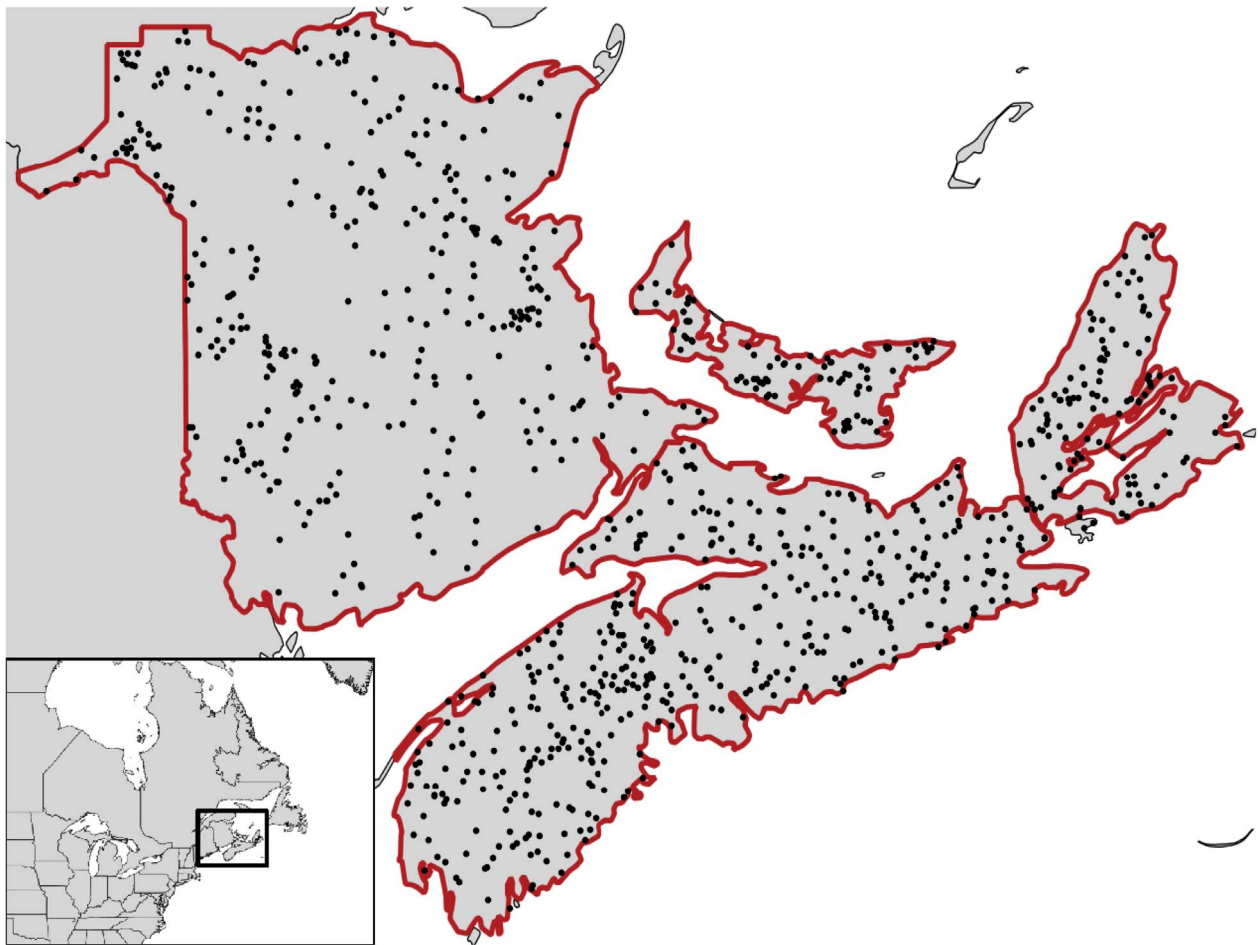


Fig. 1. Map of study area (delineated by red line), which includes the Canadian provinces of New Brunswick, Nova Scotia, and Prince Edward Island. The black dots show the distribution of the 988 provincial forest inventory sample plots (FIP) simulated by PICUS. The inset shows eastern North America. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Description of model

PICUS is an individual tree-based, spatially explicit, forest gap model (Lexer and Hönninger, 2001; Seidl et al., 2011) that simulates the establishment, growth, and mortality of individual trees on 100 m² gaps or “patches” of forest area. Usually, 100 of these patches are simulated simultaneously as interacting square cells on a contiguous 10 × 10 grid, corresponding to a 1-ha plot sample of a forest stand (Fig. 2); however, patch and grid size can be varied (e.g., 20 × 20 grid of 500 m² patches) to simulate different size forest areas. Regardless of grid and patch size, soil and climate conditions are simulated uniformly across the entire grid of patches with only light and forest inventory conditions varying among patches. PICUS runs on annual time steps and accounts for spatially explicit interactions among trees and the effects of climate and soils on forest growth and succession. A detailed description of PICUS, selected species-specific parameters, and a description of how we calibrated PICUS are presented in Appendix S1.

2.3. Simulation design and input data

2.3.1. General design

We used stratified random sampling to select a sample of 988 provincial forest inventory plots (FIP) to be simulated by PICUS using the census method. Selected plots were stratified by stand age and site quality to cover a wide variety of representative stand conditions for which recent (< 10-year-old) measurement data were available (Fig. 1). The FIP were evenly distributed across the study area, with

those from New Brunswick and Nova Scotia measuring 400 m², whereas those from PEI were 200 m². The total counts of live trees, > 9.0 cm diameter at breast height (DBH), from each FIP were scaled up to estimate the total number of such trees per ha. These 988 standardized data sets were then used to initialize each plot location as a 1-ha plot in PICUS, with each of the live trees being assigned randomly to one of the 100, 10 × 10 m grid patches in the 1-ha plot.

Because PICUS contains stochastic processes in its model design (namely, seedling establishment and tree mortality), we ran five replicate, 90-year (2011–2100) simulations, initialized with current forest inventory conditions (as described above), for each of three different climate scenarios: a baseline scenario, in which the models were run using historic, detrended 1981–2010 climate data (repeated three times over the 90-year period); and two different radiative forcing scenarios, RCP 2.6 and RCP 8.5.

2.3.2. Soil data

PICUS requires plot-level estimates of soil pH, available nitrogen (kg/ha), and water-holding capacity (i.e., field capacity, cm), to initialize and simulate each 1-ha plot. Because the FIP had very limited soil records, all soil information was derived for each FIP from the spatial soil data layer produced by Mansuy et al. (2014).

2.3.3. Climate data

Monthly time series of current (baseline) climate were interpolated to the coordinates of the 988 FIP from climate station records using well-tested thin-plate spline software (ANUSPLIN, e.g., McKenney et al.,

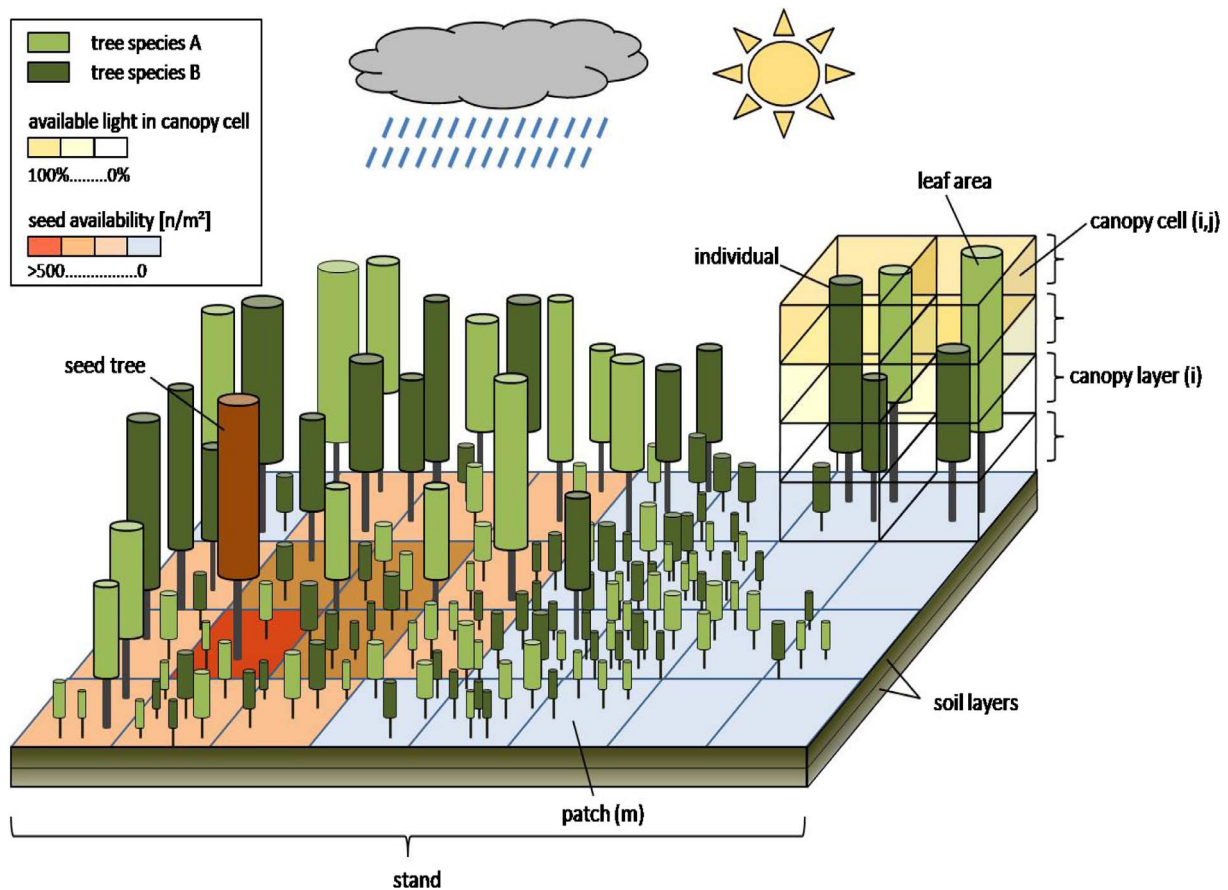


Fig. 2. Graphical interpretation of the PICUS simulation environment, showing a grid of spatially interacting cells or “patches” of trees, which together represent a plot sample of a forest stand.

Source: <http://picus.boku.ac.at/doku.php> (accessed: March 18, 2017).

2011a) and treating temperature and precipitation as dependent variables, with latitude, longitude and elevation as independent variables. Slope and aspect were not included explicitly. Future climate projections were obtained from the Canadian Earth System Model version 2 (CanESM2) using monthly data downloaded from the World Climate Research Program (WCRP) Climate Model Intercomparison Project Phase 5 (CMIP5) archive for two different radiative forcing scenarios. The RCP 2.6 scenario represents a situation where radiative forcing peaks at $\sim 3 \text{ W}\cdot\text{m}^{-2}$ before 2100 and then declines to reach $2.6 \text{ W}\cdot\text{m}^{-2}$ by 2100. This situation permits the possibility that global mean temperature will increase by $1.5\text{--}2.0 \text{ }^\circ\text{C}$ by mid-century, but humanity will find a way to decrease the forcing and begin to reduce mean temperatures by 2100. Conversely, under the RCP 8.5 scenario, the forcing reaches $8.5 \text{ W}\cdot\text{m}^{-2}$ in 2100 and continues to increase for some time afterward. Warming in Canada is expected to proceed at approximately double the global rate, hence under these two scenarios, mean climate in our study area is expected to warm by about $3.0 \text{ }^\circ\text{C}$ (RCP 2.6) to $7.0 \text{ }^\circ\text{C}$ (RCP 8.5) by 2100 (compared with the baseline). Average annual precipitation is projected to increase by 5–10%, with high spatial and interannual variability but relatively small differences between the forcing scenarios (Appendix S2, Fig. S2.1). The linkage between radiative forcing and projected warming has been well-established, and climate projections consistently show greater differences among forcing scenarios than among general circulation models (GCM) (IPCC, 2013). Hence, we chose to focus the study on the response of the Acadian Forest Region to two “extreme” scenarios as simulated by a single GCM, rather than assess its sensitivity to detailed (and potentially misleading) differences caused by using multiple climate models.

2.3.4. Tree species pool

Although our study area contains approximately 32 tree species, many of these contribute $< 0.5\%$ of total forest biomass at the regional scale. For simplicity, we reduced the total species pool to 18 species. For a tree species to be included in our species pool, it had to represent at least 0.3% of total aboveground biomass in the study area according to the 2001 NFI forest properties maps (Beaudoin et al., 2014).

In PICUS, the stand conditions at each simulated plot were initialized using the most up-to-date forest inventory for the corresponding FIP; however, tree species included in the initialization and simulations were restricted to dominant species whose biogeographical ranges overlapped with the geographic location of the FIP, as determined from tree distribution maps for North America (<http://gec.cr.usgs.gov/data/little/>). For example, FIP in northern New Brunswick were not permitted to allow red oak to colonize and form part of the forest community as these plots are well outside the present-day natural range of red oak. This assumption is reasonable over the span of our 90-year simulation period because the influence of natural tree species migration over long distances is likely to be minimal (Iverson et al., 2011). Therefore, the influence of climate change on forest composition and growth in our PICUS simulations is restricted to the direct effects of climate on individual tree species performance and biotic interactions among tree species currently found within the study area.

2.3.5. Disturbances

PICUS includes mortality subroutines that account for the death of individual trees (e.g., self-thinning) due to stress and age-related mortality. However, we also included four stand-replacing disturbance agents in our simulations, namely: forest fire, spruce budworm (SBW)

outbreaks, windthrow, and forest harvesting, which account for the majority of large areas disturbed in the Acadian Forest Region.

Although climate change is expected to affect the frequency and severity of disturbances in the region (Régnière et al., 2010; Gray, 2013; Boulanger et al., 2014), we did not include the effect of climate change on disturbances in our simulations. Rather, incidence of forest fire, SBW, windthrow, and harvesting were all based on current baseline rates and did not vary with forcing scenario or time. We acknowledge that climate-driven changes to disturbances are likely to have an effect on the future forest, but we chose to hold this additional level of complexity constant at known baseline rates and instead focus our analysis on how climate change may directly effect forest composition and growth.

We included stand-replacing disturbances for two major reasons. First, it ensured all age classes of post-disturbance stands were included in the simulations. Many researchers have proposed that young regenerating stands may be the most susceptible to shifts in composition due to climate change (e.g., Johnstone et al., 2010). Second, it allowed us to simulate forest landscape dynamics more realistically because the landscape is composed of a mosaic of different stand age classes.

The inclusion of stand-replacing disturbance was made possible through the use of the PICUS Management Module scheduling tool, which permits users to prescribe plot-specific disturbance schedules that instruct PICUS to periodically “disturb” each forest plot being simulated. A disturbance schedule was developed for each of the 988 plots and described what years the plot would be disturbed and by what disturbance. Scheduled disturbance events were selected, randomly, from annual disturbance probabilities (described in detail below). Plot disturbance schedules were kept constant for all simulation replicates.

Our aim here was not to simulate each type of disturbance in detail, but rather to design simple disturbance scenarios to impose the type of structural change on each simulated plot typically caused by a given disturbance type. For fire, a scenario was prescribed that killed a random selection of 90% of trees > 1.3 m (height) and all trees < 1.3 m in a plot when a scheduled fire event occurred. Annual probabilities of fire occurrence ranged from as low as 0.03% to as high as 0.24%, which corresponds, approximately, to a 400–3000 year fire return interval, and were estimated from baseline projections of annual area burned in the vicinity of each plot being simulated (Boulanger et al., 2013). Based on published data (e.g., Koller and Leonard, 1981), spruce budworm disturbance was prescribed assuming 80% of balsam fir and 40% of white spruce > 1.3 m tall would be randomly killed in a single year when a plot was subjected to scheduled SBW outbreak disturbance. The annual probability of SBW outbreak was set as 0.1%, and was derived from observed, historic recurrence cycles in our study area of approximately 35 years in which outbreaks typically affect < 5% of total forest area (Boulanger et al., 2012; MacLean, 1980). For wind disturbance (i.e., windthrow), a random selection of 80% of all trees > 1.3 m in a plot were killed when a scheduled wind event occurred. The annual probability of stand-replacing windthrow was determined as 0.15%, corresponding to a conservative 600-year return interval, derived from a review of historical reports on the frequency and extent of strong wind storms observed in our study area (Dwyer, 1979; Johnson, 1986; Seymour et al., 2002). Because clearcutting is the dominant form of harvesting in the region, harvesting was simulated in PICUS as the annual probability of being clearcut (i.e., 90% removal of all trees > 1.3 m in plots where the mean height was > 10 m), determined from the current known rate of clearcut harvesting in the Maritime Provinces (approximately 0.3% annually by area) (NSDNR, 2008).

2.4. Analysis of simulation outputs

All pre- and post-model data processing and analyses were conducted using the R software environment (version 3.2.3). For species composition, we calculated the mean annual relative abundance (%) of each tree species over the entire study area using all 988 FIP. Relative

abundance is a measure of plant community structure, specifically a species’ representation in the composition of a community, with respect to other species (Smith and Smith, 2012). Relative abundance was calculated from the simulated aboveground biomass (AGB) of all tree stems (including seedlings) as:

$$RA_i = 100 \left(\frac{AGB_i}{\sum_{i=1}^n AGB_i} \right) \quad (1)$$

where RA_i is the relative abundance of species i (% of total AGB) and AGB_i is the total aboveground biomass of species i in the study area. Aboveground biomass of tree stems is estimated in PICUS using allometric functions that relate individual tree stem height and diameter to biomass of the stem, branches and leaves based on Lambert et al. (2005) and Ung et al. (2008).

For forest growth, PICUS produces annual, plot-level estimates of current annual increment (CAI, $m^3 \cdot ha^{-1} \cdot yr^{-1}$) of all trees ≥ 1.3 m tall. Current annual increment is calculated in PICUS as the merchantable tree volume at the end of each year plus any volume removed that year by mortality, minus the total volume calculated at the end of the previous year. The mean CAI was calculated for each simulation year over the entire study area using all 988 FIP.

To help simplify our investigation of how changes in radiative forcing will affect the composition and growth of the Acadian Forest compared with baseline climate conditions, we calculated the annual departure (i.e., the fractional difference) at year y of simulated composition and growth obtained from the baseline scenario with results obtained from each RCP scenario, over the simulation period (i.e., 2011–2100). Using “departure from baseline” as a metric of change provides several advantages. Firstly, it provides a straightforward means of assessing how different the future forest might become under each radiative forcing scenario relative to baseline conditions, but, also, it helps correct for inherent model biases, allowing us to focus on divergence in forest response as caused by differences in radiative forcing (not differences due to model idiosyncrasies).

Departure in relative abundance between each RCP scenario and the baseline scenario was calculated as the fractional difference for each simulation year, y , as:

$$\Delta RA_{iy} = \frac{rcpRA_{iy} - baselineRA_{iy}}{baselineRA_{iy}} \quad (2)$$

where ΔRA_{iy} is the annual departure (expressed as a ratio) in the relative abundance of species i between the RCP scenario, $rcpRA_{iy}$ and the baseline scenario, $baselineRA_{iy}$, for each simulation year, y . For example, if the relative abundance of species i is 60% at year y under baseline, but is only 30% under RCP 8.5 at year y , then ΔRA_{iy} is -0.50 (i.e., only half of what it was under baseline), indicating a substantial decrease in relative abundance.

For departure in growth between each RCP scenario and the baseline scenario, we calculated the fractional difference for each simulation year as:

$$\Delta G_y = \frac{rcpG_y - baselineG_y}{baselineG_y} \quad (3)$$

where ΔG_y is the annual departure (expressed as a ratio) in growth between the RCP scenario, $rcpG_y$, and the baseline scenario, $baselineG_y$, for each simulation year, y .

To assist in the interpretation of our model results, we calculated and graphed the mean of ΔG_y and ΔRA_{iy} for three 30-year time periods, to represent short-term (2011–2040), medium-term (2041–2070) and long-term (2071–2100) changes. Changes in ΔG_y and ΔRA_{iy} are reported here as mean values only because stochastic variation among replicates was generally < 10% (Appendix S2, Fig. S2.2). No formal statistical significance tests were performed as statistical analyses are inappropriate to interpret simulation model results (White et al., 2014); rather, we assessed mean trends among RCP scenarios through visual

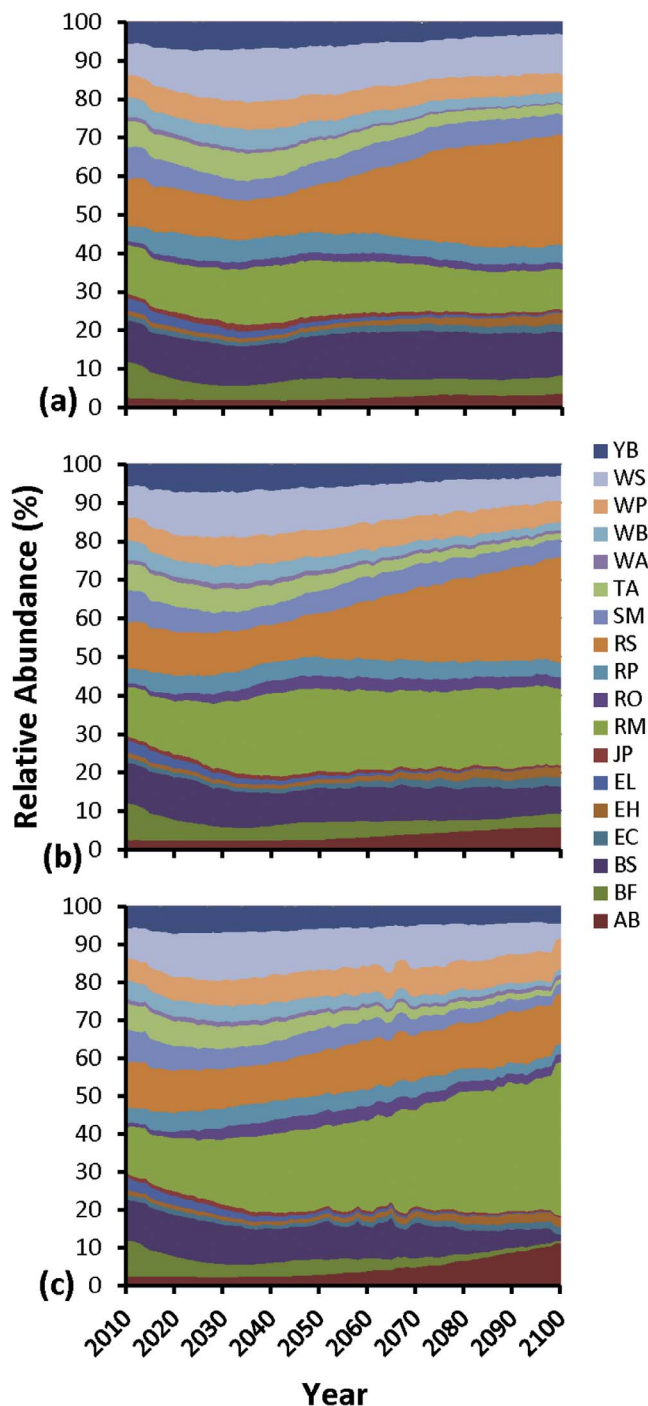


Fig. 3. Tree species relative abundance (%) for the time period 2011–2100 for the baseline climate (a) and each radiative forcing scenario: RCP 2.6 (b) and RCP 8.5 (c). AB = American beech, BF = balsam fir, BS = black spruce, EC = eastern white cedar, EH = eastern hemlock, EL = eastern larch, JP = jack pine, RM = red maple, RP = red pine, RO = red oak, RS = red spruce, SM = sugar maple, TA = trembling aspen, WA = white ash, WB = white birch, WP = white pine, WS = white spruce YB = yellow birch.

inspection of graphs and comparisons of the calculated means. We acknowledge that without direct measurement of deviation of model parameters and output, we have limited ability to assess uncertainty in the results; however, our intent in this analysis is simply to explore climate change impacts on future forest conditions and identify potential trends that may warrant further investigation.

Further, during our preliminary simulations and analyses we stratified our results according to sub-regions (e.g., northern New

Brunswick versus southern New Brunswick) to examine potential spatial variation in climate change impacts. However, we did not detect any noteworthy differences in mean response of forest composition or growth as most responses were within 10% of one another; thus we did not pursue any further spatial analysis of inter-regional trends.

3. Results

3.1. Forest composition

Relative abundances of all 18 tree species were comparatively constant over the 90-year simulation period under the baseline scenario (Fig. 3a), except for red spruce, which was initially only approximately 12% of relative abundance, but increased in abundance during the simulation to a maximum of 29%. This shift in red spruce abundance was largely a result of simulated changes in composition due to the disturbance regime we imposed on the plots, with red spruce being quite sensitive to changes in disturbance interval. The abundance of red spruce became relatively constant, at approximately 30%, when baseline simulations were run beyond the year 2100 (data not shown).

When subjected to projected changes in future climate, however, PICUS projected overall increases in the relative abundance of warm-adapted deciduous tree species and decreases in cold-adapted conifer species (Figs. 3–5). Generally, simulated changes in relative abundance were small (< 0.20 departure from baseline) in the short term (2011–2040; Figs. 4 and 5). However, over the medium and long terms (2041–2100), PICUS projected increasing departures from the baseline, with the largest changes occurring under RCP 8.5 toward the end of the century. More specifically, PICUS projected a persistent increase in the relative abundance of temperate forest species (American beech, red maple, red oak, white ash, and white pine) over time and decreases in the relative abundance of boreal species (balsam fir, white, black and red spruces, eastern larch, jack pine, trembling aspen, and white birch).

PICUS projected a substantial decrease in the relative abundance of sugar maple (Figs. 3c and 4), which was unexpected because sugar maple is considered a warm-adapted, competitive shade-tolerant species. Subsequent examination of our model simulations revealed this was partially caused by strong competition from American beech and red maple. Because our simulations do not take into consideration the strong negative impact of beech bark disease in our region (Taylor et al., 2013) and given the strong, generalist nature of red maple (Abrams, 1998), both of which share similar traits with sugar maple, PICUS likely underestimated the overall abundance of sugar maple. Other, less clear, patterns of change were observed for eastern white cedar, yellow birch, and eastern hemlock, where the projected direction of change for each time period varied considerably.

Although there were some large departures from the baseline reported (e.g., 1.96 increase in the relative abundance of red maple, Fig. 4), the absolute change in relative abundance was often quite small for such species because they contributed only a minor portion of the actual forest composition, estimated from simulated biomass (Fig. 3). For example, PICUS projected a departure of 1.26 for white ash in the long term under RCP 8.5 (Fig. 4), but white ash contributed only $\sim 0.3\%$ of baseline forest composition, increasing to $\sim 0.7\%$ of projected future forest composition (Fig. 3).

3.2. Forest growth

In the short term (2011–2040), little to no difference in forest growth was projected between the baseline and the two radiative forcing scenarios (< 0.01 departure from baseline levels, Fig. 6a and b). In the medium and long terms (2041–2100), however, PICUS showed diverging patterns in growth among the three scenarios. Under the baseline and RCP 2.6 scenarios mean forest growth increased from $\sim 8.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ to 11.9 and $10.8 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, respectively, by the end of the century (2071–2100 period), whereas under RCP 8.5 growth

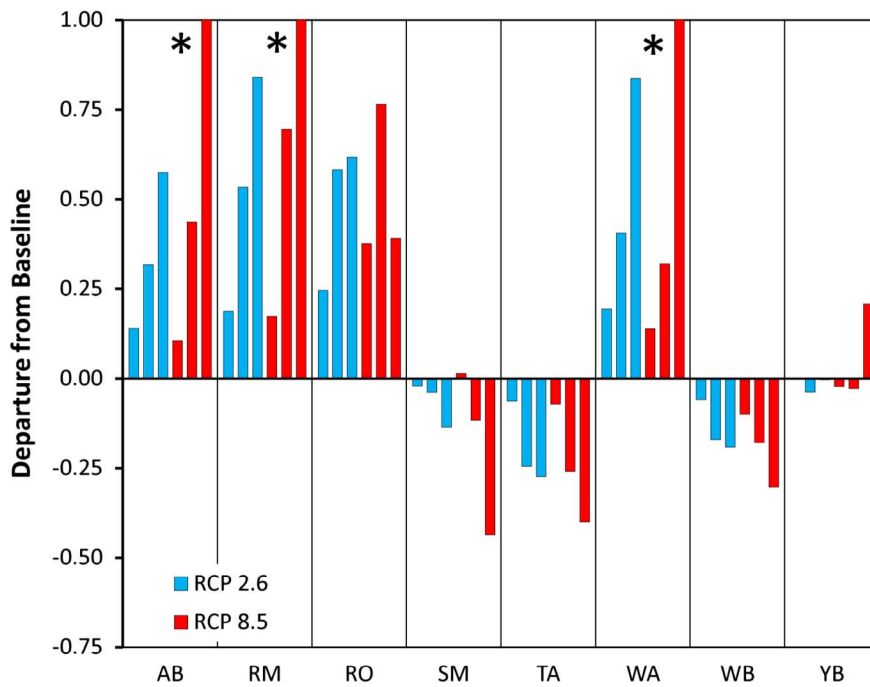


Fig. 4. Departure (fractional difference expressed as a ratio) of relative abundance of each broadleaf deciduous tree species between the baseline climate and each radiative forcing scenario (RCP 2.6: blue bars, RCP 8.5: red bars) for each time period, ordered from left to right as short term (2011–2040), medium term (2041–2070), and long term (2071–2100) in each panel. Abbreviations are the same as in Fig. 3. Note, the responses of three species, under RCP 8.5, extended beyond the Y-axis limit, and are marked with an asterisk. These values are 1.37, 1.96, 1.26 for AB, RM and WA, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

decreased to $6.9 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 6a). Under RCP 2.6, PICUS projected little to no change in growth relative to the baseline scenario (< -0.06 departure overall), but with RCP 8.5, growth decreased substantially by mid-century, with a departure of -0.42 in the long term (2071–2100) (Fig. 6b). The overall decline in growth under RCP 8.5 was primarily attributed to the strong decrease in the CAI of boreal species versus temperate species (Fig. 6c).

4. Discussion

4.1. Changes in composition and growth

Results from the PICUS simulations support our hypothesis that under the business-as-usual, high radiative forcing scenario (RCP 8.5), the Acadian Forest Region will undergo major changes in forest

composition by mid to late 21st century. More specifically, PICUS projected an increase in the relative abundance of warm-adapted, temperate tree species (e.g., American beech, red maple, and red oak), and a decrease in cold-adapted boreal species (e.g., trembling aspen, balsam fir, and black and red spruce), representing the beginning of a “deborealization” of the Acadian Forest. Our simulations corroborate other modeling studies conducted in this region (e.g., Bourque and Hassan, 2008; Ashraf et al., 2015; Boulanger et al., 2016; Rogers et al., 2016) and align with a growing number of empirical studies from across North America’s boreal–temperate forest transition zone that propose cold-adapted boreal species, particularly balsam fir and black spruce, will become increasingly maladapted under RCP 8.5 (e.g., Fisichelli et al., 2014; Reich et al., 2015; D’Orangeville et al., 2016; Searle and Chen, 2016; Pedlar and McKenney 2017).

Changes in forest composition projected by PICUS were largely

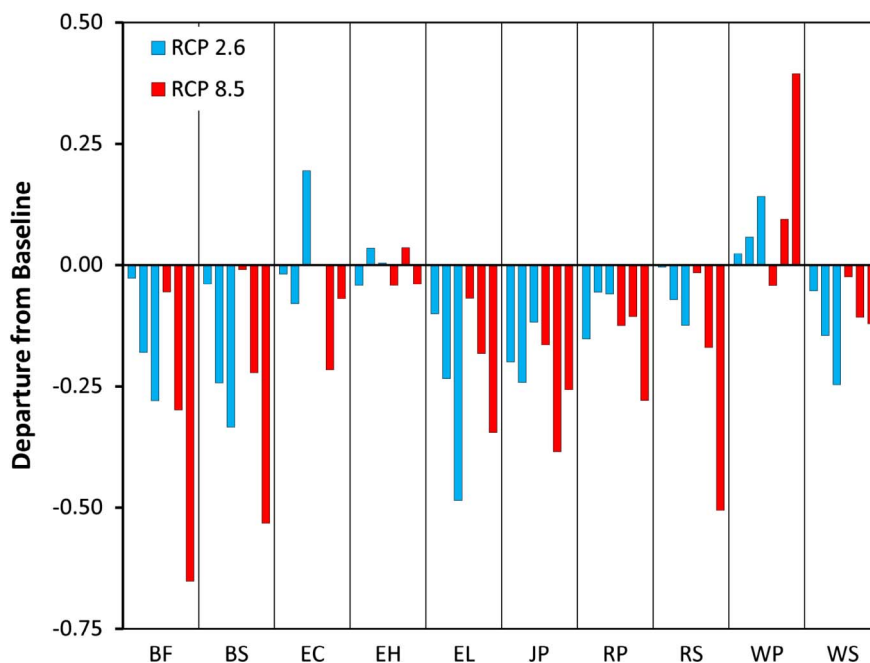


Fig. 5. Departure (fractional difference expressed as a ratio) of relative abundance of each coniferous tree species between the baseline climate and each radiative forcing scenario (RCP 2.6: blue bars, RCP 8.5: red bars) for each time period, ordered from left to right as short term (2011–2040), medium term (2041–2070), and long term (2071–2100) in each panel. Abbreviations are the same as in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

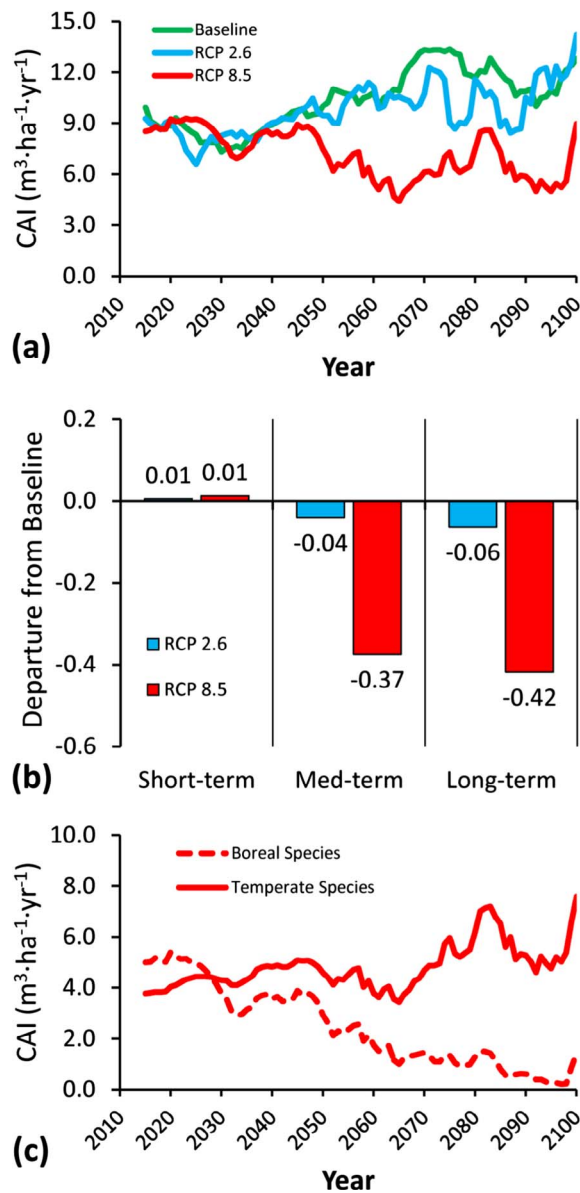


Fig. 6. (a) Current annual increment (CAI, $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) for the time period 2011–2100 for the baseline climate (green line) and each radiative forcing scenario: RCP 2.6 (blue line) and RCP 8.5 (red line). (b) Departure (fractional difference expressed as ratio) of forest growth between the baseline climate and each radiative forcing scenario (RCP 2.6: blue bars, RCP 8.5: red bars) for each time period: short term (2011–2040), medium term (2041–2070), and long term (2071–2100). (c) CAI for the time period 2011–2100 for the RCP 8.5 radiative forcing scenario for boreal species (dashed red line: balsam fir, black spruce, eastern white cedar, eastern larch, jack pine, red spruce, trembling aspen, white birch, white spruce) versus temperate species (solid red line: American beech, eastern hemlock, red maple, red pine, red oak, sugar maple, white ash, white pine, yellow birch). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

driven by shifts in the simulated competitiveness of individual tree species. Appendix S2 (Table S2.1) provides an index of species-specific response values, which indicate how well each species performed in response to changes in each environmental variable (controlling establishment, growth, and mortality) during our model simulations. Under RCP 8.5, boreal species generally responded poorly to increased growing season heat sums (growing degree days) and reduced soil moisture levels as simulated soil moisture levels decreased (Appendix S2, Fig. S2.3) due to higher temperatures in spite of general increases in annual precipitation amounts (Appendix S2, Fig. S2.1) which constrained the growth and ability of boreal species to compete with better-

adapted temperate species. Similar declines in the performance of boreal versus temperate species have been observed through climate manipulation experiments (Reich et al., 2015) and analyses of provenance trials (Pedlar and McKenney, 2017). Further, a recent analysis of historic growth trends in our study region over the past century has revealed that some boreal species are already showing signs of reduced growth due to warming and soil moisture stress (Girardin et al., 2016).

Although the projected changes in climate under RCP 8.5 caused simulated reductions in growth via physiological stress, the main driver of community change was rather the indirect effects of warmer/drier climate on interspecific competition. For instance, when monospecific stands of each species were simulated independently under each forcing scenario (Appendix S2, Fig. S2.4), almost all species were able to survive. However, when mixed-species communities were simulated under the same forcing scenarios, species that were better adapted to warmer conditions prevailed, occupying growing space left by declines in the more susceptible species. Indeed, the indirect effects of climate change on interspecific relationships and how they alter community-level responses to environmental forcing are becoming increasingly recognized (Adler et al., 2012; Zarnetske et al., 2012), and are likely more important than the effects of species migration and invasion on local community dynamics in the near term, i.e., 50–100 years (Ibanez et al., 2009; Zhu et al., 2014). Our simulations provide further theoretical evidence, which aligns with recent field experiments (e.g., Reich et al., 2015), that climate-induced shifts in the competitiveness of individual tree species will drive near-term changes in forest composition.

Corresponding with projected changes in composition, our results showed little to no change in growth (CAI) in the short term (2011–2041), but an overall decrease in growth by the mid to late 21st century, mainly under RCP 8.5. The main factor driving the decrease in growth in PICUS was the diminished performance of boreal tree species (mainly balsam fir and black spruce, which constitute a large proportion of the composition of the current Acadian Forest) in response to increasing temperature and reduced soil moisture availability, especially in the long term (2071–2100) under RCP 8.5 (Appendix S2, Fig. S2.3 and Table S2.1). These results are consistent with recent field studies that have observed similar negative responses of boreal species along Canada's southern boreal forest (e.g., Beck et al., 2011; Michaelian et al., 2011; Peng et al., 2011; Girardin et al., 2014; Pedlar and McKenney, 2017).

Although some temperate tree species (e.g., red maple and red oak) in our simulations also responded negatively to reductions in soil moisture, their simulated responses to warmer temperatures permitted them to remain productive and competitive, compared with the boreal species, even under the severe radiative forcing scenario. However, gains in simulated relative abundance and growth of temperate species did not compensate for the decreases in growth of cold-adapted, boreal species under warming, driving down overall growth across the simulated area. This “lag effect”, which has been reported in previous studies (e.g., Bertrand et al., 2011; Zhu et al., 2014), emerged in our PICUS simulations primarily from what we interpret as a “blocking mechanism”, whereby maladapted, but still living, boreal trees, continue to “block” potential growing space that would be more productive if it were occupied by faster growing, temperate trees. It is possible, however, that this observed lag effect may only be a temporary adjustment period (i.e., 50–100 years duration), at least until many of the boreal species are eventually replaced by better adapted temperate species. For instance, Wang et al. (2016), conducted a study similar to ours for the northeastern US temperate forest immediately south of our study area, finding an opposite trend, with projected increases in growth. This is not surprising, as their study area contains a substantially lower proportion of boreal species and a higher proportion of established temperate species, which are presently close to their northern (i.e., cold limited) climatic range limit and therefore ready to benefit from generally warmer conditions and available growing space. However, it is worth noting that Wang et al. (2016) used the LANDIS PRO forest

landscape model to conduct their analysis, which differs in construct from PICUS, and some differences in results are likely attributable to model differences. Nonetheless, this divergence in simulation results supports the concept that there may be great regional variability in how forests respond to climate change.

4.2. Forest management implications

Our study indicates that under a “business-as-usual” climate warming scenario, increased growth and establishment by warm-adapted temperate tree species will alter the commercial tree species mix, changing the availability of some species-specific wood products. In particular, our results show a substantial reduction in the abundance of balsam fir and black and red spruce by the end of this century. The local forestry sector presently depends greatly on these species for the production of softwood lumber and pulp and paper. Our results also project a considerable gain in the abundance of red maple, which does not seem unreasonable given its generalist, competitive nature and recent, past expansion throughout much of its northern range (Abrams, 1998; Zhang et al., 2015). Red maple is already an important source of fuel wood and hardwood lumber in the Acadian Forest Region (NSDNR, 2008); our projections indicate it will likely become an even more important economic species in the long term (late 21st century and beyond).

However, our results also show it is unlikely that the projected increase in growth and establishment by warm-adapted temperate tree species will keep pace with the loss of cold-adapted boreal species in the Acadian Forest, leading to a potential, overall decrease in average forest growth and wood supply during the latter part of this century. Our results support a growing body of evidence (e.g., McKenney et al., 2016) that traditional commercial reliance on boreal conifers along North America’s boreal–temperate transition zone may become unsustainable in the near future and that adaptive forest management strategies, such as assisted migration or pre-commercial thinning treatments that favor temperate species, may have to be considered.

4.3. Limitations of results

Our results imply climate change may have a serious impact on the Acadian Forest Region and, more broadly, North America’s boreal–temperate forest transition zone; however, we acknowledge that the power of these results is limited and should be interpreted carefully.

One key limitation to our study is the quality of our calibration of PICUS. While we made a large effort to verify that PICUS is sufficiently calibrated to simulate forest dynamics in our study region (see Appendix S1), there were some discrepancies we could not overcome. More specifically, when comparing the ability of PICUS to emulate natural succession in our study region with locally available empirical data (Appendix S1, Step Four), PICUS tended to project lower balsam fir biomass during early succession, lower black spruce biomass throughout succession, and substantially higher biomass of trembling aspen during early succession. Overall, however, PICUS conformed well to known patterns of succession and, for the most part, simulated species biomass within the confidence limits of the empirical data. Therefore, we feel the final calibration was sufficient for the purposes of our study, but that our results should be interpreted carefully, in light of our calibration.

Further limiting our results is the exclusion of climate change effects on natural disturbances. For simplicity, we did not attempt to incorporate climate-mediated disturbances in our study; however, climate change is anticipated to influence the frequency and severity of disturbances in the Acadian Forest Region. For instance, although a warmer climate is expected to become less favorable for some native insect pests, such as spruce budworm (Régnière et al., 2010; Gray, 2013), others, such as hemlock woolly adelgid (*Adelges tsugae* Annand), currently constrained to the south by cooler northern temperatures,

may become increasingly problematic (Paradis et al., 2008), which could offset any potential gains in the abundance of warm-adapted eastern hemlock.

Finally, the omission of confidence intervals surrounding our projections reduces our ability to assess how certain we can be in our findings. Some of this originates from the fact that many processes modeled within PICUS are deterministic, but also because for some parameters that characterize species’ traits, few empirical data exist from which to derive statistically reliable estimates and measures of uncertainty. This issue is not unique to PICUS and, in fact, impedes the application of many forms of process-based ecological models (Drescher et al., 2008; McMahon et al., 2011). Consequently, there are increasing calls for research to improve the quality of data used to parameterize process-based models, which would strengthen our ability to quantify and understand the reliability of projections (Franklin et al., 2016; Urban et al., 2016).

5. Conclusion

Using a well-established forest ecosystem simulation model, PICUS, our study has shown that the Acadian Forest Region, part of North America’s boreal–temperate forest transition zone, is likely to undergo a considerable change in forest composition and growth under the “business-as-usual” RCP 8.5 radiative forcing scenario. In comparison, the low-radiative forcing scenario (RCP 2.6) would have relatively minor impacts by 2100. However, it appears increasingly unlikely that humanity will succeed in keeping global warming below 1.5 °C (i.e., comparable to the RCP 2.6 projection) and that increased growth and establishment by warm-adapted temperate tree species are unlikely to keep pace with the loss of cold-adapted boreal species, leading to the beginning of a deborealization of the Acadian Forest and a potential decrease in the availability of commercial softwood species during the latter part of this century. Adaptive forest management strategies that favor temperate broadleaf species (e.g., red maple and American beech) should be considered.

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Author contributions

A.R.T., Y.B., and D.T.P. conceived research. A.R.T., Y.B., D.T.P., D.C. E.M., W.R. and J.A.K. compiled and analysed data. A.R.T., Y.B., D.T.P., D.C., and W.R. wrote paper.

Conflict of interest

The authors declare no conflict of interest.

Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.07.033>.

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