Projected climate change effects on Alberta’s boreal forests imply future challenges for oil sands reclamation

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Climate change will drive significant changes in vegetation cover and also impact efforts to restore ecosystems that have been disturbed by human activities. Bitumen mining in the Alberta oil sands region of western Canada requires reclamation to “equivalent land capability,” implying establishment of vegetation similar to undisturbed boreal ecosystems. However, there is consensus that this region will be exposed to relatively severe climate warming, causing increased occurrence of drought and wildfire, which threaten the persistence of both natural and reclaimed ecosystems. We used a landscape model, LANDIS-II, to simulate plant responses to climate change and disturbances, forecasting changes to boreal forests within the oil sands region. Under the most severe climate forcing scenarios (representative concentration pathway [RCP] 8.5) the model projected substantial decreases in forest biomass, with the future forest being dominated by drought- and fire-tolerant species characteristic of parkland or prairie ecosystems. In contrast, less extreme climate forcing scenarios (RCPs 2.6 and 4.5) had relatively minor effects on forest composition and biomass with boreal conifers continuing to dominate the landscape. If the climate continues to change along a trajectory similar to those simulated by climate models for the RCP 8.5 forcing scenario, current reclamation goals to reestablish spruce-dominated boreal forest will likely be difficult to achieve. Results from scenario modeling studies such as ours, and continued monitoring of change in the boreal forest, will help inform reclamation practices, which could include establishment of species better adapted to warmer and drier conditions.

Key words: boreal forest, climate change, fire, forest landscape model, natural disturbances, oil sands, reclamation

Implications for Practice

- Successful ecosystem restoration after oil sands mining contributes to the creation of ecologically, economically, and socially valuable forests, but may be compromised by climate change.
- Landscape model simulations of natural forest dynamics suggest that spruce-dominated forests will be replaced by parkland or prairie ecosystems under the most severe climate change scenarios.
- Reclamation must take into account which species will survive under future climates, as reliance on maladapted species would compromise the success of reclamation efforts.

Introduction

Throughout the world, human activities continue to degrade terrestrial ecosystems (Foley et al. 2005). In many regions, programs and policies have been put in place to restore degraded ecosystems (Parks Canada 2008; Zedler et al. 2012; Chazdon 2019). There are many environmental and social motivations for ecological restoration including the preservation of species, prevention of soil erosion and flooding, maintenance of biological diversity and cultural values, sequestration of carbon to mitigate climate change, or legislative requirements for land reparation following development or mining (Suding 2011; Chazdon & Brancalion 2019; Jellinek et al. 2019). Traditional restoration practices, which continue in many places, aim to return ecosystems to their original state (Perring et al. 2015). However, as the global climate continues to change (IPCC 2014), achieving such restoration goals may become increasingly untenable (Harris et al. 2006). Many natural ecosystems...
have already become maladapted to the present-day climate and may transition to fundamentally different ecosystem states under future climate change (Johnstone et al. 2016; Serra-Díaz et al. 2018; Stevens-Rumann et al. 2018). Setting realistic, and socially acceptable, restoration goals in changing environments is an ongoing challenge to restoration practices but there is a growing consensus that such goals should be more dynamic, and that a large-scale landscape perspective is required (Perring et al. 2013; Audet et al. 2015).

Globally, mining disturbances are a significant cause of forest losses (Bridge 2004; Sonter et al. 2017) and a cause of deforestation in Canada (Environment and Climate Change Canada 2018). As of December 2016, oil sands mining in Canada had removed 895 km² of Alberta’s boreal forest cover (Alberta Environment and Parks Government of Alberta 2017) with future extraction and subsequent reclamation expected to occur over much of the remaining surface-mineable area of 4,800 km² (Fig. 1) (Government of Alberta 2017). Alberta’s provincial government has legally mandated that mine operators restore the land and return it to “equivalent land capability” (Province of Alberta 2016). Revegetation guidelines state that “one of the primary goals of revegetation programs is re-establishment of vegetation communities characteristic of the locally common boreal forest” (Alberta Environment 2010). Recommendations suggest that reclaimed land should be “capable of supporting a diverse, self-sustaining” landscape with end uses that include conservation of biodiversity and wildlife habitat, commercial forestry, traditional uses, and recreation (Alberta Environment and Sustainable Resource Development 2012). However, these legislative requirements and non-binding guidelines are based on the assumption that future climates will closely resemble those of the past. Little attention has been given to the implications of a rapidly changing climate on reclaimed landscapes. Here we explore whether it is practical to reestablish boreal forest (i.e. structurally and functionally similar to the natural forest that was removed), given projected rates of warming in the region. It may be important for long-term strategic management planning to consider how climate change is likely to alter boreal forest ecosystems in the future, before defining potential reclamation targets (Choi 2007; Rooney et al. 2015).

Mean annual temperatures in northern Alberta are projected to increase 6–10°C by 2100 compared with 1981–2010, if future greenhouse gas (GHG) emissions approximate the IPCC representative concentration pathway (RCP) 8.5 (3; see also van Vuuren et al. 2011). Previous projections have indicated that climate zones suitable for parklands and prairie grasslands will expand northward into areas that presently support upland boreal forest (Schneider et al. 2009). Other work simulating species-specific succession has projected up to 50% decreases in average boreal forest biomass, with late-successional conifers nearly disappearing from the landscape by 2100 under the most extreme climate projections (Boulanger et al. 2017).

Climate change can affect forests in two ways: direct effects on the biota resulting primarily from changes in temperature and precipitation, and indirect effects due to climate-driven changes in natural disturbance regimes (Boulanger et al. 2018b). Disturbances, such as drought, insect outbreaks, tree pathogens, and wildfire, can all cause significant forest mortality, triggering changes in forest growth rates and/or successional pathways (Anderson-Teixeira et al. 2013). In Alberta, a future warmer climate will be characterized by increased drought frequency and severity (Price et al. 2013) despite anticipated changes in precipitation. Prolonged droughts have already occurred in the forest parkland–grassland ecotone in southern Alberta and have contributed to widespread die-back and decline of trembling aspen (Populus tremuloides, Hogg et al. 2008), one of the most widespread species in western Canada’s boreal forests. Drought will likely be a major driver of climate-induced ecosystem change in western interior North America (Hember et al. 2017), but episodic drought effects are rarely considered in vegetation models. Warmer and drier conditions are also expected to increase the frequency and severity of wildfires in boreal forests (Flannigan et al. 2013; Boulanger et al. 2014).

Climate-driven disturbances are likely to interact, often amplifying their individual effects on ecosystem structure and function (Price et al. 2013; Millar & Stephenson 2015; Seidl et al. 2017). With a changing climate, these interactions can contribute to faster alterations in postdisturbance patterns of stand recovery and forest succession (Anderson-Teixeira et al. 2013; Kulakowski et al. 2013; Johnstone et al. 2016). A disturbance-driven change in vegetation composition may

Figure 1. The Canadian oil sands region. The study area (red) lies within the surface mineable area (dark gray) and the oil sands deposits (light gray). The oil sands are located within the Boreal Plains ecozone (green).
cause a decrease in another disturbance (dampening, negative feedbacks). For instance, increased drought typically drives a reduction in average vegetation biomass (e.g. from pine-dominated forest to grassland), which produces lower fuel densities that, in turn, reduce the average intensity of wildfires (Terrier et al. 2013). Alternatively, change in one disturbance may lead to an increase in another disturbance (amplifying, positive feedbacks); for instance, increased forest mortality caused by pathogens increases fuel accumulation, and hence probability of intense fire (Jenkins et al. 2014).

Assessment of the effects of future climate on reclaimed landscapes and restored vegetation requires a baseline for comparison, that is, how would future climate have affected natural vegetation in the Alberta oil sands region if no bitumen mining had occurred? Our goal was to provide realistic and detailed simulations of the future landscape to improve understanding of climate change effects on natural areas and facilitate the development of climate-resilient reclamation policies and practices. Here we used the well-established LANDIS-II forest landscape model which is able to account for interactions among multiple disturbances (human-caused and natural) to investigate how future climate change could affect these interactions and their consequent impacts on boreal forest composition in Canada’s oil sands region. Given the uncertainty surrounding future GHG emission trajectories, we investigated how local boreal forests might respond to alternative scenarios of future climate derived from three Earth system models (ESMs). We simulated both the direct effects of climate change on forest growth and its indirect effects operating through projected changes in natural disturbances.

Methods

Study Area

Approximately half of our 270 km$^2$ study area in the Alberta oil sands is presently disturbed by bitumen mines and associated industrial operations (Fig. 1). The area lies within the Boreal Plains ecozone (Ecological Stratification Working Group 1995), which is characterized by a cool continental climate (mean annual temperature approximately 0$\degree$C) and low annual precipitation (approximately 400 mm with about 50% falling in June–August). Soil types include brunisols, luvisols, gleyisols, and organic soils (Turchenek & Lindsay 1982). The Boreal Plains are a relatively dry, flat portion of North America’s western boreal zone bordered to the south by the Aspen Parkland, characterized by patches of broad-leaved deciduous trees separated by prairie grasslands, and to the north by the Boreal Shield, characterized by extensive conifer-dominated forest (Fig. 1). In the Boreal Plains, upland forest vegetation is dominated by mixed stands with varying proportions of coniferous Picea glauca (white spruce) and Pinus banksiana (jack pine), and broad-leaved Populus tremuloides (trembling aspen), Populus balsamifera (balsam poplar), and Betula papyrifera (paper birch). Lower elevation areas include wetlands and treed peatlands dominated by Picea mariana (black spruce) and Larix laricina (tamarack) (Johnson & Miyaniishi 2008).

Simulation Design Overview

We projected future vegetation composition and structure by combining output from the PICUS forest gap model (Lexer & Hönninger 2001) and the LANDIS-II forest landscape model (Scheller & Mladenoff 2004). PICUS was used to assess how climate (temperature and precipitation) and soil conditions (water-holding capacity, nitrogen status, and pH) affect growth of individual tree species (Taylor et al. 2017). The PICUS-derived growth results for each species, under unique combinations of soil and climate conditions (termed “landtypes”), were then used to parameterize species establishment, maximum aboveground biomass, and maximum net primary productivity for LANDIS-II simulations in the Boreal Plains ecozone (as reported by Boulanger et al. 2017).

LANDIS-II simulates forest landscape changes by integrating topography (e.g. soil wetness, nutrients), stand-level processes (e.g. intraspecies and interspecies competition, natural and postdisturbance establishment, growth) and landscape-level processes (e.g. disturbances, seed dispersal) that are all important to projecting plausible impacts of climate change on forest landscapes (Gustafson 2013). It is a spatially explicit, raster-based model that begins each simulation with an initial distribution of species cohorts that grow, compete, and disperse according to species- and site-specific parameters, while drought, fire, and harvesting occur episodically.

We ran LANDIS-II simulations with different anthropogenic climate forcings and disturbances to determine their effects on total aboveground biomass and forest landscape species composition. We simulated nine different climate scenarios for the period 2010–2100, as projected by three different ESMs, each forced by three RCP scenarios, namely RCP 2.6, RCP 4.5, and RCP 8.5. As a baseline we also simulated future landscape-scale responses assuming recent climate (based on data for 1981–2010) persisted throughout the twenty-first century. To assess the effects of different disturbances, three disturbance types (fire, harvesting, and drought) were applied either singly, or all three in combination, during each simulation, along with a no-disturbance scenario (i.e. five disturbance treatments in total). Separating the disturbances allowed us to assess the specific effects of each disturbance and how they interact.

In total, there were (3 ESMs $\times$ 3 RCPs + baseline) $\times$ (5 disturbance treatments) = 50 different simulations, each of which was replicated 20 times. We found there was little variability in the results among replications, with most of the differences caused by stochasticity in simulated fire occurrence. Simulations were initialized for year 2000 and run to year 2300, on a 5-year time step (reflecting the temporal resolution of drought-induced mortality data). After 2100, dynamic parameters from 2070 to 2100 were held constant until 2300, to simulate the long-term effects of projected climate change on growth and mortality, and hence the consequences for forest succession (Table 1). Moreover, running to 2300 allowed the simulations of fire disturbances over multiple fire-return intervals to stabilize, along with the feedbacks between disturbances and postfire succession. A simulation period ending in 2100 would not show the long-term effects of disturbances on forest succession. The LANDIS-II simulations ran on a total domain of 8,526 grid cells at 250 m
resolution (6.25 ha) as this approximately represented the spatial resolution of the underlying soils maps (10 ha, see next section). A model validation procedure was undertaken by comparing baseline LANDIS-II simulation results with inventory plot data from the same region (Supplement S1).

Data Sources

Soils. The Alberta Oil Sands Environmental Research Program (AOSERP) supported work in the mid-1970s to map dominant soil groups and their characteristics using air-photo interpretation, with field validation from 130 soil profiles. This produced a detailed soils inventory for the study area in which the smallest soil polygon was 10 ha (Turchenek & Lindsay 1982). We digitized the AOSERP soils inventory and accompanying data, including pH range and texture for each soil group (Soundarapandian et al. 2019), and used these as soils data for the PICUS growth performance simulations for each landtype (Supplement S2). Landtypes with water and steep rocky soils were assumed unsuitable for tree growth and excluded from the simulations. To adequately represent large-scale landscape processes (fire and seed dispersal), we created a buffer around the study area, with attributes set to the spatial means of those within the study area.

The landtype map and associated data provided the necessary input variables for PICUS, namely pH, water-holding capacity (WHC), and available nitrogen (N). The soil texture triangle (Canada Soil Survey Committee 1998) was used to estimate sand and clay fractions from the reported soil texture classes for each landtype, and hence to estimate soil WHC (Saxton et al. 1986). Available soil N values were needed to project forest productivity in PICUS but were difficult to estimate for individual sites because they are influenced by vegetation cover (Quideau et al. 2013). Jerabkova et al. (2006) reported values of total soil N content for boreal forest floor in the range 109–134 g N/m², with a mean of 116 g N/m²; we therefore set available soil N to 34.8 kg N/ha throughout the study area assuming 3% of total soil N is inorganic and available to plants (see sensitivity test in Supplement S7).

Climate. PICUS simulations required monthly climate data to simulate the growth of tree species under different conditions. Monthly climate data for 1981–2010 (McKenney et al. 2011) were used to represent present-day (baseline) climate. Future monthly mean precipitation, specific humidity, and daily maximum and minimum temperatures were obtained from the Coupled Model Intercomparison Project Phase 5 archive (CMIP5, https://cmip peny et al. 2017). Climate change scenarios were used to project future climate conditions for the period 2006–2100. The RCP 8.5 scenario is the most extreme warming projection and assumes stabilized emissions by 2100. Under RCP 2.6 scenario, GHG emissions stabilize during the twenty-first century and mitigation actions are sufficient to reverse much of the global radiative forcing before 2100. Under RCP 8.5, GHG emissions continue to increase, following a near exponential trend to 2100 and beyond. The RCP 4.5 scenario is intermediate between RCP 2.6 and RCP 8.5 and assumes stabilized emissions by 2100.

The bias-corrected ESM projections were used to create spline surfaces for each month for each climate variable using the ANUSPLIN (Hutchinson 2011; McKenney et al. 2011). These spline surfaces were then interrogated using the ANUSPLIN LAPPNT program (Hutchinson 2011) to generate monthly climate data values for the centroids of each soil polygon in the study region. These monthly data were used to calculate annual climate moisture index (CMI, cm) for each landtype, following Hogg (1997) and Hogg et al. (2008) where

\[ \text{CMI} = P - PET, \]

where P and PET are annual precipitation and annual potential evapotranspiration, respectively. A simplified form of the

Table 1. Species life-history traits used to parameterize forest landscape simulation model LANDIS-II. Species-specific drought tolerance slope is based on Hogg et al. (2008) but all other parameters follow Boulanger et al. (2017).

<table>
<thead>
<tr>
<th>Species</th>
<th>Longevity</th>
<th>Sexual Maturity</th>
<th>Shade Tolerance</th>
<th>Fire Tolerance</th>
<th>Seed Dispersal Dist, Effective</th>
<th>Seed Dispersal Dist, Maximum</th>
<th>Vegetative Reproduction Probability</th>
<th>Sprout Age, Min</th>
<th>Sprout Age, Max</th>
<th>Post-fire Regeneration</th>
<th>Drought Tolerance Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula papyrifera</td>
<td>150</td>
<td>20</td>
<td>2</td>
<td>1</td>
<td>200</td>
<td>5,000</td>
<td>0.5</td>
<td>10</td>
<td>70</td>
<td>None</td>
<td>0.158</td>
</tr>
<tr>
<td>Larix laricina</td>
<td>150</td>
<td>40</td>
<td>1</td>
<td>1</td>
<td>50</td>
<td>200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>None</td>
<td>0.159</td>
</tr>
<tr>
<td>Picea glauca</td>
<td>200</td>
<td>30</td>
<td>3</td>
<td>2</td>
<td>100</td>
<td>300</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>None</td>
<td>0.111</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>200</td>
<td>30</td>
<td>4</td>
<td>2</td>
<td>80</td>
<td>200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>None</td>
<td>0.159</td>
</tr>
<tr>
<td>Pinus banksiana</td>
<td>180</td>
<td>20</td>
<td>1</td>
<td>2</td>
<td>30</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>Strict serotiny</td>
<td>0.080</td>
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<tr>
<td>Populus balsamifera</td>
<td>140</td>
<td>20</td>
<td>1</td>
<td>2</td>
<td>1,000</td>
<td>5,000</td>
<td>0.9</td>
<td>10</td>
<td>130</td>
<td>Resprout</td>
<td>0.180</td>
</tr>
<tr>
<td>Populus tremaloides</td>
<td>150</td>
<td>20</td>
<td>1</td>
<td>2</td>
<td>1,000</td>
<td>5,000</td>
<td>0.9</td>
<td>10</td>
<td>150</td>
<td>Resprout</td>
<td>0.180</td>
</tr>
</tbody>
</table>
Penman–Monteith equation was used to estimate PET from monthly vapor pressure deficit (kPa, derived from monthly specific humidity and temperature data) and monthly mean temperature (Hogg 1997). Severe drought during 1 year often reduces tree growth over multiple years (Hogg et al. 2008), so we used the minimum annual CMI calculated for the previous 5 years (Supplement S5).

**Initial Communities.** LANDIS-II simulations were initialized using Alberta Vegetation Inventory (AVI) data for 1987–2014 (Alberta Agriculture and Forestry 2017). The AVI uses air-photo interpretation and field sample plot data to map the five most common tree species present, along with year of stand origin, for both overstory and understory species. As oil sands mining had already disturbed a significant fraction of the study area when AVI data were collected, we “gap-filled” disturbed areas with potential past vegetation based on the landtypes. To identify which species were most likely present on each landtype, we included all species in the inventoried stands that intersected each landtype (by more than 1% of its area). For example, one landtype polygon may be intersected by two AVI polygons, one with 100-year-old *P. mariana* overstory and 10-year-old understory, and one with 40-year-old *P. tremuloides*. Therefore, this landtype would be initialized with 10- and 100-year-old *P. mariana* cohorts and a 40-year-old *P. tremuloides* cohort.

The years of stand origin for overstory and understory tree species in each stand were used to set 10-year-old cohorts. AVI estimates of stand age were rounded to the closest 10-year interval. Because the AVI vegetation age estimates mostly predated the start of our simulations (2010), we aged all cohorts. For example, if stand origin year was reported as 1940, stand age was set to 70 years in the first year of simulations (2010). All grid cells in the buffer region were filled with the 60 most common species cohorts to provide sources of outside colonization into the study area.

**Species Information.** We used the LANDIS-II Biomass Succession extension version 6.2 (Scheller & Mladenoff 2004) to simulate species growth and regeneration in the study region. PICUS simulation results were used to generate three species-specific dynamic growth parameters dependent on climate and soil conditions for each landtype and each climate change scenario. The three parameters were: maximum aboveground biomass ($B_{\text{max}}$), maximum annual net primary productivity ($\text{NPP}_{\text{max}}$), and species establishment probability ($\text{SEP}$) (Supplement S4). Other species’ attributes such as shade tolerance, seed dispersal distance, demographic parameters, and disturbance tolerance (Table 1) were assumed constant throughout the simulations and independent of climate and soil conditions. We recognize that these parameters could change due to evolutionary pressures—allowing future genotypes to be better adapted to the changed climate. However, in this study, we did not speculate how genotypes might change, or how rapidly. Succession and postfire tree regeneration strategies were implemented in the biomass succession extension and varied by species (Table 1). Early-successional species such as *Populus* spp. were considered shade-intolerant and able to disperse buoyant seeds over long distances, whereas late-successional species such as *Picea* spp. were considered shade-tolerant with longer lifespans, and able to disperse seeds only over short distances. Because *P. banksiana* is a strictly serotinous species, regeneration was assumed to occur only following fire. Given *P. mariana* is considered a semiserotinous species, it was also assumed to regenerate immediately following fire, but additionally seeds of *P. mariana* were allowed to disperse into burned areas from seed-bearing trees (>30 years old) in nearby unburned stands, along with seeds of *L. laricina* and *P. glauca*. Resprouting from stumps was considered possible for *B. papyrifera* and *Populus* spp. following fire. These parameters were all based on previously published sources (Boulanger et al. 2017).

**Disturbances.** Based on numerous observations over the last 20 years or more, drought is projected to cause extensive tree mortality in the Boreal Plains region as climate becomes warmer and drier (Hogg & Bernier 2005). Hogg et al. (2008) established a strong correlation between CMI and field measurements of *P. tremuloides* mortality in severe drought conditions. Annual rates of drought-related tree mortality were estimated from observed relationships between water stress-induced mortality of *P. tremuloides* (Hogg et al. 2008), extrapolated to other species and annual variations in CMI (Supplement S6). To estimate mortality rates in the LANDIS-II Biomass Succession extension, we first used the reported correlations between CMI and mortality of *P. tremuloides* to simulate the effect of drought on *P. tremuloides* (Supplement S6). We then used the slope parameter (representing sensitivity to drought stress) for *P. tremuloides*, adjusted according to relative drought tolerances of other species obtained from published sources compiled by Niinemets and Valladares (2006) to estimate drought parameters for the other modeled species. We did not include the mortality intercept estimate because background mortality was already accounted for in LANDIS-II (through species-specific age mortality and competition). Instead, we assumed that drought-induced mortality was zero for CMI > 0 (i.e. no drought-induced mortality when seasonal precipitation exceeds seasonal PET). Through this method we estimated percentage mortality (per year) for each species as a function of calculated CMI (Supplement S6).

As we wanted to implement these predefined, dynamic, and species-specific mortality rates, we used the Biomass Harvest extension v3.0 (Gustafson et al. 2000) as a surrogate to simulate drought mortality. The harvest extension was suitable for simulating these drought effects because it was possible to set the exact percentage of biomass removed for each species corresponding to the CMI, and hence mortality, occurring during each 5-year time step. The percentage of drought-killed biomass was removed equally from all cohorts over 5 years old, but *B. papyrifera* and *Populus* spp. were allowed to resprout (Table 1). After 2100, randomly selected values calculated for the period 2071–2100 were used to simulate mortality.

Timber harvesting was simulated using the LANDIS-II Biomass Harvest extension. The timber harvest rate used for simulations was calculated on the basis of historical harvest data.
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(expressed as changes in aboveground biomass estimated from MODIS-based annual forest disturbance maps for the period 2001–2011) developed by Guindon et al. (2014). Throughout the simulations and over the entire landscape, the annual harvest rate in the Boreal Plains was held constant at 0.18% of forest area per year (Guindon et al. 2014), with the maximum size of a harvested patch set to five 250 m grid cells (31.25 ha). Stands (grid cells) harvested at each time step were selected only from stands more than 60 years old, which approximates ecosystem-based forest harvesting practices in the study region (e.g. Song 2002). All cohorts over 10 years old were harvested with no species preference. Regeneration was assumed to occur by natural seeding (i.e. no artificial replanting of cleared areas), though *Populus* spp. and *B. papyrifera* were assumed also able to resprout from stumps. The LANDIS-II Biomass Harvest extension does not allow two “harvest” treatments to occur in a single time step in the same grid cell, so harvested stands were never subjected to drought mortality effects in the same simulation year.

Fire is an important landscape-scale disturbance in the boreal forest (e.g. Bond-Lamberty et al. 2007) and was simulated stochastically in LANDIS-II using the Base Fire extension (Yang et al. 2004). Baseline and future fire regime parameters were calibrated using the Southern Prairie Homogeneous Fire Regime zone model (Boulanger et al. 2014) and projected according to different RCP scenarios (Gauthier et al. 2015). Fire regimes derived from the CCCma’s Coupled Global Climate Model (CGCM3) were applied to all simulations as variations in fire parameters among different ESMs were small (Boulanger et al. 2018a). In the LANDIS-II Base Fire extension, there is no feedback between future modeled vegetation and future burn rates (i.e. vegetation fuel loads were assumed to be constant, even though in reality, increasingly frequent fires would be expected to reduce fuel accumulations and eventually stabilize mean fire return intervals).

Results

Biomass densities in disturbed grid cells simulated by LANDIS-II were generally lower than the mean biomass in the NFI ground plot inventory (Supplement S1). The simulated mean biomass was 50 tons/ha compared to 80 tons/ha reported at the NFI ground plots. LANDIS-II simulated very few stands dominated by *Picea* spp. even 250 years after disturbance. The variability of biomass in each stand was much greater in the sample plot data. Observed biomass in some plots exceeded 200 tons/ha, but LANDIS-II was unable to simulate any stands with such high biomass densities.

Effect of Climate Change Scenarios and Disturbances on Biomass Projections

Projections of future forest biomass were most sensitive to the anthropogenic climate forcing scenario, while the differences among climate models and disturbances had smaller effects (Fig. 2; see discussion in Supplement S8). For simulations that included all disturbance types (drought, fire, and harvesting), average total aboveground biomass under RCP 8.5 was approximately 60 tons/ha (for CanESM2 and MIROC-ESM) but only approximately 23 tons/ha (for HadGEM2-ES), compared with approximately 81 tons/ha for the baseline simulation. Under less severe climate forcing, average projected biomass was more similar among all three ESMs: 75–85 tons/ha for RCP 2.6 and 60–80 tons/ha for RCP 4.5 (Fig. 2). In the case of CanESM2 forced by RCP 2.6, biomass was projected to increase relative to that obtained with the baseline climate, evidently because the increases in precipitation, combined with relatively small temperature increases, projected by CanESM2, benefited the simulated growth rates (Supplement S4).

Even though LANDIS-II projected that direct effects of climate change would cause large declines in aboveground biomass, indirect effects of climate change, in the form of

![Figure 2. The impacts of climate change on average aboveground biomass in the study area under different ESMs, climate-forcing scenarios, and disturbance scenarios. The ESMs were (A) CanESM2, (B) HadGEM2, and (C) MIROC-ESM. The biomass averages and error bars (±SD) were calculated from LANDIS-II simulation results during the last year of simulations (2300) for 20 replicate simulations. Note that for comparison the baseline results without climate change are repeated for each ESM.](image-url)
climate-driven disturbances, were also projected to drive changes in average biomass. Simulated harvesting generally reduced the negative effects of climate change, causing average biomass to increase compared to simulations with no disturbances (Fig. 2). This was because regrowth of young stands occurred over a larger area, increasing the proportion of faster-growing broad-leaved biomass, which compensated for harvest removals of approximately 10 tons biomass ha$^{-1}$ year$^{-1}$ in the long term (Supplement S7). Fire and drought caused either positive or negative feedbacks with direct climate change, depending on the ESM and climate-forcing scenario (Fig. 2; Supplement S7). Under more severe forcing scenarios, however, the harvesting effect did not mitigate the direct effects of climate change, so average biomass decreased for all three ESMs (Fig. 2). Because the results obtained from simulations using different ESM projections with the same RCP forcing were very similar, but much larger differences in simulation outcomes were obtained using different forcings (Supplement S7), we chose to limit further discussion to the results obtained from CanESM2. Biomass results obtained using the CanESM2 climate projections generally fell between those obtained from the other two ESMs (HadGEM2 projected more severe climate change while the MIROC-ESM projected milder climate change, see Supplement S3).

Projected Changes in Forest Landscape Composition for CanESM2 ESM Climate Projections

We used the parameterized LANDIS-II model to simulate how natural vegetation in the Alberta oil sands region would respond to climate changes projected for the period 2010–2100. Over the simulation period, the mean aboveground biomass of species in the landscape varied depending on future climate and disturbance scenarios (Fig. 3; see Supplement S7 for means of all replicated simulations). Climate warming generally led to projected declines in spruces (Picea glauca and Picea mariana) and their replacement by broad-leaved deciduous species, a shift that occurred most rapidly under RCP 8.5 (Fig. 3A, F, K, & P). Spruces are cold-adapted conifers with relatively low tolerance for drought and wildfire, and hence appeared most vulnerable to projected climate change: spruce biomass was projected to decrease even under RCP 2.6 when all three disturbance types were included in the simulation (Fig. 3F).

Climate-driven disturbances were also important in determining future species composition. Fire favored broad-leaved species and jack pine (Pinus banksiana) compared to scenarios without that disturbance. When fire alone was simulated, P. banksiana and Populus tremuloides survived better and produced more biomass than without fire, owing to their serotinous and resprouting habits, respectively (Fig. 3C, H, M, & R). Late-successional spruces persisted on the simulated landscape under RCP 2.6 and 4.5 without disturbances (Fig. 3G, H, I, & J), but were greatly reduced when disturbances were included. As noted earlier, the projected shifts in forest composition toward predominance of younger stands of early-successional broad-leaved species (which accumulate biomass faster than conifers), explained why harvesting generated higher average biomass and dampened the direct effects of moderate changes in climate (Fig. 3I & N). However, with RCP 8.5, the dampening effect of harvesting on biomass decline disappeared and the disturbance-tolerance of broad-leaved species also decreased, particularly when all disturbance types were simulated (Fig. 3P).

Discussion

Effects of Climate Change on Average Forest Landscape Biomass

In general, LANDIS-II projected major decreases in total forest biomass in the Boreal Plains ecozone as a consequence of the direct and indirect effects of projected future changes in climate. Future forests in this region could become more sparse, resembling the dispersed patchy woodlands presently found in the Aspen Parkland ecozone further south, where average forest biomass density is about 59 tons/ha (National Forest Inventory) (Gillis et al. 2005). Our projections are consistent with niche model projections of boreal forest transitions to grassland or parkland ecosystems (Rehfeldt et al. 2012; Schneider 2013; Stralberg et al. 2018) although they might underestimate future biomass. While we did not explicitly model shrub- and/or grass-dominated ecosystems, we expect them to expand in the study area as forest cover becomes increasingly maladapted due to more frequent and severe droughts and fires.

Interactions Between Direct and Indirect Effects of Climate Change

Interactions among disturbances tend to amplify their effects on ecosystems (Seidl et al. 2017). However, we found that under RCP 2.6, harvesting and fire increased average biomass compared to scenarios without disturbances, generating a stabilizing, negative feedback between direct and indirect effects. This occurred because broad-leaved species displaced conifers on disturbed sites, and being faster-growing in the early-successional stages, they accumulated biomass more rapidly, offsetting the overall effect of more frequent disturbances on average biomass over the entire landscape. Severe stand-replacing disturbances may therefore mitigate the effect of climate change on forest biomass in boreal landscapes while altering the species composition (generally increasing broad-leaved component). Other model simulations of boreal and subalpine forests have also found that disturbances may alter species composition in ways that mitigate the negative effects of climate change (Temperli et al. 2015; Lucash et al. 2018). However, the negative feedback we observed did not occur under more severe climate change scenarios that evidently exceeded the simulated ecosystem’s tolerance to disturbance.

Forest responses to climate change are driven by individual species’ life-history traits (Anderson-Teixeira et al. 2013; Aubin et al. 2016). Our simulations indicated that Picea glauca will decline in a warmer (drier) climate, primarily because it is better adapted to cool, moist environments (Reich et al. 2015) where soil water is typically nonlimiting to growth and survival. When we included climate-driven changes to
Figure 3. LANDIS-II projections of mean aboveground biomass (tonnes/ha) for all major forest tree species, by RCP scenario and disturbance scenario. The projections were carried either with current baseline climate (A–E), RCP 2.6 (F–J), RCP 4.5 (K–O), or RCP 8.5 (P–T). Results are shown for one of the replicate simulations using the ESM CanESM2 and the sharp declines in biomass are due to fires. For results using other ESMs refer to (Supplement S3).

Disturbances in our simulations, biomass of late-successional *P. glauca* decreased, probably because it had less opportunity to reach maturity and reproduce, as reported by Brown and Johnstone (2012), and because short seed dispersal distances limited its ability to recolonize disturbed areas from neighboring patches of mature trees. With more severe climate warming (e.g. RCP 8.5), the projected shifts in climate were very rapid, which then limited the opportunities for *P. glauca* to seed into climate-suitable sites. In contrast, *Pinus banksiana* is better adapted to warmer temperatures, and more frequent fires and droughts projected under climate change, so the interactions between temperature-driven and disturbance-driven effects of climate change both favor increased biomass of this species. Broad-leaved boreal species are generally better adapted to reestablish after stand-replacing disturbances such as fire and harvesting, both through their ability to resprout following die-back of aboveground biomass, and because they can disperse wind-borne seeds over long distances; both traits enabled broad-leaved species to attain greater average biomass when these disturbances were included in the simulations. Climate change may already be causing observed postdisturbance transition to early-successional broad-leaved forests (e.g. Searle & Chen 2017; Stevens-Rumann et al. 2018). Our species-level modeling helps explain how individual species with unique trait combinations can respond to climate change and interspecific competition, leading to more realistic and detailed projections of successional changes in future vegetation.

**Model Limitations**

After comparing baseline simulations with inventory data from the oil sands region, we found that average biomass could be estimated relatively accurately by LANDIS-II, suggesting that our projections of future changes in the forest landscape are plausible. The simulations typically underestimated the occurrence of forest stands with exceptionally high or low biomass, particularly those dominated by spruces (Supplement S1). These discrepancies may have been due to the assumption of spatially constant nitrogen levels in our simulations. In nature, nitrogen levels evidently influence species composition, such that nutrient-rich sites are generally dominated by broad-leaves (Jerabkova et al. 2006). Furthermore, simulated species growth was not linked to spatial hydrology and the presence of soil water in low-lying areas (or wetlands). Notably, *Picea mariana* is a characteristic species of wetter lowland sites; conversely, on upland sites, *P. banksiana* is typically more drought-tolerant than *P. glauca*. Another reason for the discrepancy between simulations and data could be that climate change is already affecting forest structure (i.e. species composition and biomass). With rapid climate warming in the region since circa 1970,
the present-day distribution of conifers may be in climate “dis-equilibrium.” Note that AVI vegetation data collected during 1987–2014 report on forest stands established several decades earlier, while our baseline climate (for 1980–2010) represents a period generally much warmer than previous decades. Hence, it may be realistic that some conifer decline was projected in long-term simulations forced by the baseline climate.

Our simulations have not taken into account the effects of on-going reclamation activities or impacts of climate change on wetlands (including lowland bogs with tree cover). Next steps should include assessments of the performance of restored vegetation compared to natural vegetation (Errington & Pinno 2015; Dhar et al. 2018), integrating this information into new model simulations. Current reclamation prescriptions increase the proportion of upland forest in the oil sands region at the expense of low-lying peatland systems. More work would also be needed to simulate the responses of wetter lowland sites to climate warming, and the role of oil sands wetland reclamation practices, in altering boreal forest vegetation.

A further potential limitation of our study could be that the forest landscape model did not explicitly represent phenotypic or genotypic changes that may allow species to adapt to changing conditions. While these may be important processes, we are not aware of any forest landscape model that accounts for them. The reasons likely include lack of data, increased model complexity, and potential for error propagation (McMahon et al. 2011, but see Razgour et al. 2019 on using ecological niche models).

Climate Change Implications for Ecosystem Restoration

Reclamation success in the Alberta oil sands would possibly be improved in coming decades if model simulations of future forests, such as ours, were used to guide ecosystem restoration strategies (Dooley et al. 2012). Our results suggest current practices could shift toward planting species that are more drought- and fire-tolerant (e.g. Laughlin et al. 2017). Other simulation studies have demonstrated that planting climate-suitable species leads to greater tree survival and C sequestration (Hof et al. 2017; Lucash et al. 2017). Planting populations of trees that are better adapted to future local climates underpins the concept of assisted migration as a forest management adaptation to climate change (e.g. Aitken et al. 2008; Ste-Marie et al. 2011; Williams & Dumroose 2013; O’Neill et al. 2017). Such modifications to reclamation practices could also increase boreal forest ecosystem resilience to future disturbances (Timpane-Padgham et al. 2017), another important goal in oil sands reclamation (Alberta Environment and Sustainable Resource Development 2012). For example, increasing the proportion of broad-leaved species might be a silvicultural practice to decrease fire hazard and increase drought-tolerance of restored boreal forest cover (Astrup et al. 2018; Stockdale et al. 2019). Given the likely and imminent effects of climate warming on natural systems, it is important to consider the challenges attached to current mine-reclamation, and other ecosystem restoration policies, which aim to reestablish ecosystems in regions where they are unlikely to persist naturally. Factoring projected impacts of climate change on forest composition and growth will facilitate the development of climate-resilient reclamation policies and practices.

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Code availability

Simulation input data and associated code will be available at www.github.com.

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Supporting Information
The following information may be found in the online version of this article:

Supplement S1. Comparison of LANDIS-II simulation results with Forest Vegetation Inventories.
Supplement S2. Soil groups.

Supplement S3. Climate data.
Supplement S4. PICUS input data and results.
Supplement S5. Calculating climate moisture index (CMI).
Supplement S7. LANDIS simulation results.
Supplement S8. Analysis of drought and fire effects.

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