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ARTICLE

Climate Ecology

Oil sands restoration with warm-adapted trees improves outcomes under moderate but not severe warming scenarios

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Abstract

Successful restoration of human-disturbed landscapes and ecosystems will be increasingly compromised by the impacts of climate warming. Assisted migration and climate-informed restoration, in which populations and species adapted to future climates are selected for restoration planting, have emerged as management tools to mitigate climate change effects. However, it is unclear whether climate-informed restoration could offset the negative effects of climate change and enable successful restoration. We used a forest landscape model to evaluate the potential for reclamation activities to restore western Canadian boreal forest landscapes severely degraded by oil sands mining. We parametrized tree populations adapted to growing in warmer climates and then simulated the planting of local or southern tree populations under different climate change, mining, and wildfire disturbance scenarios. We found that planting trees better adapted to a warmer climate mitigated climate-change and wildfire-caused decreases in biomass across the landscape, but only under moderate climate change scenarios. The compensatory effect of planting populations adapted to warmer southern climates disappeared under a more severe climate change scenario. The advantage of planting southern populations also disappeared under wildfire scenarios, generally doubling the biomass loss compared with scenarios without wildfire. With wildfire and strong climate change effects, forest cover disappeared from much of the landscape, regardless of the planting scenario, causing it to change markedly from present-day continuous boreal forest cover. We argue that such conditions would have large ecological and economic consequences. Scenario modeling with forest landscape models could be used as a tool to identify the long-term success of restoration actions and to understand possible consequences of climate-informed restoration.

KEYWORDS
assisted migration, climate change, land-use change, oil sands mining, reclamation, restoration, simulation

INTRODUCTION

Ecological restoration of degraded lands is an increasingly common and important tool for climate change mitigation and adaptation (Griscom et al., 2017). We are currently in the "UN Decade on Ecosystem Restoration," and the Bonn Challenge aims to "bring 350 million ha of degraded and deforested landscapes into restoration by 2030." Successful restoration is key for future ecosystem health and is valuable for recreation, Indigenous uses, carbon sequestration, economic activities, and wildlife habitat. However, there is an increasing consensus that restoration must take into account potential effects of climate change. Climate change is expected to have large impacts on natural forests (e.g., Anderegg et al., 2013; Price et al., 2013), and restored forests are as vulnerable to future climate changes as natural forests. For example, Stralberg et al. (2019) estimated that 14%–42% of Canada's boreal biome could experience climate conditions unsuitable for boreal species by 2100. Restoration that accounts for future climate conditions has variously been called "climate-informed," "climate-smart," "future-proofed," "preadapted," "managed relocation," or "prestoration" (Butterfield et al., 2017; Schwartz et al., 2012; Simonson et al., 2021). Assisted migration (managed relocation) is focused on the protection of individual species and has received increasing attention as a method to ensure continuity of forest cover under future climate change, especially in a forestry context (Pedlar et al., 2012).

Climate-informed restoration is advancing in the field of forestry, where adaptive silviculture is receiving increased attention (Choi, 2008; Keenan, 2015). In forestry, climate-informed restoration is more commonly referred to as climate-based seed transfer (O'Neill et al., 2017) which involves planting seedlings using seed sources from populations in warmer climates, typically more southerly or lower elevation locations (Booth, 2016; Dalrymple et al., 2021). Climate-based seed transfer is based on plant translocations, or transplant studies that test the responses of genotypes and populations to novel climate conditions (Dalrymple et al., 2021; Pedlar et al., 2012). Traditionally, translocation and transplant studies were mostly carried out for ecological research, or for tree-improvement programs (Aitken et al., 2008), but they are now also providing information about tree growth and survival as the climate changes and guiding management strategies to mitigate climate change-induced ecosystem changes that could generate major socioeconomic losses.

Climate-informed restoration is increasingly proposed to offset climate change effects, but how exactly to implement it, and its potential ecosystem effects, is unclear. There is a need to assess how restoration is likely to perform over the long term under projected changes in environmental conditions. Scenario modeling is useful for determining if ecosystem restoration goals can be achieved (Mayer & Rietkerk, 2004; Schneider et al., 2009) and can guide policy-makers and managers in adjusting restoration goals to account for expected changes in regional climate (Hof et al., 2017). Previous modeling studies of climate-informed restoration have relied largely on single-species models to determine how a species would be suited to new climates (Barragán et al., 2023; Butterfield et al., 2017). However, when determining how to restore forest ecosystems, land managers must consider how climate-informed restoration could affect the whole landscape and the entire community of species. This requires forest simulation models that include stand- and landscape-scale interactions among the ecological processes that structure forest ecosystems, including propagule dispersal, tree growth, interspecific competition, forest succession, and natural or anthropogenic disturbances (Scheller & Mladenoff, 2007). Previous studies have simulated planting of local or novel species (Gustafson et al., 2023; Hof et al., 2017; Lucash et al., 2017). To our knowledge, no studies have attempted to model assisted migration scenarios with populations parameterized according to results from regionally appropriate climate-based seed transfer studies.

We modeled climate-informed restoration in the oil sands region in Alberta, where open-pit mining activities have cleared 895 km^2 of boreal forest and could expand to a disturbance footprint of 4800 km^2 in the coming decades (Government of Alberta, 2017). Provincial regulations require mine operators to return disturbed areas to "equivalent land capability," which coarsely translates to equivalent proportions of productive forests, other uplands, and wetlands as were present in the landscape prior to industrial disturbance (Province of Alberta, 2016). The regulations stipulate that only native species grown from "local" seed zones can be planted. In this region, anticipated future climate warming and associated increases in wildfire occurrence seem likely to trigger major decreases in aboveground biomass and drive transitions from spruce-dominated forest ecosystems to ecosystems dominated by pines and/or deciduous species

(Baltzer et al., 2021; Nenzén et al., 2020; Price et al., 2013) or even by grasslands (Cadieux et al., 2020). Previous models of restoration have not taken into account planting trees better suited to future climates (Daniel & Frid, 2012; Welham, 2014). If boreal ecosystems restored with native tree species cannot successfully regenerate and grow in the future, then the expected disturbance-mediated transition from boreal forest to grass-dominated ecosystems could be accelerated (Stralberg et al., 2018). Of note, here we will call this process "restoration," even though in the context of mining, it is really "reclamation"; that is, restoration of severely degraded lands after mining activities has removed and replaced soils at mine sites (Gann et al., 2019).

Here we test how climate-informed restoration could facilitate ecosystem persistence in a changing climate. Our objective was to test whether climate-informed restoration with different forest tree populations (variously called provenances, genotypes, source populations) better adapted to new climates would be sufficient to offset potential ecosystem biomass reductions due to anthropogenic climate warming. As alternative adaptation strategies for the planting scenarios, we considered either tree populations adapted to southern climate conditions, representing climate-informed ecosystem restoration guided by translocation experiments or locally adapted populations representing restoration as currently implemented. We tested how forests could develop under scenarios representing different combinations of restoration actions, climate change, wildfire, and scenarios of mining disturbance. Our specific questions were: (1) How is overall forest biomass expected to change under different climate change, mining, and planting scenarios? (2) At what temperature optima for southern populations could we maintain current biomass levels? (3) Can planting populations adapted to more southerly climates compensate for loss of biomass and species diversity? We assessed boreal forest restoration success by evaluating changes in total aboveground forest biomass and forest tree species composition.

METHODS

Study area

The study area encompasses a 14,000-km^2 region in the Alberta oil sands, of which approximately 6% is disturbed by bitumen mines and associated industrial operations (Figure 1). Located within the Boreal Plains ecozone (Ecological Stratification Working Group, 1995), the region is characterized by a continental climate. The mean annual temperature is ~0°C, and approximately 50% of annual precipitation (~400 mm) falls as rain from June to August. Soil types include brunisols, luvisols, gleysols, 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 aspen parkland (patches of broadleaved deciduous trees distributed within prairie grasslands) that transitions to prairie grassland. Within the Boreal Plains, upland forest is dominated by a mix of coniferous (*Picea glauca* [white spruce] on fine-textured soils and *Pinus banksiana* [jack pine] on coarse-textured soils) and broadleaved (*Populus tremuloides* [trembling aspen], *Populus balsamifera* [balsam poplar], and *Betula papyrifera* [paper birch]) tree species (Johnson & Miyanishi, 2008). *Picea mariana* (black spruce) and *Larix laricina* (tamarack) occur in low-lying areas.

Simulation design overview

We projected future vegetation composition and structure using the LANDIS-II 7.0 forest landscape model (FLM; Scheller & Mladenoff, 2004) with the PnET-Succession extension to incorporate tree physiological responses to climate change (de Bruijn et al., 2014). LANDIS-II projects change in forest composition and biomass by simulating stand- and landscape-level ecological processes (e.g., forest succession, intra- and interspecies competition, and natural and post-disturbance establishment), across a range of topoedaphic conditions and landscape-level processes (e.g., disturbances and seed dispersal) (Gustafson, 2013). LANDIS-II simulations are spatially explicit; the raster-based model simulates an initial distribution of species cohorts that grow, compete, and disperse according to species- and site-specific parameters. Wildfire, harvesting, and mining land-use changes occur episodically (described in *Disturbances* below).

We ran LANDIS-II simulations with three planting scenarios, two mining scenarios, three climate-change scenarios, and two wildfire scenarios in a full factorial design (36 combinations in total) (Table 1). To test the efficacy of climate-based seed transfer as a tool for ecosystem restoration in a changing climate, we compared a "status quo" scenario that planted trees adapted to the historical climate conditions with "restoration scenarios" that planted more southern tree populations likely better adapted to warmer climates. To represent uncertainty about the extent of future land use in the study area, we developed three scenarios of open-pit mining: (1) all mining activities cease and current mines are restored (reclaimed) immediately (i.e., only 6.5% of landscape area is disturbed); (2) exploitation continues in the leases where mining has already been started and (3) the entire mineable area is mined and then restored (27.5% of landscape area disturbed) (Figure 1, Appendix S1: Figures S5-S8). As mining

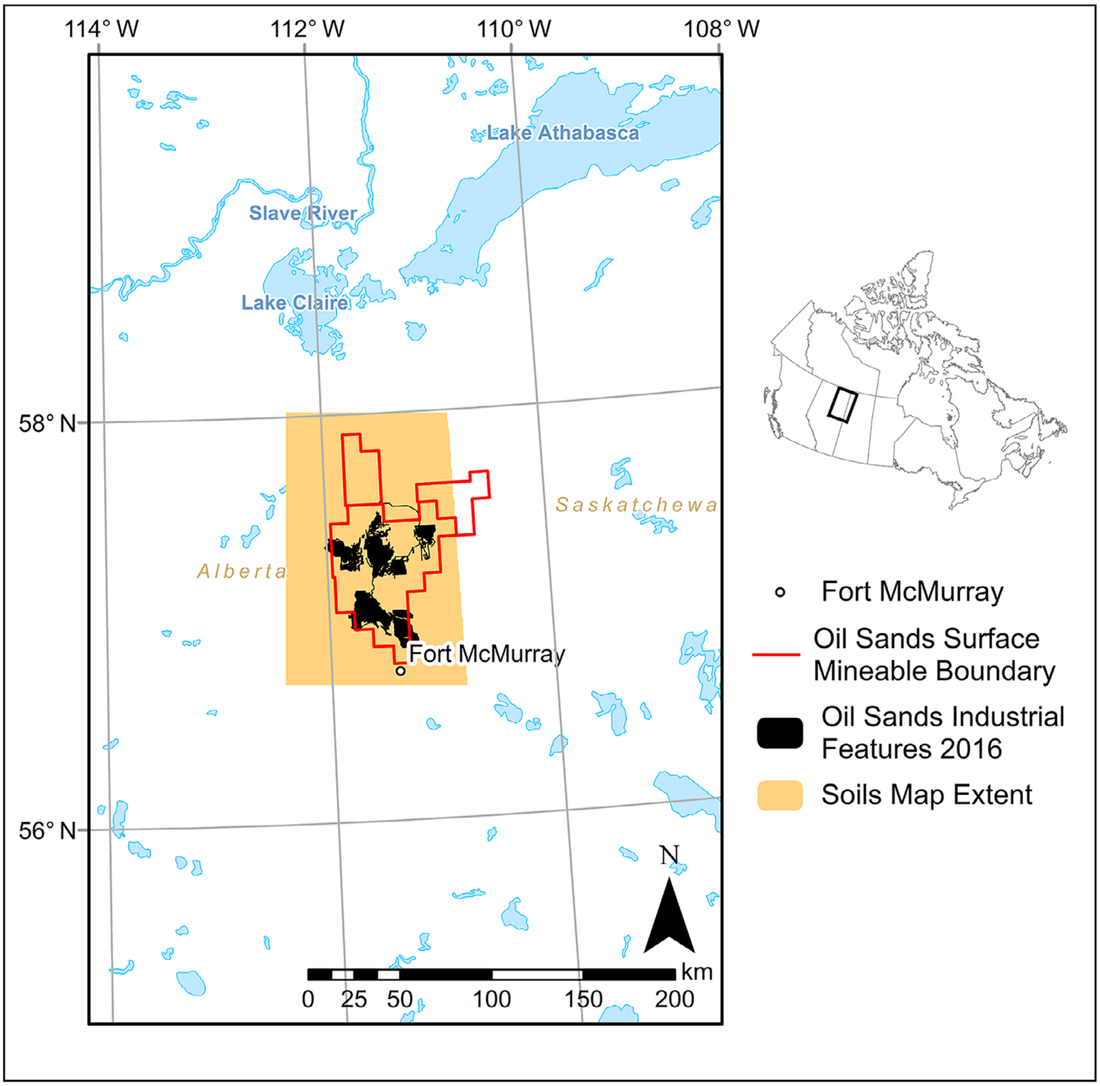

FIGURE 1 Oil sands study region located in northern Alberta, Canada. The industrial features footprint includes areas currently (2016) disturbed by surface mining, consisting of the cleared, mined, and restored (reclaimed) areas. The surface mineable boundary shows where future surface mining may occur. Disturbances by in situ mining or any other human disturbance (roads, settlements, agriculture, etc.) were not represented in the map or in simulations.

scenario did not have a large effect, we only show results for the third scenario (all mineable lands mined and restored) in the main manuscript; results from the other scenarios are shown in Appendix S1: Figure S12. Simulations were initialized in the year 2000 and run with a 10-year time step to 2200 to capture long-term effects of projected climate change on growth and mortality, along with the feedbacks between disturbances and postfire succession (Nenzén et al., 2020).

Soils data

We used the Alberta Oil Sands Environmental Research Program (AOSERP) soils inventory data of Turchenek and Lindsay (1982) as digitized by Soundarapandian et al. (2018) as inputs for PnET-Succession for each landtype (termed "ecoregions" in LANDIS-II). The landtype polygons were rasterized to 500 m resolution. Landtypes consisting of pure sand or rocky outcrops were considered unsuitable for vegetation growth and excluded from simulations, as were lakes and rivers. We also excluded landtypes classified as peatlands in the soil inventory, and thus our simulations were restricted to upland soils (~66% of the study area; Appendix S1: Table S1 and Figure S3). Landtypes classed as human settlement, disturbed lands and reserves, or unsurveyed land, were set to the third most common soil group in the region, namely, clay-loam.

TABLE 1 The experimental setup simulated in this study.

Factor	No. levels	Levels
Mining scenarios	3	Current (mining ends after current disturbance), lease (currently exploited leases are completely mined), mineable (mining extends over all mineable oil sands)
Climate scenarios	3	No climate change, SSP2-4.5, SSP3-7.0
Wildfire scenarios	2	No wildfire, wildfire
Planting scenarios	3	Planting local populations, planting southern populations (+1°, +3°) in restored areas

Abbreviation: SSP, Shared Socioeconomic Pathways.

Climate data

Historical and future monthly mean precipitation (in millimeters), solar radiation (in megajoules per square meter per day), and monthly maximum and minimum temperatures (in degrees Celsius), were obtained from ClimateNA (Wang et al., 2016; Appendix S1: Figures S1-S2). For the spin-up period before the simulations start in 2000, LANDIS-II requires climate values before 1901. For those years, we substituted randomly selected years from 1901 to 1940. Future climate data were obtained from CNRM-ESM2-1 projections (Séférian et al., 2019). For scenarios involving increased anthropogenic climate forcing, climate values between 2101 and 2200 (ClimateNA data were available up to 2100), we substituted randomly selected years from 2070 to 2100 (Nenzén et al., 2020). In the "no climate change" scenario, yearly climate data were sampled at random from 1961 to 1990 for the entire simulation period. As there is little evidence for CO_2 fertilization in our drought-prone region (Girardin et al., 2016; Peng et al., 2011; Wang et al., 2023), atmospheric CO_2 concentrations for all scenarios and years were held constant at 400 ppm, which represents concentrations of CO_2 around 2015. Supplementary simulation results show that increasing CO_2 did not compensate for effects of increasing temperature (Appendix S1: Figure S13). As weather patterns are synoptic in scale and not likely to strongly vary within such a flat landscape, all climate data were obtained for a single point in the center of the study region (57.15° N, 111.81° W).

For the future climate projections, we used Shared Socioeconomic Pathways 2 (SSP2-4.5, Middle of the Road) and 3 (SSP3-7.0, Rocky Road) (Table 1). SSP2 represents a narrative of moderate future climate change whereby some countries progress in achieving sustainable development goals and greenhouse gas reduction goals while others do not (Riahi et al., 2017). Under SSP2, CO_2 emissions are stable until 2050 and almost reach net-zero by 2100, radiative forcing reaches 4.5 W/m^2, and global mean temperature increases 2.5°C by 2100 (O'Neill et al., 2016). SSP3 represents a narrative with more severe climate change, where countries focus on achieving energy and food security goals within their own regions and progress toward sustainable development goals is slow (Riahi et al., 2017). Under SSP3, CO_2 emissions continue to increase at the current rate, radiative forcing reaches 7.0 W/m^2, and global mean temperature increases 4°C by 2100 (O'Neill et al., 2016).

Initial communities

LANDIS-II simulations were initialized using Alberta Vegetation Inventory (AVI) data provided by Alberta-Pacific Forest Industries. The AVI uses air-photo interpretation and field plot data to map the five most common tree species present and identifies stand-origin year for overstory and understory tree species. Stand-origin year for overstory and understory species in each stand was used to set 10-year age cohorts. AVI estimates of stand age were rounded to the closest 10-year interval. Because the AVI vegetation age estimates mostly pre-dated the start year of our simulations, we aged all cohorts as the difference between the first year of simulations (2000) and the stand-origin year reported in the AVI. For example, for a stand originating in 1940, stand age was set to 60 years in 2000, for both under- and overstory cohorts.

Because the AVI does not extend throughout the soils map area, we limited our study area to a smaller region where complete vegetation information existed. Also, because oil sands mining had already disturbed part of the study region when AVI data were first collected (Appendix S1: Figure S4), we assigned these disturbed areas a possible past vegetation based on the landtype (i.e., the 34 different "dominant soil units" in the soils map data). In other words, where mining had occurred and no AVI vegetation data existed, we spatially imputed the most common species to the disturbed area. To determine what species were likely present on each landtype, we first selected all species–cohort combinations in the inventoried stands that intersected each landtype. We then selected the three most common cohorts and species present in each landtype. This method generated proportions of cohorts and species in the initial communities comparable with the AVI data, generated a species cover proportion in each landtype representative of the AVI data, and used these data to fill in the areas disturbed by mining (Appendix S1: Figure S9).

Species succession modeling

We used the LANDIS-II PnET-Succession extension version 4.0.1 (de Bruijn et al., 2014) to simulate species growth and regeneration. The PnET-Succession extension is based on the tree physiology model PnET-II (Aber et al., 1992), which simulates the local competition between tree species cohorts for water and light as a function of photosynthetic processes. It uses first principles of tree physiology and physical shading to calculate species establishment probabilities in each time step as a function of soil moisture content, radiation, temperature, and cohort age (see de Bruijn et al., 2014 for more information).

Species parameters that describe growth in response to varying climatic conditions and competition intensity (Appendix S1: Table S4) were mostly set according to previously published parameters (Aber et al., 1992; de Bruijn et al., 2014, Appendix S1: Table S5). However, our study region has a significantly colder climate than the regions of these previous studies, so we modified published parameters such that biomass and species composition were similar to independent validation data (obtained from forest inventory plots, Appendix S1: Figures S10-S11) following the steps in PnET-Succession manual appendix (Gustafson & Miranda, 2022). Dispersal and post-fire tree regeneration strategies were implemented in LANDIS-II and varied by species according to published sources (Boulanger et al., 2017) (Appendix S1: Table S6). Because *P. banksiana* and *P. mariana* have serotinous cones, we parameterized regeneration of these species immediately following wildfire (option "serotiny" under Post-Fire Regen in the LANDIS-II species input). We parameterized *B. papyrifera* and *Populus* spp. regeneration following wildfire by stump resprouting (option "resprout"). All species were parameterized to disperse as seeds after a disturbance (Appendix S1: Table S6).

Parameterizing local and southern populations

To represent local and southern populations for climate-informed restoration, we parameterized two populations with different temperature optima and maxima for growth. Local populations were parameterized to be adapted to local climates, and southern populations were parameterized to be adapted to more southerly regional climates, based on provenance trials, using two temperature parameters (Table 1). For local populations adapted to historic climate, we set the optimal temperature for species growth (PsnTOpt parameter in PnET-Succession, expressed at mean daytime temperature) to the observed mean summer daytime temperature during 1961–1990 at the center of the study region (19.17°C). The maximum monthly temperature, beyond which photosynthesis is not possible (PsnTMax parameter in PnET-Succession), was set to the maximum average monthly summer temperature observed during 1961–1990 (23.60°C; Figure 2, Table 2). We acknowledge that making local populations completely adapted to local conditions might be a simplification, because some recent transplant experiments have shown increased growth in local populations that were moved to warmer and wetter areas (Gray et al., 2016).

To set temperature tolerances for optimal growth of southern populations, we identified populations that tolerate warmer climates but exhibit increased growth when moved to a colder region (Gray et al., 2016). We considered it important to select southern populations that are also adapted to a cold climate, in case climate stays the same as today or cold snaps occur more often (Francis & Vavrus, 2015). We used the outcomes of a study assessing risks associated with the movement of tree genotypes among forest tree breeding regions in Alberta to identify populations of native tree species that might be suitable for planting in the oil sands region as the climate changes. White spruce (*P. glauca*) populations with provenance from around Edmonton (seed zone area E2) translocated to the oil sands region (breeding region E1) were the only populations that grew better than local populations (tab. 2 in Gray & Hamann, 2015). This area was also recommended by the Seedlot Selection tool as its current climate matches the future climate of the local area (https://seedlotselectiontool.org/sst; St. Clair et al., 2022). In the southern E2 region (specifically at the coordinates 53.97° N, −111.58° W, approx. 3° latitude and 300 km south of our study region), the mean summer daytime temperature during 1961–1990 was 19.25°C (0.08° warmer than our study region), and the maximum temperature was 25.13°C (1.53° warmer than the study region) (Wang et al., 2016). To represent assisted migration/climate-informed restoration scenarios, we shifted the climate tolerance curve 1°C for southern populations (i.e., we added 1°C to the PsnTOpt and PsnTMax parameter values, Figure 2, Table 2; hereafter named as Pop+1), while all other species parameters remained identical. As provenance performance was only available for *P. glauca*, we assumed that *P. banksiana* and *P. tremuloides* had the same temperature tolerance optima and maxima (Gray et al., 2011 for similar trends with *P. tremuloides*, but see Schreiber et al., 2013). We selected these three species because they are the most common in the landscape and

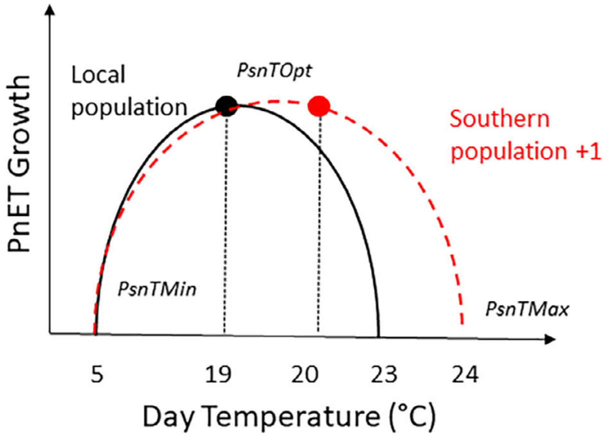

FIGURE 2 Schema of relationship between temperature and growth in PnET-Succession (photosynthesis and evapotranspiration) extension of LANDIS-II, for local (black) and southern/climate-informed (red) populations. PsnTMin (PsnTmax) = minimum (maximum) monthly temperature, beyond which photosynthesis is not possible; PsnTOpt = optimal temperature for species growth.

TABLE 2 Temperature parameters of the local and southern populations. PsnTMin (PsnTmax) = minimum (maximum) monthly temperature, beyond which photosynthesis is not possible; PsnTOpt = optimal temperature for species growth.

Populations	PsnTMin (°C)	PsnTOpt (°C)	PsnTMax (°C)
Local populations	5	19.17[a]	23.60[b]
Southern populations +1	5	20.17	24.60
Southern populations +3	5	22.17	26.60

Note: Local population parameters were set to match the local climate so that they are suited to the study area climate, and the southern populations approximately suited to a climate 300 km south.

[a] Local mean summer daytime temperature 1961–1990.

[b] Local maximum temperature maximum 1961–1990.

are the predominant species currently used in boreal forest restoration projects in the oil sands region.

Because an increase of 1°C in the temperature tolerance of local populations may not be sufficient to allow them to survive projected future climate changes, we also evaluated some even more southerly populations. We ran simulations based on theoretical populations for which tolerances were increased by 3°C (hereafter Pop+3) for *P. banksiana* and *P. tremuloides*, but not for *P. glauca*, as populations of this species are found only in warmer climates that are also significantly wetter (e.g., eastern Canada) or in locally sheltered conditions (e.g., shaded river valley slopes in southern Alberta, Estevo et al., 2022).

Disturbances

Mining scenarios

Future mining activity is likely to change depending on socioeconomic factors such as future oil prices, technological advances in renewable energy, and the success of efforts to reduce societal dependence on fossil fuels. We represented uncertainty in the spatial extent of future mining activity across our study area by using three mining scenarios (Appendix S1: Figure S5). The first scenario ("current") represents a situation where mining becomes unprofitable within a decade of simulation initiation, and all mining stops at its current extent (6% of the study region, black areas in Figure 1). The second scenario ("lease") represents a situation where the currently exploited leases would be completely mined and reclaimed. The third scenario ("mineable") assumes that mining continues for as long as it takes to extract all mineable bitumen (27% of the study region, red outline in Figure 1). Vegetation outside the minable area was assumed to remain undisturbed by land-use conversion but was subject to fire and harvesting disturbances. As mining scenarios had a minor effect on biomass, we only present results from the mineable scenario in the main manuscript and other scenarios in Appendix S1: Figure S12.

We simulated mining activity that progressed at a rate similar to past mining with a cellular automata model. To generate spatially realistic projections of the future mining scenario, we obtained historical rates of newly disturbed areas in the oil sands region (Government of Alberta, 2019, 10–287 km^2/year, Appendix S1: Table S2; see detailed methods in Appendix S1). We devised a spatial cellular automata routine in which new mines were opened at a random location within each lease, and the disturbance size was determined from past disturbance rates. We assumed that mines remained open for 40 years after the soil was cleared—a period during which trees were not allowed to grow. After 40 years, mined sites were restored.

Restoration

To represent land-use changes stemming from oil sands mining and subsequent restoration, we used the Land Use Plus (LU+) LANDIS-II extension (Thompson et al., 2016). This extension is able to simulate land-use changes but not changes in soil type. Therefore, the soil type before and after mining remains constant in our simulations, which is not a realistic representation of oil sands mining practices, in which the soils are removed to a 100 m depth and then recreated (Johnson & Miyanishi, 2008). Moreover, according to closure plans, the proportion of uplands will increase after reclamation while wetland areas would decrease, with excess water stored in deep end-pit lakes (Rooney et al., 2015).

At each 10-year time step, a land-use map indicated where trees would be cut to clear land for mining, where the land would remain in a disturbed state due to mining, and where trees would be planted to restore mined sites. After mining, the land-use extension simulated vegetation restoration by planting trees according to a predefined prescription; these trees were then left to grow until the end of the simulation (2200). The replanted species combinations and proportions were based on the actual species combinations planted in restoration projects during 2000–2016 (Government of Alberta, 2019) (Appendix S1: Table S3). The most common planting prescriptions were mixed species stands of *Populus tremuloides* and *Picea glauca*, and single-species stands of *P. glauca*. The 15 most common prescriptions, weighted by their occurrence frequencies in the data, were planted in the simulated restoration in all scenarios. For restoration with southern populations, we planted only the southern populations, not a mixture of local and southern populations. After restoration, trees were allowed to grow naturally.

Fire

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 wildfire regime parameters were calibrated using the Southern Prairie Homogenous Fire Regime zone model (Boulanger et al., 2014) and projected according to different RCP scenarios (Gauthier et al., 2015). Fire regimes derived from the Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (CGCM3) were applied to all simulations as variations in parameters among different Earth System Models were small (Boulanger et al., 2018). As fire projections driven by SSP scenarios were not available for this area, we used projections from RCP2.6 for simulations conducted under SSP2-4.5 and projections from RCP4.5 for simulations conducted under SSP3-7.0. The LANDIS-II Base Fire extension does not simulate feedbacks between future modeled vegetation and future burn rates. Therefore, our simulations assumed fuel loads remained constant even though frequent fires are expected to reduce fuel accumulation and ultimately lengthen fire return intervals.

Harvesting and replanting

Forest harvesting was simulated using the LANDIS-II Biomass Harvest extension. The harvest rate used for simulations was calculated from observed forest disturbance rates. Guindon et al. (2014) detected harvest disturbances from annual forest disturbance maps based on MODIS imagery. They calculated that 0.18% of study area forest was harvested per year during the period 2001–2011. Therefore, throughout the simulations, the annual harvest rate in the Boreal Plains was held constant at 0.18% of forest area, with the maximum size of a harvested patch set to 31.25 ha. Stands (grid cells) to be harvested during 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). Harvesting only took place in the natural areas, not in the mined and subsequently restored areas. When a stand was selected for harvest, all cohorts over 10 years old within the stand were harvested with no species preference. After harvesting, local populations of all species were planted (no southern populations were planted after harvesting). *Populus* spp. and *B. papyrifera* were also able to reproduce vegetatively, and all species were able to disperse in by seed from neighboring areas.

RESULTS

How does forest biomass change under different scenarios of climate, disturbance and planting?

Climate warming decreased average aboveground forest biomass in the study area. With no simulated climate warming, average landscape-wide aboveground biomass density in 2200 was 90 t/ha (Figures 3a and 4a). The two future climate change scenarios generated progressive reductions in average biomass density by 2200; biomass was reduced to 40 t/ha under SSP3-7.0 in the absence of wildfire disturbance (Figures 3e and 4m). The negative effects of climate change were exacerbated when wildfire disturbances were included in the simulations. For the SSP2-4.5 and SSP3-7.0 climate change scenarios, forest biomass decreased to ~20 and ~12 t/ha, respectively, in simulations including wildfire disturbance (Figure 3d,f). *Abies balsamea* (a late-successional species with low abundance in the study region) achieved only very low biomass in the simulations (with or without wildfire disturbances).

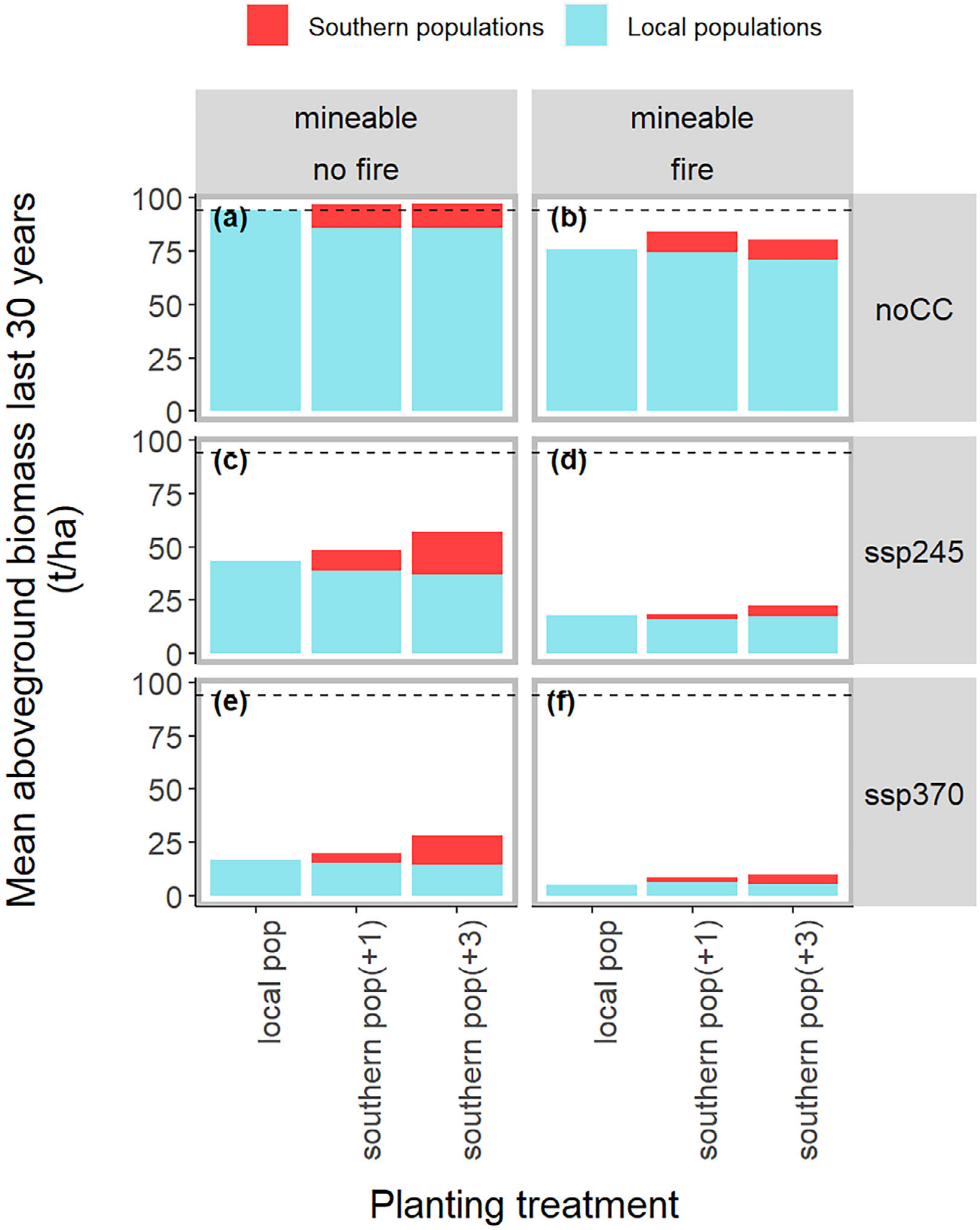

FIGURE 3 LANDIS-II projections of mean landscape-wide aboveground biomass during 2180–2200 (last 30 years of simulations) by Shared Socioeconomic Pathway (SSP) scenario, fire scenario, and planting scenarios (only for mining scenario where all surface mineable oil sands were exploited). The biomass average was calculated across the entire study area, including areas without forest biomass. The horizontal dashed line indicates the mean biomass for the fire, no-climate-change, local-planting scenario, that is, maintaining "equivalent capacity." See Table 1 for scenario definitions and Table 2 for temperature parameters of the local and southern populations.

Planting southern-adapted populations can partly mitigate climate change-related losses of biomass

Climate-informed restoration increased average biomass but only partly mitigated the impact of climate change (Figure 3). Under increased anthropogenic climate forcing but without wildfire, simulated biomass in 2200 was higher when southern populations were planted but did not reach the biomass densities simulated without climate change. Under SSP2-4.5, the biomass in simulations with Pop+1 (southern populations shifted 1°) was higher than scenarios with only local populations (Figure 3c), but biomass still did not reach levels simulated in the no-climate-change scenarios (dotted lines on Figure 3). Populations drawn from climates 3°C warmer (Pop+3)

FIGURE 4 Biomass levels over time through 2200 by Shared Socioeconomic Pathway (SSP) scenario, fire scenario, and restoration/planting scenario for the entire study region (mineable scenario only). See Table 1 for scenario definitions and Table 2 for temperature parameters of the local and southern populations.

than the oil sands region compensated more for climate change-induced growth decline of local populations and seemed more suited to future climate change than Pop+1 populations. The average simulated biomass for Pop+1 was ~50 t/ha, compared with ~60 t/ha for Pop+3 under SSP2-4.5 (Figure 3c), so planting southern populations would appear to improve restoration outcomes in a changing climate. However, the benefit of climate-informed restoration was smaller when the effects of wildfire were included in the simulations such that under SSP2-4.5 with wildfire, average simulated biomass was only ~20 t/ha even with Pop+3 populations (Figure 3d).

The increase in average biomass achieved due to planting southern populations was smaller under stronger climate change and fire scenarios. Under SSP3-7.0, the advantage of restoration with southern populations was less evident than it was under SPP2-4.5 scenarios; for +1 populations, biomass was ~20 and ~25 t/ha for +3 populations (Figure 3e). When wildfire was included in the simulations, planting southern populations on harvested sites did not mitigate landscape-level biomass losses at all. For SSP3-7.0 with wildfires included, simulated biomass density was ~10 t/ha (Figure 3f).

While warming future climate and fire substantially reduced conifer biomass across the study area, disturbance-tolerant deciduous trees (especially *P. tremuloides*) became more prevalent. Under a moderate climate change scenario (SSP2-4.5) without fire, local populations of *Picea glauca* and *P. mariana* persisted in the landscape, albeit at low biomass densities (Figure 4g). But when fire was included, the biomass of *Picea* spp., which are less tolerant to fire disturbance than *P. tremuloides*, decreased (Figure 4j). The biomass of deciduous species increased slightly if southern-adapted populations were planted (Figure 4h,i) but less when fire was included in simulations (Figure 4k,l). Assisted migration of populations particularly increased landscape biomass during the last 50 years of simulations (Figure 4h,i,o), but when climate-induced changes in fire were included, this final increase in biomass was much smaller (Figure 4k,l) and did not occur under more severe climate change (Figure 4q,r). When climate-induced changes in fire occurrence were included under SSP3-7.0, biomass values for all species and population origins were low (Figure 4p).

How warm-adapted do populations need to be to maintain current species biomass within the restored areas?

We found that planting southern tree populations within the restored areas always increased total aboveground biomass compared with planting local populations (Figure 5). Populations parameterized to represent plantings of seed sources from more southerly parts of the province (+1) had higher simulated biomass than planted local populations, under all climate-change scenarios. Under SSP3-7.0, Pop+3 populations had a simulated biomass of 17 t/ha in 2200 (Figure 5e), which was almost double that achieved by local populations planted in restored areas at the same time (10 t/ha) and higher to biomass simulated without climate change (Figure 5a, dotted lines). Under all climate-change scenarios, fire strongly reduced landscape biomass compared with no-fire scenarios, to the point where there was little advantage to restoration by planting southern populations (Figure 5d,f).

DISCUSSION

Our simulations of climate-informed restoration suggest that assisted migration of southern tree populations better adapted to future climate could generate positive outcomes, though the overall improvements could be small. Restoration with trees better adapted to future warmer climates should be able to partly compensate for the expected climate-induced declines in biomass of local tree populations. However, growth of southern populations decreased under more extreme climate-change scenarios because their temperature tolerance was set to be 1°C, higher than that of the local populations. The projected increase in maximum temperature was approximately 5°C under SSP2-4.5 by 2100 in the study area (Appendix S1: Figure S1). Given climate warming under SSP3-7.0, and increased wildfire disturbance, the simulated landscape biomass density in 2200 was ~5 t/ha. This was lower than the current average biomass of the aspen parkland ecozone (~59 t/ha) farther south (National Forest Inventory; Gillis et al., 2005). These results suggest it is quite unlikely that the current recommendation to reclaim to “equivalent capacity” of boreal forest can be achieved for standard site conditions, especially if the area burned increases as projected under most plausible climate scenarios (Boulanger et al., 2014).

The selection of species and populations to plant in regions expected to undergo significant climate change involves complex decision-making (Schwartz et al., 2012). In our simulations, although optimal temperatures were assumed equivalent across tree species, aspen (*P. tremuloides*) dominated the landscape when we planted southern populations, partly because it was the most common species planted after reclamation and partly because it is disturbance-tolerant and fast-growing. In the simulations, local aspen populations were outcompeted as they were less suited to warmer climates than southern populations, while conifer biomass decreased because of increasing disturbance rates. Given that aspen survived best under climate change and multiple disturbances (see also Anoszko et al., 2022), this species is likely to be an important focus of future restoration treatments. Moreover, planting aspen may be advantageous because deciduous trees are less flammable and can help reduce wildfire spread (Astrup et al., 2018). However, such a forest change would also accelerate a biome shift where dominant vegetation changes from boreal mixedwood forest to aspen-dominated forest or aspen parkland. This would have negative impacts on biodiversity (Cadieux et al., 2020) and cultural values, as well as softwood timber supply, and would alter ecosystem functioning (e.g., carbon sequestration and storage; Frelich et al., 2020). With knowledge about the potential forest changes we projected for this region, land managers and local communities can prepare to mitigate the negative impacts of this change (Hagerman & Kozak, 2021; Schwartz et al., 2012).

Simulated ecosystem restoration with southern tree populations was unable to fully compensate for climate change effects on the boreal forest, which suggests land managers could consider other ways to assist tree survival in a changing climate. For example, restoration could encourage the creation of cooler microsites (Caughlin et al., 2019; Suggitt et al., 2018). Through careful site manipulations, the impacts of future temperature increases could be offset by increasing water availability, something that is particularly important in the forested areas immediately north of the prairies where droughts can be destructive (e.g., Hogg et al., 2008). Trees can generally tolerate warmer climates if they have sufficient access to water (Reich et al., 2018), so restoration could include peatland conservation and intensive site preparation to retain as much water as possible in the landscape (Rooney et al., 2015; Stralberg et al., 2020). Silviculture prescriptions that affect water availability, for example altering tree planting density and spatial arrangement (North et al., 2019), could also be assessed with field and landscape simulation studies. In some regions, climate change will require land managers to shift their

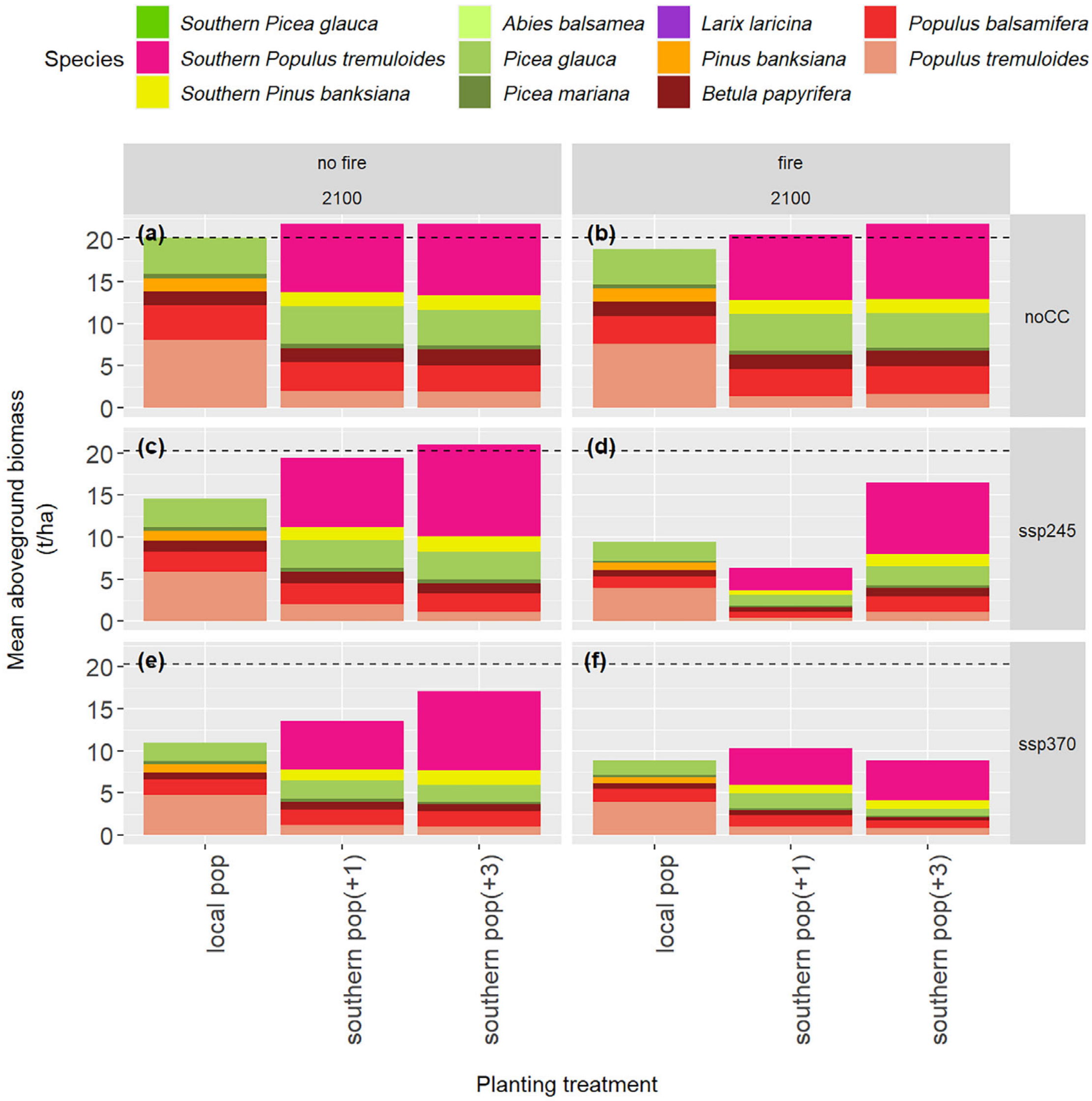

FIGURE 5 LANDIS-II projections of mean aboveground biomass in only restored areas in each simulation, in 2100 (mean values from 2090 to 2110, 30 years of simulations centered around 2100) by Shared Socioeconomic Pathway (SSP) scenario, fire scenario, and restoration/planting scenario (mineable scenario only). The biomass is calculated in the mined and subsequently restored areas only. The horizontal dashed line indicates the biomass levels in the reference scenario: no climate change, no fire with local populations planted ("equivalent capacity," a). See Table 1 for scenario definitions and Table 2 for temperature parameters of the local and southern populations.

restoration goals and facilitate transitions to different ecosystems. This could include the use of novel species (Millar et al., 2007; Zedler et al., 2012). Here we did not consider introducing tree species from outside Alberta because this is not encouraged by reclamation guidelines (Province of Alberta, 2016). In this region, a possible alternative restoration goal (Zedler et al., 2012) could be to facilitate transitions to the native grasslands that characterize the drier prairies south of the aspen parkland (Hogg, 1997). Prairies are one of the most threatened North American ecosystems (Frelich & Reich, 2010) but can store large amounts of carbon in the soil (Scurlock & Hall, 1998) and would likely develop as forests decline. Strategies for implementing climate-informed restoration might first consider restoration to "equivalent capacity" (i.e., boreal forest), but also rule out unachievable targets—through experimentation model simulations—and identify alternate targets (i.e., aspen parkland or prairie; Frelich & Reich, 2010).

Although the current Alberta genetic resource management standards were not designed for climate-informed restoration, use of seeds and seedlings from alternate provenances (seed transfer) is possible through registration and review by the province (Government of Alberta, 2016). There has been, and continues to be, active research in this area by forest companies and the provincial governments of both BC and Alberta (Aitken & Bemmels, 2016; Rweyongeza et al., 2015). Given the advanced state of the research, it is expected that more mature standards and frameworks around seed transfer will emerge in the coming years.

While landscape-level simulations of forest dynamics like ours can provide land managers with important insight about ecosystem restoration in a changing climate, our results come with caveats. Our model simulations represent *restoration* on "degraded, damaged, or destroyed land," but they do not include *reclamation* of "severely degraded land" (Gann et al., 2019), as is likely to be required after oil sands mining. Our LANDIS-II simulations did not represent reclamation of "severely degraded land" because the soil types were assumed to be constant. Changes in soil quality during mining and reclamation are an important area of active research and are presently very difficult to predict. A major reclamation uncertainty is how the physical and chemical properties of mine tailings affect the soil water and nutrient regimes in the restored landscape. Short-term greenhouse experiments show that substrates containing a high proportion of tailings decrease plant seedling growth (Hemstock, 2008; Luna Wolter & Naeth, 2014; Noah et al., 2014). Field trials on tailings are rare, as past reclamation has mostly occurred on natural "overburden" soils that were moved when excavating mines (Dhar et al., 2018). When sufficient data are available, future modeling work should include the effect of soil quality on vegetation growth (Brickner, 2013; Welegedara et al., 2020). Nonetheless, our work demonstrates that even "successful" forest reclamation is likely to be severely challenged by the warmer and drier climates that are anticipated in coming decades and centuries.

Our study is one of the first attempts to model assisted migration of climate-adapted populations using a FLM (but see Gustafson et al., 2023), and we took a simple approach to generate populations adapted to warmer climates. For example, we only altered the temperature tolerance parameters of the southern populations even though the physiological phenotypes of southern populations are likely to be different in many respects, including their capacity to tolerate drought. If land managers restored disturbed sites with populations that were both more drought-tolerant and warm-tolerant, they might offset biomass losses. However, it is difficult to represent drought tolerance in model simulations because drought-induced mortality is the outcome of many interacting physiological processes driven by species-specific traits (Gustafson et al., 2016). For example, while southern tree populations are tolerant to drought, they may be less frost-tolerant and vulnerable to "cold snaps" at the beginning and end of the growing season (Girardin et al., 2022; Schreiber et al., 2013). If restoration focused on aspen, identifying southern populations that are also drought-tolerant would increase the chances of restoration success (Gray et al., 2011; Landhäusser et al., 2019). Our simple approach to generating genotypes adapted to warmer climates was also hampered by lack of data on species/population temperature tolerances. We assumed all southern species had temperature tolerances similar to those of *P. glauca*. In reality, tolerances are likely to vary; *P. tremuloides*, in particular, may have higher temperature tolerances than *P. glauca* given its geographic distribution extends much further south.

A significant limitation of our landscape simulations was that the wildfire model used in LANDIS-II does not account for feedbacks between climate change and fire, which may result in future fire being less severe than we projected. Therefore, our wildfire scenario is an extreme condition that may represent unrealistically high fire rates. We compensated for this by including a no-fire scenario to "bookend" these extremes. Given high uncertainty about future climate-fuel feedbacks (Marchal et al., 2020), we felt that the bookend approach was a pragmatic alternative to developing more realistic fire models. The LANDIS-II Dynamic Fire Extension does have fuel feedbacks, but its parameterization was beyond the scope of this work.

In conclusion, we show that planting southern-adapted populations could partially maintain biomass after restoration but may not mitigate biomass losses under the cumulative effects of severe climate change and with an increased wildfire activity. As other studies have also indicated (Cadieux et al., 2020; Mbogga et al., 2010; Rehfeldt et al., 2012; Reich et al., 2022; Schneider et al., 2009), our results suggest that boreal mixedwood forests could transition relatively quickly to aspen-dominated stands. Furthermore, we found that these stands could have lower mean biomass density than those found in the current aspen parkland region south of the present-day closed boreal forest. Given this anticipated change, our simulations indicated that planting southern populations could increase the chances of maintaining a forested landscape though not under more severe climate change. The highly disturbed oil sands region could serve as a test region for developing new restoration treatments that could benefit forestry within the wider boreal region (Doley & Audet, 2013; Perring et al., 2013). Scenario modeling with FLMs could be used as a tool to identify restoration practices that fulfill multiple objectives, to understand possible consequences of introducing new populations and southern nonlocal species, and to communicate possible future outcomes to stakeholders (Hagerman & Kozak, 2021).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Alberta Vegetation Inventory data for the study area are owned by Alberta-Pacific Forest Industries Inc (Al-Pac; alpac.ca/contact-us/). Other data are publicly available (Soils inventory, Soundrapandian et al., 2018; ClimateNA, Wang et al., 2016; Oil Sands Information Portal, Government of Alberta, 2019). More information on the AVI dataset can be found here: https://open.alberta.ca/opendata/gda-3dbcfa02-e97a-4059-9414-1ed8e0700e80.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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