Simulated decline of a northern forest due to anthropogenic controls on the regeneration-mortality balance

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Abstract

The population structure of forests is shaped by balancing the opposing forces of
regeneration and mortality, each of which influence C turnover rates and are sensitive to climate.
Regeneration underlies the migrational potential of forests to climatic change and remains
underserved in modeling studies. Our objective was to test the hypothesis that warming may
reduce tree regeneration rates while amplifying fire regimes, producing forest loss. Absent sites
within dispersal limits, trees may fail to track the velocity of warming, producing a decline in
forested area. Long-term implications include changes to biogeochemical and energetic balances,
species composition, and evolutionary trajectories. We performed hybrid model simulations to
assess the resilience of forests to past-century conditions over the next fifty years in western
Canada. We conducted simulations at a species-level taxonomic resolution to capture
genotypic/phenotypic variability in response to climate. A recent shift toward small, frequent,
human-caused fires and warming-reduced regeneration diminished species migration potential.
The simulated rate of forest migration lagged behind temperature equilibria by 319 m yr⁻¹.
Understanding species migrational potential is particularly critical for northern forests, which
have warmed at a rate twice the global mean. Our findings highlight the effect of diminished
regeneration due to climatic change, a process neglected in current global-scale terrestrial
biosphere models used in climate studies. We suggest that future terrestrial biosphere model
studies incorporate these demographic rates in their findings on global change, as they carry
substantial climatic and evolutionary implications.
Introduction

Seasonal fire and climate cycles played a central role in the evolution of boreal forests. Here, large stand-replacing fires have been the dominant disturbance type for millennia (Rowe and Scotter 1973; Davis and Shaw 2001; Rogers et al. 2015), while temperatures historically reached cold extremes. In North America, boreal tree species evolved a diversity of adaptations to fire, including vegetative resprouting, cone serotiny, aerial seed banks, fire-enhanced regeneration, and increased flammability (Schwikl and Ackerly 2001; Keeley et al. 2014; Pounden et al. 2014; Rogers et al. 2015). These adaptations are believed to impart trees with a competitive advantage in the successional phases of disturbance and regeneration.

Trees in the Canadian boreal exhibit a high degree of intraspecific genetic variation and local adaptation (Davis and Shaw 2001). Trees respond to periodic climatic cycles in situ via phenotype plasticity (i.e., gene expression) and to long-term climatic change through emigration (Aitken et al. 2008; Matzke and Mosher 2014). Extreme events beyond physiological tolerances produce damage or mortality. While the distribution of tree species correlates well with historical climate at coarse spatiotemporal scales, disturbance responses dominate fine-scale patterns (Prentice 1986). Trees often lag behind climatic optima (Bertrand et al. 2011), requiring a semi-sequential process of mortality, reproduction, dispersal, and regeneration to transition forest composition toward optimality.

When the land velocity of temperature or moisture changes outpace the availability of sites for recruitment given disturbance patterns and dispersal rates (Clark et al. 1998), climatic change may occur too rapidly for tree migration to track warming. Given a failure to migrate, in situ regeneration conditions can become increasingly suboptimal (Nitschke and Innes 2008). When multiple species fail to track warming, absent new migrants, forest decline can occur,
which may explain recently observed reduced forest cover for the greater Rocky Mountain
region (Hogg et al. 2008; van Mantgem et al. 2009; Allen et al. 2010; Michaelian et al. 2011;
Cohen et al. 2016). Over longer timescales, gradual forest decline may give way to
compositional or landcover change. Reduced mortality rates (e.g., due to increased fire
suppression) may inhibit compositional changes, obfuscating latent migration processes
underway. This may result in more pronounced compositional changes when disturbance rates
recover to pre-suppression levels.

Due to the accelerated pace of high-latitude warming, boreal climatic conditions are
shifting northward at a rate of 430 m yr\(^{-1}\) (Loarie et al. 2009; Hamann et al. 2015). The rate of
recent warming surpasses observed Quaternary rates of species range shifts inferred from the
pollen record (Davis and Shaw 2001), while landscape fragmentation may pose a further
constraint on climatic optimality (Lazarus and McGill 2014). While direct measurements of
species migrations and other forest dynamics remain limited by the large spatiotemporal scales
of the processes involved, simulation models provide a useful tool for discerning likely historical
and future patterns. The combination of simulation models and adaptive management (Holling
1978) may eventually facilitate ecological optimization of management goals, such as
maximizing carbon storage, structural heterogeneity, or tree species diversity.

Here, forest compositional and structural changes given past-century climate and fire
trends are simulated for 50 years in the Alberta study area, beginning at year 2000 conditions.
This was done to infer the resilience of contemporary forests given the persistence of past-
century climate and fire patterns. We focus on recent observations rather than future climate and
fire projections to minimize the uncertainty regarding the likelihood of the simulated conditions
by utilizing well-described historical periods. Our hybrid forest landscape model was initialized at year 2000 conditions using modeled tree species distributions (Gray and Hamann 2012) classified into Canadian landcover classes, given the high quality of data available for this period. Four historical joint climate-fire-anthropogenic periods were used to simulate past-century forest successional trajectories. Differences in stand conditions were assessed after 50 years of simulation, with the initial ten years used for model spin-up. By simulating these four historical scenarios, we assess the resilience of extant forests to the persistence of past-century climate, fire, and anthropogenic trends.

Material and methods

We combined the Tree and Climate Assessment Establishment Model, TACA-EM (Nitschke and Innes 2008), within the second LANDscape DIsturbance and Succession model, LANDIS-II (Scheller et al. 2007), to simulate forest dynamics across a 25.2 Mha landscape in the southern Canadian Rocky Mountain region at one-hectare resolution. While the western Alberta study area is comprised of 25.2 M one-ha cells, 71% or 18 M cells are active (containing natural vegetation), after masking out developed land, waterbodies, and bare rock (Figure 1). The study area represents an elevational and latitudinal gradient between boreal, montane Cordilleran forests, and prairie. Here, differences in elevation-related climatic and edaphic patterns are believed to control vegetation species assemblages though disturbances and soil moisture effects (White and Mathewes 1986; Hogg 1994; Moss 2012). Using the Natural Regions and Subregions of Alberta (Natural Regions Committee 2006), the majority of the study area is located in the Boreal region (46.2% of the study area), followed by the Foothills (25.5%) and Rocky Mountain (19.5%) regions. The Parkland and Grassland regions together comprise less than 10% of the
study area, making over 90% of the study area boreal and montane, characterized by a strong east-west elevational gradient (Erickson et al. 2015).

Figure 1. Study area, historical wildfire perimeters, biogeoclimatic subregions, and landscape initialization process: (top-left) regional context; (top-middle) NASA SRTM topography (meters); (top-right) historical wildfire perimeters overlaid on biogeoclimatic subregions; (bottom-left) inactive (static) sites and active (dynamic) sites with and without trees; (bottom-
rules-based forest composition classification; (bottom-right) forest composition classes with inactive sites masked from the landscape initialization; all raster data used in the model was resampled to 100-meter resolution and co-registered.

The TACA-EM and LANDIS-II models and their parameterization are detailed in the supplementary materials. Both models previously underwent validation and sensitivity analysis in North America (Mladenoff et al. 1993; Scheller and Mladenoff 2004; Scheller et al. 2007; Nitschke and Innes 2008; Nitschke et al. 2008, 2012; Simons-Legaard et al. 2015). Within LANDIS-II, two types of wildfire models were applied: (1) a simple statistical fire-spread model; (2) a semi-mechanistic cost-path fire-spread model incorporating fire weather inputs and landcover change to dynamically update site fuel conditions. The semi-mechanistic fire model was developed from forest fire data in Canada (Wagner 1977; Van Wagner 1987, 1989; Forestry Canada Fire Danger Group 1992). For each fire model, a stochastic optimization algorithm based on stochastic gradient descent (Widrow and Hoff 1960) was applied for parameter tuning, overcoming a long-standing practical limitation to large-scale simulations (He and Mladenoff 1999). The overall simulation framework is shown in the supplementary materials (Figure S1).

TACA-EM was run separately for each of the climate scenarios and biogeoclimatic regions similar to previous research (Erickson et al. 2015). The resultant tree species establishment probabilities were fed into LANDIS-II together with the other parameters for each scenario. Simulations were run for 50 years at annual resolution, with the first 10 years used for model spin-up. Model spin-up was used to produce empirical disturbance-driven age class patterns given the importance of fire in shaping these patterns (Boychuk and Perera 1997). The LANDIS-II model was initially run at 500 m resolution to accelerate convergence of parameter
optimization using stochastic gradient descent (Widrow and Hoff 1960), or SGD, a variant of the steepest descent method (shown in yellow in Figure S1). In SGD, parameter values are updated in the direction and magnitude, or generally, gradient $\nabla$ of reduced model error, iteratively updated with stochasticity based on previous simulations. The SGD algorithm relies on principles common to iterative gradient-based optimization methods (Supplementary materials).

In this work, we utilized the inherently stochastic nature of the LANDIS-II model to provide stochastic updates, while the gradient direction $\vec{p}_i$ and step width $l_i$ were calculated by hand after each simulation iteration. The SGD optimization method is widely used alongside the backpropagation algorithm (Dreyfus 1962; Linnainmaa 1970) in deep learning for training artificial neural networks (LeCun et al. 2015). Final model optimization runs were conducted at 100 m resolution to balance computational cost and the grain size needed to capture the effects of fine-scale disturbance patterns, approaching the resolution limits of the LANDIS-II model.

**Historical fire regimes**

Regional fire regime parameters were derived from the Canadian National Fire Database (NFDB) spatial wildfire data. The NFDB database was produced from an analysis of airborne and satellite imagery together with field plot data. Fire rotation period (FRP), or fire cycle, is one of the most commonly applied metrics to indicate the severity of fire regimes, with lower values indicating greater severity. FRP is typically calculated alongside the mean fire return interval (MFRI), or average time between fires for a given area or individual site – an indicator of fire frequency. FRP is the mean time required for the sum of fire sizes within an area to equal that area in size, calculated over a given time interval. Hence, FRP is the area-normalized MFRI. Applied to individual sites, FRP is simply equal to MFRI. By normalizing for area, FRP provides
more information about fire regimes at scales greater than the individual site without requiring additional data collection. MFRI values calculated for areas of different sizes are not directly comparable, unless normalized for area, which produces FRP values. Accordingly, we focus on FRP in our historical fire regime analysis. While other changes in the distribution of fires provide added information, FRP provides a single robust indicator of fire regimes. Calculations for FRP and MFRI are given below.

\[
FRP = \frac{Time \ Interval}{\text{Sum of Fire Sizes or Sites Burned in Area / Area Size}}
\]

\[
MFRI = \frac{Time \ Interval}{\text{Number of Fires in Site or Area}}
\]

**Model scenarios**

Fourteen 50-year simulations were run at an annual resolution, corresponding to four historical periods, three model configurations, and two extremes scenarios, to determine forest resilience under the persistence of past-century climate and fire trends with year 2000 initial conditions. A 50-year simulation duration was selected for its relevance to management timescales and to balance initial conditions and model behavior (e.g., equilibrium at 500-year timescales), as error propagates over time in simulations, increasing uncertainty. Historical climate and fire conditions were classified into the following three 30-year periods: Pre-Suppression Era (1923-1952), Early Suppression Era (1953-1982), and Global Change Era (1983-2012), corresponding to changes in fire suppression, climate, and human activity. A Most Recent Decade (2003-2012) scenario was included to encapsulate current regimes, based on an observed inflection point in fire frequency and size.
With the exception of the Extremes scenarios, each of the four scenarios was run under three different model configurations: (1) Succession only \((ao)\); (2) Succession with Base Fire \((ao-bf)\); (3) Succession with Dynamic Fire \((ao-dffs)\). This was done to control for the effects of climate and fire on forest structural and compositional change. For the two Extremes scenarios, Pre-Suppression Era fire regimes – the most severe burn rate – were applied to Most Recent Decade climatic conditions – the warmest conditions – to determine the relative contributions of climate and fire on forest compositional and structural change in the most extreme cases. The simulation scenarios (configuration and period combinations) are abbreviated as shown in the supplementary information (Table S1).

For each scenario, spatiotemporal metrics indicative of directional change at the landscape scale were tracked, including latitudinal and elevational variation in species regeneration and relative abundance, as well as changes to forest structure (inferred from site age classes) and area. A focus on climate and fire is intended to represent changes to the two primary controls on boreal forest dynamics.

**Results**

*Three-fold decline in fire rotation period despite warming*

Fire rotation period (FRP) increased by 298% between the 30-year Pre-Suppression (1923-1952) and Global Change (1983-2012) periods, indicating an approximate three-fold reduction in fire regime severity during a period of known warming. FRP increased by 166% between the Pre-Suppression and Early Suppression (1953-1982) periods, before increasing by another 50% between the Early Suppression and Global Change periods. FRP was effectively unchanged between the Global Change and Most Recent Decade (2003-2012) periods, deviating
by -0.1% compared to the 30-year mean. However, Most Recent Decade fires were nearly twice
as frequent at half the mean fire size (MFRI ∆ = -45%; annual frequency ∆ = +82%; MFS ∆ = -
43.3%).

Adjusted for area, across all periods, the Boreal region had the shortest fire rotation
period (FRP), followed by the Foothills and Rocky Mountain regions. The lower-elevation
Parkland region had the longest FRP, followed by the Grassland region. The Boreal shows the
greatest area burned and, by a lower margin, greatest proportion of the study area. FRP increased
across the three periods, indicative of diminished burning. Between the Pre-suppression and
Global Change Eras, FRP lengthened the most in the Boreal and Foothills regions while
decreasing the most in the Parkland and Rocky Mountain regions. An analysis at the finer scale
shows an acute increase in the FRP for the Peace River Parkland and Dry Mixedwood
subregions, while the Upper Foothills subregion declined. All higher elevation subregions
showed intensifying burning indicative of warming (Supplementary material, Figure S2).

Our stochastic gradient descent-based optimization algorithm markedly improved fire
model calibration ($R^2 = 0.96; \Delta R^2 = +0.14$), yielding simulation results closely matching
observations from the Canadian National Fire Database. Based on a visual analysis of simulation
results for maximum cohort age classes resulting from fire region parameterizations, the boreal
region exhibited the greatest fire-related structural (i.e., mean and standard deviation of site age
class) change across scenarios. Frequent large fires during the Pre-Suppression Era produced a
homogeneous structural patchwork of forests, while frequent small fires in the two most recent
scenarios produced a diffuse forest landscape age pattern and decline in area burned,
corresponding to observed empirical changes.
While base fire better fit aggregate 30-year statistics for observed fire regimes, time-series comparisons between simulated and observed regimes showed that dynamic fire better captured the mean and variability for both annual fire frequency and area burned. Wavelet spectra for annual 1-D time-series showed higher and lower wavelet dissimilarity (Rouyer et al., 2008) for dynamic fire area burned and fire frequency, respectively, compared to base fire (Supplementary material, Table S5). Wavelet spectra decompose the variance of 1-D time-series over a 2-D time-frequency plane and can be used to analyze the covariance of non-stationary signals with noise (Rouyer et al., 2008).

In the dynamic fire model results, iteratively updated landscape fuel conditions, based on 2012-2013 fire weather, reduced fire frequency and area burned in each scenario compared to base fire. For the most severe fires, in the Pre-Suppression Era, base fire model results showed large fires during the initial simulation year and relatively flat activity until simulation year ~ 45. The temporal distribution of fire frequency was more stable and realistic in the dynamic fire scenarios due to the fuel-limited semi-mechanistic model design, while base fire exhibited brute-force application of statistical model parameters (Figure 2).
Figure 2. Simulated annual fire regimes by period (top) and scenario (bottom): (top-left) annual simulated area burned by period; (top-right) annual simulated fire frequency by period; (bottom-left) annual simulated area burned by scenario; (bottom-right) annual simulated fire frequency by scenario; refer to Table S1 for scenario codes.

Reduced regeneration potential under warming

TACA-EM model results indicate that conditions for tree regeneration were increasingly suboptimal, declining across the 1923-2012 study period (Figure 3). Optimal regeneration conditions occurred most frequently in the Rocky Mountain, Parkland, and Foothills regions. The Boreal region remained the most stable, while Montane regions maintained higher overall regeneration potential. An increased frequency and depth of modeled drought, due to changes to
soil water balance, most limited regeneration conditions in the Grassland region, where fluvial and aeolian soils are abundant. These results were critical to changes observed in LANDIS-II simulations, due to interactions between mortality and regeneration.

Figure 3. Probability of tree species regeneration for thirteen subregions within five biogeoclimatic regions, 1923 to 2012: blue = 1923-1952; green = 1953-1982; orange = 1983-2012; red = 2003-2012

LANDIS-II model results showed a decline in forested area for the most severe fire scenarios and an increase in forested area for mild disturbance scenarios. Forest decline indicates a failure to regenerate post-disturbance and/or an annual rate of burning outpacing the rate of regeneration. Resprouting and serotinous species regenerate post-fire each simulation year, the latter requiring that seed availability and establishment conditions be met. An initial rapid
increase in forested area for most scenarios is attributable to recruitment into sites classified as open (i.e., untreed active cells) in the initial landscape. The maximum total forested area was 38% greater than the minimum area, resulting from differences in fire regime severity and regeneration suitability. For the Pre-Suppression Era and Extremes scenarios, base fire produced the largest disturbances and thus the greatest change in forested area. While greater fire disturbances removed more species-age cohorts, warming climatic conditions reduced post-fire regeneration, further diminishing the forested area (Figure 4).

While warming reduced the likelihood of regeneration over the simulation period, variation in fire regimes produced more rapid changes, with the interaction of the two processes explaining changes in forested area. Results showed minor declines in the abundance of *Picea*, *Larix*, and *Betula* genera, and minor increases in *Pinus*, across the simulation period. Species richness declined for all scenarios, declining the most under more severe disturbances (Figure 4).
The mean number of age classes present at one-hectare sites followed similar patterns but recovered over time for succession-only scenarios (Figure 5b). The central tendency (i.e., median) of the spatial distribution of forests mildly increased in latitude and elevation under the most severe disturbances. While the mean forest latitude increased for all scenarios modeled, mean forest elevation was generally flat or declined (Figures 5c and 5d).
Figure 5. Individual and ensemble (i.e., simulation mean) model results by scenario and species: (a) species richness by scenario; (b) age class count by scenario; (c) mean forest latitude by scenario in WGS84 decimal degrees; (d) mean forest elevation by scenario; (e) incremental mean forest latitude change by species in WGS84 decimal degrees; (f) incremental mean forest elevation change by species; refer to Table S1 for scenario codes.
A downhill mean forest distribution shift was shown for the Global Change and Most Recent Decade periods (Figure 5d). This is explained by an increase in high-elevation burning and reduction in regeneration suitability here, due to modeled water holding capacity limitations of rocky soils for the Montane region. A previous analysis of the region showed that available water storage capacity was the most important model predictor of regeneration here (Erickson et al. 2015). In the Pre-Suppression and Extreme scenarios, the spatial distribution of forests shifted uphill on average due to high fire mortality rates at low elevations that surpassed the rate of regeneration. The difference in mean forest elevation between the two scenarios indicates that warming climatic conditions slowed rather than accelerated an uphill mean distribution shift (Figure 5d).

Latitudinal and elevational changes were produced by the spatiotemporal distribution of fire mortality more than climate over the 50-year simulation period. This is evidenced by large incremental changes in species elevation and latitude in the initial simulation years (Figures 5e and 5f), when disturbances were greatest in magnitude. While this spin-up period is often omitted from simulation studies, it is shown here to make model behavior transparent. The weaker effect of warming is also evident in a comparison of Extremes scenarios with Pre-suppression Era fire scenarios, which differed only in climate. Species responses varied in mean latitudinal and elevational distribution shifts resulting from fire. Rather than attributable to life history strategy or functional type, differences in species response appear primarily attributable to the initial location of species. This is evidenced by the observation that the greatest mean species distribution shifts were shown by species endemic to the boreal region, in the northeastern portion of the study area, where the rate of burning was greatest. These changes were particularly evident for the large fires of the base fire scenarios (Figures 5e and 5f).
The velocity of warming outpaced tree migration four-fold

In the full ensemble results (the mean of all scenarios), the mean latitude of forests shifted mildly poleward while the mean elevation was static (mean latitude = +111 m yr\(^{-1}\); mean elevation = -0.02 m yr\(^{-1}\)). All periods showed agreement in a mean latitudinal increase in forests, which may partially be explained by recruitment during the model spin-up period. Forest composition remained stable under the two most recent scenarios (Global Change and Most Recent Decade), but less stable during previous scenarios (Pre-Suppression and Early Suppression) due to greater disturbances. Extreme scenarios combining the most area burned with the warmest climatic conditions showed the most rapid changes in forest demographics (Figure 5b) and composition (Supplementary material, Figure S3).

Ensemble model results showed agreement in forested area decline (Supplementary material, Figure S3). An analysis of simulated annual mean incremental changes in area burned, fire frequency, and, forest latitude and elevation (Supplementary material, Figure S4) using Spearman’s rank correlation coefficient (\(\rho\)) to probe for monotonicity showed that latitudinal and elevational changes were strongly correlated (\(\rho = 0.71\)), positively correlated with area burned (\(\rho = 0.49; \rho = 0.34\)), and negatively correlated with fire frequency (\(\rho = -0.34; \rho = -0.50\)). Total forested area was negatively correlated with fire frequency more than area burned (\(\rho = -0.54; \rho = -0.11\)) (Supplementary material, Figure S3c).

The periodicity (i.e., autocorrelation) of elevational changes was strongly correlated with changes to fire frequency (\(\rho = 0.90\)). The periodicity of changes in total forested area was negatively correlated with changes to area burned, fire frequency, and, latitude and elevation (\(\rho = -0.32; \rho = -0.31; \rho = -0.06; \rho = -0.24\)). The periodicity of changes in mean forest latitude and elevation were positively correlated with changes in area burned and fire frequency, with forest...
elevation and fire frequency showing the highest correlation (Supplementary material, Figure S3d).

During the model spin-up decade, where age class distributions were initially homogeneous, distributional shifts occurred at their most rapid rate. This result was produced by a combination of high severity boreal fires given an even availability of fuels and frequent initial recruitment events. Given an even initial age class distribution, the sexual maturity of trees had equally even coverage, facilitating seed dispersal. These spin-up patterns are critical to note for their role in influencing the interpretation of simulation results. Following the 10-year model spin-up period, all scenarios with fire showed a mild decline in forested area (Figure 4).

**Conclusions**

A combination of reduced regeneration potential and more severe fires produced a significant reduction to the total forested area in simulations. This suggests that declining modeled regeneration potential together with reduced burning in the Global Change Era may potentially diminish the ability of tree species to track the velocity of warming. The simulated mean northward shift in forest distribution was 319 m yr\(^{-1}\) slower than the velocity of climate change (Loarie et al. 2009; Hamann et al. 2015), with agreement shown across simulations. Even under the greatest burning and thus migration rates, northward forest migration lagged 291 m yr\(^{-1}\) behind warming. As exhibited by the Extremes scenarios, migration rates were highest in periods where disturbance rates were the most severe, despite cooler temperatures. This is indicative of reduced competitive limitations to migration.

Changes in the distribution of tree species and forests were primarily attributable to fire. Forests tended to shift toward higher latitudes and lower elevations across simulation scenarios,
while higher fire mortality reduced species and age-class diversity. The mean of the spatial
distribution of forests increased in elevation and latitude when disturbance severity was highest,
facilitating more rapid migrations with the removal of stands. Although shifts in mean spatial
distribution were mild, they are notable given the simulation period of fifty years, short relative
to the duration of successional processes. Despite being confined within a fixed study area at a
regional scale, changes in the mean spatial distribution of forests may be indicative of broader
migrational patterns. Changes in the mean spatial distribution of forests are potentially more
robust than range minima or maxima as indicators of migrational change, given the larger sample
sizes involved and reduced sensitivity to episodic events produced by leptokurtic (i.e., heavy-
tailed) seed dispersal kernels.

In addition to fire suppression (Cumming 2005), recent changes to forest demographics
may partially explain the empirically observed increase in fire rotation period in Alberta (Zhang
et al. 2015), due to the bottom-up nature of fire mortality (i.e., younger cohorts are more
susceptible to mortality for a given fire intensity, limiting fire crowning through ladder fuels in
the absence of young trees). Fire suppression, forest aging, reduced recruitment rates, and related
fire energetic constraints may together explain the modest increase in area burned under
warming (Kelly et al. 2013; Héon et al. 2014; Zhang et al. 2015). This dynamic was reproduced
in simulations with the elimination of young trees during the model spin-up period, yielding
older and less diverse stands with a reduced rate of burning. Simulation results also suggest that,
while secondary to fire, declining regeneration potential may play a role in the decline in forested
area observed for the Global Change Era in the adjacent montane Western United States (Cohen
et al. 2016).
Some studies have indicated increased forest carbon sequestration under global change conditions (Chen et al. 2006; Fang et al. 2014), while a recent tree-ring analysis indicates no effect of warming on biomass increment in the Canadian boreal (Girardin et al. 2016). These projections fail to account for expected changes to fire regimes and tree regeneration under warming. Empirical evidence shows diminished recruitment rates for the region (Zhang et al. 2015), in agreement with TACA model results, while burning is projected to increase under warming in the short-term (Flannigan et al. 2001; Groot et al. 2003), before being limited by energetic constraints (Héon et al. 2014). The presented simulation results indicate that the interaction of higher burn rates and diminishing regeneration potential may offset any potential gains to carbon storage over centennial time-scales by reducing the forested area. This dynamic may also offset increases to forest biomass attributable to stand aging (Huang et al. 2013; Uyeda et al. 2017).

Diminished resilience, or capacity of forests in their current state to respond elastically to perturbation, is evidenced by changes to regeneration, which regulates forest change at a basal physiological level. Although variability in interspecific regeneration potential was evident for the region, the dominant regeneration signal across the study period was a long-term decrease in forested area, in agreement with recent ground plot- and remote sensing-based findings on recruitment and forest cover across the greater region (Bond-Lamberty et al. 2014; Zhang et al. 2015; Cohen et al. 2016). While Zhang et al. (2015) attributed reduced growth and recruitment rates in western Canada primarily to competition and secondly to climate, their analysis focused on undisturbed sites, making growth and recruitment rates primarily a function of stand development.
Meanwhile, fire is the dominant driver of mortality in boreal forests (Rowe 1961; Rowe and Scotter 1973; Bond-Lamberty et al. 2007), providing sites for recruitment (Clark 1991; Lavoie and Sirois 1998; Johnstone et al. 2010; Bond-Lamberty et al. 2014), while competition and climate cannot be disentangled. Competitive or mutualistic interactions are a function of climate space, evident in phenotype plasticity (i.e., gene expression) and evolutionary legacies (Aitken et al. 2008). The TACA model results presented herein suggest an alternative interpretation of the results of Zhang et al. (2015), as our modeling results indicate that diminished recruitment rates in the western Canadian boreal are due to a climatically-induced decline in regeneration potential.

Combined with available empirical evidence for Canada (Leithead et al. 2012; Fisichelli et al. 2014; Zhang et al. 2015; Cohen et al. 2016), our results suggest that a mild decline in forested area observed for some parts of intermountain western North America in recent decades may be attributable to a combination of increased fire regime severity (i.e., mortality) and diminished regeneration potential. Future studies should explore the interplay of disturbance, dispersal, and regeneration rates in changes to forested area observed for northwest North America. Empirical studies should focus on biome interfaces experiencing the highest rate of forest change. Simulation studies should expand beyond current species ranges to incorporate shifts at the edge of range limits. Improved spaceborne monitoring, data assimilation, and landscape genetic analyses will be important to understanding these dynamics, granting ecological forecasting greater predictive power. By conducting experiments in silico, the resilience of forests can be tested under different future scenarios, enabling managers to adjust policies to achieve desired targets. These applications may be considered first steps toward simulation-based management optimization.
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The TACA-EM model is designed to assess climate change impacts on the regeneration niche, the niche most sensitive to climatic change (Nitschke and Innes 2008). In TACA-EM, regeneration is a function of the biophysical space of each species in relation to soils and daily weather. Each year is simulated at daily resolution to capture phenologically driven regeneration events. Phenology is an important driver of species distributions (Chuine and Beaubien 2001) and plant fitness (Chuine 2010), necessitating its inclusion. Regeneration carries particular importance in global change studies, as it regulates directional change at the lowest level (Fischelli et al. 2014).

The LANDIS-II model is a hybrid model (i.e., empirical, process-based, and stochastic) of forest dynamics (Kimmins et al. 2010) designed to operate at a stand resolution (~one hectare) and a landscape scale (~10^6 hectares) (Scheller et al. 2007). The LANDIS-II model applies life history strategies within a cellular automaton (von Neumann 1966) using a stochastic number generator and rules-based processes within and across two-dimensional probability matrices or grids. We combined TACA-EM within LANDIS-II to generate species regeneration probabilities under different conditions. Within LANDIS-II, fire is modeled as a blend of stochastic,
empirical, mechanistic, and rules-based processes. By coupling TACA-EM with LANDIS-II, we are able to explicitly model forest dynamics under global change.

**TACA-EM**

**Model Overview**

The TACA-EM model simulates tree species regeneration as a function of climatic and edaphic conditions relative to species biophysical constraints, as previously described (Nitschke and Innes 2008). TACA-EM relies upon empirically derived biophysical relationships for specific regeneration processes in a process-based approach. The model incorporates species parameters for growing degree days, temperature thresholds, chilling requirements, bud break, drought, and frost. Modeled species navigate biologically relevant thresholds in order to regenerate each year. The overall regeneration probability is the sum of these probabilities divided by the number of scenarios in each simulation, producing an average probability for a given decade. Unlike Bayesian methods, TACA-EM explicitly represents biological processes known to be critical to regeneration. As such, TACA-EM is more likely to maintain model realism under novel conditions where a priori information is unavailable.

**Model Requirements**

In addition to species biophysical parameters, TACA-EM requires daily weather, soils, and solar radiation parameters for each site modeled. The parameters are decadal-scale daily resolution temperature minima and maxima, precipitation, soil moisture regime, soil texture, rooting zone depth, coarse fragment percent, percolation rate, an optional nitrogen modifier for productivity, and latitude. Within TACA-EM, solar radiation and evapotranspiration are
calculated using existing formulations (Hargreaves and Samani 1985; Waring and Running 1998). Soil available water storage capacity and annual heat moisture index are modeled using equations incorporating vapor pressure deficit (Wang et al. 2006). Available water storage capacity is the most sensitive model variable; when it falls to zero, soils are assumed to be at the permanent wilting point, below the minimum amount of soil moisture required to prevent permanent turgor loss. TACA-EM produces a drought index as a function of the actual-to-potential evapotranspiration ratio within a soil moisture submodel. The model includes species-specific phenology events, such as bud break, winter hardening, growing season length, and the occurrence of physiological drought and frost at critical times during development.

**Model Parameterization**

We wrote custom R functions (R Core Team 2015) to download and process NOAA Global Historical Climate Network-Daily (GHCN-Daily) data (Menne et al. 2012), subsequently released within the rnoaa package (Chamberlain et al. 2016). Our scripts produce daily resolution temperature and precipitation values for each biogeoclimatic region as the mean of all station values within a region for each day. We utilized the expectation-maximization (EM) algorithm (Dempster et al. 1977) to impute missing values with the R FastImputation package, based on Amelia-II (Honaker et al. 2011).

We used the National Soil Database Soil Landscapes of Canada (SLC) v3.2 (Soil Landscapes of Canada Working Group 2010) to generate soil parameters for Natural Subregions of Alberta (Natural Regions Committee 2006) (Supplementary material, Table S1). Soil texture, rooting zone depth, coarse fragment percent, and available water soil capacity were derived from the SLC database for the dominant soil types. We used the Canadian System of Soil
Classification (Soil Classification Working Group 1998) to produce textural classes for these soil
types before deriving percolation rates for textural classes from the literature (Derr et al. 1969).

Elevational and latitudinal parameters were sourced from a provincial report (Natural Regions
Committee 2006) and verified in ArcGIS using 90-meter NASA SRTM data. Our TACA-EM
parameterization method is the first to offer climate and soils parameters Canada-wide.

Tree species biophysical attributes were derived from previous studies (Nitschke and
Innes 2008; Nitschke et al. 2012) and the literature. Species parameters include physiological
base temperature, heat sum for bud break, chilling requirements, minimum temperature, drought
tolerance, growing-degree-day minima and maxima, frost tolerance, frost season, wet soils, and
heat moisture index responses (Supplementary material, Table S2).

Tree species biophysical parameters were derived from the following literature sources:
balsam fir (Abies balsamea) (Burns and Honkala 1990; Thompson et al. 1999; Greenwood et al.
2008); subalpine fir (Abies lasiocarpa) (Edwards 1982; Leadem 1989; Burns and Honkala 1990;
Li et al. 1994; Thompson et al. 1999; Klinka et al. 2000; Nitschke and Innes 2008; Nitschke et al.
2012); white birch (Betula papyrifera) (Bevington and Hoyle 1981; Bevington 1986; Burns and
Honkala 1990; Thompson et al. 1999; Klinka et al. 2000; Nitschke and Innes 2008; Grenier and
Sirois 2009); tamarack (Larix laricina) (Pitel and Cheliak 1986; Burns and Honkala 1990;
Thompson et al. 1999; Klinka et al. 2000; Nitschke and Innes 2008; Klinka et al.
1999; Klinka et al. 2000); western larch (Larix occidentalis) (Burns and
Honkala 1990; Sorenson 1990; Li et al. 1994; Carlson 1994; Thompson et al. 1999; Klinka et al.
2000; Nitschke and Innes 2008); Engelmann spruce (Picea engelmannii) (Woodard 1983; Burns
and Honkala 1990; Thompson et al. 1999; Klinka et al. 2000; Nitschke and Innes 2008); white
spruce (Picea glauca) (Burns and Honkala 1990; Li et al. 1994; Thompson et al. 1999; Klinka et
al. 2000; Renault et al. 2000; Nitschke and Innes 2008; Nitschke et al. 2012); black spruce

**LANDIS-II**

**Model Overview**

The LANDIS-II model is based on the JABOWA-FORET genre of gap models and LANDSIM (Mladenoff and He 1999). The model incorporates dynamics important at the landscape scale. The LANDIS-II model core is the central hub of a modular system that allows users to specify submodels at a user-defined time-step. In LANDIS-II, each grid cell in the landscape matrix is either active or inactive. Inactive cells are static and active cells are dynamic. Active grid cells can be forested or non-forested. Grasslands are typically the only active non-forested cells, where trees may establish given favorable conditions. Each active forested grid cell is a stand of trees comprised of horizontally homogeneous species-age cohort classes.
To better represent variation in regional climate, soils, and fire, we divided the landscape into biogeoclimatic regions. In our simulations, we utilize three submodel configurations: Age-Only Succession, Base Fire, and the Dynamic Fuels and Fire System.

We used the Age-Only Succession submodel to model light, reproduction, ontogeny, senescence, seed dispersal, and interspecific competition. In LANDIS-II, light is modeled as a function of the maximum shade tolerance for sexually mature species present at a site. The presence of shade tolerant species, which fare poorly in open stands (Spies and Franklin 1989), are used as an indicator of poor light conditions. When fires initiate within a cell, younger, more shade tolerant species typically have higher mortality rates, increasing modeled light values.

Reproduction is limited by propagule presence and light availability given regeneration probabilities output from TACA-EM. Fire directly interacts with regeneration through mortality, resprouting, and serotiny. Cohort mortality is a function of species maximum age, with an increasing probability of mortality once species reach 80% of their maximum age. Seed dispersal is represented by a two-part negative exponential probability distribution with a leptokurtic dispersal kernel (Ward et al. 2004), based on observed migration rates (Clark et al. 1998). Interspecific competition occurs through the intersection of species life history attributes, establishment probabilities, and local disturbance patterns.

We apply two conceptually different LANDIS-II extensions for modeling wildfire: Base Fire and the Dynamic Fuels and Fire System. Base Fire is an empirically based stochastic fire-growth model that reproduces parameterized statistical distributions, with variability a result of its stochastic core. In contrast, the Dynamic Fuels and Fire System is a semi-mechanistic stochastic fire-growth model that uses topography, fuel conditions, fire weather, and empirical fire distributions to shape fire patterns. The Dynamic Fuels and Fire System is conceptually
analogous to Prometheus in Canada (Tymstra et al. 2010) and FARSITE in the US (Finney 2004), which are based on the Fire Behaviour Prediction (FBP) System (Forestry Canada Fire Danger Group 1992) and BEHAVE (Andrews and Chase 1989), respectively. In both LANDIS-II fire models, fires begin through separate ignition and initiation events (Yang et al. 2004). Mean fire return intervals (Pickett and Thompson 1978) are used to model fire frequency.

In the Base Fire model, the frequency of ignitions follows a Poisson distribution. Fire initiation is based on Bernoulli trials, with ignition probability a function of time-since-last-fire. Fire sizes are drawn from a log-normal distribution (Yang et al. 2004), producing periodic large fires. Fire shape is a product of a stochastic percolation algorithm representing wind vectors. Inactive cells may act as fire breaks, stopping fire spread before reaching its target size. Fire severity is determined by fuel and wind curves representing fuel buildup and decay; a site’s position on these curves is determined by time-since-last-fire. Fire is modeled as a bottom-up disturbance, whereby younger cohorts have a higher probability of mortality (He and Mladenoff 1999).

The Dynamic Fuels and Fire System is a process-based fire model that uses a semi-mechanistic representation of fire growth (Sturtevant et al. 2009). Similar to Base Fire, fires are hierarchically split into ignition and initiation events (Yang et al. 2004). Ignition frequency also follows a Poisson distribution, with cells in each fire region selected stochastically. Unlike Base Fire, fire initiation is modeled probabilistically based on site fuel conditions, calculated using cohort information and daily weather data within FBP and Fire Weather Index (FWI) Systems equations (Van Wagner 1987; Forestry Canada Fire Danger Group 1992). Fire sizes are drawn from a log-normal distribution, while users can alternatively specify duration-based sizes. Fire shape is modeled using fuel-specific rate-of-spread equations (Hirsch 1993) and a modified
minimal-travel-time cost-path method. The minimum-travel-time method is based on Huygens’ Principle of wave propagation, also used in Prometheus and FARSITE. Yet, LANDIS-II implements the most efficient algorithm of the three fire simulators (Finney 2002).

In the Dynamic Fuels and Fire System, the fire spread algorithm contains two core components: wind bias and fuel conditions. Wind bias has an ellipsoidal shape with the length and width based on the magnitude of a wind velocity vector (Finney 2002). Fuel-based spread is a function of fuel class, wind speed, and topography, using FBP System fuel classes. A cost surface is created using the inverse rate-of-spread to calculate a minimum-travel-time path. The cumulative minimum-travel-time and fire size selected determine the shape of each fire, producing improved disturbance pattern realism.

The probability of fire sizes being selected from the log-normal size distribution are classified into five equally spaced bins. These bins correspond to five fire weather bins, based on the logic that larger fires occur during more severe fire weather conditions. The fire weather bins are typically parameterized by classifying FWI values. The seasonal distribution of fire frequency is represented probabilistically, incorporating leaf status. Detailed model information and equations are provided in the literature (Forestry Canada Fire Danger Group 1992; Finney 2002; Sturtevant et al. 2009). Model requirements are provided in the supplementary materials.

**Model Requirements**

The LANDIS-II model core requires a list containing life history attributes for tree species. These attributes include species longevity, sexual maturity age, shade tolerance, fire tolerance, seed dispersal, vegetative reproduction, and serotiny. The model core also requires a matrix and lookup table specifying tree species-age cohort classes present in each cell. Cohort
classes are dynamically updated at each time step. A biogeoclimatic regions matrix and corresponding lookup tables are optional. A succession model table requires species regeneration probabilities.

The Base Fire model requires statistical fire distributions for fire regime regions, typically set to the biogeoclimatic region matrix. Base Fire requires parameters for the mean, minimum, and maximum event size, ignition probability ($\lambda$), and the mean fire rotation period for each of the fire regions. These parameters require adjustment to reproduce empirical fire distributions, typically achieved by manual approximation of the ignition probability and fire rotation period parameters (Syphard et al. 2007). To produce the desired fire regimes with high accuracy, we applied gradient descent for parameter optimization.

The Dynamic Fuels and Fire System (Dynamic Fire) model similarly requires fire regions, typically using the biogeoclimatic region matrix, and a corresponding lookup table. The model requires the expected mean ($\mu$), standard deviation ($\sigma$), and maximum fire size for the log-normal distribution. The model also requires seasonal foliar moisture content (FMC) low and high averages, proportion of fires during high FMC conditions, open fuels class designation, and the annual frequency of fire initiation for each region. Dynamic Fire also requires a fire seasonality table containing leaf status, proportion of fires, percent curing, and fire-day-length-proportion parameters for each season. The model additionally requires a fuel-type table based on FBP System classes, which consists of parameters for base type, surface type, initiation probability, three fuel type-specific rate-of-spread constants, buildup index (BUI$_S$ in the FBP System), maximum buildup effect ($q$ in the FBP System), and crown base height, used to modify the initial spread index. The equations requiring these parameters have previously been described (Forestry Canada Fire Danger Group 1992; Finney 2002; Sturtevant et al. 2009).
The Dynamic Fire model’s fire damage table requires parameters for the upper bound of the cohort age range and the minimum difference between fire severity and tolerance for mortality to occur. An initial weather database incorporating daily fire weather data, including fine fuel moisture code, buildup index, wind speed velocity, fire weather index, fire weather index bin, season, and ecoregion, is used to modify fuel conditions. To model the effects of topography on fire shape, users may input percent-slope and upslope-azimuth matrices, which we include using 90-meter NASA SRTM elevation data. The Dynamic Fire model requires a fuel coefficient for each species and a maximum-site-hardwood-percentage to be classified as a coniferous fuel group. The optional Dynamic Fuels submodel, which we include, requires a fuel type classification table in order to reclassify site fuel conditions following succession and/or disturbance. The table contains parameters for base fuel type, age range, and species presence/absence. A disturbance conversion table can optionally be used to allow other disturbance types to modify the site fuel classification (Sturtevant et al. 2009).

Model Parameterization

To parameterize the LANDIS-II model core, we used local species parameters derived from the literature and species compendiums (Burns and Honkala 1990; Farrar 1995). We applied Ward’s leptokurtic double-exponential seed dispersal algorithm within the succession model (Ward et al. 2004). To parameterize the initial landscape, we used a rules-based classification of species distributions for western North America (Gray and Hamann 2012). While bioclimatic envelope, or climate-equilibrium, models may not be suitable for forecasting under novel conditions, they can be used to accurately predict existing species distributions – a parameter difficult to estimate using remote sensing.
We classified modeled species frequency values into species cohorts using FBP System classes (Forestry Canada Fire Danger Group 1992). We binned forested sites into the following classes (FBP System code): Aspen (D-1); Boreal Spruce (C-2); Lodgepole or Jack Pine (C-3/C-4); Douglas-fir (C-7); Boreal Mixedwood (M-1/M-2). We set each site to even 0, 30, 60, and 90 year old age classes, relying on model spin-up to create historical forest structure patterns, given an absence of reliable forest age maps. For biogeoclimatic regions, we used a provincial classification scheme (Natural Regions Committee 2006).

We combined and reclassified Landcover for Agricultural Regions of Canada (Agriculture and Agri-Food Canada 2012) and Earth Observation for Sustainable Development of Forests (Wulder et al. 2007) data, each set to year 2000 conditions. We defined three base cell states: active-treed, active-untreed, and inactive. We classified the initial landscape to active-treed cells where species cohorts were present. We set herb, grassland, and shrubland landcover classes, to active-untreed, while setting agriculture, annual cropland, perennial crops and pasture, wetland, water, exposed land, snow/ice, rock/rubble, and built-up cells to inactive. Hence, forests and fires could expand into open natural areas given suitable conditions, but not into developed or resource-limited sites.

For Base Fire, we utilized historical fire data from the Canadian National Fire Database (Canadian Forest Service 2015) for 1923 to 2012, analyzed in a parallel study (Erickson et al., In Review). For the fire regions, we used the biogeoclimatic regions. We used the default fuel curve table to represent five fire severity classes, as it was created based on Canadian forests. We wrote R functions (R Core Team 2015) to calculate the mean, minimum, and maximum fire size, ignition probability, and fire rotation period for each fire region.
We developed a new parameter optimization technique for both fire models based on stochastic gradient descent (Widrow and Hoff 1960). First, coarse-resolution (500 m cell) simulations are run for the maximum duration (~1,000 years) to efficiently estimate the model signal for a given parameter space. Fire parameters for each region are then updated using the difference between actual and simulated values, before a new simulation begins. The process is repeated until the difference between actual and simulated fire regimes reaches a minimum. Specifically, the ignition probability is adjusted for each region until the simulated fire frequency is within 1% of the target range before the same optimization process is applied to $k$ values, equivalent to the fire rotation period. We then computed final optimizations by running simulations at full resolution for the target duration, often producing little difference. Our fire parameter optimization method conceptually fuses sparse approximation with Monte Carlo signal processing methods and gradient descent. Our method reliably produced fire frequencies within 1% of the target values and area burned $R^2$ values over 0.99, compared to unoptimized values of 20% and 0.75, respectively. If fire regimes deviate significantly from a log-normal size distribution, Base Fire will be limited in its ability to reproduce them, but we did not experience that here.

For Dynamic Fire, we wrote R scripts (R Core Team 2015) to calculate the expected mean, standard deviation, maximum fire size, and annual fire frequency for each region and period. We wrote functions derived from the FBP System to calculate seasonal foliar moisture content (FMC) values. To do so, we calculated the regional minimum FMC date based on the mean latitude, longitude and elevation, before calculating the mid-season FMC using ordinal dates for the vernal equinox, summer solstice, autumnal equinox, and winter solstice. We used
these values to calculate the proportion of fires occurring during the high FMC period. Low and
high FMC thresholds were set to 25% and 75% of the maximum, respectively.

We used biogeoclimatic regions as the fire regions matrix. For percent ground slope and
uphill azimuth, we used NASA SRTM3 version 2 data. For the fire seasons table, we set the leaf
status for spring, summer, and fall to leaf-off, leaf-on, and leaf-off, respectively. We calculated
the proportion of fires during each season by using a subset of the fire database, with dates
converted to ordinal dates and seasons. The percent curing values were calculated as a function
of FMC values, using a grassland curing index equation (Dilley et al. 2004), with the mean index
value used to represent each season. Fire day length proportion was set to the standard value of
one.

We calculated an initial fire weather database using Alberta Agriculture and Rural
Development’s historical fire weather station data. We selected fire weather stations with the
shortest Euclidean distance to the centroid of each region. We used daily resolution fire weather
data for the April 2012 through March 2013 fire weather season to represent recent climatic
influences on fuels, as historical fire weather data is unavailable here. The weather metrics used
include precipitation, mean temperature, mean humidity, wind speed at 10m above ground, and
wind direction at 10m above ground. We used the R mtsdi package (Junger and de Leon 2012) to
impute missing values for the period, using the default EM algorithm and splines method. We
then used the R fwi/fbp package (Wang et al. 2014) to calculate daily fine fuel moisture content,
build-up index, and fire weather index using standard equations (Van Wagner 1987). We
segmented fire weather index values into five bins based on quantile groups using the R Hmisc
package (Harrell and Dupont 2015).
To parameterize the fuel type table, we used FBP System fuel classes and parameters developed for Canada (Forestry Canada Fire Danger Group 1992). These parameters include base type, surface type, initiation probability, $a$, $b$, and $c$ rate-of-spread parameters, $q$ depth dryness parameter, build-up index, maximum build-up effect, and crown base height. We set the fuel types not currently present in the landscape to inactive. We used a standard fire damage table, with probability of mortality inversely related to cohort age. The table includes species-specific fire tolerances, with standard transitions at 20%, 50%, 85% and 100% age percent of longevity.

We used the optional dynamic fuels submodel, reclassifying site fuel conditions at the end of each simulation year. This enables fire behavior to more realistically respond to succession and disturbance. To parameterize the fuels model, we assigned species an even fuel reclassification weighting coefficient of 1.0. We set deciduous species maximum composition for conifer stands to the standard 10%. We based the fuel type reclassification table on the FBP System, utilizing its definitions for species composition and age classes (Forestry Canada Fire Danger Group 1992).

Tree species life history attributes for LANDIS-II (Supplementary material, Table S3) were derived from the following sources: balsam fir (Abies balsamea) (Xu et al. 2010); subalpine fir (Abies lasiocarpa) (Burns and Honkala 1990; Farrar 1995); paper birch (Betula papyrifera) (Peterson et al. 1997; Government of Alberta 2009); larch (Larix laricina) (Burns and Honkala 1990; Farrar 1995); western larch (Larix occidentalis) (Burns and Honkala 1990; Engelmann spruce (Picea engelmannii) (McCune and Allen 1985; Burns and Honkala 1990; Government of Alberta 2009); white spruce (Picea glauca) (Dobbs 1976; Groot et al. 2003; Government of Alberta 2009); black spruce (Picea mariana) (Stanek 1961; Burns and Honkala 1990;

**Gradient-based Optimization**

Generally, gradient-based strategies search for a minimum to a $D$-dimensional target (also objective or cost) function $f(\vec{x})$ approximated by a terminated Taylor series expansion around $\vec{x}_0$:

$$f(\vec{x}_0 + \vec{x}) \approx f(\vec{x}_0) + (\nabla f(\vec{x}_0))^T \vec{x} + \frac{1}{2} \vec{x}^T \nabla^2 f(\vec{x}_0) \vec{x}$$

Optimization is performed iteratively by beginning at an initial value $x_{i=0}$ and computing its target function $f(\vec{x}_i)$ value, before searching for a minimum in the following loop:

1. Check for convergence of $f(\vec{x}_i)$ per a given criterion; if fulfilled, accept $\vec{x}_i$
2. Compute the gradient direction $\vec{p}_i$ and step width or learning rate $l_i$
3. Evaluate the new point in the parameter space $\vec{x}_{i+1} = \vec{x}_i + \vec{p}_i \cdot l_i$; compute the target $f(\vec{x}_{i+1})$ and return to step 1
A first-order linear approximation can be used to compute the step direction $p_i$ of the target function:

$$f(\mathbf{x}_0 + \mathbf{p}) \approx f(\mathbf{x}_0) + \nabla f(\mathbf{x}_0)^T \mathbf{p}$$

This results in the following step direction $p_i$, known as the steepest descent method:

$$\mathbf{p} = -\nabla f(\mathbf{x}_0)$$

The gradient vector is orthogonal to the plane tangent to the isosurfaces of the function $f(\mathbf{x})$. Gradient descent adds stochasticity to the optimization process in order to improve search space coverage and convergence toward a global minimum, avoiding local minima or saddle points. The standard gradient descent algorithm updates the parameters $\mathbf{x}$ of target function $f(\mathbf{x})$:

$$\mathbf{x} = \mathbf{x} - \eta \nabla_x \mathbb{E}[f(\mathbf{x})]$$

The expectation $\mathbb{E}$ is calculated by evaluating the gradient over the entire training dataset.

Stochastic gradient descent removes the expectation in the update and instead computes the gradient of parameters using one to few training samples.

The SGD update is as follows:

$$\mathbf{x} = \mathbf{x} - \eta \nabla_x f(\mathbf{x}; x_i, y_i)$$
### Table S1. Simulation scenario codes based on model configuration and period

<table>
<thead>
<tr>
<th>LANDIS-II Configuration</th>
<th>Period</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-only succession</td>
<td>1923-1952</td>
<td>ao-1923-1952</td>
</tr>
<tr>
<td>Age-only succession</td>
<td>1953-1982</td>
<td>ao-1953-1982</td>
</tr>
<tr>
<td>Age-only succession</td>
<td>1983-2012</td>
<td>ao-1983-2012</td>
</tr>
<tr>
<td>Age-only succession</td>
<td>2003-2012</td>
<td>ao-2003-2012</td>
</tr>
<tr>
<td>Age-only succession with base fire</td>
<td>1923-1952</td>
<td>ao-bf-1923-1952</td>
</tr>
<tr>
<td>Age-only succession with base fire</td>
<td>1953-1982</td>
<td>ao-bf-1953-1982</td>
</tr>
<tr>
<td>Age-only succession with base fire</td>
<td>1983-2012</td>
<td>ao-bf-1983-2012</td>
</tr>
<tr>
<td>Age-only succession with base fire</td>
<td>2003-2012</td>
<td>ao-bf-2003-2012</td>
</tr>
<tr>
<td>Age-only succession with dynamic fire</td>
<td>1923-1952</td>
<td>ao-dffs-1923-1952</td>
</tr>
<tr>
<td>Age-only succession with dynamic fire</td>
<td>1953-1982</td>
<td>ao-dffs-1953-1982</td>
</tr>
<tr>
<td>Age-only succession with dynamic fire</td>
<td>1983-2012</td>
<td>ao-dffs-1983-2012</td>
</tr>
<tr>
<td>Age-only succession with dynamic fire</td>
<td>2003-2012</td>
<td>ao-dffs-2003-2012</td>
</tr>
<tr>
<td>Age-only succession with base fire</td>
<td>Extremes</td>
<td>ao-bf-extremes</td>
</tr>
<tr>
<td>Age-only succession with dynamic fire</td>
<td>Extremes</td>
<td>ao-dffs-extremes</td>
</tr>
</tbody>
</table>

### Table S2. Soils parameters used in TACA-EM

<table>
<thead>
<tr>
<th>Natural Subregion</th>
<th>Soil Texture</th>
<th>Rooting Zone Depth (m)</th>
<th>Coarse Fragment %</th>
<th>AWWC (mm/m)</th>
<th>Field Capacity (mm/m)</th>
<th>Percolation (mm/day)</th>
<th>Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Mixedwood</td>
<td>SiCL</td>
<td>1.0</td>
<td>5%</td>
<td>452</td>
<td>560</td>
<td>93.1</td>
<td>55°</td>
</tr>
<tr>
<td>Central Parkland</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>50°</td>
</tr>
<tr>
<td>Dry Mixedwood</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>55°</td>
</tr>
<tr>
<td>Foothills Fescue</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>50°</td>
</tr>
<tr>
<td>Foothills Parkland</td>
<td>CL</td>
<td>1.0</td>
<td>20%</td>
<td>341</td>
<td>470</td>
<td>103.2</td>
<td>50°</td>
</tr>
<tr>
<td>Lower Boreal Highlands</td>
<td>CL</td>
<td>1.0</td>
<td>20%</td>
<td>341</td>
<td>470</td>
<td>103.2</td>
<td>55°</td>
</tr>
<tr>
<td>Lower Foothills</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>55°</td>
</tr>
<tr>
<td>Mixedgrass</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>50°</td>
</tr>
<tr>
<td>Montane</td>
<td>L</td>
<td>1.0</td>
<td>20%</td>
<td>377</td>
<td>460</td>
<td>66.4</td>
<td>50°</td>
</tr>
<tr>
<td>Peace River Parkland</td>
<td>CL</td>
<td>1.0</td>
<td>5%</td>
<td>341</td>
<td>470</td>
<td>122.6</td>
<td>55°</td>
</tr>
<tr>
<td>Subalpine</td>
<td>L</td>
<td>1.0</td>
<td>20%</td>
<td>377</td>
<td>460</td>
<td>66.4</td>
<td>50°</td>
</tr>
<tr>
<td>Upper Boreal Highlands</td>
<td>CL</td>
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<td>20%</td>
<td>341</td>
<td>470</td>
<td>103.2</td>
<td>55°</td>
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<tr>
<td>Upper Foothills</td>
<td>CL</td>
<td>1.0</td>
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<td>341</td>
<td>470</td>
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### Table S3. Tree species biophysical parameters used in TACA-EM

<table>
<thead>
<tr>
<th>Species</th>
<th>Mode I Code</th>
<th>Physiological Base Temperature (°C)</th>
<th>Heat Sum for Bud Burst (GDD)</th>
<th>Chilling Requirements (Days)</th>
<th>Minimum Temperature (°C)</th>
<th>Drought Tolerance</th>
<th>GDD Minimum m</th>
<th>GDD Maximum m</th>
<th>Frost Tolerance</th>
<th>Frost Season</th>
<th>We T Moisture Index</th>
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<tbody>
<tr>
<td>Abies balsamea</td>
<td>Sp1</td>
<td>2.8</td>
<td>121</td>
<td>49</td>
<td>-62</td>
<td>0.20</td>
<td>560.0</td>
<td>2,386</td>
<td>0.9</td>
<td>305</td>
<td>0.5</td>
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<tr>
<td>Abies lasiocarpa</td>
<td>Sp3</td>
<td>2.6</td>
<td>119</td>
<td>70</td>
<td>-67</td>
<td>0.25</td>
<td>197.6</td>
<td>5,444</td>
<td>0.9</td>
<td>320</td>
<td>0.7</td>
</tr>
<tr>
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<td>Sp5</td>
<td>3.7</td>
<td>231</td>
<td>77</td>
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<td>236.8</td>
<td>4,122</td>
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<td>285</td>
<td>0.3</td>
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<td>42</td>
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<td>0.20</td>
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<tr>
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<td>Pinus contorta</td>
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<td>63</td>
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<tr>
<td>Pinus monticola</td>
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<td>0.9</td>
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<td>Populus tremuloides</td>
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### Table S4. Tree species life history attribute parameters used in LANDIS-II

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<thead>
<tr>
<th>Species</th>
<th>Longevity</th>
<th>Sexual Maturity Age</th>
<th>Shade Tolerance</th>
<th>Fire Tolerance</th>
<th>Effective Seed Dispersal Distance</th>
<th>Maximum Seed Dispersal Distance</th>
<th>Vegetative Reproduction Probability</th>
<th>Sprouting Minimum Age</th>
<th>Sprouting Maximum Age</th>
<th>Post-Fire Regeneration</th>
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<tbody>
<tr>
<td>Abies balsamea</td>
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<td>5</td>
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<td>1</td>
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<td>Abies lasiocarpa</td>
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<td>3</td>
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<td>80</td>
<td>0.05</td>
<td>20</td>
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<td>None</td>
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<td>Betula papyrifera</td>
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<td>1</td>
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<td>Larix laricina</td>
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<td>1</td>
<td>3</td>
<td>100</td>
<td>60</td>
<td>0.05</td>
<td>10</td>
<td>150</td>
<td>None</td>
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<tr>
<td>Larix occidentalis</td>
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<td>100</td>
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<td>Pinus contorta</td>
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<td>-1</td>
<td>-1</td>
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<td>Serotiny</td>
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<td>5000</td>
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<td>9</td>
<td>200</td>
<td>Resprout</td>
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<tr>
<td>Populus tremuloides</td>
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<td>2</td>
<td>1</td>
<td>4</td>
<td>uni</td>
<td>5000</td>
<td>0.95</td>
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<td>200</td>
<td>Resprout</td>
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Table S5. Fire regime statistics by period for the study area

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<th>Period</th>
<th>Burned (ha)</th>
<th>Area (ha)</th>
<th>FRP</th>
<th>MFRI</th>
<th>MFS</th>
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<tbody>
<tr>
<td>1923-1952</td>
<td>3,224,691</td>
<td>24,972,634</td>
<td>232.326</td>
<td>0.011</td>
<td>1,148.394</td>
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<td>1953-1982</td>
<td>1,211,806</td>
<td>24,972,634</td>
<td>618.234</td>
<td>0.020</td>
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<tr>
<td>1983-2012</td>
<td>809,967</td>
<td>24,972,634</td>
<td>924.950</td>
<td>0.020</td>
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<tr>
<td>2003-2012</td>
<td>270,287</td>
<td>24,972,634</td>
<td>923.931</td>
<td>0.011</td>
<td>308.899</td>
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Table S6. Simulated and observed fire time-series statistics; WD = wavelet dissimilarity

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<tr>
<th>Period</th>
<th>Simulation</th>
<th>Mean$_{area}$</th>
<th>SD$_{area}$</th>
<th>$r_{area}$</th>
<th>WD$_{area}$</th>
<th>Mean$_{freq.}$</th>
<th>SD$_{freq.}$</th>
<th>$r_{freq.}$</th>
<th>WD$_{freq.}$</th>
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</thead>
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<tr>
<td>1923-1952</td>
<td>Base Fire</td>
<td>+70,282</td>
<td>+375,027</td>
<td>-0.10</td>
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<td>+82.9</td>
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<td>46.976</td>
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<tr>
<td>1923-1952</td>
<td>Dynamic Fire</td>
<td>-18,385</td>
<td>-168,825</td>
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<td>+54.3</td>
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<td>0.05</td>
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</tr>
<tr>
<td>1953-1982</td>
<td>Base Fire</td>
<td>-27,265</td>
<td>-66,458</td>
<td>0.25</td>
<td>+357.6</td>
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<td>1953-1982</td>
<td>Dynamic Fire</td>
<td>-3,338</td>
<td>-59,027</td>
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<td>+39.9</td>
<td>-2.7</td>
<td>0.11</td>
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<td>1983-2012</td>
<td>Base Fire</td>
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<td>-51,047</td>
<td>0.21</td>
<td>+202.3</td>
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<td>-40,783</td>
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Figure S1. Overall simulation framework used in this study
Figure S2. Historical fire statistics by region and time period; change metrics are computed between the periods 1923-1952 and 1983-2012: (top-left) Fire rotation period (FRP) change by subregion; (top-middle) FRP change by region; (top-right) FRP by period; (bottom-left) fraction of area burned by region; (bottom-middle) total area burned by region; (bottom-right) FRP by region; Montane region = Rocky Mountain; red = decline; green = increase
Figure S3. Mean annual simulated forest change: (a) total forested area for all scenarios with a 95% confidence interval; (b) re-scaled forested area, latitude, elevation, area burned, and fire frequency for all scenarios; (c) Spearman’s $\rho$ for re-scaled metrics; (d) Spearman’s $\rho$ for autocorrelations of re-scaled metrics; Abun = forest area; Lat = forest latitude; Elev = forest elevation; Area = area burned; Freq = fire frequency
Figure S4. Simulated annual incremental change in species abundance by scenario; refer to Table S1 for scenario codes.