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Integrating remotely sensed imagery in a forest gap model to study North American boreal forests in a changing world

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Supplementary material for this article is available [online](#)

Abstract

Boreal forests of Alaska and Western Canada are experiencing rapid climate change characterized by higher temperatures, more extreme droughts, and changing disturbance regimes, resulting in forest mortality and composition changes. Mechanistic models are increasingly important for predicting future forest trends as the region experiences novel environmental change. Previously, many process-based models have generated starting conditions by ‘spinning up’ to equilibrium. However, setting appropriate initial conditions remains a persistent challenge in using mechanistic forest models, where stochastic events and latent parameters governing tree establishment have long-lasting impacts on simulation outcomes. Recent advances in remote sensing analysis provide information that can help address this issue. We updated an individual-based gap model, the University of Virginia Forest Model Enhanced (UVAFME), to include initial conditions derived from aerial and satellite imagery at two locations. Following these updates, material legacies (e.g. trees, seed banks, soil organic layer) allowed new forest types to persist in UVAFME simulations, landscape-level forest heterogeneity increased, and forest-wide biomass estimates increased. At both study sites, initialization from remotely sensed data had a strong impact on forest cover and volume. Climate change impacts were simulated decades earlier than when the model was ‘spun up’. In Alaska’s Tanana Valley State Forest, warmer climate scenarios drove deciduous expansion, increased drought stress, and resulted in a 28% decrease in overall biomass by 2100 between historical and high emissions climate scenarios. At a lowland site in Northern British Columbia, lodgepole pine (*Pinus contorta*) remained dominant and became more productive with exogenous climate forcing as temperature, nutrient, and flooding limitations decreased. These case studies demonstrate a new framework for forest modeling and emphasize the advantages of integrating remotely sensed data with mechanistic models, thereby laying groundwork for future research that explores near-term impacts of non-stationary ecological change.

1. Introduction

Mechanistic forest models provide ecologists and natural resource planners with the capacity to predict ecosystem responses in non-stationary systems. By incorporating biological processes, such models can adequately examine rapid disturbances such as fire (Shuman *et al* 2017, Foster *et al* 2022) and insect outbreaks (Foster *et al* 2018), and thus simulate vegetation dynamics that allow for the existence of alternative stable states. Traditionally, these mechanistic models have been used to evaluate overarching ecological dynamics (Shugart *et al* 2020), given their ability to document such substantial transitions in forest communities. In contrast, empirical (e.g. growth and yield) and machine learning models, which both

rely on previous observations to predict future growth, have been used to predict near-term, high-resolution forest change (Wang *et al* 2023a, Burrell *et al* 2024), but are only able to predict changes represented in their training data. Global models, which face tradeoffs between extent, resolution, and complexity (Scheller and Mladenoff 2007), may lack important processes like fire and species interactions altogether (Wang *et al* 2021). In forests where climate impacts are rapidly changing community dynamics, empirical and global-scale models may be limited in their ability to predict future state changes (Yates *et al* 2018). Consequently, updating regional mechanistic models to simulate high-resolution, near-term change facilitates a better understanding of the dramatic pressures faced by forest ecosystems today.

Tree establishment has long been a challenge for mechanistic forest models: it is highly stochastic, difficult to observe and quantify, and yet exerts a strong influence on forest outcomes (Shugart 1998). Many forest models still implement the simplistic assumptions of early models like JABOWA (Botkin *et al* 1972), where small trees establish based on a seedling quantity and simulated site conditions (Huber *et al* 2020). Small variation in model parameters like recruitment limit, seed production, and seedling survival may produce large biases in long-term forest dynamics (Coomes and Grubb 2003, Foster *et al* 2017, Huber *et al* 2020). For instance, Raiho *et al* (2020) found that initial conditions were the dominant source of uncertainty in a forest gap model's performance. As a result, improving initialization and establishment procedures in these models may allow for more appropriate simulation of modern forest conditions; in other words, it is difficult to apply models to today's urgent questions without a precise set of starting conditions that mirrors existing stands (Shugart *et al* 2018).

Data-model integration is a critical research frontier as remote sensing technologies and data collection rapidly expand (Shugart *et al* 2015, Fer *et al* 2021). Forest stand characteristics across large spatial scales are now commonplace and come from a variety of types of remote sensing instruments and platforms (Hansen *et al* 2013, Kennedy *et al* 2018, Neuenschwander *et al* 2020, Coops *et al* 2021). Aerial imagery and multispectral remotely sensed data have long been used to provide information about forest stand characteristics (Spurr 1948, Loetsch and Haller 1964, Trotter *et al* 1997, Hyyppä *et al* 2000) and spatial patterns (Wulder 1998). In forest models, such data have recently been used to validate allometric scaling (Fischer *et al* 2019), spatial heterogeneity and forest structure (Rödig *et al* 2017), and mortality rates (Hiltner *et al* 2022). Articles suggesting the integration of remotely sensed data to vegetation and forest models have circulated over the past several decades (Shugart *et al* 2015, LaDeau *et al* 2017), yet wide-scale efforts to achieve this fusion are infrequent (Hurtt *et al* 2004, Thomas *et al* 2008, Köhler and Huth 2010, Antonarakis *et al* 2011, Ma *et al* 2023).

Boreal forests of North America are well-suited systems for testing such data-model integration because they are both well-studied and experiencing rapid environmental change (Fisher *et al* 2018). These forests store vast amounts of carbon (Bradshaw and Warkentin 2015) yet are increasingly vulnerable to warming surface temperatures and changing disturbance regimes that may lead to alternative states (Walker *et al* 2015, Johnstone *et al* 2020, Wang *et al* 2023b). For instance, black spruce forests, which maintain large carbon stocks in deep organic soils, are exhibiting limited resilience to today's droughts and increasingly active fire regime, which itself is exacerbated by drought (Johnstone *et al* 2010b, Walker *et al* 2019, Baltzer *et al* 2021). A large-scale shift in demography from evergreen to deciduous forest as a result of fire and climate change in boreal North America has already been observed via remote sensing (Beck *et al* 2011, Wang *et al* 2020, Berner and Goetz 2022), and these patterns are important for predicting future wildfire, ecosystem services, and climate feedbacks (Bonan 2008, Gauthier *et al* 2015, Anderegg *et al* 2022). The boreal forest's vulnerability and low species diversity render it an ideal study location, where mechanistic models are urgently applicable and remotely sensed data can provide robust estimates of present forest characteristics.

In prior efforts, the University of Virginia Forest Model Enhanced (UVAFME), an individual-based forest gap model which simulates forest dynamics and processes, has been updated and validated in boreal forests of Alaska and Western Canada (Foster *et al* 2019, 2022). Raiho *et al* (2021) explored long-term competitive dynamics by optimizing species-level parameters in Denali National Park and Preserve. The model has recently been used to estimate climate change impacts (Foster *et al* 2019) and test the self-limiting feedback between fire and vegetation in the same region (Foster *et al* 2022). However, UVAFME has previously taken an approach to stand initialization that will 'spin up' forest conditions to reach either known stand age or to equilibrium conditions. Consequently, previous applications UVAFME were limited to investigating long-term dynamics (50–100+ years) including long-term species interactions (Raiho *et al* 2021), climate change responses (Lutz *et al* 2013, Foster *et al* 2017, 2019, Shuman *et al* 2017), cyclical insect outbreaks (Foster *et al* 2018), and fire (Shuman *et al* 2017, Foster *et al* 2022). Previous attempts to account for initial conditions include time-intensive local stand age reconstruction and disturbance history but fail to include information about other influential factors like seed banks and fuel characteristics (Foster *et al* 2019, 2022, Raiho *et al* 2021).

Here we describe a set of advancements aimed at initializing the UVAFME model with current stand information as collected by remotely sensed instruments. These developments were designed to appropriately represent forest heterogeneity and account for observed outcomes of stochastic events that were missed in a traditional ‘spin-up’ approach. We monitor the prevalence of initialized and simulated trees as a proxy for the persistence of initialized conditions and compare our new approach to traditional methods which use a spin-up period. Our areas of focus are two regions of the North American boreal forest zone which have been previously modeled using UVAFME and for which extensive remotely sensed data products already exist. With this framing, we seek to address the following questions:

- How may existing data be utilized as initial conditions for an individual tree-based forest gap model?
- How do predictions of forest composition and biomass differ when the model is ‘spun up’ from bare ground versus initialized from remotely sensed data and what drives these differences?
- How does climate change impact forest composition and biomass at initialized sites, and what drives these impacts?

With this set of analyses, we describe an attempt to inform an individual-based forest gap model with remotely sensed data, assess the simulation outcomes, and predict ecological responses to climate change at local scales. Our experiment describes a scalable approach for incorporating initial conditions data into a mechanistic forest model to address both applied and fundamental research questions.

2. Methods

2.1. Study area

We selected two case study regions for our experiments. Together, the two areas provided a range of boreal forest conditions that span upland white spruce stands, floodplain deciduous and mixed forests, and mesic black spruce stands in Interior Alaska, and lodgepole pine, black spruce, and deciduous forests on low slopes and in valley bottoms in Northern British Columbia. The different regions allow for two different forms of remotely sensed inventory data to be used for initialization.

Our first study area is the Tanana Valley State Forest (TVSF), which encompasses roughly 367 000 hectares across 14 individual management units that straddle the Tanana River of Interior Alaska (figure 1). The Tanana Basin has thick, relatively productive soils and shallow underlying permafrost in low, wet areas and on north-facing slopes (Tanana Valley State Forest Management Plan 2001). The TVSF is managed by the Alaska Division of Forestry, although poor access limits intensive activities like harvest and fire suppression (Paragi *et al* 2020). Dominant species here are white spruce (*Picea glauca*), black spruce (*Picea mariana*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Two dominant, distinct types of forest are maintained by feedbacks between fire, vegetation, and soils. Black spruce tends to grow in dense, highly flammable stands, accumulate moss and deep organic soils underlain by permafrost, and regenerate after stand-replacing fires which only partially burn the soil organic layer (Viereck *et al* 1983, Johnstone *et al* 2010a, 2010b). In contrast, mixed and broadleaf-deciduous forests are more productive, experience more rapid nutrient cycling, and establish from wind-blown seeds and suckers on exposed mineral soils following fire (Johnstone and Chapin 2006, Johnstone *et al* 2010a, Alexander and Mack 2016). Forests on sites with intermediate drainage (e.g. side slopes, well-drained lowlands) are stabilized by existing fire-vegetation-soil feedbacks, and are most vulnerable to fire-driven transitions (Johnstone and Chapin 2006). At these high latitudes, climate change manifests as rapidly rising temperatures and increasing moisture deficits as runoff increases and soil moisture decreases (Cook *et al* 2020).

Our second study area is a 1° tile, about 630 000 hectares, in Northern British Columbia between 59–60° N and 127–128° W (figure 1). This area is a broad valley in the Northern Rocky Mountain Trench and contains the confluence of the Kechika and Liard rivers (hereafter, Kechika–Liard Confluence; KLC); it is less mountainous than much of the Boreal Cordillera. It experiences a continental climate with a large annual temperature range, long and cold winters, and short and cool summers (Brandt *et al* 2013). Dominant species are white and black spruce, quaking aspen, balsam poplar, and lodgepole pine (*Pinus contorta*) (figure S1). Lodgepole pine, the most common species in this study area, is resilient to stand-replacing fire and often succeeded by more shade-tolerant species like spruce (*Picea spp.*) in absence of disturbance (Burns and Honkala 1990). When repeated fires eliminate seed sources from other species, lodgepole pine is self-perpetuating (Burns and Honkala 1990). Part of this study area lies within the Muskwa-Kechika Management Area. Development pressure is low and only one major highway runs through the area. Unlike many forests in Alberta and Saskatchewan, this area has no systematic seismic survey tracks or oil development (Dabros *et al* 2018).



Figure 1. Map of study area. The Tanana Valley State Forest (TVSF; green polygons in left inset) is located on near the Tanana River within the Tanana watershed (outlined) in Interior Alaska. Modeled sites in TVSF are initialized from an aerial survey and corresponding forest inventory. This contrasts with our second study region, a 1° tile in Northern British Columbia (59–60 N, 127–128 W; right inset), occupied by the confluence of the Kechika and Liard rivers, where sites are initialized from satellite-derived products. The inset maps use Esri's National Geographic base map (service layer credits: National Geographic, Esri, DeLorme, HERE, UNEP-WCWC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC).

2.2. Forest gap model

The UVAFME model is an individual-based gap model that simulates the annual establishment, growth, and death of individual trees within independent forested plots of a user-defined size and number (typically 200 plots at 500 m²). It is the direct descendant of the FAREAST model (Xiaodong and Shugart 2005) that was designed to simulate Eurasian boreal forest ecosystems (e.g. Shuman and Shugart 2009, Shuman *et al* 2015). UVAFME traditionally initializes bare-ground sites from input including topography, soil characteristics, climate, and available species range data (Foster *et al* 2019). UVAFME updates biogeochemical and hydrological cycle processes daily and calculates canopy characteristics and individual trees annually. The model simulates and stores fine-scale variables at each model site such as soil nutrient levels and the height, diameter, and species of each individual tree, allowing for a wide range of potential output metrics. UVAFME has been updated to simulate boreal processes including permafrost and concomitant nutrient dynamics, the presence and impact of moss, interactions between litter decay and fire, and species-level fire responses (Shuman *et al* 2017, Foster *et al* 2019). Recently, the inclusion of more mechanistic fire dynamics to UVAFME has allowed for the investigation of explicit relationships between fire, vegetation, and climate (Foster *et al* 2018). UVAFME has been shown to accurately produce boreal forest dynamics and characteristics in Alaska and Western Canada (Foster *et al* 2019, 2022).

While the majority of our updates related to initializing UVAFME with aerial and remotely sensed data, we needed to modify several existing components of the model for these changes to be implemented. We reduced the general output number of plots running at each site from a previous default value of 100 to 1, allowing us to better characterize the impacts of disturbance and more adequately represent forest heterogeneity, which had been previously masked when heteroskedastic outputs were averaged. Although disaggregating output at the site level runs counter to previous work with gap models, we re-aggregate output across the landscape scale for interpretation. We also created a new mechanism to annually classify forests at the site level based on TVSF forest strata (table S1), which aids in interpretation of landscape-scale dynamics. Most stand classifications are based on dominant species and volume, but we also indicate reproduction-sized stands composed largely of seedlings and small trees.

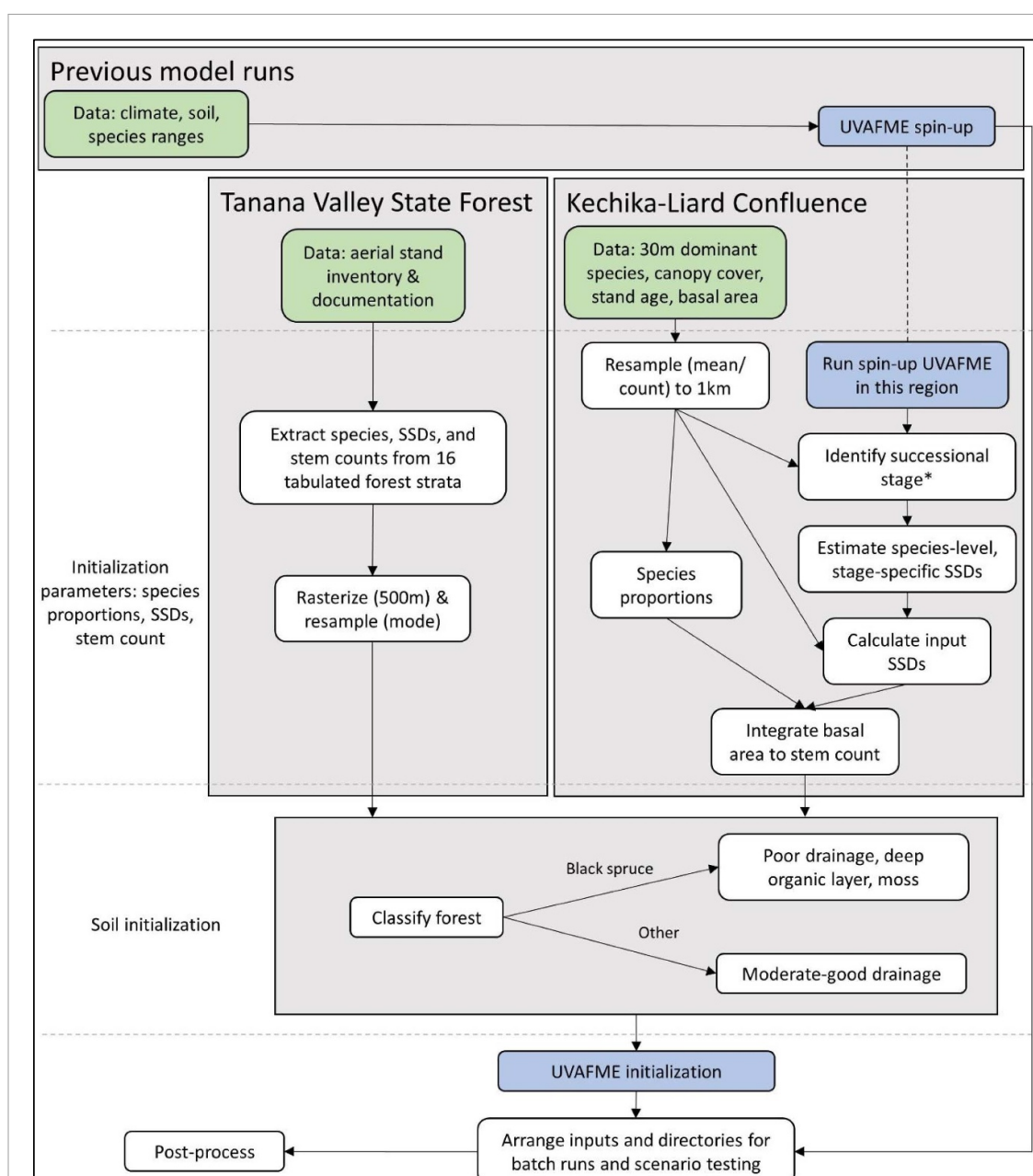


Figure 2. In previous experiments using UVAFME, the model was ‘spun up’ for forests to approach equilibrium conditions (top box). This manuscript’s analyses used additional data for the Tanana Valley State Forest (middle left box) and Kechika–Liard Confluence (middle right box) sites to initialize forest conditions at each site that was modeled. SSD is short for stem size distribution. Criteria to identify stand successional stages are listed in table S3. Soil initialization (bottom box) was used to improve how drainage was modeled in black spruce dominated sites. Green boxes indicate raw data, blue boxes indicate UVAFME runs, and white boxes indicate data processing.

We added the ability for the model to initialize mature trees based on input species proportions, species-level size distributions, and stem count. In this new routine, the model utilizes set information on the number of trees initialized upon each site and selects the species and then size of each tree based on input distributions. Because litter and moss accumulate at some sites during the spin-up period and have substantial impacts on nutrient cycling, hydrology, and tree growth, we also modified soil inputs to better match stand conditions following initialization with tree data (figure 2). For example, when dwarf black spruce sites were initialized with no moss, they were unrealistically productive until moss accumulated, nutrient turnover slowed, and soils became more insulated (figure S2(a)). Similarly, white spruce sites initialized on poorly drained sites would immediately die and be replaced by black spruce (figure S2(b)). Consequently, we made several adjustments to soil cycling within the model (table S2). These alterations mimic soil and litter differences between black spruce and hardwood forests (Légaré *et al* 2005, Laganière *et al* 2010) and produced realistic successional trajectories where, in absence of disturbance, deciduous

Interior Alaskan forests gradually transition to white spruce, overmature white spruce without excellent drainage transition to black spruce, and black spruce forests maintain unproductive stands.

Field observations indicate that positive feedback loops between trees, litter, and soil result in a thicker soil organic layer, shallower permafrost, lower soil nitrogen content, higher soil water content, and more moss in black spruce stands (Johnstone *et al* 2010a, Turetsky *et al* 2012, Jean *et al* 2020). We fine-tuned black spruce soil initialization variables by iterative testing until these sites maintained stable tree and moss biomass levels as well as appropriate organic soil and permafrost depths after initialization (table S2). Soil starting conditions for black spruce sites were selected so that sites were in equilibrium immediately after initialization. When starting values we tested were inappropriate, we observed two outcomes: (1) when soil conditions were too favorable (e.g. drier, warmer, moss-free, or higher nutrients), black spruce were unrealistically productive for a few decades, then nearly all suddenly died when soils cooled and permafrost became extremely shallow, or (2) black spruce could not grow at all, and the site was covered in moss. Because black spruce stands were not very sensitive to small differences in these soil inputs, we generalize starting values to all sites.

2.3. Updated initialization using remotely sensed data

Updated initialization of the TVSF sites was performed by making use of an existing forest-wide inventory effort undertaken by the Alaska Division of Forestry in 2013. Inventories carried out to surveil state forest resources help provide managers with updated information regarding the volume of various timber types to update future management plans and calculate sustainable harvesting rates. The 2013 inventory was built through a combination of field sampling of 487 individual timber stands making up 4870 measurement plots and color infrared aerial photographs (Hanson 2013). All photographs were orthorectified, geo-rectified, and mosaiced prior to classification (Hanson 2013). In order to create a geographic database of forest types, the Division of Forestry used DAT/EM Summit Evolution photogrammetric software to evaluate forest type boundaries and create GIS feature classes in ESRI ArcMap GIS software; the interpretation of imagery and categorization into types was based on the color, texture, tree height, and location of each feature (Hanson 2013). Altogether, the aerial survey covers over 1.1 million hectares of the state forest and consists of features no smaller than 0.2 hectares representing 16 forest strata with various species, tree size classes, and crown densities (e.g. white spruce sawtimber or poletimber, birch open or closed).

The TVSF aerial survey served as the primary data source for the initialization routine in that study area (figure 2). Using the R package terra v1.7–3 (Hijmans *et al* 2023), we rasterized the survey to a 500 m grid and assigned species proportions, species-level size distributions, and stem counts from corresponding tabulated inventory data (Hanson 2013) for average conditions of each forest strata. For dwarf black spruce stands, which were not included in the inventory, we tested an initialization input configuration which produces stable forest conditions in UVAFME (figure S3). Aerial data was from both 2013 and 1983, and we initialized 15 819 total sites in their respective years. Input data for climate, site, soil, species, and litter were derived as in Foster *et al* (2019) and Foster *et al* (2022); see supplementary material.

Our updated initialization procedure for the KLC area utilized Landsat-based forestry products to initialize 5693 sites on a 1 km grid (figure 2). These products were constructed at 30 m pixels and consisted of maps of dominant tree species in the year 2019 (Hermosilla *et al* 2022), stand age in 2019 (Maltman *et al* 2023), forest canopy cover for 2015 (Matasci *et al* 2018), and basal area for 2015 (Matasci *et al* 2018). These products were created as part of a campaign to generate country-wide maps of forest characteristics from remote sensing data in Canada (Coops *et al* 2021). Stand age was estimated by a combination of remotely sensed time series data, for stands disturbed after 1965, and forest structure allometries for older stands (Maltman *et al* 2023). Canopy cover and basal area were imputed by combining airborne LiDAR and annual Landsat composites (Matasci *et al* 2018). Dominant species were classified by Landsat reflectance and phenology data and ancillary data (Hermosilla *et al* 2022). Because we could not directly extract stem size distributions (SSDs) from these data, we ran UVAFME from spin-up for 150 years on 500 sites across the study area representing a stratified sample of forest types. We then classified UVAFME output into four stand phases—stand initiation, stem exclusion, canopy transition, and gap dynamics (Chen and Popadiouk 2002; table S3)—and estimated SSDs for each species and phase. UVAFME-generated SSDs were consistent with other field studies (figure S4; Mulverhill *et al* 2018, 2019).

We resampled and combined the Landsat-based data products on a 1 km grid. Species proportions were calculated from the dominant species data product. We classified the stand phase at each gridded site (table S3) and species-level SSDs were assigned with parameters estimated from the UVAFME spin-up output (table S9). Additionally, we updated the initialization routine in UVAFME to add trees at each site until the input basal area was reached, whereas previously this step relied on satisfying the value of the stem count. These

sites were initialized in 2015, the year corresponding to our basal area product. Where the stand age was less than four years, indicating that a site had experienced disturbance between 2015 and 2019, we forced a fire in the corresponding year. In the absence of disturbance, we combined data products from different years.

Repeated stand-level inventories in the study region were no more than 15 years apart and covered a narrow range of forest conditions, preventing robust quantitative validation of forest trajectories after initialization. However, we performed three qualitative checks on the validity of outputs from our updated model, listed below. These also follow validation efforts from Foster *et al* (2019) and Foster *et al* (2022). (1) We manually reviewed output for species-level biomass, stem counts, tree size distributions, stressors, mortality, and litter and soil characteristics at many sites to verify that initialized mature stands began in equilibrium and experienced only gradual change in the model. (2) We compared forest dynamics in the model (e.g. feedbacks between vegetation and soils, competitive interactions between species) to the literature to verify that model processes agreed with observations (Burns and Honkala 1990, Johnstone and Chapin 2003, Johnstone *et al* 2010a). (3) We met with Alaska Division of Forestry employees and shared figures of site-level outputs to verify that model runs under historic climate matched the successional trajectories and timelines typical of their experience (Personal communication 2022). As many of these employees have lived and worked in this landscape for decades, we highly value their experience and feedback.

2.4. Model simulation of future conditions

We obtained historic and future temperature and precipitation data from the ClimateNA v7.31 software (Wang *et al* 2016). For model runs under the historic climate scenario, we used climate means between 1961 and 1990. We used annual projected climate data from an 8-model ensemble to simulate Shared Socioeconomic Pathways (SSPs) 2–4.5 and 5–8.5 for future years.

To better understand how model outcomes varied between simulations containing spin-up vs. initialization procedures, we calculated the prevalence of initialized trees. This metric provides a numerical indication of the influence of stochastic events in the model since initialization. It is calculated as the proportion of basal area composed of initialized trees (as opposed to stochastically established trees) in UVAFME; as new trees are established and grow in the model, this value diminishes. While the prevalence of initialized trees correlates strongly with stand age after several decades of simulation, it is a useful indicator of stand viability—and therefore, congruent input variables—immediately after initialization.

3. Results

3.1. Model spin-up versus initialization at TVSF

Initialization of sites in UVAFME prior to simulation increased forest heterogeneity and perpetuated different forest types in the TVSF site runs (figure 3). Sites that were modeled using spin-up followed a common forest trajectory from reproductive stands to mixed and deciduous forests to black spruce under a historic climate scenario. In contrast, sites initialized using remotely sensed data incorporated materials (e.g. mature trees, soil properties, seed banks) which facilitated different forest types. Modeled mature forest landscapes do not generally revert to the reproduction stage in spin-up model runs because these sites each aggregate 100 plots which experience independent, asynchronous disturbances. Initialized UVAFME, which runs 1 plot per site ($n = 15\,819$ sites in TVSF), consistently had a small number of reproduction-age stands which transition to mixed, black spruce, and aspen forests by order of occurrence. After fifty years of simulation, the proportion of initialized sites occupied by black spruce stands had increased from 46.7% to 48.9%. In contrast, 72.4% of spun-up sites were black spruce after the same interval, and after 100 years of simulation all spin-up sites were dominated by black spruce and did not change again for the rest of the simulation (figure 3), or even when the spin-up period was extended to 500 years (figure S5(a)). While UVAFME has a strong tendency to produce sites dominated by black spruce, stand initialization mediates this for 100–150 years of simulation (figure S6).

At the site level, spun-up sites generally had lower biomass than initialized sites, largely due to variation in forest type (figure 4). In 2020, site-level biomass differences were relatively low (mean 1.23 tC ha^{-1}), owing to the low proportion of highly productive white spruce on the initialized landscape. By 2060, initialized white spruce stands occupied more than triple their original area, producing large (mean -21.8 tC ha^{-1} under historic climate scenario) differences in biomass between model versions. An increase in initialized black spruce forests and spun-up deciduous and mixed stands (figure 4(b)) accounted for tapering biomass differences by 2100 (figure 4(a)). While the absolute biomass difference shrinks in some scenarios, forest dynamics are misrepresented by the spin-up runs.

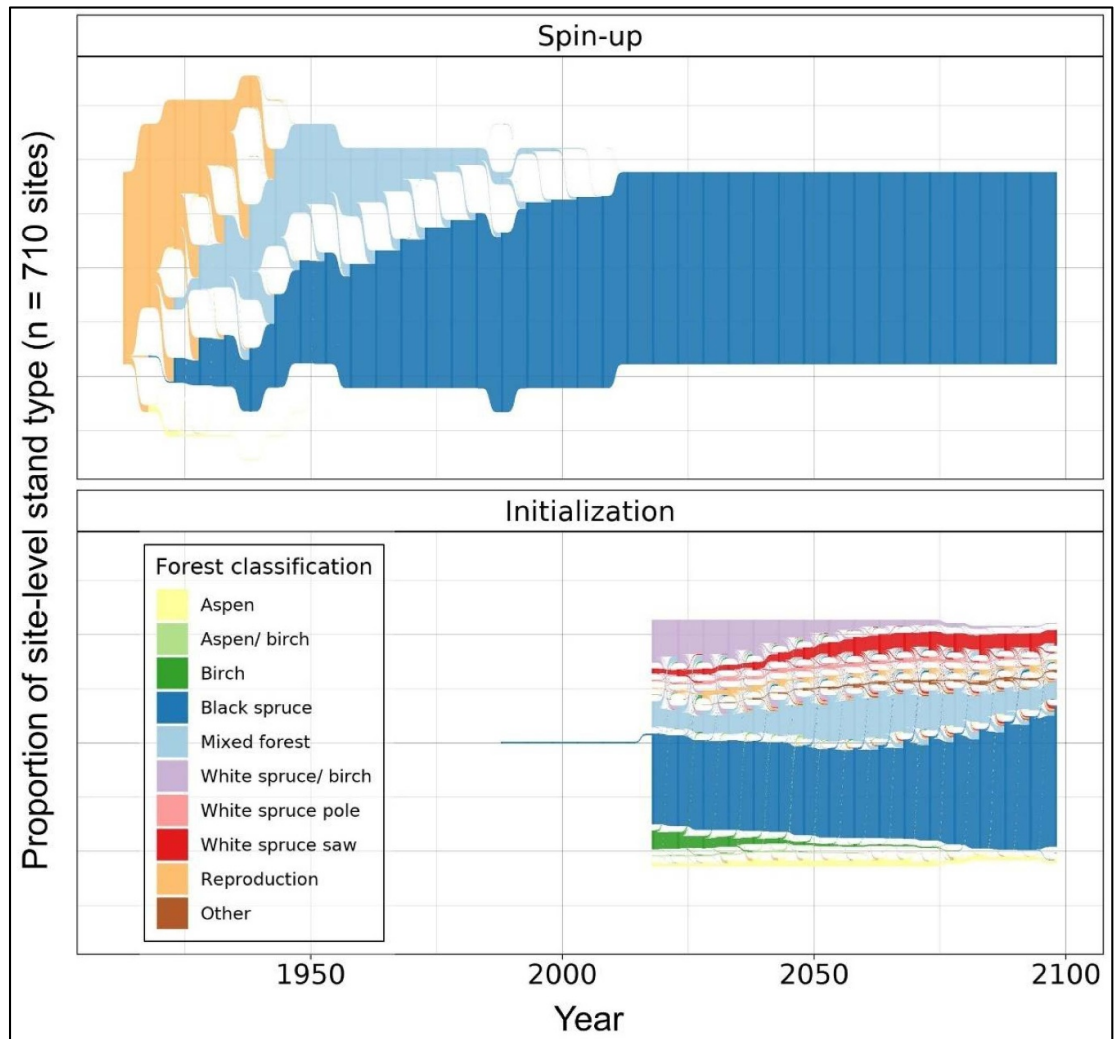


Figure 3. UVAFME simulation of forest change under a historic climate scenario on 710 Tanana Valley State Forest sites in subunit 4 C when run with spin-up procedures (top) and initial conditions from aerial survey and inventory data (bottom). The vertical width of each color represents the proportion of sites occupied by each stand type at 5-year intervals and ribbons between colors indicate stand type transitions. The spin-up scenario begins in 1913, allowing 100 years, roughly the average stand age in Interior Alaska, for stands to reach equilibrium. Using spin-up methods, these sites were projected to be dominated by black spruce, whereas utilizing aerial inventory data facilitates the simulation of a variety of forest stand types.

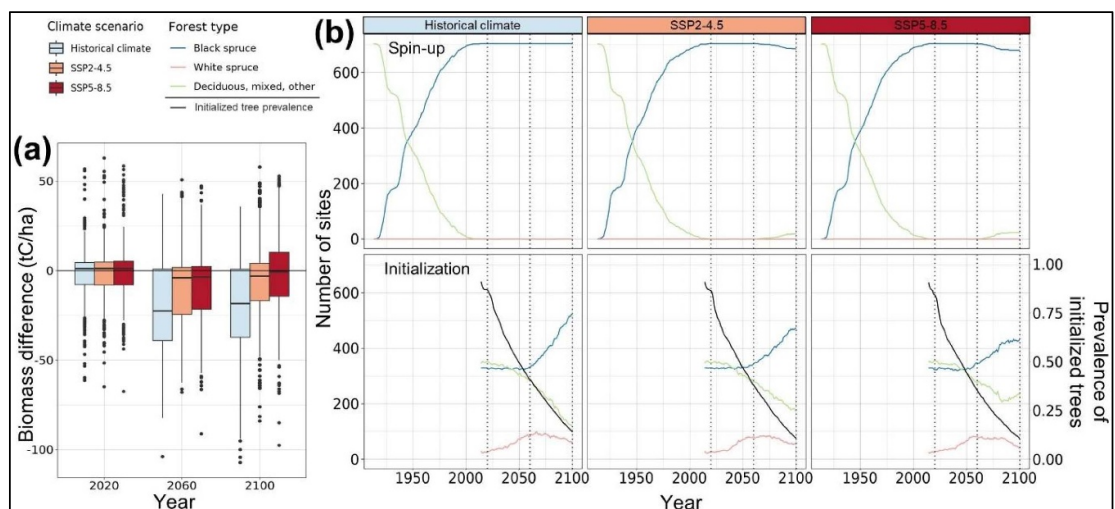


Figure 4. Trends in forest composition and biomass for spin-up vs. initialization runs of UVAFME for 704 sites in Tanana Valley State Forest subunit 4 C under different climate scenarios. (a) Biomass difference between the same sites in initialized and spun-up model runs. (b) Frequency of stand types over time across the study area. On the bottom panel, the black line represents the mean prevalence of initialized trees across sites (0–1), an indicator of the influence of stochastic events in the model since initialization.

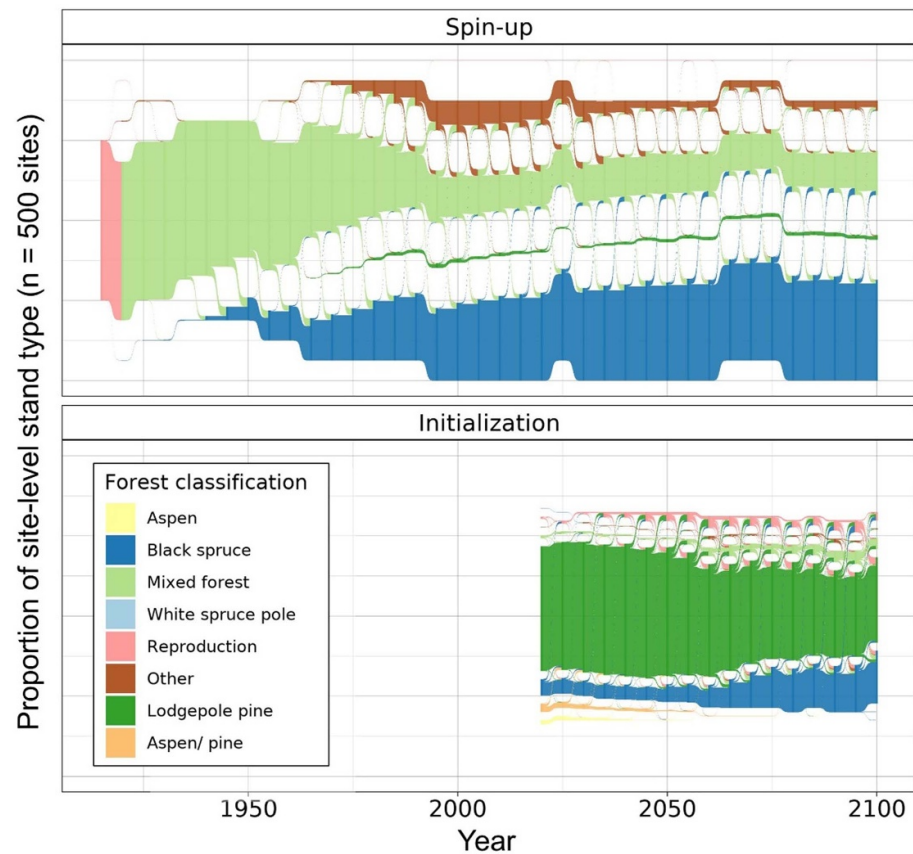


Figure 5. UVAFME simulation forest change under a historic climate scenario on 500 Kechika–Liard Confluence sites when run with spin-up procedures (top) and initial conditions from Landsat-derived products (bottom). The vertical width of each color represents the number of sites occupied by each stand type at 5-year intervals and ribbons between colors indicate stand type transitions. The spin-up scenario begins in 1915, allowing 100 years for stands to reach equilibrium. Using spin-up methods, these sites were projected to be dominated by mixed forests and black spruce, whereas initialization from satellite data facilitates pine dominance and a slowly increasing proportion of black spruce.

Across the landscape in the TVSE, forest composition is vastly different between spin-up and initialization run by the end of the simulation in 2100 (figures 3 and 4). When UVAFME spins up, black spruce increases across the landscape as deciduous and mixed forests decline (figure 4(b)). White spruce stands are completely absent. In warmer climate scenarios a small proportion of these sites transition to mixed or deciduous forests after 2050 (figure 4(b)). In contrast, initialized UVAFME begins with 46.7% black spruce, 49.1% deciduous, mixed, and other intermediate stage stands, and 4.3% white spruce forests. The proportions of black and white spruce gradually increase. In warmer climate scenarios, transition to black or white spruce stands are delayed for initialized sites. The prevalence of initialized trees in 2100 decreases from 0.20 to 0.14 in warmer climate scenarios, indicating increased mortality among initialized trees and a decline in mean stand age (figure 4(b)).

3.2. Model spin-up versus initialization at KLC study area

In the KLC area, initialization in UVAFME had a strong effect on dominant stand type (figures 5 and S5(b)). Sites modeled using spin-up generally followed a trajectory from young mixed forests to increasing dominance of black spruce. After spinning up for 100 years, most of these sites are composed of mixed forest (27.2%) and black spruce (54.0%). Lodgepole pine stands are virtually absent. In contrast, most initialized sites are composed of lodgepole pine (76.6% in 2016) which persist for decades after initialization (figures 5 and 6).

At the site level, spun-up sites had lower biomass and higher proportions of spruce and mixed forests than initialized sites (figure 6(a)). In 2020, site-level biomass differences were greatest (mean -9.44 tC ha^{-1}) because initialized pine stands were more productive than spun-up black spruce sites. In 2060 and 2100 this difference shrinks, especially in the historic climate scenario. This is because biomass in lodgepole pine stands decreases after initialization (table S5). In scenarios with climate change, the spun-up version of

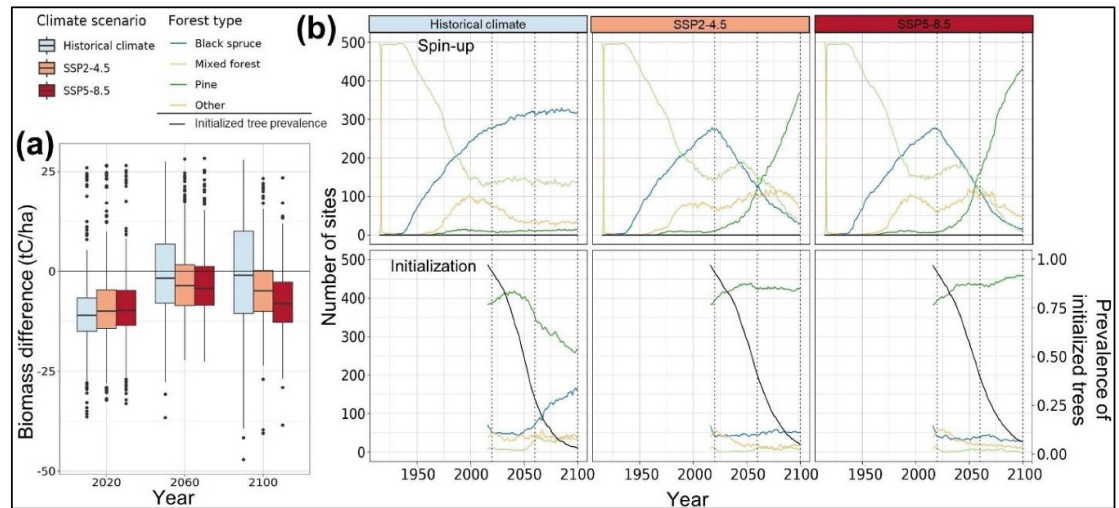


Figure 6. Trends in forest composition and biomass for spin-up vs. initialization runs of UVAFME for 500 sites in the Kechika–Liard Confluence area under different climate scenarios. (a) Biomass difference between the same sites in initialized and spun-up model runs. (b) Frequency of stand types over time across the study area. On the bottom panel, the black line represents mean prevalence of initialized trees across sites (0–1), an indicator of the influence of stochastic events in the model since initialization.

UVAFME predicts pine at more sites beginning around 2030 (figure 6(b)). By 2100, pine extent in spun-up UVAFME is nearly as great as in the initialized version of the model (in SSP 5, 86.8% compared to 91.8%). However, forest composition changes in the spin-up projections lagged several decades behind predicted changes in the initialized model.

3.3. Climate impacts on TVSF study area

After initialization, black spruce stands are the most common in TVSF (34.5% sites) and have a mean biomass of 27.1 tC ha^{-1} (table S4). Deciduous forests, most often composed of aspen, store more carbon (mean 58.6 tC ha^{-1}) while white spruce is the most productive stand type in TVSF (mean 74.4 tC ha^{-1}) and occupies a relatively small area (9.0%) (table S4). The mean aboveground biomass across TVSF following initialization using remotely sensed products was 46.5 tC ha^{-1} . Under a historic climate scenario, UVAFME maintains stand-type and biomass distributions similar to those at initialization for several decades (figure S7).

Under the SSP 5 climate scenario, UVAFME projected a 27.8% decline in aboveground biomass by 2100 when compared to a historic climate scenario (figure 7(a)). Warmer scenarios produced shifts towards more reproductive-age and deciduous stands as fire activity increased (figure 7(b)). Under SSP 2, black spruce coverage of the study area was reduced from 58.0% under a historic climate run to 42.7% in 2100, while deciduous forests expanded to occupy an additional 4.4% of the landscape and reproductive forests, an additional 11.4% (table S4). In SSP 5 these shifts were amplified: black spruce extent decreased by 25.7%, deciduous cover increased by 8.2%, and the extent reproductive stands nearly tripled from 13.2% to 36.9% (table S4). Black spruce forests which did not transition became more productive under warmer scenarios as nutrient limitation decreased (figures 7(c) and S8(a)). The model scenarios projected a strong (up to 38%) decline in biomass of deciduous stands by the end of the century (figure 7(c)), which was driven by growth reduction and higher mortality under increasing drought conditions (figure S8(b)). Mixed stands experience a similar, though less severe, decline while climate impacts are more moderate in white spruce forests (figures 7(b) and (c), table S4). Drought-induced productivity loss in deciduous forests outweighed black spruce gains by the end of the century, reducing overall carbon sequestration in this study area.

3.4. Climate impacts on KLC study area

Lodgepole pine stands are dominant in KLC, initially occupying 76.0% of the study area. After initialization in 2016, mean biomass was 31.8 tC ha^{-1} in these stands (table S5). Because white spruce stands are extremely uncommon, making up only 0.18% of spruce observations, black and white spruce stands were combined in this study area. Spruce stands initially occupied 15.3% of sites with mean 28.2 tC ha^{-1} aboveground biomass

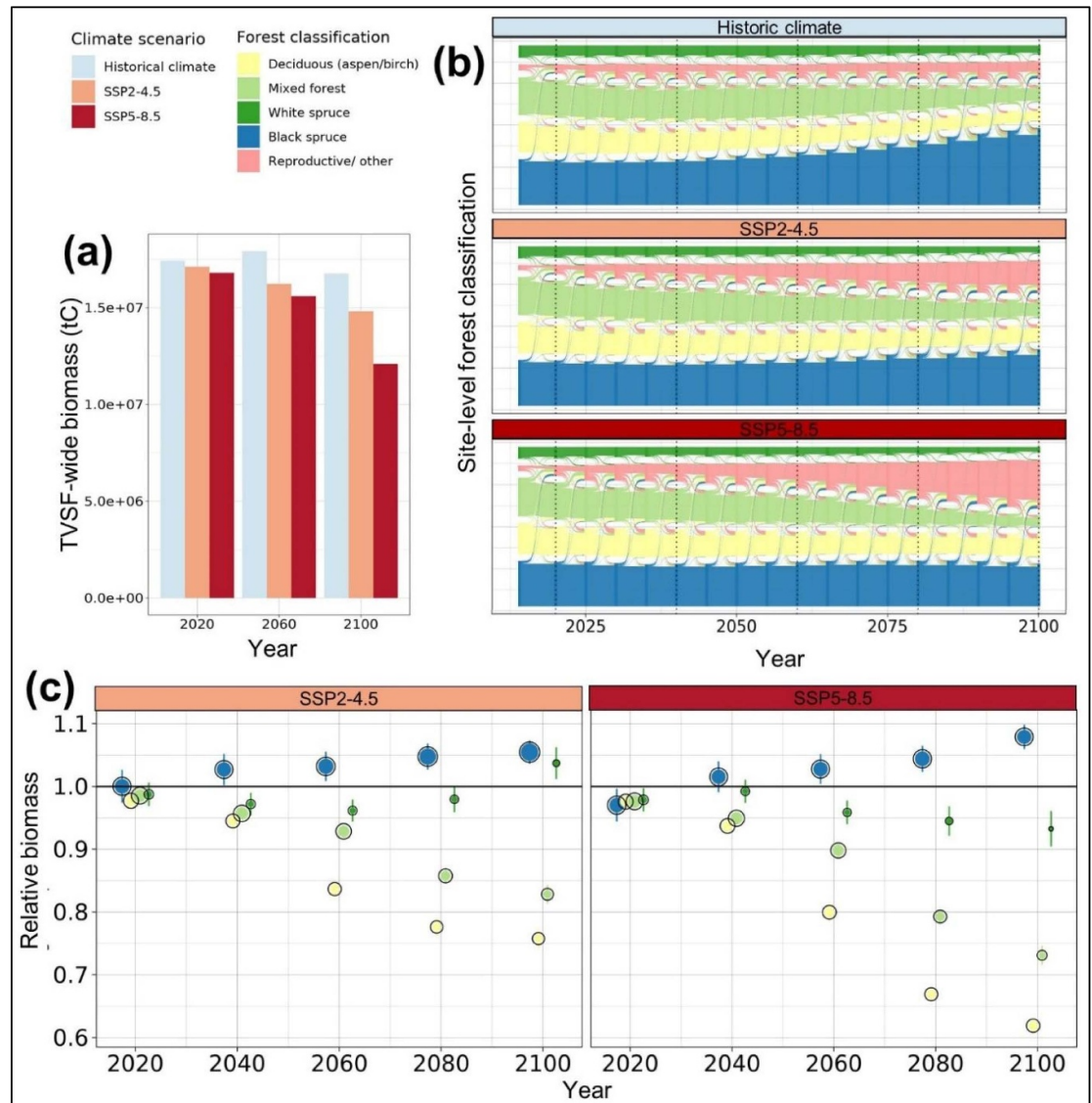


Figure 7. Tanana Valley State Forest-wide biomass and forest composition change under different climate scenarios. (a) Modeled landscape-wide biomass between different climate scenarios over the 367 000 ha study area. (b) Site-level forest transitions across the landscape under different climate scenarios. The vertical width of each color represents the proportion of sites occupied by each stand type at 5-year intervals and ribbons between colors indicate stand type transitions. (c) Relative biomass with exogenous forcing (differences between climate scenarios in corresponding years) by forest type. Point size represents a stand type's occurrence across the landscape.

(table S5). Deciduous and mixed forests are uncommon at initialization, occupying only 8.6% of the study area (table S5).

By 2100, UVAFME projects a decline in biomass under all climate scenarios (figure 8(a)), indicating model-endogenous processes that limit productivity for pine-dominated forests (figure S9). Under SSP 2, exogenous climate change results in an increase in forest-wide biomass (13.4%) by 2100 compared to the historical climate scenario (figure 8(a)). These gains are the result of reduced flood, nutrient, and cold limitations on lodgepole pine (figure S10(a)). Under SSP 5, forest-wide biomass increased by 13.8% by the end of the century compared to the historic climate run (figure 8(c); table S5). In this climate scenario, drought limitation rises after 2060 (figure S10(a)), resulting in a slight reduction in pine stand biomass between 2060 and 2100 (figure 8(c); table S5). In both climate change scenarios, spruce, which are more sensitive to drought (figure S10(b)), are gradually replaced by pine stands (figure 8(b)).

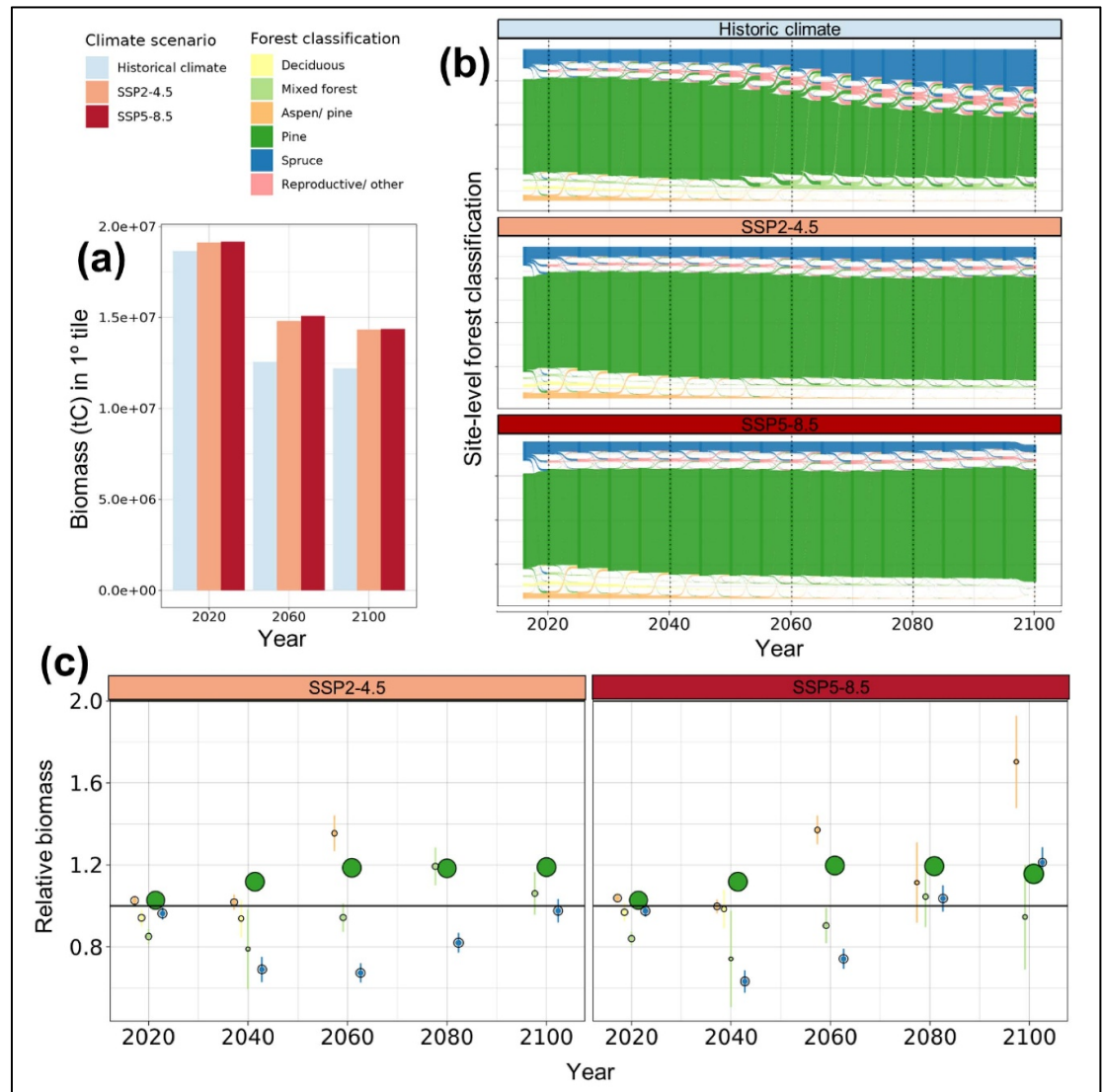


Figure 8. Forest biomass and forest composition change under different climate scenarios in the Kechika–Liard Confluence study region. (a) Modeled landscape-wide biomass between different climate scenarios over our 630 000 ha study area. (b) Site-level forest transitions across the landscape under different climate scenarios. The vertical width of each color represents the number of sites occupied by each stand type at 5-year intervals and ribbons between colors indicate stand type transitions. (c) Relative biomass with exogenous forcing (differences between climate scenarios in corresponding years) by forest type. Point size represents a stand type's occurrence across the landscape.

4. Discussion

Because boreal forests are characterized by disturbances—particularly stand-replacing fire in North America—and exist in a state of dynamic equilibrium, accurate initial conditions are essential for modeling forest composition and making near-term predictions in the face of climate change (Johnstone *et al* 2010a, Rogers *et al* 2015, Zhang *et al* 2022). Following disturbance, material legacies like seed banks and soil characteristics (Johnstone *et al* 2016) heavily influence regeneration, often determining forest composition for decades (Turner *et al* 1999, Huber *et al* 2020). Most of today's gap models, including UVAFME's predecessor FAREAST, derive from a genealogy designed to simulate old-growth forest dynamics in the US Northeast (Botkin *et al* 1972, Shugart 1984, Liu and Ashton 1995, Shugart *et al* 2018). Gap models have dealt with stochasticity by simulating many independent runs and aggregating results (Shugart *et al* 2018). However, this modeling framework lacks mechanisms to adequately account for short-interval disturbances and a landscape where endogenous gap dynamics are the exception, not the rule (McCarthy 2001). Precision is lost during the spin-up process as stochastic events occur, model biases accumulate, and spatial patterns that influence disturbances and establishment are unaccounted for. We found that material legacies (i.e. initial conditions) were critical for accurately predicting forest composition and landscape-level

ecological variability. Employees at the Alaska Division of Forestry confirmed that near-term results from our updated model matched their expectations.

Previous work with LINKAGES, a similar model, demonstrated that initial conditions were the dominant source of uncertainty in a 60 year hindcast, followed by process, meteorological, then parameter uncertainties (Raiho *et al* 2020). Similarly, Temperli *et al* (2013) found a forest landscape model to be highly sensitive to initial conditions. Baltzer *et al* (2021), who optimized parameters for two species in UVAFME with tree ring data, note that parameter optimization may be more important for simulating long-term species coexistence than forest succession for models that already characterize the trade-offs driving successional processes. Here, we demonstrated that a long spin-up period did not improve model accuracy. Because feedback loops between vegetation, soils, and disturbance have strong influences on regeneration in the boreal zone, future forest composition is best predicted by including information about present stand and soil characteristics. Gradual change in mature initialized forests indicated that model processes and parameters supported forest conditions as observed on the ground, improving our confidence in the model.

Compared to the spin-up version of UVAFME, our updated version with initial conditions from remotely sensed data in Interior Alaska produces more deciduous and white spruce forests and fewer black spruce stands. Similarly, in Western Canada UVAFME produces lodgepole pine stands that were virtually non-existent when the model ran from spin-up. The causes are twofold: material legacies associated with initialized forests were established in the model and we removed within-site plot-level aggregation in lieu of landscape-level aggregation. For example, in UVAFME *Populus* and *Betula* reproduce by sprouting when there are reproductive-size trees on a plot (i.e. a material legacy already exists). If there are no existing parent trees or deciduous seedlings are shaded out by competing understory conifers, black spruce will almost always establish and persist on a site. Similarly, because UVAFME has no mechanism for masting processes, sites dominated by large white spruce—which often establishes when mast years coincide with fire that exposes mineral soils (Gärtner *et al* 2011)—could not be produced from spin-up. In the KLC, a centuries-long legacy of disturbance preceded the dominance of lodgepole pine by eliminating other seed sources (Burns and Honkala 1990). Second, in UVAFME disturbances including fire are asynchronous between plots within a site because fuels (calculated from plot-level trees, litter, and soils) are independent between plots. Previously, model output was summarized by means and variances for species-level biomass. Site-level means often implied an evenly mixed forest landscape while heteroskedastic plot-level output was summarized as constant variance. Consequently, when site-level means and variances were aggregated across the landscape, stochastic events including disturbance and seed establishment were ‘averaged out’ with the result that stand heterogeneity was severely diminished. In the updated model version, we avoid this double-aggregation challenge by running one plot per site then aggregate several sites within new forest classifications to characterize landscape-level trends. This approach better reflects observed landscape dynamics where forests are not uniformly distributed with given proportions of species, but rather, composed of discrete stands with unique disturbance histories that contribute to a dynamic equilibrium across the landscape (Hansson 1992).

Initial conditions proved significant in modeling future climate impacts on the boreal forest. Deciduous expansion and spruce decline under climate warming occurred earlier in our updated model. In TVSF, black spruce dominance in the spin-up version of the model resulted in underestimation of aboveground biomass and implied greater carbon sequestration under warmer climate scenarios (a 2.0% increase between 2020 and 2100 under SSP 5 in TVSF subunit 4 C). This is a stark contrast to the updated model’s prediction of a 28% reduction in the same scenario.

While gap models are generally limited to characterizing regional, decades- to centuries-long dynamics, the initialized version of UVAFME is better able to predict localized changes in the upcoming years and decades. For example, our latest results agree with recent observations that deciduous expansion is already underway (Wang *et al* 2020, Baltzer *et al* 2021, Walker *et al* 2023) and limitations on growth are easing at colder, wetter sites (Sullivan *et al* 2017, Dial *et al* 2022). Similarly, our model indicates future moisture deficits will limit forest biomass, especially in the most productive TVSF sites, a trend already observed in boreal forests (Walker *et al* 2015, Sulla-Menashe *et al* 2018, Berner and Goetz 2022, Sánchez-Pinillos *et al* 2022). In agreement with Walker *et al* (2024) we found lodgepole pine in the KLC has a competitive advantage over spruce as the climate warms and fire activity increases. Previous applications of UVAFME have predicted broad-scale trends in forest demography in response to climate change (Foster *et al* 2019, 2022). However, our latest work suggests that these climate impacts (e.g. increasing deciduous fraction, increased productivity at cold sites, decreased productivity at upland sites) may occur earlier than previously predicted.

We tested two case studies for integrating remotely sensed data in a forest gap model, but many opportunities and challenges remain. For example, we did not incorporate errors from remote-sensing derived maps in UVAFME but in future, initial conditions uncertainty may be estimated by running the model many times with inputs probabilistically adjusted to remote sensing accuracy assessments. Model

output (e.g. forest height, leaf area) may be validated from optical or LiDAR data, and stochastic events (e.g. fire, insect outbreak, assisted migration) may be updated in real time. More data may be integrated into UVAFME by optimizing species and environmental parameters with field data, as demonstrated by Baltzer *et al* (2021). Similarly, sensitivity to climate scenarios and their uncertainties may be assessed. In UVAFME, the additions of spatially interactive fire and seed dispersal would represent more realistic disturbance/recovery dynamics and landscape heterogeneity in long-term projections. Similarly, the boreal version of UVAFME does not contain mechanisms for insect and pathogen outbreaks, although several biotic agents have recently had unprecedented outbreaks (Bleiker *et al* 2019, Boyd *et al* 2021, Ruess *et al* 2021, Anderegg *et al* 2022). Because short- and long-term predictions are vastly improved, mechanistic models that incorporate initial conditions are well positioned to address questions about region-wide ecological responses and adaptive forest management in a changing climate. While the capability to initialize stands is particularly important in boreal forests where stand-replacing disturbance occurs frequently, it is also increasingly relevant for tropical and temperate forests where deforestation is widespread (Hansen *et al* 2013). Data availability and processing (i.e. creating species maps from remotely sensed reflectance) remain substantial limitations, but we demonstrate the value of coordinated efforts to quantify forest characteristics (Coops *et al* 2021).

5. Conclusion

By incorporating remotely sensed data into forest initialization in the UVAFME model, we found that model results captured observed stochastic events like disturbance history and seedling success that determined forest structure. Compared to the spin-up version of the model, updated model results better represented landscape heterogeneity and dynamic equilibrium under frequent disturbances. Furthermore, because it can reflect present on-the-ground conditions, the updated model is more applicable to small-scale, short-term scenarios.

Dominant model trends under climate warming generally agree with field studies and other modeling efforts and indicate four main outcomes: (1) as fire activity increases in Interior Alaska, deciduous forests expand and conifer recruitment declines in the decades following the fire event, (2) deciduous forests that displace black spruce are more productive than their predecessors, (3) warming releases trees from permafrost and nutrient limitations at colder sites, and (4) moisture deficits reduce future forest productivity at warmer sites. When we spun up the model, these impacts were predicted later and at smaller magnitudes than in the updated version of the model. Our findings demonstrate the value and urgency of data-model integration for understanding ecological change and managing forests where appropriate in a warming future.

Our study showcases the importance of accurate initial conditions in simulating vegetation's response to current and future climate and disturbance regimes. At a local scale, spin-up from bare ground created mismatches between observed and modeled historical conditions which were propagated into the future to create disparate responses to climate change. Determining accurate spin-up and/or initialization is a key problem for both calibration and application of local, regional, and global models. Often model spin-up to equilibrium is selected, especially for global models, due to a cited lack of relevant observational data. This choice adds uncertainty as well as computational constraints to simulations. Our study demonstrates an approach for initializing a detailed vegetation demographics model with satellite observations, which are publicly available, spatially continuous, and span decades. We recommend that other forest demography modelers test similar initialization procedures, and if results show consistent improvements over the previous approach, update standard workflows where feasible. For boreal forests, starting conditions had a strong influence on the timing and magnitude of responses to climate change. This may be the case for other ecological and earth system models as well, and we emphasize the importance of using free, high-quality data for parameterizing, initializing, and benchmarking models.

Data availability statement

The data and code that support these findings are openly available at the following URL: https://github.com/shelby147/UVAFME_model_init. The Landsat-based data products for the KLC study areas were obtained from National Terrestrial Ecosystem Monitoring System for Canada and can be accessed at the following URL: https://opendata.nfis.org/mapserver/nfis-change_eng.html.

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