

Fire disturbance and climate change: implications for Russian forests

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

Abstract

Change in the Russian boreal forest has the capacity to alter global carbon and climate dynamics. Fire disturbance is an integral determinant of the forest's composition and structure, and changing climate conditions are expected to create more frequent and severe fires. Using the individual tree-based forest gap model UVAFME, along with an updated fire disturbance module that tracks mortality based on tree-species and –size level effects, biomass and species dynamics are simulated across Russia for multiple scenarios: with and without fire, and with and without altered climate. Historical fire return intervals and percent of forest stand mortality are calculated for the Russian eco-regions and applied to 31 010 simulation points across Russia. Simulation results from the scenarios are compared to assess changes in biomass, composition, and stand structure after 600 years of successional change following bare-ground initiation. Simulations that include fire disturbance show an increase in biomass across the region compared to equivalent simulations without fire. Fire disturbance allows the deciduous needle-leaved conifer larch to maintain dominance across much of the region due to their high growth rate and fire tolerance relative to other species. Larch remain dominant under the scenario of altered climate conditions with fire disturbance. The distribution of age cohorts shifts for the scenario of altered climate with fire disturbance, displaying a bimodal distribution with a peak of 280-year-old trees and another of 100-year-old cohorts. In these simulations, fire disturbance acts to increase the turnover rate and patterns of biomass accumulation, though species and tree size are also important factors in determining mortality and competitive success. These results reinforce the importance of the inclusion of complex competition at the species level in evaluating forest response to fire and climate.

1. Introduction

Boreal forests sit atop the largest reservoir of terrestrial carbon (C), two-thirds of which are in Russia (Hare and Ritchie 1972, Alexeyev and Birdsey 1998). Fire is a dominant disturbance in this region that alters C stores and forest composition (Sukhinin *et al*

2004). Warming has resulted in intensification in both fire frequency (i.e. the number of fire occurrences per unit time within an area (Pyne *et al* 1996)) and severity, as well as larger areas burned (Kasischke *et al* 2004, Kasischke and Turetsky 2006, Kharuk *et al* 2008). Boreal fire frequency and area burned are predicted to continue increasing (Overpeck *et al* 1990,

Stocks *et al* 1998, Stocks *et al* 2000, Flannigan *et al* 2009), potentially leading to shifts in species composition and tree demography, and alteration of the annual C budget. The temporal effects of fire depend on the combined effects of fuel state, residence time of burn and fire intensity (Van Wagner 1973, Pyne *et al* 1996). The subsequent loss of above- and below-ground organic material defines the fire severity (Keeley 2009). Fire severity and variations in duff consumption shape post-fire successional pathways (Johnstone and Kasischke 2005, Shorohova *et al* 2009, Johnstone *et al* 2010a, Barrett *et al* 2011, Shenoy *et al* 2011). Low-severity, frequent fires can prevent young trees from reaching maturity, and severe, stand-replacing fires reset the successional cycle (Johnstone *et al* 2010a, Johnstone *et al* 2010b). Some species tolerate and regenerate quickly after fire, and others are negatively impacted by frequent or severe fires, thus impacting composition (Johnstone and Kasischke 2005, Shorohova *et al* 2009, Johnstone *et al* 2010a, Shenoy *et al* 2011, Schulze *et al* 2012). Through its effects on stand structure and species composition, fire will be a strong driver of forest composition and C dynamics within Russia.

In addition to its impact on fire dynamics, climate change is also likely to bring about changes to aboveground boreal C dynamics through alteration of tree growth, vigor, and mortality (Allen *et al* 2010, Kharuk *et al* 2005, Schaphoff *et al* 2016, Soja *et al* 2007, Tchebakova *et al* 2009). It is unclear how these may interact, especially with the concurrent effects of changing fire disturbance. Schaphoff *et al* (2016) reported that the current fire-affected area is ~20% larger than mean area found for the period of 1960–2007 (Soja *et al* 2007). Forest lost to stand-replacing fires has also increased (Schaphoff *et al* 2016). Within Siberia, more frequent or more severe fire alters stand density and diameter increment, resulting in increased aboveground C storage (Kharuk *et al* 2005, Furyaev *et al* 2001, Alexander *et al* 2012, Kharuk *et al* 2011). High severity fires and the combustion of duff and organic soil layers can create a shift in the dominant species through changes in soil depth and moisture, impacting species-specific recruitment and growth (Johnstone *et al* 2010a, Johnstone *et al* 2010b, Barrett *et al* 2011). Field studies have demonstrated differential species response to fire, with *Pinus sylvestris* forests in lower and central Siberia displaying a 50% and 83% loss of biomass, respectively, whereas lower Siberian larch (*Larix* spp.) forests lose between 47% and 23% of biomass to fires of variable severities (Ivanova *et al* 2011, Kukavskaya *et al* 2014). Evaluating the ultimate response of boreal forests and associated aboveground C storage thus requires consideration of the response of individual species.

Individual tree-based gap models, which simulate the establishment, growth, and death of trees on patches across a landscape, can explore the impact of changing disturbance and climate regimes on forest characteristics and aboveground biomass. Gap models established

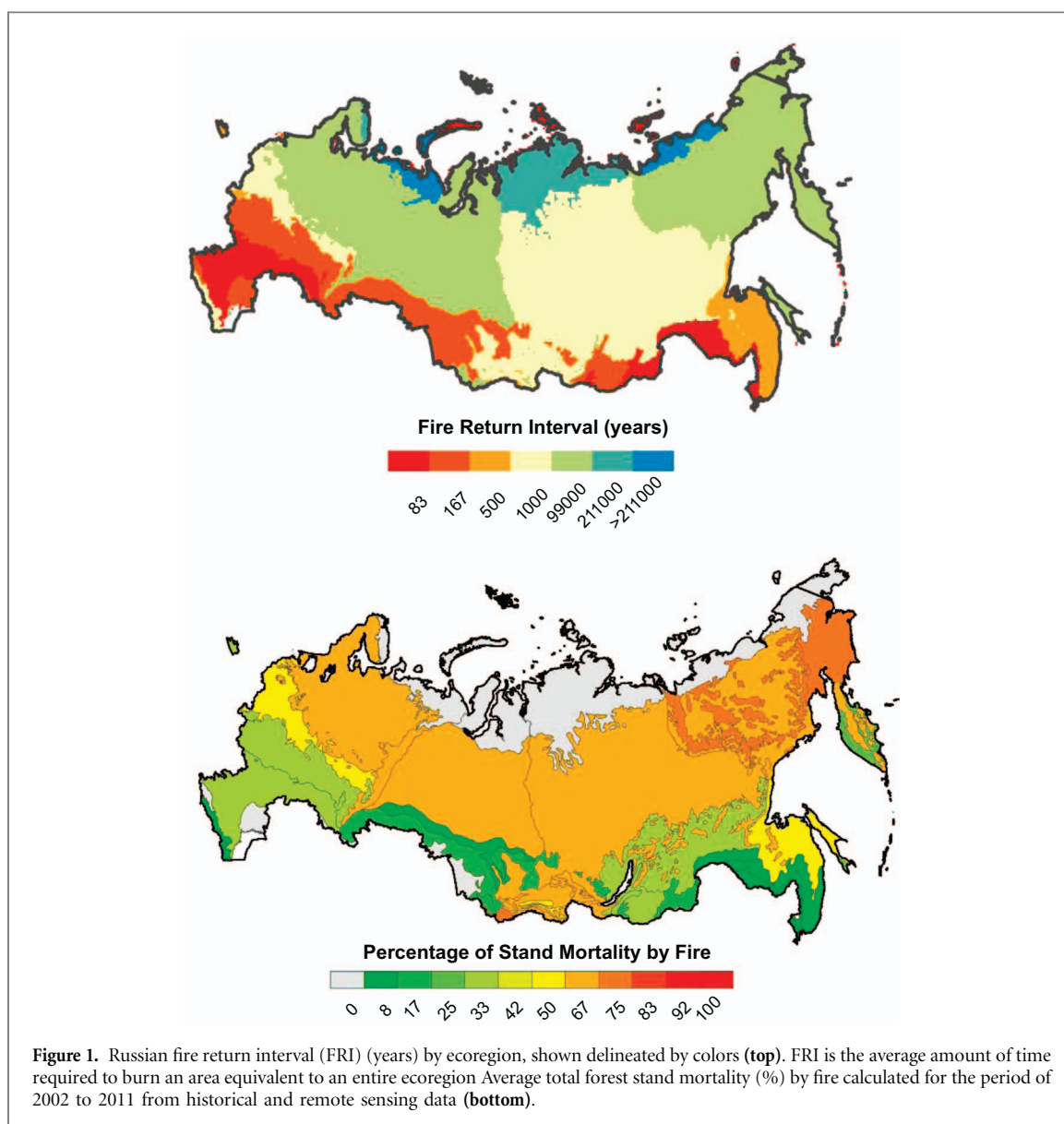
according to the approach of Botkin *et al* (1972) and Shugart and West (1977) are driven by successional dynamics and the concept of ‘gap phase’ replacement introduced by Watt (1947). As a simulated tree dies, new and existing trees establish and grow within this gap through greater access to light and resources (Shugart and West 1980). Unlike dynamic global vegetation models (DGVMs), which typically only simulate biomass at the level of plant functional types (PFTs) the strengths of gap models lie in their simulation of trees and species, thus allowing prediction of fine-scale changes in forest structure and composition. Field studies demonstrate that prior stand structure, regeneration, and within-stand disturbances act as important controls on landscape aboveground C storage (Kashian *et al* 2013). By tracking each stem, individual-based models capture changes to aboveground biomass and stand structure resulting from environmental factors such as shading and moisture stress, or size- and species-specific mortality events such as fires.

We use the individual-based gap model University of Virginia Forest Model Enhanced (UVAFME) to simulate forest dynamics across Russia in response to historical fire disturbance probability and fire disturbance altered by changing climate. The fire disturbance portion of the model is updated to include size- and species-level effects of fire on tree mortality and regeneration. The historical fire return interval is calculated for eco-regions across Russia, from which we derive the probability of fire. The associated percent of stand mortality across Russia is derived and applied to calculate the mean intensity of fire at model-simulated locations. Using four simulation scenarios, which include or exclude fire and use either historical or altered climate, we evaluate the impact of changing climate and fire disturbance regimes on species biomass, composition, and stand characteristics across Russia. These results are an important step towards understanding how C and species dynamics may change.

2. Methods

Model description

UVAFME is an individual tree-based model used to simulate forest succession. It is an object-oriented version of FAREAST (Yan and Shugart 2005). Simulated species biomass, composition, and basal area have been validated along an elevation gradient in northeastern China and against forest type at sites in eastern Russia (Yan and Shugart 2005), against species inventory data from 44 forest locations spanning from eastern to western Russia (Shuman *et al* 2014), and against dominant species and forest biomes from a bioclimatic envelope model and two observation-based maps across Russia (Shuman *et al* 2015). A detailed description of UVAFME can be found in Supplement S2 available at stacks.iop.org/ERL/12/035003/mmedia. UVAFME



updates tree characteristics annually, accounting for competition among trees and the effects of climate, soil nutrients, and water on forest growth. Stand properties representative of a forest landscape for an area with particular climate and soil conditions are derived by averaging across several independent plots.

UVAFME incorporates equations tracking the influence of biotic and abiotic factors on ecological processes and tree characteristics. Specifically, tree growth and seedling banks are modified by changes in light transmission through the multi-layer canopy resulting from tree growth and death, changes in annual growing degree-days (GDD) from varying temperature, changes in potential evapotranspiration, and changes in available soil C and nitrogen. The effect of environmental factors on tree growth limitation has been updated in this study from a multiplicative approach to use only the most limiting factor. The response function used to calculate the effect of temperature on tree-growth has been updated according to Bugmann and Solomon (2000) from a

parabolic curve to an asymptotic curve that peaks at the species-specific temperature optimum. With this change, species no longer experience a decline in growth beyond their temperature optimum, but continue to be limited by the remaining abiotic and biotic factors.

Fire within the model

Fire disturbance within the model has been updated to allow for variable fire intensity as well as species- and size-specific effects on tree survival and regeneration. A detailed description of this module and parameterization is included in Supplement S2. Fire occurs stochastically based on a site-specific fire probability, set according to the fire return interval (FRI) in years determined from historical data (figure 1). FRIs for this study are based on values derived across Russia for eco-regions using the Regionally-Adjusted MODIS Burned Area (RAMBA) method of mapping burned area for the period of 2001 to 2014 (Loboda *et al* 2007, Loboda *et al* 2011) with the methodology of

Soja *et al* (2006). According to Soja *et al* 2006, the FRI is the average amount of time required to burn an area equivalent to an entire ecosystem. Using this method, a landscape with an average FRI of 100 years would be expected to experience 1/100 or 0.01 of that landscape to burn annually. The percentage of stand-replacing fires calculated according to Krylov *et al* (2014), which represents the percentage of total forest stand mortality (figure 1), is used to derive the site-specific mean fire intensity. Fire severity based on vegetation mortality has been shown to correlate with fire intensity in forests dominated by conifers (Wade 1993, McCaw *et al* 1997, Keeley 2009). Individual tree mortality is evaluated in the model based on size, percentage of crown scorch and cambial damage based on bark thickness. Therefore, for trees the same size and with the same crown scorch damage, those with thicker bark will have a lower probability of mortality. Removal of soil organic material by fire is not included in this version of the model. Fire affects seeds and seedlings based on species-specific characteristics with either an increase, decrease or no change to the seedling bank. Equations within this updated fire module have been successfully utilized within the western United States (Hood *et al* 2007, Keane *et al* 2011, Reinhardt and Crookston 2003, Ryan and Reinhardt 1998) and have also been successfully tested with UVAFME in the southern Rocky Mountains (Foster *et al* 2017).

Modelled fire probability increases with increasing site aridity based on the ratio of precipitation to potential evapotranspiration as in Feng and Fu (2013) (equation (5) Supplement S2). This modification allows the probability of fire to increase with increasing evaporative demand, either due to higher temperatures or lower precipitation.

Model simulations

In this study, UVAFME was used to generate forest composition and biomass for four scenarios: 1) *no disturbance*: with climate conditions derived from historical climate but without fire disturbance; 2) *fire*: with the same climate as scenario 1 but with fire return probability and intensity as determined by the methods described above; 3) *climate change without fire*: 500 years of simulation which are the same as scenario 1, followed by 100 years of altered climate derived from a 'business as usual' climate change scenario, and 4) *climate change with fire*: 500 years of simulation which are the same as scenario 2, followed by 100 years of altered climate as in scenario 3. Resulting biomass, forest composition, height, and stand age are compared for the scenarios to evaluate the response across the region.

UVAFME is used to simulate species composition and biomass at 31 010 gridded sites with a spatial resolution of 23 km × 23 km for coverage across Russia. Site and species parameters are derived as in Shuman *et al* (2015) and summarized in Supplement

S2. Historical daily temperature and precipitation conditions at each site are derived from statistical distributions of mean monthly temperature and precipitation from 60 years of weather station data for the period from 1941 to 2001 (NCDC 2005a, 2005b). Fifty-eight tree species are included from ten genera (*Abies* spp., *Betula* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Populus* spp., *Tilia* spp., *Quercus* spp., *Fraxinus* spp. and *Ulmus* spp.) and two collections of less common deciduous and coniferous species. Range maps determine which species are eligible for colonization at each site (Nikolov and Helmisaari 1992, Hytteborn *et al* 2005). Competition for light, nutrients and water determines which species establish and survive.

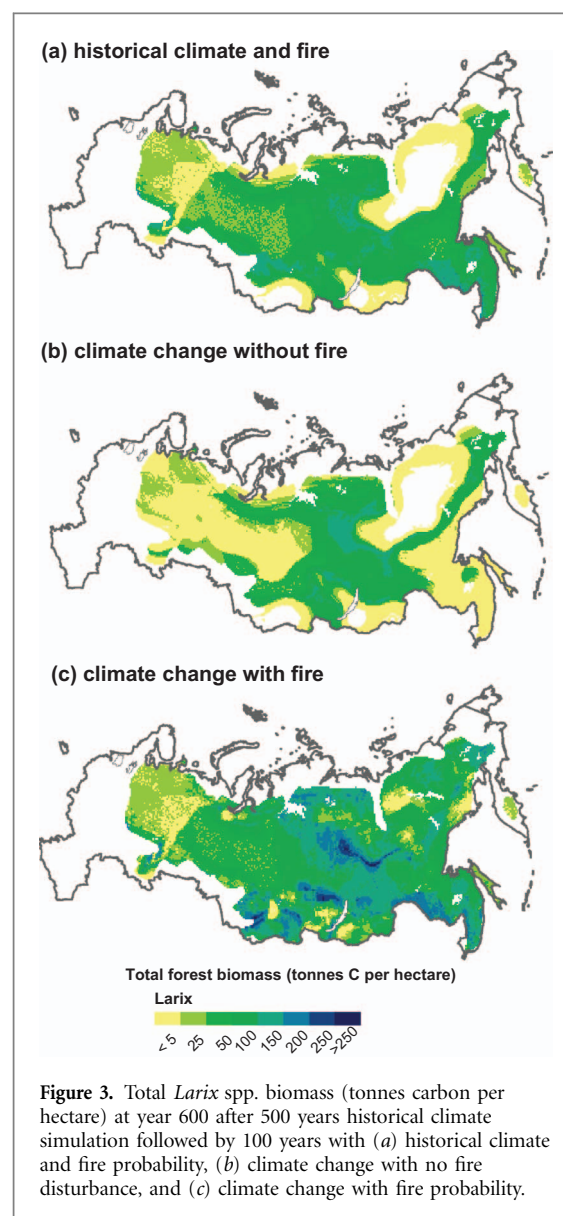
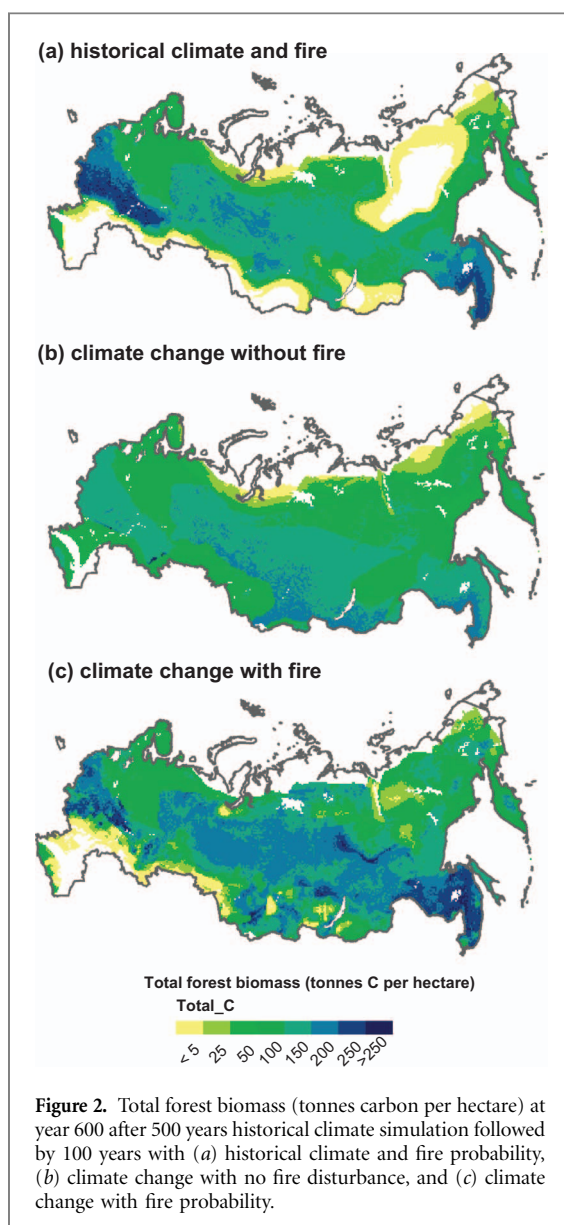
For the altered climate scenario temperature and precipitation values generated by NCAR's Community Climate System Model (Collins *et al* 2006) projected according to the 'business as usual' scenario are used. With the highest projected temperature increases by the end of the 21st century, this scenario allows evaluation of extreme climate conditions as they affect vegetation and fire probability, thus providing a likely worst-case scenario. Across Russia this scenario projects increasing temperatures and variable changes in precipitation, resulting in increases in GDD above 5 °C and annual moisture index (AMI; ratio of GDD to annual precipitation) values, indicating drying and greater probability of drought (Shuman *et al* 2015).

For each model simulation run at each site, 200 independent 500 m² plots are simulated from bare ground to year 600. The simulated forest has reached a state of quasi-equilibrium by year 500, and it is after this point, for scenarios 3 and 4, that altered climate data are substituted. Model simulation methodology and datasets are the same except for the inclusion or exclusion of fire and the use of historical or altered climate data for the final 100 years.

3. Results

The FRI and percent stand mortality across Russia show broad similarities, with the map of percent stand mortality displaying more heterogeneity than the FRI map (figure 1). The FRI shows, on average, long FRI in the north across much of Russia, and shorter FRI along the southern border and in the Amur region of the Russia Far East. Low stand mortality (i.e. less than 30%) occurs along the southern boundary of Russia and corresponds to areas of more frequent fire (figure 1). Small areas with high mortality are embedded within areas classified as having infrequent fires in far northeastern Russia.

Total mature forest biomass for historical climate simulations with (figure 2(a)) and without fire (figure S1) show areas of high biomass in the Amur region of the Russian Far East and European Russia. After 600 years of simulation for historical climate with fire (scenario 2) there is an increase in



total biomass compared to simulation without fire (scenario 1) (table 1). Under scenario 3 (altered climate without fire) the increased mean total biomass (94.50 tC ha^{-1}) reflects increased biomass across northern and southern portions of Russia (figure 2(b)). With fire disturbance under altered climate conditions (scenario 4) biomass decreases in the southern portion of western Russia and increases within far northeastern Siberia and along the Amur River border between China and the Russia (figure 2(c)). Across all of Russia, scenario 4 results in increased mean total biomass (112 tC ha^{-1}) (table 1).

The increased total biomass for scenario 4 is broadly associated with changes in larch, which is dominant across much of Russia (figures 3 and 4). Under scenario 3, evergreen conifers show increased biomass across central Russia, whereas in these same areas the biomass of larch decreases (table 1, figure 3 and S2). In contrast with fire, the biomass of larch increases for scenario 4 for areas in the Siberian transect spanning

north from Lake Baikal, displaying increases of 100 tC ha^{-1} compared to biomass for scenario 2 (historical conditions with fire) (figures 3 and 4 and S3).

Under altered climate, many species across interior Russia increase in biomass compared to historical climate conditions (figure S3). However, with the inclusion of fire in scenario 4 evergreen trees do not increase biomass compared to scenario 3 (figure 4). Warming climate and fire create a more complex pattern of height and stand age distribution across Russia. With fire and altered climate (scenario 4), UVAFME predicts, on average, taller trees in areas of increased biomass along the southern Siberia border, from the Lake Baikal region into northern Siberia, and in far northeastern Russia (figure S4). In scenario 2 the Lorey's height (i.e. mean height weighted by basal area) may reach 22 m in northern Siberia and 26 m in central and southern Siberia (figure 5). Fire disturbance with warming climate in scenario 4 results in patches of increased height in areas of newly increased

Table 1. Biomass characteristics (tonnes C per hectare) for forests at simulation year 600 for four model scenarios across Russia.

Scenario	Total Carbon			<i>Larix</i> spp.			Needle leaved evergreen			Broad leaved deciduous		
	Mean	Median	Standard deviation	Mean	Median	Standard deviation	Mean	Median	Standard deviation	Mean	Median	Standard deviation
No Fire	73.27	86.79	51.4	27.51	4.13	35.81	39.28	9.91	48.96	17.58	1.63	31.07
Climate Change no Fire	94.5	94.22	41.31	20.25	4.06	28.79	65.11	54.93	54.68	21.32	5.39	31.29
Fire	82.06	89.48	62.78	43.54	36.25	38.51	33.59	12.12	42.07	19.25	1.31	45.58
Climate Change with Fire	112	116.39	60.31	75.29	70.49	52.13	38.34	16.92	44.14	20.62	6.18	36.21

Biomass characteristics (mean, median, and standard deviation) at year 600 for total aboveground forest carbon and three groups of species, including *Larix* spp., needle leaved evergreen, and broad leaved deciduous, for four model scenarios which include or exclude fire disturbance and use either historical or climate change data from a 'business as usual' scenario in the final 100 years of simulation at 31 010 sites across Russia.

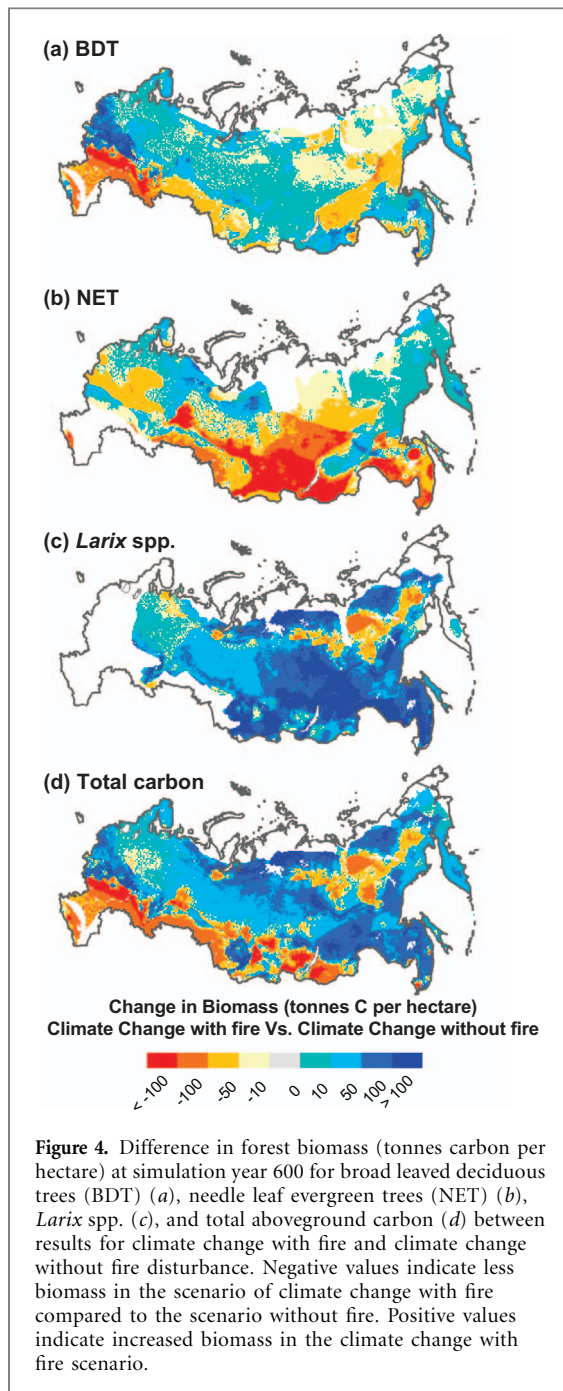
biomass, i.e. far northeastern Russia (figure 5). The scenarios also display variable patterns in the frequency of mean stand age (figure 6). With historical climate and fire in scenario 2, there is a peak in frequency for the youngest 20 year age class, and a peak for the 280 year age class (figure 6 top). Under conditions of altered climate without fire in scenario 3, there is no true peak, but a broadly older forest, indicated by a cluster of age classes from 260 to 360 years (figure 6 middle). There is clear bimodal distribution of age classes for scenario 4, with peaks at the 100 year age class and again at 280 years (figure 6 bottom).

4. Discussion

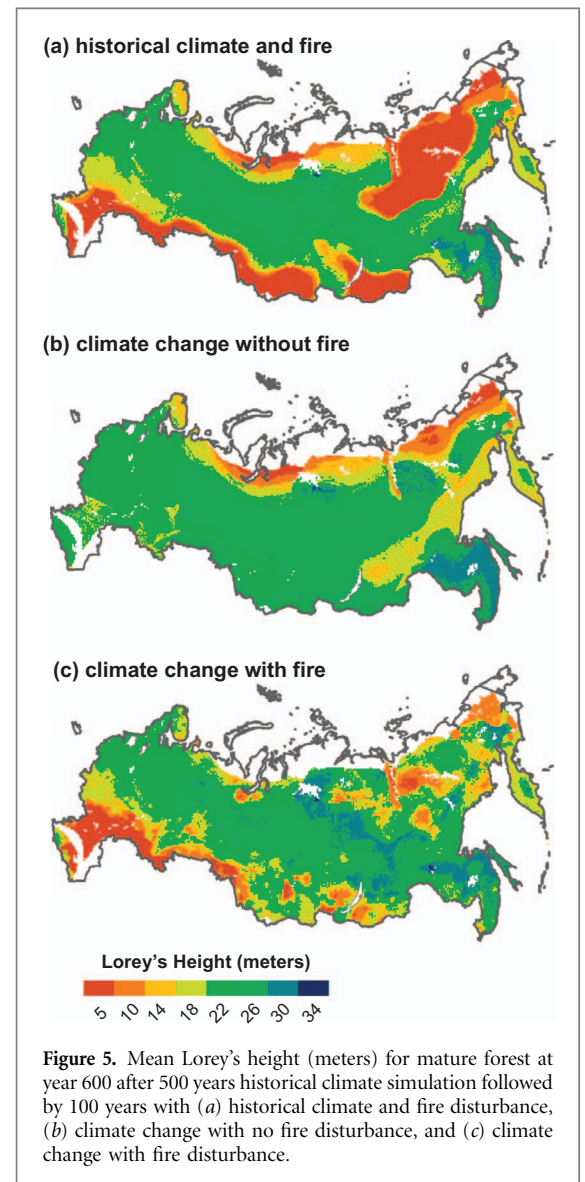
Individual-based models relate changes in external drivers (e.g. climate and fire regimes) with internal responses, and produce changes in ecosystem composition and age structure that further affect ecosystem function. Feedbacks among change in drivers and change in ecosystem function are seen in this investigation. The increase in biomass for both altered climate scenarios suggests that climate acts as a strong modulator on biomass and competition dynamics. Species with higher growth rates are more competitive in more favorable climate conditions (i.e. once released from temperature or water limitation). This increase in biomass is not seen with the inclusion of fire under historical climate. GDD increases under warming climate, resulting in increased biomass as species are released from temperature limitation (Schaphoff *et al* 2016). With increased AMI, drought tolerance is important, and larch effectively competes for resources, as seen in the increases in biomass (figures 3, 4 and S3). These results suggest that water limitation and disturbance will be determining factors for species composition in southern boreal forests. This highlights the importance of limiting species distributions based on available resources, rather than predefined limits, as in the use of a parabolic temperature response or a fixed climate envelope approach.

Peaks in age structure represent long-lived transients from stand replacement processes (i.e. succession) following stand initiation at year zero as well as the transient dynamics from changes in climate and fire in year 500 (figure 6). These results do not suggest a wholesale reduction in biomass in response to altered fire and climate, but rather an alteration of stand structure and thus C dynamics. Altered climate conditions without fire act to increase biomass, resulting in higher aboveground C stores as stand structure becomes heavily weighted towards older stands (figure 6). The inclusion of fire disturbance increases tree turnover rate, and for altered climate with fire shifts the age distribution to include young productive stands as well as mature older stands (figure 6). Associated changes in height occur alongside this change in stand age. Increases in stand height with warmer conditions (figure 5) agree with those of Tchebakova *et al* (2016), which demonstrated a similar increase in height in far northern Siberia using a simplified forest height stand model validated against the lidar-based height map of Simard *et al* (2011). The differences between the altered climate scenarios with and without fire suggest that the demographic and structural responses to fire are an important component driving biomass and species dynamics.

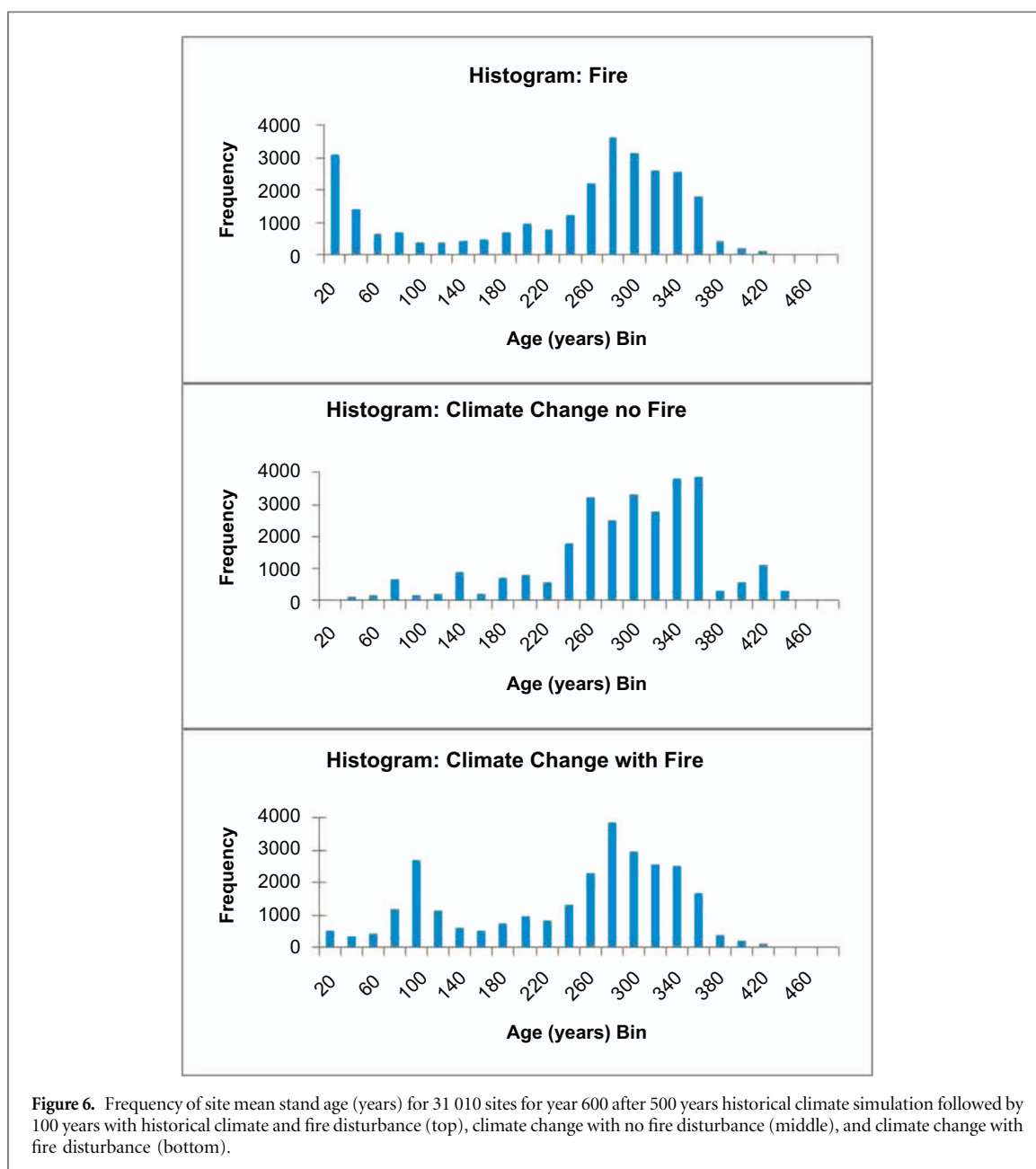
The increase in aboveground carbon storage from this study agrees with previous boreal forest modeling work by Kasischke *et al* (1995), which demonstrated an increase in aboveground storage with warming and increased fire frequency. In a field study of a transect in central Siberia which focused on fire frequency and its importance in determining species composition and performance, Schulze *et al* (2012) found that larch demonstrated a constant increase in biomass over 350 years of stand ages. The changes in biomass seen in this current study are largely due to increases in biomass for larch in the same region studied by Schulze *et al* (2012). These results demonstrate the competitive advantage that larch gains with fire disturbance due to their tolerance of fire and high growth rate compared to other species (Nikolov and Helmissari 1992, Hytteborn *et al* 2005).



Bark thickness is a key component determining tree mortality due to fire. Bark thickness increases with increasing tree diameter, thereby increasing fire resistance (Harmon 1984, Peterson and Ryan 1986, Ryan *et al* 1988, Ryan and Reinhardt 1988). Larch and *P. sylvestris* have the highest bark thickness value (0.063 cm bark per cm DBH), making them more tolerant of fires compared to other species, whose bark thickness ranges from 0.046 to 0.014 cm bark per cm DBH (table 2). Larch and *P. sylvestris* coexist across central Russia in mixed forests, with larch more dominant further north (Nikolov and Helmissari 1992, Schulze *et al* 1995, Kharuk *et al* 2011, Schulze *et al* 2012). Larch have a higher growth rate than does *P. sylvestris*, affording them an advantage in biomass accumulation following disturbance where both



species survive. In our simulations, larch are dominant in biomass for conditions of warming climate and fire across the broad Siberian region. With fire, *Pinus* spp. have a similar mean biomass under historical and warming climate conditions (figure S6). This similarity indicates that while *P. sylvestris* may be fire tolerant, its growth rate is not fast enough to result in increased biomass following fire when in competition with larch. These results match findings of Schulze *et al* (2012) for studies in central Siberia, of Kharuk *et al* (2011) for northern Siberia, and of Schulze *et al* (1995) for eastern Siberia within the Lena basin, all of which found that fire cycle is essential in maintaining larch dominance. Field and remote sensing studies in larch forests of far northeastern Russia found a range of post-fire tree survival with biomass accumulation varying according to the age of surviving stands (Berner *et al* 2012). These results demonstrate that the ecosystem response to fire derives from individual-tree attributes, as both species and individual tree size are vital for determining fire mortality.



Though there have been improvements in modeling fire at the global scale, DGVMs do not consider complex age or size structure, nor species. The SPITFIRE model (Thonicke *et al* 2010) that captures vegetation mortality based on crown scorch and cambial damage has been used to improve fire simulation within multiple DGVMs (e.g. LPJ-LMfire (Pfeiffer *et al* 2013), ORCHIDEE (Yue *et al* 2014, Yue *et al* 2015), and JSBACH, the land portion of MPI (Lasslop *et al* 2014)). These DGVMs have shown fidelity in their ability to simulate historical global burned area and fire regimes with particular improvements within boreal regions where fire is strongly driven by climate variation. They all use PFTs to represent a group of similar species, which in the boreal region reduces the vegetation to a total of 2 or 3 PFTs depending on the model. DGVMs provide valuable tools for exploring fire impacts, but do not have the ability to track the complex interactions

among individual trees and species. Size structure is essential for determining accurate biomass estimation and tracking mortality in forest systems globally, which demonstrate different behavior based on transitions following disturbance (e.g. dominance of different species in the boreal zone in response to fire as presented in this manuscript, and transitions between forest and grassland in tropical systems (Hoffman *et al* 2012, Lehmann *et al* 2014)). With their ability to provide detail size structure and demography, individual species-based models, such as UVAFME, could be used alongside DGVMs to provide a complete picture of vegetation structure and composition in response to changing disturbance and climate.

Along with forest composition and structure, FRI is an essential driver of forest dynamics. There is strong variation in FRI in association with forest type and latitude, with the northern forests having periods as

Table 2. Bark thickness and characteristics by genus or species for trees across Russian boreal forests.

Genus or Scientific Name	bark thickness (cm bark per cm DBH)	deciduous vs. evergreen	conifer vs. broadleaf	general region of occurrence	number of species
<i>Abies</i> spp.	0.046	evergreen	conifer	Middle and southern Siberia into European Russia	3
<i>Populus</i> spp.	0.014	deciduous	broadleaf	various species; all of Russia	5
<i>Picea</i> spp.	0.022	evergreen	conifer	various species; all of Russia	4
<i>Pinus</i> spp.	0.03	evergreen	conifer	Siberia and Russian Far East	3
<i>Pinus sylvestris</i>	0.063	evergreen	conifer	southern Siberia and Russian Far East, European Russia	1
<i>Betula</i> spp.	0.021	deciduous	broadleaf	various species; all of Russia	8
<i>Acer</i> spp.	0.02	deciduous	broadleaf	European Russia, Russian Far East Amur region	4
<i>Larix</i> spp.	0.063	deciduous	conifer	Siberia and Russian Far East	5
<i>Tilia</i> spp.	0.02	deciduous	broadleaf	European Russia, Russian Far East Amur region	3
<i>Fraxinus</i> spp.	0.02	deciduous	broadleaf	European Russia, Russian Far East Amur region	3
<i>Ulmus</i> spp.	0.03	deciduous	broadleaf	European Russia, Russian Far East Amur region	3
<i>Quercus</i> spp.	0.03	deciduous	broadleaf	European Russia, Russian Far East Amur region	2
<i>Taxus cuspidata</i>	0.021	evergreen	conifer	Russian Far East Amur region	1
<i>Thuja orientalis</i>	0.021	evergreen	conifer	Russian Far East Amur region	1
<i>Kalopanax ricinif</i>	0.021	deciduous	broadleaf	Russian Far East Amur region	1
<i>Phellodendron amurense</i>	0.021	deciduous	broadleaf	Russian Far East Amur region	1
<i>Juglans mandshurica</i>	0.03	deciduous	broadleaf	Russian Far East Amur region	1
<i>Chosenia macrolepis</i>	0.03	deciduous	broadleaf	Russian Far East	1
<i>Carpinus cordata</i>	0.03	deciduous	broadleaf	Russian Far East Amur region	1
<i>Micromeles almifolia</i>	0.03	deciduous	broadleaf	Russian Far East Amur region	1
<i>Maakia amurensis</i>	0.03	deciduous	broadleaf	Russian Far East Amur region	1
<i>Syringa robusta</i>	0.02	deciduous	broadleaf	Russian Far East Amur region	1
<i>Alnus</i> spp.	0.02	deciduous	broadleaf	European Russia, Russian Far East Amur region	3
<i>Carpinus betulus</i>	0.02	deciduous	broadleaf	Small presence at western border of Russia and Belarus	1

Sources for parameter values: bark thickness adapted from Keane *et al* (2011); remaining parameters from Nikolov and Helmisaari (1992) and Hytteborn *et al* (2005)

long as 350 years between fires compared to the FRI of 20 to 60 years in the larch-taiga ecotone and southern Siberian mountains (Kharuk *et al* 2008, Ivanova *et al* 2010, Kharuk *et al* 2011, Soja *et al* 2006, Furyaev *et al* 2001, Ponomarev *et al* 2016). The map of burned area created by Schaphoff *et al* (2016), which utilized data from Sukhinin (2011) and Bartalev *et al* (2015), for the period from 1996 through 2010 agrees with the FRI data used in this study in identifying the southern Russian border as an area of high fire frequency. With classification based on burned area in large eco-regions the FRI data used for this study likely under-represent areas which locally have more frequent fires. This under-representation arises out of the temporal limitation of using the available 13–14 years of data in a region known to have extreme inter-annual variability in burned area and FRI (Soja *et al* 2006, Ivanova and Ivanov 2005, Kharuk *et al* 2011, Schaphoff *et al* 2016). By using the percent stand

mortality as a determinant of mean fire intensity, UVAFME can simulate infrequent stand-replacing fires, as well as frequent low-level fires. The combined use of the detailed percentage of stand mortality of Krylov *et al* (2014) in conjunction with the broad eco-region FRI dataset allows for simulated fire intensity, and thus tree mortality, to be informed by the more detailed dataset, helping to reduce uncertainty associated with the FRI. Future analysis, however, will calculate FRI across smaller areas, as this may improve representation of FRI by capturing local areas with more frequent fires.

To determine how forest dynamics across the region might respond to a shorter FRI (i.e. a higher fire frequency), scenarios 2 and 4 are run with the longest FRI reduced to 350 years based on studies by Soja *et al* (2006), Kharuk *et al* (2008), Ivanova *et al* (2010), Kharuk *et al* (2011) and Ponomarev *et al* (2016). The results from these reduced FRI scenarios show that

total mean biomass increased for both the reduced FRI fire scenario, to 86.11 tC ha^{-1} compared to the previous mean of 82.06 tC ha^{-1} with the eco-region-determined FRI, and for the altered climate with reduced FRI fire disturbance to $119.17 \text{ tC ha}^{-1}$ from the previous mean of 112 tC ha^{-1} with the eco-region-determined FRI. Similar to the scenarios which used the eco-region FRI, the increase in biomass is from an increase in larch (figure S7). The similarity in results using a reduced FRI in comparison to those of the eco-region derived FRI suggests that competitive dynamics for resources (i.e. water resources), growth rate, and fire tolerance are key drivers determining biomass accumulation and species dominance.

This version of UVAFME does not contain a feedback between vegetation and fire, nor does it track the impact of fire on the soil layers. Many studies have suggested a relationship between regional fire dynamics, species composition, and fuels (Rogers *et al* 2015, Kukavskaya *et al* 2014, De Groot *et al* 2013, Berner *et al* 2012, Schulze *et al* 2012, Johnstone *et al* 2010a, Furyaev *et al* 2001). The implications of this connection suggest that if there is a shift in species across Russia, there may be a corresponding shift in fire regime. For such a shift in fire regime to occur there would first be a conversion of vegetation in response to altered climate or fire conditions. Shifts in previously predictable forest states in response to altered fire and climate regimes are already being observed in the boreal forests of North America (Johnstone *et al* 2010b) and Eurasia (Cai and Yang 2016). Feedbacks between the soil state, existing species, and fire severity determine the resilience and stability of the boreal forest (Johnstone *et al* 2010a, Johnstone *et al* 2010b). Future modeling work which adds a feedback between vegetation and fire by tracking changes in size and moisture of fuels and soil layers would help to better resolve this possibility while preserving the ability to simulate novel species combinations. It is expected that low to mid-severity fires, which create a thin organic layer promoting warmer soil temperatures and eliminating moss, would favor larch, as moss and thick duff are a barrier to regeneration (Alexander *et al* 2012, Sofronov and Volokitina 2010). In contrast, high severity fires which expose mineral soil are expected to favor the regeneration of deciduous species (Johnstone *et al* 2010b, Cai and Yang 2016). Given the results of this study we expect these additional interactions to maintain larch regeneration, except in cases of high severity fire, which may favor deciduous broadleaf species.

The shifts in species composition and stand structure predicted in this study have the capacity to impact both the local and regional energy budgets through changes in surface albedo, soil moisture, and thus heating/cooling through sensible and latent heat fluxes (Betts 2000, Chapin *et al* 2000, Liu *et al* 2005, Liu and Randerson 2008, Jin *et al* 2012, Rogers *et al*

2013), as well as the permafrost-C-climate feedback (Lorant *et al* 2016). Boreal forest composition and stand age have been demonstrated to have varying effects on net radiation and albedo, with magnitudes that have the capacity to affect climate locally and regionally (Amiro *et al* 2006, Liu *et al* 2005, O'Halloran *et al* 2012). Because larch is deciduous, the seasonal component and presence of snowfall will be important in evaluating the net effect of vegetation change on the energy budget, as this genus has a particularly elevated albedo in snowy conditions (Betts and Ball 1997, Hollinger *et al* 2010). These local- to global-scale radiative effects of pre- and post-fire forests within Russia emphasize the importance of characterizing the post-disturbance forest as well as the importance of using individual tree-based models to make predictions about future forest conditions.

Conclusion

Fire has long been recognized as a critically important driver of compositional and structural dynamics within the boreal region, and exploration of this disturbance driver becomes more important as fire is expected to become more frequent and more severe with warmer and drier climate conditions. Because UVAFME explicitly tracks individual trees of multiple species as they compete for resources through time, it can be used as a tool to evaluate the response of the boreal forest to fire under conditions of historical and altered climate. Results suggest that altered climate conditions allow for increased accumulation of biomass, but that fire disturbance creates a competitive situation in which the deciduous conifer larch maintain dominance across the region due to their high growth rate and tolerance to fire. Fire disturbance with altered climate conditions increases stand turnover creating a bimodal distribution of age cohorts across the region with a peak of mature older stands with a mean stand age of 280 years and productive maturing stands with a mean stand age of 100 years. The changes in biomass and age distribution are associated with a more complex distribution of tree height associated with increased turnover, growth, and stand density. These results suggest that species and tree-size level interactions are important in capturing the response of forests to changing climate and fire.

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