PAST AND FUTURE IMPACTS OF CLIMATE CHANGE ON BOREAL

FOREST TIMBER SUPPLY

AARON BRECKA

ABSTRACT

The boreal forest is home to a thriving forest industry which requires stable, long term timber to remain viable. Anthropogenic climate change, caused by the release of greenhouse gasses, is occurring rapidly in northern locations. Climate change impacts the boreal forest in many different ways and has the potential impact forestry operations considerably. While there has been significant research on both climate change and the boreal forest, few studies combine both topics to include long-term timber supply. Knowledge gaps exist in terms of how ecological impacts from climate change will affect forestry, particularly in terms of net biomass, species compositions, forest disturbances and species migrations. There is also a lack of timber forecasting studies that utilize forest disturbances and implement drought mortality. Throughout this thesis, these key areas are addressed.

We first conducted a literature review and synthesis of the impacts of climate change on boreal forest timber supply. We found that the disparity between migration rates of tree species with ongoing climate change may reduce the overall forest area of the boreal long term. Regional forest disturbances are increasing in frequency and intensity, affecting harvestable volumes and timber quality. Species compositions are changing; favoring early successional conifers and deciduous broadleaf species because of new local climates and more frequent disturbances. Most importantly, net biomass is likely in decline since regional increases in growth are outweighed by general increases in overall tree mortality. Our synthesis concluded that considerable reductions in the quality and quantity of boreal timber supply are likely to occur in the near future without forestry adaptation strategies or climate mitigation measures being implemented.

We then simulated four climate change scenarios in three boreal forest regions to test the effect on long term timber supply and the success of two harvesting intensities. By adding

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annual, species specific, drought-induced tree mortality to a previously published landscape model, we sought to more completely study this important topic. Our results show long term declines in aboveground biomass, regional increases in tree mortality (from fires, insects and drought), and species composition shifts favoring broadleaf and temperate forest species. Our area-based harvesting prescriptions show that with lower harvesting intensity, consistent harvest levels area more likely to be maintained. However, our most severe climate forcing shows considerable reductions in aboveground biomass and harvested biomass. These findings necessitate action for mitigation of climate change and forestry adaptation strategies to cope with negative climate impacts.

In summary, climate change considerably impacts the future success of boreal forestry. Our review of recent literature suggests that the consequences of climate change far outweigh the benefits. Our simulation results show annual biomass levels generally declines, especially in extreme future climates. Continued study and urgent management actions are needed to successfully adapt forest industry to the pressures of climate change.

Key words: climate change, boreal forest, aboveground biomass, forest disturbances, forestry, harvest operations

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NOTE

This is a manuscript-based thesis; chapters were written based on the submission requirements of targeted journals. Formatting and reference styles may vary.

Chapters:

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3. Brecka, A. F. J., Boulanger, Y., Searle, E. B., Taylor, A. R., Shahi, C., and Chen, H. Y. H. 2018. Above ground biomass loss from ongoing climate change compromises harvests across three Canadian boreal regions (in preparation)

CHAPTER ONE: GENERAL INTRODUCTION

Climate worldwide is experiencing changes from historical averages, trending towards warmer temperatures, greater atmospheric CO₂ concentration and shifting precipitation regimes (IPCC 2014). Changes in climate are experienced globally, however, the impact on forest health varies locally (Kellomäki 2016). Northern areas, notably the boreal forest, are expected to experience more drastic changes in climate compared to southern regions (Diffenbaugh and Field 2013) for which they may not have the adaptive capacity to handle (Bonan 2008). For example, climate in Canada is projected to continue warming over the next 40-50 years though precipitation regimes are more difficult to predict. This is a result of the complexities associated with moisture trends and methods used to forecast precipitation (Dai 2012). This will have impacts on many ecological processes and forest dynamics since climate is influential to boreal forest health (Gauthier et al. 2015a). Noteworthy changes include: site suitability for tree species (D'Orangeville et al. 2016), species composition (Searle and Chen 2017a) and boreal biome shifts (Beck et al. 2011), forest productivity (Chen and Luo 2015a, Girardin et al. 2016a), and forest disturbance regimes (Flannigan et al. 2009, Weed et al. 2013). Continued study of climate effects on boreal forest dynamics is necessary for a complete understanding of its implications.

Changes in forest dynamics and ecological processes pose problems for environmental management and forest operations across the global boreal forest. For hundreds of years, forestry has been practiced in boreal forests and currently is one of the most important industries in terms of providing jobs and exporting wood products to global markets (NRTEE 2011). Successful industry is driven by stable and predictable timber supply; this is inevitably impacted by climate change. Though the productivity of forestry may be expected to increase regionally from climate change, the overall economic viability of boreal forestry will likely be stressed. Lower market

prices from a flood of wood products (Sohngen and Tian 2016) and the increased cost of forest operations from shifting weather patterns could pose future problems (Gauthier et al. 2014, Rittenhouse and Rissman 2015). Reduced fiber and wood quality from increased growth, disease and insects can cause problems in the wood product manufacturing facilities (Lempriere et al. 2008). As well, altered species compositions (Hanewinkel et al. 2010) and the shift of forest biomes following climate change have been shown to greatly reduce the value of forest land over time (Hanewinkel et al. 2013). Understanding the full impacts of climate change is vital to maintaining a stable forest industry and resource-based economy.

There has been considerable research done on the impacts of climate change on boreal forest timber; however, there are notable gaps in our current knowledge. Complete syntheses of this issue are either older (Kirilenko and Sedjo 2007), or lacking the connection to forestry implications (Price et al. 2013). Modelling studies simulating long term timber supply in the boreal forest often are done without forest disturbances (Alam et al. 2008, Kellomäki et al. 2008) or important drought considerations (McKenney et al. 2016). These shortcomings need to be rectified to properly inform forest industry and clearly study this issue.

We begin with a detailed and comprehensive literature review of the challenge climate change poses to forestry operations and management practices. We examine the different ways that climate is affecting the boreal forest, the impact that subsequent changes will have on forest industry, potential steps to mitigate negative impacts, and future areas for continued and necessary research. From there, we conducted an analytical study simulating three boreal forest regions under different climate forcings. We focused on how ecological changes from new climate (especially drought) impacted the overall harvested biomass throughout our landscape model. This developed projections for wood supply in three boreal regions and implications to

harvesting operations. Our findings are applicable to the entire boreal forest since there are ecological similarities throughout this biome and provide timely information on the impacts of climate change on boreal forestry.

CHAPTER TWO: CLIMATE CHANGE IMPACTS ON BOREAL FOREST TIMBER SUPPLY

Abstract

Recent studies have assessed the ecological effects of climate change on boreal forests; however, our understanding of the economic impacts of climate change on timber supply remains limited. Forestry is an important boreal industry; hence, it is necessary to better understand the ecological impacts that directly and indirectly affect this sector. We reviewed published literature concerning ecological impacts of climate change on biome shifts, regional forest disturbances, and tree growth, mortality and species compositional shifts in established forest stands. Subsequently, we examined how each factor influences timber supply and forestry. Tree species ranges have been and will continue migrating north to find more suitable growing conditions, but at a slower rate than climate change. Biome shifts from forests to shrub or grasslands may occur under persistent drought conditions. Warmer temperatures and lower climate moisture availability increase forest disturbances; notably fire and insect outbreaks, creating younger forests dominated by pioneer species and limiting harvestable material. While tree growth and mortality rates are spatially variable across established forest regions, tree mortality has temporally increased with climate change; accompanied by reduced growth or increased growth at a rate lower than mortality loss, resulting in a reduced rate of volume accumulation and timber available for harvest. Moreover, climate change favors pioneer species (Pinus spp. and Populus spp.) over late successional species (*Picea* spp. and *Abies* spp.). Our findings suggest that climate change has strong negative effects on boreal timber supply but may prompt operational adaptations, opening opportunities for forest industry to incorporate species such as Populus.

Keywords: biome/ species compositional shift; forest disturbances; forest management; harvest volume; productivity; tree mortality rates

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Introduction

The boreal forest is one of Earth's largest forest biomes, with an area of 1.2 billion hectares; stretching from Russia, across Scandinavia and throughout North America (van Lierop et al. 2015). The boreal forest constitutes approximately 30% of the world's most densely forested area (Crowther et al. 2015), while storing nearly half of the global forest carbon, primarily within soils (Soja et al. 2007, Gauthier et al. 2015a). This forest region is immensely critical to the global timber products market. Roughly 33% of lumber and 25% of paper exports in the global market originate from the boreal forest (Gauthier et al. 2015a). However, most ecological functions and processes, such as tree growth, proceed slowly in the boreal forest due to short growing seasons with severe, cold winters (Kellomaki 2000, Fettig et al. 2013). Despite similar presences of tree genus (*Picea, Pinus, Populus, Larix,* and *Betula*), disturbance regimes and management histories and strategies differ between Eurasian and North American boreal forest regions (Gauthier et al. 2015a, Rogers et al. 2015, Schaphoff et al. 2016).

Climate change has a profound impact on global forestry, and continues to accelerate with increasing anthropogenic greenhouse gas emissions (IPCC 2014). Higher latitudinal areas are expected to undergo the largest increases in temperature (Diffenbaugh and Field 2013) and experience variable shifts in precipitation regimes (Gauthier et al. 2015a, Reyer et al. 2015). Changes in site conditions and frequency of disturbance regimes have also affected the boreal forest as a result of climate change (Price et al. 2013). Understanding climate change impacts on boreal forest dynamics and timber supply is crucial to the continued viability of boreal forest industry.

Timber supply, defined in this review as the quality and quantity of standing timber available for harvesting, directly impacts the forest industry; in both the short run and long run.

The difference between the two timelines is the amount of time required to transition between capital investments in equipment and product development (Zhang and Pearse 2011). Short run supply occurs within a timeframe that is too short for industry to adjust their capital stock and standing timber inventory; slower growth rates and higher rotation ages (particularly in the boreal forest) slow this process. This lack of flexibility means that industry can only adjust their variable inputs (fuel and labour) or utilize their facilities more intensively. In the long run, industry is able to reinvest in profitable areas and change supply to better suit the market (Zhang and Pearse 2011). The duration of the long run depends on products (lumber or engineered wood products), industry (logging or pulp and paper) and geographic location (boreal forest or tropical). However, long run timber supply is difficult to anticipate because of a number of factors that affect trees: growth and mortality rates, disturbances, harvesting rotation schedules and demand of forest products (Zhang and Pearse 2011). Climate change further complicates this process of product evaluation and timber supply (Sohngen 2014). Analyses of the impacts of climate change on boreal timber supply should involve both short term and long-term research to properly forecast the implications of ecological change on the economy.

Recent advances have been made toward understanding climate change impacts on forest productivity, species range shifts and forest disturbances (Boisvenue and Running 2006, Kurz et al. 2008, Hofgaard et al. 2013), though there have been few publications synthesizing these impacts. Several published reviews on the boreal forest and climate change include: global boreal forest health (Gauthier et al. 2015a), impacts to North American forests and ecosystems (Fettig et al. 2013, Price et al. 2013), implications to forest carbon balance (Kurz et al. 2013, Schaphoff et al. 2016), forestry adaptation practices (Gauthier et al. 2014), and a recently proposed concept of using biodiversity to mitigate climate change impacts on ecosystem functioning (Hisano et al. 2018). However, the impact of climate change on industrial timber supply and its economic implications is an area that demands continued investigation. The existing forestry related reviews suggested that there would likely be increases in global timber supply (though high regional variation) from greater forest productivity (Kirilenko and Sedjo 2007) leading to probable decreases in wood product prices and demand (Sohngen and Tian 2016).

Modeling studies have addressed the economic impacts of climate change in specific countries or regions (Mendelsohn et al. 2000, Solberg et al. 2003, Ochuodho et al. 2012), whereas others have considered the forest industry in a global context (Sohngen et al. 2001, Lindner et al. 2002, Perez-Garcia et al. 2002, Tian et al. 2016). Older global timber models suggest higher timber productivity from tropical regions, compared to temperate regions with ongoing climate change (Sohngen et al. 2001, Perez-Garcia et al. 2002), whereas, the latest global timber model predicts a similar overall increase in forest productivity in both regions (Tian et al. 2016). Generally, timber resources are expected to increase across the globe and result in lower product prices (Sohngen and Tian 2016, Tian et al. 2016). However, empirical evidence from tropical forests revealed that climate change has led to greater biomass loss through tree mortality than growth gain, resulting in less standing biomass (Brienen et al. 2015). Further, these studies typically simulated consistent future disturbance regimes possibly leading to yield inaccuracies (McKenney et al. 2016). Nevertheless, these modelling studies do not specifically analyze the productivity of the boreal forest under climate change; rather they have focused on temperate and tropical forests. Therefore, modeling climate change impacts on boreal forest timber supply remains needed.

The purpose of this review is to synthesize the impacts of climate change on boreal forest dynamics directly relating to available timber supply (Figure 2-1). Specifically, this review will: i) examine how climate change has affected boreal ecological processes at a variety of spatial scales (biome, regional, stand and individual levels), since the impacts to ecological processes differ across scales (McGill 2010), ii) analyze how these ecological changes will impact timber supply, iii) detail management adaptations, and iv) identify gaps in current knowledge for future research.

Literature selection criteria

Papers were systematically selected for this review via the online search engine ISI Web of Science. The reference sections of selected papers were also reviewed for relevant literature. This was done in order to capture all applicable and available literature. Key words including climate change impacts, boreal forest timber supply, and forest sector implications were used in various combinations for the search. Because of the rapid development of the study topic, we focused on reviewing recent literature; largely post 2000. Literature was subsequently analyzed, initially by title and abstract, and then through more in-depth reading. Titles were selected by having some mention of climate change and timber supply associated ecological processes including biome shift, range shift, species composition, disturbance, growth, and mortality. Papers that did not explicitly address climate change were excluded. Both reviews and original articles were considered to gather evidence from a range of perspectives. Topics were divided into themes and research was synthesized to explain the various ways climate change impacts boreal timber supply (Figure 2-1).

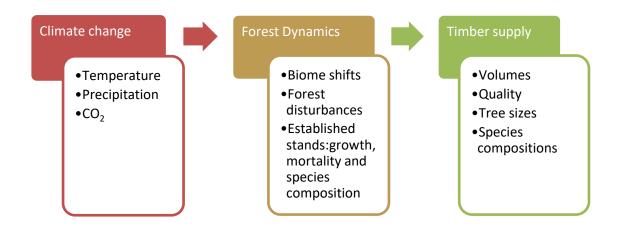


Figure 2-1. A simple representation of the focus for this review and the related factors and variables associated with each. Climate change (changes in temperature, precipitation and CO₂ levels) will influence forest dynamics (growth, mortality, species range and disturbance interactions) which then impact the volume, quality, and species of timber supply available for industrial harvest and use in the boreal forest.

Biome shifts

Biome shifts represent a landscape's transition over time from one biome to another, such as forest biome to shrub land and/ or grassland biome (Beck et al. 2011). Biome shifts are adaptations that take place between vegetation types and contrasting climates (Donoghue and Edwards 2014); the process of transition is dependent on the state of an ecosystem and the speed of climate change. In high latitude systems, biome shifts have been observed over temporal scales of multiple years or decades (Beck et al. 2011). Climate is a key factor toward determining the geographic distribution of plant species (Fettig et al. 2013, Fei et al. 2017). As the climate changes, sites can become less suitable for certain plant species over time causing them to regress or die, whereupon other more suitable species take their place (Gonzalez et al. 2010). Biome shifts tend to occur along the edge of biomes (Davis and Shaw 2001), as evidenced by the

transition from forests to shrub lands under extended droughts (Anderegg et al. 2013, Donoghue and Edwards 2014). Most of the world's forests are regarded as being extremely vulnerable to biome shifts as a result of climate change (Gonzalez et al. 2010), which stresses the importance of understanding the risks of shifting biomes.

Boreal forests have been seen steadily migrating northward in response to global warming. Researchers have observed shifts in plant and animal species ranges for decades, signifying the effect of changing climate (Parmesan and Yohe 2003, Chen et al. 2011). Tree migration has been observed most clearly in areas with temperature extremes, such as the boreal forest and tundra regions. Boreal forests have been documented as steadily growing northward into areas that were previously tundra. In Alaska, spruce populations have been declining in areas that they previously thrived in, most likely as a result of water deficiencies from high vapor pressure deficits on photosynthesis (Beck et al. 2011). Similar forest migration and compositional changes are expected in Siberia; boreal species are predicted and recorded to be migrating into more northern locations (Tchebakova et al. 2011, Berner et al. 2013). In Norway, northern regions that were once previously tree line edge are now found to be forested areas; indicating the migration of tree species (Hofgaard et al. 2013). These tree species are now moving into cooler regions so as to escape areas with high vapor pressure deficits, as well as to access more water (Fei et al. 2017). It is expected that the tundra could lose up to 50% of its area from northward expansion of the boreal (Kirilenko and Sedjo 2007). In parallel with moving northward, southern boreal forests could retreat and shift to shrub lands or grasslands due to warming-induced climate moisture deficits (Allen and Breshears 1998). It remains, however, unclear whether the northward expansion of boreal forests matches its southward retreat.

Under rapid climate change, species ranges continue to shift (Pecl et al. 2017), which imparts profound environmental and economic implications. It was reported that the historic migration rate of tree species (~20-40 km per century) was far slower than the rate required to avoid changing climate envelopes (~300-500 km per century) (Davis and Shaw 2001). Recent findings estimate that tree migration rate is actually less than 100 m per year (Aitken et al. 2008) compared to the 160 km migration requirement for every degree of temperature increase (Thuiller 2007), highlighting the disparity in migration rate requirements. More recently, there was an estimated migration rate of 16.9 km per decade, away from the equator, and 11 m per decade in elevation; still significantly lower than the required migration speed (Chen et al. 2011). This may cause unknown environmental consequences in the functioning of our ecosystems. However, assisted migration may help mitigate the mismatch between slow natural migration rates and rapid climate change (Aitken et al. 2008).

Regional forest disturbance patterns

Boreal forests are characterized by natural disturbances, such as fires, fungi and insect outbreaks (Gauthier et al. 2015a), where forest disturbances have severe implications to timber supply. Insects are suggested to have the greatest effect on forest harvest volumes and quality; even more so than forest fires (Malmstrom and Raffa 2000, Logan et al. 2003), though recent findings have suggested that fires are more impactful (Hansen et al. 2013). For example, *Dendroctonus ponderosae* (mountain pine beetle) in Canada have impacted nearly 20 million ha of pine forest during their recent epidemic outbreak, which began in the 1990's, and are projected to continue infesting boreal forests as they move eastward (Dhar et al. 2016). Insect and diseases have also affected a much greater area than fires in North American temperate forests during 2003-2012 (van Lierop et al. 2015). Climate change is expected to increase the

frequency of forest disturbances for a number of reasons, acting on both biological agents and abiotic disturbances (Ayres and Lombardero 2000, Weed et al. 2013, Ramsfield et al. 2016). One of the most powerful ecological interactions in the boreal forest, similar to temperate regions, are disturbances coupled with on-going drought. By further stressing a system with a disturbance during an ongoing drought, the severity of the interactions can be intensified and the future health of the forest compromised if threshold levels are exceeded (Millar and Stephenson 2015). Though a natural feature of boreal forest dynamics, increased forest disturbances under climate change could have strong negative impacts on timber supply.

Biotic disturbances

Insects in the boreal forest are likely to benefit from climate change due to i) lower winter mortality rates (milder temperatures) and ii) lower resistance in trees from temperature and moisture stress (Weed et al. 2013). A tree's resistance to defend itself against insect and/ or pathogen attack is lowered from drought and higher temperature (Kurz et al. 2008, Millar and Stephenson 2015). As a result of these interactions, we are likely to see more widespread and devastating insect infestations in northern forests (Pureswaran et al. 2015). Though a slight decrease frequency in spruce bud worm has been forecasted due to the reduction in suitable hosts (Candau and Fleming 2011). An increased insect (*Ips spp.* beetles) susceptibility has been forecasted in Austria and has already occurred in Lithuania and Canada (mountain pine beetle) (Seidl et al. 2008, Alfaro et al. 2009, Ozolincius 2012). Insect outbreaks in Russia appear less studied than elsewhere, though reports indicate that silk moth (a major disturbance agent) has increased substantially over the last 20 years (Schaphoff et al. 2016). The effects of fungal tree diseases under climate change are less predictable, as there have been mixed results in studies; there could be increases in particular pathogens and reduced impacts from others (Pautasso et al.

2015). For the boreal forest, it is anticipated that diseases and insects will spread due to increasing temperatures and possibly have new species introduced through global trade (Sturrock 2012, Pautasso et al. 2015, Pecl et al. 2017). Though pest and pathogen disturbances may increase in frequency through improved climate conditions, drought events assist in determining which pest could inflict the most damage by influencing the section of the tree that insects and fungi target (e.g., foliar versus woody) depending on drought severity and method of pest damage (Jactel et al. 2012). Generally, as the severity of droughts increase, infestation by certain pests will be favoured in alignment with their mode of damage (e.g. wood borers performed best on drought stressed trees).

Abiotic disturbances

Fires are projected to increase in frequency and intensity under climate change, due to higher temperatures and decreased precipitation over many areas (Flannigan et al. 2005, Moritz et al. 2012). The potential area burned annually could increase dramatically in Canada (Girardin et al. 2009, Boulanger et al. 2014) and eastern Russia with continued dry conditions (Groisman et al. 2007). Greater quantities of dead wood from fungal mortality and insect infestations provide greater fuel availability for fires, increasing the likelihood of severe burns (Gillett et al. 2004, Flannigan et al. 2009). Drought and warmer conditions potentially cause greater tree mortality, which further increase the fuel available for fire ignition (Ruthrof et al. 2016). More frequent storms are expected with new weather patterns under changing climate, increasing the probability of lightning strikes igniting a fire (Flannigan et al. 2009, Shvidenko and Schepaschenko 2014). However, it has been suggested that fire frequency and intensity could be lowered, in certain areas, as a result of greater deciduous tree species composition since they are less flammable (Terrier et al. 2013). It is necessary to consider tree species when evaluating the vulnerability of forests to fire; North America and Eurasia have different dominant tree species, which results in a contrasting level of high intensity crown fires versus lower intensity fires (Rogers et al. 2015). Though there exist areas less prone to fire (e.g., larch and spruce swamps) that have much longer fire return intervals (Johnson 1992). The risk of increased fire to timber supply in the boreal forest across Canada is generally low in many regions; however, vulnerability increases with higher temperatures and lower precipitation in the future (Gauthier et al. 2015b). Other disturbances include storm related events such as wind throw, which may increase in severity and frequency due to stressed and weakened trees (Blennow et al. 2010, Peltola et al. 2010, Girard et al. 2014), coupled with more frequent climate extremes (IPCC 2014).

Growth, mortality, and composition in established forest stands

Identifying trends in growth, mortality and species compositional shifts within local stands is necessary for gaining a clear understanding of the impacts of climate change on timber availability. Timber volume, or biomass, that is available for harvest represents the accumulation of net growth (growth minus mortality), while species composition reflects the types of timber, an aspect of timber quality, that are available for harvest.

Growth and mortality

Tree growth can be quantified at both the individual tree and stand levels, and described in a variety of ways, through increasing: size, biomass, gross primary production (GPP, the total amount of carbon accumulated from photosynthesis), or net primary productivity (the difference between GPP and plant respiration) (Luyssaert et al. 2007). We will focus on tree growth in terms of increasing size or biomass accumulation because both relate to volume (Chojnacky et al. 2013). Growth in northern regions typically improve as they warm, in contrast to dryer

southern areas (Boisvenue and Running 2006, D'Orangeville et al. 2016). However, there are instances of the opposite occurring (Table 2-1) (Boisvenue and Running 2006, Luyssaert et al. 2007, Zhao and Running 2010). Rising atmospheric CO₂ concentrations may have contributed to improved tree growth more than temperature at the stand level (Brienen et al. 2015, Chen et al. 2016a), though it is unclear which factor is most influential in the boreal as it is difficult to partition their effects (Price et al. 2013, Girardin et al. 2016a). Further, growth may fluctuate quickly in forests due to annual variations in temperature and precipitation (Toledo et al. 2011, Pretzsch et al. 2014). Throughout Europe, Picea abies (Norway spruce) has experienced greater growth rates, stand volumes and stock accumulation over the last 100 years because of changing climate (Schlyter et al. 2006, Pretzsch et al. 2014). Individual tree growth rates in Canadian boreal tree species are expected to increase with climate change (Huang et al. 2013), though significant spatial variations in historical growth rates show no collective growth gain across the landscape (Girardin et al. 2016a). Evidence of increased growth rates have been shown both in simulation scenarios (Nabuurs et al. 2002, Bergh et al. 2003), and in historical/ observational studies in certain areas (Kauppi et al. 2014, Pretzsch et al. 2014). In western Canada, however, increased tree growth tends to be restricted to young stands (Chen et al. 2016a) and/ or broadleaf dominated stands (Chen and Luo 2015a). Coupled with rising CO₂, global warming with longer growing seasons (Boisvenue and Running 2006, Linderholm 2006) could be attributable to the observed increase in tree growth (Table 2-1).

Table 2-1. Global and boreal evidence of variation in growth productivity as a result of climate change (positive influence of climate change, negative influence, and reports of mixed findings).

Positive	Study area	Methods	Findings	Causes
Bergh et al. (2003)	Scandinavia	Growth model simulations	Increased growth, provided water not limited	Longer growing seasons
Berner et al. (2013)	NE Siberia	Satellite and tree ring data	Productivity influenced by seasonal temp. and moisture	Response varies seasonally, warmer temp. and enough precip. needed
Boonstra et al. (2008)	NW Canada	Tree ring data	Higher temperatures increased growth as did the fertilizer	Cold and nutrient deprived region
Luyssaert et al. (2007)	Global	Global carbon flux database	Biomass accumulation in boreal is slower than global average	Saturation point of 10°C and 1500mm
Kauppi et al. (2014)	Finland	National Forest Inventory permanent sample plots	Growth rates increased	Longer growing seasons
Nabuurs et al. (2002)	Europe	Process based forest growth simulation	Net annual increments increased in response to climate changes	Large uncertainty surrounding future ecological changes
Pretzsch et al. (2014)	Central Europe	Long term plot sampling	Climate change increases growth rates and stand volume	Favorable climate conditions
Sato et al. (2016)	E Siberia	Simulation model	Increase in larch forest growth	More growing days, constant moisture
Ciais et al. (2008)	Europe	NFI and timber harvest statistics	Biomass accumulation increased	Increase in net primary production
Negative	Study area	Methods	Findings	Causes
Aakala and Kuuluvainen (2011)	NW Russia	Tree ring sampling	Reduced tree growth	Drought conditions
Beck et al. (2011)	Alaska	Satellite and tree ring data	Decline in southern productivity	Hydraulic limitations from high vapor pressure deficits
Chen and Luo (2015a)	W Canada	Forest inventory permanent sample plots	Net biomass declines	Tree mortality outpaces growth
Chen et al. (2016a)	W Canada	Forest inventory permanent sample plots	Net biomass declines in older stands	Less productivity in older stands
Luo and Chen (2015)	W Canada	Permanent sample plots	Biomass losses even when water is not limited	Competition

Barber et al. (2000)	Alaska	Tree sampling and ring data	Decreased growth of white spruce	Heat and drought
Girardin et al. (2016b)	Canada	Tree ring data in (climate) carbon model	Loss of black spruce productivity	Higher temperatures
Ge et al. (2010)	Finland	Integrated process-based model	Lower stem volume production	Drought and less nutrients
Ciais et al. (2005)	Europe	Eddy covariance	Decrease in productivity in European forest	High temperature
Zhao and Running (2010)	Global	Satellite imaging and drought index	Reduced global NPP-may have increased short term NPP in northern regions	Drought stress and continued drying from high temp.
Montwe et al. (2016)	W. Canada	Provenance trials	Northern seed sources' growth depressed	Not adapted to drought conditions
Mixed	Study area	Methods	Findings	Causes
Boisvenue and Running (2006)	Global	Literature review	Increases and decreases in productivity, greater changes in northern areas	Longer growing season, need adequate water
Lloyd et al. (2011)	Siberia	Tree ring analysis	Better growth in north than south	Different responses to temp. and precip.
Sitch et al. (2008)	Global	Climate carbon model and Dynamic Global Vegetation Model	Forests either sources or sinks in future: boreal projected to lose forest area	Various climate inputs based on scenarios
Ge et al. (2011)	Finland	Process based ecosystem model	Better growth in north than south	Different responses to temp. and precip based on species and latitude
Girardin et al. (2012)	Canada	Plot level tree growth analysis	Heterogeneous growth responses between species and demographics	Areas with more growth may not exceed the added mortality and site stresses
Huang et al. (2013)	Canada	Tree ring data and modeling	Better growth in north than south boreal	Temperature increase less severe in northern areas promoting growth
D'Orangeville et al. (2016)	Canada	Tree ring analysis	Latitude and climate constrain growth	Different responses to temp. and precip.
Peñuelas et al. (2011)	Global	Tree ring isotopic and growth data	Enhanced water use from higher air CO2 didn't always lead to better growth in boreal regions	Other factors restrained growth

Decreases in available climate moisture lead to droughts that lower the growth rate and raise mortality in forests (Table 2-2) (Bennett et al. 2015). Drought can be observed as an event, such as particular years of severely decreased precipitation, or as a general reduction of moisture in the area over time from changes in precipitation regimes (Dai 2011). Drought is possibly the single most influential factor in the growth of trees (Figure 2-2) (Allen et al. 2010b, Anderegg et al. 2013). Studies reporting increased tree mortality and/ or declines in growth often cite drought as the primary factor (Barber et al. 2000, Ciais et al. 2005, Zhao and Running 2010).

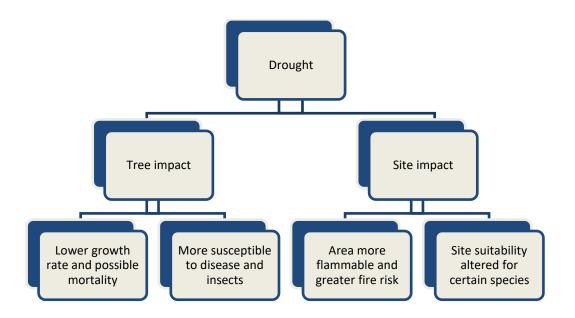


Figure 2-2. Some of the many impacts of drought in a boreal forest stand. Drought can both affect the site by making it dryer and the trees by stressing them. There are four possible end results during a drought occurence that are described.

Trees require more water under higher temperatures in order to meet evapotranspiration demands but are unable to meet these requirements under drought conditions (van Mantgem et al. 2009, Peng et al. 2011). What is even more concerning, in relation to the forest industry, is that drought has been shown to cause greater rates of mortality in larger diameter trees (Bennett et al. 2015).

Mortality Evidence	Study Area	Туре	Methods	Results
	Alea	Type	Methods	
Allen et al. (2010a)	Global	Review	Literature synthesis	Increased tree mortality both globally and in boreal regions
Allen et al. (2015)	Global	Review	Literature synthesis	Droughts have profound impact with high temp. though uncertain future in boreal
Anderegg et al. (2013)	Primarily NA	Review	Literature synthesis	Increase tree mortality impacts ecosystem functions and services, post mortality recovery takes decades in boreal settings
Barber et al. (2000)	NW USA	Article	Tree ring sampling	Depressed growth from drought
(Ciais et al. 2005)	Europe	Article	Eddy covariance	Increase tree mortality and more profound drought effect with high temp.
(Clark et al. 2016)	USA	Review	Literature	Drought intolerant boreal/ temperate species replaced by tolerant temperate
(Dai 2011)	Global	Review	Drought indices	Severe drought occurrences generally expected globally most boreal regions may have adequate precip.
(Hember et al. 2017)	NA	Article	PSP data, climate data and mortality modeling	Water-stressed tree mortality not likely increasing with tree size
(Houle et al. 2016)	E. Canada	Article	Nutrient and precipitation sampling	Decreased site quality from nutrient loss through drought
(Michaelian et al. 2011)	SW. Canada	Article	Monitoring plots	Increase tree mortality from drought
(Peng et al. 2011)	Canadian Boreal	Article	Permanent sample plots	Increase tree mortality from drought
(Trenberth et al. 2013)	Global	Review	Literature synthesis and comparison	Disparity in conclusions drawn on the future of drought, data bias in northern areas

Table 2-2. Global and boreal evidence of tree mortality as a direct result of drought from climate change.

This is a contested point, however, with different methodologies yielding contrasting evidence concerning the susceptibility of trees to drought based on their height (Greenwood et al. 2017, Hember et al. 2017). In boreal forests, after properly accounting for the increased tree mortality probability with stand ageing (Luo and Chen 2011), Luo and Chen (2013) demonstrated that climate change-induced tree mortality is greater in young stands than in older stands. More importantly, even without reduced climate moisture availability, tree mortality increases with climate change in boreal and other biomes (Brienen et al. 2015, Luo and Chen 2015), which were attributable to: reduced tree longevity, increased competition and/ or direct heat stress associated with global warming (Allen et al. 2015). Other mechanisms, including hydraulic failure, carbon starvation, greater susceptibility to biotic disturbances, and increased losses of nutrients, could also contribute to widespread increases in tree mortality worldwide (Allen et al. 2010b, Brienen et al. 2015, Rowland et al. 2015, Houle et al. 2016). Global warming coupled with continued drought occurrence could remove significant harvestable volumes from the boreal forest.

While intergovernmental reports demonstrate the increasing severity of droughts in the world (IPCC 2014), the future of drought in the boreal forest is largely uncertain due to varying reports that differ in data sets and drought indices used, as well as the unpredictability of future events (Trenberth et al. 2013). For example, historically similar total amounts of precipitation may fall in two areas but with different frequencies and individual amounts (Dai 2012, Trenberth et al. 2013). Annual precipitation levels may be identical, but droughts may occur between rain events, or a higher proportion of precipitation may fall as snow. Though there are conflicting reports of future droughts, they are likely to become more frequent in certain areas due to increased temperatures and varying precipitation regimes, making forests more vulnerable (Dai

2012, Allen et al. 2015). It is important to note that although climate change may increase tree growth in some cases, studies that simultaneously examined growth and mortality in response to climate change have shown that aboveground biomass loss is far greater than biomass gain from increased growth, reducing net growth in both boreal and tropical forests (Brienen et al. 2015, Chen and Luo 2015a, Chen et al. 2016a). This indicates that, overall, climate change has reduced biomass or timber volume available for harvest. Ongoing climate change with more warming and drought might further reduce timber volumes available due to high mortality losses.

Composition shifts

In general, tree species respond to climate change differently (Drobyshev et al. 2013). As temperature regimes shift, northern latitudes may have unsuitable environments for certain species (Perie and de Blois 2016). In the event that regional average temperatures exceed 2 °C, deciduous broadleaf trees are expected to become more dominant in Russia, whereas conifers may regress (Schaphoff et al. 2016). In Canada, *Picea mariana* (black spruce) populations have declined due to increased temperatures, making northeastern locations more suitable for their growth because of greater precipitation (D'Orangeville et al. 2016, Girardin et al. 2016b). More frequent drought occurrences favour, or have lesser impacts, on drought tolerant species such as *Pinus* spp. (Anderegg et al. 2013, Chen and Luo 2015a, Luo and Chen 2015).

The increased frequency of disturbance regimes may also impact species available for harvest. Those species that are less adapted to disturbance, such as later successional species, would likely be pushed out of heavily disturbed areas in favor of more tolerant or faster growing pioneer species (Chen et al. 2009, Johnstone et al. 2010). Among pioneer species, vegetatively reproducing *Populus* and *Betula*, are likely better at colonizing heavily disturbed sites (Chen et al. 2009, Ilisson and Chen 2009, Price et al. 2013), though deciduous trees do not thrive in areas of severe drought (Michaelian et al. 2011). Moreover, in established forest stands without stand replacing disturbances, climate change has also shifted species composition towards a greater proportion of early successional species such as *Pinus, Populus* and *Betula* at the expense of *Picea* and *Abies* in western boreal forests of Canada (Searle and Chen 2017a).

Implications to boreal forestry

Climate change influences the quantity and quality of boreal forest timber supply in different ecological ways, particularly in the three ways discussed above. Biome shifts highlight a disparity between southern forest mortality and northern forest migration rates. Northern forests are not migrating fast enough to keep up with favorable climate zones (Aitken et al. 2008), nor are they adapted to new southern boreal climate conditions (Allen and Breshears 1998). This may lead to reductions in overall productive boreal forest growing area due to the mismatch between the two (Anderegg et al. 2013, Hanewinkel et al. 2013, Tchebakova et al. 2016). Rapid climate change over the next century will likely intensify this problem (Donoghue and Edwards 2014). Reduced productive forest area has major implications to future timber supply and the forest industry. Since temperatures are higher along the southern edges of the boreal, where negative effects of climate change are most pronounced (D'Orangeville et al. 2016), forestry operations may see significant alterations in harvestable volumes and species compositions (Hanewinkel et al. 2013).

Ongoing climate change contributes to the increasing frequency and intensity of biotic and abiotic disturbances in the boreal forest, and are factors in decreasing harvestable timber volumes (van Lierop et al. 2015). This will occur as a combination of insect, pathogen (Weed et al. 2013) and fire disturbances (Flannigan et al. 2005), which are compounded by regional drought events (Allen et al. 2015, Millar and Stephenson 2015). Risk averse managers should

account for disturbances, particularly fire, when forecasting timber supply impacts especially in vulnerable areas (Savage et al. 2010). Additionally, by changing the age class structure of the forest through shortened disturbance intervals, forest managers will have a more difficult time supplying mills with mature, harvestable wood (NRTEE 2011, Gauthier et al. 2015b, McKenney et al. 2016).

Growth rates at the stand level are expected to increase in areas not limited by decreased moisture availability because of rising CO₂ levels, warmer temperatures with longer growing seasons (Boisvenue and Running 2006), and being situated in northern locations (Kellomäki et al. 2008, Ge et al. 2011). Increased growth, however, does not necessarily result in improved timber volumes (Tian et al. 2016) if mortality losses are greater than growth gains (Chen and Luo 2015a, Chen et al. 2016a). Growth trends associated with climate change seem region and site specific, but generally with the historical limiting growth factor shifting from low temperature to low moisture levels in warmer northern areas (Berner et al. 2013, Charney et al. 2016). Across the boreal biome, some areas have become more productive while others less so, collectively canceling each other out (Girardin et al. 2016a). Because increased tree mortality is projected to outpace increased growth, accompany no growth gain or even reduced growth (Chen and Luo 2015a, Chen et al. 2016a), the net effect of climate change on biomass and timber production is negative in established forests (Reyer et al. 2017). These results differ considerably from most published articles on the topic of climate change and timber supply (Table 2-3) (Tian et al. 2016) and reviews examining climate change impacts on boreal forest productivity (Kirilenko and Sedjo 2007, Price et al. 2013).

The quality of timber supply is determined not only by age structure available for harvest (NRTEE 2011, Gauthier et al. 2015b), but also the availability of certain tree species. Coupled

with more frequent disturbances, an increased abundance of deciduous broadleaf species are reproducing at the expense of late-successional conifers (Ilisson and Chen 2009, Johnstone et al. 2010, Chen and Taylor 2012). In addition, species compositions in established forests are shifting to lower abundances of late successional spruce and fir, and may continue to decrease further over time (Searle and Chen 2017a), and may continue to decrease further over time (Kellomäki et al. 2008). A greater proportion of deciduous species may benefit a portion of forest industry that utilizes aspen, and especially pine, however later-successional conifers are generally preferred in pulp/ paper and lumber. This shift in composition may allow for the development of new wood industry products if a company's financial constraints are flexible enough to adapt to changing forest supply. Simultaneously, increased growth rates in softwood species actually decreases their mechanical properties, such as density and strength (Zhang 1994), because the growth rings are spread farther apart with a lower proportion of latewood to early wood (Zhu et al. 2007). By reducing mechanical properties and skewing species composition towards less favorable options, wood quality and the value of the forest may be lessened through climate change.

As the references in Table 2-3 show, conflicting understandings of climate change impacts to forestry exist. Many of the older studies show benefits to forest industry stemming from increased growth and forest expansion (Mendelsohn et al. 2000, Sohngen et al. 2001). In some cases, economic benefits are not realized because of the flood of timber into the market lowering prices (Perez-Garcia et al. 2002, Solberg et al. 2003) or because additional temperature increases caused productivity declines (Lutz et al. 2013). In the cases of negative forestry impacts, studies showing reductions in boreal forest area (Hanewinkel et al. 2013) or increases in forest disturbances (Tian et al. 2016, Reyer et al. 2017) result in lowered available timber. The

total economic implications of reduced timber are complex but a major factor is how dependent a region's economy is on forestry (Ochuodho et al. 2012).

The forest industry requires a consistent and predictable supply of timber in order to have viable operations. However, climate change will affect forestry operations in managed forest areas. This can include earlier ground thaw with a shorter winter harvest, and more frequent extreme weather (heat, rain and snowmelt duration) making fieldwork more dangerous (Rittenhouse and Rissman 2015). Changes in weather patterns impact forest companies through: inaccessibility to forestland from flooding, more frequent and higher costs on road repair, and damage to timber from snow, ice, or storms (DeWalle et al. 2003). These factors have important implications since winter harvesting of wetlands (spruce forests) may be shortened, while more frequent storms may impact the quality of the timber and structure of forest roads (Lempriere et al. 2008). This is an important scenario since one of the greatest costs in boreal forestry is the construction and maintenance of roads. Higher moisture conditions from warmer winters and continued snow melt can lead to increased export of mercury and organic matter from the site if driven on by vehicles, causing environmental damage (Keskitalo et al. 2016). As climate continues to change, management may also be hard pressed to meet sustainability and conservation objectives (Gauthier et al. 2014). To continue having a profitable and successful forest industry, adapting management to the impacts of climate change is essential.

Area	Year	Methods	Results	Impact to Forestry	Economic Implications
Global ¹	2016	Climate data from the MIT Integrated Global Systems Model in a DGVM. NPP and die back are then used in an updated Global Timber Model (GTM).	Increases in global NPP in both temperate and tropical forests, though increases in dieback occur as well. Timber increases resulting in decreased global timber prices.	Advantage	Timber Prices
Global ²	2001	Climate data from two climate intensity models used in BIOME3 for tree species distribution and productivity. GTM then maximizes NPV of forests from outputs	Increases in NPP globally but with high variance in timber losses. Timber supply increases leads to lower timber prices. Most change occurs in inaccessible boreal regions.	Advantage	Timber Prices
Global ³	2002	Used Terrestrial Ecosystem Model to derive CO2 data to modify timber supply in a GTM. This will then show market implications for fluctuations in timber resources.	Timber increases lead to economic benefits with lower global timber prices. Market analysis found greater consumption of wood products despite some product surplus.	Advantage	Gross Domestic Product
Europe ⁴	2013	Developed a biome shift model through regionalized GCMs and NFI. Cash flows are generated through timber growth simulator for use in LEV calculations identifying the change in European forest value.	All climate scenarios resulted in less Norway spruce dominated land (migrated north) indicating a loss in land and timber value. New climate benefitted oak and pine.	Disadvantage	Land Expectation Value
Canada ⁵	2012	Used a CGE model to assess the economic impact of climate change on Canadian forests. Computed results based on varying scenarios.	Results generally show negative impacts to economy, though with high variances. Shows the importance of forestry adaptations to benefit the economy.	Both	Canadian Economy

Table 2-3. Summary of timber modeling studies with reference to forestry implications and the effect on economic areas.

Global ⁶	2000	Utilize a Global Impact Model (GIM) that combines future world scenarios, climate simulations, sectoral data, market sector response to climate change. Based on three scenarios from the IPCC	Small increases in global GDP in year 2100 under climate scenarios. Forestry market is expected to increase in wealth from increased forest productivity- primarily boreal.	Advantage	Global GDP
Europe ⁷	2003	Used a regionalised, partial equilibrium model (EFI-GTM) to model profit maximizing in the European forest market. Analysed accelerated forest growth in a variety of scenarios for a variety of products.	Increased wood production within Europe leads to lower prices and less importing in most scenarios. Lower wood prices compromise producer incomes. Logs and sawn wood are products most affected.	Both	Timber Prices
Russia ⁸	2013	Studied the combined use of an ecological gap model and economic model in Russian forests as temperatures increase over the next 90 years	Found general increases in timber yields at 2°C warming but general decreases in timber yield and carbon sequestration at 4 °C depending on site location and species	Both	Carbon pricing

1- Tian et al. 2-Sohngen et al. 3- Perez-Garcia et al. 4- Hanewinkel et al. 5 Ochuodo et al. 6-Mendelsohn et al. 7- Solberg et al. 8- Lutz et al.

Adaptations to the uncertainties of 21st century climate change

Management is vital to maintaining efficient biomass production in the boreal forest (Campioli et al. 2015) and this will only continue under climate change through adaptation. Adaptation is needed to continue receiving benefits from the environment, and the value of adaptations need to be expressed to society (Guo and Costello 2013). Adaptations can either be reactive or proactive; proactive modifications are most favorable as they reduce exposure to risk, though more often reactive adaptations are used in forestry practices (Gauthier et al. 2014). Intensive treatments through behavioral changes, or extensive treatments that apply discrete adaptations, are further strategies (Guo and Costello 2013). It is important to recognize that adaptive measures should be implemented based on context, not applying the same action to all situations (Gauthier et al. 2014). Several papers have proposed comprehensive recommendations for climate change adaptations (Park et al. 2014, Hisano et al. 2018). Here we focus on how adaptations may proceed in response to biome shifts, increased disturbances, reduced net growth and compositional shifts.

Shifting biomes and climate envelopes present new challenges to forest industry; provenance trials have demonstrated that southern populations are declining while northern ones are benefiting from warmer climate (Thomson and Parker 2008, Pedlar and McKenney 2017). As climate is altered, plant species may form isolated populations (Pearson 2006), adapt to local conditions or hybridize to survive under new climate conditions (Aitken et al. 2008). Assisted migration, therefore, may be utilized as a way ensure species are growing under optimal climate conditions (Aitken et al. 2008, Gauthier et al. 2014). This means not only migrating current (local) seed sources north, but also bringing southern species/ seed sources northward to cope with dryer and warmer conditions (Thomson and Parker 2008, Keskitalo et al. 2016). To ensure

that currently harvested and planted forests will be sustainably productive again in the future, they must be managed to succeed in a changing climate (Lempriere et al. 2008, Park et al. 2014). However, we do not yet fully know the implications of moving seed sources or southern species into northern locations.

Every year, large areas of forest land are impacted by forest disturbances (van Lierop et al. 2015), which affects the harvestable volumes from the region. In order to protect valuable mature stands, certain measures can be taken in susceptible regions; namely the management of fires and pests (NRTEE 2011). This may be accomplished through fire suppression and pesticide applications; though in the case of fire, future costs may increase drastically and impede fire management (Hope et al. 2016). When affected by a disturbance, salvage harvesting is a method sometimes employed but can lead to complications in the milling process (Lempriere et al. 2008), as well as nutrient removal with implications for long-term site productivity (Hume et al. 2018). Although, salvage harvesting can recover some of the lost timber (Seidl et al. 2008, Leduc et al. 2015), it is always better to protect areas proactively (before salvaging is necessary), to avoid negative economic impacts (NRTEE 2011, Ochuodho et al. 2012).

In monoculture conifer stands, hardwoods could be added to the composition to increase functional diversity, possibly helping to mitigate the impacts of climate change (Hisano et al. 2018) and improve productivity (Liang et al. 2016). Though not necessarily increasing harvestable volumes, mixed-woods do provide lower risk both financially and industrially, since they are more resistant to abiotic and biotic disturbances and are better able to recuperate afterwards (Knoke et al. 2007, Zhang et al. 2012, Hisano et al. 2018). Also, designing forests with greater adaptive capacity will delay the negative aspects of climate change (Park et al. 2014). As a result of altered species compositions, manufacturers may subsequently have to adapt new wood products to changing supply demographics, though at a greater expense (Lempriere et al. 2008).

Summary and future directions

Climate change affects ecological processes at different spatial scales and impacts timber supply in boreal forests. First, the area of productive boreal forest may decrease as northern migration rates are slower than the speed at which southern limits retreat from unfavorable climate conditions. Second, forest disturbances have increased in recent decades and are anticipated to increase in severity and/ or frequency, leading to younger forest age structures and increased dominance of early successional tree species over late-successional species. Third, tree growth in established forests has increased in areas where water availability is not limiting as the result of warmer temperatures, longer growing seasons and CO₂ fertilization. However, widespread increases in tree mortality have occurred over the last several decades due to direct heat stress, drought and increased disturbances. Increased mortality has occurred at a greater rate than growth increases, or has accompanied reduced growth rates, leading to decreased net growth and net volumes. Moreover, late successional tree species are more vulnerable to climate than early successional species in established forests, leading to the increased dominance of early successional conifers and broadleaves. These trends are expected to continue as warming and extreme weather conditions are anticipated to be amplified in the 21st century.

Changes in timber quantity and quality have profound impacts on the forest industry. First, lower net harvestable volumes will likely be available since climate change induced mortality losses are greater than growth gains. Second, product manufacturing will need to accommodate new supply demographics, though it is costly to alter processing facilities; despite this, new unforeseen opportunities may arise. Third, locating sufficient mature timber may

become more difficult as increased disturbances skew the forest age structure to younger levels. Lastly, the overall quality of extracted wood is likely to decline since there will be greater impact from disturbances and greater proportion of less desirable species. However, once again, this may offer a new range of opportunities for specific niches in product manufacturing. Additionally, even if there are fewer disturbance events at a given site, accelerated growth rates can lead to lower quality softwood timber because of decreased mechanical wood properties.

Therefore, adaptations in the forestry sector are needed to keep the industry viable and sustainable during this time of change. Certain adaptations are more applicable in areas over others; thus, careful planning, and in some cases new policy, is necessary. Management adaptations include: assisted migration into favorable growing areas, fire and pest management to protect mature stands, and improving resilience and adaptive capacity to disturbances by enhancing forest diversity. Innovation and research will be necessary to better understand the full scope of their consequences and to improve our understanding of future timber supply.

Continued research is required to properly assess the future impacts of climate change; there is still much uncertainty. To conclude, we propose four areas of future research.

1) It is known that boreal forests are shifting northward, yet this may differ regionally depending on climate moisture availability (Fei et al. 2017). More knowledge of species specific responses is required; the continued study of provenance trials could provide a wealth of information (Pukkala 2017). Further, more definitive rates of decline in southern boreal limits and rates of expansion in northern limits are needed since there exist many conflicting estimates (Chen et al. 2011). Better understanding this will provide information on the productive forest area available to industry in the future, which has been suggested to be decreasing (Hanewinkel

et al. 2013). Repeatedly measured satellite imagery may likely assist in accurately determining forest migration rates (Hofgaard et al. 2013).

2) Boreal forest wildfires are expected to increase in the future (Flannigan et al. 2009) but can differ considerably among boreal forest regions (Girardin et al. 2013). We need to better understand how younger, fire-origin forests feedback into wildfire regimes (Boulanger et al. 2017a). It is also necessary to improve our understanding of the changing relative importance of different disturbance types under on-going climate change, and its spatial variations (Logan et al. 2003, Hansen et al. 2013). Our knowledge is also limited concerning the development of future forest diseases; it is unclear what role they will play in conjunction with forest dynamics and other disturbances.

3) Efforts have been made to study the impacts of climate change on net forest biomass accumulation in western Canadian boreal forests (Chen and Luo 2015a, Chen et al. 2016a). However, there has been little research done on this topic in other regions. As well, there is no clear understanding of how large scale mortality will affect the succession of tree species compositions (Anderegg et al. 2013). Compositional shifts of tree species are important to forest industry. While observational (Searle and Chen 2017a) and simulation (Shuman et al. 2015) studies have shown that climate change induces compositional shifts to early successional tree species in western Canada and Russia, it remains unclear whether this trend is pan-boreal.

4) It is important to determine the economic and societal consequences of changes in the boreal forest. Intensively managed areas, providing economic benefits, may respond differently to climate change than unmanaged forests, prompting continued study. This is especially necessary for southern areas of the boreal forest as this is where most of the population and industry resides. As well, previous results based on economic and timber simulation studies

(Sohngen et al. 2001, Perez-Garcia et al. 2002) generally differ from the empirical evidence that we have synthesized. There is a need to reconcile this disparity in order to clearly inform policy makers and forest managers.

CHAPTER THREE: SUSTAINABLE BIOMASS HARVESTS ARE COMPROMISED BY CLIMATE CHANGE IN THREE BOREAL REGIONS

Abstract

Climate change poses serious risk to sustainable, long term wood supply. Accurately projecting future wood supply is a vital task when planning forestry operations. However, few studies include the cumulative and interacting impacts of climate change on forest productivity and disturbances; fewer still include drought impacts when forecasting timber. We modeled how disturbance- and drought-induced tree mortality affects wood supply in three boreal forest regions over 200 years. Using two harvesting intensities, we show that sustainable long-term harvesting is more likely achieved with lower intensities. Harvests are complicated by declines in overall aboveground biomass from increases in drought and fire-induced tree mortality without being compensated by increased tree growth rates. Furthermore, harvests are incredibly reduced under severe climate forcings despite a lower harvesting intensity. To continue having sustainable forest management, our results imply a need to adapt operations and implement climate mitigation strategies.

Keywords: LANDIS-ii, drought-induced mortality, forest disturbances, species compositions, sustainable operations, harvesting intensity, forest management

Introduction

Global change, caused by the continued release of anthropogenic greenhouse gasses (IPCC 2014), has been impacting the growth and mortality of tree species (Allen et al. 2015). The effects of global change on forests are expected to impact forestry operations in many ways; notably through changes in wood supply (Kirilenko and Sedjo 2007, Gauthier et al. 2015b). Wood supply is strongly influenced by changes in forest growth, tree species composition, and forest disturbances (Kirilenko and Sedjo 2007). There has been an important discussion for communities within the boreal forest whose economies rely largely on the forestry sector (Gauthier et al. 2015a). Whether the boreal forest industry continues to have a stable supply of merchantable timber in the near and long- term remains an important question (Brecka et al. 2018).

Perhaps the most important aspect of changing climate is the influence that future moisture conditions will have on forest dynamics (Berner et al. 2013, Girardin et al. 2016a). In addition to forest productivity losses (Ciais et al. 2005), moisture deficits lower site suitability (D'Orangeville et al. 2016), increase susceptibility to insects and disease (Jactel et al. 2012), and shorten fire frequency (Gauthier et al. 2015b). Drying has already led to regional increases in tree mortality around the world (Allen et al. 2015) and within the boreal forest specifically (Peng et al. 2011). However, boreal forests are affected differently based on species composition (Drobyshev et al. 2013, Chen and Luo 2015b) and stand age (Chen et al. 2016b). Importantly, early successional species are increasing under global change in relation to later successional conifers (Johnstone et al. 2010, Searle and Chen 2017b), while temperate species have been found to thrive compared to boreal species (Reich et al. 2015). Alternatively, under favorable conditions, growth and biomass gains may occur, though benefits are highly dependent on moisture availability (Girardin et al. 2016a). Even in areas where growth has increased, biomass loss from increased tree mortality has led to a net decrease of boreal biomass (Girardin et al. 2012, Chen and Luo 2015b). A trend in declining overall boreal standing biomass poses considerable ramifications to forestry.

Despite these adverse ecological consequences of climate change, wood supply modeling studies suggest general increases in future boreal timber due to warmer temperatures and longer growing seasons (Kellomäki et al. 2008, Lutz et al. 2013). However, many of these studies (both global and boreal) do not explicitly incorporate forest disturbances or dynamic processes that are affected by climate change within their models (Perez-Garcia et al. 1997, Sohngen et al. 2001, McKenney et al. 2016, Tian et al. 2016). Though sometimes difficult to quantify their full impacts, it is necessary to simulate disturbances (Reyer et al. 2017) as they are strongly linked to forest landscapes and wood supply, particularly in the boreal biome (Gauthier et al. 2015a). Contrary to previous studies, including dynamic disturbances may predict loss of available timber as a result of drought induced mortality (Peng et al. 2011), reduction in productivity from heat and moisture stress (Hogg et al. 2017), and disturbance related mortality (Gauthier et al. 2015b, Boucher et al. 2018). Currently, no studies have assessed the interactive and cumulative impacts of climate-induced changes on these processes on boreal Canadian wood supply.

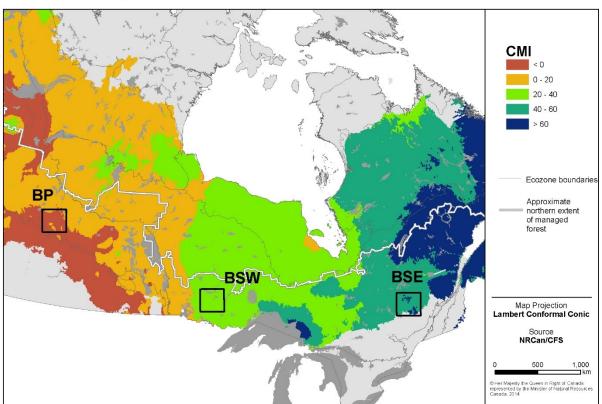
The impact of climate change on boreal wood supply, with specific concern for drought and disturbance related tree mortality, is an area that demands continued study (NRTEE 2011, McKenney et al. 2016). To do this, we simulated dynamic stand- and landscape-scale processes from 2000-2200 in three Canadian boreal forest regions. The three regions selected represent an east-west declining moisture gradient allowing us to directly model how increasing drought, along with fire and insects, will impact harvestable biomass (Mg/ha) across the boreal forest of

Canada. Our landscape simulation combined dynamic drought mortality with a previously published LANDIS-ii (Landscape Disturbance and Succession) model (Boulanger et al. 2018). We expect that as anthropogenic climate forcing increases, harvestable biomass in the boreal forest will decrease because of cumulated disturbances, resulting in lowered harvests and reduced economic viability. Specifically, we expect that: (*i*) important industrial boreal species (*Picea* spp., *Pinus banksiana*, and *Populus tremuloides*) would decline across all regions; and, (*ii*) biomass loss from tree mortality would increase over time, from east to west, and with greater climate pressures (e.g., declining water availability), reducing future harvestable biomass.

Methodology

Study areas

All three study areas are located within the boreal forest of Canada. We selected one location of approximately 25,000 km² from each of the following ecozones (Ecological Stratification Working Group 1996): Boreal Plains (BP), Boreal Shield West (BSW), and Boreal Shield East (BSE) (Boulanger et al. 2016) (Figure 3-1). These represent an east-west moisture gradient that is likely to become even more obvious as climate change alters future precipitation regimes (IPCC 2014). These boreal forest settings are comprised of softwood (*Pinus banksiana, Pinus resinosa, Pinus strobus, Picea mariana, Picea glauca,* and *Abies balsamea*) and hardwood (*Populus tremuloides, Populus balsamifera* and *Betula papyrifera*) tree species. Some temperate species are found within BSE but are not the focus of this study, though they were included in simulations. We initialized simulations with current forest composition and age structure estimated from National Forest Inventory forest cover maps (Beaudoin et al. 2014). We used simulations to project the expected future forest conditions and estimated their above ground biomass fluctuations for analysis. Permanent sample plots provide data for species-specific growth, yield and mortality curves within the study areas. Forest-level data and stand characteristics for describing forest growth and species composition were utilized from previous studies (Boulanger et al. 2016, Boulanger et al. 2017b). Initial biomass estimations were updated from methods used in Tremblay et al. (2018).



1971 - 2000 Climate moisture index

Fig. 3-1. Study locations were chosen using a Climate Moisture Index (Hogg 1997) map of Canada. We selected three sites, Saskatchewan (BP), Ontario (BSW), and Quebec (BSE) because of differing levels of projected future moisture conditions (source: NRCAN).

Climate conditions

Monthly time series of climate station observations for the period (2000 - 2010) were spatially interpolated from data of McKenney et al. (2013). Future climate scenarios were

constructed by merging projections of future monthly changes derived from the Canadian Earth System Model version 2 (CanESM2, e.g., (Arora and Boer 2010)), with 30-year monthly climate normals for 1961–1990, interpolated from the McKenney et al. (2013) station records. CanESM2 results were downloaded from the World Climate Research Program (WCRP) Climate Model Intercomparison Project Phase 5 (CMIP5) archive for each of three different radiative forcing scenarios, known as Representative Concentration Pathways (RCP, (Van Vuuren et al. 2011)), namely RCP 2.6, RCP 4.5 and RCP 8.5. These three scenarios (Fig S3-3) were included for analysis along with a historic (baseline) scenario showing current climate that was used for comparison.

Simulating the ecological impacts of climate change

Simulation of forecasted aboveground biomass and species compositions was done using LANDIS-ii (Scheller et al. 2007), derived from the original LANDIS model (Mladenoff 2004). LANDIS- ii has a core model with optional extensions that analyze specific forest attributes (Scheller et al. 2007). It is a rasterized landscape simulation model that applies various ecological processes to ecoregions that are made of individual cells (Scheller and Domingo 2012). Cells are filled by tree species of certain age cohorts. The primary processes involved are succession, and forest disturbances (fire, wind, insects, drought), which are built on ecological knowledge (Scheller et al. 2007). There are spatial interactions at the landscape level (dispersal, harvesting, natural disturbances, etc.) that scale up from cell level, aspatial processes (species establishment, cohort growth etc.) (Scheller and Mladenoff 2004). This is a flexible modeling platform, offering the user a variety of options when defining and transitioning the forest over time. It is used for landscape simulation projects to aid ecologists and foresters in understanding the impacts of forest disturbances (Sturtevant et al. 2009), harvesting operations (Steenberg et al.

2013) and climate change (Scheller and Mladenoff 2005, Steenberg et al. 2011). For full methodologies on the simulation of ecological processes see Boulanger et al. (2017b).

We initialized simulations with current forest composition and age structure estimated from National Forest Inventory forest cover maps (Beaudoin et al. 2014). We used simulations to project the expected future forest conditions and estimated their above ground biomass fluctuations for analysis. Permanent sample plots provide data for species-specific growth, yield and mortality curves within each region. Forest-level data and stand characteristics for describing forest growth and species composition were utilized from previous studies (Boulanger et al. 2016, Boulanger et al. 2017b). Initial biomass estimations were updated from methods used in Tremblay et al. (2018).

We used the climate-sensitive forest patch model PICUS 1.5 (Lexer and Hönninger 2001) to simulate climate change impacts on growth and establishment in LANDIS (Boulanger et al. 2017b). Mono-specific stands of each tree species on all ecoregions were simulated with PICUS starting from bare-ground, using parameters described in Boulanger et al. (2017b). Monthly time series of climate data for each time period (2000-2010, 2011-2040, 2041-2070, 2071-2200) and forcing scenario (baseline, RCP 2.6, RCP 4.5, RCP 8.5) were used to drive each simulation for 300 years. Species-, ecoregion- and climate-specific dynamic inputs (species establishment probabilities, maximum above ground species biomass, and annual species NPP) were then directly derived from these simulations. Full details on model parameterization and implementation are described in previous studies (Boulanger et al. 2017b, Taylor et al. 2017).

Dynamic drought-induced mortality

We sought to predict species-level tree mortality rates as climate moisture changes temporally and spatially. We did this through a linear mixed effects model using Climate Moisture Index

(CMI) to evaluate tree mortality in repeatedly measured permanent sample plots (PSP); a similar process to those done in previous studies (Peng et al. 2011, Luo and Chen 2013). CMI shows the difference between expected precipitation (cm) and potential evapotranspiration demand (cm); negative results show reduced available moisture (Wang et al. 2014). Historical monthly CMI values were generated for each PSP using BIOSIM-10. BioSIM projected daily maximum and minimum temperatures (°C), precipitation (mm), mean daily relative humidity and wind speed by matching georeferenced sources of weather data (weather station with daily weather data) to spatially georeferenced points, adjusting the weather data for differences in latitude, longitude, and elevation between the source of weather data and each cell location using spatial regressions.

Monthly values were then summed to an annual level (ACMI) and applied to our model. The baseline relationship was produced from historical PSP tree data and plot level ACMI values. First, we determined the annual plot-level, species mortality rates:

$$M = 1 - \left(1 - \frac{N_D}{N_S}\right)^{\frac{1}{L}}$$
[1]

where M is the annual mortality rate, N_D is the number of dead stems over the census period in each plot, N_S is the number of total stems over the census period in each plot, and L is total length of time the plots were censused. We then estimated the effect of ACMI on stand level annual mortality rates for each species according to the following linear mixed effects model:

$$logit(M_{ij}) = \beta_0 + \beta_1 \times ACMI_i + \beta_2 \times MBA_i + \pi_j$$
^[2]

M is the mortality rate of tree species at the *i*th census for the *j*th plot. MBA is the mean basal area for each tree, found by subtracting the previous census year's basal area from the current census' basal area. ACMI is the value calculated annually from 2010-2100 for each climate

change scenario. Our initial model included ACMI, MBA, and MSA (mean stand age), however lower AIC values caused us to select the reduced model (equation 2).

In order to project future drought-related mortality, monthly CMI values for each LANDIS-II ecoregion were generated from the years 2010-2100 (in 30 year segments) for each climate change scenario through BioSIM; projections were run with 45 replications (Régnière et al. 2014). This was done separately for all regions; three RCP scenarios and a baseline- no climate change projection (using climate normals from 1981-2010). Mortality rates for each tree species were then predicted using coefficient β_1 from equation 2 and projected ACMI values from BioSIM-10. All analyses and predictions were run in R statistical software version 3.4.4 and the *lme4* package (Bates et al. 2015, R Core Team 2017). Annual drought-related mortality was averaged over the 45 replicates and then summed over ten years in accordance with simulation time steps. Drought mortality levels were implemented accordingly in LANDIS simulations as a background mortality at each time step for each tree species, ecoregion and climate scenario.

Disturbances

Fire is an ongoing disturbance that is present in all three regions and important in boreal forest dynamics (Gauthier et al. 2015a) and was simulated using the LANDIS-II Base Fire extension (He and Mladenoff 1999). Fire regime data (annual area burned, fire occurrence, and mean fire size) were summarized into "fire regions" corresponding to the intersection of the study region and the Canadian Homogeneous Fire Regime (HFR) zones of Boulanger et al. (2014). As in Boulanger et al. (2016), baseline and future fire regime parameters within each fire region were calibrated according to models developed by Boulanger et al. (2014) and further updated for different RCP scenarios (Gauthier et al. 2015b).

Our LANDIS simulation accounts for the periodic outbreak of spruce budworm (SBW) outbreaks, which are known to cause some of the most widespread forest damage in the eastern North America's boreal forest. SBW outbreaks were simulated only in the BSW and BSE regions as it is not important in western (BP) Canada. Host tree species for SBW were, from most to least vulnerable, balsam fir (Abies balsamea), and white (Picea glauca), red (P. rubens) and black (P. mariana) spruce. Outbreaks were simulated as probabilistic events at the grid cell level with probabilities being a function of site and neighborhood resource dominance (e.g., host abundance within a 1-km radius) as well as regional outbreak status. Outbreak impacts (tree mortality) are contingent on these probabilities as well as on host species- and age-specific susceptibility. Parameters used in this study were calibrated and validated using various sources for the mixedwood forest (e.g., (Hennigar et al. 2008)). Regional outbreaks were calibrated at the highest severity level possible using the BDA extension (Sturtevant et al. 2004) and were set to last, at most, one time step (10 years) and to occur every 40 years in accordance with typical observed regional recurrence cycles (Boulanger et al. 2012). Specific parameterizations for both fire and insects are described in Boulanger et al. (2016).

Previous simulations (Boulanger et al. 2016) using this calibrated LANDIS-ii model had specific harvesting prescriptions which followed economic priorities. We built on these prescriptions to assess different levels of harvesting intensities. We used three levels of areabased harvesting; no harvest, 4% and 8% of the area per time step. This was done to determine if climate change effects on forest dynamics would influence the sustainability of harvesting operations meeting their goals. It would also show if there is enough harvest eligible land throughout the study period.

Study framework

LANDIS simulations were run according to a full factorial design with climate scenarios and harvest prescriptions as factors. The four climate scenarios were baseline, RCP 2.6, RCP 4.5 and RCP 8.5 while there were three levels of harvest prescriptions (No harvest, 4%, 8%). Scenarios were replicated 5 times in order to assess convergence of results for a total of 60 simulations (4 climate scenarios x 3 harvesting strategies x 5 replicates) per region. All simulations were run for 200 years at 10-yr time steps starting in year 2000. Climate sensitive parameters (fire regime; growth [maxANPP, maxAGB and SEP]) were allowed to change in 2010, 2040, and 2070 according to the forcing scenario and were held fixed thereafter for the 2070 - 2200 period. Parameters calibrated for the baseline climate were used for the 2000-2010 period for all simulations as well as for the spin-up phase, when initializing tree species biomass. To illustrate the temporal trends of available standing timber between the three study regions and across three climate change scenarios, we graphed the mean response from all five simulations. Trends were assessed for total AGB, species-specific AGB, total drought-related biomass mortality as well as total harvested area. We focused results on the following commercially important species: Abies balsamea (Bf), Betula papyrifera (Bw), Pinus banksiana (Pj), Populus tremuloides (Pt), Picea mariana (Sb), and Picea glauca (Sw). All others were deemed either commercially unimportant in the boreal forest or are temperate forest species; many of the additional species found in the BSE region are considered temperate species.

Results

Total biomass fluctuations

Total regional aboveground biomass (AGB) strongly declines with increasing climate forcing (Fig. 3-2). Changes in AGB were compared between study regions, climate scenarios and over

the 200-year simulation time. Declines in AGB are more extreme in the RCP 8.5 scenario, especially for the BSW and BP regions. Major changes during the RCP 8.5 scenario take place around 2050 for all regions due to a combination of increased fire occurrence (Fig. S3-5) and increasing drought related mortality (Fig. 3-4). Among three regions, the temporal changes in AGB in the BSE were less dramatic than those in the other two regions. The BSE is younger than the other two regions (Fig. S3-1), and experiences biomass accumulation until approximately 2050. AGB is relatively stable in the BSE across the entire study period for the baseline, but decline with increasing climate forcing, despite lower declines than the other two regions.

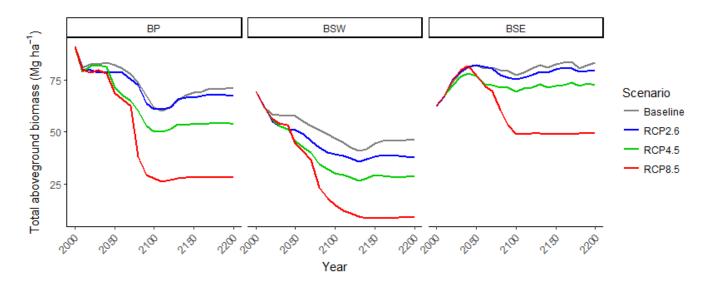


Fig. 3-2. Average AGB (Mg ha⁻¹) from the total area in each region shown through the four climate scenarios over 200 years.

Species biomass changes

Most boreal conifer species decline considerably during our study period and with increasing climate forcing, though temperate broadleaf species increase (Fig. 3-3 and Fig. S3-3a). Throughout the three study regions, broadleaf species constitute the majority of future total

biomass. This is especially true for: *Populus balsamifera* (Pb) in the BP, *Betula papyrifera* (Bw) in the BP both for RCP 4.5 and 8.5 after 2100, Populus tremuloides (Pt) in the BSW, and Acer rubra (Mr), Acer saccharum (Ms), and Pt in the BSE (Fig S3-3b). Baseline scenarios tend to show increases in later successional species over time, such as Picea spp. and Abies balsamea (Bf). However, these species decline with increasing climate forcings. Picea mariana (Sb) seems to perform well in most regions and scenarios, though this does not hold true throughout the BSW after 2100. Both Sb and Picea glauca (Sw), along with Abies balsamea (Bf), do not decline drastically in BSE except under the RCP 8.5 forcing. There are noticeable fluctuations in Bf biomass over time in the BSE and in the baseline/RCP 2.6 scenarios of the BSW (absent in the BP). Pinus banksiana (Pj) begins as the most abundant conifer throughout the simulations, especially in the BSW where it declines considerably. Losses of Pj are much more pronounced since it starts with such high initial biomass, much like Bf in the BSE and Pt in the BP. However, Pt still makes up a substantial portion of the regional biomass (top row Fig S3-3b) whereas Pj declines considerably in relative biomass in the BSW (middle row Fig. S3-3b). All species decline considerably under the RCP 8.5 forcing showing a substantial reduction in commercial boreal tree species. Despite this, broadleaf species still have greater relative abundances than conifers in general (Fig. S3-3b).

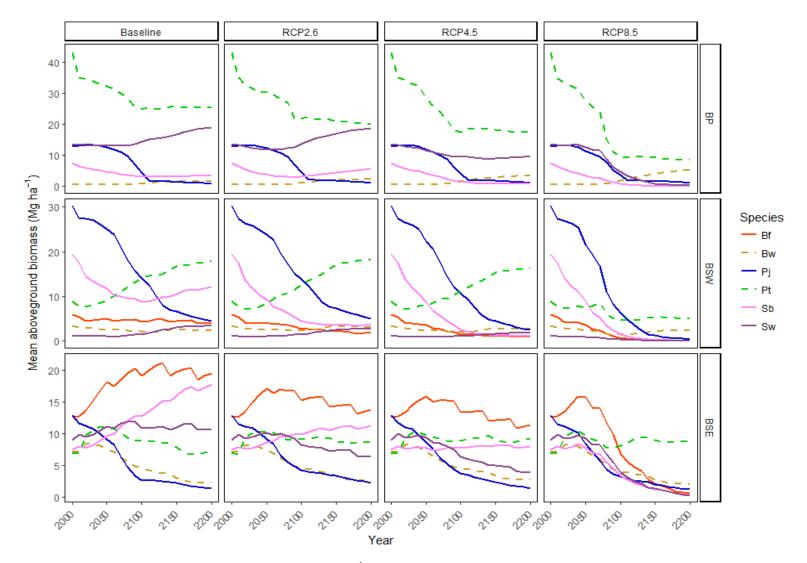


Fig. 3-3. Changes in individual species AGB (Mg ha⁻¹) with harvest, drought, fires and insect disturbances. Specific commercially important boreal species are shown for easier identification and interpretation while temperate and non-commercial species are removed (full figure is shown in Fig S3-3a). Note: the y-axis is not normalized between regions and dashed indicates broadleaf species.

Tree mortality and growth

Drought induced tree mortality is greatest in the most westerly study region, across all climate forcing scenarios. Annual trends differ between species, regions and climate change scenarios (Fig. 3-4). Drought is more impactful in western Canada as there are greater losses observed there over the study period, e.g., three times as much in the BP compared with the BSW and BSE. Surprisingly, total drought mortality declines under RCP 8.5 in both the BP and BSW. There are also much greater fluctuations in the amount lost between each climate scenario in the BP region compared with the relatively consistent losses in the BSW and BSE. Interestingly, the BSE has slightly greater drought-related losses than the BSW site, even though there is generally greater regional precipitation in eastern Canada. These losses are very similar to the biomass replaced through annual net primary production (NPP) and may therefore be balanced (Fig. 3-5). NPP is rather consistent between climate forcings except in RCP 8.5 where a negative trend occurs. For BP and BSE, NPP slightly increases after 2100 within this climate forcing.

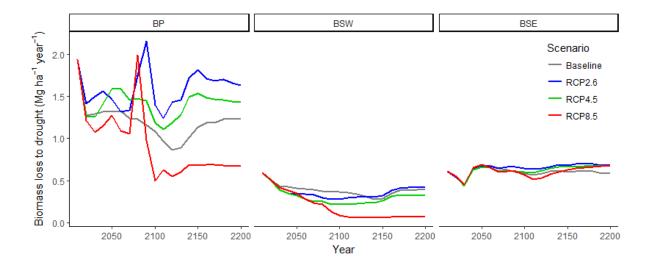


Fig. 3-4. Annual biomass losses to drought-related mortality (Mg ha⁻¹ year⁻¹) in the 3 Canadian regions across 4 climate scenarios.

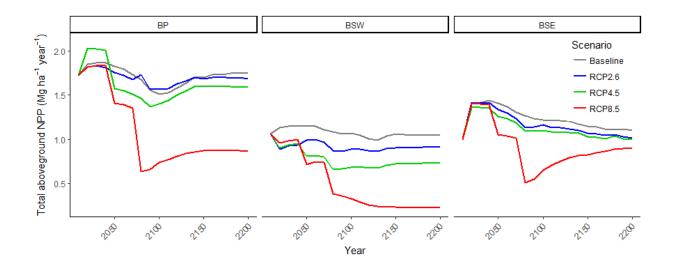


Fig. 3-5. NPP (Mg ha⁻¹ year⁻¹) trends across the three regions and 4 climate forcings.

Harvesting scenarios

Biomass harvested is strongly reduced with increased climate forcing, especially for BP and BSW. To see the impact of fire, drought and insects on the trends in boreal forest harvesting, climate change scenario harvests are compared to baseline levels (Fig. 3-6). When trend lines appear over 1.00, climate change scenarios are providing enough areas with mature timber to be harvested and exceeds baseline levels.

Generally, harvests are extremely low relative to their respective baseline harvests when considering the highest harvesting scenario (Fig. 3-6b). Harvests are least impacted in BSE and BP (RCP 2.6 and 4.5) whereas harvest levels are considerably lower in BSW under both RCP 4.5 and 8.5. Harvested biomass strongly declines under the RCP 8.5 scenario in all study sites, especially in BSW where area harvested is reduced by more than 75%. In total, losses of harvest could be around 25% less than expected for all study areas.

The lower harvesting intensity is generally able to maintain consistent harvesting levels, especially in BSW and BSE. When looking at the 4% harvesting prescription, the relative harvest

levels are slightly higher than the 8% (Fig. 3-6a). Biomass harvested in RCP 2.5 and 4.5 are much closer to the baseline scenario under these new conditions. In BP however, harvests are noticeably lower than the other areas and quite similar to Fig. 6b. In this case, harvesting 4% of the area per decade may still be too great a target under these forcing scenarios. Biomass harvesting improves in BSW as both RCP 2.6 and 4.5 surpass baseline levels. There doesn't appear to be any difference between the RCP 8.5 harvests from Fig. 3-6a and Fig. 3-6b. This probably means that, under either harvesting intensity, this climate forcing is so extreme that there just is not enough harvestable biomass to meet the criteria for harvesting eligibility requirements (minimum stand age).

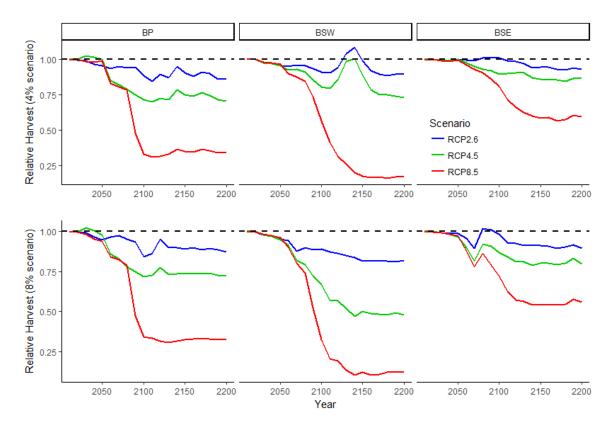


Fig. 3-6. Harvested biomass in each climate change-scenario relative to baseline levels (1.00); model shows how harvesting is impacted by fire, drought and insects. Top graphs (a) show the 4% area removed scenario compared to 8% removal scenario (b) on the bottom.

Discussion

Under increasing anthropogenic climate forcing, our simulations project a steady decline of timber resources that is consistent between regions, climate scenarios and across most boreal commercial tree species. This coincides with general increases in tree mortality (through fire or drought) which out matches future NPP, severely influencing overall harvest levels. Further, our simulations show that most major changes occur prior to the year 2100 (~2050-2075), suggesting there may be considerable risk in the near term sustainable management of these boreal forest regions.

Regional biomass trends

The more eastern BSE region is generally least impacted compared to either the BSW or BP, though which region is most negatively impacted is unclear. Indeed, the largest influence on forest resources in the BSW appears to be from fire, whereas drought seems most impactful in the BP region. Both fire (Gauthier et al. 2015b, Daniel et al. 2017) and drought-related boreal tree mortality (Michaelian et al. 2011, Peng et al. 2011, Hogg et al. 2017) have the potential to impact boreal wood supply considerably. Climate conditions under the RCP 8.5 forcing are most detrimental to biomass decline in all regions, as expected from previous studies (Charney et al. 2016, Dyderski et al. 2017, Aubin et al. 2018). This is a result of both increased mortality rates removing biomass from the landscape and increasingly frequent disturbances lowering the average age of these forests affecting their harvesting potential (Fig. S4). Younger forests encompass smaller trees which contribute less to the overall biomass pool. Ramifications for industry are potentially alarming, as finding consistent, mature timber for manufacturing may prove difficult in these regions (NRTEE 2011).

Species-specific changes

Nearly all species were negatively affected in our simulations though there are considerable differences in magnitude between climate forcings. Broadleaf species tend to be less negatively affected than conifers over time throughout each region as seen by their relative abundances. This agrees with observational studies showing that pioneer species like *Populus* tremuloides have been increasing in relative abundance over time (Johnstone et al. 2010, Searle and Chen 2017b). Increases in the relative abundance of warm-adapted temperate hardwoods (e.g., sugar and red maples) at the expense of boreal conifers in BSE are notable since it may show they have a competitive advantage with global change. These shifts in relative abundances have been observed (Fisichelli et al. 2014) and projected (Evans and Brown 2017, Taylor et al. 2017) for other areas along North America's southern boreal regions. Overall, these shifts towards greater abundance of deciduous broadleaves suggests greater prevalence of mixed wood forests or a northern shift in the boreal-temperate zone with ongoing climate change (Fisichelli et al. 2014, Evans and Brown 2017). This trend has serious economic implications since conifers are generally preferred in industry; decreases in conifer abundance will influence the type and quality of wood products that companies can manufacture (Boulanger et al. 2017a, Brecka et al. 2018). If regionally unsuitable for specific wood products, a greater presence of mixed wood forests or broadleaf trees may necessitate intensive silvicultural practices to provide a secure supply of desirable species.

Mortality and Growth Trends

Drought mortality occurs more prominently in the BP than the other regions. Climate change impacts on stand scale drivers (growth rates, species establishment etc.) were previously found to be most influential to biomass dynamics in the BP region, confirming that drought may

be more important here (Boulanger et al. 2018). However, total biomass killed by drought declines under the RCP 8.5 forcing. Though odd, this is likely the result of much lower biomass left for drought mortality than under weaker climate forcings, since all disturbances are occurring simultaneously (Lucash et al. 2018). It should be noted that drought events in our simulation are not stand-replacing disturbances; nonetheless drought-affected stands offer less volume for harvest than those unaffected. With ongoing mortality taking place throughout the simulations, regional NPP isn't great enough to compensate for increased biomass losses from all disturbance interactions. Productivity declines considerably in the most extreme climate forcing and so losses are emphasized since disturbance events are greater under this scenario. Biomass gains are then outweighed by losses from mortality leading to the overall decline in AGB and posing risk to sustainable boreal forestry operations.

Implications to forestry

Relative harvest levels decline in both harvesting scenarios, but they are generally much less severe when using a lower harvesting intensity. Of particular interest is the lower harvesting intensity in the BSW region; there are years in both RCP 2.6 and 4.5 where harvesting levels improve enough to remain similar to baseline levels. This likely means that growth rates are improving stand biomass levels while mortality rates are not great enough to compromise harvesting success. Lowering long term harvest targets under this scenario may be enough to provide timber for future operations, despite ongoing disturbance events. A buffer stock of timber may alleviate the stress of unplanned tree mortality events (Raulier et al. 2014). While this is not the case in BP, where harvesting declines in a similar fashion regardless of harvesting intensity, BSE does see an improvement in future biomass harvested. In the context of climate change mitigation, harvesting less to allow for additional growth and carbon sequestration is only

effective in the short term so other methods will need to be investigated for long term mitigation goals (Smyth et al. 2014). It should be stated that across all regions and scenarios, the RCP 8.5 scenario reduces harvesting levels to an impossibly low level. In this case, pursuing new options for improving harvesting yields is sorely needed.

Forestry will remain an important industry in the boreal forest; whether for economic purposes (Ochuodho et al. 2012, Chen et al. 2017) or carbon sequestration strategies (Antón-Fernández and Astrup 2012, Lutz et al. 2013). Forestry depends on a healthy and consistent supply of timber in the near term and long-term future to have economically viable and sustainable harvesting operations. This study provides further insight into the expected changes in aboveground biomass with important implications to boreal forestry (Boulanger et al. 2016, Boulanger et al. 2018). Drought and disturbance-related tree mortality remain vital components of wood supply projections. Here we show the importance of including drought since it is a major driver of biomass dynamics in the boreal forest and not commonly modelled in wood supply studies (Kellomäki et al. 1997, Gauthier et al. 2015b, McKenney et al. 2016, Nordström et al. 2016). Through our drought-related mortality model, a better estimation of biomass changes can be made for management decisions. Simulating disturbances in our projections provide biomass and harvesting estimates with more accountability of external factors. Moreover, visualizing trends in a variety of climate scenarios is useful for seeing a range of potential outcomes of climate change. It is clear the RCP 8.5 forcing shows the most drastic changes in aboveground biomass, with significant changes occurring around 2075. However, sustainable forest management may be achieved with careful planning in affected areas. This could simply include reduced harvest rates creating a buffer stock against high mortality events, but other, more intensive options may be warranted with ongoing climate change. The loss of

aboveground and harvested biomass should prompt decision makers toward significant climate change mitigation efforts.

CHAPTER FOUR: GENERAL CONCLUSIONS

This thesis explored the various ecological impacts of climate change and how boreal forest timber is affected. Since there are no current, comprehensive reviews on the impacts of climate change on boreal forest timber supply, my first objective was to address this knowledge gap. Secondly, though there are many timber supply studies analyzing the impact of climate change, most do not include forest disturbances. My second objective therefore, was to conduct a simulation study whereby drought-induced tree mortality was implemented into a landscape disturbance model utilizing climate projections.

In my second chapter, we found that climate change poses serious risk to the quantity and quality of boreal forest timber. Regional increases in tree growth are likely insufficient to outweigh the general, landscape wide increases in tree mortality. Increases in mortality occurs from forest disturbances, increased heat and moisture stress, and low adaptation to changing climate. Quality of extracted timber is affected by various insects and pathogens as well as new growing conditions which can negatively alter wood fibre. Chapter three utilized a published LANDIS-ii model in combination with a drought mortality factor that we produced. By studying two levels of area-based harvesting intensity, we found that harvest levels can only be maintained long term if lower intensities are used. Despite this finding, with more intense climate forcings (i.e. RCP 8.5) it still is an issue to harvest on a consistent basis.

There is a high probability of severe negative impacts of climate change in the near future. We have identified several forestry adaptation strategies to better cope with these stresses. Assisted migration is one method that continues to be studied in research but not necessarily implemented in industrial settings. Identifying species that pair favorably with local and future climates will allow industry to remain productive. Drought tolerant species in dry areas and some

temperate species along the southern areas of the boreal forest are notable suggestions. As climate continues changing, we may have to also adjust our harvesting or silvicultural intensities to be sustainable long term.

To conclude, we found evidence both from literature and our simulations that boreal timber supply may be significantly reduced. Negative impacts to the quantity and quality of timber has serious implications to industry and nations located in the boreal. This topic requires continued study and demands policy action. Mitigation of climate change is incredibly important to lessen future negative impacts. Adaptation of forestry practices will also be key to mitigation strategies, whether improving carbon sequestration methods or operational efficiency, as well as allowing forestry to remain an economically viable industry.

LITERATURE CITED

- Aakala, T., and T. Kuuluvainen. 2011. Summer droughts depress radial growth of Picea abies in pristine taiga of the Arkhangelsk province, northwestern Russia. Dendrochronologia 29:67-75.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95-111.
- Alam, A., A. Kilpeläinen, and S. Kellomäki. 2008. Impacts of thinning on growth, timber production and carbon stocks in Finland under changing climate. Scandinavian Journal of Forest Research 23:501-512.
- Alfaro, R. I., E. Campbell, and B. Hawkes. 2009. Historical frequency, intensity, and extent of mountain pine beetle disturbance in British Columbia. Natural Resources Canada, Canadian Forest Service.
- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences 95:14839-14842.
- Allen, C. D., D. D. Breshears, and N. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anhropocene. Ecosphere 6:1-55.
- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010a. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660-684.
- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010b. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660-684.
- Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change **3**:30-36.
- Antón-Fernández, C., and R. Astrup. 2012. Empirical harvest models and their use in regional business-as-usual scenarios of timber supply and carbon stock development. Scandinavian Journal of Forest Research 27:379-392.
- Arora, V., and G. Boer. 2010. Uncertainties in the 20th century carbon budget associated with land use change. Global Change Biology **16**:3327-3348.
- Aubin, I., L. Boisvert-Marsh, H. Kebli, D. McKenney, J. Pedlar, K. Lawrence, E. Hogg, Y. Boulanger, S. Gauthier, and C. Ste-Marie. 2018. Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere 9.
- Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262:263-286.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature **405**:668-673.

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.
- Beaudoin, A., P. Bernier, L. Guindon, P. Villemaire, X. Guo, G. Stinson, T. Bergeron, S. Magnussen, and R. Hall. 2014. Mapping attributes of Canada's forests at moderate resolution through k NN and MODIS imagery. Canadian Journal of Forest Research 44:521-532.
- Beck, P. S., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters 14:373-379.
- Bennett, A. C., N. G. McDowell, C. D. Allen, and K. J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. Nature Plants 1:15139.
- Bergh, J., M. Freeman, B. Sigurdsson, S. Kellomäki, K. Laitinen, S. Niinistö, H. Peltola, and S. Linder. 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. Forest Ecology and Management 183:327-340.
- Berner, L. T., P. S. A. Beck, A. G. Bunn, and S. J. Goetz. 2013. Plant response to climate change along the forest-tundra ecotone in northeastern Siberia. Global Change Biology 19:3449-3462.
- Blennow, K., M. Andersson, O. Sallnäs, and E. Olofsson. 2010. Climate change and the probability of wind damage in two Swedish forests. Forest Ecology and Management 259:818-830.
- Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity evidence since the middle of the 20th century. Global Change Biology **12**:862-882.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science **320**:1444-1449.
- Boonstra, R., L. Desantis, C. J. Krebs, and D. S. Hik. 2008. Climate and nutrient influences on the growth of white spruce trees in the boreal forests of the Yukon. Climate Research 36:123-130.
- Boucher, D., Y. Boulanger, I. Aubin, P. Y. Bernier, A. Beaudoin, L. Guindon, and S. Gauthier. 2018. Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. Ecol Appl 28:1245-1259.
- Boulanger, Y., S. Gauthier, and P. J. Burton. 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Canadian Journal of Forest Research 44:365-376.
- Boulanger, Y., M. Girardin, P. Y. Bernier, S. Gauthier, A. Beaudoin, and L. Guindon. 2017a. Changes in mean forest age in Canada's forests could limit future increases in area burned but compromise potential harvestable conifer volumes. Canadian Journal of Forest Research 47:755-764.
- Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, E. McGarrigle, W. Rammer, G. Sainte-Marie, A. Beaudoin, L. Guindon, and N. Mansuy. 2016. Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landscape Ecology 32:1415-1431.
- Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, and G. Sainte-Marie. 2017b. Stand-level drivers most important in determining boreal forest response to climate change. Journal of Ecology.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, G. Sainte-Marie, and F. Gilliam. 2018. Standlevel drivers most important in determining boreal forest response to climate change. Journal of Ecology 106:977-990.

Brecka, A. F., C. Shahi, and H. Y. Chen. 2018. Climate change impacts on boreal forest timber supply. Forest Policy and Economics **92**:11-21.

- Brienen, R. J., O. L. Phillips, T. R. Feldpausch, E. Gloor, T. R. Baker, J. Lloyd, G. Lopez-Gonzalez, A. Monteagudo-Mendoza, Y. Malhi, S. L. Lewis, R. Vasquez Martinez, M. Alexiades, E. Alvarez Davila, P. Alvarez-Loayza, A. Andrade, L. E. Aragao, A. Araujo-Murakami, E. J. Arets, L. Arroyo, C. G. Aymard, O. S. Banki, C. Baraloto, J. Barroso, D. Bonal, R. G. Boot, J. L. Camargo, C. V. Castilho, V. Chama, K. J. Chao, J. Chave, J. A. Comiskey, F. Cornejo Valverde, L. da Costa, E. A. de Oliveira, A. Di Fiore, T. L. Erwin, S. Fauset, M. Forsthofer, D. R. Galbraith, E. S. Grahame, N. Groot, B. Herault, N. Higuchi, E. N. Honorio Coronado, H. Keeling, T. J. Killeen, W. F. Laurance, S. Laurance, J. Licona, W. E. Magnussen, B. S. Marimon, B. H. Marimon-Junior, C. Mendoza, D. A. Neill, E. M. Nogueira, P. Nunez, N. C. Pallqui Camacho, A. Parada, G. Pardo-Molina, J. Peacock, M. Pena-Claros, G. C. Pickavance, N. C. Pitman, L. Poorter, A. Prieto, C. A. Quesada, F. Ramirez, H. Ramirez-Angulo, Z. Restrepo, A. Roopsind, A. Rudas, R. P. Salomao, M. Schwarz, N. Silva, J. E. Silva-Espejo, M. Silveira, J. Stropp, J. Talbot, H. ter Steege, J. Teran-Aguilar, J. Terborgh, R. Thomas-Caesar, M. Toledo, M. Torello-Raventos, R. K. Umetsu, G. M. van der Heijden, P. van der Hout, I. C. Guimaraes Vieira, S. A. Vieira, E. Vilanova, V. A. Vos, and R. J. Zagt. 2015. Long-term decline of the Amazon carbon sink. Nature 519:344-348.
- Campioli, M., S. Vicca, S. Luyssaert, J. Bilcke, E. Ceschia, F. S. Chapin Iii, P. Ciais, M. Fernández-Martínez, Y. Malhi, M. Obersteiner, D. Olefeldt, D. Papale, S. L. Piao, J. Peñuelas, P. F. Sullivan, X. Wang, T. Zenone, and I. A. Janssens. 2015. Biomass production efficiency controlled by management in temperate and boreal ecosystems. Nature Geoscience 8:843-846.
- Candau, J. N., and R. A. Fleming. 2011. Forecasting the response of spruce budworm defoliation to climate change in Ontario. Canadian Journal of Forest Research **41**:1941-1960.
- Charney, N. D., F. Babst, B. Poulter, S. Record, V. M. Trouet, D. Frank, B. J. Enquist, and M. E. Evans. 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. Ecology Letters 19:1119-1128.
- Chen, H. Y., and Y. Luo. 2015a. Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. Global Change Biology **21**:3675-3684.
- Chen, H. Y., Y. Luo, P. B. Reich, E. B. Searle, and S. R. Biswas. 2016a. Climate changeassociated trends in net biomass change are age dependent in western boreal forests of Canada. Ecology Letters 19:1150-1158.
- Chen, H. Y. H., and Y. Luo. 2015b. Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. Glob Chang Biol **21**:3675-3684.
- Chen, H. Y. H., Y. Luo, P. B. Reich, E. B. Searle, and S. R. Biswas. 2016b. Climate changeassociated trends in net biomass change are age dependent in western boreal forests of Canada. Ecol Lett **19**:1150-1158.

- Chen, H. Y. H., and A. R. Taylor. 2012. A test of ecological succession hypotheses using 55year time-series data for 361 boreal forest stands. Global Ecology and Biogeography 21:441-454.
- Chen, H. Y. H., S. Vasiliauskas, G. J. Kayahara, and T. Ilisson. 2009. Wildfire promotes broadleaves and species mixture in boreal forest. Forest Ecology and Management 257:343-350.
- Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.
- Chen, S., C. Shahi, H. Y. H. Chen, and B. McLaren. 2017. Economic analysis of forest management alternatives: Compositional objectives, rotation ages, and harvest methods in boreal forests. Forest Policy and Economics **85**:124-134.
- Chojnacky, D. C., L. S. Heath, and J. C. Jenkins. 2013. Updated generalized biomass equations for North American tree species. Forestry **87**:129-151.
- Ciais, P., M. Reichstein, N. Viovy, A. Granier, J. Ogee, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A. D. Friend, P. Friedlingstein, T. Grunwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J. F. Soussana, M. J. Sanz, E. D. Schulze, T. Vesala, and R. Valentini. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529-533.
- Ciais, P., M. J. Schelhaas, S. Zaehle, S. L. Piao, A. Cescatti, J. Liski, S. Luyssaert, G. Le-Maire, E. D. Schulze, O. Bouriaud, A. Freibauer, R. Valentini, and G. J. Nabuurs. 2008. Carbon accumulation in European forests. Nature Geoscience 1:425-429.
- Clark, J. S., L. Iverson, C. W. Woodall, C. D. Allen, D. M. Bell, D. C. Bragg, A. W. D'Amato, F. W. Davis, M. H. Hersh, I. Ibanez, S. T. Jackson, S. Matthews, N. Pederson, M. Peters, M. W. Schwartz, K. M. Waring, and N. E. Zimmermann. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22:2329-2352.
- Crowther, T. W., H. B. Glick, K. R. Covey, C. Bettigole, D. S. Maynard, S. M. Thomas, J. R. Smith, G. Hintler, M. C. Duguid, G. Amatulli, M. N. Tuanmu, W. Jetz, C. Salas, C. Stam, D. Piotto, R. Tavani, S. Green, G. Bruce, S. J. Williams, S. K. Wiser, M. O. Huber, G. M. Hengeveld, G. J. Nabuurs, E. Tikhonova, P. Borchardt, C. F. Li, L. W. Powrie, M. Fischer, A. Hemp, J. Homeier, P. Cho, A. C. Vibrans, P. M. Umunay, S. L. Piao, C. W. Rowe, M. S. Ashton, P. R. Crane, and M. A. Bradford. 2015. Mapping tree density at a global scale. Nature 525:201-205.
- D'Orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Côté, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science **352**:1452-1455.
- Dai, A. 2011. Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change **2**:45-65.
- Dai, A. 2012. Increasing drought under global warming in observations and models. Nature Climate Change **3**:52-58.
- Daniel, C. J., M. T. Ter-Mikaelian, B. M. Wotton, B. Rayfield, and M.-J. Fortin. 2017. Incorporating uncertainty into forest management planning: Timber harvest, wildfire and climate change in the boreal forest. Forest Ecology and Management 400:542-554.

- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**:673-679.
- DeWalle, D. R., A. R. Buda, and A. Fisher. 2003. Extreme weather and forest management in the mid-Atlantic region of the United States. Northern Journal of Applied Forestry **20**:61-70.
- Dhar, A., L. Parrott, and S. Heckbert. 2016. Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. Canadian Journal of Forest Research 46:987-999.
- Diffenbaugh, N. S., and C. B. Field. 2013. Changes in ecologically critical terrestrial climate conditions. Science **341**:486-492.
- Donoghue, M. J., and E. J. Edwards. 2014. Biome Shifts and Niche Evolution in Plants. Annual Review of Ecology, Evolution, and Systematics **45**:547-572.
- Drobyshev, I., S. Gewehr, F. Berninger, and Y. Bergeron. 2013. Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. Journal of Ecology **101**:231-242.
- Dyderski, M. K., S. Paz, L. E. Frelich, and A. M. Jagodzinski. 2017. How much does climate change threaten European forest tree species distributions? Global Change Biology.
- Ecological Stratification Working Group. 1996. A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/ Hull.
- Evans, P., and C. D. Brown. 2017. The boreal-temperate forest ecotone response to climate change. Environmental Reviews **25**:423-431.
- Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species responses to climate change. Science Advances **3**:e1603055.
- Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. Wang. 2013. Changing Climates, Changing Forests: A Western North American Perspective. Journal of Forestry 111:214-228.
- Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography **37**:152-161.
- Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549-560.
- Flannigan, M. D., K. A. Logan, B. D. Amiro, W. R. Skinner, and B. J. Stocks. 2005. Future Area Burned in Canada. Climatic Change 72:1-16.
- Gauthier, S., P. Bernier, P. J. Burton, J. Edwards, K. Isaac, N. Isabel, K. Jayen, H. Le Goff, and E. A. Nelson. 2014. Climate change vulnerability and adaptation in the managed Canadian boreal forest. Environmental Reviews 22:256-285.
- Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015a. Boreal forest health and global change. Science **349**:819-822.
- Gauthier, S., P. Y. Bernier, Y. Boulanger, J. Guo, L. Guindon, A. Beaudoin, and D. Boucher. 2015b. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Canadian Journal of Forest Research 45:1439-1447.
- Ge, Z. M., S. Kellomaki, H. Peltola, X. Zhou, K. Y. Wang, and H. Vaisanen. 2011. Impacts of changing climate on the productivity of Norway spruce dominant stands with a mixture of Scots pine and birch in relation to water availability in southern and northern Finland. Tree Physiology 31:323-338.

- Ge, Z. M., X. A. Zhou, S. Kellomaki, K. Y. Wang, H. Peltola, H. Vaisanen, and H. Strandman. 2010. Effects of changing climate on water and nitrogen availability with implications on the productivity of Norway spruce stands in Southern Finland. Ecological Modelling 221:1731-1743.
- Gillett, N. P., A. Weaver, F. Zwiers, and M. D. Flannigan. 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters **31**.
- Girard, F., L. De Grandpre, and J. C. Ruel. 2014. Partial windthrow as a driving process of forest dynamics in old-growth boreal forests. Canadian Journal of Forest Research **44**:1165-1176.
- Girardin, M. P., A. A. Ali, C. Carcaillet, S. Gauthier, C. Hély, H. Le Goff, A. Terrier, and Y. Bergeron. 2013. Fire in managed forests of eastern Canada: Risks and options. Forest Ecology and Management 294:238-249.
- Girardin, M. P., A. A. Ali, C. Carcaillet, M. Mudelsee, I. Drobyshev, C. Hely, and Y. Bergeron. 2009. Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. Global Change Biology 15:2751-2769.
- Girardin, M. P., O. Bouriaud, E. H. Hogg, W. Kurz, N. E. Zimmermann, J. M. Metsaranta, R. de Jong, D. C. Frank, J. Esper, U. Buntgen, X. J. Guo, and J. Bhatti. 2016a. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences 113:E8406-E8414.
- Girardin, M. P., X. J. Guo, P. Y. Bernier, F. Raulier, and S. Gauthier. 2012. Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits. Biogeosciences **9**:2523-2536.
- Girardin, M. P., E. H. Hogg, P. Y. Bernier, W. A. Kurz, X. J. Guo, and G. Cyr. 2016b. Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Global Change Biology **22**:627-643.
- Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography **19**:755-768.
- Greenwood, S., P. Ruiz-Benito, J. Martinez-Vilalta, F. Lloret, T. Kitzberger, C. D. Allen, R. Fensham, D. C. Laughlin, J. Kattge, G. Bonisch, N. J. Kraft, and A. S. Jump. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecology Letters 20:539-553.
- Groisman, P. Y., B. G. Sherstyukov, V. N. Razuvaev, R. W. Knight, J. G. Enloe, N. S.
 Stroumentova, P. H. Whitfield, E. Førland, I. Hannsen-Bauer, and H. Tuomenvirta. 2007.
 Potential forest fire danger over Northern Eurasia: changes during the 20th century.
 Global and Planetary Change 56:371-386.
- Guo, C., and C. Costello. 2013. The value of adaption: Climate change and timberland management. Journal of Environmental Economics and Management **65**:452-468.
- Hanewinkel, M., D. A. Cullmann, M. J. Schelhaas, G. J. Nabuurs, and N. E. Zimmermann. 2013. Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3:203-207.
- Hanewinkel, M., S. Hummel, and D. A. Cullmann. 2010. Modelling and economic evaluation of forest biome shifts under climate change in Southwest Germany. Forest Ecology and Management 259:710-719.
- Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini,

C. O. Justice, and J. R. G. Townsend. 2013. High- Resolution Global Maps of 21st-Century Forest Cover Change. Science **342**:850-853.

- He, H. S., and D. J. Mladenoff. 1999. SPATIALLY EXPLICIT AND STOCHASTIC SIMULATION OF FOREST-LANDSCAPE FIRE DISTURBANCE AND SUCCESSION. Ecology **80**:81-99.
- Hember, R. A., W. A. Kurz, and N. C. Coops. 2017. Relationships between individual-tree mortality and water-balance variables indicate positive trends in water stress-induced tree mortality across North America. Global Change Biology 23:1691-1710.
- Hennigar, C. R., D. A. MacLean, and L. J. Amos-Binks. 2008. A novel approach to optimize management strategies for carbon stored in both forests and wood products. Forest Ecology and Management 256:786-797.
- Hisano, M., E. B. Searle, and H. Y. H. Chen. 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biological Reviews **93**:439-456.
- Hofgaard, A., H. Tommervik, G. Rees, and F. Hanssen. 2013. Latitudinal forest advance in northernmost Norway since the early 20th century. Journal of Biogeography **40**:938-949.
- Hogg, E. H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology **84**:115-122.
- Hogg, E. H., M. Michaelian, T. I. Hook, and M. E. Undershultz. 2017. Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. Global Change Biology 23:5297-5308.
- Hope, E. S., D. W. McKenney, J. H. Pedlar, B. J. Stocks, and S. Gauthier. 2016. Wildfire Suppression Costs for Canada under a Changing Climate. PLoS One **11**:e0157425.
- Houle, D., G. Lajoie, and L. Duchesne. 2016. Major losses of nutrients following a severe drought in a boreal forest. Nature Plants **2**:16187.
- Huang, J. G., Y. Bergeron, F. Berninger, L. Zhai, J. C. Tardif, and B. Denneler. 2013. Impact of future climate on radial growth of four major boreal tree species in the Eastern Canadian boreal forest. PLoS One 8:e56758.
- Hume, A. M., H. Y. H. Chen, A. R. Taylor, and P. Kardol. 2018. Intensive forest harvesting increases susceptibility of northern forest soils to carbon, nitrogen and phosphorus loss. Journal of Applied Ecology 55:246-255.
- Ilisson, T., and H. Y. H. Chen. 2009. The direct regeneration hypothesis in northern forests. Journal of Vegetation Science **20**:735-744.
- IPCC. 2014. Summary for Policy Makers.*in* R. K. Pachauri and L. A. Meyer, editors. Climate Change 2014: Synthesis Report. Contibution of Working Groups I, II, and III to the Fifth Assessment Report if the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- Jactel, H., J. Petit, M.-L. Desprez-Loustau, S. Delzon, D. Piou, A. Battisti, and J. Koricheva. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. Global Change Biology 18:267-276.
- Johnson, E. A. 1992. Fire and vegetation dynamics: studies from North American boreal forest. Camebridge University Press, Cambirdge.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281-1295.
- Kauppi, P. E., M. Posch, and P. Pirinen. 2014. Large impacts of climate warming on growth of boreal forests since 1960. PLoS One **9**.

- Kellomaki, S. 2000. Forests of the boreal region: gaps in knowledge and research needs. Forest Ecology and Management **132**:63-71.
- Kellomäki, S. 2016. Managing Boreal Forests in the Context of Climate Change. Boca Raton, CRC Press.
- Kellomäki, S., T. Karjalainen, and H. Väisänen. 1997. More timber from boreal forests under changing climate? Forest Ecology and Management **94**:195-208.
- Kellomäki, S., H. Peltola, T. Nuutinen, K. T. Korhonen, and H. Strandman. 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2339-2349.
- Keskitalo, E., J. Bergh, A. Felton, C. Björkman, M. Berlin, P. Axelsson, E. Ring, A. Ågren, J.-M. Roberge, M. Klapwijk, and J. Boberg. 2016. Adaptation to Climate Change in Swedish Forestry. Forests 7:28.
- Kirilenko, A. P., and R. A. Sedjo. 2007. Climate change impacts on forestry. Proceedings of the National Academy of Sciences **104**:19697-19702.
- Knoke, T., C. Ammer, B. Stimm, and R. Mosandl. 2007. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. European Journal of Forest Research 127:89-101.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987-990.
- Kurz, W. A., C. H. Shaw, C. Boisvenue, G. Stinson, J. Metsaranta, D. Leckie, A. Dyk, C. Smyth, and E. T. Neilson. 2013. Carbon in Canada's boreal forest — A synthesis1. Environmental Reviews 21:260-292.
- Leduc, A., P. Y. Bernier, N. Mansuy, F. Raulier, S. Gauthier, and Y. Bergeron. 2015. Using salvage logging and tolerance to risk to reduce the impact of forest fires on timber supply calculations. Canadian Journal of Forest Research **45**:480-486.
- Lempriere, T. C., P. Bernier, A. L. Carroll, M. D. Flannigan, R. P. Gilsenan, D. W. McKenney, E. H. Hogg, J. H. Pedlar, and D. Blain. 2008. The importance of forest sector adaptation to climate change. Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada.
- Lexer, M. J., and K. Hönninger. 2001. A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. Forest Ecology and Management 144:43-65.
- Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E. D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch, S. de-Miguel, A. Paquette, B. Herault, M. Scherer-Lorenzen, C. B. Barrett, H. B. Glick, G. M. Hengeveld, G. J. Nabuurs, S. Pfautsch, H. Viana, A. C. Vibrans, C. Ammer, P. Schall, D. Verbyla, N. Tchebakova, M. Fischer, J. V. Watson, H. Y. Chen, X. Lei, M. J. Schelhaas, H. Lu, D. Gianelle, E. I. Parfenova, C. Salas, E. Lee, B. Lee, H. S. Kim, H. Bruelheide, D. A. Coomes, D. Piotto, T. Sunderland, B. Schmid, S. Gourlet-Fleury, B. Sonke, R. Tavani, J. Zhu, S. Brandl, J. Vayreda, F. Kitahara, E. B. Searle, V. J. Neldner, M. R. Ngugi, C. Baraloto, L. Frizzera, R. Balazy, J. Oleksyn, T. Zawila-Niedzwiecki, O. Bouriaud, F. Bussotti, L. Finer, B. Jaroszewicz, T. Jucker, F. Valladares, A. M. Jagodzinski, P. L. Peri, C. Gonmadje, W. Marthy, T. O'Brien, E. H. Martin, A. R. Marshall, F. Rovero, R. Bitariho, P. A. Niklaus, P. Alvarez-Loayza, N. Chamuya, R. Valencia, F. Mortier, V. Wortel, N. L. Engone-Obiang, L. V.

Ferreira, D. E. Odeke, R. M. Vasquez, S. L. Lewis, and P. B. Reich. 2016. Positive biodiversity-productivity relationship predominant in global forests. Science **354**.

- Linderholm, H. W. 2006. Growing season changes in the last century. Agricultural and Forest Meteorology **137**:1-14.
- Lindner, M., B. Sohngen, L. A. Joyce, D. T. Price, P. Y. Bernier, and T. Karjalainen. 2002. Integrated forestry assessments for climate change impacts. Forest Ecology and Management 162:117-136.
- Lloyd, A. H., A. G. Bunn, and L. Berner. 2011. A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. Global Change Biology **17**:1935-1945.
- Logan, J., J. Régnière, and J. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130-137.
- Lucash, M. S., R. M. Scheller, B. R. Sturtevant, E. J. Gustafson, A. M. Kretchun, and J. R. Foster. 2018. More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. Ecosphere 9:e02293.
- Luo, Y., and H. Y. Chen. 2013. Observations from old forests underestimate climate change effects on tree mortality. Nature communications 4:1655.
- Luo, Y., and H. Y. Chen. 2015. Climate change-associated tree mortality increases without decreasing water availability. Ecology Letters **18** 1207–1215.
- Luo, Y., and H. Y. H. Chen. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. Journal of Ecology **99**:1470-1480.
- Lutz, D. A., H. H. Shugart, and M. A. White. 2013. Sensitivity of Russian forest timber harvest and carbon storage to temperature increase. Forestry **86**:283-293.
- Luyssaert, S., I. Inglima, M. Jung, A. D. Richardson, M. Reichstein, D. Papale, S. L. Piao, E. D. Schulze, L. Wingate, G. Matteucci, L. Aragao, M. Aubinet, C. Beer, C. Bernhofer, K. G. Black, D. Bonal, J. M. Bonnefond, J. Chambers, P. Ciais, B. Cook, K. J. Davis, A. J. Dolman, B. Gielen, M. Goulden, J. Grace, A. Granier, A. Grelle, T. Griffis, T. GrÜNwald, G. Guidolotti, P. J. Hanson, R. Harding, D. Y. Hollinger, L. R. Hutyra, P. Kolari, B. Kruijt, W. Kutsch, F. Lagergren, T. Laurila, B. E. Law, G. Le Maire, A. Lindroth, D. Loustau, Y. Malhi, J. Mateus, M. Migliavacca, L. Misson, L. Montagnani, J. Moncrieff, E. Moors, J. W. Munger, E. Nikinmaa, S. V. Ollinger, G. Pita, C. Rebmann, O. Roupsard, N. Saigusa, M. J. Sanz, G. Seufert, C. Sierra, M. L. Smith, J. Tang, R. Valentini, T. Vesala, and I. A. Janssens. 2007. CO2balance of boreal, temperate, and tropical forests derived from a global database. Global Change Biology 13:2509-2537.
- Malmstrom, C. M., and K. F. Raffa. 2000. Biotic disturbance agents in the boreal forest: considerations for vegetation change models. Global Change Biology **6**:35-48.
- McGill, B. J. 2010. Ecology. Matters of scale. Science 328:575-576.
- McKenney, D., J. Pedlar, M. Hutchinson, P. Papadopol, K. Lawrence, K. Campbell, E. Milewska, R. F. Hopkinson, and D. Price. 2013. Spatial climate models for Canada's forestry community. The Forestry Chronicle 89:659-663.
- McKenney, D., D. Yemshanov, J. Pedlar, D. Allen, K. Lawrence, E. Hope, B. Lu, and B. Eddy. 2016. Canada's Timber Supply: Current Status and Future Prospects under a Changing Climate. Natural Resources Canada, Canadian Forest Service.
- Mendelsohn, R., W. Morrison, M. Schlesinger, and N. Andronova. 2000. Country-specific market impacts of climate change. Climate Change **45**:553-569.

- Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology 17:2084-2094.
- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science **349**:823-826.
- Mladenoff, D. J. 2004. LANDIS and forest landscape models. Ecological Modelling 180:7-19.
- Montwe, D., M. Isaac-Renton, A. Hamann, and H. Spiecker. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. Global Change Biology **22**:806-815.
- Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere **3**:1-22.
- Nabuurs, G. J., A. Pussinen, T. Karjalainen, M. Erhard, and K. Kramer. 2002. Stemwood volume increment changes in European forests due to climate change a simulation study with the EFISCEN model. Global Change Biology **8**:304-316.
- Nordström, E.-M., N. Forsell, A. Lundström, A. Korosuo, J. Bergh, P. Havlík, F. Kraxner, S. Frank, O. Fricko, T. Lundmark, and A. Nordin. 2016. Impacts of global climate change mitigation scenarios on forests and harvesting in Sweden1. Canadian Journal of Forest Research:1-12.
- NRTEE. 2011. Paying the price: the economic impacts of climate change for Canada. National Round Table on the Economy and Environment, A Canadian Initiative.
- Ochuodho, T. O., V. A. Lantz, P. Lloyd-Smith, and P. Benitez. 2012. Regional economic impacts of climate change and adaptation in Canadian forests: A CGE modeling analysis. Forest Policy and Economics **25**:100-112.
- Ozolincius, R. 2012. Possible Effects of Climate Change on Forest Biodiversity, Tree Growth and Condition: Review of Research in Lithuania. Baltic Forestry **18**:156-167.
- Park, A., K. Puettmann, E. Wilson, C. Messier, S. Kames, and A. Dhar. 2014. Can Boreal and Temperate Forest Management be Adapted to the Uncertainties of 21st Century Climate Change? Critical Reviews in Plant Sciences 33:251-285.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.
- Pautasso, M., M. Schlegel, and O. Holdenrieder. 2015. Forest health in a changing world. Microbrial Ecology **69**:826-842.
- Pearson, R. G. 2006. Climate change and the migration capacity of species. Trends in Ecology and Evolution **21**:111-113.
- Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I. C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengård, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-Scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, M.-N. Tuanmu, A. Vergés, C. Villanueva, T. Wernberg, E. Wapstra, and S. E. Williams. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355.
- Pedlar, J. H., and D. W. McKenney. 2017. Assessing the anticipated growth response of northern conifer populations to a warming climate. Scientific Reports 7:43881.
- Peltola, H., V. P. Ikonen, H. Gregow, H. Strandman, A. Kilpeläinen, A. Venäläinen, and S. Kellomäki. 2010. Impacts of climate change on timber production and regional risks of

wind-induced damage to forests in Finland. Forest Ecology and Management **260**:833-845.

- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change 1:467-471.
- Peñuelas, J., J. G. Canadell, and R. Ogaya. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Global Ecology and Biogeography **20**:597-608.
- Perez-Garcia, J., L. A. Joyce, A. D. McGuire, and X. M. Xiao. 2002. Impacts of climate change on the global forest sector. Climatic Change **54**:439-461.
- Perez-Garcia, J., L. A. Joyce, C. S. Binkley, and A. D. McGuire. 1997. Economic impacts of climatic change on the global forest sector: An integrated ecological/economic assessment. Critical Reviews in Environmental Science and Technology 27:123-138.
- Perie, C., and S. de Blois. 2016. Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. PeerJ 4:e2218.
- Pretzsch, H., P. Biber, G. Schutze, E. Uhl, and T. Rotzer. 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. Nature communications **5**:4967.
- Price, D. T., R. I. Alfaro, K. J. Brown, M. D. Flannigan, R. A. Fleming, E. H. Hogg, M. P. Girardin, T. Lakusta, M. Johnston, D. W. McKenney, J. H. Pedlar, T. Stratton, R. N. Sturrock, I. D. Thompson, J. A. Trofymow, and L. A. Venier. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems1. Environmental Reviews 21:322-365.
- Pukkala, T. 2017. Transfer and response functions as a means to predict the effect of climate change on timber supply. Forestry: An International Journal of Forest Research:1-8.
- Pureswaran, D. S., L. De Grandpre, D. Pare, A. Taylor, M. Barrette, H. Morin, J. Regniere, and D. D. Kneeshaw. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. Ecology 96:1480-1491.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramsfield, T. D., B. J. Bentz, M. Faccoli, H. Jactel, and E. G. Brockerhoff. 2016. Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. Forestry **89**:245-252.
- Raulier, F., N. Dhital, P. Racine, R. Tittler, and A. Fall. 2014. Increasing resilience of timber supply: How a variable buffer stock of timber can efficiently reduce exposure to shortfalls caused by wildfires. Forest Policy and Economics 46:47-55.
- Régnière, J., R. Saint-Amant, and A. Béchard. 2014. BioSIM 10- User's manual Natural Resources Canada, Canadian Forest Service, Laurentian Forest Centre.
- Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change 5:148.
- Reyer, C. P. O., S. Bathgate, K. Blennow, J. G. Borges, H. Bugmann, S. Delzon, S. P. Faias, J. Garcia-Gonzalo, B. Gardiner, J. R. Gonzalez-Olabarria, C. Gracia, J. G. Hernández, S. Kellomäki, K. Kramer, M. J. Lexer, M. Lindner, E. van der Maaten, M. Maroschek, B. Muys, B. Nicoll, M. Palahi, J. H. N. Palma, J. A. Paulo, H. Peltola, T. Pukkala, W. Rammer, D. Ray, S. Sabaté, M.-J. Schelhaas, R. Seidl, C. Temperli, M. Tomé, R. Yousefpour, N. E. Zimmermann, and M. Hanewinkel. 2017. Are forest disturbances

amplifying or canceling out climate change-induced productivity changes in European forests? Environmental Research Letters **12**:034027.

- Reyer, C. P. O., N. Brouwers, A. Rammig, B. W. Brook, J. Epila, R. F. Grant, M. Holmgren, F. Langerwisch, S. Leuzinger, W. Lucht, B. Medlyn, M. Pfeifer, J. Steinkamp, M. C. Vanderwel, H. Verbeeck, D. M. Villela, and D. Coomes. 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of Ecology 103:5-15.
- Rittenhouse, C. D., and A. R. Rissman. 2015. Changes in winter conditions impact forest management in north temperate forests. J Environ Manage **149**:157-167.
- Rogers, B. M., A. J. Soja, M. L. Goulden, and J. T. Randerson. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. Nature Geoscience 8:228-234.
- Rowland, L., A. C. da Costa, D. R. Galbraith, R. S. Oliveira, O. J. Binks, A. A. Oliveira, A. M. Pullen, C. E. Doughty, D. B. Metcalfe, S. S. Vasconcelos, L. V. Ferreira, Y. Malhi, J. Grace, M. Mencuccini, and P. Meir. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature 528:119-122.
- Ruthrof, K. X., J. B. Fontaine, G. Matusick, D. D. Breshears, D. J. Law, S. Powell, and G. Hardy. 2016. How drought-induced forest die-off alters microclimate and increases fuel loadings and fire potentials. International Journal of Wildland Fire 25:819.
- Sato, H., H. Kobayashi, G. Iwahana, and T. Ohta. 2016. Endurance of larch forest ecosystems in eastern Siberia under warming trends. Ecology and Evolution **6**:5690-5704.
- Savage, D. W., D. L. Martell, and B. M. Wotton. 2010. Evaluation of two risk mitigation strategies for dealing with fire-related uncertainty in timber supply modelling. Canadian Journal of Forest Research **40**:1136-1154.
- Schaphoff, S., C. P. O. Reyer, D. Schepaschenko, D. Gerten, and A. Shvidenko. 2016. Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. Forest Ecology and Management 361:432-444.
- Scheller, R. M., and J. B. Domingo. 2012. LANDIS-II Model v6.0 Conceptual Description. Portland State University.
- Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecological Modelling 201:409-419.
- Scheller, R. M., and D. J. Mladenoff. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecological Modelling 180:211-229.
- Scheller, R. M., and D. J. Mladenoff. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biology **11**:307-321.
- Schlyter, P., I. Stjernquist, L. Barring, A. M. Jonsson, and C. Nilsson. 2006. Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. Climate Research 31:75-84.
- Searle, E. B., and H. Y. Chen. 2017a. Persistent and pervasive compositional shifts of western boreal forest plots in Canada. Global Change Biology **23**:857-866.
- Searle, E. B., and H. Y. H. Chen. 2017b. Persistent and pervasive compositional shifts of western boreal forest plots in Canada. Glob Chang Biol **23**:857-866.

- Seidl, R., W. Rammer, D. Jäger, and M. J. Lexer. 2008. Impact of bark beetle (Ips typographus L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. Forest Ecology and Management 256:209-220.
- Shuman, J. K., N. M. Tchebakova, E. I. Parfenova, A. J. Soja, H. H. Shugart, D. Ershov, and K. Holcomb. 2015. Forest forecasting with vegetation models across Russia1. Canadian Journal of Forest Research 45:175-184.
- Shvidenko, A. Z., and D. G. Schepaschenko. 2014. Climate change and wildfires in Russia. Contemporary Problems of Ecology **6**:683-692.
- Sitch, S., C. Huntingford, N. Gedney, P. E. Levy, M. Lomas, S. L. Piao, R. Betts, P. Ciais, P. Cox, P. Friedlingstein, C. D. Jones, I. C. Prentice, and F. I. Woodward. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biology 14:2015-2039.
- Smyth, C. E., G. Stinson, E. Neilson, T. C. Lempriere, M. Hafer, G. J. Rampley, and W. A. Kurz. 2014. Quantifying the biophysical climate change mitigation potential of Canada's forest sector. Biogeosciences 11:3515-3529.
- Sohngen, B. 2014. Forests and Climate Change: Economic perspectives. Pages 227-242 *in* S. Kant and J. R. R. Alavalapati, editors. Handbook of Forest Reouce Economics. Routledge, London, UK and New York, USA.
- Sohngen, B., R. Mendelsohn, and R. Sedjo. 2001. A global model of climate change impacts on timber markets. Journal of Agricultural and Resource Economics **26**:326-343.
- Sohngen, B., and X. Tian. 2016. Global climate change impacts on forests and markets. Forest Policy and Economics **72**:18-26.
- Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin, and P. W. Stackhouse. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56:274-296.
- Solberg, B., A. Moiseyev, and A. M. I. Kallio. 2003. Economic impacts of accelerating forest growth in Europe. Forest Policy and Economics **5**:157-171.
- Steenberg, J. W. N., P. N. Duinker, and P. G. Bush. 2011. Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. Forest Ecology and Management 262:2316-2327.
- Steenberg, J. W. N., P. N. Duinker, and P. G. Bush. 2013. Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. Annals of Forest Science 70:61-73.
- Sturrock, R. N. 2012. Climate change and forest diseases: using today's knowledge to address future challenges. Forest Systems **21**:329-336.
- Sturtevant, B. R., E. J. Gustafson, W. Li, and H. S. He. 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecological Modelling 180:153-174.
- Sturtevant, B. R., R. M. Scheller, B. R. Miranda, D. Shinneman, and A. Syphard. 2009. Simulating dynamic and mixed-severity fire regimes: A process-based fire extension for LANDIS-II. Ecological Modelling 220:3380-3393.
- Taylor, A. R., Y. Boulanger, D. T. Price, D. Cyr, E. McGarrigle, W. Rammer, and J. A. Kershaw. 2017. Rapid 21st century climate change projected to shift composition and

growth of Canada's Acadian Forest Region. Forest Ecology and Management **405**:284-294.

- Tchebakova, N. M., E. I. Parfenova, M. A. Korets, and S. G. Conard. 2016. Potential change in forest types and stand heights in central Siberia in a warming climate. Environmental Research Letters **11**.
- Tchebakova, N. M., E. I. Parfenova, and A. J. Soja. 2011. Climate change and climate-induced hot spots in forest shifts in central Siberia from observed data. Regional Environmental Change **11**:817-827.
- Terrier, A., M. P. Girardin, C. Perie, P. Legendre, and Y. Bergeron. 2013. Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecological Applications 23:21-35.
- Thomson, A. M., and W. H. Parker. 2008. Boreal forest provenance tests used to predict optimal growth and response to climate change. 1. Jack pine. Canadian Journal of Forest Research **38**:157-170.
- Thuiller, W. 2007. Biodiversity: climate change and the ecologist. Nature 448:550-552.
- Tian, X., B. Sohngen, J. B. Kim, S. Ohrel, and J. Cole. 2016. Global climate change impacts on forests and markets. Environmental Research Letters **11**:035011.
- Toledo, M., L. Poorter, M. Peña-Claros, A. Alarcón, J. Balcázar, C. Leaño, J. C. Licona, O. Llanque, V. Vroomans, P. Zuidema, and F. Bongers. 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. Journal of Ecology 99:254-264.
- Tremblay, J. A., Y. Boulanger, D. Cyr, A. R. Taylor, D. T. Price, and M.-H. St-Laurent. 2018. Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. PLoS One **13**:e0191645.
- Trenberth, K. E., A. Dai, G. van der Schrier, P. D. Jones, J. Barichivich, K. R. Briffa, and J. Sheffield. 2013. Global warming and changes in drought. Nature Climate Change 4:17-22.
- van Lierop, P., E. Lindquist, S. Sathyapala, and G. Franceschini. 2015. Global forest area disturbance from fire, insect pests, diseases and severe weather events. Forest Ecology and Management **352**:78-88.
- van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. Science 323:521-524.
- Van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, T. Kram, V. Krey, and J.-F. Lamarque. 2011. The representative concentration pathways: an overview. Climatic Change 109:5.
- Wang, Y., E. H. Hogg, D. T. Price, J. Edwards, and T. Williamson. 2014. Past and projected future changes in moisture conditions in the Canadian boreal forest. The Forestry Chronicle 90:678-691.
- Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs **83**:441-470.
- Zhang, D., and P. Pearse. 2011. Forest Economics. UBC Press, Vancouver, British Columbia.
- Zhang, S. Y. 1994. Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. Wood Science and Technology 29:451-465.

- Zhang, Y., H. Y. H. Chen, and P. B. Reich. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology **100**:742-749.
- Zhao, M. S., and S. W. Running. 2010. Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009. Science **329**:940-943.
- Zhu, J. Y., C. T. Scott, K. L. Scallon, and G. C. Myers. 2007. Effects of plantation density on wood density and anatomical properties of red pine (Pinus resinosa Ait.). Wood and Fiber Science 39:502-512.

SUPPLEMENTARY INFORMATION: CHAPTER THREE

Parameterization

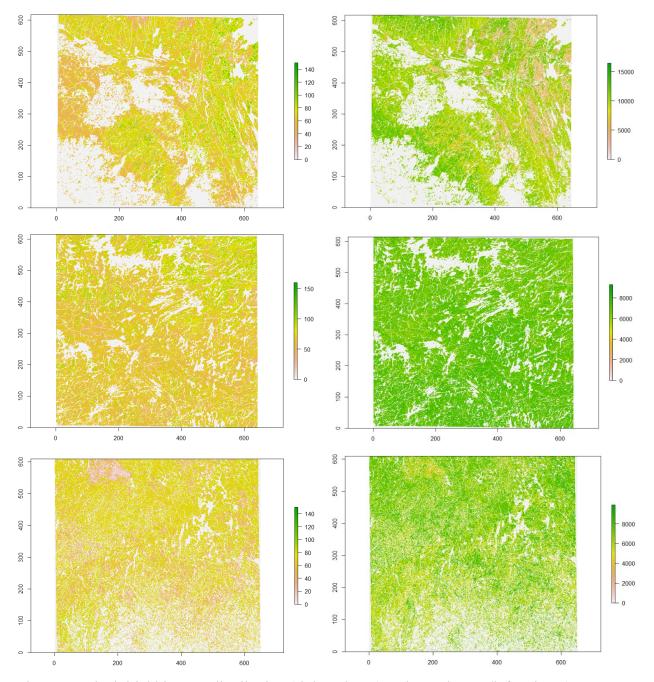


Fig. S3-1. The initial biomass distribution (right column) and age classes (left column) present across the Boreal Plains (top row), Boreal Shield West (middle row) and Boreal Shield East (bottom row). Some of the densest stands are found in the BP whereas the youngest and least dense region is the BSE.

Climate change projections

This study utilized climate projections from the Canadian Coupled Global Climate Model CanESM2. This model was used for each of the three RCP scenario. Important climate components within the LANDIS modelling framework are both long term temperature (°C) and precipitation (mm). Below are the mean annual values used for both factors throughout the three regions.

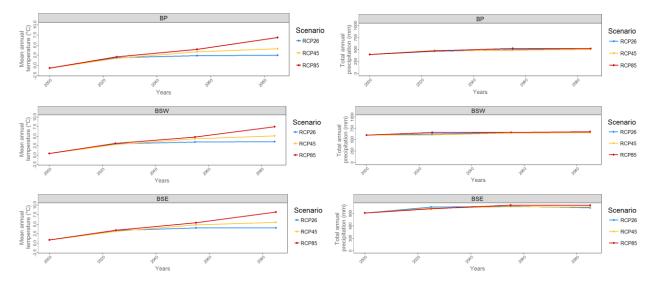
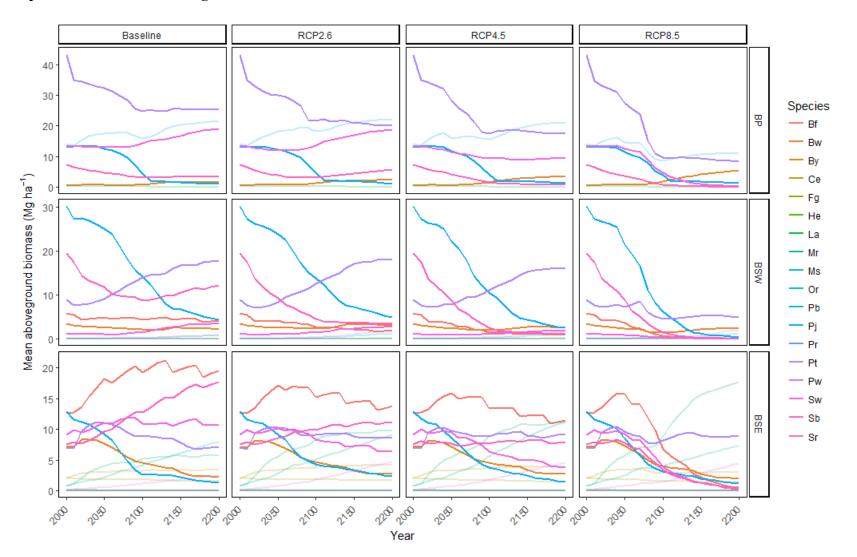
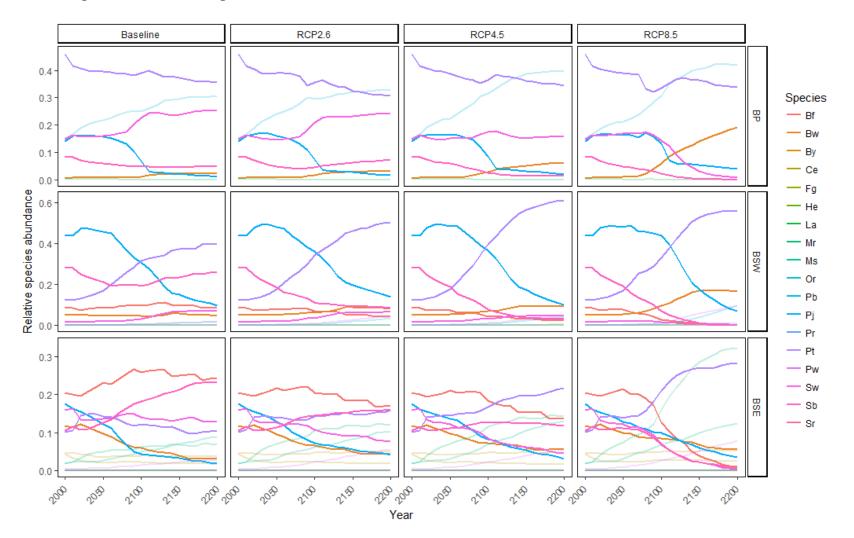


Fig. S3-2. Climate projections used in the simulations: temperature (left) and precipitation (right) within BP (top), BSW (middle) and BSE (bottom).



Species level biomass changes

Fig. S3-3a. Changes in individual species mean aboveground biomass (Mg ha⁻¹) shown across 4 climate scenarios in three study regions. Specific commercially important boreal species are highlighted for easier identification and interpretation.



Relative species biomass changes

Fig. S3-3b. Relative abundances of all species throughout the simulations. Specific commercially important boreal species are highlighted for easier identification and interpretation.

Harvestable area (%)

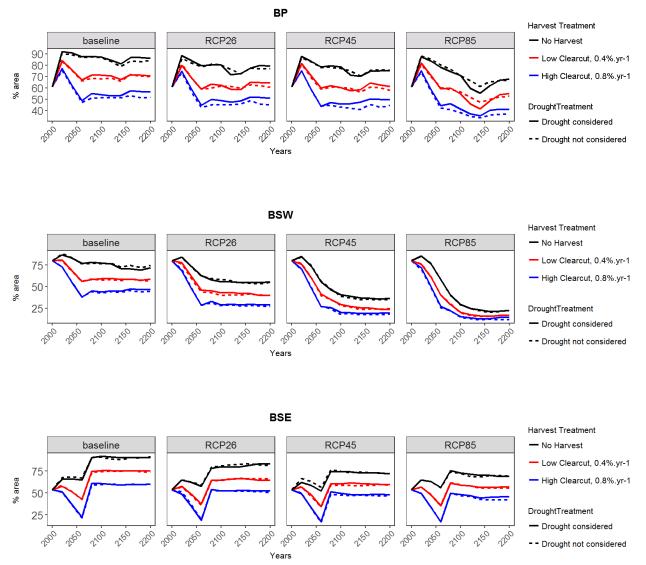


Fig. S3-4. Percent of land available for harvest in each harvesting scenario considering the impact of forest disturbances, particularly drought.

Fire disturbance

The area burned each year by fire is extremely variable between study sites and climate scenarios. Stand age is an important factor for this simulation because it relates to the amount of fuel present whereas time since last disturbance is the driver between likelihood of ignition. It is evident that there is much greater impact, in terms of biomass removal, in the BSW site, especially the RCP 8.5 scenario. In fact, RCP 8.5 affected the greatest area for all sites as expected. The reasons for this include, warmer temperatures and slightly less precipitation over the study period (Fig. S4, S4a). Greater fire return interval in the study, and the RCP 8.5 scenario in particular, contributes to the decreased stand volumes as there are lower stand ages present. This may also shift some of the species compositions that are better adapted to fire, as mentioned earlier; Pj regenerates through serotinous cones and broadleaf species are better at colonizing disturbed sites. Planning for fires will remain crucial in forecasting wood supply, especially in such fire prone areas.

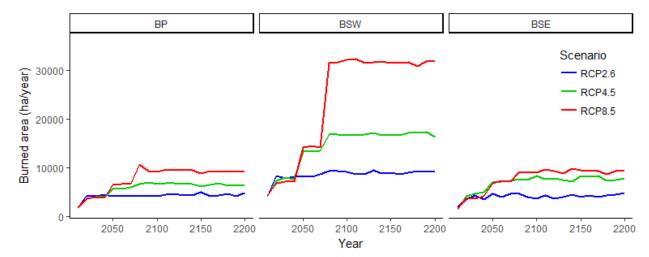


Fig. S3-5. Amount of burned area (ha/ year) for the three study regions and three climate scenarios over 200 years.