# Modeling the Impacts of Global Change on Tree Growth and Stand Density of Boreal Forests in Canada

by

Kun Xu

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Forest Biology and Management

Department of Renewable Resources
University of Alberta

# Abstract

Global change of environment and human activity has profoundly impacted boreal forests in structure, dynamics and function, imposing serious challenges for maintaining forest growth and yield in Canada. In this thesis, I address three questions important for understanding and predicting dynamics of boreal forests in the face of global change: how to estimate tree biomass under global warming, how to maintain long-term forest plots under intensified fire disturbances, and what is the spatial distribution of tree density in boreal forests. I answered the three questions based on unprecedented datasets compiled from over 30,000 plots established since 1949. My effort comprises three main chapters of my thesis.

In Chapter 2, I assessed the effects of climate on tree allometric biomass equations and proposed to incorporate climatic factors into allometric models. I focused on five major timber species of Canada and built climate-based allometric models by explicitly testing the effect of each climatic factor, e.g., temperature, precipitation, etc. I found that the allometries of three species, i.e., white spruce (*Picea glauca*), black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), were not sensitive to climate, but the allometric models for trembling aspen (*Populus tremuloides*) and tamarack (*Larix laricina*) performed significantly better after incorporating frost-free period and mean annual temperature respectively into their conventional, climate-independent allometric models. Under the modest warming scenario, if the conventional models for trembling aspen and tamarack were still in use in 2030, the aboveground biomass of these two species would be underestimated by 10% in Canada. This chapter suggests the necessity to proactively develop climate-based allometric equations for more accurate and reliable tree biomass estimation.

In Chapter 3, I addressed the challenge of maintaining long-term forest plots in facing intensified fire disturbances in northern forests. Based on 60-year fire burning data of 919 permanent sample plots (PSPs) in Alberta, Canada, I built Cox proportional hazards models to quantify the effects of stand conditions and climate on plot fire hazards. The results showed that 17% of the plots were burned with an average 28.7-year lifespan. I found that plots established more recently suffered higher fire hazards, and plots in the Boreal ecoregion suffered 2.85 and 3.36 times higher risks than those in the Foothills and Rocky Mountain ecoregions, respectively. Higher tree species richness and density of deciduous trees were found associated with lower plot fire hazards, while warming increased fire hazards. Based on the estimated Cox proportional hazards model, I projected plot fire hazards in 2050 to be 1.63 times higher than the current level due to warming. This chapter emphasizes the need to consider intensified natural disturbances, including fire, for the maintenance of long-term forest plots.

In Chapter 4, I attempted to model tree density variation in North American boreal forest by incorporating stand height into an existing biome model. By validating this biome model for density estimation, I identified that it underestimated tree density of 4,367 plots by 32.3%. The tree density model that I developed outperformed the previous biome model as judged by all measures of goodness-of-fit, with only 0.6% underestimation. Based on my model, I estimated there were 351.3 billion trees in the boreal forest of North America, compared to 211.2 billion estimated from the previous model. The underestimation by the previous model was equivalent to a missing of 14.0 trillion kg biomass. I also produced a 1-km resolution boreal tree density map of North America, and projected tree density distribution in 2050. This chapter updates understanding of the role of boreal forests in regulating forest ecosystem functions. It also

addresses the urgent need to improve boreal forest models to inform adaptation and mitigation planning.

By modeling biomass allometry for major timber species, fire hazards of long-term forest plots, and tree density distribution across boreal forests, my thesis contributes to data, models and understanding for sustainable management of forests and the impacts of global change on forest ecosystems in Canada.

# Preface

This thesis is an original work by Kun Xu. The forest data for Chapter 2 were from the Energy from the Forest (ENFOR) Canada Biomass Data contributed by Canadian Forest Service, Natural Resources Canada and C-H. Ung, M.C. Lambert, F. Raulier, J. Guo and P.Y. Bernier under the Open Government License – Canada. The forest data for Chapter 3 were provincial Permanent Sample Plot (PSP) data requested from Forest Stewardship and Trade Branch of the Government of Alberta. The forest data for Chapter 4 were PSP data requested from local governments and forestry departments of provinces and territories of Canada and from Cooperative Alaska Forest Inventory, which were compiled by Kun Xu, together with the Canadian National Forest Inventory and ABMI data requested from Canadian Council of Forest Ministers and Alberta Biodiversity Monitoring Institute respectively. The climate data for Chapter 2 and 3 were generated from ClimateNA v7.21 contributed by T. Wang, A. Hamann, D. Spittlehouse and D. Carroll, and the climate data for Chapter 4 were accessed from WorldClim v2.1 contributed by S.E. Fick and R.J. Hijmans and CCAFS GCM downscaled data portal contributed by C. Navarro-Racines, C. Tarapues, P. Thornton, et al. Human development, topographic and vegetative data used in Chapter 4 were individually acknowledged in the supplementary Table S6 of this chapter. Apart from the credits for the data collection, management and sharing, all others are my original work.

Chapter 2 of this thesis has been published as

Xu, K., Jiang, J., & He, F. (2021). Climate-based Allometric Biomass Equations for Five Major Canadian Timber Species, *Canadian Journal of Forest Research*, 51, 1633-1642. https://doi.org/10.1139/cjfr-2020-0485.

K. Xu was responsible for the concept formation, data analysis, and manuscript writing. J. Jiang assisted with the data quality check. F. He supervised the study and was involved with concept formation and manuscript writing.

Chapter 3 of this thesis has been published as

Xu, K., Huang, S., & He, F. (2022). Modeling fire hazards for the maintenance of long-term forest inventory plots in Alberta, Canada, *Forest Ecology and Management*, 513, 120206. https://doi.org/10.1016/j.foreco.2022.120206.

K. Xu was responsible for concept formation, data preparation and analysis, validation, manuscript writing and revision. S. Huang assisted with resources, data curation, and manuscript revision. F. He supervised the study and was involved with concept formation, manuscript writing and revision.

Chapter 3 was also presented as a contributed talk in fire management for the 2022 ESA & CSEE Joint Meeting in Montreal (Abstract ID: 1230778) on the 18th of August 2022.

Chapter 4 of this thesis was submitted to *Nature Communications* for peer reviewing.

# Acknowledgements

My PhD thesis is funded by the CSC-University of Alberta Joint Doctoral Scholarship awarded by China Scholarship Council (CSC) in 2018, the Doctoral Recruitment Scholarship of the Faculty of Graduate Studies and Research of the University of Alberta in 2017, and graduate research assistantship from Prof. Fangliang He sponsored by Natural Sciences and Engineering Research Council of Canada (NSERC) in 2017 and 2021. I also received the J Gordin Kaplan Graduate Student Award in support for my conference participation in 2022. Without these sources of funding, I would not have succeeded in completing my PhD.

I thank the continuous supervision of Prof. Fangliang He, my committee members, Prof. Victor Lieffers and Dr. Shongming Huang, and the Candidacy Examination committee members, Dr. Charles Nock and Dr. Jaime Pinzon. I particularly thank Prof. Victor Lieffers and Dr. Shongming Huang for their careful review of my thesis. My first-year enhancement learning in statistics, success in CSC scholarship application, continental forest data compilation, straight pass in candidacy exam, two 1st-author publications in *Canadian Journal of Forest Research* and *Forest Ecology and Management*, and thesis completion would not have been realized if there were no continuous encouragement and support of Prof. Fangliang He, who is the most admirable scientist and supervisor in forest ecology to me.

Understanding the enormous effort invested in sampling forest data and data management, I sincerely thank the following agencies and individuals for generously sharing their precious and valuable data with me:

Chapter 2 – the Energy from the Forest (ENFOR) Canada Biomass Data contributed and maintained by Canadian Forest Service, Natural Resources Canada and C-H. Ung, M.C. Lambert, F. Raulier, J. Guo and P.Y. Bernier.

Chapter 3 – the Alberta Permanent Sample Plot data sharing partner, Forest Stewardship and Trade Branch, Ministry of Agriculture, Forestry and Rural Economic Development of Alberta, Government of Alberta, and the forest analyst in charge of data management, K. Stadt.

Chapter 4 – the Alaskan Permanent Sample Plot data contributed by T. Malone, J. Liang and E.C. Packee of Forest Service, United States Department of Agriculture and M. Stevens of University of Alaska Fairbanks; the Canadian Permanent Sample Plot data points of contact, K. Stadt of Alberta, R.D. Jong of British Columbia, S. Meng of

Manitoba, B. Pittman and C. Cohlmeyer of Newfoundland and Labrador, K. Groenewegen, T. Rea and T. Lakusta of Northwest Territories, T. Little of Ontario, Direction des inventaires forestiers, Ministère des Forêts, de la Faune et des Parcs of Quebec, P. Loseth of Saskatchewan, and A. Geoppel of Yukon; the Canadian National Forest Inventory data contributed by Canadian Council of Forest Ministers; the ABMI data contributed by Alberta Biodiversity Monitoring Institute.

I want to thank the lab mates of He's lab, including Youhua Chen, Dingliang Xing, Jessica Akande, David Deane, Pembegul Moradaogu, Scott Boyce and Jingye Li, for their encouragement, support and many good suggestions on my study and life.

I especially want to thank the following five persons for helping transform me from an inexperienced student to what I am today. Dr. Adam Kashlak from the Department of Mathematical and Statistical Sciences led me to the world of mathematical statistics and showed me the power of statistics. Prof. Fangliang He, Dr. Jaime Pinzon and Dr. Charlene Nielsen offered me valuable teaching assistant opportunities for their courses, which greatly built up my independent teaching skills that will be very valuable for my future career. Dr. Ting Ma and Dr. Shiyu Ma kindly invited me to collaborate on their research that excited me and also offered me opportunities to transform my expertise to outcome. I prepared myself for future opportunities and challenges from these precious learning, teaching and collaboration experiences.

Lastly, without the loving support from my parents, relatives, friends and peers for my PhD study in Canada, I would not have had the strength to overcome every difficulty throughout my journey to PhD. Without Prof. Fangliang He's strict but extremely constructive advice on my analysis and writing, it would not be possible for me to complete this thesis study. I owe my successful completion of the PhD to their enormously generous support.

## Table of Contents

# List of Tables

## List of Figures

# Chapter 1 Introduction

## 1.1 Canadian boreal forests under global change

Boreal forests, the second largest terrestrial biome (accounting for 28% of global forests and 75% forests in Canada; Natural Resources Canada 2020), are teeming with a great diversity of life, including over 300 bird and 200 fish and mammal species (Kayes and Mallik 2020). Boreal forests contain approximately 800 Pg C in biomass (Apps et al. 1993), support the economy of countries at high latitudes (Östlund et al. 1997; Burton et al. 2006; Bogdanski 2008), and contribute net carbon sink to the reduction of global carbon dioxide ($CO_2$) emission (Liski et al. 2003). Modern silviculture practices, stand development, increased temperature and enhanced $CO_2$ fertilization contributed to boreal tree growth and yield increase to certain degrees (Jarvis and Linder 2000; Kirilenko and Sedjo 2007; Jucker et al. 2020; Ameray et al. 2021; Burkhart and Yang 2022). However, the capacity of net carbon sink of boreal forests has decreased due to intensified negative impacts of global change in environment and human activity, making them a potential carbon source (Apps et al. 1993; Vanderwel, Coomes and Purves 2013; Gauthier et al. 2015). Much evidence has shown that the overall forest growth, yield and biomass stock of Canada have decreased over the past half century due to forest harvesting (Burton et al. 2006; Bogdanski 2008) and global change (Spittlehouse and Stewart 2004; Duchesne et al. 2005; Peng et al. 2011; Ma et al. 2012; Lemprière et al. 2013; Chen and Luo 2015; Searls et al. 2021). Intensifying draught was found as a major culprit that limited tree growth and induced tree mortality in Canada under global warming (Balshi et al. 2009; Peng et al. 2011; Ma et al. 2012), which also triggered disturbances such as forest fires (Lee et al. 2002; Boulanger, Gauthier and Button 2014) and pest infestation (Safranyik et al. 2010; Cortini and Comeau 2020). Tree mortality rates were found to have increased by 4.7% per year from 1963 to 2008 across Canada mainly due to increasing climate change induced water stress (Peng et al. 2011). Meanwhile, intensifying natural disturbances, such as insect, pathogen and fire disturbances, also resulted in mortality increase and growth and yield decline in Canada over the past decades (Duchesne et al. 2005; Wotton, Nock and Flannigan 2010; Gauthier et al. 2015). Taking fire disturbances as an example, the forest area burned, length of fire season, and number of large fires all increased since 1959 in Canada according to the National Fire Information Database (Lee et al. 2002; Hanes et al. 2018). And the national carbon emissions due to forest fire were expected to surpass the increase of forest carbon stock under warming and intensifying drought (Balshi et al. 2009).

These would not only impact the global carbon cycle, but also inevitably alter the dynamics and succession of boreal forests (Bergeron et al. 1998; Peng et al. 2011; Chen and Luo 2015; Zhang, Huang and He 2015) where stands with higher competition stress and mortality rotated faster and yielded less biomass (Vanderwel et al. 2016; Luo et al. 2020; Searls et al. 2021). These increased uncertainties in forest dynamics will further jeopardize the maintenance of forest growth and yield in Canada (Duchesne et al. 2005; Taylor et al. 2017). To assess such impacts and uncertainties, it is necessary to understand how forest dynamics and structure, such as growth, stand density, and the maintenance of forest stands are affected by climate change and intensified natural disturbances in Canada (Park et al. 2014; Gauthier et al. 2015; Trumbore, Brando and Hartmann 2015; Girardin et al. 2016). My thesis aims to test how climate affects biomass accumulation of tree species, plot fire hazards and tree density distribution across landscape to support sustainable growth of forests in Canada under global change.

## 1.2 Allometric biomass equations for growth and yield estimation

Allometric biomass equations are a major tool in supporting estimation and projection of forest growth and yield (Monserud 2003). These equations have been developed since the 1960s based on the allometric relationship between tree size, as measured by diameter at breast height (DBH), and height and biomass of individual trees (Pastor et al. 1984; Weiner 2004), and have been widely used for forest biomass estimation (Jucker et al. 2017; Réjou-Méchain et al. 2019). In Canada, allometric biomass equations were built for individual tree species with pooled biomass data by sites (Lambert, Ung and Raulier 2005; Ung, Bernier and Guo 2008), and they have been subsequently used for forest biomass estimation by summing the biomass per stand per species. Studies on forest carbon stock and growth and yield in Canada have adopted these equations for aboveground forest biomass estimation, e.g. Chen and Luo (2015) and Taylor et al. (2017). But the results and projection of these studies may be unreliable as these models were developed without accounting for the possible effect of climate change on tree biomass allometries (Lambert, Ung and Raulier 2005; Ung, Bernier and Guo 2008). Contrary to the conventional climate-independent allometric models, the biomass allometries are often found to vary among different environmental conditions (McMahon, Parker and Miller 2010; Lloyd, Bunn and Berner 2011; Yang et al. 2020).

Biophysical evidence has shown that wood density could vary considerably among trees of the same species when growing in different climate or habitat conditions, leading to differential accumulation of biomass of trees of the same size (Chave et al. 2014). It is documented that the wood density of deciduous trees, e.g., tamarack, growing in warmer regions is denser than those of the same species in colder regions (McMahon et al. 2010; Clough et al. 2017). Also, some trees of a species grow taller in warmer temperature than others of the same age or DBH in colder regions (Yang et al. 2020). However, not every tree species grows larger under elevated temperature (Bouriaud et al. 2004; Way and Oren 2010; Yang et al. 2020). For example, the volume and stem biomass of evergreen trees, such as spruce and fir, remains unchanged under elevated temperature (Way and Oren 2010). It is thus necessary to incorporate the variation of climate in allometric models to account for the effect of climate on biomass estimation (Chave et al. 2014; Álvarez-Dávila et al. 2017; Fu et al. 2017). By building climate-based allometric models for neotropical (Chave et al. 2014) and temperate trees (Álvarez-Dávila et al. 2017; Fu et al. 2017), these studies were able to assess and predict the possible impact of climate change on forest biomass. However, there is little understanding nor quantitative assessment on how tree biomass allometries in Canada are affected by climate and how the omission of climate from the allometric equations may contribute to the high estimation errors associated with the conventional climate-independent models (Case and Hall 2008; Silesh 2014; Xing et al. 2019). One of the objectives of my thesis research was to incorporate climate into the conventional allometric models for estimating biomass of individual tree species to account for the possible effect of climate on biomass estimation. My attempt was to improve the widely used Canada's national allometric models developed on data collected four decades ago (Lambert, Ung and Raulier 2005; Ung, Bernier and Guo 2008). This study is presented in Chapter 2 of my thesis.

### 1.3 Long-term forest inventory data

Long-term forest data afford understanding the factors impacting forest growth and yield and contribute to modeling and predicting forest dynamics and biomass accumulation (Næsset 2002; Ahokas, Kaartinen and Hyyppä 2003; Zhang et al. 2014; Crowther et al. 2015; MacDicken 2015; Liang et al. 2016). Compared to airborne data, ground plots are particularly important for building models for accurate projection of growth, yield and forest dynamics (Hyyppä et al. 2008; van Leeuwen et al. 2011; Wulder et al. 2012; Mahoney et al. 2018). Of these ground samples, forest inventory plots with repeated censuses, such as permanent sample plots (PSPs), have played an increasingly important role in forest modeling in response to global change (Vanclay, Skovsgaard and Hansen 1995; Labrecque et al. 2006; Schepaschenko et al. 2019; Baker et al. 2021). Studies on forest growth, mortality, disturbances and maintenance under climate change in Canada were based on these long-term forest inventory plots (Peng et al. 2011; Ma et al. 2012; Chen and Luo 2015; Zhang, Huang and He 2015; Searl et al. 2021). In boreal forests, long-term inventory data in general are not as widely available as in other forest biomes (MacDicken 2015; Mackey, Skinner and Norman 2021). However, Canadian provincial permanent sample plot programs are exceptional. Established since the early 1950s, PSPs were designed for long-term repeated censuses of forest stands (Marshall, Lencar and Hassani 2000). Over 30,000 plots were established in all provinces and territories of Canada, with varied sizes from 100 to 8,000 $m^2$ and census intervals from 3 to 10 years, according to provincial field protocols (Fortin 1983; Alberta Forest Service 2000; Marshall, Lencar and Hassani 2000; Porter, MacLean and Beaton 2001; Townsend 2004; Stearns-Smith and Basaraba 2006; Perron and Morin 2011). These plots provide exceptionally long-term forest data valuable for modeling forest growth and yield, monitoring forest dynamics, predicting impacts of global change, and informing sustainable forest management (Houghton 2005; Zhang et al. 2014; Zhang, Huang and He 2015; Altrell 2019; Morimoto and Juday 2019). I compiled an unprecedented dataset consisting of 28,604 PSPs from all provinces and territories of Canada (except Nunavut; in total 13 jurisdictions) and Alaska of the USA. In my thesis, I used the PSPs to model plot fire hazards to quantify the risk of fire disturbance for the PSPs and to predict the increased fire risk of the PSPs in facing global warming (Chapter 3). I further used the PSPs to map tree density in the boreal forests of North America and address how many trees are there in the region and how climate change would affect tree density (Chapter 4).

## 1.4 Maintaining forest inventory plots from disturbances

Long-term forest plots are essential in affording data for modeling growth and yield, predicting impacts of global change, and making sustainable management decisions. However, the long-term maintenance of such plots has been a challenge given the ever-increasing frequency and intensity of natural and anthropocentric disturbances (Seidl et al. 2011; Frelich et al. 2018). These disturbances lead to faster stand rotation and higher tree mortality, and are transforming an otherwise carbon sink to a carbon source with reduced growth and yield potential (Trumbore, Brando and Hartmann 2015). Although forest stands regenerate and set off new succession after disturbances, disturbed inventory plots could lose their function as monitoring sites. It is costly to reestablish those destroyed plots, and it also decreases or permanently damages the quality of the long-term data (Vanclay et al. 1995; Salvati et al. 2017; Baker et al. 2021). Forest plots are subject to many different disturbances. Of them, fire has stood out as the single most damaging regime. For example, in 2015, fire alone affected 98 million hectares of forests globally, 58 million hectares larger than the total area affected by insects, pathogen diseases and severe weather events together (MacDicken 2015). In boreal forests, wildfires play a particularly important role in the forested landscape (Bergeron et al. 1998; Kuuluvainen and Gauthier 2018). This role has increasingly become a problem with increased fire intensity, frequency, and extremity over the past decades due to the change in climate (Larsen 1997; Wotton, Nock and Flannigan 2010; Girardin et al. 2013; Rogeau et al. 2016; Hanes et al. 2019). Warming reduces moisture in forest stands faster and in a greater extent from soil to air, piling up dry fuel for ignition and spread of fire (Wotton, Nock and Flannigan 2010). This trend also applies to forest plots which also contain fuel and are vulnerable to fire, with the expectation for shorter fire survival time of the plots. Moreover, the effect of warming on fire among ecoregions varies by fuel type, soil profile and tree composition (Cumming 2001; Tilman, Isbell and Cowles 2014; Beverly 2017). This challenges us for determining priority for fire management and maintenance of the plots in different regions.

Within expectation, fire disturbance has seriously threatened the maintenance of forest inventory plots. Having recognized the problem of fire disturbance, PSP programs in Canada have particularly recorded fire disturbance in the censuses of plots since establishment (Fortin 1983; Alberta Forest Service 2000; Marshall, Lencar and Hassani 2000; Porter, MacLean and Beaton 2001; Townsend 2004; Stearns-Smith and Basaraba 2006; Perron and Morin 2011). However, there remains surprisingly little quantitative understanding of fire hazards of the forest inventory plots in Canada as well as other countries, compromising our ability of protecting those invaluable long-term forest plots and our understanding of the magnitude and consequence of hazards climate change would further inflict on these plots (McRoberts, Tomppo and Næsset 2010). I attempted to fill in this knowledge gap in Chapter 3 by modeling fire hazards of the PSPs in Alberta where fire disturbance is a major disturbance regime in its forests (Flannigan, Stocks and Wotton 2000; Boulanger, Gauthier and Burton 2014; Rogeau et al. 2016; Mrozewski 2018), posing increased threats to maintenance of its forest plots. Alberta has the most detailed records on fire disturbances on its PSPs than other jurisdictions in Canada (Alberta Forest Service 2000; Marshall, Lencar and Hassani 2000). The censuses of these PSPs allowed me to not only model plot fire hazards but also quantify the coupling effect of climatic factors. The fire hazards model I developed and the quantification of the hazards would support the maintenance and management of long-term forest plots in Alberta and also elsewhere (Monserud 2003; Altrell 2019; Baker et al. 2021).

## 1.5 Tree density distribution in boreal forests of North America

Tree density (i.e., the number of trees per unit area) is a baseline forest quantity and a stand structure index informative to forest management (Kays and Harper 1974; Ghazoul, Liston and Boyle 1998; Greene et al. 1999), biodiversity maintenance (Clark and Clark 1984; Ter Steege et al. 2013; Chen et al. 2018; Sugiyama et al. 2018), understanding ecosystem functioning (Gram and Sork 2001; Tobner et al. 2014; Song and Lee 2017), and formulating climate change mitigation policy (Gonzalez, Tucker and Sy 2012). At the stand level, tree density has been found closely related to stand volume or biomass (Mohler, Marks and Sprugel 1978; Westoby 1984; Xu et al. 2019), and tree size (White and Harper 1970). Tree density is also useful for modeling forest growth and yield at the landscape level (Mohammadi et al. 2010; Luo et al. 2020). However, tree density has been documented to vary vastly across landscapes, regions and forest biomes (Crowther et al. 2015). For example, tree density in boreal forests can range from 100s to 1,000s of trees per hectare (Martin 2005). This variation makes any effort of estimating tree density a challenge. Attempts on modeling tree density distribution have been made at the local (Mohammadi et al. 2010; Solarik et al. 2010; Günlü et al. 2015; Dar and Sundarapandian 2016), regional (Gonzalez, Tucker and Sy 2012; Humagain et al. 2017), and global scales (Crowther et al. 2015). However, the accuracy of these estimations is poorly known, and knowledge about tree density in boreal forests is particularly limited (Solarik et al. 2010; Gonzalez, Tucker and Sy 2012). According to Crowther et al. (2015), boreal tree density was very difficult to estimate, and their tree density model for the boreal biome was the worst of the 14 global biomes they developed, partly due to the lack of data and the large variation in boreal tree density. A key group of factors missing from their model were stand characteristics depicting competition within and succession of the stands (Hart, Hart and Murphy 1989). Trees compete for light and nutrients and the associated mortality contributes to fluctuation in stand tree density (Huston 1980; Xu et al. 2019). As forest stands develop in different succession stages, tree density of these stands varies drastically with an initial increase, a relatively steady stage, and a decline by self-thinning (Reyes-Hernández and Comeau 2014).

Indeed, tree density is subjected to the effects of many factors, including stand age, succession stage, size structure, topography, soil profile, climate, vegetation, and natural and human disturbances (White and Harper 1970; Hart, Hart and Murphy 1989; MacFarlane, Green and Burkhart 2000; Crowther et al. 2015), making it challenging for modeling tree density with limited available data across boreal forests. How each of these factors would affect tree density at the regional or global scale is not well quantified. In particular, we know very little how the ongoing and projected climate change is affecting and will affect tree density across spatial scales. Furthermore, how large the impact of climate change on tree density might be comparing against that of many other factors is highly uncertain. I dedicated Chapter 4 of my thesis to estimate tree density in the boreal forests of North America which account for over 40% of the global boreal forests (FAO and UNEP 2020). This chapter fills in an important knowledge gap given the importance of boreal forests in the global terrestrial system (boreal forests account for 28% trees of global forests; Crowther et al. 2015) and their role in regulating global climate (Bonan, Pollard and Thompson 1992). Accurate estimation of tree density for North American boreal forests is thus needed for understanding tree density distribution and the impacts of global change on this region.

## 1.6 Objectives

The overall objective of my thesis is to develop models to estimate tree biomass allometries, plot fire risks, and boreal tree density distribution in Canada. I hypothesized that (i) some if not all tree species accumulate biomass differently under different climatic conditions; (ii) the intensifying trend and heterogeneity of fire disturbances in boreal forests under warming should be observed and expected for long-term forest plots in the same region; and (iii) stand tree height as a key stand characteristic factor should play an important role in regulating boreal tree density. As such, the incorporation of stand tree height in tree density model should improve the accuracy of the estimation of the total number of trees in North American boreal forests. Specifically, I addressed the following three questions at the species, plot and biome scales.

(i) To develop climate-based tree biomass allometric models. I was interested to determine whether there is an individual or a set of common climatic factors that would consistently affect biomass allometries across species, or, alternatively, whether species respond to climatic variables differently. The models I built would also address the need to develop climate-based allometric models for improving biomass estimation.

(ii) To model fire hazards of forest inventory plots. I aimed to answer the question of how the fire hazards of forest plots in Alberta vary by their spatial locations and stand characteristics, and how climate warming may intensify the effect of fire risks on the survival of these long-term plots. The plot fire hazards model I built also quantified the challenges for long-term maintenance of forest inventory plots.

(iii) To estimate tree density in boreal forests. I developed an innovative model to estimate boreal tree density in North America. This model took account of the effect of competition on stand tree density and is thus a mechanism-based model. The model addressed the question of how many boreal trees are there in North America, and identified stand structure and climatic factors key to boreal tree density.

To address these questions, I compiled data from the Energy from the Forest Biomass (ENFOR) Program, and from provincial Permanent Sample Plot (PSP), the Canadian National Forest Inventory (NFI), the Alberta Biodiversity Monitoring Institute (ABMI), and the Cooperative Alaska Forest Inventory (CAFI) plots. I developed climate-based allometric biomass models for five major timber species (i.e., black spruce, white spruce, trembling aspen, tamarack, and balsam fir) sampled from 267 ENFOR sites in Canada to address question (i). To address question (ii), I took a survival analysis approach to model the survival time of 919 PSPs in Alberta from fire disturbance. Finally, I developed a stand height based model to estimate boreal tree density in North America to address question (iii).

This thesis identified three species insensitive to climate in terms of biomass allometries, built climate-based allometric models for trembling aspen and tamarack, quantified fire hazards of PSPs in Alberta, and improved estimates of boreal tree density across North America. The three chapters also contribute to understanding how climate change may affect tree biomass allometries, increase fire hazards of permanent forest inventory plots, and alter tree density distribution in boreal forests of Canada. Under the modest emission scenario, 10% underestimation of aboveground biomass would be expected for trembling aspen and tamarack, two major timber species of Canada, if the climate-independent allometric equations were still in use in 2030, five decades after biomass data collection. By 2050, fire hazards for PSPs in Alberta are projected to be 1.63 times higher than the current level under the present trend of warming, and the plots in the boreal ecoregion suffer most from fire disturbances. The number of trees in North American boreal forests is estimated as 351.3 billion, and the ratio of trees per person in the region is 67.9 thousand, 160 times higher than the global average 422 trees per person. Moreover, stand height, together with climate, topography and vegetation, are key factors for the variation of boreal tree density. This improved knowledge about tree density in boreal forests is important for forest managers to model and predict forest growth, yield and carbon stock, and to make mitigation plans for climate change.

Because of the ever-increasing effects of global change on boreal forests, e.g., the resultant higher tree mortality, larger variability in stand dynamics, the increased risk of transition to carbon source, it is critically important to take account of the effect of climate change for modeling dynamics of forest ecosystems in the boreal. This thesis addresses urgent needs to update our understanding of ecological relationships and natural processes in shaping the structure and dynamics of forests in Canada. Should the current climate-independent models continue to be used, change of climate will likely increase the uncertainty in management planning and policy making. Sustainable forest management will consequently be compromised. With the aid of valuable long-term forest inventory plot data, it is possible, as this thesis shows, to develop models to improve our understanding of forest dynamics to guide management of forest ecosystems in the face of global change.

## 1.7 References

Ahokas, E., Kaartinen, H. & Hyyppä, J. (2003). A quality assessment of airborne laser scanner data. *International Archives of Photogrammetry and Remote Sensing*, 34, W13.

Alberta Forest Service (2000). *Permanent Sample Plot Field Procedures Manual*. Alberta Forest Service Edmonton, Alberta.

Altrell, D. (2019). Multipurpose National Forest Inventory in Mongolia, 2014-2017-A tool to support sustainable forest management. *Geography, Environment, Sustainability*, 12, 167-183.

Álvarez-Dávila, E., Cayuela, L., González-Caro, S., Aldana, A.M., Stevenson, P.R., Phillips, O. *et al.* (2017). Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS One*, 12, e0171072.

Ameray, A., Bergeron, Y., Valeria, O., Montoro Girona, M., & Cavard, X. (2021). Forest carbon management: A review of silvicultural practices and management strategies across boreal, temperate and tropical forests. *Current Forestry Reports*, 7, 245-266.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R. *et al.* (1993). Boreal forests and tundra. *Water, Air, and Soil Pollution*, 70, 39-53.

Baker, T.R., Vicuña Miñano, E., Banda-R, K., del Castillo Torres, D., Farfan-Rios, W., Lawson, I.T. *et al.* (2021). From plots to policy: How to ensure long-term forest plot data supports environmental management in intact tropical forest landscapes. *Plants, People, Planet*, 3, 229-237.

Balshi, M.S., McGuire, A.D., Duffy, P., Flannigan, M., Kicklighter, D.W. & Melillo, J. (2009). Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century. *Global Change Biology*, 15, 1491-1510.

Bergeron, Y., Richard, P.J.H., Carcaillet, C., Gauthier, S., Flannigan, M. & Prairie, Y.T. (1998). Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. *Conservation Ecology*, 2, 2.

Beverly, J.L. (2017). Time since prior wildfire affects subsequent fire containment in black spruce. *International Journal of Wildland Fire*, 26, 919-929.

Bogdanski, B.E.C. (2008). *Canada's boreal forest economy: economic and socioeconomic issues and research opportunities*. Pacific Forestry Centre, Victoria, B.C.

Bonan, G. B., Pollard, D., & Thompson, S. L. (1992). Effects of boreal forest vegetation on global climate. *Nature*, 359, 716-718.

Boulanger, Y., Gauthier, S. & Burton, P.J. (2014). A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research*, 44, 365-376.

Bouriaud, O., Bréda, N., Le Moguedec, G. & Nepveu, G. (2004). Modelling variability of wood density in beech as affected by ring age, radial growth and climate. *Trees*, 18, 264-276.

Burkhart, H. E., & Yang, S. I. (2022). A retrospective comparison of carrying capacity of two generations of loblolly pine plantations. *Forest Ecology and Management*, *504*, 119834.

Burton, P.J., Messier, C., Adamowicz, W.L. & Kuuluvainen, T. (2006). Sustainable management of Canada's boreal forests: progress and prospects. *Ecoscience*, 13, 234-248.

Case, B.S. & Hall, R.J. (2008). Assessing prediction errors of generalized tree biomass and volume equations for the boreal forest region of west-central Canada. *Canadian Journal of Forest Research*, 38, 878-889.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C. *et al.* (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20, 3177-3190.

Chen, H.Y.H. & Luo, Y. (2015). 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.

Clough, B.J., Curzon, M.T., Domke, G.M., Russell, M.B. & Woodall, C.W. (2017). Climate-driven trends in stem wood density of tree species in the eastern United States: Ecological impact and implications for national forest carbon assessments. *Global Ecology and Biogeography*, 26, 1153-1164.

Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C., Maynard, D.S., Thomas, S.M. *et al.* (2015). Mapping tree density at a global scale. *Nature*, 525, 201-205.

Cumming, S.G. (2001). Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological Applications*, 11, 97-110.

Duchesne, L., Ouimet, R., Moore, J.-D. & Paquin, R. (2005). Changes in structure and composition of maple–beech stands following sugar maple decline in Québec, Canada. *Forest ecology and Management*, 208, 223-236.

MacDicken, K.G. (2015). Global forest resources assessment 2015: what, why and how? *Forest Ecology and Management*, 352, 3-8.

FAO & UNEP (2020). *The State of the World's Forests 2020: Forests, biodiversity and people*. Rome.

Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000). Climate change and forest fires. *Science of the Total Environment*, 262, 221-229.

Fortin, J. (1983). *Les placettes-échantillons permanentes et leurs utilisations.* Ministère de l'énergie et des ressources, Gouvernement du Québec, Quebec.

Frelich, L.E., Jõgiste, K., Stanturf, J.A., Parro, K. & Baders, E. (2018). Natural disturbances and forest management: interacting patterns on the landscape. In: *Ecosystem Services from Forest Landscapes*. Springer, pp. 221-248.

Fu, L., Lei, X., Hu, Z., Zeng, W., Tang, S., Marshall, P. *et al.* (2017). Integrating regional climate change into allometric equations for estimating tree aboveground biomass of Masson pine in China. *Annals of Forest Science*, 74, 42.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest health and global change. *Science*, 349, 819-822.

Girardin, M.P., Ali, A.A., Carcaillet, C., Gauthier, S., Hély, C., Le Goff, H. *et al.* (2013). Fire in managed forests of eastern Canada: Risks and options. *Forest Ecology and Management*, 294, 238-249.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M. *et al.* (2016). No growth stimulation of Canada's boreal forest under half-century of combined warming and $CO_2$ fertilization. *Proceedings of the National Academy of Sciences*, 113, E8406-E8414.

Hanes, C.C., Wang, X., Jain, P., Parisien, M.-A., Little, J.M. & Flannigan, M.D. (2019). Fire-regime changes in Canada over the last half century. *Canadian Journal of Forest Research*, 49, 256-269.

Hart, T.B., Hart, J.A., Murphy, P.G. (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist*, 133, 613-633.

Houghton, R.A. (2005). Aboveground forest biomass and the global carbon balance. *Global Change Biology*, 11, 945-958.

Huston, M. (1980) Soil nutrients and tree species richness in Costa Rican forests. *Journal of*

*Biogeography*, 7, 147-157.

Hyyppä, J., Hyyppä, H., Leckie, D., Gougeon, F., Yu, X. & Maltamo, M. (2008). Review of methods of small-footprint airborne laser scanning for extracting forest inventory data in boreal forests. *International Journal of Remote Sensing*, 29, 1339-1366.

Jarvis, P., & Linder, S. (2000). Constraints to growth of boreal forests. *Nature*, 405, 904-905.

Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F. *et al.* (2017). Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Global Change Biology*, 23, 177-190.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., & Coomes, D. A. (2020). Good things take time—Diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology*, 108, 2198-2211.

Kayes, I., & Mallik, A. (2020). Boreal Forests: Distributions, Biodiversity, and Management. *Life on Land*, 1-12.

Kirilenko, A. P., & Sedjo, R. A. (2007). Climate change impacts on forestry. *Proceedings of the National Academy of Sciences*, 104, 19697-19702.

Kuuluvainen, T. & Gauthier, S. (2018). Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems*, 5, 1-15.

Labrecque, S., Fournier, R.A., Luther, J.E. & Piercey, D. (2006). A comparison of four methods to map biomass from Landsat-TM and inventory data in western Newfoundland. *Forest Ecology and Management*, 226, 129-144.

Lambert, M.C., Ung, C.H. & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research*, 35, 1996-2018.

Larsen, C.P.S. (1997). Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography*, 24, 663-673.

Lemprière, T.C., Kurz, W.A., Hogg, E.H., Schmoll, C., Rampley, G.J., Yemshanov, D. *et al.* (2013). Canadian boreal forests and climate change mitigation. *Environmental Reviews*, 21, 293-321.

Liski, J., Korotkov, A.V., Prins, C.F.L., Karjalainen, T., Victor, D.G. & Kauppi, P.E. (2003). Increased carbon sink in temperate and boreal forests. *Climatic Change*, 61, 89-99.

Lloyd, A.H., Bunn, A.G. & Berner, L. (2011). A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, 17, 1935-1945.

Luo, Y., McIntire, E.J.B., Boisvenue, C., Nikiema, P.P. & Chen, H.Y.H. (2020). Climatic change only stimulated growth for trees under weak competition in central boreal forests. *Journal of Ecology*, 108, 36-46.

Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W. *et al.* (2012). Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences*, 109, 2423-2427.

MacFarlane, D.W., Green, E.J., Burkhart, H.E. (2000) Population density influences assessment and application of site index. *Canadian Journal of Forest Research,* 30, 1472-1475.

Mackey, B., Skinner, E. & Norman, P. (2021). A Review of Definitions, Data, and Methods for Country-level Assessment and Reporting of Primary Forest. *Griffith Climate Action Beacon*, 1-21.

Mahoney, C., Hall, R.J., Hopkinson, C., Filiatrault, M., Beaudoin, A. & Chen, Q. (2018). A forest attribute mapping framework: a pilot study in a northern boreal forest, Northwest Territories, Canada. *Remote Sensing*, 10, 1338.

Marshall, P.L., Lencar, C. & Hassani, B. (2000). *Review of PSP Systems Employed Outside of British Columbia*. Vancouver, BC.

Martin, P.J. (2005). Design of regeneration standards to sustain boreal mixedwoods in western Canada. *International Forestry Review*, 7, 135-146.

McMahon, S.M., Parker, G.G. & Miller, D.R. (2010). Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences*, 107, 3611-3615.

McRoberts, R.E., Tomppo, E.O. & Næsset, E. (2010). Advances and emerging issues in national forest inventories. *Scandinavian Journal of Forest Research*, 25, 368-381.

Mohammadi, J., Shataee Joibary, S., Yaghmaee, F. & Mahiny, A.S. (2010). Modelling forest stand volume and tree density using Landsat ETM data. *International Journal of Remote Sensing*, 31, 2959-2975.

Monserud, R.A. (2003). Evaluating forest models in a sustainable forest management context. *Forest Biometry, Modelling and Information Sciences*, 1, 35-47.

Morimoto, M. & Juday, G. (2019). Perspectives on Sustainable Forest Management in Interior Alaska Boreal Forest: Recent History and Challenges. *Forests*, 10, 484.

Mrozewski, T. (2018). Canadian Forest Fire Data. *Bulletin-Association of Canadian Map Libraries and Archives (ACMLA)*, 160, 17-19.

Næsset, E. (2002). Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. *Remote Sensing of Environment*, 80, 88-99.

Natural Resources Canada. (2020). 8 facts about Canada's boreal forest. Available at: https://www.nrcan.gc.ca/our-natural-resources/forests-forestry/sustainable-forest-management/boreal-forest/8-facts-about-canadas-boreal-forest/17394. Last accessed 2022-07-15.

Östlund, L., Zackrisson, O. & Axelsson, A.L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, 27, 1198-1206.

Park, A., Puettmann, K., Wilson, E., Messier, C., Kames, S. & Dhar, A. (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.

Pastor, J., Aber, J.D. & Melillo, J.M. (1984). Biomass prediction using generalized allometric regressions for some northeast tree species. *Forest Ecology and Management*, 7, 265-274.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W. et al. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1, 467-471.

Perron, J. & Morin, P. (2011). *Normes d’inventaire forestier: Placettes-échantillons permanentes*. Ministry of Forests: Quebec, QC, Canada.

Porter, K.B., MacLean, D.A., Beaton, K.P. & Upshall, J. (2001). *New Brunswick Permanent Sample Plot Database (PSPDB v1. 0)*. NB.

Réjou-Méchain, M., Barbier, N., Couteron, P., Ploton, P., Vincent, G., Herold, M. *et al.* (2019). Upscaling Forest biomass from field to satellite measurements: sources of errors and ways to reduce them. *Surveys in Geophysics*, 40, 881-911.

Reyes-Hernández, V. & Comeau, P.G. (2014). Survival probability of white spruce and trembling aspen in boreal pure and mixed stands experiencing self-thinning. *Forest Ecology and Management*, 323, 105-113.

Rogeau, M.-P., Flannigan, M.D., Hawkes, B.C., Parisien, M.-A. & Arthur, R. (2016). Spatial and temporal variations of fire regimes in the Canadian Rocky Mountains and foothills of southern Alberta. *International Journal of Wildland Fire*, 25, 1117-1130.

Salvati, L., Becagli, C., Bertini, G., Cantiani, P., Ferrara, C. & Fabbio, G. (2017). Toward sustainable forest management indicators? A data mining approach to evaluate the impact of silvicultural practices on stand structure. *International Journal of Sustainable Development & World Ecology*, 24, 372-382.

Schepaschenko, D., Chave, J., Phillips, O.L., Lewis, S.L., Davies, S.J., Réjou-Méchain, M. *et al.* (2019). The Forest Observation System, building a global reference dataset for remote sensing of forest biomass. *Scientific Data*, 6, 1-11.

Searls, T., Zhu, X., McKenney, D., Mazumder, R., Steenberg, J., Yan, G. et al. (2021). Assessing the influence of climate on the growth rate of boreal tree species in northeastern Canada through long-term permanent sample plot data sets. *Canadian Journal of Forest Research*, 51, 1039-1049.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K. *et al.* (2011). Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling*, 222, 903-924.

Sileshi, G.W. (2014). A critical review of forest biomass estimation models, common mistakes and corrective measures. *Forest Ecology and Management*, 329, 237-254.

Song, H.-S. & Lee, S.-H. (2017). Effects of wind and tree density on forest fire patterns in a mixed-tree species forest. *Forest Science and Technology*, 13, 9-16.

Spittlehouse, D.L. & Stewart, R.B. (2004). Adaptation to climate change in forest management. *Journal of Ecosystems and Management*, 4, 1-11.

Stearns-Smith, S., Cf, R.P.F. & Basaraba, D. (2006). *Provincial PSP Remeasurement Priorities (BC's PSP Strategy Revisited)*. Ministry of Forests, Range Sooke, BC.

Taylor, A.R., Boulanger, Y., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W. *et al.* (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.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471-493.

Townsend, P. (2004). *Nova Scotia forest inventory based on permanent sample plots measured between 1999 and 2003.* Report FOR 2004-3. Nova Scotia Department of Natural Resources, Truro, NS.

Trumbore, S., Brando, P. & Hartmann, H. (2015). Forest health and global change. *Science*, 349, 814-818.

Ung, C.-H., Bernier, P. & Guo, X.-J. (2008). Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, 38, 1123-1132.

van Leeuwen, M., Hilker, T., Coops, N.C., Frazer, G., Wulder, M.A., Newnham, G.J. *et al.* (2011). Assessment of standing wood and fiber quality using ground and airborne laser scanning: A review. *Forest Ecology and Management*, 261, 1467-1478.

Vanclay, J.K., Skovsgaard, J.P. & Hansen, C.P. (1995). Assessing the quality of permanent sample plot databases for growth modelling in forest plantations. *Forest Ecology and Management*, 71, 177-186.

Vanderwel, M. C., Coomes, D. A., & Purves, D. W. (2013). Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology*, 19, 1504-1517.

Vanderwel, M. C., Zeng, H., Caspersen, J. P., Kunstler, G., & Lichstein, J. W. (2016). Demographic controls of aboveground forest biomass across North America. *Ecology Letters*, 19, 414-423.

Way, D.A. & Oren, R. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, 30, 669-688.

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 6, 207-215.

Westoby, M. (1984). The self-thinning rule. *Advances in Ecological Research*, 14, 167-225.

Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997). Strong density-and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences*, 94, 1252-1257.

Wotton, B.M., Nock, C.A. & Flannigan, M.D. (2010). Forest fire occurrence and climate change in Canada. *International Journal of Wildland Fire*, 19, 253-271.

Wulder, M.A., White, J.C., Nelson, R.F., Næsset, E., Ørka, H.O., Coops, N.C. *et al.* (2012). Lidar sampling for large-area forest characterization: A review. *Remote Sensing of Environment*, 121, 196-209.

Xing, D., Bergeron, J.A.C., Solarik, K.A., Tomm, B., Macdonald, S.E., Spence, J.R. *et al.* (2019). Challenges in estimating forest biomass: use of allometric equations for three boreal tree species. *Canadian Journal of Forest Research*, 49, 1613-1622.

Xu, Y., Li, C., Sun, Z., Jiang, L., Fang, J. (2019) Tree height explains stand volume of closed-canopy stands: Evidence from forest inventory data of China. *Forest Ecology and Management*, 438, 51-56.

Yang, Y., Huang, S., Vassov, R., Pinno, B. & Chhin, S. (2020). Climate-sensitive height–age models for top height trees in natural and reclaimed oil sands stands in Alberta, Canada. *Canadian Journal of Forest Research*, 50, 297-307.

Zhang, J., Huang, S. & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, 112, 4009-4014.

Zhang, J., Huang, S., Hogg, E.H., Lieffers, V., Qin, Y. & He, F. (2014). Estimating spatial variation in Alberta forest biomass from a combination of forest inventory and remote sensing data. *Biogeosciences*, 11, 2793.

# Chapter 2 Climate-based Allometric Biomass Equations for Five Major Canadian Timber Species

## 2.1 Abstract

Accurate estimation of forest biomass is essential to quantify the role forests play at balancing terrestrial carbon. Allometric equations based on tree size have been used for this purpose worldwide. There is little quantitative understanding on how environmental variation may affect tree allometries. Even less known is how to incorporate environmental factors into such equations to improve estimation. Here I tested the effects of climate on tree allometric equations and proposed to model forest biomass by explicitly incorporating climatic factors. Among the five major Canadian timber species tested, the incorporation of climate was not found to improve the allometric models for three species. For trembling aspen and tamarack, the residuals of their conventional allometric models were found strongly related to frost-free period and mean annual temperature, respectively. The predictions of the two best climate-based models were significantly improved, which indicate that trembling aspen and tamarack store more aboveground biomass when growing in warmer than in colder regions. I showed that, under the RCP4.5 modest climate change scenario, there would be a 10% underestimation of aboveground biomass for these two species if the conventional non-climate models would still be in use in 2030. This study suggests the necessity to proactively develop climate-based allometric equations for more accurate and reliable forest biomass estimation.

Keywords: Allometric equation, aboveground biomass, climate change, Canadian timber species, trembling aspen and tamarack.

## 2.2 Introduction

A great proportion of the estimation error of the terrestrial carbon balance arises from the uncertainty of forest biomass estimation (van Breugel et al. 2011). Improving estimation accuracy is essential for evaluating changes in global carbon cycle (Le Toan et al. 2011), predicting forest growth (Fang et al. 2014), carbon budget modeling (Kurz et al. 1996), and developing mitigation and sustainable forestry strategies (van Breugel et al. 2011). Much effort has been invested to improve existing models for more accurate forest biomass estimation, such as by further including height (Yang et al. 2020), crown dimensions (Goodman et al. 2014) and wood density (Ketterings et al. 2001) into "existing models", by developing stem taper models and using laser scanning techniques to acquire data on stem form (McTague and Weiskittel 2021), or by modifying the mathematical forms of the allometric models (Hame et al. 1997). Of them, improving tree allometric equations has been the major focus. These equations commonly model tree biomass in terms of the allometric relationship that links biomass to tree size and height (Pastor et al. 1984; Niklas 2004; Weiner 2004).

Tree growth is subject to the effect of different abiotic conditions, such as site-specific heterogeneity and climatic variables, due to biophysical (White et al. 1999; Beaubien and Freeland 2000; Bouriaud et al. 2004; McMahon et al. 2010) and ecophysiological processes (Karlsson et al. 2005; Littell et al. 2008; Clough et al. 2017). Despite this recognition, it is not a common practice to model tree allometric growth by considering the impacts of habitat (Bond-Lamberty et al. 2014) and climate (Lloyd et al. 2011). I found only a handful of studies that have examined how tree allometric relationships are affected by different environmental conditions and climate (Chave et al. 2014; Fu et al. 2017; Yang et al. 2020). One of the notable examples is the recent development of climate-based allometric equations for improving biomass estimation in pantropical forests (Chave et al. 2014). In that study, the conventional allometric equations with tree diameter, height and wood density as predictors were fitted to the observed stand-level biomass data. For stands where data on height are not available, a climate-for-height model, using temperature seasonality, precipitation seasonality and climate water deficit as predictors, is proposed to estimate height. Although Chave et al. (2014) offer a promising approach for developing climate-based allometric models, their approach does not consider the difference of individual species but pools biomass data across all species and applies a single allometric equation. This pooling of the data is necessary for species-rich tropical forests, but the bias associated with this approach is unknown because species that differ in architecture and ecophysiology could result in starkly different responses to the effect of climate (Way and Oren 2010). For example, in boreal and temperate forests, Jucker et al. (2017) found that pooled-species (i.e. stand-level) allometric equations overestimated up to 30% of biomass compared to that estimated from the widely used individual species allometric equations developed by Lambert et al. (2005) in Canada. Along this line, Xing et al. (2019) showed that regional allometric equations could either overestimate or underestimate local stand biomass in Alberta, Canada, presumably due to the variation in climate and site conditions. Fu et al. (2017) is another example that considers the effect of climate on allometric equation for estimating biomass for Masson pine in Southern China. However, this single species study, including 2 dummy and 4 climatic variables, is data demanding and seems overly complex. It is thus clear that there is a need to develop climate-based biomass models for individual species for understanding interspecific variation in the effect of climate on tree biomass accumulation and for improving future estimation of forest biomass (McCarthy and Enquist 2007).

This study aims to quantify the effect of climate on aboveground biomass of five major Canadian timber species (i.e., black spruce, white spruce, trembling aspen, tamarack, and balsam fir). I focus on biomass-DBH allometries without including height because DBH-only allometric equations are commonly used in most regional and global studies (Peichl and Arain 2007; Chojnack et al. 2014; Chen and Luo 2015) partly due to the lack of height data (Marshall, Lencar and Hassani 2000). I first assessed the effect of climate, including temperature, precipitation and aridity, on the allometric equations for each of the five species in Canada to identify the potential climatic factors that affect the growth of these species. I was interested in finding out whether there is a common or a set of common climatic factors (e.g. temperature, precipitation, and aridity) that consistently affect growth across species, or, alternatively, whether species respond to climatic variables differently. I then developed allometric models by incorporating the significant climatic factors identified for the species. These climate-based allometric equations were further used to predict the impact of the projected climate scenarios on forest biomass estimation. The climate-based allometric models so developed are expected to improve forest biomass estimation in Canada and strengthen our ability of mitigation for greenhouse emission.

## 2.3 Materials and methods

### 2.3.1 Biomass dataset

I compiled biomass data from the Energy from the Forest Research (ENFOR) program of Canadian Forest Service (Ung et al. 2008). Between 1978 and 1983, ENFOR destructively sampled 9,454 stems of 49 commercial tree species at over 300 sites across Canada. Oven dry aboveground biomass (including the biomass components from stem wood, stem bark, branches, foliage and twigs), diameter at breast height (DBH) and height of each tree were measured in the field and data quality control was followed with check on possible erroneous values (Lambert et al. 2005; Ung et al. 2008). The sites were distributed in 10 ecozones with a wide range of climatic conditions from the pacific maritime in British Columbia to the boreal shield in Newfoundland and Labrador (Ecological Stratification Working Group 1996). Field measurements and site locations of each stem sampled were assembled into the ENFOR Canada Biomass Data (accessible online at https://doi.org/10.23687/fbad665e-8ac9-4635-9f84-e4fd53a6253c).

### 2.3.2 Study species

Of the total, 5,732 stems from 45 species sampled at 267 sites had a complete set of total aboveground biomass measurements (hereafter referred to as aboveground biomass; AGB) and site coordinates. The number of sites surveyed varied from 1 to 76 (mean 13.1 and median 7) sites and the number of stems per species sampled ranged from 1 to 783 (mean 127.4 and median 78). However, only five species (*Picea mariana*, black spruce; *Picea glauca*, white spruce; *Populus tremuloides*, trembling aspen; *Larix laricina*, tamarack; and *Abies balsamea*, balsam fir) were sampled in more than 3 jurisdictions (provinces and territories) and at more than 25 sites across Canada (Table 2.1; also see Table S1 for the ranges of site locations, DBH and aboveground biomass). The sampling locations of these five species consisted of 162 sites within their natural distributions in Canada (Fig. 2.1; Pavlic et al. 2007). These species are the primary timber species in Canada (Pavlic et al. 2007), which reportedly stock over 7 billion tons of biomass in the country (Power and Gillis 2001). Here I attempt to build climate-based allometric biomass equations for each of them.

### 2.3.3 Climatic variables

I selected climatic variables based on their documented significance for tree growth (Vanganov et al. 1999; Friedrichs et al. 2009). In total, thirty-year annual averages from 1961 to 1990 of 16 climatic variables (i.e., climate normal; Table 2.2; also see Fig. 2.1 for mean annual temperature) were used to represent the climatic conditions of those sites for the sampling period (1978 to 1983). All these climatic variables were georeferenced based on the site locations and extracted from the 4-km resolution climate grids from downscaled PRISM (Daly et al. 2008) using ClimateNA v6.20 (Wang et al. 2016; see Table S1 for the ranges of the 16 climatic variables), which are the current highest quality temporal climate data available representing the period over which the ENFOR data were collected.

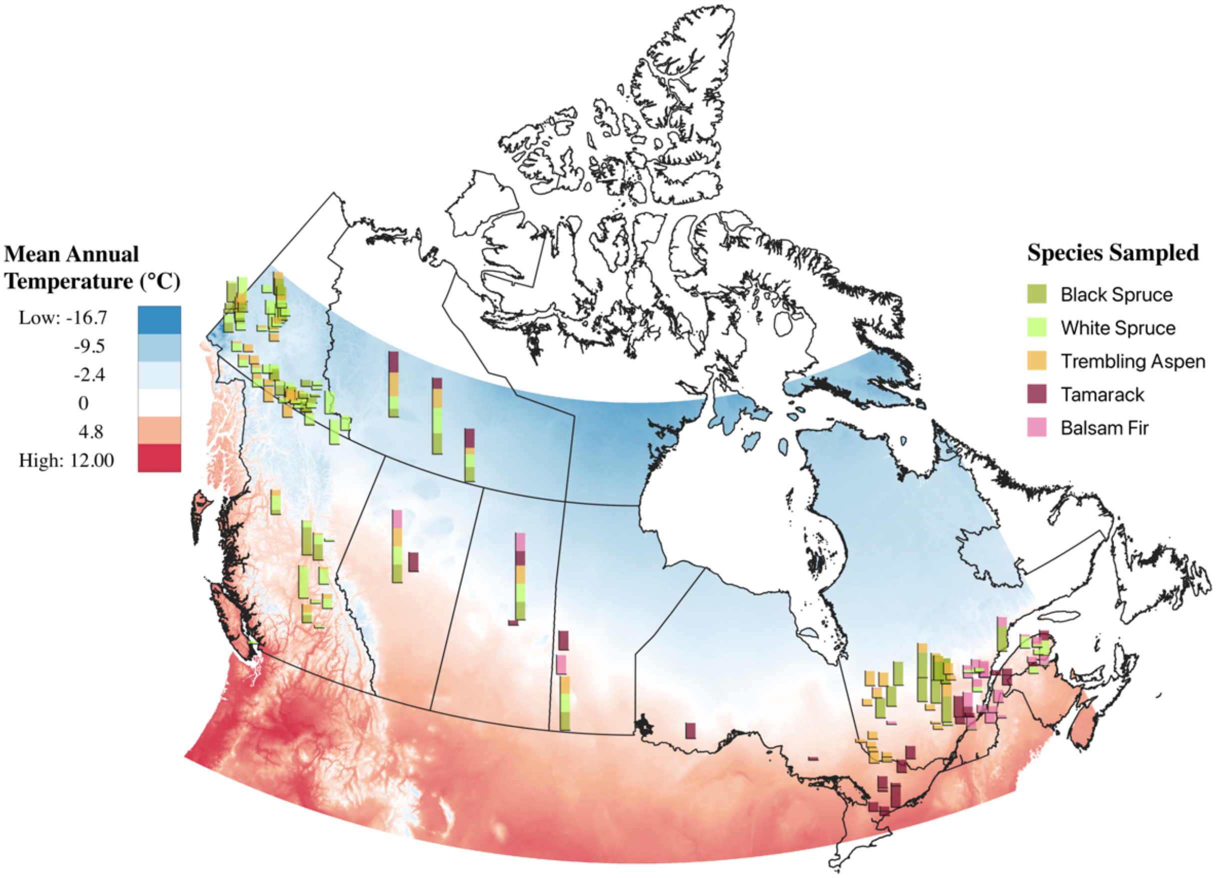

Fig. 2.1 Distribution of all 162 sampling sites for black spruce, white spruce, trembling aspen, tamarack and balsam fir. The base map is the thirty-year mean annual temperature from 1961 to 1990 with blue the coldest and red the warmest regions. At each sampling site, the tree species are represented in dark green, light green, brown, red and pink, respectively, on a stack. The height of each color bar represents the relative number of stems for the species sampled at that site.

Table 2.1 Number of stems and sites (in parenthesis) sampled from each province and territory for black spruce, white spruce, trembling aspen, tamarack and balsam fir that have complete information of aboveground biomass and site location in the ENFOR Canada Biomass Data.

| Species | YT | NT | BC | AB | SK | MB | ON | QC | Total |
|---|---|---|---|---|---|---|---|---|---|
| Black Spruce | 290 | 48 | 60 | 20 | 20 | 20 | | 325 | 783 |
| | (31) | (3) | (4) | (1) | (1) | (1) | | (31) | (54) |
| White Spruce | 354 | 56 | 100 | 20 | 20 | 20 | | 62 | 632 |
| | (46) | (3) | (11) | (1) | (1) | (1) | | (13) | (76) |
| Trembling Aspen | 188 | 54 | 26 | 20 | 20 | 19 | | 133 | 460 |
| | (29) | (3) | (8) | (1) | (2) | (1) | | (20) | (63) |
| Tamarack | | 56 | | 20 | 20 | 20 | 84 | 87 | 287 |
| | | (3) | | (1) | (1) | (1) | (10) | (10) | (27) |
| Balsam Fir | | | | 20 | 20 | 20 | | 165 | 225 |
| | | | | (1) | (1) | (1) | | (23) | (26) |

Note: AB – Alberta, BC – British Columbia, MB – Manitoba, NT – Northwest Territories, ON – Ontario, QC – Quebec, SK – Saskatchewan, and YT – Yukon.

Table 2.2 List of 16 climatic variables, their abbreviations and definitions extracted from ClimateNA v6.20 for 1961-1990 annual means per ENFOR Canada biomass sample site. The sources and definitions of all the 16 climatic variables are detailed in Wang et al. (2016) except for climate moisture index in Hogg and Schwarz (1997).

| Abbreviation | Variable | Definition |
|---|---|---|
| MAT | Mean annual temperature | Mean of monthly temperature per year; °C |
| MWMT | Mean warmest-month temperature | Mean temperature of the warmest month in each year; °C |
| MCMT | Mean coldest-month temperature | Mean temperature of the coldest month in each year; °C |
| TD | Continentality | Difference between MWMT and MCMT; MWMT – MCMT; °C |
| MAP | Mean annual precipitation | Mean of the sum of monthly precipitation per year; mm |
| MSP | Mean summer precipitation | Mean of the sum of May-to-September precipitation in each year; mm |
| AHM | Annual heat-to-moisture index | (MAT + 10) / (MAP / 1000); °C $mm^{-1}$ |
| SHM | Summer heat-to-moisture index | MWMT / (MSP / 1000); °C $mm^{-1}$ |
| DD5 | Degree-days above 5°C | Sum of degree-days above 5°C in each year; °C |
| FFP | Frost-free period | Length between the day of the year on which frost-free period begins and the day it ends; day |
| PAS | Precipitation as snow | Sum of precipitation as snow (for an individual year, it covers the period between August of the previous year and July of the target year); mm |
| $E_{ref}$ | Hargreaves reference evaporative demand | Derived from the water equivalent of the radiation above the atmosphere and mean daily temperature; mm |

| | | |
|---|---|---|
| CMD | Climatic moisture deficit | Sum of the monthly difference between $E_{ref}$ and precipitation (if $E_{ref}$ is smaller than precipitation, the CMD of that month is 0, not a negative value); mm |
| MAR | Mean annual solar radiation | Sum of the monthly solar radiation; MJ $m^{-2}$ $d^{-1}$ |
| RH | Mean annual relative humidity | Derived from monthly maximum and minimum temperature; % |
| CMI | Climate moisture index | Difference between annual precipitation and potential evapotranspiration as defined in Hogg and Schwarz (1997); mm |

### 2.3.4 Climate-based allometric modeling

The conventional biomass equations developed by the ENFOR program for the Canadian tree species were in the common form of allometry:

$$(1)\ AGB = a \times DBH^{d}$$

where *AGB* is the aboveground biomass in kg, *DBH* is the diameter at breast height of a stem in cm, and *a* and *d* are two parameters controlling the intercept and slope of the equation, respectively.

Because of the nested sampling structure of the ENFOR biomass data, trees of the same species sampled at the same site were possibly correlated. Adopting nonlinear mixed-effect models with site as the random term, I was able to control the site level variation and use the correct degrees of freedom (Dutchã et al. 2018) for inference. A random term, *site*, can be added to account for the site level variation in *a* or *d* as:

$$(2)\ AGB = (a + site_{i}) \times DBH^{d}$$

$$(3)\ AGB = a \times DBH^{(d + site_{i})}$$

To account for the possible effect of climate, I formulated the mixed-effect models (2) and (3) by incorporating climatic variables to Eqs. (4) - (9) as shown below. Here, I added one climatic variable (denoted as $Clim_{i}$) each time to Eqs. (4) - (9), respectively. Each of the 16 climatic variables presented in Table 2.2 was modeled with *b* as the estimated coefficient of *Clim*. In total, there were 96 candidate climate-based models for each species.

(4) $AGB = (a + site_i + b \times Clim_i) \times DBH^d$

(5) $AGB = (a + b \times Clim_i) \times DBH^{(d + site_i)}$

(6) $AGB = (a + site_i) \times DBH^{(d + b \times Clim_i)}$

(7) $AGB = a \times DBH^{(d + site_i + b \times Clim_i)}$

(8) $AGB = (a + site_i) \times DBH^d + b \times Clim_i$

(9) $AGB = a \times DBH^{(d + site_i)} + b \times Clim_i$

The above 99 models (the 96 plus Eqs. 1, 2 and 3) for each of the five species were estimated using maximum likelihood from the nlme package (Pinheiro et al. 2022) in R 3.5.1 (https://www.r-project.org/).

### 2.3.5 Model comparison

For each species, I compared the 99 candidate models to select the best model and identify climatic variables that significantly affect the allometric model (1). For this study, the ten-fold cross-validation approach was applied to compare the predictive ability of the candidate models for each species while avoiding over-fitting (Arlot and Celisse 2010). I ran 1,000 iterations for each of the 99 models for a species. At each iteration, I randomly extracted one tenth of the sample sites as the testing data and used the remaining nine tenths of the sites as the training data for model fitting for cross-validation. For example, tamarack had data sampled from 27 sites and 287 stems (Table 2.1). Three of the sites were randomly selected for validation, while the remaining 24 sites were used for fitting (training) each of the 99 models for this species. The same training and testing sites were used to train and validate each of the 99 candidate models.

Aboveground biomass was then estimated for the sites of the testing data set using DBH and the corresponding climatic variable that was modeled for each model. I adopted two widely used statistics, mean absolute error (MAE) and root-mean-square error (RMSE), for assessing the predictive performance of these models.

(10) $\text{MAE} = \frac{\sum |\hat{y}_i - y_i|}{n}$

(11) $\text{RMSE} = \sqrt{\frac{\sum (\hat{y}_i - y_i)^2}{n}}$

where $\hat{y}_i$ and $y_i$ are the estimated and the observed aboveground biomass for the *i*th tree, and *n* is the total number of trees in the testing data set.

A climate-based model was considered to be superior if it yielded a significantly lower MAE than that of the conventional model (1) and the two mixed-effect models (2) and (3). Also, considering model reliability (Wehrens et al. 2011), a superior climate-based model should yield lower MAE than the three competing models in no fewer than 700 times out of the 1,000 iterations (i.e., 70% of the iterations). These repeatedly lower MAE justified the climatic allometric model. Because MAE varied in each training and testing data set among the 1,000 resampling iterations, mean MAE was calculated over the 1,000 iterations for each model. One tail paired $t$-test was used to assess if a climatic allometric model had significantly lower MAE than the non-climatic allometric models (1), (2) and (3). This test was also repeated for RMSE.

Further attempts were made to add more than one climatic variable to the conventional allometric models, but that did not improve the models. I also tried to include a second random term, e.g., combining the two random terms from Eqs. (4) and (5), but that did not improve the models either and in some cases the estimation did not actually converge. I thus just focused on the allometric equations of a single climatic variable and a single random term (Eqs. 4 - 9).

### 2.3.6 Validation of the best climate-based model

After determining the best climate-based models, I refitted them and the conventional model to the entire samples of trees for each species and compared the goodness of fit and the percentage errors (%Error, Eq. 12) between the best model and the conventional model. I then plotted the estimated aboveground biomass against the observed aboveground biomass for each species, and calculated the pseudo $R^2$ $(1 - \frac{\Sigma(y_{obs_i} - y_{hat_i})^2}{\Sigma(y_{obs_i} - \bar{y}_{obs_i})^2})$ for each model. I also performed likelihood ratio tests between the best climate-based model and the conventional model for statistical comparison.

(12) $\%Error = \frac{\hat{y}_i - y_i}{y_i} \times 100\%$

where $\hat{y}_i$ and $y_i$ are the model prediction and the observed aboveground biomass for the $i^{th}$ tree of the entire samples for the species of interest.

### 2.3.7 Prediction error under the modest warming scenario

I predicted the estimation biases of aboveground biomass of trembling aspen and tamarack (the species found sensitive to climate) in Canada in 2030 (i.e. 50 years after the collection of the data) using models estimated from the ENFOR biomass data (collected between 1978 and 1983). I adopted the modest warming scenario, RCP4.5 (a stabilization scenario with the radiative forcing level fixed at 4.5 W/m$^2$ after effort in reducing greenhouse gas emissions; Thomson et al. 2011), to evaluate biomass prediction errors for the two species in 2030. I first derived the mean climatic variables (i.e. frost-free period and mean annual temperature for this study) in 2030 from RCP4.5. I then assessed the model percentage errors (%Error, Eq. 12) by regressing the %Error of the conventional model (1) and the best climatic model separately against the selected 1961-1990 mean frost-free period and mean annual temperature for trembling aspen and tamarack respectively using ordinary least squares. %Error should be independent of the climatic variable if the model is no longer affected by the variable, but not the case for the conventional model (1). The %Error for aspen and tamarack biomass in 2030 was then estimated by substituting the RCP4.5 projected frost-free period and mean annual temperature in 2030 to the respective regression models. These estimated %Errors multiplying the total aboveground biomass stock of the two species in Canada given by Power and Gillis (2006) are the prediction errors if the conventional allometric model were still in use in 2030.

## 2.4 Results

### 2.4.1 Best climate-based models

I found that the best climate-based models for trembling aspen and tamarack outperformed the conventional and the two mixed-effect allometric models (Eqs. 1 - 3) based on MAE and RMSE (Table 2.3; see Table S2 for the cross-validation result in which Eq. (5) outperforms equations for both species), while no significantly better climate-based models were found for the other three species.

For trembling aspen, the best climate-based models is

$$(13)\ \widehat{AGB} = (0.0389 + 0.000513 \times FFP) \times DBH^{2.453}$$

where FFP is the frost-free period of the site where aboveground biomass is estimated.

For tamarack, the model is

$$(14)\ \widehat{AGB} = (0.142 + 0.00613 \times MAT) \times DBH^{2.261}$$

where MAT is the mean annual temperature.

Table 2.3 Paired *t*-test comparing the best climate-based models for trembling aspen and tamarack and the conventional allometric Eq. (1) and the two mixed-effect allometric models (Eqs. 2 and 3) based on MAE and RMSE from the 1,000-time cross validation. The mean MAE and RMSE of the best climate-based models (i.e. Eq. 13 for trembling aspen and Eq. 14 for tamarack), and the difference in MAE (and RMSE) between the best models and their conventional allometric models are presented together with *t*-test *p*-values.

| | Trembling Aspen - Eq. (13) | Tamarack - Eq. (14) |
|---|---|---|
| Mean MAE | 21.264 | 17.318 |
| Mean RMSE | 36.112 | 25.542 |
| vs Eq. (1) | MAE: -3.404 ($p<10^{-16}$)<br>RMSE: -4.145 ($p<10^{-16}$) | MAE: -5.747 ($p<10^{-16}$)<br>RMSE: -8.029 ($p<10^{-16}$) |
| vs Eq. (2) | MAE: -3.471 (p<$10^{-16}$)<br>RMSE: -4.714 (p<$10^{-16}$) | MAE: -5.270 (p<$10^{-16}$)<br>RMSE: -7.470 (p<$10^{-16}$) |
| vs Eq. (3) | MAE: -4.339 ($p<10^{-16}$)<br>RMSE: -7.233 ($p<10^{-16}$) | MAE: -5.189 ($p<10^{-16}$)<br>RMSE: -7.071 ($p<10^{-16}$) |

### 2.4.2 Model validation

Goodness of fit of the best climate-based models for trembling aspen and tamarack were compared against the conventional model (1) as shown in Fig. 2.2. The pseudo $R^2$ for the conventional models are 0.966 and 0.943 for trembling aspen and tamarack, respectively, while the $R^2$ for the best climate-based models are respectively 0.978 and 0.980. The log-likelihood ratio tests confirmed that the best climate-based model, for both species, performed significantly better than the conventional model (1) when fitting the ENFOR biomass data for trembling aspen (likelihood ratio = 178.05, $df = 2$, $p < 0.0001$) and tamarack (likelihood ratio = 167.85, $df = 2$, $p < 0.0001$).

By residual diagnosis, I found that the %Error of allometric model (1) for trembling aspen (Figs. 2.3a) and tamarack (Figs. 2.3c) were negatively related to FFP and MAT, respectively. The slope of the linear regression model between %Error and FFP for trembling aspen is -0.47 (Fig. 2.3a), indicating that the model estimate is 4.7% lower than the actual aboveground biomass if the FFP increases by 10 days. Similarly, the slope for the regression between %Error and MAT for tamarack is -4.91 (Fig. 2.3c), indicating that there is 4.9% underestimation if the

MAT increases by 1°C. In contrast, the best climate-based models for both species show no sign of relationship with either FFP (Fig. 2.3b) and MAT (Fig. 2.3d), respectively, indicating the climate-based allometric models are unbiased in estimating the aboveground biomass for trembling aspen and tamarack.

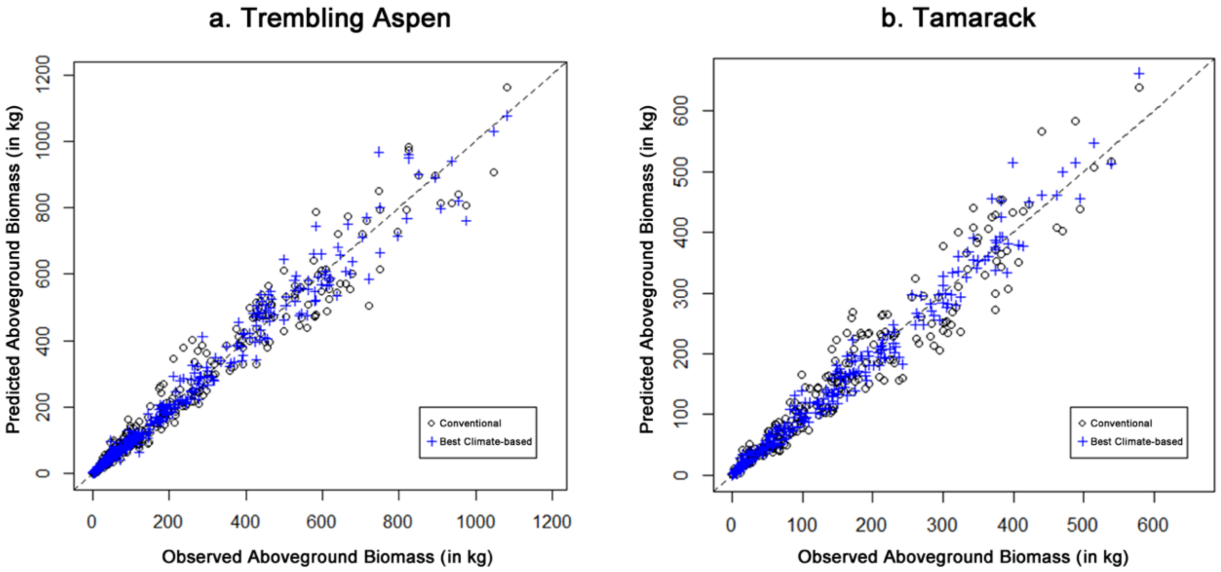

Fig. 2.2 The aboveground biomass predicted by the conventional model (1) and the best climate-based models (13) and (14) plotted against the observed aboveground biomass for trembling aspen (a) and tamarack (b). The black circles are the conventional model and the blue crosses are the climate-based models. The dashed lines are the 1:1 lines between the predicted and observed aboveground biomass.

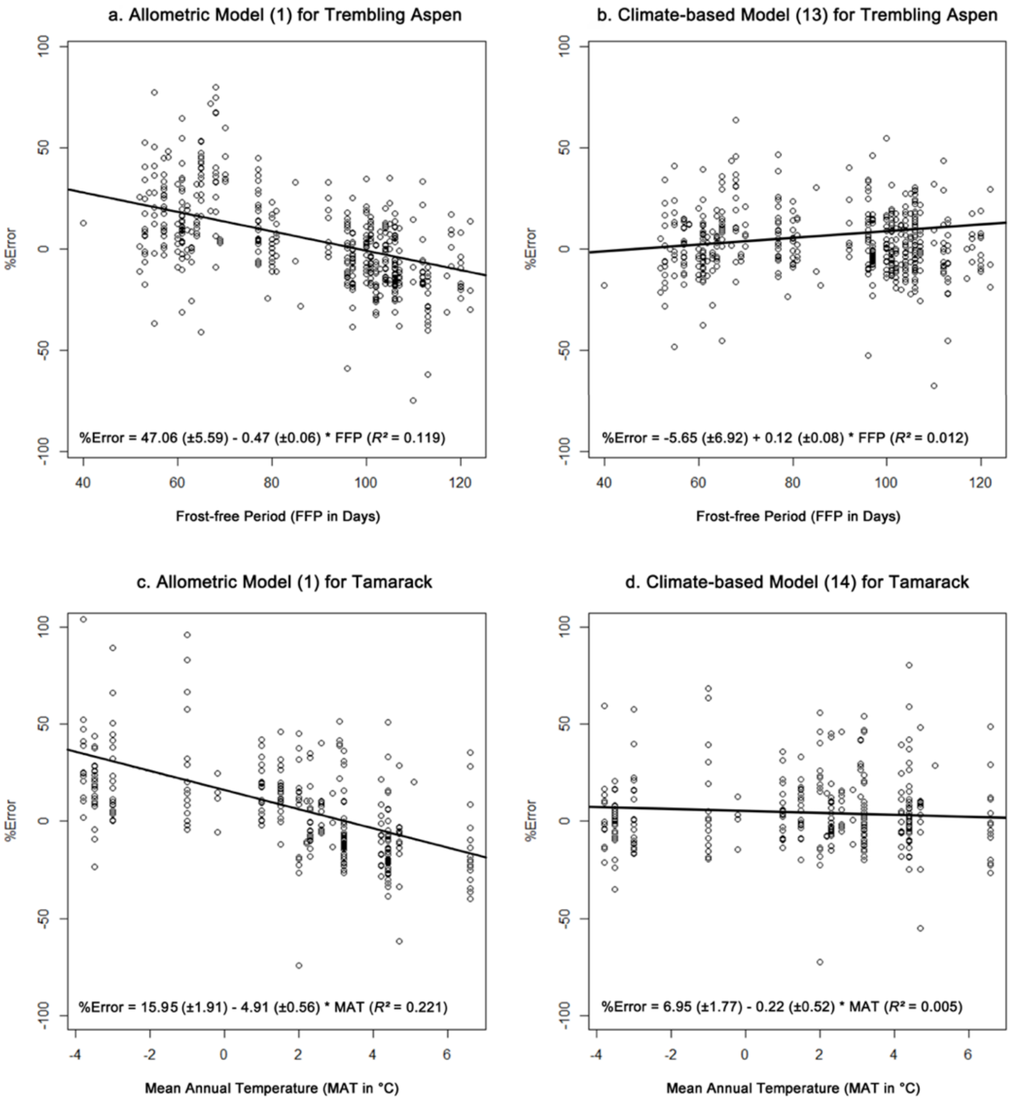

Fig. 2.3 (a) The %Error of the conventional allometric model (1) for trembling aspen is plotted against FFP. The slope of the linear regression line is -0.47, significantly smaller than 0 ($p$-value $< 10^{-13}$ for one-tail $t$-test). (b) The %Error of the best climate-based model (13) for trembling aspen plotted against FFP. The slope (0.12) of the regression line is not significantly different from 0 ($p$-value = 0.16 for two-tail $t$-test). (c) The %Error of the allometric model (1) for tamarack plotted against MAT. The slope (-4.91) of the regression line is significantly smaller than 0 ($p$-value $< 10^{-15}$ for one-tail $t$-test). (d) The %Error of the best climate-based model (14) for tamarack plotted against MAT. The slope (-0.22) of the regression line is not significantly different from 0 ($p$-value = 0.67 for two-tail $t$-test). The fitted models and $R^2$ for the four linear regression models are shown in each panel.

### 2.4.3 Potential underestimation under climate change

Under the climate change scenario, RCP4.5, the mean FFP and MAT in Canada are expected to increase by 20 days and 2°C, respectively, in 2030 compared to the time (1978-1983) when the ENFOR biomass data were collected (Wang et al. 2016). If the current conventional allometric models (1) for trembling aspen and tamarack were still in use in 2030, a 9.5% ± 1.2% ($20 \times (0.47\% \pm 0.06\%)$; from the fitted line in Fig. 2.3a) and a 9.8% ± 1.1% ($2 \times (4.91\% \pm 0.56\%)$; from the fitted line in Fig. 2.3c) underestimation in aboveground biomass for trembling aspen and tamarack, respectively, in Canada would be expected in 2030. Based on the estimated total amounts of aboveground biomass published in the Canada's Forest Inventory 2001 (Power and Gillis 2006), potential underestimation of aboveground biomass for trembling aspen would be 134.22 ± 16.95 million tons and for tamarack 6.00 ± 0.67 million tons in 2030 if the conventional biomass equations for these two species were used without considering the effect of climate change.

## 2.5 Discussion

### 2.5.1 Improvement of model performance

To minimize the increasing uncertainty in predicting forest biomass under climate change (van Breugel et al. 2011), it is necessary to take account of the effect of climate on the conventional allometric biomass models (Chave et al. 2014; Fu et al. 2017; Yang et al. 2020). In this study, I found that incorporation of climatic variables into those conventional models did not improve biomass estimation for three of the five species. For the two species (trembling aspen and tamarack) whose allometric models were significantly modified by climatic variables, I found that the %Error of the conventional allometric models were significantly negatively correlated with frost-free period (Fig. 2.3a) and mean annual temperature (Fig. 2.3c), respectively, suggesting the necessity to consider the climatic variables in modeling biomass of these two species. After incorporating FFP and MAT, respectively, to each species, the correlations of the %Error of models with FFP (Eq. 13; Fig. 2.3b) and MAT (Eq. 14; Fig. 2.3d) were no longer significant. For black spruce, white spruce and balsam fir, I found that conventional allometric models are sufficient to estimate biomass and the incorporation of climatic variables is not needed.

Among all the 96 climate-based models for each species, none of them with the climatic variable as additive terms in Eqs. (8) and (9) is significantly better than the allometric model (1), which suggests that the effect of climate on tree biomass accumulation in relation to DBH increment are not simply additive. Instead, the best climate-based models for trembling aspen and tamarack both have the form of Eq. (5) where the climatic variables multiply DBH, and the random effect, *site*, is at the exponent term. The significantly positive coefficients for the FFP (0.000513; Eq. 13) and MAT (0.00613; Eq. 14) indicate that trembling aspen growing in areas with longer frost-free periods and tamarack in warmer regions maintain higher biomass than those trembling aspen in areas with shorter frost-free periods and tamarack in colder regions, respectively.

### 2.5.2 Evidence in support for climate-based models

Biophysical and ecophysiological evidence offers support to the best climate-based models for trembling aspen and tamarack (White et al. 1999; Beaubien and Freeland 2000; Bouriaud et al. 2004; McMahon et al. 2010; Clough et al. 2017; Yang et al. 2020) as well as the finding of non-significant improvement in allometric models for black spruce, white spruce and balsam fir (Wilson and Elling 2004; Choat et al. 2005; Way and Oren 2010; Killi et al. 2018). It is documented that tamarack growing in warmer regions store more biomass with denser wood than those in colder regions (McMahon et al. 2010; Clough et al. 2017). FFP is found closely related to the primary production of deciduous forest, including trembling aspen stands (White et al. 1999), and elongation of FFP leads to longer growing activity of trembling aspen (Beaubien and Freeland 2000). Notably, trembling aspen and tamarack are deciduous trees, while the other three are evergreen. Indeed, deciduous and evergreen trees are found to respond differently to elevated temperature in stem biomass growth due to differential growth rates in volume (Way and Oren 2010) and physiological changes in wood density (Killi et al. 2018). In general, evergreen trees do not show as significant increase in stem volume (determined by height and tamper) as deciduous trees when temperature increases (Way and Oren 2010), as evidenced by studies for natural forests (Yang et al. 2020) and experimental forests (Bouriaud et al. 2004). On the other hand, deciduous trees develop denser woods for stronger water storage and transportation capacity in warmer regions, while evergreen trees have lower water pressure and show little increase of wood density under the same warming scenario (Choat et al. 2005; Clough et al. 2017). Also, evergreen trees, such as spruce, are found less sensitive to the variation of climatic conditions in terms of aboveground biomass accumulation than deciduous trees (Wilson and Elling 2004).

### 2.5.3 Necessity for climate-based models

Because of growth dependence on climate, allometric biomass models estimated from the ENFOR Canada biomass data may not reflect today's biomass-DBH allometries, let alone tomorrow's. The mean annual temperature in Canada has increased by 0.8 °C and the frost-free period has elongated by 8 days since the 1980's sampling period (Wang et al. 2016) as a result of the effects of climate change. Given such a warming trend, the climate-based allometric models predict by 2030, under the modest climate change scenario (RCP4.5), near 10% underestimation of aboveground biomass for trembling aspen and tamarack in Canada would be expected if the allometric model (1) were still in use. This accounts for an estimated aboveground biomass deficit of 134 and 6 million tons for trembling aspen and tamarack, respectively. In addition to trembling aspen and tamarack, there are other deciduous timber species in Canada, such as maples, birches and other poplar species, whose biomass may be underestimated too by the conventional allometric models. Unfortunately, I do not have the data to model biomass allometries for these species, but expect that some (if not all) could also be sensitive to climate change in terms of their biomass-DBH allometries.

This study is an attempt to develop growth-yield models that account for the effect of climate change. Different from previous efforts, e.g. Chave et al. (2014), I modeled biomass of individual species and directly incorporated climatic factors into the allometric models. The results show that species respond to the effect of climate differently; there is no single climatic factor that would universally affect growth across species. While for species-rich tropical forests it is necessary to model forest biomass by combining tree biomass across species as in the pantropical model of Chave et al. (2014), this study suggests this will likely introduce climate-driven bias in biomass estimation, as is also confirmed by Chave et al. (2014) in which their climate-for-height pantropical model performs considerably worse than the height-diameter model (their Fig. 5). The number of tree species is much smaller in northern forests, making it possible to build species specific allometric models (Lambert et al. 2005; Ung et al. 2008). Here, I particularly suggest testing and modeling effects of climate on biomass of individual species to improve estimation accuracy for tree species in Canada. It is also interesting to note that climatological water deficit appears to be the only climatic factor that was identified to influence Chave et al.'s (2014) height-diameter biomass model (although three climatic factors were found to influence tree height in their study). This study is consistent to this result in which only one climatic variable was found to affect trembling aspen and tamarack, respectively.

### 2.5.4 Limitations and recommendations

The lack of empirical biomass data prevents me from building climate-based allometric models for other species in Canada. The ENFOR biomass data is the only data I can find that cover sufficiently large spatial extent required for this study. Even for the ENFOR data, most species were only sampled for aboveground biomass at fewer than 10 sites, and site conditions such as vegetation condition, soil nutrition, basal area, crown class and stand top height were not recorded. These conditions could also alter (Weiner 2004) or interact with climate (Buechling et al. 2017) to affect the growth patterns of tree species. In this study, to minimize the potential effect of site conditions on tree growth, I included *site* as the random term in the allometric equations. It is also important to mention that genetic stock could also substantially affect tree growth (Zobel and Talbert 1984) and thus their allometry. In addition to site condition and climate, it would be necessary to consider genetic variation of trees in order to improve biomass estimation. However, such genetic-dependent growth data are currently not available for assessing genetic effect on biomass estimation. I stress the importance to collect more empirical field data, including genetic data, on tree biomass for developing climate-based allometric equations, despite the cost and labor demand for collecting such data. I would also like to acknowledge that the 4-km resolution for the climate data used in this study is inevitably coarse. That could potentially introduce some undue inaccuracy in the site-level climate data. Ideally, more localized climate data with higher resolution, whenever available, should be used for modeling forest biomass.

## 2.6 Conclusion

In conclusion, this study assessed the effect of climate on allometric biomass models for five major tree species in Canada. I found three of them were insensitive to the effect of climatic factors. For the other two species, Eq. (13) is identified as the best model for trembling aspen, and Eq. (14) is the best model for tamarack. These best, unbiased models are corroborated by previous studies that show how warming impacts the growth of deciduous trees like trembling aspen and tamarack. Under the RCP4.5 modest climate change scenario in Canada, 10% underestimation of aboveground biomass would be expected if the allometric model (1) for these two species were still in use in 2030. There remain over 40 common tree species in Canada without sufficient field sampled biomass data to test whether climate-based allometric equations may also improve the conventional allometries. It is important to expand the ENFOR biomass database by collecting more empirical field biomass samples with broad geographic coverage in order to improve existing allometric models for predicting forest biomass under climate change.

## 2.7 References

Arlot, S. & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys*, 4, 40-79.

Beaubien, E.G. & Freeland, H.J. (2000). Spring phenology trends in Alberta, Canada: links to ocean temperature. *International Journal of Biometeorology*, 44, 53-59.

Bond-Lamberty, B., Rocha, A.V., Calvin, K., Holmes, B., Wang, C. & Goulden, M.L. (2014). Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Global Change Biology*, 20, 216-227.

Bouriaud, O., Bréda, N., Le Moguedec, G. & Nepveu, G. (2004). Modelling variability of wood density in beech as affected by ring age, radial growth and climate. *Trees*, 18, 264-276.

Buechling, A., Martin, P.H. & Canham, C.D. (2017). Climate and competition effects on tree growth in Rocky Mountain forests. *Journal of Ecology*, 105, 1636-1647.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C. *et al.* (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20, 3177-3190.

Chen, H.Y.H. & Luo, Y. (2015). 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.

Choat, B., Ball, M.C., Luly, J.G. & Holtum, J.A.M. (2005). Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees*, 19, 305-311.

Chojnacky, D.C., Heath, L.S. & Jenkins, J.C. (2014). Updated generalized biomass equations for North American tree species. *Forestry*, 87, 129-151.

Clough, B.J., Curzon, M.T., Domke, G.M., Russell, M.B. & Woodall, C.W. (2017). Climate-driven trends in stem wood density of tree species in the eastern United States: Ecological impact and implications for national forest carbon assessments. *Global Ecology and Biogeography*, 26, 1153-1164.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H. *et al.* (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, 28, 2031-2064.

Dutcă, I., Stăncioiu, P.T., Abrudan, I.V. & Ioraş, F. (2018). Using clustered data to develop biomass allometric models: The consequences of ignoring the clustered data structure. *PLoS One*, 13, e0200123.

Ecological Stratification Working Group. (1996). *A National Ecological Framework for Canada.* Environment Canada Ottawa, Ontario.

Fang, J., Guo, Z., Hu, H., Kato, T., Muraoka, H. & Son, Y. (2014). Forest biomass carbon sinks in East Asia, with special reference to the relative contributions of forest expansion and forest growth. *Global Change Biology*, 20, 2019-2030.

Friedrichs, D.A., Trouet, V., Buentgen, U., Frank, D.C., Esper, J., Neuwirth, B. *et al.* (2009). Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees-Structure and Function*, 23, 729-739.

Fu, C., Yang, W., Tan, B., Xu, Z., Zhang, Y., Yang, J. *et al.* (2017). Seasonal Dynamics of Litterfall in a sub-alpine spruce-fir forest on the Eastern Tibetan Plateau: Allometric scaling relationships based on one year of observations. *Forests*, 8, 314.

Goodman, R.C., Phillips, O.L. & Baker, T.R. (2014). The importance of crown dimensions to improve tropical tree biomass estimates. *Ecological Applications*, 24, 680-698.

Hame, T., Salli, A., Andersson, K. & Lohi, A. (1997). A new methodology for the estimation of biomass of conifer-dominated boreal forest using NOAA AVHRR data. *International Journal of Remote Sensing*, 18, 3211-3243.

Hogg, E.H. & Schwarz, A.G. (1997). Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. *Journal of Biogeography*, 24, 527-534.

Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F. *et al.* (2017). Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Global Change Biology*, 23, 177-190.

Karlsson, P.S., Weih, M. & Borg, C. (2005). Mountain birch growth in relation to climate and herbivores. In: *Plant ecology, herbivory, and human impact in Nordic mountain birch forests* (eds. Caldwell, MM & et al.). Springer Berlin, Heidelberg, pp. 71-86.

Ketterings, Q.M., Coe, R., van Noordwijk, M. & Palm, C.A. (2001). Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management*, 146, 199-209.

Killi, D., Bussotti, F., Gottardini, E., Pollastrini, M., Mori, J., Tani, C. *et al.* (2018). Photosynthetic and morphological responses of oak species to temperature and [$CO_2$] increased to levels predicted for 2050. *Urban Forestry & Urban Greening*, 31, 26-37.

Kurz, W.A., Beukema, S.J. & Apps, M.J. (1996). Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. *Canadian Journal of Forest Research*, 26, 1973-1979.

Lambert, M.C., Ung, C.H. & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research*, 35, 1996-2018.

Le Toan, T., Quegan, S., Davidson, M.W.J., Balzter, H., Paillou, P., Papathanassiou, K. *et al.* (2011). The BIOMASS mission: Mapping global forest biomass to better understand the terrestrial carbon cycle. *Remote Sensing of Environment*, 115, 2850-2860.

Littell, J.S., Peterson, D.L. & Tjoelker, M. (2008). Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecological Monographs*, 78, 349-368.

Lloyd, A.H., Bunn, A.G. & Berner, L. (2011). A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, 17, 1935-1945.

Marshall, P.L., Lencar, C. & Hassani, B. (2000). *Review of PSP Systems Employed Outside of British Columbia.* Vancouver, BC.

McCarthy, M.C. & Enquist, B.J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*, 21, 713-720.

McMahon, S.M., Parker, G.G. & Miller, D.R. (2010). Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences*, 107, 3611-3615.

McTague, J.P. & Weiskittel, A. (2021). Evolution, history, and use of stem taper equations: a review of their development, application, and implementation. *Canadian Journal of Forest Research*, 51, 210-235.

Niklas, K.J. (2004). Plant allometry: is there a grand unifying theory? *Biological Reviews*, 79, 871-889.

Pastor, J., Aber, J.D. & Melillo, J.M. (1984). Biomass prediction using generalized allometric regressions for some northeast tree species. *Forest Ecology and Management*, 7, 265-274.

Pavlic, G., Chen, W., Fernandes, R., Cihlar, J., Price, D.T., Latifovic, R. *et al.* (2007). Canada-wide maps of dominant tree species from remotely sensed and ground data. *Geocarto International*, 22, 185-204.

Peichl, M. & Arain, M.A. (2007). Allometry and partitioning of above-and belowground tree biomass in an age-sequence of white pine forests. *Forest Ecology and Management*, 253, 68-80.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team, R.C. (2020). nlme: linear and nonlinear mixed effects models. R package version 3.1-149. Vienna, Austria.

Power, K. & Gillis, M.D. (2006). *Canada's Forest Inventory 2001*. Pacific Forestry Centre Victoria, British Columbia.

Thomson, A.M., Calvin, K.V., Smith, S.J., Kyle, G.P., Volke, A., Patel, P. *et al.* (2011). RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Climatic Change*, 109, 77-94.

Ung, C.-H., Bernier, P. & Guo, X.-J. (2008). Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, 38, 1123-1132.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H. & Silkin, P.P. (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, 400, 149-151.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J.S. (2011). Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management*, 262, 1648-1657.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLoS One*, 11, e0156720.

Way, D.A. & Oren, R. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, 30, 669-688.

Wehrens, R., Franceschi, P., Vrhovsek, U. & Mattivi, F. (2011). Stability-based biomarker selection. *Analytica Chimica Acta*, 705, 15-23.

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 6, 207-215.

White, M.A., Running, S.W. & Thornton, P.E. (1999). The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, 42, 139-145.

Wilson, R. & Elling, W. (2004). Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. *Trees-Structure and Function*, 18, 19-28.

Xing, D., Bergeron, J.A.C., Solarik, K.A., Tomm, B., Macdonald, S.E., Spence, J.R. *et al.* (2019). Challenges in estimating forest biomass: use of allometric equations for three boreal tree species. *Canadian Journal of Forest Research*, 49, 1613-1622.

Yang, Y., Huang, S., Vassov, R., Pinno, B. & Chhin, S. (2020). Climate-sensitive height–age models for top height trees in natural and reclaimed oil sands stands in Alberta, Canada. *Canadian Journal of Forest Research*, 50, 297-307.

Zobel, B. & Talbert, J. (1984). *Applied Forest Tree Improvement*. Wiley, New York.

# Chapter 3 Modeling Fire Hazards for the Maintenance of Long-term Forest Inventory Plots in Alberta, Canada

## 3.1 Abstract

Long-term forest inventory plots provide important data for forest research and management. Maintaining such sites is a challenge as they are vulnerable to numerous unforeseeable anthropogenic and natural disturbances. This is particular so given the ongoing global change and the resultant risks of intensified disturbances. Of these disturbances, fire is the most important regime that dictates the dynamics of northern forests. However, little is known about how fire may threaten the forest inventory plots in the region. To address this question, I compiled data on forest fires occurred over the past six decades for permanent sample plots in Alberta, Canada. I employed the Cox proportional hazards model to quantify the effects of stand conditions and climate on the fire hazards of these plots. The results showed that 17% of the plots were burned, and they had an average 28.7-year lifespan, and more recently established plots suffered higher fire hazards. My model predicted that 15% of the plots in Alberta would be disturbed due to fire 30 years after plot establishment, and that prediction increased to 35% after 50 years. The plots located in the Boreal ecoregion suffered 2.85 and 3.36 times higher fire risk than those in the Foothills and Rocky Mountain ecoregions, respectively. Tree species richness and density of deciduous trees of the plots were found to reduce their fire hazards, while mean annual temperature increased the hazards. By 2050, the mean fire hazards of the plots are projected to be 1.63 times higher than the current level as global warming persists, posing a great threat to the long-term maintenance of forest inventory plots.

Keywords: Northern forests, Cox proportional hazards model, fire hazards, plot maintenance, permanent sample plots.

## 3.2 Introduction

Long-term forest data are essential for understanding forest dynamics and functioning (Rees et al. 2001; Pan et al. 2011; Lindenmayer, Laurance and Franklin 2012; Zhang, Huang and He 2015; Liang et al. 2016), quantifying and mapping temporal changes in forest resources, biomass and biodiversity (MacDicken 2015; Blowes et al. 2019; Chave et al. 2019; Liang and Gamarra 2020; Besnard et al. 2021; Davies et al. 2021), predicting impacts of changes in climate (Peng et al. 2011; Chen et al. 2016) and land use (MacDicken 2015), and practicing resource management and conservation (Kangas and Maltamo 2006; MacDicken 2015; Davies et al. 2021). To collect such data, researchers and forest managers have established long-term monitoring plots at the local (Stadt, Schieck and Stelfox 2006; Alberta Agriculture and Forestry 2015), regional (Ribeiro, Borges and Oliveira 2004; Phillips et al. 2009) and global scales (Tomppo et al. 2010; Condit et al. 2014). Despite that the history of forest sampling sites could date back as far as to the 1860s (Spurr 1952), the use of permanent forest plots for collecting long-term inventory data started in the early 1900s (Munger 1946; Burgess and Robinson 1998). It is not until the 1920s that large scale inventory plots have been established (Tomppo et al. 2010; MacDicken 2015). These inventory plot programs include Alberta Biodiversity Monitoring plots (Stadt, Schieck and Stelfox 2006) and permanent sample plots (Alberta Agriculture and Forestry 2015), the Barro Colorado Island (BCI) 50-ha plot (Condit et al. 1998), and national inventory plots of Canada and the USA, China and many European and other countries (Smith 2002; Kangas and Maltamo 2006; Tomppo et al. 2010). These inventory plots, together with plots established for other purposes, contribute to several regional and global forest plot networks, including the Amazon Forest Inventory Network (RAINFOR) (Phillips et al. 2009), ForestPlots.net (Lopez-Gonzalez et al. 2011), ForestGEO (Anderson-Teixeira et al. 2015; Davies et al. 2021), and Global Forest Biodiversity Initiative (GFBI) (Liang et al. 2016). However, the maintenance of long-term forest plots has been a global challenge given the ever increasing natural and anthropogenic disturbances as well as the haphazard nature of these disturbances. This problem compounding with the lack of long-term funding and collaboration makes the maintenance of field plots even more challenging (Ribeiro, Borges and Oliveira 2004; Kangas and Maltamo 2006; Kovač et al. 2010; Tomppo et al. 2010). While efforts have been taken to protect plots from anthropogenic disturbances (Kangas and Maltamo 2006), less attention has been paid to the protection of these plots from the bashing of increasing natural disturbances resulted from global change (Flannigan, Stocks and Wotton 2000; Stephens et al. 2013). This is particularly a problem for the plots at high latitudes where the magnitudes of change in climate are larger and the risk of natural disturbances is higher (Weber and Flannigan 1997; Li, Flannigan and Corns 2000; De Groot et al. 2003; Tymstra et al. 2007; Safranyik et al. 2010; Cortini and Comeau 2020). In this study, I focus on the permanent sample plots in Alberta, Canada, by assessing the existing and rising threats of fire disturbance to plot maintenance.

The permanent sample plot (PSP) network in Alberta was first established in the early 1960s, with an initial set of near 200 plots (Alberta Agriculture and Forestry 2015). The provincial PSP network has since been expanded to about 1,200 plots as of today. Plots, with sizes varying from 200 to 2,034 $m^2$, were established by tagging and repeatedly measuring every stem with diameter at breast height (DBH) larger than 9 cm every 5 to 10 years. These plots provide invaluable long-term data in Alberta for growth-yield modeling (Hogg et al. 2017; Yang et al. 2020), biomass estimation (Monserud, Huang and Yang 2006; Zhang et al. 2014), climate change impact assessment (Peng et al. 2011; Zhang, Huang and He 2015; Chen et al. 2016), biodiversity conservation (Stadt, Schieck and Stelfox 2006) and silvicultural planning (Metsaranta and Lieffers 2009). Over the past six decades, the PSP network has been subjected to the threats of many natural and anthropogenic risk factors (Alberta Agriculture and Forestry 2015). Forest fire as measured by its intensity and frequency is a primary disturbance regime shaping forested landscapes in Alberta (Larsen 1997; Cumming 2001). For example, between 2006 and 2015, on average 1,581 wildfires occurred annually, and the total area burned in this decadal period was equivalent to near 12% of the harvestable forests in Alberta (Beverly and McLoughlin 2019). Fire returns, on average, every 28 years in southern and 35 years in northern Alberta (Larsen 1997; Johnstone and Chapin 2006), depending on stand characteristics (Cumming 2001; Taylor, McCarthy and Lindenmayer 2014) and climate (Tymstra et al. 2007). Forest fires are expected to intensify and occur more frequently as climate becomes warmer and drier (Weber and Flannigan 1997; Li, Flannigan and Corns 2000; De Groot et al. 2003; Tymstra et al. 2007; Boulanger, Gauthier and Burton 2014; Beverly and McLoughlin 2019; Rupasinghe and Chow-Fraser 2021), challenging the long-term maintenance of permanent forest plots in Alberta.

Despite of the dictating role of forest fire in shaping the northern forests (Larsen 1997; Cumming 2001; Tymstra et al. 2007; Rogeau et al. 2016; Beverly and McLoughlin 2019) and that fire damages have become more severe and fire seasons have elongated (Rupasinghe and Chow-Fraser 2021), there is little understanding of how fire threatens the forest plots in Alberta. In this study, my overall objective is to provide a quantitative assessment of the fire hazards on the PSPs in Alberta. To this end, I first built fire hazards models to quantify the variation of fire hazards across the PSPs in three ecoregions. I then identified the risk factors, including stand structural, compositional and climatic variables, and estimated their effects on fire hazards. Based on the fire hazards models that were developed, I finally projected the impact of climate on fire hazards of the PSPs in 2050 under a moderate emission scenario. The results of this study are expected to contribute to quantitative understanding of fire hazards of PSPs in Alberta and support the management and maintenance of long-term forest plots in the face of climate change.

## 3.3 Materials and methods

### 3.3.1 Plot data

This study included 1,125 permanent sample plots (PSPs) distributed in northern forests across the Boreal, Foothills and Rocky Mountain ecoregions of Alberta (Natural Regions Committee 2006). Of the total plots, 452 were established under the 4-subplot design (Alberta Agriculture and Forestry 2015), for which I merged the records of the four subplots at each site to represent a whole plot. Further, 182 plots did not have complete coordinates and another 24 had no repeated measures, two pieces of key information needed for modeling. Consequently, these plots were excluded from this study, resulting in 919 plots ($n$ = 306, 509 and 104 in the Boreal, Foothills and Rocky Mountain ecoregions, respectively; Fig. 3.1a). The plot dominant tree species in the Foothills and Rocky Mountain ecoregions include *Pinus contorta* (lodgepole pine), *Picea glauca* (white spruce) and *Populus tremuloides* (trembling aspen). And those in the Boreal ecoregion include *Abies balsamea* (Balsam fir), *Picea mariana* (black spruce), *Picea glauca* (white spruce) and *Populus tremuloides* (trembling aspen). *Populus balsamifera* (Balsam popular) and *Betula papyrifera* (paper birch) were common species of plots across ecoregions. All these 919 plots were established in forests of natural origin, with 84% of them established before 1990 (Fig. 3.1b). I recorded their year of establishment ($y_0$), ranging from 1960 to 2009, from the plot data (Alberta Agriculture and Forestry 2015). And for PSPs with no record of establishment year, I assigned the year of the first census to $y_0$. I also recorded the year of the last census (the most recent census; $y_{last}$) of each PSP. The distributions of $y_0$ and $y_{last}$ are shown in Fig. 3.1b. Of the 919 PSPs, 48% were last measured after 2010.

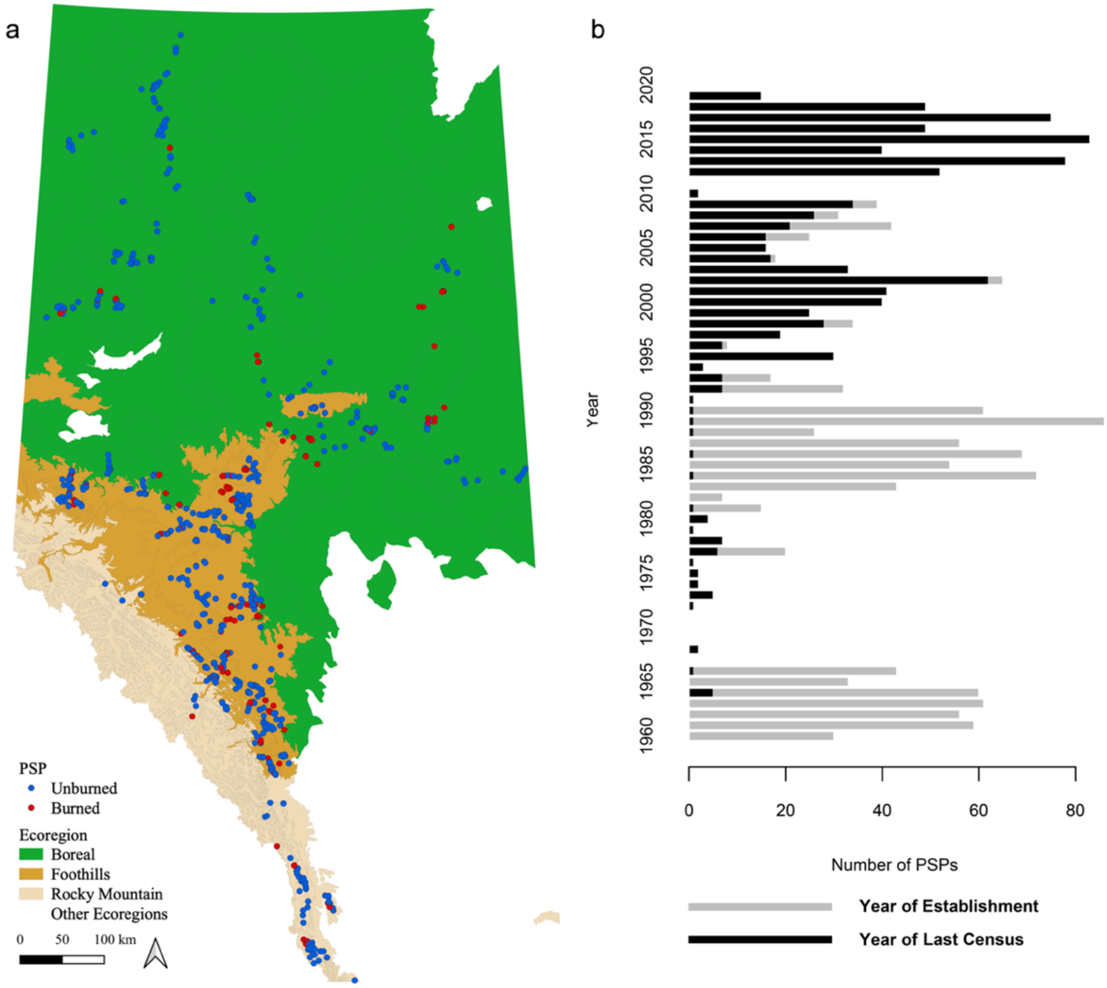

Fig. 3.1. (a) Distribution of the 919 permanent sample plots (PSPs) across the Boreal (*n* = 306), Foothills (*n* = 509) and Rocky Mountain (*n* = 104) ecoregions of Alberta, Canada. Unburned and burned plots are displayed as blue and red dots respectively. (b) Distribution of the year of establishment (in grey) and last census (in black) of the 919 PSPs from 1960 to 2020.

### 3.3.2 Fire data

Alberta has detailed fire records at both plot- and tree-levels of all PSPs (though records for other types of disturbances are either incomplete or undocumented; Alberta Agriculture and Forestry 2015). In this study, those PSPs that were abandoned from the PSP network because of fire disturbance (with fire records for the plot or with over 10% trees burned in the last census) were regarded as burned plots, whereas the rest were considered as unburned plots. The year of fire ($y_f$) of each burned PSP was then recorded. Of the 919 PSPs, I identified 152 plots (17% of the PSPs) were burned and counted the time between the year of establishment and the year of fire as persistence (or "survival") time ($= y_f - y_0$) of each burned plot. Of the remaining 767 unburned plots, 465 remained active by the end of the study period (which is 2019), and their survival times were counted as right-censored. The survival times of the other 302 plots that were discontinued but for reasons other than fire disturbance were also right-censored. The right-censored survival time for each of these 767 unburned plots was counted as the years between the last census and establishment ($survival\ time\ = y_{last} - y_0$). I estimated the survival function $S(t)$, i.e., the probability a plot survived up to *t* years since plot establishment without fire disturbance (*t* ranges from 1 to 57 years in this study) using the Kaplan-Meier estimator (Lawless 2011):

$$\hat{S}(t) = \prod_{i:t_i \le t} (1 - \frac{d_i}{n_i}), \tag{1}$$

where $t_i$ is the time of the $i^{\text{th}}$ fire occurrence after plot establishment, $d_i$ is the number of plots burned at time $t_i$, and $n_i$ is the number of plots known to have survived up to time $t_i$.

### 3.3.3 Modeling fire hazards

I adopted the Cox proportional hazards regression (Lawless 2011) to model the survival times of the 919 PSPs, which assumes proportionality (i.e., each factor imposes a constant impact on the hazard over time). The model has the form:

$$h(t) = h_0(t)\, e^{(b_1 x_1 + b_2 x_2 + \dots + b_p x_p)}, \tag{2}$$

which describes the effects of explanatory variables ($x_i$, $i = 1, 2, \dots, p$) on the fire hazards of a plot, $h(t)$, i.e., the probability of fire occurrence for a plot *t* years after establishment. $h_0(t)$ is the baseline hazard when every explanatory variable $x_i$ equals 0. $b_i$ is a coefficient, representing the change in the expected log of hazard ratio, $\ln(\frac{h(t)}{h_0(t)})$, with a one unit change in $x_i$ given that other variables are fixed. A hazard ratio of 3 means that the number of burned plots under the given combination of explanatory variables is three time higher than that under the baseline condition.

Data for 19 explanatory variables that describe stand characteristics and climatic conditions were compiled for the Cox proportional hazards modeling (Table S3). Variables that describe plot physical characteristics include plot size, year of establishment, stand age at establishment, latitude, longitude, altitude, ecoregion, aspect and slope. Data on plot aspect and slope were extracted from LiDAR 7.5 Digital Elevation Model (DEM) (Chang and Tsai 1991). Variables describing stand structure of each plot include species richness of live trees with DBH > 9 cm (the PSP DBH cutoff; same for other variables), canopy height (mean height of 3 trees with the largest DBH of the plot), tree density (number of trees per hectare) and basal area ($\sum \frac{DBH_i^2 \times \pi}{4}$ per hectare). I also calculated the density and basal area of deciduous trees. Each of the six stand structural variables was the average across the censuses of each plot. In addition, I extracted four mean annual climatic variables for each plot from ClimateNA v7.21 (Wang et al. 2016): mean annual temperature (MAT), difference between mean warmest and mean coldest month temperature (TD), mean annual precipitation (MAP) and climate moisture index (CMI; Hogg and Schwarz 1997). These four variables are commonly used to model the occurrences of forest fires (Weber and Flannigan 1997; Flannigan, Stocks and Wotton 2000; Tymstra et al. 2007; Stephens et al. 2013). The collinearity of these variables was not a concern as the highest Pearson's correlation of the variable pairs was < 0.8. Ecoregion was the only categorical variable, which allowed to detect the difference in fire hazards among the three ecoregions. All numeric variables were standardized to the 0-1 scale using the transformation $\frac{x - x_{min}}{x_{max} - x_{min}}$. I also fitted the model using stand structural and climatic variables at the most recent census, and their means during the last two censuses, and found no difference in the results (neither changed the list of significant factors nor the signs of their effects) from the model fitted using the averages across censuses. I thus only report the results of the census-averaged model in this study.

The Cox proportional hazards models (2) for the 919 PSPs were estimated using the *coxph* function of the *survival* package (Therneau 2021) in R 3.6.1 (https://www.r-project.org). For each model, I tested the proportional hazards assumption (proportionality) using the *cox.zph* function of the same package. No evidence of non-proportionality was detected in these models (*p*-value > 0.05). The model selection was carried out using likelihood ratio tests on the nested models (Fan and Li 2002). I also predicted the fire hazards of PSPs in Alberta in 2050, 30 years after this study. I adopted the modest emission scenario (SSP245; Shared Socioeconomic Pathway 2 with a 4.5 $W \cdot m^2$ additional radiative forcing) of the 13-GCM CMIP6 ensemble (GCM for global climate model and CMIP6 for Coupled Model Intercomparison Project 6;

Mahony et al. 2022) to estimate plot fire hazards by substituting the projected plot mean annual temperature increase in the 2040-2060 period from the 2000-2020 baseline (extracted from ClimateNA v7.21; Wang et al. 2016) into the best selected model. The estimated fire hazards reflect how much higher fire risk the PSPs in Alberta may suffer in 2050 due to warming under the modest emission scenario than the current risk level.

## 3.4 Results

Survival times of the 919 PSPs in Alberta range from 1 to 57 years with a mean of 28.7 years (standard deviation 13.4 years), and those of the 152 burned plots range from 1 to 56 years with a mean of 25.6 years (standard deviation 15.3 years). The distribution of the survival times of the 919 PSPs is shown in Fig. 3.2a, and the Kaplan-Meier survival probability curve for these plots in Fig. 3.2b. The estimated survival probability of PSPs in Alberta dropped to 0.85 30 years after plot establishment, then sharply decreased after 45 years, and reached 0.65 in year 50 and further down to 0.55 in year 57 (the end of this study). For PSPs in the three ecoregions, their survival curves are shown in Fig. 3.2c. The survival probability of PSPs in each ecoregion has been consistently above 0.8 up to 30 years since establishment. For PSPs in the Rocky Mountain ecoregion, the survival probability had remained above 0.75 until year 57, whereas that for PSPs in the Foothills ecoregion had dropped from 0.85 in year 45 to 0.58 by the end of the study. The survival probability for PSPs in the Boreal ecoregion dropped steadily to 0.33 55 years after establishment.

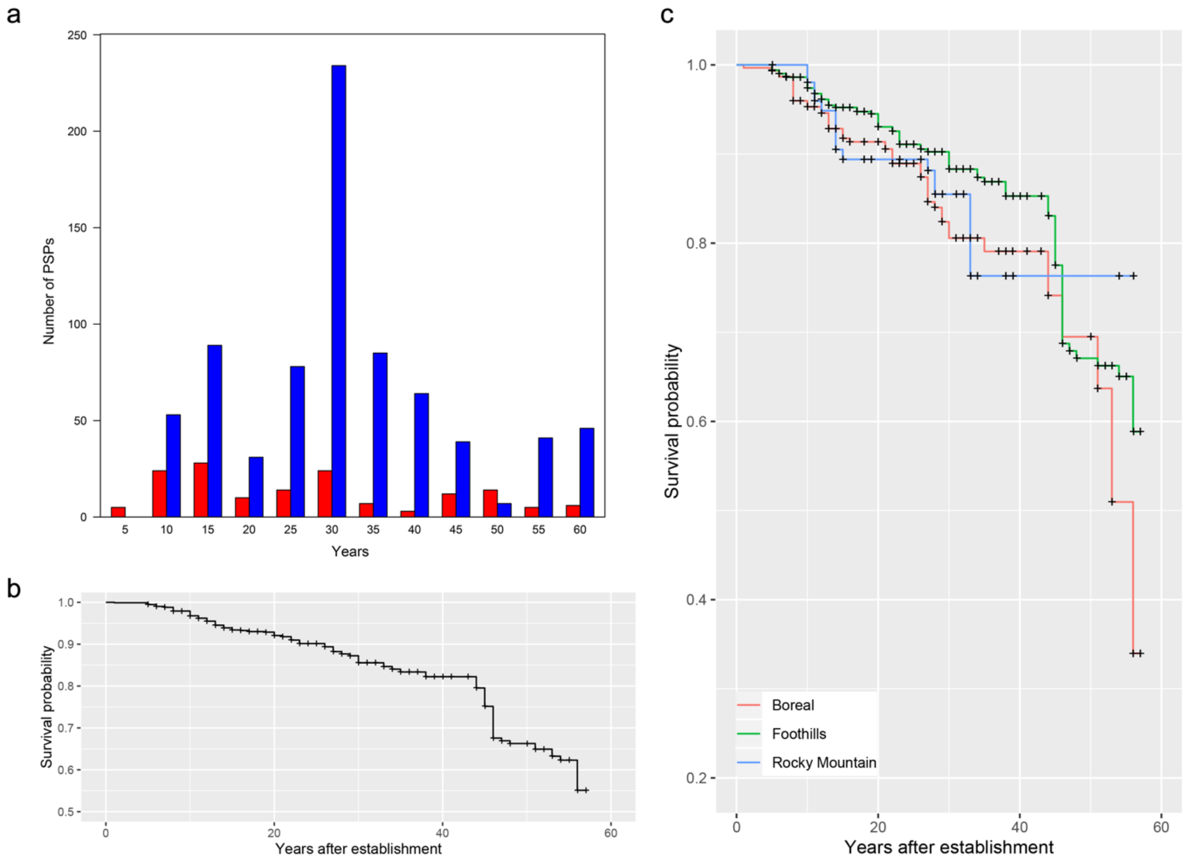

Fig. 3.2. (a) Distributions of the survival times (in years) of the 152 burned PSPs (in red) and of the right-censored survival times of the 767 unburned PSPs (in blue) in Alberta. (b) The Kaplan-Meier survival curve of fire occurrence estimated for all 919 PSPs in Alberta. (c) The survival curves of fire occurrence estimated for the PSPs in the Boreal (in red), Foothills (in green) and Rocky Mountain (in blue) ecoregions.

The best selected Cox proportional hazards model is presented in Table 3.1 where five explanatory variables are retained, including ecoregion (Boreal, Foothills and Rocky Mountain), year of establishment, tree species richness, density of deciduous trees and mean annual temperature. The estimated coefficients of the four numeric variables in Table 3.1 indicate their effects on fire hazards. The interpretations of their effects are as follows. Taking mean annual temperature as an example, for 1 degree increase in mean annual temperature, given other variables fixed, the probability of plot fire occurrence increases by 30.1%. This is calculated from $(e^{\frac{1}{6.47}\times 1.700} - 1) \times 100\%$, where 6.47 °C is the range of mean annual temperature across the 919 PSPs (i.e., the difference between the highest and lowest mean annual temperature of the

919 plots). This range is needed because the variable is standardized (see Table S3 for the range of the other numeric variables). The model also indicates that plots established more recently have higher fire risks than those established earlier. For example, the fire hazards of plots established one year later would increase by 6.6% ($(e^{\frac{1}{49}\times 3.151} - 1) \times 100\%$) than those established a year earlier. The Cox model also shows that tree species diversity of a plot would reduce fire hazards, with 36.4% reduction if one new tree species is added to the plot. The density of deciduous trees would also reduce fire risks, by 10.3% if the density of deciduous trees (with DBH > 9.0 cm) increases by 100 stems per hectare within the plot.

Table 3.1. The best selected Cox proportional hazards model for the survival times of 919 PSPs in Alberta. The model overall likelihood ratio = 117.8 on 6 degrees of freedom with $p$-value < $10^{-16}$. The Boreal ecoregion is the baseline for the Ecoregion factor.

| Factor | Coefficient | Standard error | $Z$-value | $p$-value |
|---|---|---|---|---|
| Ecoregion: Foothills | -1.048 | 0.351 | -4.248 | $2.15 \times 10^{-5}$ |
| Ecoregion: Rocky Mountain | -1.213 | 0.297 | -3.759 | $1.71 \times 10^{-4}$ |
| Year of establishment | 3.151 | 0.454 | 6.935 | $4.05 \times 10^{-12}$ |
| Tree species richness | -2.172 | 0.454 | -4.787 | $1.70 \times 10^{-6}$ |
| Density of deciduous trees | -2.081 | 0.778 | -2.676 | $7.45 \times 10^{-3}$ |
| Mean annual temperature | 1.700 | 0.690 | 2.464 | $1.38 \times 10^{-2}$ |

The results in Table 3.1 also show that fire hazards of PSPs in the Foothills and Rocky Mountain ecoregions are respectively 0.35 (i.e., $e^{-1.048}$) and 0.30 (i.e., $e^{-1.213}$) times the risk level in the Boreal ecoregion, or, in other words, the fire hazards in the Boreal ecoregion are 2.85 (i.e., $\frac{1}{e^{-1.048}}$) and 3.36 (i.e., $\frac{1}{e^{-1.213}}$) times higher than the Foothills and Rocky Mountain ecoregions. There was a significant difference in fire hazards between the Boreal and the other two ecoregions (both $p < 0.001$), while no significant difference was detected between the Foothills and Rocky Mountain ecoregions ($p = 0.56$; $t$ test on the estimated coefficients of these two ecoregions).

Under the moderate climate change scenario of the 13-GCM CMIP6 ensemble (Mahony et al. 2022) that projects a 1.15 – 2.30 °C increase in plot mean annual temperature for the 2040-

2060 period from the 2000-2020 baseline, my Cox proportional hazards model (Table 3.1) predicts that the fire hazards of the PSPs in Alberta would be 1.63 (ranging from 1.35 to 1.83) times higher than the current level given that other variables remain unchanged. The hazards would be 1.68 (ranging from 1.46 to 1.83), 1.61 (1.41 to 1.76) and 1.56 (1.35 to 1.71) times higher for those in the Boreal, Foothills and Rocky Mountain ecoregions, respectively.

## 3.5 Discussion

Maintaining long-term ecological research sites has been a global challenge, yet it is essential for supporting ecological research and management (Rees et al. 2001; Lindenmayer, Laurance and Franklin 2012; MacDicken 2015; Liang and Gamarra 2020). Field sites are subject to numerous threats of natural and anthropogenic disturbances. Of the 919 PSPs analyzed in this study, 302 of them were discontinued due to unknown reasons. To my best knowledge, their loss could be due to many undocumented factors, such as pest infestation (e.g. Mountain pine beetle outbreak in the 2000s in the Foothills and Rocky Mountain ecoregions; Safranyik et al. 2010), lack of supporting resources for maintenance (Alberta Agriculture and Forestry 2015), and even erratic causes. Nonetheless, fire disturbance represents the single most important risk factor for the PSPs in Alberta (Alberta Agriculture and Forestry 2015) and Alberta's forests in general (Larsen 1997; Cumming 2001; Tymstra et al. 2007; Rogeau et al. 2016; Beverly and McLoughlin 2019; Rupasinghe and Chow-Fraser 2021). This study found that the PSPs in Alberta have on average 28.7 years of fire survival time. This is short compared to the 28-to-35-year mean forest fire return interval in Alberta (Larsen 1997; Johnstone and Chapin 2006) particularly because most PSPs were not established immediately after stand replacing fires. In fact, most PSPs were established in mature forests (Alberta Agriculture and Forestry 2015). This study also showed that the PSPs in Alberta had an estimated survival probability of 0.85 (i.e., 15% of plots lost; Fig. 3.2b) 30 years after plot establishment, which dropped to 0.65 (i.e., 35% of plots lost; Fig. 3.2b) after 50 years. These are surprisingly high rates of loss of plots to fires given that the age of a typical old stand in Alberta is around 130 years (Morgantini and Kansas 2003; Natural Regions Committee 2006), and these rates speak for the importance to protect the PSPs. In addition, fire hazards of the PSPs varied across ecoregions. The plots in the Boreal ecoregion suffered significantly higher fire hazards than those in the Foothills and Rocky Mountain ecoregions (by 2.85 and 3.36 times higher, respectively). This is consistent with the general understanding that fire hazards in Alberta are higher in the Boreal ecoregion (Larsen 1997; Li, Flannigan and Corns 2000; Rogeau et al. 2016). The non-significant difference in fire hazards between the Foothills and Rocky Mountain ecoregions ($p = 0.56$) detected in my model is consistent with the reported similar hazards in these two ecoregions (Natural Regions Committee 2006; Rogeau et al. 2016).

In addition to the variation among the ecoregions, I found that fire hazards were not associated with plot longitude, latitude, altitude, slope or aspect as none of these variables was selected by the Cox proportional hazards model. Instead, the Cox model indicates that fire hazards of PSPs were significantly dependent on the year of plot establishment, tree species richness, density of deciduous trees and mean annual temperature (Table 3.1). The Cox model predicts that the PSPs established more recently suffered higher fire risks than those established earlier. This might be due to two reasons. First, 43% of the PSPs established between 2000 and 2009 were for replacing burned plots where fires occurred frequently (Alberta Agriculture and Forestry 2015). Second, 55% of the PSPs established in the 2000s were located in the Boreal ecoregion where the risks of fire occurrence are higher than those in the other two ecoregions (Cumming 2001; Johnstone and Chapin 2006). Both of these reasons imply that the PSPs established in the 2000s were exposed to higher fire hazards than those established before 2000. However, I did not find that plot fire hazards were related to stand age, though younger forest stands in Alberta are in general less likely to be burned (Taylor, McCarthy and Lindenmayer 2014). This is probably because most PSPs are in mature forests.

Among the many stand structure variables (Table S3), only tree species richness and density of deciduous trees were significantly associated with fire hazards of the PSPs in Alberta. The Cox model (Table 3.1) shows that the fire hazards would decrease by 36.4% by adding a new species to an existing plot. One possible reason for high diversity plots to have low fire risks is that species-rich plots may diversify fuel types and also lower fuel load (Cumming 2001; Beverly 2017). Another reason could be that plots with high richness are often younger (in contrast to stands at the old-growth stage) which are less likely to be burned (Cumming 2001; Johnstone and Chapin 2006; Taylor, McCarthy and Lindenmayer 2014). Species diversity is widely documented to be functionally important in maintaining ecosystem stability, resisting exotic invasions and increasing productivity (Tilman, Isbell and Cowles 2014). My result reveals a previously little recognized function of biodiversity in reducing forest fire hazards. Plot fire hazards were also found lower with higher density of deciduous trees, consisting of trembling aspen, balsam poplar and white birch. This is to a great part due to that coniferous trees are better fuel types than deciduous trees, particularly in mixedwood stands in Alberta (Cumming 2001; Beverly 2017). In this study, the fire hazards of the PSPs with the highest density of deciduous trees (DBH > 9.0 cm; 2113 trees per hectare) are only 0.12 ($e^{-2.081}$) times the fire hazards of the PSPs of pure coniferous trees. Considering these effects of tree species diversity and deciduous tree density, due attention is needed to consider tree species compositions and density of deciduous trees when assessing plot fire hazards.

Apart from those effects, my model in Table 3.1 shows that mean annual temperature (MAT) would significantly raise fire hazards of PSPs. From 1948 to 2016, MAT in Alberta had increased by 1.9 °C (Zhang et al. 2019). This increase in MAT, else being unchanged, would have increased fire hazards of PSPs in Alberta by 64.7% as projected from my Cox model (Table 3.1). Under the SSP245 moderate emission scenario (Mahony et al. 2022), my model projects that the fire hazards of PSPs in Alberta would be 1.63 times higher in 2050 than the current level. This is a conservative estimation as the SSP245 scenario assumes efforts in reducing radiative forcing and considers only medium challenges to global mitigation and adaptation (Mahony et al. 2022). Fire hazards of the PSPs will be likely higher than this estimation as more PSPs in the Boreal (22%) than in the Foothills (3%) and Rocky Mountain (0%) ecoregions are projected to suffer >1.75 times higher risks under the SSP245 scenario in 2050. The hazards should also increase unevenly across the landscape because warming effect is spatially heterogeneous (Jiang et al. 2017) and would reduce biodiversity (Price et al. 2013) as well as intensify tree mortality (Peng et al. 2011), particularly of deciduous trees, e.g. trembling aspen, due to drought (Michaelian et al. 2011). Such a heterogeneous effect of warming on plot fire hazards would further challenge the maintenance of PSPs in Alberta, requiring proactive plans for those expecting higher risks.

Fire disturbances are pervasive not only in Alberta but also in other regions of Canada (Lee et al. 2002; Johnstone and Chapin 2006; Boulanger, Gauthier and Button 2014) and globally (Flannigan, Stocks and Wotton 2000; Stephens et al. 2013). As such, protection of forest inventory plots from fire threat is both a regional and a global challenge. This study quantified fire hazards of forest plots in Alberta and showcased modeling of fire risks. The approach and the methodology demonstrated here are applicable to other regions of Canada or elsewhere, and can also be applied to modeling the hazards of other types of disturbances if data were available, e.g. the effect of moose browsing on the PSPs in Newfoundland and Labrador where moose activity has been the major disturbance (Charron and Hermanutz 2017).

I would like to note some limitations associated with this study. The first is that data were not available for me to identify the causes of the 302 discontinued plots which could be abandoned for various reasons, e.g. pest infestation (Safranyik et al. 2010; Cortini and Comeau 2020) and lack of supporting resources (Alberta Agriculture and Forestry 2015). Without further data, I was not able to identify other causes for the loss of PSPs, thus complicating the effort of plot maintenance. The second limitation is that fire hazards might be underestimated in my study, again due to two limitations of the data. One is that some of those 302 discontinued plots could be burned but were not recorded as so. The other is that the actual survival times of those 152 burned PSPs could be shorter than the recorded data because plot censuses did not take place every year or immediately after the burns. Instead, the time intervals between two consecutive censuses varied from 5 to 10 years. In most cases, fires usually occurred between the last two censuses but were recorded and assigned to the year of last census. Note that because of lacking accurate locations of PSPs, it is not feasible to refer to the provincial fire polygons for historical fire years of these plots. To improve the fire data, a comprehensive fire scar examination should be conducted in future surveys, or tree ring samples be collected to more precisely date the occurrences of fires (Jones and Daniels 2012).

Failing to address the threats field research plots face could increase the cost of plot maintenance to an unaffordable level. It is estimated that the cost of replacing lost sites could be 3 to 5 times higher than that of maintaining existing plots (Kovač et al. 2010). Although there has always been an interest in establishing new plots to extend spatial coverage and increase sample sizes of ecological monitoring programs (Condit et al. 2014; Anderson-Teixeira et al. 2015; Liang and Gamarra 2020), I argue that it is equally important and is cost-effective to improve the maintenance of existing plots. While I recognize the practical challenges to prevent fire occurrences (or other disturbances), my study provides a model for identifying risk factors and for quantifying fire hazards of the PSPs in Alberta. For example, if our goal is to maintain a constant number of plots in the PSP network, the life expectancy (28.7 years) of the PSPs estimated from this study affords key information for plot replacement to achieve that goal. This information could also aid to determine census intervals to optimize data collection for plots at different risk levels. On another front, forest managers and planners always face the challenge to distribute limiting resources to meet management needs. This study suggests that we should allocate more resources to protect and monitor those plots with higher fire risks (e.g. new plots and plots in the Boreal ecoregion) by taking a shorter census interval. To better understand post-fire regeneration and stand dynamics, I suggest installing extra plots in fire-prone areas and stand types, and continuing monitoring burned stands wherever possible. In conclusion, my study is of value to contribute to the goal of improving the maintenance of long-term forest inventory plots by addressing the need to model disturbances, identifying the key risk factors and quantifying their impacts for maintaining the long-term forest inventory plots.

### 3.6 References

Alberta Agriculture and Forestry (2015). *Minimum Standards and Suggested Protocol and Priorities for Establishing and Measuring Permanent Sample Plots in Alberta.* Forest Management Branch, Alberta Agriculture and Forestry, Edmonton, Alberta.

Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Joseph Wright, S., et al. & Zimmerman, J. (2015). CTFS-Forest GEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21, 528-549.

Besnard, S., Koirala, S., Santoro, M., Weber, U., Nelson, J., Gütter, J., et al. & Carvalhais, N. (2021). Mapping global forest age from forest inventories, biomass and climate data. *Earth System Science Data Discussions*, 13, 4881-4896.

Beverly, J.L. (2017). Time since prior wildfire affects subsequent fire containment in black spruce. *International Journal of Wildland Fire*, 26, 919-929.

Beverly, J.L. & McLoughlin, N. (2019). Burn probability simulation and subsequent wildland fire activity in Alberta, Canada–Implications for risk assessment and strategic planning. *Forest Ecology and Management*, 451, 117490.

Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., et al. & Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339-345.

Boulanger, Y., Gauthier, S. & Burton, P.J. (2014). A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research*, 44, 365-376.

Burgess, D., & Robinson, C. (1998). Canada's oldest permanent sample plots—thinning in white and red pine. *The Forestry Chronicle*, 74, 606-616.

Chang, K.-t. & Tsai, B.-w. (1991). The effect of DEM resolution on slope and aspect mapping. *Cartography and Geographic Information Systems*, 18, 69-77.

Charron, L. & Hermanutz, L. (2017). Simplicity is key: Restoration protocols for nonregenerating forests degraded by overabundant herbivores. *Restoration Ecology*, 25, 432-441.

Chave, J., Davies, S.J., Phillips, O.L., Lewis, S.L., Sist, P., Schepaschenko, D. *et al.* (2019). Ground data are essential for biomass remote sensing missions. *Surveys in Geophysics*, 40, 863-880.

Chen, H.Y., Luo, Y., Reich, P.B., Searle, E.B. & Biswas, S.R. (2016). Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecology Letters*, 19, 1150-1158.

Condit, R., Sukumar, R., Hubbell, S. P., & Foster, R. B. (1998). Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist*, 152, 495-509.

Condit, R., Lao, S., Singh, A., Esufali, S. & Dolins, S. (2014). Data and database standards for permanent forest plots in a global network. *Forest Ecology and Management*, 316, 21-31.

Cortini, F. & Comeau, P.G. (2020). Pests, climate and competition effects on survival and growth of trembling aspen in western Canada. *New Forests*, 51, 175-190.

Cumming, S.G. (2001). Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological Applications*, 11, 97-110.

Davies, S. J., Abiem, I., Salim, K. A., Aguilar, S., Allen, D., Alonso, A., et al. & Yap, S. L. (2021). ForestGEO: Understanding forest diversity and dynamics through a global observatory network. *Biological Conservation*, 253, 108907.

De Groot, W.J., Bothwell, P.M., Carlsson, D.H. & Logan, K.A. (2003). Simulating the effects of future fire regimes on western Canadian boreal forests. *Journal of Vegetation Science*, 14, 355-364.

Fan, J. & Li, R. (2002). Variable selection for Cox's proportional hazards model and frailty model. *Annals of Statistics*, 30, 74-99.

Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000). Climate change and forest fires. *Science of the Total Environment*, 262, 221-229.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017). Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology*, 23, 5297-5308.

Hogg, E.H. & Schwarz, A.G. (1997). Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. *Journal of Biogeography*, 24, 527-534.

Jiang, R., Gan, T.Y., Xie, J., Wang, N. & Kuo, C.-C. (2017). Historical and potential changes of precipitation and temperature of Alberta subjected to climate change impact: 1900–2100. *Theoretical and Applied Climatology*, 127, 725-739.

Johnstone, J.F. & Chapin, F.S. (2006). Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems*, 9, 268-277.

Jones, E.L. & Daniels, L.D. (2012). Assessment of dendrochronological year-of-death estimates using permanent sample plot data. *Tree-Ring Research*, 68, 3-16.

Kangas, A. & Maltamo, M. (2006). *Forest inventory: methodology and applications*. Springer, Dordrecht, The Netherlands.

Kovač, M., Kušar, G., Hočevar, M., Simončič, P., Poljanec, A., Skudnik, M., Gartner, A. & Kozorog, E. (2010). Control sampling method in Slovenia-History, Characteristics and Use. *Studia Forestalia Slovenica*, 136, 1-66.

Larsen, C.P.S. (1997). Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography*, 24, 663-673.

Lawless, J. F. (2011). *Statistical models and methods for lifetime data*. John Wiley & Sons, 362pp.

Lee, B.S., Alexander, M.E., Hawkes, B.C., Lynham, T.J., Stocks, B.J. & Englefield, P. (2002). Information systems in support of wildland fire management decision making in Canada. *Computers and Electronics in Agriculture*, 37, 185-198.

Li, C., Flannigan, M.D. & Corns, I.G. (2000). Influence of potential climate change on forest landscape dynamics of west-central Alberta. *Canadian Journal of Forest Research*, 30, 1905-1912.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G. *et al.* (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, 354, aaf8957.

Liang, J. & Gamarra, J.G. (2020). The importance of sharing global forest data in a world of crises. *Scientific Data*, 7, 1-5.

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Global decline in large old trees. *Science*, 338, 1305-1306.

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., & Phillips, O. L. (2011). ForestPlots. net: a web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science*, 22, 610-613.

MacDicken, K.G. (2015). Global forest resources assessment 2015: what, why and how? *Forest Ecology and Management*, 352, 3-8.

Mahony, C.R., Wang. T., Hamann, A. & Cannon, A.J. (2022). A CMIP6 ensemble for downscaled monthly climate normal over North America. *International Journal of Climatology*, doi: 10.1002/joc.7566.

Metsaranta, J. M., & Lieffers, V. J. (2009). Using dendrochronology to obtain annual data for modelling stand development: a supplement to permanent sample plots. *Forestry*, 82, 163-173.

Michaelian, M., Hogg, E. H., Hall, R. J., & Arsenault, E. (2011). Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, 17, 2084-2094.

Monserud, R. A., Huang, S., & Yang, Y. (2006). Biomass and biomass change in lodgepole pine stands in Alberta. *Tree physiology*, 26, 819-831.

Morgantini, L. E., & Kansas, J. L. (2003). Differentiating mature and old-growth forests in the upper foothills and subalpine subregions of west-central Alberta. *The Forestry Chronicle*, 79, 602-612

Munger, T.T. (1946). Watching a Douglas-fir forest for thirty-five years. *Journal of Forestry*, 44, 705-708.

Natural Regions Committee. (2006). *Natural Regions and Subregions of Alberta*. Government of Alberta, Edmonton, Alberta.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., et al. & Hayes, D. (2011). A large and persistent carbon sink in the world’s forests. *Science*, 333, 988-993.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., et al. & Zhou, X. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1, 467-471.

Phillips, O. L., Aragão, L. E., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G. *et al*. (2009). Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344-1347.

Price, D. T., Alfaro, R. I., Brown, K. J., Flannigan, M. D., Fleming, R. A., Hogg, E. H., et al. & Venier, L. A. (2013). Anticipating the consequences of climate change for Canada’s boreal forest ecosystems. *Environmental Reviews*, 21, 322-365.

Rees, M., Condit, R., Crawley, M., Pacala, S., & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293, 650-655.

Ribeiro, R.P., Borges, J.G. & Oliveira, V. (2004). A framework for data quality for Mediterranean sustainable ecosystem management. *Annals of Forest Science*, 61, 557-568.

Rogeau, M.-P., Flannigan, M.D., Hawkes, B.C., Parisien, M.-A. & Arthur, R. (2016). Spatial and temporal variations of fire regimes in the Canadian Rocky Mountains and foothills of southern Alberta. *International Journal of Wildland Fire*, 25, 1117-1130.

Rupasinghe, P.A. & Chow-Fraser, P. (2021). Relating pre-fire canopy species, fire season, and proximity to surface waters to burn severity of boreal wildfires in Alberta, Canada. *Forest Ecology and Management*, 496, 119386

Safranyik, L., Carroll, A. L., Régnière, J., Langor, D. W., Riel, W. G., Shore, T. L., et al. & Taylor, S. W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, 142, 415-442.

Smith, W.B. (2002). Forest inventory and analysis: a national inventory and monitoring program. *Environmental Pollution*, 116, S233-S242.

Spurr, S.H. 1952. *Forest Inventory*. Ronald Press, New York.

Stadt, J. J., Schieck, J., & Stelfox, H. A. (2006). Alberta Biodiversity Monitoring Program–monitoring effectiveness of sustainable forest management planning. *Environmental Monitoring and Assessment*, 121, 33-46.

Stephens, S.L., Agee, J.K., Fule, P.Z., North, M.P., Romme, W.H., Swetnam, T.W. *et al.* (2013). Managing forests and fire in changing climates. *Science*, 342, 41-42.

Taylor, C., McCarthy, M.A. & Lindenmayer, D.B. (2014). Nonlinear effects of stand age on fire severity. *Conservation Letters*, 7, 355-370.

Therneau, T.M. (2021). A package for survival analysis in R. Version 3.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471-493.

Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., Gabler, K., Schadauer, K. *et al.* (2010). National forest inventories. *Pathways for Common Reporting. European Science Foundation*, 1, 541-553.

Tymstra, C., Flannigan, M.D., Armitage, O.B. & Logan, K. (2007). Impact of climate change on area burned in Alberta's boreal forest. *International Journal of Wildland Fire*, 16, 153-160.

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11, e0156720.

Weber, M.G. & Flannigan, M.D. (1997). Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. *Environmental Reviews*, 5, 145-166.

Yang, Y., Huang, S., Vassov, R., Pinno, B., & Chhin, S. (2020). Climate-sensitive height–age models for top height trees in natural and reclaimed oil sands stands in Alberta, Canada. *Canadian Journal of Forest Research*, 50, 297-307.

Zhang, J., Huang, S. & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, 112, 4009-4014.

Zhang, J., Huang, S., Hogg, E.H., Lieffers, V., Qin, Y. & He, F. (2014). Estimating spatial variation in Alberta forest biomass from a combination of forest inventory and remote sensing data. *Biogeosciences*, 11, 2793.

Zhang, X., Flato, G., Kirchmeier-Young, M., Vincent, L., Wan, H., Wang, X., et al. & Kharin, V. V. (2019). Changes in Temperature and Precipitation Across Canada; Chapter 4. In *Canada's Changing Climate Report* (eds Bush, E. & Lemmen, D.S.), Government of Canada, Ottawa, Ontario, 112-193.

# Chapter 4 Estimating Tree Density of North American Boreal Forest

## 4.1 Abstract

Boreal forests, the largest terrestrial biome on Earth, are highly varied in local tree density. Despite the recent attempt of Crowther et al. (2015) to estimate tree density in boreal forests from a biome-level model, accurate estimates are still lacking, leaving the question how many trees there are in boreal forests unanswered. In this study, I compiled tree density data from 4,367 plots in North American boreal forest to address this question. My results showed that the biome model consistently underestimated boreal tree density by 32.3%, compared to a 0.6% underestimation of my model that incorporated stand height as a predictor. I estimated a total number of 351.3 billion trees in North American boreal forest compared to 211.2 billion estimated by the biome model. The underestimation of 140.1 billion trees is equivalent to missing 14.0 trillion kg biomass. I further produced a boreal tree density map of North America, and projected tree density distribution in 2050 under the RCP2.6, 4.5 and 8.5 emission scenarios. This improved knowledge about boreal tree density contributes to understanding of the role of boreal forests in regulating forest ecosystem functions and informs adaptation and mitigation planning and policy-making.

Keywords: Tree density, biome model, North American boreal forest, stand height, forest plots.

## 4.2 Introduction

Knowledge about tree density (number of trees per unit area; hereafter per hectare) at local, regional and global scales is critical to forest management (Kays and Harper 1974; Ghazoul, Liston and Boyle 1998; Greene et al. 1999), biodiversity maintenance (Clark and Clark 1984; Ter Steege et al. 2013; Chen et al. 2018; Sugiyama et al. 2018), understanding ecosystem functioning (Gram and Sork 2001; Tobner et al. 2014), and informing climate change mitigation (Seppälä, Alexander and Katila 2009). Underlying these multifaceted roles of tree density is the process of competition that drives stand dynamics and promotes the development of stand structure, leading to quantitative relationships between tree density and stand volume or biomass (Mohler, Marks and Sprugel 1978; Westoby 1984), and mean tree size (White and Harper 1970). Much of the foundation of growth and yield modeling and silviculture is based on managing stand density to minimize the negative effects of competition (Puettmann, Coates and Messier 2009). Despite the wide importance of stand density, our knowledge about it and the factors responsible for its variation across landscapes remains limited. Tree density in a forest can be subject to as many factors as the number of trees themselves, including geography, topography, soils, climate, stand structure, stand age, disturbances, etc. (Huston 1980; Seidl et al. 2017). It is thus challenging to develop models that would capture the variation in stand density across forests. Crowther et al. (2015) have taken up this challenge to model global tree density at the biome level (thereafter the biome model). This exceptional effort led to an estimate of 3.04 trillion trees on Earth with tree abundance estimation for each of the 14 biomes. Their model was developed on the assumption that stand density is determined by stand topographic and vegetative characteristics and regulated by climate, with a possible association with human development. While the biome model fills in a long-missing knowledge gap critical to the management of forest resources and global carbon cycling, the quality of these estimates varies greatly across different biomes, with particularly poor estimation for boreal forest and tundra biomes as evidenced in Fig. 2 of Crowther et al. (2015).

Boreal forests are the largest biome on Earth, storing approximately 11% of global terrestrial carbon (Gauthier et al. 2015). Boreal forests also play important roles in maintaining biodiversity, mitigating climate change impacts, and supporting livelihood and economy of northern regions (Seppälä, Alexander and Katila 2009; Ma et al. 2012; Gauthier et al. 2015). Given the importance of boreal forests, knowledge about tree density and its variation in distribution is necessary for sustainable management of boreal forests and policy-making (D'Amato et al. 2011; Brecka, Shahi and Chen 2018). However, accurate estimation of boreal tree density has proven to be challenging because boreal forests are one of the most heterogenous forest ecosystems, with stand density varying from hundreds to thousands stems per hectare (Brandt 2009). Crowther et al. (2015) estimated 749.3 billion trees in the boreal biome (accounting for 25% of the total number of trees globally), and 211.2 billion trees in North American boreal forest (estimated from their tree density map). However, the accuracy of this estimation is unknown given that the boreal biome model in Crowther et al. (2015) is one of the two most poorly performed models. Various reasons can contribute to the poor performance of their boreal biome model. Notably, lack of data and missing important explanatory variables from the model are two of them. The 8,688 ground plots used by Crowther et al.'s (2015) to build their boreal biome model only included a small set of 346 ground plots from North American boreal forest, despite the fact that it covers a vast terrestrial area of 627 million hectares. On the other hand, although stand topographic, vegetative and climatic conditions have been considered to dictate the formation and distribution of global vegetation (Peel, Finlayson and McMahon 2007), they are insufficient in capturing the local variation of tree density (Aussenac 2000; Weiner et al. 2001). An important process that regulates stand density is competition, e.g., for light (Krajicek, Brinkman and Gingrich 1961; Hart, Hart and Murphy 1989). Tree canopy height has been widely recognized as a key stand architecture that controls light conditions in forests (Krajicek, Brinkman and Gingrich 1961; Hart, Hart and Murphy 1989; MacFarlane, Green and Burkhart 2000; Xu et al. 2019), and should be considered in modeling stand density. This is particularly so given that data on tree canopy height are widely available from both ground and airborne data.

In this study, I aimed to estimate tree density of boreal forest of North America with improvement on the above shortcomings of Crowther et al.'s (2015) boreal biome model. I compiled a large set of data consisting of 4,367 ground plots across the region, and developed a stand density model that includes the effects of climate, topography and vegetative characteristics as well as stand height. The results would inform how tree density varies spatially in North American boreal forest and how many boreal trees there are in the continent.

## 4.3 Materials and methods

### 4.3.1 Tree density data

I compiled ground plot data from three data sources, including permanent sample plots (PSPs), National Forest Inventory plots (NFI, which was the data source of Crowther et al.'s study in North American boreal forest; Gillis, Omule and Brierley 2005) and Alberta Biodiversity Monitoring Institute plots (ABMI; Stadt, Schieck and Stelfox 2006). The PSPs consist of Canadian provincial and territorial forest inventory plot data (Bonnor and Magnussen 1987) and the Cooperative Alaska Forest Inventory (CAFI; Malone, Liang and Packee 2009). These PSPs, NFI and ABMI plots together cover the North American boreal zone (Brandt 2009), including Alaska (the USA) and 9 Canadian provinces and territories (Fig. 4.1). To be consistent with Crowther et al. (2015), in this study I included alive trees with diameter at breast height (DBH) ≥ 10.0 cm. Plots were selected for this study if: (1) they were ≥ 100 $m^2$ in size with complete coordinates, (2) there were ≥ 5 trees and field-measured height for ≥ 3 largest trees, (3) they were naturally regenerated without silviculture treatments (e.g., fertilizing or thinning) and no records of disturbances (e.g., fire, pest, landslide, flood or other extreme weather events), and (4) they were censused between 1999 and 2019. For plots with multiple censuses, the census closest to 2009 was used to minimize the within-plot temporal variation because this census is comparable to the ground data used in Crowther et al. (2015). The final data included 4,367 ground plots, of which 3,829 were from PSPs, 346 from NFI and 192 from ABMI plots (Fig. 4.1; Table S4).

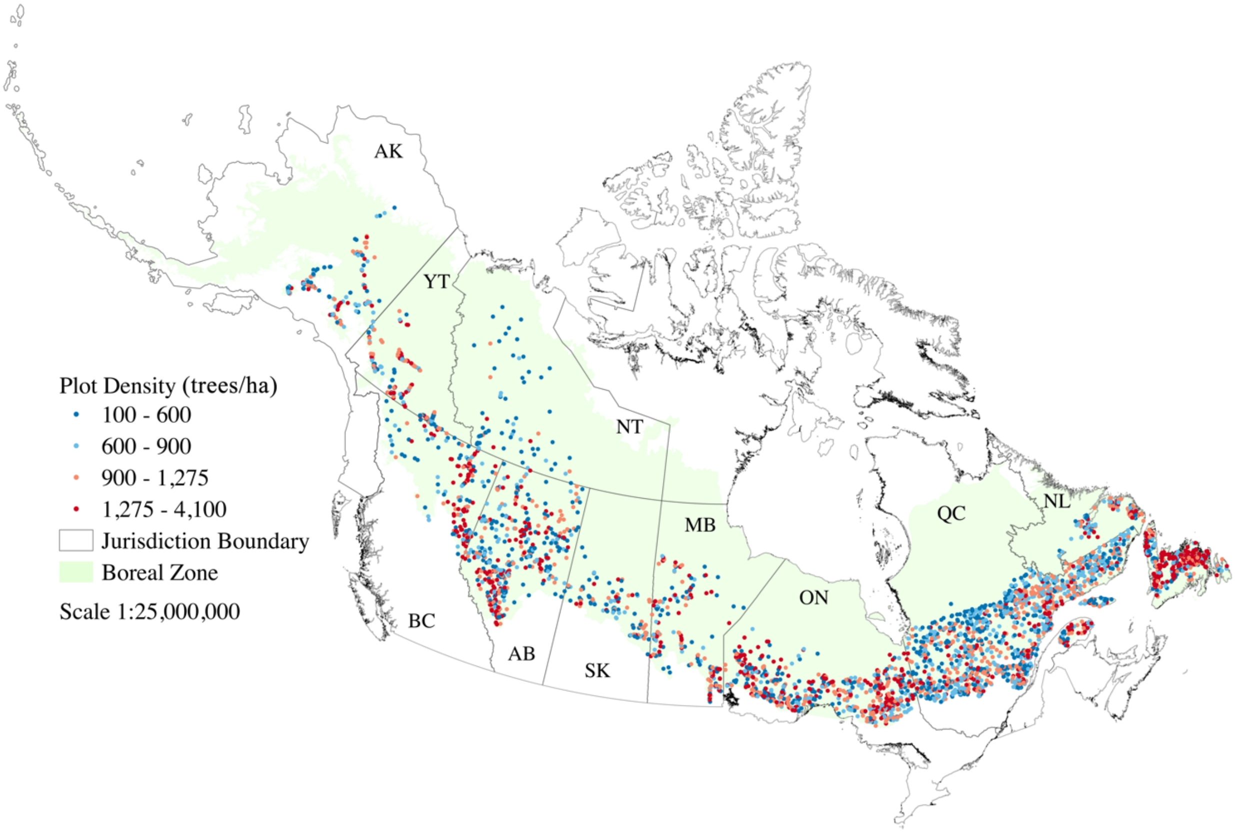

Fig. 4.1 Distribution of 4,367 plots in North American boreal zone (light green area; scaled at 1:25,000,000 for N40°, W55° – N90°, W180°). The observed tree density of these plots varies from 110 to 4,100 stems/ha (categorized into 4 blue-to-red gradients from the lowest to highest density). From the left to the right, the jurisdictions are Alaska (AK), Yukon (YT), British Columbia (BC), Northwest Territories (NT), Alberta (AB), Saskatchewan (SK), Manitoba (MB), Ontario (ON), Quebec (QC), and Newfoundland and Labrador (NL).

For each plot, the following data were compiled or calculated: (1) plot location (latitude, longitude and elevation), (2) stand height (mean height of the tallest 3 trees), and (3) the observed tree density (number of trees per ha; Fig. S1a). I also extracted plot canopy height data from the 2006 1-km global canopy height map (Simard et al. 2011). I compiled the same set of 20 explanatory variables of Crowther et al. (2015), that is, human development, six topographic, eight climatic and five vegetative variables. In this study, I included 13 additional bioclimatic variables (BIO; Hijmans et al. 2005) plus two stand height variables and the widely used normalized difference vegetation index (NDVI). The bioclimatic variables were 1970-2000 annual means and NDVI was 2000-2009 monthly mean. There were in total 36 explanatory variables in this study (see Table S5 for the descriptions of these variables, and Table S6 for a summary of them). In cases where data of the above variables were not available at the plot location, I set 10 km as the maximum radius in searching the nearest location where such data were available.

### 4.3.2 Modeling tree density

Any model aiming to describe stand tree density should consider factors that regulate stand density. For this purpose, I followed Crowther et al. (2015) to include human development, topography, vegetation and climate as predictors. I further included stand height as a proxy for competition because height as a measure of stand architecture plays a key role in controlling stand light condition (MacFarlane, Green and Burkhart 2000). My exploratory data analysis confirmed that stand height had a linear and quadratic relationship with stand density (Fig. S1b). In addition to its link to stand density, stand height was also one of the few stand architecture variables available in both ground measurement and airborne data. I thus proposed a linear mixed-effects model as:

$$y_{ij} = \beta_0 + \beta_1 ht_{ij} + \beta_2 {ht_{ij}}^2 + HUM_{ij} + TOPO_{ij} + VEG_{ij} + CLIM_{ij} + \Upsilon_j + \varepsilon_{ij}, \quad (1)$$

where $y_{ij}$ is tree density, $ht_{ij}$ is stand height, and $HUM_{ij}$, $TOPO_{ij}$, $VEG_{ij}$ and $CLIM_{ij}$ are sets of human development, topographic, vegetative and climatic variables of the $i^{\text{th}}$ plot from the $j^{\text{th}}$ jurisdiction, respectively. Note canopy height was not used for parameterizing the model. The random intercept term $\Upsilon_j$ (~1|*Jurisdiction*) was necessary for modeling the within-cluster (i.e., within jurisdiction) dependence of the plots (Hall and Bailey 2001). I detected heterogeneous variance in the residuals ($\varepsilon_{ij}$), and thus, I used a combined variance structure that included an exponential function for stand height, a power function for BIO6 and an exponential function for BIO8. The variance structure I used in the model was of the form: *varComb*(*varExp*(form = ~*ht*), *varPower*(form = ~BIO6), *varExp*(form = ~BIO8)). Stepwise model selection both forward and backward was conducted based on AIC values (Bozdogan 1987).

The mixed-effects model (1) was estimated using the density data of 4,367 plots. Multicollinearity was dealt with by screening pairwise Pearson's correlations with $R^2 > 0.9$ among the 36 explanatory variables and between stand height and the remaining 35 variables. None of the 35 variables was collinear with stand height, while eight climatic variables were excluded due to collinearities among them. Thus, the final dataset included BIO1, 2, 3, 5, 6, 7, 8, 9, 15, 16 and 17, aridity index and evapotranspiration as climatic variables, and all of the human development, topographic and vegetative variables plus stand height.

In addition to my model (1), two forms of Crowther et al.'s (2015) models were used in this study. One was their boreal biome model, which was estimated using data from 8,688 plots (346 from North America and the remaining from Scandinavia and Siberia), with tree density estimates extracted from their density map. The other was the model that included the same set of explanatory variables as their boreal biome model, but was refitted using data from the 4,367 plots in North America. My model (1) and Crowther et al.'s North American model were estimated using the *lme* function from the R package *nlme* (Pinheiro et al. 2022) in R 4.0.2 (https://www.r-project.org), and the spatial correlation of residuals was checked using the *Variogram* function from the same package.

### 4.3.3 Model validation

I assessed the adequacy of the three models, i.e., model (1), Crowther et al.'s boreal biome model and Crowther et al.'s North American refitted model. For each of the 4,367 plots, stand tree density was estimated by substituting stand height and the other data to the parameterized model (1). Two height data were used to estimate plot tree density: one was stand height (i.e., the mean height of the 3 tallest trees in each plot), and the other was canopy height (extracted from a global canopy height map; Simard et al. 2011). The reason that I also used canopy height for estimation was to test the utility of this globally available height data. I thus had two stand density estimates for each plot, one predicted from the stand height and the other from the canopy height, denoted as $\hat{y}_s$ and $\hat{y}_c$, respectively. There were also two density estimates from Crowther et al.'s biome model, denoted as $\hat{y}_G$ and $\hat{y}_{NA}$, where $\hat{y}_G$ was extracted from their published boreal density map (i.e., estimates of the boreal biome model) and $\hat{y}_{NA}$ was estimated from the refitted model to the 4,367 North American plots. For each of these four estimates ($\hat{y}_s$, $\hat{y}_c$, $\hat{y}_G$ and $\hat{y}_{NA}$), I evaluated their individual performances based on the following measures.

These measures include: (1) percent bias (%bias), calculated as $\frac{\sum_{i=1}^{n}(\hat{y}_i - y_i)}{\sum_{i=1}^{n} y_i} \times 100\%$ to assess estimation accuracy (positive %bias means overestimation, otherwise negative %bias); (2) $R^2$ between the observed and estimated density, also represented in heatscatter plots; (3) mean absolute error (MAE: $\frac{\sum_{i=1}^{n}|y_i - \hat{y}_i|}{n}$) and (4) root mean square error (RMSE: $\sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n}}$). In these formulas, *n* was the number of plots, $\hat{y}_i$ estimated density (either $\hat{y}_{s_i}$, $\hat{y}_{c_i}$, $\hat{y}_{G_i}$ or $\hat{y}_{NA_i}$), and $y_i$ the observed tree density of the *i*th plot. $\overline{\hat{y}}$ and $\bar{y}$ were the mean estimated and mean observed density of the *n* plots, respectively. MAE and RMSE are in the same unit as *y* (trees/ha).

To compare the spatial aggregations of the four estimates, I first applied the optimized Getis-Ord GI* hotspot analysis (Getis and Ord 2010) in ArcGIS 10.3 (https://www.arcgis.com) for the observed density and each estimate, respectively. Hot spots were defined as plots surrounded by high density plots falling in the upper 95th quantile, and vice versa for cold spots (Nelson and Boots 2008).

### 4.3.4 Mapping tree density and estimating tree abundance

Upon checking the utility of canopy height for estimating stand density, I mapped tree density estimated from canopy height (i.e., $\hat{y}_c$) at 1-km grid resolution (the same resolution as the global canopy height map) for the North American boreal zone defined by Brandt (2009). Note for non-forested areas where canopy height values did not exist, a density value of 0 was assigned. I also calculated the mean ($\bar{y}$), standard deviation (*SD*) and coefficient of variation ($CV = \frac{SD}{\bar{y}} \times 100\%$) of grid estimates from this map, as well as from Crowther et al.'s map ($\hat{y}_G$). These would allow me to compare the distributions of estimated densities of different models.

I estimated the total number of trees in North American boreal forest across all forested grids of my map as $\sum_{i=1}^{n}(\hat{y}_i \times s_i)$, where $s_i$ was the size (in ha) of the *i*th of all *n* grids. I repeated this estimation using Crowther et al.'s map. I further calculated the biomass equivalent to the estimated total number of trees in the region by multiplying each by 100.0 kg. This multiplier was the estimated aboveground biomass of an individual tree at the mean stand DBH, 17.0 cm, based on the Canadian national allometric biomass equation for all tree species (Ung, Bernier and Guo 2008). This calculation was conservative because of the power-law relation between aboveground biomass and DBH (i.e., larger trees weighed disproportionally more than smaller ones with respect to their DBH ratio; Ung, Bernier and Guo 2008), and because of unaccounted belowground biomass. Like Crowther et al. (2015), I also calculated the ratio of trees per person by dividing the total number of boreal trees in North America by the population size of the region (the sum of grid values from the Gridded Population of the World (GPWv4; https://sedac.ciesin.columbia.edu/data/collection/gpw-v4).

My last analysis was to project boreal tree density in 2050 under three emission scenarios assuming else being equal, e.g., no change in stand height and human development (though those factors are likely to change). The three emission scenarios were Representative Concentration Pathways (RCPs) 2.6, 4.5 and 8.5 for the moderate, intermediate and severe scenarios, respectively (Meinshausen et al. 2011). For each RCP, the climatic variables were averages of the 2050 projections by 23 General Circulation Models (GCMs; Table S4; Flato et al. 2014) from the ensembled CMIP5 climate data (30-arc-second spatial resolution; http://ccafs-climate.org/data_spatial_downscaling). Maps of tree density distribution and its change over the baseline (the current distribution) for the three emission scenarios were produced. Based on each map, I projected the total number of trees of North American boreal forest in 2050.

## 4.4 Results

The mean (± standard deviation) of observed tree density of the 4,367 plots was 991.6 ± 545.1, with a range of 110 – 4,100 trees/ha (Fig. S1a). The best selected model for stand tree density was:

$$\hat{y}_i = -157.82 + 152.32ht_i - 4.56{ht_i}^2 + 18.23\text{Eastness}_i + 661.53\text{NDVI}_i - 14.01\text{Dissimilarity}_i + 11.90\text{BIO6}_i - 8.42\text{BIO8}_i - 8.62\text{BIO9}_i,$$

where the predictors include *ht* (stand height), Eastness (sine of terrain aspect), NDVI (normalized difference vegetation index), Dissimilarity (of enhanced vegetation index; EVI), BIO6 (minimum temperature of coldest month), BIO8 (mean temperature of wettest quarter), and BIO9 (mean temperature of driest quarter). Further descriptions of this model including its random term and variance structure are presented in Table S8.

The performance tests showed that my model estimated tree density well, with smaller %bias, MAE and RMSE and higher $R^2$ than Crowther et al.'s models (Table 4.1). Although refitting Crowther et al.'s model exclusively to North American plot data improved its accuracy, the refitted model still performed poorly with a $R^2$ smaller than 0.1 (Table 4.1; Fig. S2). Although my model using canopy height as a predictor slightly overestimated the density by 3.4%, it outperformed Crowther et al.'s models by all other measures (Table 4.1). This confirms the usefulness of the global canopy height map (Simard et al. 2011) for estimating tree density distribution wherever data on ground tree height measures are not available.

Table 4.1 Comparison of tree density model performance. The estimated densities include the two estimated from my model (1) using stand height ($\hat{y}_s$) and canopy height ($\hat{y}_c$) and the two from Crowther et al.'s boreal biome model ($\hat{y}_G$) and the refitted North American model ($\hat{y}_{NA}$). The measures for model comparison include percent bias (%bias), $R^2$, mean absolute error (MAE) and root mean squared error (RMSE). The units of MAE and RMSE are trees/ha.

| Model (estimate) | %bias | $R^2$ | MAE | RMSE |
|---|---|---|---|---|
| Stand height ($\hat{y}_s$) | -0.6% | 0.22 | 367.6 | 480.9 |
| Canopy height ($\hat{y}_c$) | 3.4% | 0.16 | 389.7 | 500.8 |
| Crowther Biome ($\hat{y}_G$) | -32.3% | 0.03 | 473.3 | 635.5 |
| Crowther Refitted ($\hat{y}_{NA}$) | -0.2% | 0.09 | 405.7 | 521.0 |

My model estimated a total number of 351.3 billion trees in North American boreal forest, compared to 211.2 billion trees estimated from Crowther et al.'s biome model (Table 4.2). The underestimation of 140.1 billion trees by their model amounts to a missing of 14.0 trillion kg biomass. The ratio of trees per person was 67.9 thousand (351.3 billion trees divided by an estimated 5.17 million population in the region), 160 times higher than the global average that was 422 trees per person given by Crowther et al. (2015). The 1-km resolution tree density map with grid density ($\hat{y}_c$) for North American boreal forest is shown in Fig. 4.2. The spatial aggregation of hot and cold spots of the observed plot density, and of the estimated tree density by my model and Crowther et al.'s model are shown in Fig. S3.

I projected that the total number of trees in North American boreal forest in 2050 would be reduced by 4.8, 1.9 and 2.1 billion from the currently estimated 351.3 billion trees under the moderate (RCP2.6), intermediate (RCP4.5) and severe (RCP8.5) emission scenarios, respectively. The projected tree density maps show an overwhelming trend of decrease in tree density in the Canadian Prairies and the Pacific Northwest in 2050 (Fig. S4).

Table 4.2 Estimated total number of trees, mean, standard deviation and coefficient of variation (CV) of the 1-km grid tree density estimated from my model ($\hat{y}_c$) and Crowther et al.'s boreal biome model ($\hat{y}_G$) for North American boreal forest.

| Model (grid estimates) | Total number of trees (in billion) | Mean grid tree density (trees/ha) | Standard deviation (trees/ha) | CV (%) |
|---|---|---|---|---|
| My model ($\hat{y}_c$) | 351.3 | 577.0 | 364.7 | 63.2 |
| Crowther et al.'s boreal biome ($\hat{y}_G$) | 211.2 | 346.9 | 262.5 | 75.7 |

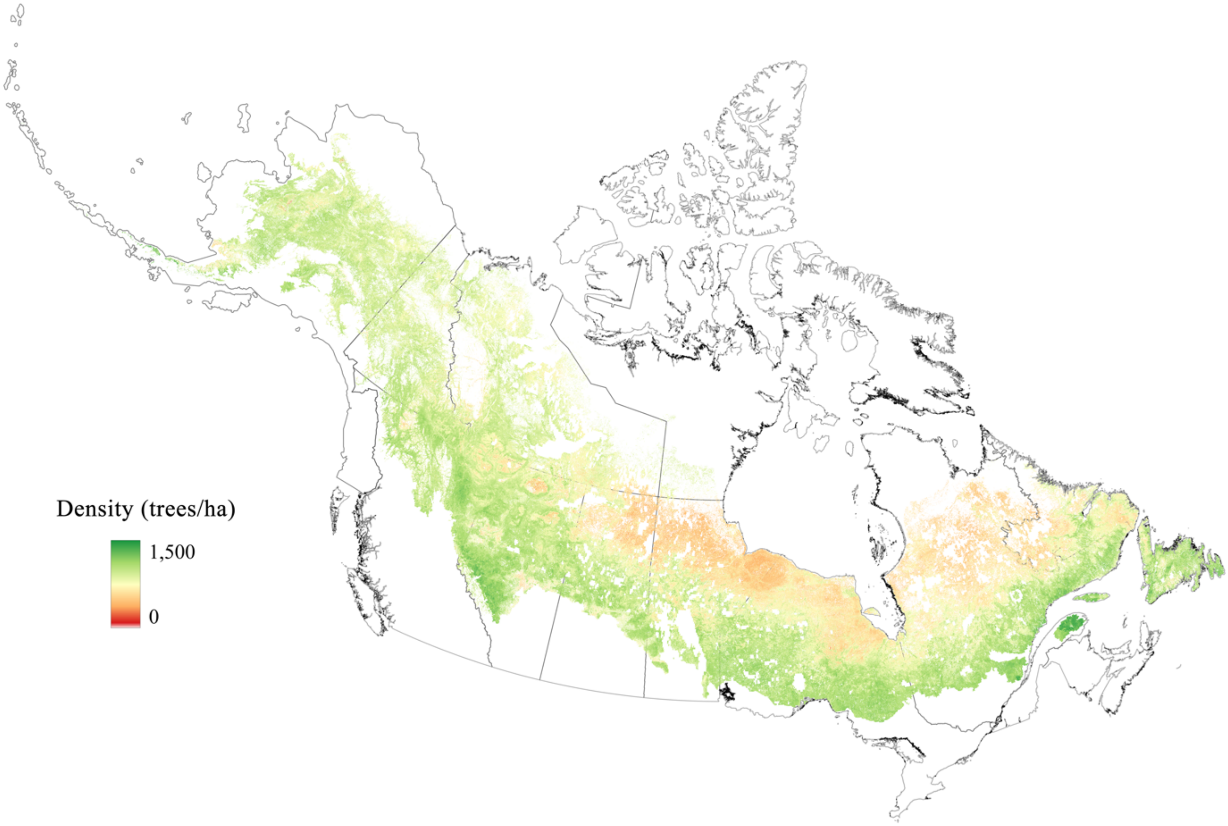

Fig. 4.2 Tree density map of North American boreal forest at 1-km resolution with grid density $\hat{y}_c$.

## 4.5 Discussion

Knowledge about tree density at local, regional and global scales is important for forest management, understanding functioning of forest ecosystems, and formulating resource-based climate mitigation policies. However, such knowledge is often not available at the regional and global scales. Crowther et al.'s (2015) was the first effort to estimate the global tree density at the biome scale. The performance of their model varied greatly, with density in some biomes estimated better than in others. The poor performance of their model for the boreal biome is not surprising given the large variation in density in the region as shown in their Fig. 1, this study (Table S6), and others (Gillis, Omule and Brierley 2005; Brandt 2009). Estimated from 4,367 plots in North America, my model (1) performed well as assessed by the goodness-of-fit measures (Table 4.1).

I estimated a total number of 351.3 billion trees in North American boreal forest, 140.1 billion (66.3%) higher than the number estimated from Crowther et al.'s model for the region (Table 4.2). The underestimation of 140.1 billion boreal trees in North America is equivalent to at least 14.0 trillion kg biomass (about 1,186 times the total emission of carbon dioxide equivalent due to deforestation in Canada in 2016; Natural Resources Canada 2018). If this level of underestimation also occurred in Scandinavian and Siberian boreal forests, after a correction, the expected number of trees globally in the boreal biome would be 1.23 trillion trees ($1.663 \times 0.74$; where 0.74 trillion was the number of global boreal trees given by Crowther et al. (2015)). This underestimation of 0.49 trillion boreal trees was equivalent to 16.1% of their estimate of 3.04 trillion global trees. How many trees there are on Earth remains uncertain, but the estimate provided by Crowther et al. (2015) of 3.04 trillion is probably low considering how many trees were already missing from boreal forests (according to the results of my proposed model).

The substantial improvement of my model over Crowther et al.'s is due to two reasons. The first one is ecological, by which I incorporated stand height into my model. Tree height is a key stand architecture that controls stand light condition (MacFarlane, Green and Burkhart 2000) and drives tree competition (Hart, Hart and Murphy 1989; MacFarlane, Green and Burkhart 2000) and thinning mortality (Westoby 1984; Reyes-Hernández and Comeau 2014). My model indeed identified stand height as the most important factor among the factors associated with tree density (Table S5). This revelation makes my model easier to interpret in mechanism. The second reason is statistical, by which I formulated my model as a mixed-effects model that allowed me to take into account the variation among jurisdictions in plot sampling design and in geography (Bonnor and Magnussen 1987; Gillis, Omule and Brierley 2005; Stadt, Schieck and

Stelfox 2006; Malone, Liang and Packee 2009). It is worth noting that this linear mixed-effects model does not impose any statistical burden compared to the multiple linear regression model of Crowther et al. (2015).

My model shows that the effect of stand height on tree density comes from linear and quadratic terms (Fig. S1b). These terms indicate that stand density initially increases with stand height but decreases as stand becomes taller. Empirical evidence shows that when stands are short, canopy space is ample and competition for light is low, in favor of an initial increase in density (MacFarlane, Green and Burkhart 2000; Xu et al. 2019). With growing stand height, competition for canopy space, light, and soil nutrients builds up (Huston 1980), intensifying self-thinning (Reyes-Hernández and Comeau 2014) and resulting in density decline. However, the overall relation between stand density and height might should not be specifically applied to infer stand height for maximum density due to highly varied abiotic and biotic stand conditions in North American boreal forests. In addition to stand height, my model also found plot eastness, NDVI, dissimilarity of EVI, and three bioclimatic variables (BIO6, 8 and 9) to be important. In contrast to Crowther et al. (2015), my model did not find plot latitude, elevation, northness, roughness, or EVI to be useful in predicting tree density. The reason the four plot topographic variables and EVI were not significant in my model could be that NDVI captured terrain vegetative variation more accurately than EVI in boreal forests (Chen 1996; Sulla-Menashe, Friedl and Woodcock 2016). Crowther et al. (2015) did not consider stand height nor NDVI. Besides these differences, my model predicted that higher minimum temperature of the coldest month (BIO6), lower temperature of the wettest quarter (BIO8) and lower temperature of the driest quarter (BIO9) were associated with higher tree density. This is expected as temperature is a major climatic factor related to tree growth, reproduction and mortality (Vayreda et al. 2012; Dulamsuren et al. 2013; Seidl et al. 2017; Lett and Dorrepaal 2018). Warmer winter (higher BIO6), cooler fall (lower BIO8) and milder summer (lower BIO9) stimulate boreal tree growth and reproduction (Vayreda et al. 2012; Lett and Dorrepaal 2018) while extreme cold (lower BIO6) or severe heat before snow (higher BIO8 and BIO9) would increase tree mortality (Seidl et al. 2017) and reduce seeding survival rates (Dulamsuren et al. 2013). Different from my model, mean annual temperature (BIO1) and mean precipitation of the driest quarter (BIO17) were selected in Crowther et al.'s boreal biome model. Human development was not significant in my model, which could be due to the relatively low population density in North American boreal zone (as both mean and median of human development of the 4,367 plots are 0; Table S6).

The three RCP emission scenarios showed varied degrees of change in tree density in 2050 (Fig. S4). The projected 2050 total numbers of trees in North American boreal forest were slightly lower than the 351.3 billion estimated from my current model. However, the projection of change in density (Fig. S4) is more complicated than a simple decrease in total number of trees. In general, tree density in the Canadian Prairies and the Northwest Pacific is expected to decrease in 2050, regardless of the RCP emission scenarios, while the density would increase in Eastern Canada (Fig. S4). It is important to note, however, this impact analysis only assumes "else being equal" but the change in emission scenarios. This space-for-time estimation should be interpreted with caution as the estimated effect of climatic variables on the spatial variation of tree density might change by time. In reality, many other factors, and even some key factors, could also change over the next 30 years. For example, human development may increase and stand tree height could also increase due to the warming climate.

Despite the effort made in this study, I identified that data availability and quality issues remain the major limitations to modeling tree density variation in boreal forests. First, the exact spatial coordinates of ABMI and NFI plots were not available to the public for the purpose of plot protection. Because of that, the spatial locations of ABMI and NFI plots are 10-km approximates to their published coordinates (Gillis, Omule and Brierley 2005; Stadt, Schieck and Stelfox 2006). This would inevitably increase uncertainty in density estimation regardless of which models are used. Second, there is a considerable spatial variation in the distribution of ground plots, with fewer or no plots in northern and remote forests (Franklin, Ahmed and Williams 2017). Third, although I confirmed the utility of canopy height for estimating density (Table 4.1), the estimation accuracy is subjected to the accuracy and resolution of canopy height data (as shown in Fig. S2). Also, LiDAR-based canopy height data are not as accurate as ground-measured stand height ($R^2 = 0.39$ between the two height variables of the 4,367 plots), especially at latitudes above 60°N due to extrapolation (Simard et al. 2011) and in boreal forests (Yang and Kondoh 2020). Fine-resolution canopy height data are not yet available for forests at high latitudes (e.g., 30-m canopy height data not yet available above 52°N; Potapov et al. 2021). Substituting canopy height in my proposed model to estimate grid tree density thus unavoidably introduced uncertainty that should not be ignored. Due to the lack of resources and logistic support, both ground and airborne data availability and quality in boreal forests are behind those in temperate and tropical forests, compromising our understanding of the functions and dynamics of boreal forests (Liang and Gamarra 2020). The same situation occurred when I attempted to include additional explanatory variables from data for dominant species and soil profile, which poorly aligned with plot records.

In conclusion, my model improves the estimation of boreal tree density in North America and sheds light on tree density of the global boreal biome. The maps of boreal tree density provide baseline data for modeling forest carbon stock and forest productivity, estimating forest biodiversity, and competition-driven dynamics of boreal forests. For example, hot and cold spots of plot density identified may inform the spatial aggregation of wood resources in Canada. The Government of Canada has made a commitment to planting 2 billion trees over the 2020-2030 decade as a nature-based climate solution (https://www.canada.ca/en/campaign/2-billion-trees.html). However, 2 billion planted trees only account for 0.57% of my estimated total number of 351.3 billion trees in North American boreal forest, speaking for the mitigation challenge through tree planting in the region. Considering the rapidly changing forest dynamics in boreal forests (Seppälä, Alexander and Katila 2009; D'Amato et al. 2011; Brecka, Shahi and Chen 2018), there is an urgent need for advanced and accurate models for effective adaptation and mitigation planning and policy-making.

## 4.6 References

Aussenac, G. (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57, 287-301.

Bonnor, G.M., Magnussen, S. (1987) Forest inventories in Canada: a framework for change. *The Forestry Chronicle*, 63, 193-198.

Bozdogan, H. (1987) Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. *Psychometrika,* 52, 345-370.

Brandt, J.P. (2009) The extent of the North American boreal zone. *Environmental Reviews,* 17, 101-161.

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

Chen, J.M. (1996) Evaluation of vegetation indices and a modified simple ratio for boreal applications. *Canadian Journal of Remote Sensing,* 22, 229-242.

Chen, L., Comita, L.S., Wright, S.J., Swenson, N.G., Zimmerman, J.K., Mi, X. *et al* (2018) Forest tree neighborhoods are structured more by negative conspecific density dependence than by interactions among closely related species. *Ecography*, 41, 1114-1123.

Clark, D.A., Clark, D.B (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *The American Naturalist*, 124, 769-788.

Crowther, T.W., Glick, H.B., Covey, K.R. *et al.* (2015) Mapping tree density at a global scale. *Nature,* 525, 201-205.

D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J. (2011) Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *Forest Ecology and Management,* 262, 803-816.

Dulamsuren, C., Wommelsdorf, T., Zhao, F., Xue, Y., Zhumadilov, B.Z., Leuschner, C., Hauck, M. (2013) Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of eastern Kazakhstan. *Ecosystems,* 16, 1536-1549.

Flato, G., Marotzke, J., Abiodun, B. *et al.* (2014) Evaluation of climate models. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (pp. 741-866). Cambridge University Press, Cambridge, UK.

Franklin, S.E., Ahmed, O.S., Williams, G. (2017) Northern conifer forest species classification using multispectral data acquired from an unmanned aerial vehicle. *Photogrammetric Engineering & Remote Sensing,* 83, 501-507.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G. (2015) Boreal forest health and global change. *Science,* 349, 819-822.

Getis, A., Ord, J.K. (2010) The analysis of spatial association by use of distance statistics. In: *Perspectives on Spatial Data Analysis.* (pp. 127-145). Springer, Berlin, Heidelberg.

Ghazoul, J., Liston, K.A., Boyle, T. (1998) Disturbance-induced density-dependent seed set in *Shorea siamensis (Dipterocarpaceae)*, a tropical forest tree. *Journal of Ecology*, 86, 462-473.

Gillis, M.D., Omule, A., Brierley, T. (2005) Monitoring Canada's forests: the national forest inventory. *The Forestry Chronicle*, 81, 214-221.

Gram, W.K., Sork, V.L. (2001) Association between environmental and genetic heterogeneity in forest tree populations. *Ecology*, 82, 2012-2021.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. *et al.* (1999) A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, 29, 824-839.

Hall, D.B., Bailey, R.L. (2001) Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. *Forest Science,* 47, 311-321.

Hart, T.B., Hart, J.A., Murphy, P.G. (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist*, 133, 613-633.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965-1978.

Huston, M. (1980) Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography*, 7, 147-157.

Kays, S., Harper, J. L. (1974) The regulation of plant and tiller density in a grass sward. *Journal of Ecology*, 62, 97-105.

Krajicek, J.E., Brinkman, K.A., Gingrich, S.F. (1961) Crown competition—a measure of density. *Forest Science*, 7, 35-42.

Lett, S., Dorrepaal, E. (2018) Global drivers of tree seedling establishment at alpine treelines in a changing climate. *Functional Ecology,* 32, 1666-1680.

Liang, J., Gamarra, J. G. (2020) The importance of sharing global forest data in a world of crises. *Scientific Data*, 7, 1-5.

Ma, Z., Peng, C., Zhu, Q. *et al.* (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences,* 109, 2423-2427.

MacFarlane, D.W., Green, E.J., Burkhart, H.E. (2000) Population density influences assessment and application of site index. *Canadian Journal of Forest Research,* 30, 1472-1475.

Malone, T., Liang, J., Packee, E.C. (2009) *Cooperative Alaska Forest Inventory*, General Technical Report PNW-GTR-785, USDA Forest Service, Pacific Northwest Research Station.

Meinshausen, M., Smith, S.J., Calvin, K., *et al.* (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change,* 109, 213-241.

Mohler, C. L., Marks, P. L., Sprugel, D. G. (1978) Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology*, 66, 599-614.

Natural Resources Canada (2018) *The State of Canada's Forests: Annual Report 2018*. Ottawa, ON, Canada

Nelson, T.A., Boots, B. (2008) Detecting spatial hot spots in landscape ecology. *Ecography,* 31, 556-566.

Peel, M.C., Finlayson, B.L., McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633-1644.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. (2022) Linear and nonlinear mixed effects models. R package 'nlme' version 3.1-155. https://cran.r-project.org/web/packages/nlme/index.html

Potapov, P., Li, X., Hernandez-Serna, A., *et al.* (2021) Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote Sensing of Environment,* 253, 112165.

Puettmann, K., Coates, K.D., Messier, C. (2009) *A Critique of Silviculture: Managing for Complexity*. Island Press, Washington, DC.

Reyes-Hernández, V., Comeau, P.G. (2014) Survival probability of white spruce and trembling aspen in boreal pure and mixed stands experiencing self-thinning. *Forest Ecology and Management*, 323, 105-113.

Seidl, R., Thom, D., Kautz, M., *et al.* (2017) Forest disturbances under climate change. *Nature Climate Change,* 7, 395-402.

Seppälä, R., Alexander, B., Katila, P. (2009) *Adaptation of forests and people to climate change: A global assessment report (No. 22)*. IUFRO World Series, International Union of Forestry Research Organizations (IUFRO), Helsinki, Finland.

Simard, M., Pinto, N., Fisher, J.B., Baccini, A. (2011) Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research: Biogeosciences,* 116, G04021.

Stadt, J.J., Schieck, J., Stelfox, H.A. (2006) Alberta Biodiversity Monitoring Program–monitoring effectiveness of sustainable forest management planning. *Environmental Monitoring and Assessment*, 121, 33-46.

Sugiyama, A., Comita, L. S., Masaki, T., Condit, R., Hubbell, S. P. (2018) Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species. *Ecology*, 99, 2583-2591.

Sulla-Menashe, D., Friedl, M.A., Woodcock, C.E. (2016) Sources of bias and variability in long-term Landsat time series over Canadian boreal forests. *Remote Sensing of Environment*, 177, 206-219.

Ter Steege, H., Pitman, N. C., Sabatier, D., Baraloto, C., Salomão, R. P., *et al.* (2013) Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092.

Tobner, C. M., Paquette, A., Reich, P. B., Gravel, D., Messier, C. (2014) Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, 174, 609-621.

Ung, C.H., Bernier, P., Guo, X.J. (2008) Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, 38, 1123-1132.

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Retana, J. (2012) Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. *Global Change Biology*, 18, 1028-1041.

Weiner, J., Stoll, P., Muller-Landau, H., Jasentuliyana, A. (2001) The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *The American Naturalist*, 158, 438-450.

Westoby, M. (1984) The self-thinning rule. *Advances in Ecological Research,* 14, 167-225.

White, J., Harper, J.L. (1970) Correlated changes in plant size and number in plant populations. *Journal of Ecology*, 58, 467-485.

Xu, Y., Li, C., Sun, Z., Jiang, L., Fang, J. (2019) Tree height explains stand volume of closed-canopy stands: Evidence from forest inventory data of China. *Forest Ecology and Management*, 438, 51-56.

Yang, W., Kondoh, A. (2020) Evaluation of the Simard et al. 2011 Global Canopy Height Map in Boreal Forests. *Remote Sensing,* 12, 1114.

# Chapter 5 Conclusion

The contribution of this thesis to forest ecology and management includes both conceptual components and technical advances. On the conceptual side, the proposal of climate-based tree allometric models in essence integrates the conventional allometric models with the concept of site condition, i.e., incorporating the climatic condition of local specific sites into the allometric models. Another example is the development of my tree density model by taking account of the effect of tree height regulated competition. The inclusion of competition makes the model mechanistic and improves its performance. On the technical side, my thesis quantifies how climate affects tree biomass allometries, plot fire hazards, and boreal forest stand density. I took innovative approaches (e.g., survival analysis to model fire hazards of long-term forest plots) to address my proposed objectives and led to important and sensible results, including that (1) failing to account for the variation in biomass allometries induced by climate change could result in 10% underestimation in aboveground biomass of two timber species in 2030, equivalent to a missing of 140 trillion kg biomass from the current calculation; (2) warming threatens the already short-lived PSPs in in Alberta (mean survival time 28.7 years) and would increase fire hazards of these plots in 2050 by 1.63 times higher than the current risk under the moderate emission scenario; and (3) both stand height and climate are important to tree density with height being a dominant factor driving density change. The tree density model developed in this thesis estimated 351.3 billion boreal trees in North America, 66.3% higher than a previous estimate in the literature. Below, I summarize the major findings of my thesis, state some limitations of the research and findings, and discuss possible future research directions following this thesis.

## 5.1 Major contributions

Supported by rigorous statistical methods and large forest datasets, my thesis addressed the three questions hypothesized in the objective Section 1.6. The major contributions are summarized in the following.

In Chapter 2, I tested the impacts of climate on tree allometric equations by building climate-based allometric models for five major Canadian timber species based on the biomass data used for estimating the allometric equations in Canada (conventional equations). I found that three species were insensitive to climate. The climate-based allometric models for trembling aspen and tamarack performed significantly better than the conventional equations. I identified that frost-free period and mean annual temperature were the significant climatic variables for the best models for trembling aspen and tamarack, respectively. Based on the climate-based models, under the moderate emission scenario, there would be a 10% underestimation in the aboveground biomass for the two species if the conventional equations were still in use in Canada in 2030. This chapter addresses the need to develop climate-based allometric models for more tree species to support forest growth and yield in Canada.

In Chapter 3, I quantified the risks of long-term forest plots under global warming by modeling fire hazards of permanent sample plots (PSPs). By thoroughly examining the fire records of 919 PSPs established since 1960 in Alberta, I compiled plot fire data and built Cox proportional hazards models for the survival time of these plots. Based on the selected model, I identified that the PSPs established more recently with lower tree species diversity and lower deciduous tree density suffered higher fire risks. The plots located in the Boreal ecoregion suffered 2.85 and 3.36 times higher fire risks than those in the Foothills and Rocky Mountain ecoregions, respectively. Under the moderate climate change scenario, the fire hazards of PSPs in Alberta was projected 1.63 times higher than the current level. These results inform challenges for maintaining long-term forest inventory plots as valuable data sources for sustainable management under intensified fire risks in face of climate change.

In Chapter 4, I incorporated stand height to improve the model based on 4,367 forest plots. My tree density model outperformed the biome model by every goodness-of-fit metric with a 0.6% underestimation and smaller errors. The new model estimated the total number of trees in the region as 351.3 billion, which was 140.1 billion more trees than previously estimated. These missing trees were equivalent to at least 14.0 trillion kg biomass. I also produced a 1-km resolution tree density map for North American boreal forests, and projected tree density distribution in 2050 under three emission scenarios. The improved tree density model, map and projections are informative for understanding boreal tree density variation and forest dynamics of North America under global change.

In addition to the above three major contributions, this thesis also addressed the need to incorporate climate into existing tree and forest models. It was also important to use the best available data to develop models for understanding tree growth, yield and density variation. To reduce uncertainty in our understanding of impacts of global change on forests, it is necessary to maintain existing long-term forest plots, increase sample coverage, develop proven models for quantifying key forest quantities (e.g., biomass, fire hazards, and stand density), projecting forest dynamics, and making management and policy decisions.

## 5.2 Limitations

It is worth noting that the scope of my thesis is on naturally occurring and growing stands, rather than recently regenerated stands, given plot data availability. Despite my effort in compiling the best available data, there are certain limitations in each data chapter, particularly from ground plots (Fortin 1983; Honer and Hegyi 1990; Hayden 1995; Alberta Forest Service 2000; Marshall, Lencar and Hassani 2000; Porter, MacLean and Beaton 2001; Townsend 2004; Stearns-Smith and Basaraba 2006; Malone, Liang and Packee 2009; Perron and Morin 2011; Bourgeois et al. 2018). Higher sampling errors were found in plot censuses during the mid 1950s than those censused more recently (Fortin 1983; Perron and Morin 2011). Meanwhile, a large proportion of plots established for forest growth and yield monitoring are located in young and dense forests (Honer and Hegyi 1990; Hayden 1995; Malone, Liang and Packee 2009). The impacts of the variation in those data qualities on data modeling and results are not known, but it is important to keep the issue in mind. For plot protection purposes, only approximate coordinates of ABMI and NFI plots were available for public use (Alberta Forest Service 2000; Gillis, Omule and Brierley 2005; Burrill et al. 2021). This approximation, if ignored, could result in substantial estimation biases (Bugmann 2001; Johnson 2006; Thompson et al. 2007; Newbold 2010; Neyeloff, Fuchs and Moreira 2012). Although I adopted the data processing methods following the literature (Peng et al. 2011; Chen and Luo 2015; Zhang, Huang and He 2015; Zhu et al. 2018), specific issues could still arise in each data chapter. In Chapter 2, the ENFOR biomass data were collected nearly 40 years ago by different researchers (Lambert, Ung and Raulier 2005; Ung, Bernier and Guo 2008), covering limited area (Fig. 2.1) and species (Table 2.1). These biomass data were less representative than data collected more recently for the tree biomass allometries under the decadal impact of climate warming. In Chapter 3, for forest monitoring purposes (Alberta Forest Service 2000), the 919 PSPs were not completely randomly sampled (Fig. 3.1). This increases uncertainty of the plot fire hazards model across the ecoregions. In Chapter 4, despite my extensive effort in compiling data from 4,367 plots, plot distribution was limited in northern forests (Fig. 4.1), increasing the estimation error in tree density of these stands.

In addition to plot data limitations, the availability, e.g., limited data for stand architecture, and quality of airborne data, e.g., climate and canopy height data, could be two other concerns. No airborne data other than canopy height were available for depicting stand architecture, such as stand mean DBH, age and composition, which might be more closely related to stand density than height (Burkhart and Yang 2022). If such data become available, the tree density model in Chapter 4 could be improved by trying to incorporate these key stand factors. On the other hand, the historical climate data used in Chapters 2 and 3 were at the 4-km resolution (Wang et al. 2016; Wang, Hamann and Spittlehouse 2019), lower than Daymet version 3 (Thornton et al. 2016) and WorldClim v2.1 (Hijmans et al. 2005) data. But these higher resolution data were not available for the complete sampling periods of the ENFOR (1978 – 1983) and Alberta PSP (1960 – 2020) plots. If the temporal coverages of Daymet or WorldClim data are extended in the future, models in Chapters 2 and 3 could be improved by fitting higher resolution climate data. Similar improvement for Chapter 4 could be achievable if fine resolution canopy height data were available in boreal forests. Canopy height data used in Chapter 4 were found only moderately correlated with ground measured stand height ($R^2 = 0.39$), and their quality for the region at above 60°N was low compared to that at lower latitudes. Data for historical fire events, forest dominant species, and soil profile aligned poorly with plot records on these variables, probably due to the lack of the accuracy of plot coordinates and the lack of fine resolution spatial data for such variables. In addition, data limitations also challenged projection. Extrapolation by projecting tree biomass, plot fire hazards and stand density for future climate scenarios should be interpreted with caution because the trends may not sustain the relationships identified in the models (Miller et al. 2004; Peters and Herrick 2004). Meanwhile, the space-for-time estimation in Chapter 4 for projected tree density in 2050 should also be interpreted with caution because of possible effects of changes in the other factors associated with density. Because of these limitations, planning for forest management based on projections in this thesis should be practiced prudently.

## 5.3 Future research directions

Future research may (1) expand research scales, (2) apply new analytical methods, and (3) extend spatial analyses to the spatiotemporal scope. The first step forward is to model more species in broader area. Following Chapter 2, climate-based allometric equations for at least 30 individual tree species in Canada remain to be modeled. Extended spatial representability of these allometric equations is also possible, such as building a regional climate-based allometric model for trembling aspen in Canada and northwestern USA (Mitton and Grant 1996; Jenkins et al. 2004; Lambert, Ung and Raulier 2005; Ung, Bernier and Guo 2008). The spatial coverage of Chapters 3 and 4 can also be extended. Extended plot fire hazards models could be built for western Canada (Weir, Johnson and Miyanishi 2000; Axelson, Alfaro and Hawkes 2009; Brown et al. 2017) and for the North American boreal zone (Girardin et al. 2013; Boucher et al. 2018). The tree density model and map can be extended to the entire North America and other continents by compiling national forest data, such as the US Forest Inventory and Analysis Program (FIA) data (Burrill et al. 2021).

Methods of this thesis can be applied to answer a wide range of questions, such as belowground biomass and height-age allometries (Yang et al. 2000), risks of other types of disturbances for plot maintenance (Charron and Hermanutz 2017; Audley et al. 2021), and other forest quantities such as carbon stock, $CO_2$ flux, growth and mortality rates, reproduction and regeneration (Vanderwel, Coomes and Purves 2013; Vanderwel et al. 2016; Zhu et al. 2018). This extension would provide deeper understanding of the impacts of global change on forest dynamics and support sustainable management of forests, as supplementary knowledge to the currently debates on net biomass change due to global change (Kirilenko and Sedjo 2007; Gauthier et al. 2015; Girardin et al. 2016; Burkhart and Yang 2022).

Last, our understanding of forest dynamics can be extended from the space-for-time perspective in Chapters 2 and 4 to the spatiotemporal dimension based on the repeated censuses from the unprecedented long-term forest data. Much work has already been done to model the temporal variation and trends in forest growth and mortality under global change (Peng et al. 2011; Ma et al. 2012; Chen and Luo 2015; Zhang, Huang and He 2015; Seidl et al. 2017; Zhang et al. 2018, Zhu et al. 2018; Searle and Chen 2020). The extension to spatial dimension of similar analyses would make forest dynamics study spatiotemporal and provide a more complete understanding in forest dynamics (Trumbore, Brando and Hartmann 2015). In sum, future studies can focus on widening the research scale, applying innovative analytical methods, and extending the spatiotemporal dimension, following this thesis.

## 5.4 References

Alberta Agriculture and Forestry (2016). *Alberta Government Forestry Permanent Sample Plots Stand Dynamics System, Alberta Forest Service and Forest Management Branch Types Re-Measurement, Maintenance and Establishment Procedures.* Alberta Agriculture and Forestry Edmonton, Alberta.

Alberta Forest Service (2000). *Permanent Sample Plot Field Procedures Manual.* Alberta Forest Service Edmonton, Alberta.

Audley, J.P., Fettig, C.J., Munson, A.S., Runyon, J.B., Mortenson, L.A., Steed, B.E. *et al.* (2021). Dynamics of beetle-killed snags following mountain pine beetle outbreaks in lodgepole pine forests. *Forest Ecology and Management*, 482, 118870.

Axelson, J.N., Alfaro, R.I. & Hawkes, B.C. (2009). Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management*, 257, 1874-1882.

Boucher, D., Boulanger, Y., Aubin, I., Bernier, P.Y., Beaudoin, A., Guindon, L. *et al.* (2018). Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. *Ecological Applications*, 28, 1245-1259.

Bourgeois, W., Binkley, C., LeMay, V., Moss, I. & Reynolds, N. (2018). *British Columbia Forest Inventory Review Panel Technical Background Report*. British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development.

Brown, K.J., Hebda, N.J., Conder, N., Golinski, K.G., Hawkes, B., Schoups, G. *et al.* (2017). Changing climate, vegetation, and fire disturbance in a sub-boreal pine-dominated forest, British Columbia, Canada. *Canadian Journal of Forest Research*, 47, 615-627.

Bugmann, H. (2001). A review of forest gap models. *Climatic Change*, 51, 259-305.

Burkhart, H. E., & Yang, S. I. (2022). A retrospective comparison of carrying capacity of two generations of loblolly pine plantations. *Forest Ecology and Management*, 504, 119834.

Burrill, E.A., DiTommaso, A.M., Turner, J.A., Pugh, S.A., Menlove, J., Christiansen, G. *et al.* (2021). *The Forest Inventory and Analysis Database: database description and user guide version 9.0 for Phase 2*. U.S. Department of Agriculture Forest Service.

Charron, L. & Hermanutz, L. (2017). Simplicity is key: Restoration protocols for nonregenerating forests degraded by overabundant herbivores. *Restoration Ecology*, 25, 432-441.

Chen, H.Y.H. & Luo, Y. (2015). 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.

Fortin, J. (1983). *Les placettes-échantillons permanentes et leurs utilisations.* Ministère de l'énergie et des ressources, Gouvernement du Québec, Quebec.

Gillis, M.D., Omule, A.Y. & Brierley, T. (2005). Monitoring Canada's forests: the national forest inventory. *The Forestry Chronicle*, 81, 214-221.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest health and global change. *Science*, 349, 819-822.

Girardin, M.P., Ali, A.A., Carcaillet, C., Gauthier, S., Hély, C., Le Goff, H. *et al.* (2013). Fire in managed forests of eastern Canada: Risks and options. *Forest Ecology and Management*, 294, 238-249.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M. *et al.* (2016). No growth stimulation of Canada’s boreal forest under half-century of combined warming and $CO_2$ fertilization. *Proceedings of the National Academy of Sciences*, 113, E8406-E8414.

Hayden, J. (1995). *Ontario forest growth and yield program: field manual for establishing and measuring permanent sample plots*. Ontario.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 25, 1965-1978.

Honer, T.G. & Hegyi, F. (1990). Forest Inventory—Growth and Yield in Canada: Past, Present and Future. *The Forestry Chronicle*, 66, 112-119.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. & Birdsey, R.A. (2004). *Comprehensive database of diameter-based biomass regressions for North American tree species.* USDA Forest Service, Northeastern Research Station. Gen.Tech.Rep.NE-GTR-319.

Johnson, D.W. (2006). Progressive N limitation in forests: review and implications for long-term responses to elevated CO2. *Ecology*, 87, 64-75.

Kirilenko, A. P., & Sedjo, R. A. (2007). Climate change impacts on forestry. *Proceedings of the National Academy of Sciences*, 104, 19697-19702.

Lambert, M.C., Ung, C.H. & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research*, 35, 1996-2018.

Malone, T., Liang, J. & Packee, E.C. (2009). *Cooperative Alaska forest inventory*. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Marshall, P.L., Lencar, C. & Hassani, B. (2000). *Review of PSP Systems Employed Outside of British Columbia*. Vancouver, BC.

Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L. & Stanley, E.H. (2004). Spatial extrapolation: the science of predicting ecological patterns and processes. *Bioscience*, 54, 310-320.

Mitton, J.B. & Grant, M.C. (1996). Genetic variation and the natural history of quaking aspen. *Bioscience*, 46, 25-31.

Newbold, T. (2010). Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography*, 34, 3-29.

Neyeloff, J.L., Fuchs, S.C. & Moreira, L.B. (2012). Meta-analyses and Forest plots using a Microsoft Excel spreadsheet: step-by-step guide focusing on descriptive data analysis. *BMC Research Notes*, 5, 1-6.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W. *et al.* (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1, 467-471.

Perron, J. & Morin, P. (2011). *Normes d'inventaire forestier: Placettes-échantillons permanentes.* Ministry of Forests: Quebec, QC, Canada.

Peters, D.P.C. & Herrick, J.E. (2004). Strategies for ecological extrapolation. *Oikos*, 106, 627-636.

Porter, K.B., MacLean, D.A., Beaton, K.P. & Upshall, J. (2001). *New Brunswick Permanent Sample Plot Database (PSPDB v1. 0)*. NB.

Stearns-Smith, S., Cf, R.P.F. & Basaraba, D. (2006). *Provincial PSP Remeasurement Priorities (BC's PSP Strategy Revisited).* Ministry of Forests, Range Sooke, B.C.

Thompson, I.D., Maher, S.C., Rouillard, D.P., Fryxell, J.M. & Baker, J.A. (2007). Accuracy of forest inventory mapping: Some implications for boreal forest management. *Forest Ecology and Management*, 252, 208-221.

Thornton, P.E., Thornton, M.M., Mayer, B.W., Wei, Y., Devarakonda, R., Vose, R.S. *et al.* (2016). Daymet: daily surface weather data on a 1-km grid for North America, version 3. ORNL DAAC, Oak Ridge, Tennessee, USA. In: *USDA-NASS, 2019. 2017 Census of Agriculture, Summary and State Data, Geographic Area Series, Part 51, AC-17-A-51*.

Townsend, P. (2004). *Nova Scotia forest inventory based on permanent sample plots measured between 1999 and 2003.* Report FOR 2004-3. Nova Scotia Department of Natural Resources, Truro, NS.

Ung, C.-H., Bernier, P. & Guo, X.-J. (2008). Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, 38, 1123-1132.

Vanderwel, M. C., Coomes, D. A., & Purves, D. W. (2013). Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology*, 19, 1504-1517.

Vanderwel, M. C., Zeng, H., Caspersen, J. P., Kunstler, G., & Lichstein, J. W. (2016). Demographic controls of aboveground forest biomass across North America. *Ecology Letters*, 19, 414-423.

Wang, T., Hamann, A. & Spittlehouse, D. (2019). ClimateNA v6.20. BC.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11, e0156720.

Weir, J.M.H., Johnson, E.A. & Miyanishi, K. (2000). Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. *Ecological Applications*, 10, 1162-1177.

Yang, Y., Huang, S., Vassov, R., Pinno, B. & Chhin, S. (2020). Climate-sensitive height–age models for top height trees in natural and reclaimed oil sands stands in Alberta, Canada. *Canadian Journal of Forest Research*, 50, 297-307.

Zhang, J., Huang, S. & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, 112, 4009-4014.

Zhu, K., Zhang, J., Niu, S., Chu, C. & Luo, Y. (2018). Limits to growth of forest biomass carbon sink under climate change. *Nature Communications*, 9, 1-8.

# Bibliography

Ahokas, E., Kaartinen, H. & Hyyppä, J. (2003). A quality assessment of airborne laser scanner data. *International Archives of Photogrammetry and Remote Sensing*, 34, W13.

Alberta Agriculture and Forestry (2015). *Minimum Standards and Suggested Protocol and Priorities for Establishing and Measuring Permanent Sample Plots in Alberta.* Forest Management Branch, Alberta Agriculture and Forestry, Edmonton, Alberta.

Alberta Agriculture and Forestry (2016). *Alberta Government Forestry Permanent Sample Plots Stand Dynamics System, Alberta Forest Service and Forest Management Branch Types Re-Measurement, Maintenance and Establishment Procedures.* Alberta Agriculture and Forestry Edmonton, Alberta.

Alberta Forest Service (2000). *Permanent Sample Plot Field Procedures Manual.* Alberta Forest Service Edmonton, Alberta.

Altrell, D. (2019). Multipurpose National Forest Inventory in Mongolia, 2014-2017-A tool to support sustainable forest management. *Geography, Environment, Sustainability*, 12, 167-183.

Álvarez-Dávila, E., Cayuela, L., González-Caro, S., Aldana, A.M., Stevenson, P.R., Phillips, O. *et al.* (2017). Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS One*, 12, e0171072.

Ameray, A., Bergeron, Y., Valeria, O., Montoro Girona, M., & Cavard, X. (2021). Forest carbon management: A review of silvicultural practices and management strategies across boreal, temperate and tropical forests. *Current Forestry Reports*, 7, 245-266.

Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Joseph Wright, S., et al. & Zimmerman, J. (2015). CTFS-Forest GEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21, 528-549.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R. *et al.* (1993). Boreal forests and tundra. *Water, Air, and Soil Pollution*, 70, 39-53.

Arlot, S. & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys*, 4, 40-79.

Audley, J.P., Fettig, C.J., Munson, A.S., Runyon, J.B., Mortenson, L.A., Steed, B.E. *et al.* (2021). Dynamics of beetle-killed snags following mountain pine beetle outbreaks in lodgepole pine forests. *Forest Ecology and Management*, 482, 118870.

Aussenac, G. (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57, 287-301.

Axelson, J.N., Alfaro, R.I. & Hawkes, B.C. (2009). Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management*, 257, 1874-1882.

Baek H, Lee J, Lee H *et al.* (2013) Climate change in the 21st century simulated by HadGEM2-AO under representative concentration pathways. *Asia-Pacific Journal of Atmospheric Sciences,* 49, 603-618.

Baker, T.R., Vicuña Miñano, E., Banda-R, K., del Castillo Torres, D., Farfan-Rios, W., Lawson, I.T. *et al.* (2021). From plots to policy: How to ensure long-term forest plot data supports environmental management in intact tropical forest landscapes. *Plants, People, Planet*, 3, 229-237.

Balshi, M.S., McGuire, A.D., Duffy, P., Flannigan, M., Kicklighter, D.W. & Melillo, J. (2009). Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century. *Global Change Biology*, 15, 1491-1510.

Beaubien, E.G. & Freeland, H.J. (2000). Spring phenology trends in Alberta, Canada: links to ocean temperature. *International Journal of Biometeorology*, 44, 53-59.

Bellouin N, Collins WJ, Culverwell ID *et al.* (2011) The HadGEM2 family of met office unified model climate configurations. *Geoscientific Model Development,* 4, 723-757.

Bentsen M, Bethke I, Debernard JB *et al.* (2013) The Norwegian Earth System Model, NorESM1-M–Part 1: description and basic evaluation of the physical climate. *Geoscientific Model Development,* 6, 687-720.

Bergeron, Y., Richard, P.J.H., Carcaillet, C., Gauthier, S., Flannigan, M. & Prairie, Y.T. (1998). Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. *Conservation Ecology*, 2, 2.

Besnard, S., Koirala, S., Santoro, M., Weber, U., Nelson, J., Gütter, J., et al. & Carvalhais, N. (2021). Mapping global forest age from forest inventories, biomass and climate data. *Earth System Science Data Discussions*, 13, 4881-4896.

Beverly, J.L. (2017). Time since prior wildfire affects subsequent fire containment in black spruce. *International Journal of Wildland Fire*, 26, 919-929.

Beverly, J.L. & McLoughlin, N. (2019). Burn probability simulation and subsequent wildland fire activity in Alberta, Canada–Implications for risk assessment and strategic planning. *Forest Ecology and Management*, 451, 117490.

Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., et al. & Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339-345.

Bogdanski, B.E.C. (2008). *Canada's Boreal Forest Economy: Economic and Socioeconomic Issues and Research Opportunities*. Pacific Forestry Centre, Victoria, B.C.

Bonan, G. B., Pollard, D., & Thompson, S. L. (1992). Effects of boreal forest vegetation on global climate. *Nature*, 359, 716-718.

Bonnor, G.M., Magnussen, S. (1987) Forest inventories in Canada: a framework for change. *The Forestry Chronicle*, 63, 193-198.

Bond-Lamberty, B., Rocha, A.V., Calvin, K., Holmes, B., Wang, C. & Goulden, M.L. (2014). Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Global Change Biology*, 20, 216-227.

Boucher, D., Boulanger, Y., Aubin, I., Bernier, P.Y., Beaudoin, A., Guindon, L. *et al.* (2018). Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. *Ecological Applications*, 28, 1245-1259.

Boulanger, Y., Gauthier, S. & Burton, P.J. (2014). A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research*, 44, 365-376.

Bourgeois, W., Binkley, C., LeMay, V., Moss, I. & Reynolds, N. (2018). *British Columbia Forest Inventory Review Panel Technical Background Report*. British Columbia Ministry of Forests, Lands. Natural Resource Operations and Rural Development.

Bouriaud, O., Bréda, N., Le Moguedec, G. & Nepveu, G. (2004). Modelling variability of wood density in beech as affected by ring age, radial growth and climate. *Trees*, 18, 264-276.

Bozdogan H (1987) Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. *Psychometrika,* 52, 345-370.

Brandt JP (2009) The extent of the North American boreal zone. *Environmental*

*Reviews,* 17, 101-161.

Brecka AF, Shahi C, Chen HY (2018) Climate change impacts on boreal forest timber supply. *Forest Policy and Economics,* 92, 11-21.

Brown, K.J., Hebda, N.J., Conder, N., Golinski, K.G., Hawkes, B., Schoups, G. *et al.* (2017). Changing climate, vegetation, and fire disturbance in a sub-boreal pine-dominated forest, British Columbia, Canada. *Canadian Journal of Forest Research*, 47, 615-627.

Buechling, A., Martin, P.H. & Canham, C.D. (2017). Climate and competition effects on tree growth in Rocky Mountain forests. *Journal of Ecology*, 105, 1636-1647.

Bugmann, H. (2001). A review of forest gap models. *Climatic Change*, 51, 259-305.

Burgess, D., & Robinson, C. (1998). Canada's oldest permanent sample plots—thinning in white and red pine. *The Forestry Chronicle*, 74, 606-616.

Burkhart, H. E., & Yang, S. I. (2022). A retrospective comparison of carrying capacity of two generations of loblolly pine plantations. *Forest Ecology and Management*, 504, 119834.

Burrill, E.A., DiTommaso, A.M., Turner, J.A., Pugh, S.A., Menlove, J., Christiansen, G. *et al.* (2021). *The Forest Inventory and Analysis Database: database description and user guide version 9.0 for Phase 2.* U.S. Department of Agriculture, Forest Service.

Burton, P.J., Messier, C., Adamowicz, W.L. & Kuuluvainen, T. (2006). Sustainable management of Canada's boreal forests: progress and prospects. *Ecoscience*, 13, 234-248.

Case, B.S. & Hall, R.J. (2008). Assessing prediction errors of generalized tree biomass and volume equations for the boreal forest region of west-central Canada. *Canadian Journal of Forest Research*, 38, 878-889.

Chang, K.-t. & Tsai, B.-w. (1991). The effect of DEM resolution on slope and aspect mapping. *Cartography and Geographic Information Systems*, 18, 69-77.

Charron, L. & Hermanutz, L. (2017). Simplicity is key: Restoration protocols for nonregenerating forests degraded by overabundant herbivores. *Restoration Ecology*, 25, 432-441.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C. *et al.* (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20, 3177-3190.

Chave, J., Davies, S.J., Phillips, O.L., Lewis, S.L., Sist, P., Schepaschenko, D. *et al.* (2019). Ground data are essential for biomass remote sensing missions. *Surveys in Geophysics*, 40, 863-880.

Chen, H.Y.H. & Luo, Y. (2015). 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., Luo, Y., Reich, P.B., Searle, E.B. & Biswas, S.R. (2016). Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecology Letters*, 19, 1150-1158.

Chen JM (1996) Evaluation of vegetation indices and a modified simple ratio for boreal applications. *Canadian Journal of Remote Sensing,* 22, 229-242.

Chen, L., Comita, L.S., Wright, S.J., Swenson, N.G., Zimmerman, J.K., Mi, X. *et al.* (2018). Forest tree neighborhoods are structured more by negative conspecific density dependence than by interactions among closely related species. *Ecography*, 41, 1114-1123.

Choat, B., Ball, M.C., Luly, J.G. & Holtum, J.A.M. (2005). Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees*, 19, 305-311.

Chojnacky, D.C., Heath, L.S. & Jenkins, J.C. (2014). Updated generalized biomass equations for North American tree species. *Forestry*, 87, 129-151.

Chylek P, Li J, Dubey MK, Wang M, Lesins G (2011) Observed and model simulated 20th century Arctic temperature variability: Canadian earth system model CanESM2. *Atmospheric Chemistry and Physics Discussions,* 11, 22893-22907.

Clark, D.A., Clark, D.B. (1984). Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *The American Naturalist*, 124, 769-788.

Cleveland WS (1981) LOWESS: A Program for Smoothing Scatterplots by Robust Locally Weighted Regression. *The American Statistician,* 35, 54.

Clough, B.J., Curzon, M.T., Domke, G.M., Russell, M.B. & Woodall, C.W. (2017). Climate-driven trends in stem wood density of tree species in the eastern United States: Ecological impact and implications for national forest carbon assessments. *Global Ecology and Biogeography*, 26, 1153-1164.

Condit, R., Sukumar, R., Hubbell, S. P., & Foster, R. B. (1998). Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist*, 152, 495-509.

Condit, R., Lao, S., Singh, A., Esufali, S. & Dolins, S. (2014). Data and database standards for permanent forest plots in a global network. *Forest Ecology and Management*, 316, 21-31.

Cortini, F. & Comeau, P.G. (2020). Pests, climate and competition effects on survival and growth of trembling aspen in western Canada. *New Forests*, 51, 175-190.

Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C., Maynard, D.S., Thomas, S.M. *et al.* (2015). Mapping tree density at a global scale. *Nature*, 525, 201-205.

Cumming, S.G. (2001). Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological Applications*, 11, 97-110.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H. *et al.* (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, 28, 2031-2064.

D'Amato AW, Bradford JB, Fraver S, Palik BJ (2011) Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *Forest Ecology and Management,* 262, 803-816.

Davies, S. J., Abiem, I., Salim, K. A., Aguilar, S., Allen, D., Alonso, A., et al. & Yap, S. L. (2021). ForestGEO: Understanding forest diversity and dynamics through a global observatory network. *Biological Conservation*, 253, 108907.

De Groot, W.J., Bothwell, P.M., Carlsson, D.H. & Logan, K.A. (2003). Simulating the effects of future fire regimes on western Canadian boreal forests. *Journal of Vegetation Science*, 14, 355-364.

Duchesne, L., Ouimet, R., Moore, J.-D. & Paquin, R. (2005). Changes in structure and composition of maple–beech stands following sugar maple decline in Québec, Canada. *Forest ecology and Management*, 208, 223-236.

Dulamsuren C, Wommelsdorf T, Zhao F, Xue Y, Zhumadilov BZ, Leuschner C, Hauck M (2013) Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of eastern Kazakhstan. *Ecosystems,* 16, 1536-1549.

Dutcă, I., Stăncioiu, P.T., Abrudan, I.V. & Ioraş, F. (2018). Using clustered data to develop biomass allometric models: The consequences of ignoring the clustered data structure. *PLoS One*, 13, e0200123.

Ecological Stratification Working Group. (1996). *A National Ecological Framework for Canada.* Environment Canada Ottawa, Ontario.

Fan, J. & Li, R. (2002). Variable selection for Cox's proportional hazards model and frailty model. *Annals of Statistics*, 30, 74-99.

Fang, J., Guo, Z., Hu, H., Kato, T., Muraoka, H. & Son, Y. (2014). Forest biomass carbon sinks in East Asia, with special reference to the relative contributions of forest expansion and forest growth. *Global Change Biology*, 20, 2019-2030.

FAO & UNEP (2020). *The State of the World's Forests 2020: Forests, biodiversity and people.* Rome.

Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000). Climate change and forest fires. *Science of the Total Environment*, 262, 221-229.

Flato G, Marotzke J, Abiodun B *et al.* (2014) Evaluation of climate models. In: *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (pp. 741-866). Cambridge University Press, Cambridge, UK.

Fortin, J. (1983). *Les placettes-échantillons permanentes et leurs utilisations.* Ministère de l'énergie et des ressources, Gouvernement du Québec, Quebec.

Franklin SE, Ahmed OS, Williams G (2017) Northern conifer forest species classification using multispectral data acquired from an unmanned aerial vehicle. *Photogrammetric Engineering & Remote Sensing,* 83, 501-507.

Frelich, L.E., Jõgiste, K., Stanturf, J.A., Parro, K. & Baders, E. (2018). Natural disturbances and forest management: interacting patterns on the landscape. In: *Ecosystem Services from Forest Landscapes*. Springer, pp. 221-248.

Friedrichs, D.A., Trouet, V., Buentgen, U., Frank, D.C., Esper, J., Neuwirth, B. *et al.* (2009). Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees-Structure and Function*, 23, 729-739.

Fu, C., Yang, W., Tan, B., Xu, Z., Zhang, Y., Yang, J. *et al.* (2017). Seasonal Dynamics of Litterfall in a sub-alpine spruce-fir forest on the Eastern Tibetan Plateau: Allometric scaling relationships based on one year of observations. *Forests*, 8, 314.

Fu, L., Lei, X., Hu, Z., Zeng, W., Tang, S., Marshall, P. *et al.* (2017). Integrating regional climate change into allometric equations for estimating tree aboveground biomass of Masson pine in China. *Annals of Forest Science*, 74, 42.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest health and global change. *Science*, 349, 819-822.

Gent PR, Danabasoglu G, Donner LJ, Holland MM, Hunke EC, Jayne SR, Lawrence DM, Neale RB, Rasch PJ, Vertenstein M, Worley PH (2011) The community climate system model version 4. *Journal of Climate*, 24, 4973-4991.

Getis A, Ord JK (2010) The analysis of spatial association by use of distance statistics. In: *Perspectives on Spatial Data Analysis.* (pp. 127-145). Springer, Berlin, Heidelberg.

Ghazoul, J., Liston, K.A., Boyle, T. (1998). Disturbance-induced density-dependent seed set in *Shorea siamensis (Dipterocarpaceae)*, a tropical forest tree. *Journal of Ecology*, 86, 462-473.

Gillis, M.D., Omule, A., Brierley, T. (2005). Monitoring Canada's forests: the national forest inventory. *The Forestry Chronicle*, 81, 214-221.

Giorgetta MA, Jungclaus J, Reick CH, Legutke S, Bader J, Böttinger M *et al.* (2013) Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *Journal of Advances in Modeling Earth Systems*, 5, 572-597.

Girardin, M.P., Ali, A.A., Carcaillet, C., Gauthier, S., Hély, C., Le Goff, H. *et al.* (2013). Fire in managed forests of eastern Canada: Risks and options. *Forest Ecology and Management*, 294, 238-249.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M. *et al.* (2016). No growth stimulation of Canada's boreal forest under half-century of combined warming and $CO_2$ fertilization. *Proceedings of the National Academy of Sciences*, 113, E8406-E8414.

Goodman, R.C., Phillips, O.L. & Baker, T.R. (2014). The importance of crown dimensions to improve tropical tree biomass estimates. *Ecological Applications*, 24, 680-698.

Gram, W.K., Sork, V.L. (2001). Association between environmental and genetic heterogeneity in forest tree populations. *Ecology*, 82, 2012-2021.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. *et al.* (1999). A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, 29, 824-839.

Gu H, Yu Z, Wang J *et al.* (2015) Assessing CMIP5 general circulation model simulations of precipitation and temperature over China. *International Journal of Climatology,* 35, 2431-2440.

Hall, D.B., Bailey, R.L. (2001) Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. *Forest Science,* 47, 311-321.

Hame, T., Salli, A., Andersson, K. & Lohi, A. (1997). A new methodology for the estimation of biomass of conifer-dominated boreal forest using NOAA AVHRR data. *International Journal of Remote Sensing*, 18, 3211-3243.

Hanes, C.C., Wang, X., Jain, P., Parisien, M.-A., Little, J.M. & Flannigan, M.D. (2019). Fire-regime changes in Canada over the last half century. *Canadian Journal of Forest Research*, 49, 256-269.

Hart, T.B., Hart, J.A., Murphy, P.G. (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist*, 133, 613-633.

Hayden, J. (1995). *Ontario Forest Growth and Yield Program: Field manual for establishing and measuring permanent sample plots*. Ontario.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965-1978.

Hogg, E.H. & Schwarz, A.G. (1997). Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. *Journal of Biogeography*, 24, 527-534.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017). Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology*, 23, 5297-5308.

Honer, T.G. & Hegyi, F. (1990). Forest Inventory—Growth and Yield in Canada: Past, Present and Future. *The Forestry Chronicle*, 66, 112-119.

Houghton, R.A. (2005). Aboveground forest biomass and the global carbon balance. *Global Change Biology*, 11, 945-958.

Hourdin F, Foujols M, Codron F *et al.* (2013) Impact of the LMDZ atmospheric grid configuration on the climate and sensitivity of the IPSL-CM5A coupled model. *Climate Dynamics,* 40, 2167-2192.

Huston, M. (1980). Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography*, 7, 147-157.

Hyyppä, J., Hyyppä, H., Leckie, D., Gougeon, F., Yu, X. & Maltamo, M. (2008). Review of methods of small-footprint airborne laser scanning for extracting forest inventory data in boreal forests. *International Journal of Remote Sensing*, 29, 1339-1366.

Jarvis, P., & Linder, S. (2000). Constraints to growth of boreal forests. *Nature*, 405, 904-905.

Jeffrey S, Syktus J (2011) The CSIRO-Mk3.6.0 Atmosphere-Ocean GCM: participation in CMIP5 and data publication. *International Congress on Modelling and Simulation – MODSIM 2011,* Perth, Western Australia.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. & Birdsey, R.A. (2004). *Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species.* USDA Forest Service, Northeastern Research Station. Gen.Tech.Rep.NE-GTR-319.

Jiang, R., Gan, T.Y., Xie, J., Wang, N. & Kuo, C.-C. (2017). Historical and potential changes of precipitation and temperature of Alberta subjected to climate change impact: 1900–2100. *Theoretical and Applied Climatology*, 127, 725-739.

Johnson, D.W. (2006). Progressive N limitation in forests: review and implications for long-term responses to elevated $CO_2$. *Ecology*, 87, 64-75.

Johnstone, J.F. & Chapin, F.S. (2006). Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems*, 9, 268-277.

Jones, E.L. & Daniels, L.D. (2012). Assessment of dendrochronological year-of-death estimates using permanent sample plot data. *Tree-Ring Research*, 68, 3-16.

Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F. *et al.* (2017). Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Global Change Biology*, 23, 177-190.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., & Coomes, D. A. (2020). Good things take time—Diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology*, 108, 2198-2211.

Kangas, A. & Maltamo, M. (2006). *Forest inventory: methodology and applications*. Springer, Dordrecht, The Netherlands.

Karlsson, P.S., Weih, M. & Borg, C. (2005). Mountain birch growth in relation to climate and herbivores. In: *Plant ecology, herbivory, and human impact in Nordic mountain birch forests* (eds. Caldwell, MM & et al.). Springer Berlin, Heidelberg, pp. 71-86.

Kayes, I., & Mallik, A. (2020). Boreal Forests: Distributions, Biodiversity, and Management. *Life on Land*, 1-12.

Kays, S., Harper, J. L. (1974) The regulation of plant and tiller density in a grass sward. *Journal of Ecology*, 62, 97-105.

Ketterings, Q.M., Coe, R., van Noordwijk, M. & Palm, C.A. (2001). Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management*, 146, 199-209.

Killi, D., Bussotti, F., Gottardini, E., Pollastrini, M., Mori, J., Tani, C. *et al.* (2018). Photosynthetic and morphological responses of oak species to temperature and [$CO_2$] increased to levels predicted for 2050. *Urban Forestry & Urban Greening*, 31, 26-37.

Kirilenko, A. P., & Sedjo, R. A. (2007). Climate change impacts on forestry. *Proceedings of the National Academy of Sciences*, 104, 19697-19702.

Knutti R, Masson D, Gettelman A (2013) Climate model genealogy: Generation CMIP5 and how we got there. *Geophysical Research Letters*, 40, 1194-1199.

Kovač, M., Kušar, G., Hočevar, M., Simončič, P., Poljanec, A., Skudnik, M., Gartner, A. & Kozorog, E. (2010). Control sampling method in Slovenia-History, Characteristics and Use. *Studia Forestalia Slovenica*, 136, 1-66.

Krajicek, J.E., Brinkman, K.A., Gingrich, S.F. (1961). Crown competition—a measure of density. *Forest Science*, 7, 35-42.

Kurz, W.A., Beukema, S.J. & Apps, M.J. (1996). Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. *Canadian Journal of Forest Research*, 26, 1973-1979.

Kuuluvainen, T. & Gauthier, S. (2018). Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems*, 5, 1-15.

Labrecque, S., Fournier, R.A., Luther, J.E. & Piercey, D. (2006). A comparison of four methods to map biomass from Landsat-TM and inventory data in western Newfoundland. *Forest Ecology and Management*, 226, 129-144.

Lambert, M.C., Ung, C.H. & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research*, 35, 1996-2018.

Larsen, C.P.S. (1997). Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography*, 24, 663-673.

Lawless, J. F. (2011). *Statistical models and methods for lifetime data*. John Wiley & Sons, 362pp.

Le Toan, T., Quegan, S., Davidson, M.W.J., Balzter, H., Paillou, P., Papathanassiou, K. *et al.* (2011). The BIOMASS mission: Mapping global forest biomass to better understand the terrestrial carbon cycle. *Remote Sensing of Environment*, 115, 2850-2860.

Lee, B.S., Alexander, M.E., Hawkes, B.C., Lynham, T.J., Stocks, B.J. & Englefield, P. (2002). Information systems in support of wildland fire management decision making in Canada. *Computers and Electronics in Agriculture*, 37, 185-198.

Lemprière, T.C., Kurz, W.A., Hogg, E.H., Schmoll, C., Rampley, G.J., Yemshanov, D. *et al.* (2013). Canadian boreal forests and climate change mitigation. *Environmental Reviews*, 21, 293-321.

Lett S, Dorrepaal E (2018) Global drivers of tree seedling establishment at alpine treelines in a changing climate. *Functional Ecology,* 32, 1666-1680.

Li, C., Flannigan, M.D. & Corns, I.G. (2000). Influence of potential climate change on forest landscape dynamics of west-central Alberta. *Canadian Journal of Forest Research*, 30, 1905-1912.

Liski, J., Korotkov, A.V., Prins, C.F.L., Karjalainen, T., Victor, D.G. & Kauppi, P.E. (2003). Increased carbon sink in temperate and boreal forests. *Climatic Change*, 61, 89-99.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G. *et al.* (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, 354, aaf8957.

Liang, J. & Gamarra, J.G. (2020). The importance of sharing global forest data in a world of crises. *Scientific Data*, 7, 1-5.

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Global decline in large old trees. *Science*, 338, 1305-1306.

Littell, J.S., Peterson, D.L. & Tjoelker, M. (2008). Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecological Monographs*, 78, 349-368.

Lloyd, A.H., Bunn, A.G. & Berner, L. (2011). A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, 17, 1935-1945.

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., & Phillips, O. L. (2011). ForestPlots. net: a web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science*, 22, 610-613.

Luo, Y., McIntire, E.J.B., Boisvenue, C., Nikiema, P.P. & Chen, H.Y.H. (2020). Climatic change only stimulated growth for trees under weak competition in central boreal forests. *Journal of Ecology*, 108, 36-46.

Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W. *et al.* (2012). Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences*, 109, 2423-2427.

MacDicken, K.G. (2015). Global forest resources assessment 2015: what, why and how? *Forest Ecology and Management*, 352, 3-8.

MacFarlane DW, Green EJ, Burkhart HE (2000) Population density influences assessment and application of site index. *Canadian Journal of Forest Research,* 30, 1472-1475.

Mackey, B., Skinner, E. & Norman, P. (2021). A Review of Definitions, Data, and Methods for Country-level Assessment and Reporting of Primary Forest. *Griffith Climate Action Beacon*, 1-21.

Mahony, C.R., Wang. T., Hamann, A. & Cannon, A.J. (2022). A CMIP6 ensemble for downscaled monthly climate normal over North America. *International Journal of Climatology*, doi: 10.1002/joc.7566.

Mahoney, C., Hall, R.J., Hopkinson, C., Filiatrault, M., Beaudoin, A. & Chen, Q. (2018). A forest attribute mapping framework: a pilot study in a northern boreal forest, Northwest Territories, Canada. *Remote Sensing*, 10, 1338.

Malone T, Liang J, Packee EC (2009) *Cooperative Alaska Forest Inventory*, General Technical Report PNW-GTR-785, USDA Forest Service, Pacific Northwest Research Station.

Marshall, P.L., Lencar, C. & Hassani, B. (2000). *Review of PSP Systems Employed Outside of British Columbia.* Vancouver, BC.

Martin, P.J. (2005). Design of regeneration standards to sustain boreal mixedwoods in western Canada. *International Forestry Review*, 7, 135-146.

McCarthy, M.C. & Enquist, B.J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*, 21, 713-720.

McMahon, S.M., Parker, G.G. & Miller, D.R. (2010). Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences*, 107, 3611-3615.

McRoberts, R.E., Tomppo, E.O. & Næsset, E. (2010). Advances and emerging issues in national forest inventories. *Scandinavian Journal of Forest Research*, 25, 368-381.

McTague, J.P. & Weiskittel, A. (2021). Evolution, history, and use of stem taper equations: a review of their development, application, and implementation. *Canadian Journal of Forest Research*, 51, 210-235.

Meinshausen M, Smith SJ, Calvin K *et al.* (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change,* 109, 213-241.

Metsaranta, J. M., & Lieffers, V. J. (2009). Using dendrochronology to obtain annual data for modelling stand development: a supplement to permanent sample plots. *Forestry*, 82, 163-173.

Michaelian, M., Hogg, E. H., Hall, R. J., & Arsenault, E. (2011). Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, 17, 2084-2094.

Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L. & Stanley, E.H. (2004). Spatial extrapolation: the science of predicting ecological patterns and processes. *Bioscience*, 54, 310-320.

Mitton, J.B. & Grant, M.C. (1996). Genetic variation and the natural history of quaking aspen. *Bioscience*, 46, 25-31.

Mohammadi, J., Shataee Joibary, S., Yaghmaee, F. & Mahiny, A.S. (2010). Modelling forest stand volume and tree density using Landsat ETM data. *International Journal of Remote Sensing*, 31, 2959-2975.

Mohler, C. L., Marks, P. L., Sprugel, D. G. (1978). Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology*, 66, 599-614.

Monserud, R.A. (2003). Evaluating forest models in a sustainable forest management context. *Forest Biometry, Modelling and Information Sciences*, 1, 35-47.

Monserud, R. A., Huang, S., & Yang, Y. (2006). Biomass and biomass change in lodgepole pine stands in Alberta. *Tree physiology*, 26, 819-831.

Morgantini, L. E., & Kansas, J. L. (2003). Differentiating mature and old-growth forests in the upper foothills and subalpine subregions of west-central Alberta. *The Forestry Chronicle*, 79, 602-612

Morimoto, M. & Juday, G. (2019). Perspectives on Sustainable Forest Management in Interior Alaska Boreal Forest: Recent History and Challenges. *Forests*, 10, 484.

Mrozewski, T. (2018). Canadian Forest Fire Data. *Bulletin-Association of Canadian Map Libraries and Archives (ACMLA)*, 160, 17-19.

Munger, T.T. (1946). Watching a Douglas-fir forest for thirty-five years. *Journal of Forestry*, 44, 705-708.

Næsset, E. (2002). Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. *Remote Sensing of Environment*, 80, 88-99.

Natural Regions Committee. (2006). *Natural Regions and Subregions of Alberta.* Government of Alberta, Edmonton, Alberta.

Natural Resources Canada. (2020). 8 facts about Canada's boreal forest. Available at: https://www.nrcan.gc.ca/our-natural-resources/forests-forestry/sustainable-forest-management/boreal-forest/8-facts-about-canadas-boreal-forest/17394. Last accessed 2022-07-15.

Natural Resources Canada (2018) *The State of Canada's Forests: Annual Report 2018*. Ottawa, ON, Canada

Nelson. T.A., Boots, B. (2008) Detecting spatial hot spots in landscape ecology. *Ecography,* 31, 556-566.

Newbold, T. (2010). Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography*, 34, 3-29.

Neyeloff, J.L., Fuchs, S.C. & Moreira, L.B. (2012). Meta-analyses and Forest plots using a Microsoft Excel spreadsheet: step-by-step guide focusing on descriptive data analysis. *BMC Research Notes*, 5, 1-6.

Niklas, K.J. (2004). Plant allometry: is there a grand unifying theory? *Biological Reviews*, 79, 871-889.

Östlund, L., Zackrisson, O. & Axelsson, A.L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, 27, 1198-1206.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., et al. & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333, 988-993.

Park, A., Puettmann, K., Wilson, E., Messier, C., Kames, S. & Dhar, A. (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.

Pastor, J., Aber, J.D. & Melillo, J.M. (1984). Biomass prediction using generalized allometric regressions for some northeast tree species. *Forest Ecology and Management*, 7, 265-274.

Pavlic, G., Chen, W., Fernandes, R., Cihlar, J., Price, D.T., Latifovic, R. *et al.* (2007). Canada-wide maps of dominant tree species from remotely sensed and ground data. *Geocarto International*, 22, 185-204.

Peel, M.C., Finlayson, B.L., McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633-1644.

Peichl, M. & Arain, M.A. (2007). Allometry and partitioning of above-and belowground tree biomass in an age-sequence of white pine forests. *Forest Ecology and Management*, 253, 68-80.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W. et al. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1, 467-471.

Perron, J. & Morin, P. (2011). *Normes d'inventaire forestier: Placettes-échantillons permanentes*. Ministry of Forests: Quebec, QC, Canada.

Peters, D.P.C. & Herrick, J.E. (2004). Strategies for ecological extrapolation. *Oikos*, 106, 627-636.

Phillips, O. L., Aragão, L. E., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G. *et al.* (2009). Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344-1347.

Pinheiro J, Bates D, DebRoy S, Sarkar D (2022) Linear and nonlinear mixed effects models. R package 'nlme' version 3.1-155. https://cran.r-project.org/web/packages/nlme/index.html

Porter, K.B., MacLean, D.A., Beaton, K.P. & Upshall, J. (2001). *New Brunswick Permanent Sample Plot Database (PSPDB v1. 0).* NB.

Potapov P, Li X, Hernandez-Serna A *et al.* (2021). Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote Sensing of Environment,* 253, 112165.

Power, K. & Gillis, M.D. (2006). *Canada's Forest Inventory 2001*. Pacific Forestry Centre Victoria, British Columbia.

Price, D. T., Alfaro, R. I., Brown, K. J., Flannigan, M. D., Fleming, R. A., Hogg, E. H., et al. & Venier, L. A. (2013). Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, 21, 322-365.

Puettmann, K., Coates, K.D., Messier, C. (2009). *A Critique of Silviculture: Managing for Complexity*. Island Press, Washington, DC.

Rees, M., Condit, R., Crawley, M., Pacala, S., & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293, 650-655.

Réjou-Méchain, M., Barbier, N., Couteron, P., Ploton, P., Vincent, G., Herold, M. *et al.* (2019). Upscaling Forest biomass from field to satellite measurements: sources of errors and ways to reduce them. *Surveys in Geophysics*, 40, 881-911.

Reyes-Hernández, V. & Comeau, P.G. (2014). Survival probability of white spruce and trembling aspen in boreal pure and mixed stands experiencing self-thinning. *Forest Ecology and Management*, 323, 105-113.

Ribeiro, R.P., Borges, J.G. & Oliveira, V. (2004). A framework for data quality for Mediterranean sustainable ecosystem management. *Annals of Forest Science*, 61, 557-568.

Riley SJ, DeGloria SD, Elliot R (1999) Index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23-27.

Rogeau, M.-P., Flannigan, M.D., Hawkes, B.C., Parisien, M.-A. & Arthur, R. (2016). Spatial and temporal variations of fire regimes in the Canadian Rocky Mountains and foothills of southern Alberta. *International Journal of Wildland Fire*, 25, 1117-1130.

Rupasinghe, P.A. & Chow-Fraser, P. (2021). Relating pre-fire canopy species, fire season, and proximity to surface waters to burn severity of boreal wildfires in Alberta, Canada. *Forest Ecology and Management*, 496, 119386.

Safranyik, L., Carroll, A. L., Régnière, J., Langor, D. W., Riel, W. G., Shore, T. L., et al. & Taylor, S. W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, 142, 415-442.

Salvati, L., Becagli, C., Bertini, G., Cantiani, P., Ferrara, C. & Fabbio, G. (2017). Toward sustainable forest management indicators? A data mining approach to evaluate the impact of silvicultural practices on stand structure. *International Journal of Sustainable Development & World Ecology*, 24, 372-382.

Schepaschenko, D., Chave, J., Phillips, O.L., Lewis, S.L., Davies, S.J., Réjou-Méchain, M. *et al.* (2019). The Forest Observation System, building a global reference dataset for remote sensing of forest biomass. *Scientific Data*, 6, 1-11.

Searls, T., Zhu, X., McKenney, D., Mazumder, R., Steenberg, J., Yan, G. et al. (2021). Assessing the influence of climate on the growth rate of boreal tree species in northeastern Canada through long-term permanent sample plot data sets. *Canadian Journal of Forest Research*, 51, 1039-1049.

Seidl R, Thom D, Kautz M *et al.* (2017) Forest disturbances under climate change. *Nature Climate Change,* 7, 395-402.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K. *et al.* (2011). Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling*, 222, 903-924.

Seppälä, R., Alexander, B., Katila, P. (2009) *Adaptation of forests and people to climate change: A global assessment report (No. 22)*. IUFRO World Series, International Union of Forestry Research Organizations (IUFRO), Helsinki, Finland.

Sileshi, G.W. (2014). A critical review of forest biomass estimation models, common mistakes and corrective measures. *Forest Ecology and Management*, 329, 237-254.

Simard M, Pinto N, Fisher JB, Baccini A (2011) Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research: Biogeosciences,* 116, G04021.

Smith, W.B. (2002). Forest inventory and analysis: a national inventory and monitoring program. *Environmental Pollution*, 116, S233-S242.

Song, H.-S. & Lee, S.-H. (2017). Effects of wind and tree density on forest fire patterns in a mixed-tree species forest. *Forest Science and Technology*, 13, 9-16.

Spittlehouse, D.L. & Stewart, R.B. (2004). Adaptation to climate change in forest management. *Journal of Ecosystems and Management*, 4, 1-11.

Spurr, S.H. 1952. *Forest inventory*. Ronald Press, New York. 476pp.

Stadt, J. J., Schieck, J., & Stelfox, H. A. (2006). Alberta Biodiversity Monitoring Program– monitoring effectiveness of sustainable forest management planning. *Environmental Monitoring and Assessment*, 121, 33-46.

Stearns-Smith, S., Cf, R.P.F. & Basaraba, D. (2006). *Provincial PSP Remeasurement Priorities (BC's PSP Strategy Revisited)*. Ministry of Forests, Range Sooke, B.C.

Stephens, S.L., Agee, J.K., Fule, P.Z., North, M.P., Romme, W.H., Swetnam, T.W. *et al.* (2013). Managing forests and fire in changing climates. *Science*, 342, 41-42.

Sugiyama, A., Comita, L. S., Masaki, T., Condit, R., Hubbell, S. P. (2018) Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species. *Ecology*, 99, 2583-2591.

Sulla-Menashe, D., Friedl, M.A., Woodcock, C.E. (2016) Sources of bias and variability in long-term Landsat time series over Canadian boreal forests. *Remote Sensing of Environment*, 177, 206-219.

Taylor, A.R., Boulanger, Y., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W. *et al.* (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.

Taylor, C., McCarthy, M.A. & Lindenmayer, D.B. (2014). Nonlinear effects of stand age on fire severity. *Conservation Letters*, 7, 355-370.

Ter Steege, H., Pitman, N. C., Sabatier, D., Baraloto, C., Salomão, R. P., ..., Silman, M. R. (2013) Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092.

Therneau, T.M. (2021). A package for survival analysis in R. Version 3.

Thompson, I.D., Maher, S.C., Rouillard, D.P., Fryxell, J.M. & Baker, J.A. (2007). Accuracy of forest inventory mapping: Some implications for boreal forest management. *Forest Ecology and Management*, 252, 208-221.

Thomson, A.M., Calvin, K.V., Smith, S.J., Kyle, G.P., Volke, A., Patel, P. *et al.* (2011). RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Climatic Change*, 109, 77-94.

Thornton, P.E., Thornton, M.M., Mayer, B.W., Wei, Y., Devarakonda, R., Vose, R.S. *et al.* (2016). Daymet: daily surface weather data on a 1-km grid for North America, version 3.

ORNL DAAC, Oak Ridge, Tennessee, USA. In: *USDA-NASS, 2019. 2017 Census of Agriculture, Summary and State Data, Geographic Area Series, Part 51, AC-17-A-51*.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471-493.

Tobner, C. M., Paquette, A., Reich, P. B., Gravel, D., Messier, C. (2014) Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, 174, 609-621.

Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., Gabler, K., Schadauer, K. *et al.* (2010). National forest inventories. *Pathways for Common Reporting. European Science Foundation*, 1, 541-553.

Townsend, P. (2004). *Nova Scotia Forest Inventory Based on Permanent Sample Plots Measured between 1999 and 2003*. Report FOR 2004-3. Nova Scotia Department of Natural Resources, Truro, NS.

Trabucco A, Zomer RJ (2018) Global aridity index and potential evapotranspiration (ET0) climate database v2. *Consortium for Spatial Information,* 10, 9.

Trumbore, S., Brando, P. & Hartmann, H. (2015). Forest health and global change. *Science*, 349, 814-818.

Tuanmu MN, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23, 1031-1045.

Tuanmu MN, Jetz W (2015) A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 24, 1329-1339.

Tymstra, C., Flannigan, M.D., Armitage, O.B. & Logan, K. (2007). Impact of climate change on area burned in Alberta's boreal forest. *International Journal of Wildland Fire*, 16, 153-160.

Ung, C.-H., Bernier, P. & Guo, X.-J. (2008). Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research*, 38, 1123-1132.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H. & Silkin, P.P. (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, 400, 149-151.

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Retana, J. (2012) Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. *Global Change Biology*, 18, 1028-1041.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J.S. (2011). Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management*, 262, 1648-1657.

van Leeuwen, M., Hilker, T., Coops, N.C., Frazer, G., Wulder, M.A., Newnham, G.J. *et al.* (2011). Assessment of standing wood and fiber quality using ground and airborne laser scanning: A review. *Forest Ecology and Management*, 261, 1467-1478.

Vanclay, J.K., Skovsgaard, J.P. & Hansen, C.P. (1995). Assessing the quality of permanent sample plot databases for growth modelling in forest plantations. *Forest Ecology and Management*, 71, 177-186.

Vanderwel, M. C., Coomes, D. A., & Purves, D. W. (2013). Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology*, 19, 1504-1517.

Vanderwel, M. C., Zeng, H., Caspersen, J. P., Kunstler, G., & Lichstein, J. W. (2016). Demographic controls of aboveground forest biomass across North America. *Ecology Letters*, 19, 414-423.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLoS One*, 11, e0156720.

Wang, T., Hamann, A. & Spittlehouse, D. (2019). ClimateNA v6.20. BC.

Watanabe M, Suzuki T, O'ishi R *et al.* (2010) Improved climate simulation by MIROC5: Mean states, variability, and climate sensitivity. *Journal of Climate,* 23, 6312-6335.

Way, D.A. & Oren, R. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, 30, 669-688.

Weber, M.G. & Flannigan, M.D. (1997). Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. *Environmental Reviews*, 5, 145-166.

Wehrens, R., Franceschi, P., Vrhovsek, U. & Mattivi, F. (2011). Stability-based biomarker selection. *Analytica Chimica Acta*, 705, 15-23.

Weiner, J., Stoll, P., Muller-Landau, H., Jasentuliyana, A. (2001) The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *The American Naturalist*, 158, 438-450.

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 6, 207-215.

Weir, J.M.H., Johnson, E.A. & Miyanishi, K. (2000). Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. *Ecological Applications*, 10, 1162-1177.

Westoby, M. (1984). The self-thinning rule. *Advances in Ecological Research*, 14, 167-225.

White, M.A., Running, S.W. & Thornton, P.E. (1999). The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, 42, 139-145.

White, J., Harper, J. L. (1970) Correlated changes in plant size and number in plant populations. *Journal of Ecology*, 58, 467-485.

Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997). Strong density-and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences*, 94, 1252-1257.

Wilson, R. & Elling, W. (2004). Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. *Trees-Structure and Function*, 18, 19-28.

Wotton, B.M., Nock, C.A. & Flannigan, M.D. (2010). Forest fire occurrence and climate change in Canada. *International Journal of Wildland Fire*, 19, 253-271.

Wulder, M.A., White, J.C., Nelson, R.F., Næsset, E., Ørka, H.O., Coops, N.C. *et al.* (2012). Lidar sampling for large-area forest characterization: A review. *Remote Sensing of Environment*, 121, 196-209.

Xing, D., Bergeron, J.A.C., Solarik, K.A., Tomm, B., Macdonald, S.E., Spence, J.R. *et al.* (2019). Challenges in estimating forest biomass: use of allometric equations for three boreal tree species. *Canadian Journal of Forest Research*, 49, 1613-1622.

Xu, Y., Li, C., Sun, Z., Jiang, L., Fang, J. (2019) Tree height explains stand volume of closed-canopy stands: Evidence from forest inventory data of China. *Forest Ecology and Management*, 438, 51-56.

Yang W, Kondoh A (2020) Evaluation of the Simard et al. 2011 Global Canopy Height Map in

Boreal Forests. *Remote Sensing,* 12, 1114.

Yang, Y., Huang, S., Vassov, R., Pinno, B. & Chhin, S. (2020). Climate-sensitive height–age models for top height trees in natural and reclaimed oil sands stands in Alberta, Canada. *Canadian Journal of Forest Research*, 50, 297-307.

Zhang, J., Huang, S. & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, 112, 4009-4014.

Zhang, J., Huang, S., Hogg, E.H., Lieffers, V., Qin, Y. & He, F. (2014). Estimating spatial variation in Alberta forest biomass from a combination of forest inventory and remote sensing data. *Biogeosciences*, 11, 2793.

Zhang, X., Flato, G., Kirchmeier-Young, M., Vincent, L., Wan, H., Wang, X., et al. & Kharin, V. V. (2019). Changes in Temperature and Precipitation Across Canada; Chapter 4. In *Canada's Changing Climate Report* (eds Bush, E. & Lemmen, D.S.), Government of Canada, Ottawa, Ontario, 112-193.

Zhu, K., Zhang, J., Niu, S., Chu, C. & Luo, Y. (2018). Limits to growth of forest biomass carbon sink under climate change. *Nature Communications*, 9, 1-8.

Zobel, B. & Talbert, J. (1984). *Applied Forest Tree Improvement*. Wiley, New York.

## Appendices

Table S1. Ranges of site locations, diameter at breast height, aboveground biomass and the 16 climatic variables for black spruce, white spruce, trembling aspen, tamarack and balsam fir modeled in Chapter 2.

| Species | Black Spruce | White Spruce | Trembling Aspen | Tamarack | Balsam Fir |
|---|---|---|---|---|---|
| Longitude (°) | 140.96W - 68.26W | 140.96W - 65.66W | 140.85W - 72.37W | 121.23W - 65.67W | 115.50W - 65.66W |
| Latitude (°) | 48.84N - 63.95N | 46.43N - 63.98N | 46.43N - 63.95N | 44.00N - 61.75N | 46.44N - 54.33 N |
| DBH (cm) | 1.1 - 38.4 | 2.4 - 57.6 | 1.5 - 47.2 | 1.9 - 44.5 | 1.8 - 42.4 |
| AGB (kg) | 0.57 - 685.1 | 0.89 - 1,577.70 | 0.13 - 1,081.55 | 0.42 - 938.88 | 0.55 - 649.02 |
| MAT (°C) | -5.6 - 3.3 | -5.2 - 7.0 | -5.6 - 4.0 | -3.8 - 6.6 | -1.0 - 3.5 |
| MWMT (°C) | 9.9 - 17.5 | 9.9 - 18.0 | 9.9 - 18.5 | 15.2 - 19.9 | 15.0 - 18.3 |
| MCMT (°C) | -27.4 - -8.7 | -27.6 - -0.2 | -27.6 - -8.2 | -26.4 - -7.4 | -21.5 - -11.6 |
| TD (°C) | 20.3 - 43.3 | 15.7 - 43.3 | 20.3 - 43.3 | 27.3 - 43.3 | 27.5 - 37.7 |
| MAP (mm) | 281 - 983 | 263 - 1,822 | 263 - 1,238 | 341 - 1,137 | 484 - 1,160 |
| MSP (mm) | 158 - 516 | 149 - 574 | 149 - 530 | 185 - 548 | 315 - 574 |
| AHM (°C $mm^{-1}$) | 10.2 - 31.4 | 7.5 - 31.4 | 9.1 - 30.9 | 11.3 - 24.5 | 8.5 - 21.3 |
| SHM (°C $mm^{-1}$) | 30.9 - 86.7 | 24.5 - 88.0 | 26.0 - 88.0 | 32.8 - 82.0 | 26.9 - 54.3 |
| DD5 (°C) | 507 - 1,425 | 490 - 1,557 | 506 - 1,631 | 961 - 2,029 | 999 - 1,583 |
| FFP (day) | 40 - 112 | 40 - 167 | 40 - 122 | 96 - 143 | 93 - 121 |

| | | | | | |
|---|---|---|---|---|---|
| PAS (mm) | 107 - 590 | 82 - 770 | 101 - 663 | 116 - 441 | 136 - 552 |
| $E_{ref}$ (mm) | 323 - 576 | 323 - 644 | 323 - 644 | 354 - 688 | 414 - 632 |
| CMD (mm) | 20 - 303 | 0 - 330 | 0 - 330 | 15 - 229 | 0 - 198 |
| MAR (MJ $m^{-2}$ $d^{-1}$) | 9.1 - 12.7 | 9.1 - 12.8 | 9.1 - 12.9 | 10.1 - 13.6 | 11.8 - 12.8 |
| RH (%) | 51 - 68 | 51 - 75 | 51 - 68 | 55 - 68 | 56 - 69 |
| CMI (mm) | -162 - 576 | -162 - 1233 | -146 - 793 | -123 - 600 | -80 - 736 |

Table S2. Results of ten-fold cross-validation with climate-based models for trembling aspen and tamarack based on 1,000 iterations. Models with the highest 5 numbers of times designated as “good” (shown in the parenthesis) through the MAE and RMSE comparisons are under the column of MAE and RMSE, respectively. As an example for interpretation, FFP (715) at the first row under the trembling aspen-MAE column indicates that the model of Eq (4) with FFP as the climatic variable. It has a lower MAE than the conventional model (Eq. 1) and the two nonlinear mixed models (Eqs. 2 and 3) for 715 times out of the 1,000 iterations. The models in bold are the best climate-based models for trembling aspen and tamarack. No climate-based model for black spruce, white spruce and balsam fir yields lower MAE and RMSE than the conventional and the two non-linear mixed models for over 700 times out of the 1,000 iterations.

| | Trembling Aspen | | Tamarack | |
|---|---|---|---|---|
| Model | MAE | RMSE | MAE | RMSE |
| Eq. (4) $AGB = (a + site_i + b \times Clim_i) \times DBH^d$ | FFP (715) | FFP (620) | MAT (880) | MAT (839) |
| Eq. (5) $AGB = (a + b \times Clim_i) \times DBH^{(d+site_i)}$ | DD5 (730)<br>**FFP (754)** | MWMT (627)<br>DD5 (707)<br>**FFP (721)** | **MAT (887)** | **MAT (871)**<br>MCMT (840)<br>MAP (831) |
| Eq. (6) $AGB = (a + site_i) \times DBH^{(d+b\times Clim_i)}$ | NA | NA | MAT (885) | MAT (832) |
| Eq. (7) $AGB = a \times DBH^{(d+site_i+b\times Clim_i)}$ | DD5 (704)<br>FFP (731) | FFP (629) | MAT (881)<br>MCMT (850) | NA |
| Eq. (8) $AGB = (a + site_i) \times DBH^d + b \times Clim_i$ | NA | NA | NA | NA |
| Eq. (9) $AGB = a \times DBH^{(d + site_i)} + b \times Clim_i$ | NA | NA | NA | NA |

Table S3. Summary of 19 plot physical, stand characteristic and climatic variables for the 919 PSPs in Alberta

| Type | Variable | Range (Median) | Source |
|---|---|---|---|
| Plot physical | Plot size ($m^2$) | 200 – 2,034 (1,000) | Plot records |
| | Year of establishment | 1960 – 2009 (1984) | |
| | Stand age at establishment (years) | 18 – 262 (121) | |
| | Latitude (° N) | 49.01 – 59.73 (54.39) | |
| | Longitude (° W) | 110.1 – 119.7 (115.6) | |
| | Altitude (m) | 291 – 2,089 (980) | |
| | Ecoregion (Categorical) | Boreal (*n* = 306), Foothills (*n* = 509), and Rocky Mountain (*n* = 104) Ecoregions | |
| | Aspect (° to North) | 1.53 – 179.93 (96.3) | LiDAR 7.5 DEM |
| | Slope (°) | 0 – 60 (3) | |
| Stand structural | Tree species richness | 1 – 7 (2.5) | Tree records |
| | Canopy height (m) | 3.70 – 40.24 (18.92) | |
| | Tree density of all trees ($hectare^{-1}$) | 10 – 3,637 (1,050) | |
| | Basal area of all trees ($m^2 \cdot hectare^{-1}$) | 0.07 – 79.70 (30.51) | |
| | Tree density of deciduous trees ($hectare^{-1}$) | 0 – 2,113 (15) | |
| | Basal area of deciduous trees ($m^2 \cdot hectare^{-1}$) | 0 – 50.61 (0.38) | |
| Climatic | Mean annual temperature (MAT, °C) | -2.62 – 3.85 (2.11) | ClimateNA v7.21 |
| | Difference between mean warmest and mean coldest month temperature (TD, °C) | 22.73 – 41.00 (27.60) | |
| | Mean annual precipitation (MAP, mm) | 371.6 – 1,054.1 (554.8) | |
| | Climate moisture index (CMI, mm) | -113.4 – 589.6 (23.0) | |

Table S4. Summary of 4,367 forest inventory plots analyzed in this study, consisting of 3,829 PSPs across 10 jurisdictions, 346 NFI and 192 ABMI plots. The mean observed tree density, DBH and stand height (standard deviation in brackets) are presented. Alaska-AK, Alberta-AB, British Columbia-BC, Manitoba-MB, Newfoundland and Labrador-NL, Northwest Territories-NT, Ontario-ON, Quebec-QC, Saskatchewan-SK, and Yukon-YT.

| Plot type | Number of plots | Mean observed tree density (trees/ha) | Mean DBH (cm) | Mean stand height (m) |
|---|---|---|---|---|
| AB | 321 | 1,035 (576) | 22.0 (5.6) | 19.4 (3.9) |
| AK | 154 | 823 (381) | 18.5 (4.9) | 14.6 (3.3) |
| BC | 135 | 1,415 (594) | 17.3 (4.8) | 18.2 (4.2) |
| MB | 158 | 1,056 (524) | 14.4 (3.1) | 13.5 (3.2) |
| NL | 518 | 1,460 (747) | 15.2 (2.8) | 10.7 (2.0) |
| NT | 26 | 500 (204) | 25.8 (5.6) | 16.9 (3.6) |
| ON | 739 | 1,096 (477) | 16.3 (3.8) | 15.1 (3.5) |
| QC | 1,320 | 840 (367) | 15.2 (2.5) | 12.4 (3.2) |
| SK | 230 | 771 (344) | 23.0 (4.6) | 20.6 (3.0) |
| YT | 228 | 362 (84) | 16.5 (3.6) | 14.5 (3.4) |
| All PSP | 3,829 | 983 (553) | 16.8 (4.4) | 14.3 (4.3) |
| NFI | 346 | 759 (518) | 17.2 (4.7) | 13.4 (4.5) |
| ABMI | 192 | 847 (498) | 20.8 (7.1) | 18.1 (5.4) |
| Total | 4,367 | 992 (545) | 17.0 (4.0) | 14.4 (4.5) |

Table S5. Definitions and data sources for the 36 human development, topographic, stand height, climatic and vegetative variables used in this study. Variables used in Crowther et al.'s (2015) study are denoted in italics. All variables are at 1-km (30-arc-second) spatial resolution, except for Leaf Area Index (500-m), and for plot latitude, elevation and stand height (the accuracy of plot spatial location ranges from 10 m to 10 km).

| Type | Variable | Definition | Reference |
|---|---|---|---|
| Human Development | *Percent of developed and managed land* | Consensus prevalence of urban or built-up land cover in percentage | Tuanmu and Jetz (2014); https://www.earthenv.org/landcover |
| Topographic | *Latitude* | Plot latitudinal coordinate | Plot record |
|  | *Elevation* | Plot altitude |  |
|  | *Slope* | Angle of inclination of the terrain | USGS EROS Archive – Digital Elevation – Global 30 Arc-Second Elevation (GTOPO30); https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-global-30-arc-second-elevation-gtopo30?qt-science_center_objects=0 |
|  | *Eastness* | Sine of aspect (to north) |  |
|  | *Northness* | Cosine of aspect (to north) |  |
|  | *Roughness (TRI)* | Terrain ruggedness index (Riley et al. 1999) |  |
| Stand height | Stand height | Mean height of the 3 tallest trees at a plot | Plot record |
|  | Canopy height | Lidar-based canopy height | Simard et al. (2011); https://landscape.jpl.nasa.gov/cgi-bin/data-search.pl |
| Vegetative index | *Leaf Area Index (LAI)* | The Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices based on the calculation of radiometer reflectance | MODIS MOD15A2Hv061; https://lpdaac.usgs.gov/products/mod15a2hv061/ |
|  | *Enhanced Vegetation Index (EVI)* |  | MODIS MOD13A3v061; https://lpdaac.usgs.gov/products/mod13a3v061/ |

| | | | |
|---|---|---|---|
| | Normalized difference vegetation index (NDVI) | bands for global monitoring of vegetation conditions | |
| Second-order texture measures of vegetative index | *EVI: Angular Second Moment* | Uniformity (orderliness) of EVI | Tuanmu and Jetz (2015);<br>https://www.earthenv.org/texture |
| | *EVI: Contrast* | Exponentially weighted difference in EVI between adjacent pixels | |
| | *EVI: Dissimilarity* | Difference in EVI between adjacent pixels | |
| Climatic | *BIO1* | Mean annual temperature | Worldclim v2.1 1970-2000 climate data;<br>https://www.worldclim.org/data/index.html |
| | BIO2 | Mean Diurnal Range | |
| | BIO3 | Isothermality | |
| | *BIO4* | Temperature seasonality | |
| | BIO5 | Maximum temperature of warmest month | |
| | BIO6 | Minimum temperature of coldest month | |
| | BIO7 | Temperature annual range | |
| | BIO8 | Mean temperature of wettest quarter | |
| | BIO9 | Mean temperature of driest quarter | |
| | BIO10 | Mean temperature of warmest quarter | |
| | BIO11 | Mean temperature of coldest quarter | |
| | *BIO12* | Annual precipitation | |
| | BIO13 | Precipitation of wettest month | |

| | | | |
|---|---|---|---|
| | *BIO14* | Precipitation: driest month | |
| | *BIO15* | Precipitation: seasonality | |
| | BIO16 | Precipitation of wettest quarter | |
| | *BIO17* | Precipitation: driest quarter | |
| | BIO18 | Precipitation of warmest quarter | |
| | BIO19 | Precipitation of coldest quarter | |
| | *Aridity index* | Ratio between precipitation and $ET_0$ | Trabucco and Zomer (2019); https://figshare.com/articles/dataset/Global_Aridity_Index_and_Potential_Evapotranspiration_ET0_Climate_Database_v2/7504448/5 |
| | *Evapotranspiration* | Penman-Monteith Reference Evapotranspiration ($ET_0$) | |

Table S6. Summary information about the 4,367 plots analyzed in this study, including plot coordinates, census information, stand density, height and the other explanatory variables.

| Variable | Range | Median | Mean | Standard Deviation |
|---|---|---|---|---|
| Latitude (°) | 47.08 – 67.93 | 51.18 | 52.45 | 4.26 |
| Longitude (°) | -150.83 – -52.77 | -82.49 | -89.94 | 25.79 |
| Elevation (m) | 1 – 1,855 | 397 | 458.4 | 287.9 |
| Year of establishment | 1949 – 2018 | 1990 | 1988 | 13.3 |
| Year of census | 1999 – 2019 | 2009 | 2009 | 4.4 |
| Number of census | 1 – 9 | 3 | 3.4 | 1.4 |
| Mean diameter at breast height (cm) | 10.4 – 44.2 | 15.5 | 16.8 | 4.4 |
| Tree species richness | 1 – 8 | 2 | 2.6 | 1.4 |
| Plot size ($m^2$) | 100 – 8,092 | 500.3 | 771.3 | 881.2 |
| Observed tree density, $y$ (trees/ha) | 110 – 4,100 | 900 | 991.6 | 545.1 |
| Estimated tree density by Crowther et al.'s biome model, $y_b$ (trees/ha) | 13.5 – 1,483.1 | 678.1 | 670.9 | 202.5 |
| Stand height (m) | 1.0 – 34.8 | 13.8 | 14.4 | 4.5 |
| Estimated canopy height (m) | 6 – 26 | 15 | 14.8 | 3.6 |
| Human development (%) | 0 – 16 | 0 | 0.004 | 0.24 |
| Slope (°) | 0 – 27.5 | 0.7 | 1.4 | 2.0 |
| Eastness | -1 – 1 | 0 | 0.02 | 0.66 |
| Northness | -1 – 1 | 0.06 | 0.03 | 0.75 |
| Terrain ruggedness index, TRI | 0 – 0.917 | 0.131 | 0.204 | 0.192 |
| Leaf area index, LAI | 0.02 – 0.60 | 0.30 | 0.22 | 0.12 |
| Enhanced vegetation index, EVI | 0.032 – 0.532 | 0.354 | 0.332 | 0.077 |
| Normalized differential vegetation index, NDVI | 0.060 – 0.741 | 0.495 | 0.487 | 0.085 |

|  |  |  |  |  |
|---|---|---|---|---|
| Angular Second Moment of EVI, ASM: EVI | 0.050 – 0.543 | 0.073 | 0.085 | 0.037 |
| Contrast of EVI | 0.46 – 163.72 | 12.86 | 18.03 | 17.08 |
| Dissimilarity of EVI | 0.37 – 11.29 | 2.77 | 2.98 | 1.39 |
|  |  |  |  |  |
| BIO1, Annual mean temperature (°C) | -9.55 – 5.23 | 0.45 | 0.18 | 1.9 |
| BIO2, Mean diurnal range (mean of monthly maximum – minimum temperature, °C) | 7.39 – 14.68 | 11.29 | 11.06 | 1.4 |
| BIO3, Isothermality $(\frac{BIO2}{BIO7} \times 100)$ | 17.2 – 37.7 | 24.6 | 25.3 | 3.1 |
| BIO4, Temperature seasonality (standard deviation of temperature $\times 100$, °C) | 726 – 1,692 | 1,234 | 1,183 | 171.3 |
| BIO5, Maximum temperature of warmest month (°C) | 13.7 – 25.3 | 21.6 | 21.4 | 1.9 |
| BIO6, Minimum temperature of coldest month (°C) | -32.4 – -8.0 | -24.0 | -22.7 | 4.4 |
| BIO7, Temperature annual range (BIO5 – BIO6, °C) | 27.2 – 54.7 | 46.1 | 44.0 | 5.3 |
| BIO8, Mean temperature of wettest quarter (°C) | -12.6 – 17.9 | 13.5 | 12.1 | 4.5 |
| BIO9, Mean temperature of driest quarter (°C) | -22.1 – 14.6 | -9.4 | -9.1 | 6.0 |
| BIO10, Mean temperature of warmest quarter (°C) | 6.6 – 17.9 | 14.4 | 14.1 | 1.6 |
| BIO11, Mean temperature of coldest quarter (°C) | -27.0 – -3.5 | -15.9 | -15.0 | 3.9 |
| BIO12, Annual precipitation (mm) | 218 – 1,746 | 808 | 795 | 300 |
| BIO13, Precipitation of wettest month (mm) | 34 – 173 | 103 | 102 | 23 |
| BIO14, Precipitation of driest month (mm) | 3 – 113 | 37 | 38 | 23 |

| | | | | |
|---|---|---|---|---|
| BIO15, Precipitation seasonality ($\frac{standard\ deviation\ of\ precipitation}{mean\ of\ precipitation}$) | 7.6 – 93.1 | 35.3 | 38.0 | 17.4 |
| BIO16, Precipitation of wettest quarter (mm) | 97 – 508 | 288 | 283 | 70 |
| BIO17, Precipitation of driest quarter (mm) | 14 – 369 | 121 | 128 | 72 |
| BIO18, Precipitation of warmest quarter (mm) | 90 – 454 | 279 | 273 | 63 |
| BIO19, Precipitation of coldest quarter (mm) | 20 – 477 | 141 | 150 | 88 |
| Aridity index | 0.35 – 2.58 | 1.09 | 1.12 | 0.50 |
| Evapotranspiration (mm) | 475 - 996 | 734 | 735.1 | 98.2 |

Table S7. The 23 General Circulation Models used for the projected mean climate in 2050 under the RCP2.6, 4.5 and 8.5 emission scenarios.

| Country of Sponsor | General Circulation Model ID(s) | Reference(s) |
|---|---|---|
| Australia | CSIRO-Mk3.6.0 | Jeffrey and Syktus 2011 |
| Canada | CCCMA-CanESM2 | Chylek et al. 2011 |
| China | BCC-CSM1.1 | Gu et al. 2015 |
| | BCC-CSM1.1(m) | |
| | BNU-ESM | |
| | FIO-ESM | |
| | LASG-FGOALS-G2 | |
| France | IPSL-CM5A-LR | Hourdin et al. 2013 |
| | IPSL-CM5A-MR | |
| Germany | MPI-ESM-LR | Giorgetta et al. 2013 |
| Japan | MIROC-ESM | Watanabe et al. 2010 |
| | MIROC-ESM-CHEM | |
| | MIROC-MIROC5 | |
| | MRI-CGCM3 | |
| Korea | NIMR-HadGEM2-AO | Baek et al. 2013 |
| Norway | NCC-NorESM1-M | Bentsen et al. 2013 |
| UK | MOHC-HadGEM2-ES | Bellouin et al. 2011 |
| USA | CESM1-CAM5 | Gent et al. 2011; Knutti, Masson and Gettelman 2013 |
| | GFDL-CM3 | |
| | GFDL-ESM2G | |
| | GFDL-ESM2M | |
| | GISS-E2R | |
| | NCAR-CCSM4 | |

Table S8. Summary of the parameterized model (1) with its random effect and variance structure. Fixed effects are presented in the descent order of their importance in the stepwise selection based on AIC. The random effects are a random slope $\gamma_j$ by jurisdiction (~1|*Jurisdiction*), accounting for 192.26 standard deviation with the residual standard deviation 9021.33. The combination of variance functions is $\sigma^2(ht, BIO6, BIO8) = e^{2\times-0.011\mathrm{ht}}|BIO6|^{2\times-0.97}e^{2\times-0.015\mathrm{BIO8}}$. The total number of observations is 4,367 and the number of jurisdictions is 10, leaving the degrees of freedom of the intercept and each predictor as 4,349.

| | Estimated coefficient | Standard error | *t*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | -157.82 | 130.48 | -1.21 | 0.2265 |
| Stand height | 152.32 | 8.13 | 18.72 | <0.0001 |
| Stand height$^2$ | -4.56 | 0.25 | -18.28 | <0.0001 |
| NDVI | 661.53 | 109.38 | 6.05 | <0.0001 |
| Dissimilarity of EVI | -14.01 | 5.28 | -2.65 | 0.0080 |
| BIO6 | 11.90 | 3.33 | 3.58 | 0.0004 |
| BIO8 | -8.62 | 2.37 | -3.63 | 0.0003 |
| BIO9 | -8.42 | 2.11 | -3.99 | 0.0001 |
| Eastness | 18.23 | 9.44 | 1.93 | 0.0267 |

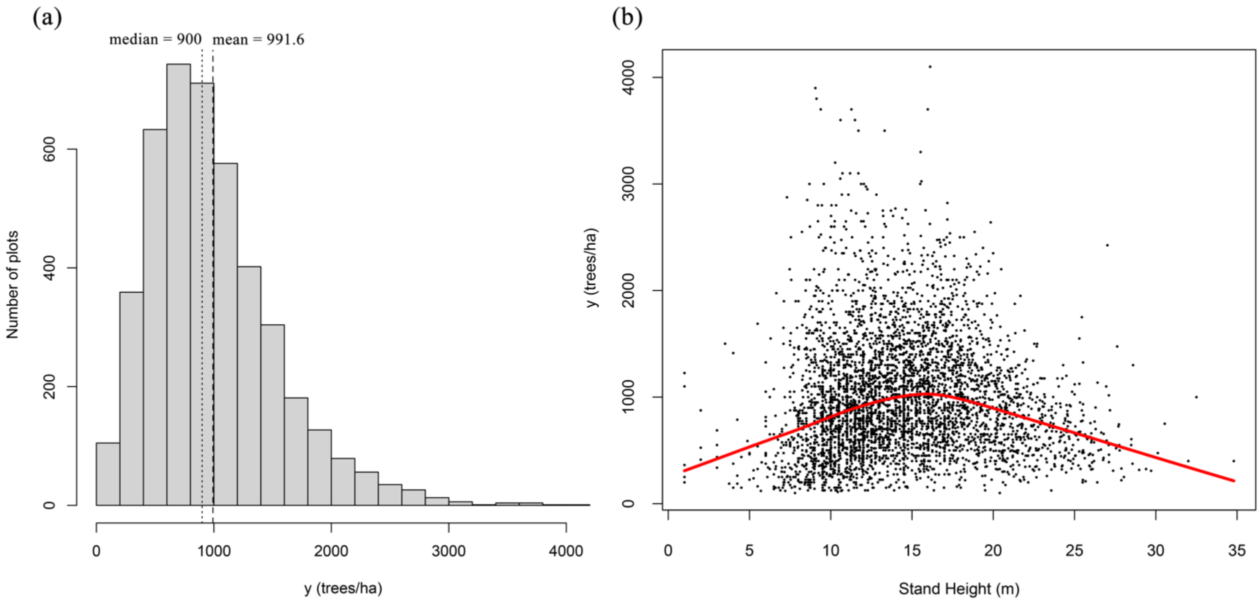

Fig. S1 (a) Histogram of observed tree density (y) of the 4,367 plots with mean 991.6 and median 900 trees/ha. (b) Locally weighted smoothing (LOWESS; Cleveland 1981) curve fitted to the scatterplot between observed tree density and stand height of the 4,367 plots.

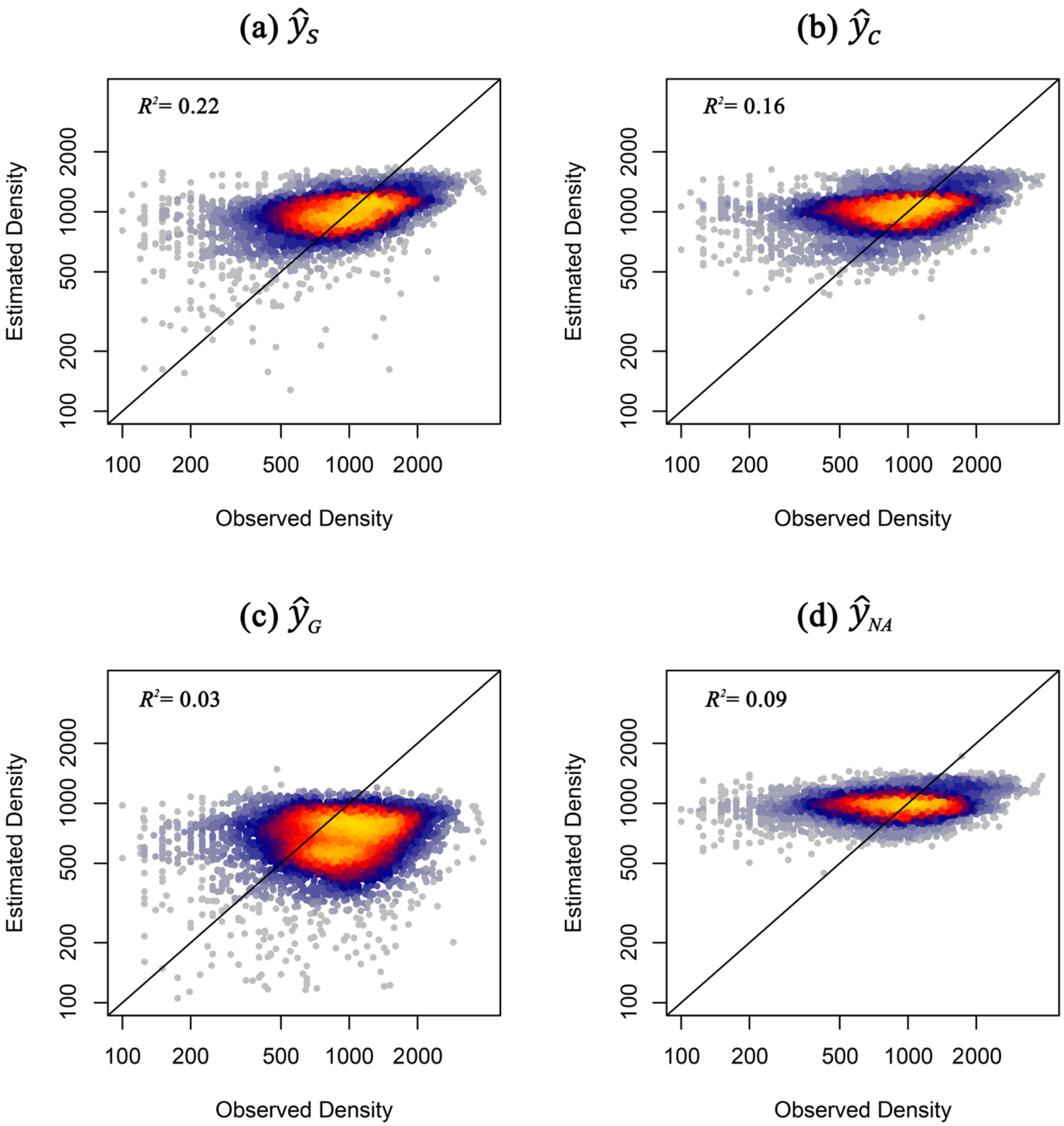

Fig. S2 Heatscatter plots of the four density estimates ($\hat{y}_S$, $\hat{y}_C$, $\hat{y}_G$ and $\hat{y}_{NA}$) versus the observed plot tree density ($y$) at the log-log scale for the 4,367 plots. $R^2$ between the estimated and observed density is shown at each panel. The black line is the 1:1 line.

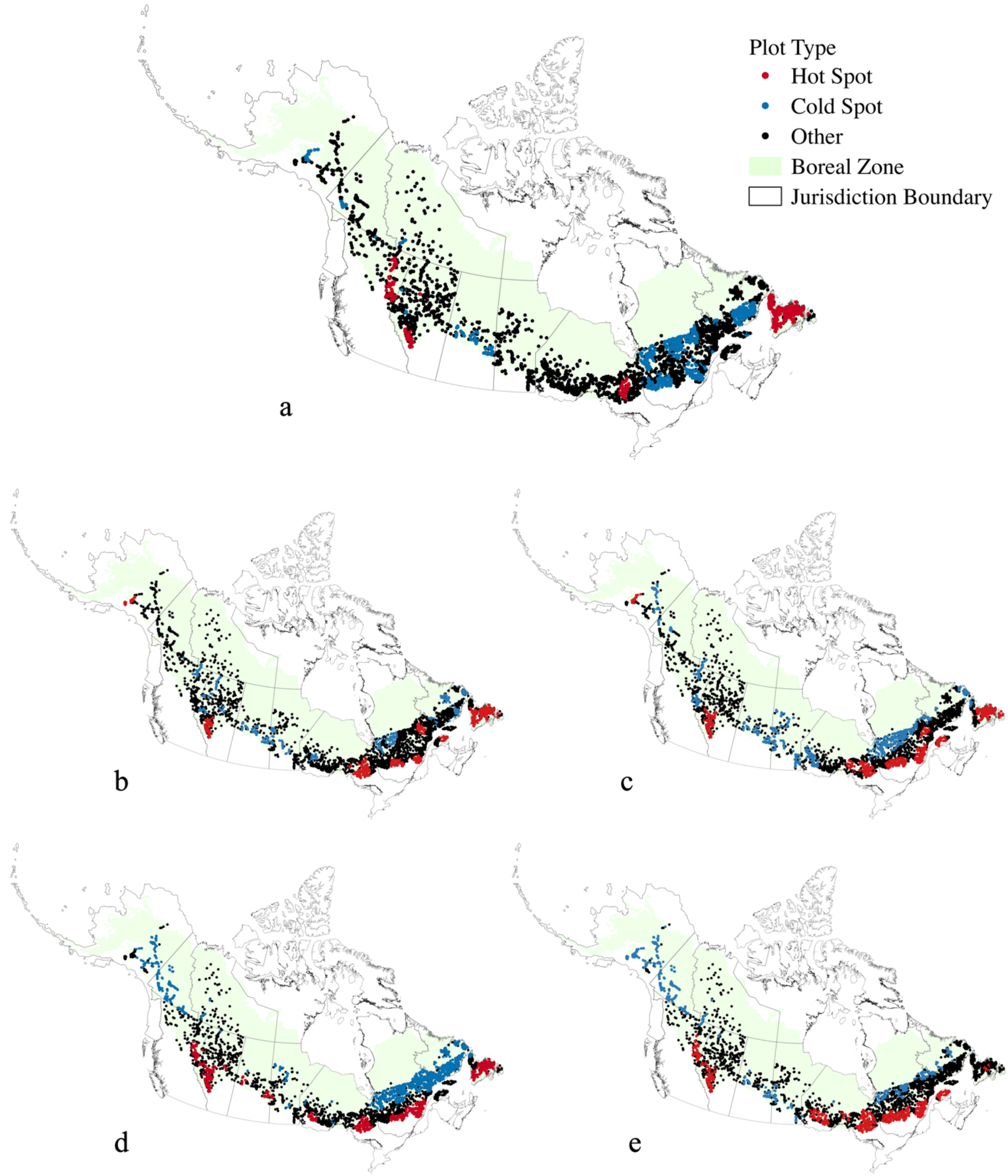

Fig. S3 Hot (red dots) and cold (blue dots) spots identified by the 95th quantile of the distributions of observed tree density (a), estimates of model (1) by stand height (b) and canopy height (c), and those of Crowther et al.'s boreal biome model (d) and refitted model (e) for the 4,367 plots (black dots if neither hot or cold spots) in the North American boreal zone.

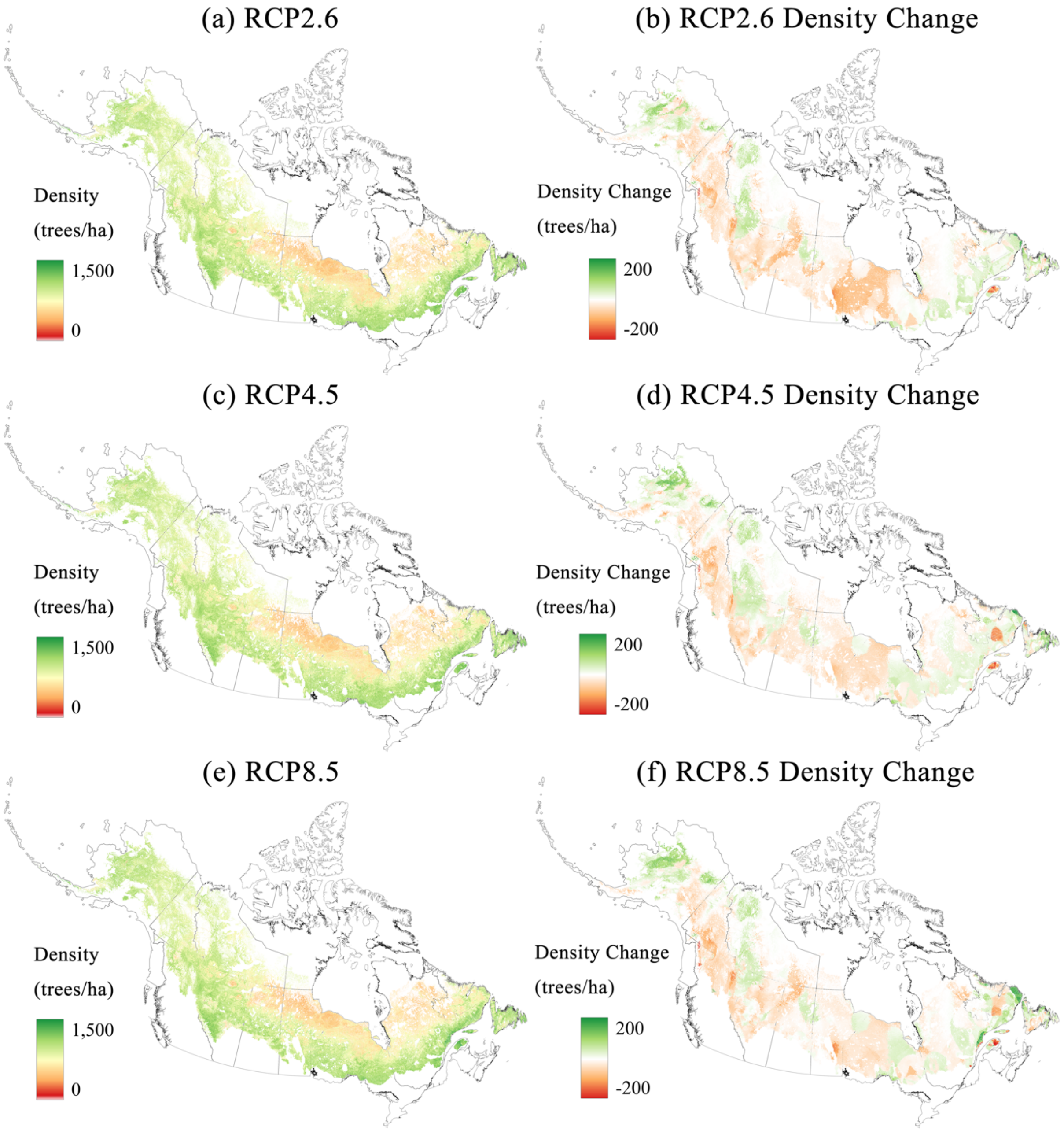

Fig. S4 Maps at 1-km resolution for projected tree density of North American boreal forest in 2050 under the RCP2.6 (a), 4.5 (c), and 8.5 (e) emission scenarios assuming other variables unchanged. Maps of changes of boreal tree density in North America showing the difference between projected density under RCP2.6 (b), 4.5 (d), and 8.5 (f) and the current estimates. There is an overwhelming trend of decrease in tree density in Canadian Prairies and the Pacific Northwest.