CLIMATE CHANGE-ASSOCIATED TEMPORAL INCREASE OF TREE MORTALITY AND ITS CONSEQUENCES IN CENTRAL AND WESTERN CANADIAN BOREAL FORESTS

By

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Abstract

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Keywords: Boosted Regression Trees (BRT), boreal forest, carbon, endogenous factors, global warming, global-change-type drought, Hierarchical Bayesian model, individual tree mortality analysis, neighborhood analysis, old forests, permanent sampling plot, plant competition, species aging, species composition, species interaction, stand development, tree mortality, young forests

Tree mortality influences forest structure, composition and ecosystem functions. To assess how recent climate changes affected tree mortality, observational studies conducted in old-growth forests have shown that tree mortality has increased with recent global warming, increasing atmospheric CO_2, and decreasing water availability in tropical, temperate, and boreal forests. These studies could lead to biased estimation of climate effects on boreal forests. Boreal forests are a mosaic of stands at various developmental stages, with old forests accounting for only a small portion of the landscape. Additionally, uncertainty exists whether the observed temporal increases in tree mortality are attributable to climate changes or stand developmental processes. The overall objective of this thesis was to investigate how recent climate changes affected North American boreal forests, encompassing the variety of of tree sizes, stand developmental stages and stand compositions which typify the boreal region. The aboveground biomass carbon pool had been examined and related to tree mortality.

In the first tree mortality study, I examined how endogenous factors, such as competition, species interaction and aging, affect tree mortality. I simultaneously tested, using Boosted Regression Trees (BRT) models, the effects of an individual's relative size, stand crowding, species interaction and ageing on mortality of *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh. and *Picea mariana* Mill. Data from 109 permanent sampling plots (PSPs) located in Ontario had been used for these analyses. I found that mortality increased significantly with decreasing relative size for all study species, and the size-dependent mortality was stronger for shade-intolerant than for shade-tolerant species. With increasing stand basal area, mortality increased for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana*, but decreased for *Betula papyrifera*. Mortality was higher in stands with more conspecific neighbours for *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, but was lower for *Pinus banksiana*. Mortality also increased with stand age for all species. Furthermore, the size-dependent mortality was stronger in more crowded stands. These results suggest that tree mortality in boreal forest is driven by endogenous factors such as competition, aging, and species interaction.

The objective of the second tree mortality study was to disentangle the effects of climate change and endogenous processes on tree mortality. I conducted individual mortality probability analyses for five major boreal tree species *Populus tremuloides*, *Populus balsamifera* L., *Pinus banksiana*, *Picea mariana*, and *Picea glauca* (Moench)

Voss, using Hierarchical Bayesian logistic regression model (HBLogit). The analyses were based on data from 887 PSPs that covered a wide range of stand developmental stages in the western boreal region, i.e., Alberta and Saskatchewan. I found that both climate change and forest development processes influenced temporal mortality increases. When endogenous factors were considered for all study species, the overall tree mortality increased during study period (1958-2007). Climate change-associated increases in tree mortality were significantly higher in young than old forests. I also found that, over the study period, annual temperature anomaly increased, and climate moisture index anomaly decreased, showing a global-change-type drought. Further analyses revealed that higher increases of tree mortality in younger forests were a result of their higher sensitivity to regional warming and drought.

Additionally, I examined climate change-induced tree mortality using data from 148 PSPs in Manitoba. I partitioned climate change effects from endogenous effects on tree mortality by developing individual tree mortality models using HBLogit. The analyses were conducted for five major boreal tree species *Populus tremuloides*, *Populus balsamifera*, *Pinus banksiana*, *Picea mariana*, and *Picea glauca*,. I found that tree mortality increased over the last three decades. Although there was significant warming in the Manitoba study area (i.e., annual temperature anomaly increased by 0.038 ^{o}C year^{-1} over the study period), there was also an increase in annual climate moisture index anomaly, suggesting that the study area did not experience global-change-type drought. Collectively, the mechanism that led to temporal increases of tree mortality in this area could be different from other areas of western North America where global-change-type drought may be the mechanism for observed increases in tree mortality. The neighborhood analyses provide the evidence that the temporal increases of temperature and water availability likely have increased tree-tree competition on tree mortality and led to a temporal increase of tree mortality.

Finally, I investigated temporal changes of biomass carbon pool and related it to recent increases of tree mortality in western boreal forest region. Using data from 871 permanent plots in Alberta and Saskatchewan, I found that aboveground biomass change (ΔAGB) averaged at 1.11 (95% credible interval (CI), 1.02~1.21) Mg ha^{-1} yr^{-1} over study period (1958-2009), suggesting that the forests have been a strong carbon sink. After accounting for forest age-dependent decreases, I found that ΔAGB has declined at -0.031 (CI, -0.037~-0.024) Mg ha^{-1} yr^{-1} yr^{-1} due to increased tree mortality and reduced growth of surviving trees with no increase in recruitment. The highest decline rate was found for late-successional coniferous forests that dominated by shallow-rooted *Picea* spp. at a rate of -0.074 (CI, -0.093~-0.053) Mg ha^{-1} yr^{-1} yr^{-1}. Further analyses indicated that regional warming and drought were likely contributors to shrinkage of forest aboveground biomass carbon sink in this region.

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Chapter 1. General introduction

Tree mortality is a natural process in forest ecosystems. Among three demographic attributes, i.e., mortality, recruitment and growth, mortality has long been the least understood component because of little available mortality data and relative longevity of tree species (Franklin et al. 1987, Lutz and Halpern 2006). Tree mortality is important in several ways. First, tree mortality affects forest structure and composition. Differences in mortality among tree sizes/ages lead to changes in stand structure (Chen and Popadiouk 2002, Busing 2005), while differences in mortality rates among tree species may lead to changes in species composition (Mueller et al. 2005, Lutz and Halpern 2006, Fauset et al. 2012).

Tree mortality is also important to understanding coexistence of tree species and the maintenance of tree diversity (Janzen 1970, Harms et al. 2000, Condit et al. 2006, Comita et al. 2010). Tree mortality redefines the local community assemblages by altering micro-climatic conditions and creating habitats for newcomers. For instance, a forest gap created by death of large trees changes light condition, which in turn affects understory plant species diversity (Bartels and Chen 2010), while dead tree itself can serve as habitats for decomposers such as fungi (Franklin et al. 1987).

As forest ecosystems play a key role in biosphere-atmosphere interactions, tree mortality likely influences forest ecosystem functions in several ways. Firstly, it could alter the forest surface energy fluxes by changing reflection of solar radiation and latent heat (Bonan 2008). Hydrological fluxes may also be affected by tree mortality through alteration of canopy evapotranspiration, ground drainage and runoff (Anderegg et al.

2013). Furthermore, tree mortality affects the forest carbon uptake and storage by changing forest productivity (Ma et al. 2012).

The causes of individual tree mortality are complex because they involve multiple processes, which sometimes interact (Franklin et al. 1987). A tree could die because of carbon starvation that caused by the respiratory loss larger than photosynthetic gain (Guneralp and Gertner 2007), or failure to allocate sufficient energy to defend against disturbance agents such as pests and herbivores (Loehle 1988). Significant mechanical damages such as breaking, uprooting or crushing, can also lead to death of a tree (Lutz and Halpern 2006, Larson and Franklin 2010). Furthermore, xylem cavitation (hydraulic failure) also could be mechanism driving tree mortality when a tree is under drought condition (McDowell et al. 2008, McDowell et al. 2011). The factors that lead to tree mortality can be categorized into three groups: predisposing factors, inciting factors and contributing factors (Manion 1991). Predisposing factors stress the trees during years or decades, e.g., growth suppression by shading from large trees or poor edaphic location. The effect of predisposing factors on tree mortality is often indicated as a gradual decline of tree vigor or growth before death (e.g., Wyckoff and Clark 2002). Inciting factors lead to quick and intensive tree mortality, for example drought-induced tree mortality (Phillips et al. 2010). Contributing factors are those that could accelerate tree mortality by negatively influencing trees that are already stressed. For example, the presence of forest pests in drought area can lead to higher tree mortality (Marchetti et al. 2011, Gaylord et al. 2013).

In the context of forest development, the causes of tree mortality can be divided into two groups, i.e., endogenous and exogenous factors (Luo and Chen 2011, 2013).

Endogenous factors are determined by the state of forest development. The endogenous factors include tree-tree competition, species interaction and aging (Lutz and Halpern 2006). In contrast to endogenous factors, exogenous factors of tree mortality are independent from forest development such as recent climate changes (van Mantgem et al. 2009).

The goal of this thesis is to examine how the recent climate change has affected tree mortality and its consequences on forest carbon function in central and western boreal forests of North America. To achieve this goal, the aspects of the overarching objective have been disseminated into the following chapters. In chapter 2, I examined how tree mortality is affected by endogenous factors. Chapter 2 provided a foundation for the following two chapters. In chapters 3 and 4, I expanded the analyses by including exogenous factors to examine how recent climate change has affected tree mortality in western and central boreal forests. Finally, in chapter 5 I examined whether recent climate change had altered the biomass carbon pool in western boreal forests, and related the change of biomass carbon to tree mortality.

In this thesis, I employed long-term measured data from permanent sampling plots (PSPs) in central and western boreal forests (Figure 1.1). Since data is longitudinal and violated the assumptions of conventional statistics, more sophisticated modeling methods were used to link tree mortality and its contributors. Boosted Regression Trees (BRT) approach was used in chapter 2. In chapters 3~5, the Bayesian Hierarchical models were used to account for the uncertainties associated with data and parameters.

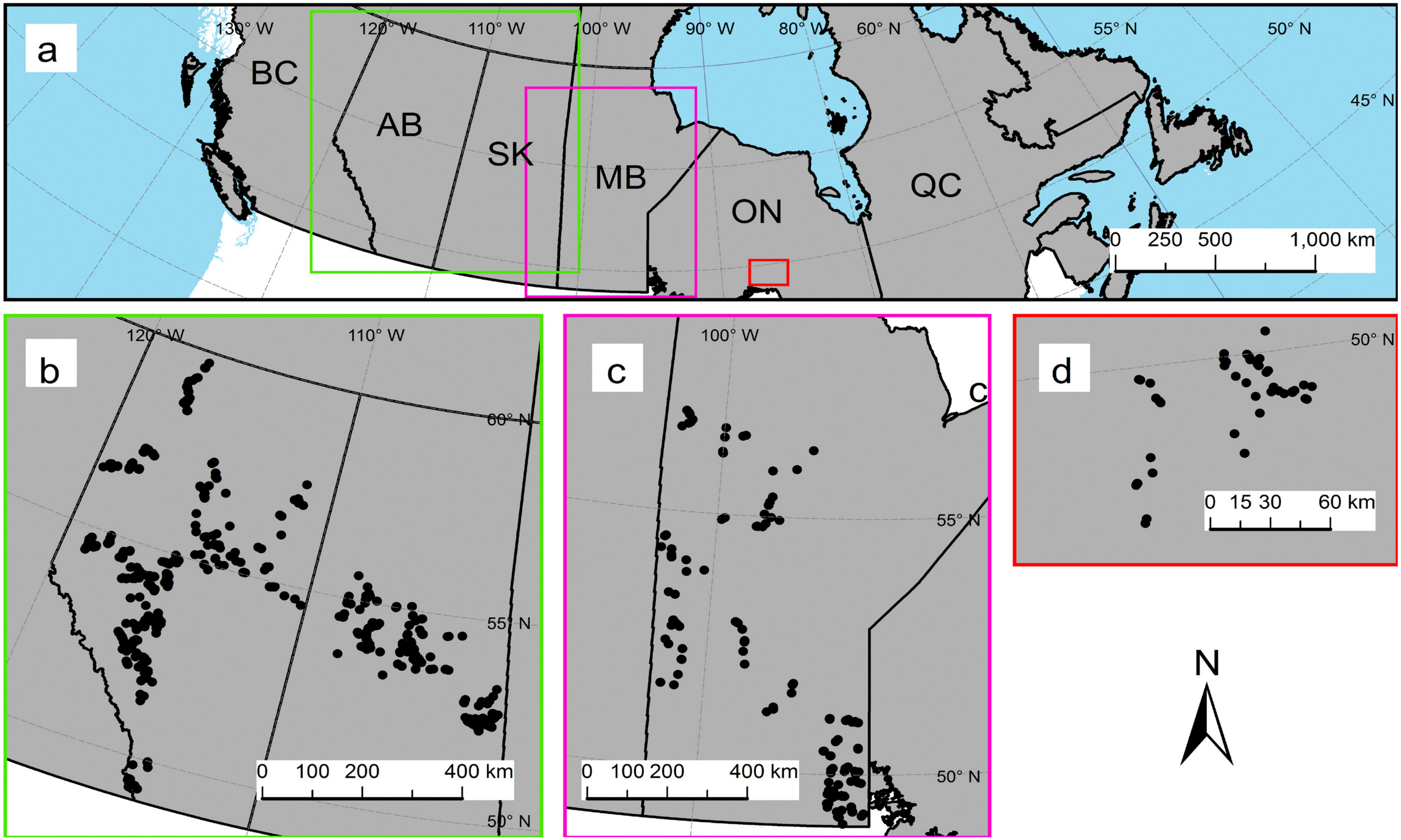


Figure 1. 1. Study area and plot locations. An overview of study area in Canada (a), plot locations for chapter 3 and chapter 5 (b), for chapter 4 (c), and chapter 2 (d).

Chapter 2. Competition, species interaction and ageing control tree mortality in boreal forests

Introduction

Tree mortality is a critical process in forest ecosystems, influencing forest structure, composition and biodiversity (Laurance et al. 2004, Lutz and Halpern 2006, Phillips et al. 2009, Comita et al. 2010). The direct causes of tree mortality are generally understood to be carbon starvation caused by the respiratory losses larger than photosynthetic production (Guneralp and Gertner 2007), failure to allocate sufficient energy to defend against disturbance agents such as pests and herbivores (Loehle 1988), or mechanical damages such as breaking, uprooting or crushing (Lutz and Halpern 2006, Larson and Franklin 2010). A tree also could die as a result of hydraulic failure due to short of water supply (McDowell et al. 2008, McDowell et al. 2011). A major challenge for ecologists is to predict tree mortality over a wide range of environmental conditions. While the metabolic ecology theory predicts that tree mortality is scaled to -1/4 of body mass or -2/3 tree diameter in equilibrium forest communities, where mortality rates nearly equal fecundity rates (Brown et al. 2004, Enquist et al. 2009), in non-equilibrium boreal and temperate forests (Chen and Popadiouk 2002, Franklin et al. 2002), previous studies have focused on competition-driven mortality and typically have been restricted to a limited range of stand developmental stages (Lutz and Halpern 2006) or juvenile trees such as seedlings and saplings under forest canopy (e.g., Kobe et al. 1995, Wyckoff and Clark 2002). Few studies have considered a wide range of tree sizes, stand developmental stages and stand composition types to identify how tree mortality is affected by multiple mechanisms such as competition, species interaction, ageing and their interactions with minor disturbances (Franklin et al. 1987, Peet and Christensen 1987).

Assuming that tree mortality is a result of carbon starvation or failure to tolerate the disturbance agents, and their interactions, regardless of stand development stages, trees with relatively small sizes are expected to experience size-asymmetric competition for light and other resources, and to be more susceptibility to mechanical damages, resulting in a higher mortality (Weiner 1990, Muller-Landau et al. 2006, Larson and Franklin 2010). This asymmetric relationship between mortality and size may differ with species' life-history traits that affect growth, allocation, resource uptake and resource utilization in stressed environments (Schwinning and Weiner 1998). Tree species differ in their ability to survive under shaded environments (Kobe et al. 1995, Wyckoff and Clark 2002) because of their variations in morphological and physiological traits. For example, the lower leaf-mass ratios, lower whole-plant respiration rates, higher plasticity in crown architecture and lower light compensation points of shade-tolerant species allow them a net carbon gain in shaded environments (Niinemets and Valladares 2006). Furthermore, their thicker bark and higher wood densities make them more resistant to disturbance agents (Poorter et al. 2010) and their higher carbohydrate storage in roots and stems leads to a quicker recovery from damages (Canham et al. 1999). Consequently, I hypothesize that mortality is dependent on relative size, but shade-tolerant species present less sensitivity of relative-size-dependent mortality than shade-intolerant species.

Second, stand crowding influences resource uptake, available growing space and crown development of the individual within a stand (Canham et al. 2004, Coates et al. 2009), consequently affecting tree mortality. The higher resource competition in more crowded stands also has below-ground effects since root competition influences the performance of the focal individuals (Schnitzer et al. 2005, Kueffer et al. 2007). Therefore, I hypothesize that individuals within more crowded stands have higher rates of mortality.

Third, intra-specific competition may be stronger than inter-specific competition because individuals of the same species may occupy the same ecological niche, e.g. resource and space. Additionally, facilitation may occur among species (Callaway 1995) by ameliorating environmental variability, altering substrate characteristics, or improving resource use efficiency through mycorrhizal networks. Furthermore, the Janzen–Connell hypothesis (Janzen 1970, Connell et al. 1984) predicts that nearby conspecific trees reduce the focal tree's performance (i.e. survival) in the presence of host-specific pests. For example, the negative plant–soil feedback mediated by soil biota such as soil-borne fungi, bacteria and fauna may be responsible for mortality (Mangan et al. 2010). The individuals' performances may also be reduced by insects associated with conspecific neighbours since they may act as either an attractant or a source of the herbivores. As a result, my third hypothesis is that tree mortality is higher in stands with more conspecific individuals.

Finally, as trees age and grow in size, their physiological functions such as photosynthesis rates decline, resulting in mortality from carbon starvation or minor disturbances (Lugo and Scatena 1996). Furthermore, larger trees may have a higher risk of mortality from limitations imposed by size on water and nutrient transport to their canopy (Domec et al. 2008). However, the ageing-related mortality of tree species has not been adequately studied because most studies covered a small range of ages for tree species, and age information of individual trees is often hard to obtain (Peet and Christensen 1987). In boreal forests, most trees are established following stand-replacing disturbances such as fire, thus they form relatively even-aged stands (Greene et al. 1999) and increasing mortality rates of large trees occur at the time of stand decline (Lugo and Scatena 1996). Consequently, I hypothesize that tree mortality increases with stand age in boreal forests.

In this chapter, I attempt to understand how the mechanisms of competition, species interaction and ageing influence the mortality in boreal forests for four tree species with increasing shade tolerance, i.e. *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh. and *Picea mariana* Mill. Specifically, I tested my four hypotheses by using data from the repeatedly measured permanent sampling plots (PSP) from the Ontario forest inventory program, which covers a wide range of tree sizes, stand compositions and stand ages. To simultaneously test these hypotheses, I used boosted regression tree models to disentangle the influences of relative tree size within a stand (relative basal area, RBA), stand basal area (SBA), the ratio of focal species' basal area to stand basal area (rFSBA), and stand age (SA) on tree mortality.

Method and materials

Study area and data collection

The study area is located in the eastern-central part of the Canadian Boreal Shield, near the town of Longlac, Ontario, Canada (49º24'-50º10'N, 85º93'-87º24'W) (Figure 1.1). Elevation ranges from 290 m to 411 m a.s.l. Mean annual precipitation in 1971-

2000 was ~760 mm, of which ~214 mm was snow (Geraldton A meteorological station) (Environment Canada2005). Mean annual temperature in 1971-2000 was ~0.3 °C. This area is a largely forested glacial region, with little topographic relief, interspersed with lakes, rivers, marshes and bogs. Forest soils originate from a variety of modes of glacial deposition, including tills, glaciofluvial, glaciolacustrine and organic deposits. The major stand-replacing disturbance in this area is fire with an estimated average fire return interval of ~100 years (Senici et al. 2010). In addition to the study species, *Populus balsamifera* L., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill. and *Thuja occidentalis* L. occur as minor components in stands.

A total of 123 plots originating from stand-replacing fire, each measuring 809 m^2 in area, were established from 1952 to 1965 by the Kimberly–Clark Canada. These plots were located on mesic sites, the most productive segment of the boreal forest; they were established in stands (> 1 ha in area) that were visually homogeneous in structure and composition, and were at least 100 m from any openings to minimize edge effects. The plots, if not damaged by fire or cutting, were re-measured until 2000 at varying, but mostly 5-year, intervals. Trees larger than 2 cm in diameter at breast height (DBH) were identified by species, tagged, and recorded as either dead or alive at each measurement. Diameter at breast height was measured for all live trees at each census. When a plot experienced a major disturbance from fire, windthrow, outbreak of insects, or cutting since its establishment, it was abandoned from further measurement.

To eliminate the effect of different measurement lengths on mortality, sample plots with measurements occurring in 5-year intervals were used. In this chapter, analyses were limited to *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and

Picea mariana because sample sizes of other species were too small to conduct a meaningful analysis. Of a total of 123 plots, 109 plots, each with 2 to 5 measurements, were used. The total observations for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana* were 20,157, 5743, 2924 and 31,413 with mortality cases being 1778, 716, 217 and 2724, respectively (Table 2.1). The numbers of plots involved were 91, 51, 48 and 98 for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively (Appendix 2.1). The size distribution analyses following the method by Enquist *et al.* (2009) indicated that these stands are non-equilibrium stands (Appendix 2.2).

Explanatory variables

All explanatory variables were calculated using the preceding measurements of each interval. Since the realized resource uptake for individuals depends not only on individual's uptake ability but also on resource availability for individuals, I used relative size and stand crowding as proxies for these two factors. I used relative size, rather than the absolute size (i.e. DBH) used in studies in equilibrium forests (Brown et al. 2004, Muller-Landau et al. 2006), because this study covered a wide range of stand developmental stages, and relative size better reflects the competitiveness of individuals when encountering other individuals in the same forest community. For example, I observed that trees with 16-cm DBH were the largest in some ~38 year-old plots, but were smallest in some ~100 year-old plots. The correlation between DBH and height indicated that the basal area can be utilized as approximate plant biomass. Thus, I used relative basal area (RBA), a ratio of a subject tree's basal area to the mean tree basal area at each measurement of the stand, to represent the relative size. To examine whether DBH has additional explanatory power in addition to RBA, I added DBH as an additional explanatory variable to my models, and the resulted models had the same or less predictive ability (Appendix 2.3). Thus, DBH was not included in the final models. Stand crowding determines the average resource availability for trees within a stand. The higher stand crowding suggests fewer resources available per individual. As in other empirical studies (e.g., Coomes and Allen 2007a), I used stand basal area (SBA) as a surrogate for stand crowding.

To take into account the effect of species interactions on mortality, I used the ratio of focal species basal area to stand basal area (rFSBA). Stand age (SA) was derived from the plot establishment records (Table 2.1).

Table 2. 1. Summary statistics (mean±1 SD and range in brackets) for explanatory variables. The explanatory variables were calculated based on the previous census (5 years before the observed tree's status). The summary statistics for the stand-level explanatory variables (SBA, rFSBA, SA and STD) may be identical for live and dead trees because stands may include both live and dead trees

Explanatory variable	*Pinus banksiana*		*Populus tremuloides*		*Betula papyrifera*		*Picea mariana*	
	Live trees	Dead trees	Live trees	Dead trees	Live trees	Dead trees	Live trees	Dead trees
	n = 18379	*n* = 1778	*n* = 5027	*n* = 716	*n* = 2707	*n* = 217	*n* = 28689	*n* = 2724
RBA	1.34±0.71	0.66±0.48	1.21±0.76	0.50±0.42	0.52±0.45	0.30±0.22	0.89±0.57	0.52±0.42
	(0.02~9.65)	(0.05~6.01)	(0.02~5.70)	(0.03~3.72)	(0.03~3.89)	(0.04~1.06)	(0.01~5.28)	(0.02~2.72)
SBA	34.90±6.02	34.75±6.11	36.43±6.25	35.21±5.88	37.01±5.25	37.34±5.59	38.13±6.72	38.97±6.41
	(16.6~53.4)	(16.6~52.6)	(17.6~53.4)	(17.6~52.6)	(20.6~50.8)	(23.9~49.9)	(16.6~53.4)	(17.6~53.4)
rFSBA	0.76±0.24	0.78±0.24	0.58±0.36	0.60±0.38	0.13±0.12	0.15±0.12	0.67±0.28	0.71±0.25
	(0.002~1.00)	(0.003~1.00)	(0.003~1.00)	(0.009~1.00)	(0.001~0.38)	(0.001~0.38)	(0.001~1.00)	(0.005~1.00)
SA	75.86±28.50	70.78±30.16	66.50±22.96	56.50±21.00	73.53±24.15	82.55±24.60	93.92±28.20	96.01±27.99
	(34~154)	(34~154)	(34~120)	(34~115)	(34~154)	(35~154)	(34~155)	(34~155)
STD	2515±1325	2867±1476	2236±1125	2690±1159	2258±1195	1981±992	2732±945	2777±924
	(815~6461)	(815~6461)	(519~6462)	(519~5201)	(519~5226)	(581~5226)	(581~5226)	(741~5226)

Statistical analysis

I used boosted regression trees (BRT) to model the relationships between explanatory variables and the response variable. Boosted regression trees combines two simple algorithms, regression trees and boosting (Elith et al. 2008). Specifically, a large number of simple trees are produced using recursive binary splits based on the value of a single predictor variable at each node that results in the two most homogeneous subsets of the response variable. Each tree is built from a random subset of the data, which is known as bagging, and introduces stochasticity to the model. The terms are fitted in a stage-wise manner by building trees from the residuals of the prior collection of trees, thereby allowing the model to put more emphasis on the points that are more difficult to classify. The resulting BRT model can be viewed as an additive regression model in which every term is a tree. More information about BRT can be found in references (De'ath 2007, Elith et al. 2008, Hastie et al. 2008).

Boosted regression trees (BRT) was chosen for my analyses because of the following advantages. First, with a "Bernoulli" error structure (Ridgeway 2007), BRT can be employed to analyse discrete data like ours (i.e. live trees or dead trees) (Elith et al. 2008). Second, as a tree-based method, BRT automatically takes into account interactions among variables (i.e. every successive tree node constitutes a potential interaction) and the nonlinearity between the dependent variable and the predictors, without the need of data transformation. Third, BRT is able to deal with multi-dimensionality of predictors and disentangle the effect for each variable.

There are three input settings for BRT models: tree complexity, learning rate and bagging. Tree complexity consists of the number of nodes or variable interactions in each tree. The learning rate is shrinkage parameter, and it regulates the amount of learning possible in each tree. Typically, a low learning rate, used in conjunction with a large number of trees, enables BRT to generate highly complex response functions. A fast learning rate requires fewer trees, but is subject to more noise induced by the bagging and a lack of smoothness in the response functions. Bagging fraction specifies the proportion of data to be randomly sampled without replacement for sequent fitting, in order to introduce stochasticity into BRT models.

For each species, BRTs with a range of values for tree complexity (2, 3, 4), learning rate (0.01, 0.005, 0.001) and a bagging fraction 0.5 or 0.75 were fitted. To prevent over-fitting the training data, a cross-validation method was used (Hastie et al. 2008). I used default 10-fold cross-validation procedures described by Elith et al.(2008). The model with the smallest predictive error—which represents the unexplained variation by the model—for cross-validation was considered the best model. Finally, based on the overall trend of mortality probability against each predictor, the monotonic BRT models were also fitted, using BRT settings for the best model, to facilitate the interpretation of the relationship between response variable and each predictor. The predictive performances of the monotonic BRT models were also assessed. The BRTs were computed in R 2.10.1 (R Development Core Team 2009) with the '*gbm*' package using a Bernoulli error structure (Ridgeway 2007), and with *brt.functions* written by Elith *et al.* (2008).

I interpreted the results by examining the relative influence of predictors from the best model, the predictive value plot of response to individual predictors, and the main interactions in each model (De'ath 2007, Elith et al. 2008). The relative influence of each predictor in the model was measured based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman and Meulman 2003). Predictive value plot of a predictor quantifies the relationship between the predictor in the model and the response variable after accounting for the effects of other predictors. Finally, I conservatively reported top-ranked interactions among predictors in each monotonically fitted model, because, first, BRT provides the relative strength of interaction rather than the absolute value provided by traditional statistical methods (e.g. p value in logistic regression) and second, the accommodation of outliers in BRT might introduce more noise to a best model than to a monotonically fitted model. The strength of interaction was determined following De'ath (2007) and Elith *et al.* (2008). Essentially, predictions were simulated from BRT using a temporary data set, which contained involved pair variables representing combinations of values at fixed intervals along each of their range, as well as other variables of their respective means. Then, the predictions were related to the marginal predictors using a linear model and fitting the marginal predictors as factors. The residual variance in this linear model indicated the relative strength of the interactions fitted by BRT.

To determine the sensitivity of the size-dependent mortality among species, I compared linear regression slopes of predicted mortality probability against RBA. A greater slope indicates more sensitivity between mortality and RBA. At equal intervals of RBA, I chose 1000 data points of predicted mortality probability against RBA from each best model. Then linear regression analyses were conducted with the RBA range from the smallest value up to the value at which the predicted mortality probability became consistent. I calculated 95% confidence intervals for slopes to facilitate the comparison among species. Since *Pinus banksiana* had an initial increase of the marginal effect size of RBA, I developed slopes both with and without the initial increase of marginal effect size.

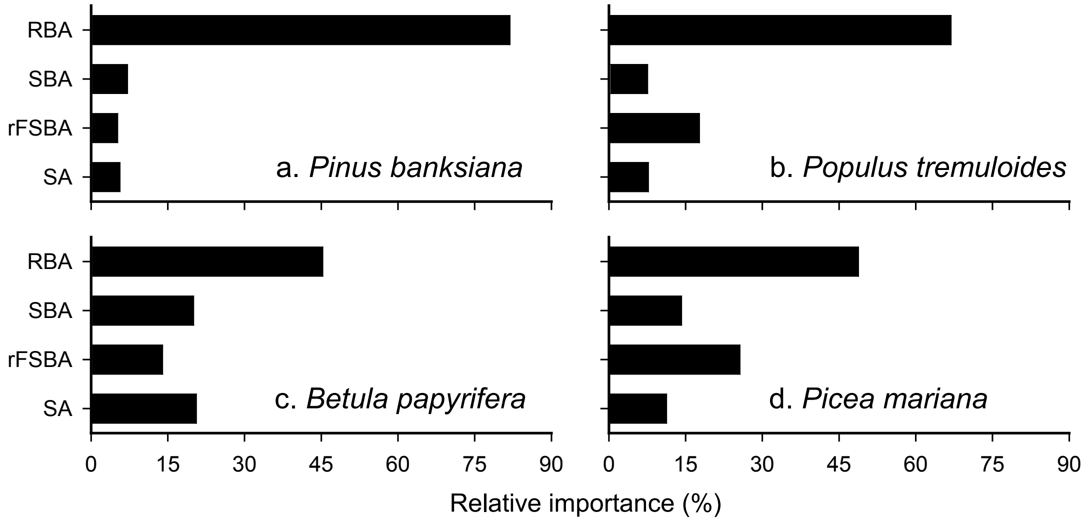


Figure 2. 1. The relative influences of independent variables on tree mortality probability. The total values add to 100% for each model. In each model, predictors with larger values in relative influence have more explanatory power.

Results

The predictive errors of the best models were 0.427, 0.529, 0.458 and 0.489 for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively (Table 2.2); these models predicted nearly half of the observed variation in mortality. These models also had high discriminate power as indicated by the area under Receiver Operating Characteristic curve (AUC) ≥ 0.78 for crossing-validation data (Table 2.2). The monotonically fitted models were also able to explain nearly half observed variation of response variables and had high discriminate power (Table 2.2). But the monotonically fitted models slightly decreased the model predictive performances, indicated by a slight increase of predictive error and a decrease of AUC.

Size-dependent mortality

Relative basal area (RBA) was the most important variable among predictors, accounting for 81.94%, 66.93%, 45.31% and 48.81% relative influence on mortality of *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively (Figure 2.1). For all species, the predicted value plots from the fitted model indicated that, when other predictors were held constant, individuals with small RBA generally had a higher probability of mortality (Figures 2.2a-d). The RBA values at which the marginal effect sizes became constant were ~1.29, ~1.29, ~1.08 and ~1.88 for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively. However, for *Pinus banksiana*, the mortality probability increased initially to ~0.18 of RBA (Figure 2.2a).

Linear regressions fitted data very well as indicated by the high r^2 and narrow confidence interval (Table 2.3). The regression analyses between predicted mortality probability and RBA showed that, with or without the initial increase of predicted mortality probability for *Pinus banksiana*, the sensitivity of RBA-dependent mortality was the highest for two shade-intolerant species, *Pinus banksiana* and *Populus tremuloides*. The sensitivity of RBA-dependent mortality for *Betula papyrifera* was medium, and that for *Picea mariana* was the lowest. With 0.1 unit of increase in RBA, the decline of predicted mortality probability was about 0.417, 0.473, 0.453, 0.218 and 0.152 for *Pinus banksiana* (with initial increase), *Pinus banksiana* (without initial increase), *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively (Table 2.3). The 95% confidence intervals for slopes did not overlap among species except for two shade-intolerant species, *Pinus banksiana* and *Populus tremuloides* (Table 2.3).

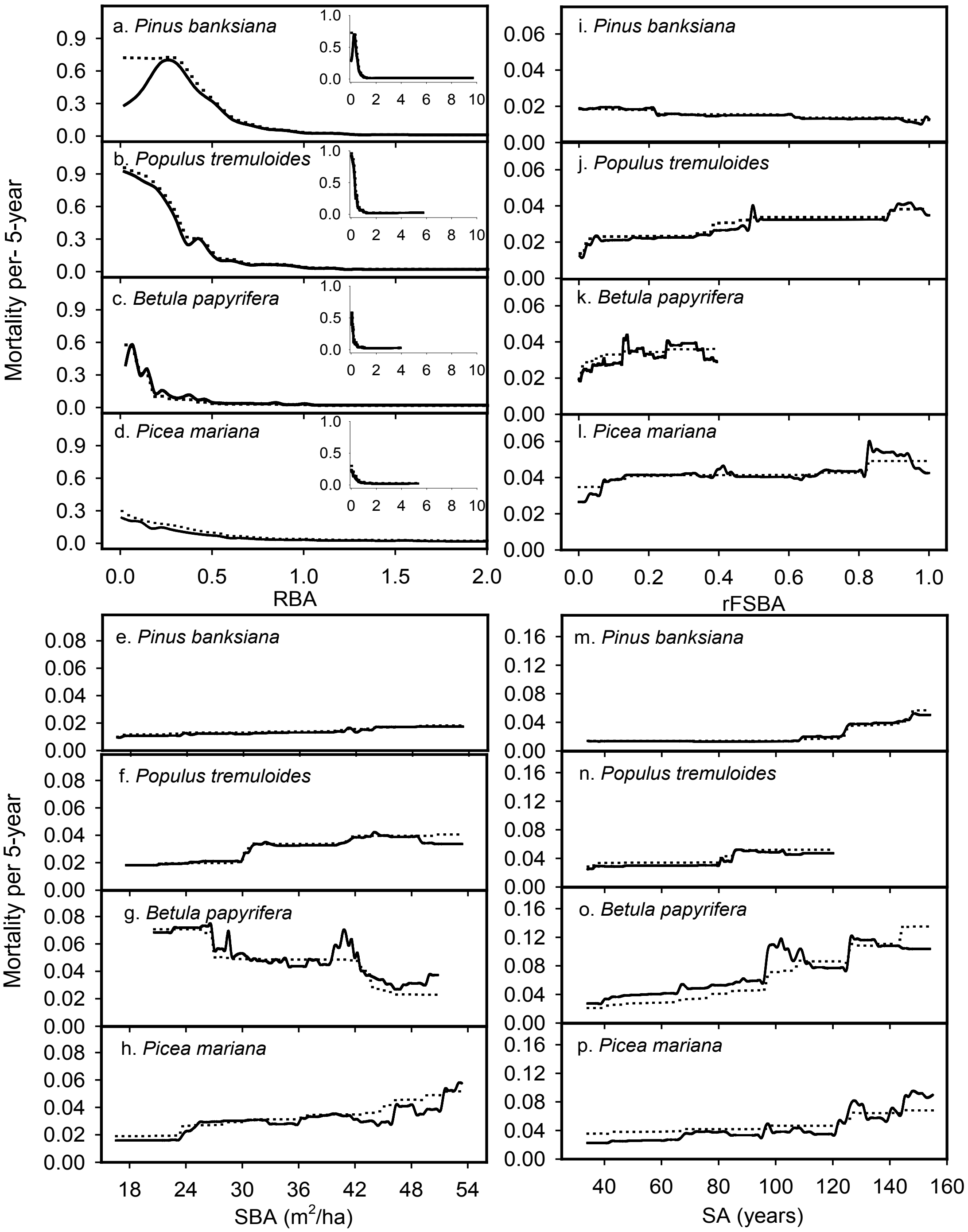


Figure 2. 2. Predicted mortality per 5-year in relation to independent variables. Inset graphs of a-d show predicted 5-year mortality probability across the full range of observed RBA. The black lines indicate the predicted values from best models, and dotted lines indicate the predicted values from monotonically fitted models.

Table 2. 2. Optimal settings and predictive performances of boosted regression trees. The best models (BM) were determined by smallest mean predictive error for crossing-validation data (CV predictive error). CV AUC is the area under Receiver Operating Characteristic curve (ROC) for crossing-validation data. The MFM is monotonically fitted model, using BRT settings for best model of each species

Tree species	Learning rate	Tree complexity	Bag fraction	Number of trees		CV predictive error		CV AUC	
				BM	MFM	BM	MFM	BM	MFM
Pinus banksiana	0.01	4	0.75	1750	900	0.427	0.433	0.87	0.86
Populus tremuloides	0.01	4	0.50	1350	750	0.529	0.544	0.87	0.86
Betula papyrifera	0.01	4	0.50	1150	450	0.458	0.469	0.78	0.77
Picea mariana	0.01	4	0.75	3050	1450	0.489	0.510	0.80	0.77

Table 2. 3. Sensitivity analysis of size-dependent mortality using linear regression between predicted mortality probability and relative basal area (RBA). A steeper slope indicates higher sensitivity of size-dependent mortality

Tree species	Range of RBA	Slope	95% Confidence interval		r^2
			Lower	Upper	
Pinus banksiana (with initial increase)	0.02~1.29	-4.17	-4.40	-3.94	0.91
Pinus banksiana (without initial increase)	0.18~1.29	-4.73	-4.91	-4.56	0.96
Populus tremuloides	0.02~1.29	-4.53	-4.73	-4.32	0.89
Betula papyrifera	0.03~1.08	-2.18	-2.31	-2.05	0.81
Picea mariana	0.01~1.88	-1.52	-1.58	-1.46	0.87

Crowding-induced mortality

The relative influence of SBA on mortality was 7.15%, 7.6%, 20.08% and 14.22% for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, respectively (Figure 2.1). Two general trends of mortality against SBA are shown in predicted value plots (Figures 2.2e-h). For *Pinus banksiana*, *Populus tremuloides* and *Picea mariana*, mortality increased with SBA (Figures 2.2e, 2.2f, and 2.2h). The mortality of *Pinus banksiana* gradually increased with SBA and reached its plateau at ~46 m^2 ha^{-1} in SBA (Figure 2.2e). The mortality of *Populus tremuloides* and *Picea mariana* dramatically increased at ~30 m^2 ha^{-1} and ~24 m^2 ha^{-1} in SBA, respectively, and remained at a higher level (Figures 2.2f and 2.2h). Mortality of *Betula papyrifera*, however, decreased with SBA (Figure 2.2g).

Specific interactions on mortality

The ratio of focal species' basal area to stand basal area had the weakest influence on mortality among the four predictors for *Pinus banksiana* and *Betula papyrifera* with 5.24% and 14% in relative importance, respectively (Figures 2.1a and 2.1c). The ratio of focal species' basal area to stand basal area ranked as the second strongest predictor in the models for *Populus tremuloides* and *Picea mariana*, accounting for 17.72% and 25.66% in relative importance, respectively (Figures 2.1b and 2.1d). The predicted value plots indicated that the mortality of *Pinus banksiana* decreased, whereas those of *Populus tremuloides* and *Picea mariana* increased with increasing rFSBA (Figures 2.2j-l). Even with a narrow range of rFSBA, *Betula papyrifera* presented an increase of mortality with rFSBA (Figure 2.2k).

Age-related mortality

For *Pinus banksiana* and *Populus tremuloides*, the relative influence of SA on mortality was weak as indicated by its small relative influence value (<8%) (Figures 2.1a-b). For *Betula papyrifera*, SA had the second strongest influence on mortality with 20.61% in relative influence (Figure 2.1c). Stand age was the weakest variable in the model for *Picea mariana* with 11.31% in relative influence (Figure 2.1d). The predicted value plots showed that mortality increased with stand age for all study species (Figures 2.2m-p). The patterns, however, differed among the study species. For *Pinus banksiana*, mortality increased in stands > 110 years of age with an apparent increase at ~120 in SA (Figure 2.2m). For *Populus tremuloides*, mortality had a steep increase between 80 and 90 years and then remained at the higher level with a few fluctuations (Figure 2.2n). For *Betula papyrifera*, mortality increased through the whole range of stand age (Figure 2.3o). For *Picea mariana*, mortality began to increase at a stand age of ~125 years (Figure 2.2p).

Main interactions

In the monotonically fitted model, the interactions between RBA and SBA were found for all species (Figures 2.3a-d). For *Pinus banksiana*, *Populus tremuloides* and *Picea mariana*, individuals with smaller RBA had a higher probability of mortality in stands with higher SBA (Figures 2.3a-b, and 2.3d), but *Betula papyrifera* had a lower probability of mortality in the stands with higher SBA (Figure 2.3c). Interaction was also found between RBA and rFSBA for *Populus tremuloides* and *Picea mariana*, i.e. the individuals with smaller RBA had a higher probability of mortality in stands with higher rFSBA (Figures 2.3e and 2.3g). For *Betula papyrifera*, mortality probability was higher for individuals in stands with a combination of less SBA and higher SA (Figure 2.3f).

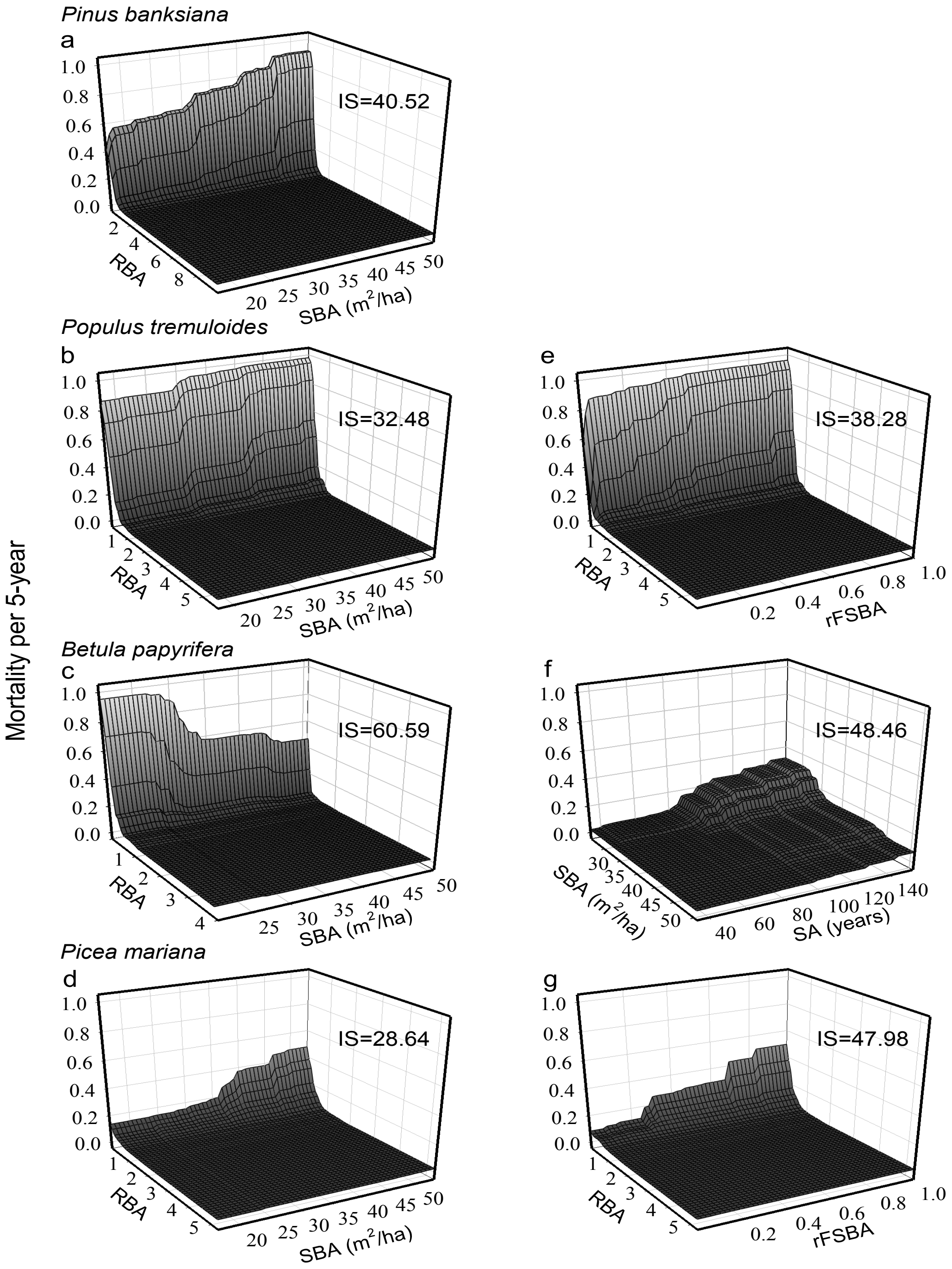


Figure 2. 3. Predicted mortality per 5-year showing the main interactions in the monotonically fitted BRT model. IS is the interaction size, indicating relative interaction strength in the model.

Discussion

Size-dependent mortality

The first hypothesis that tree mortality is dependent on relative size is strongly supported, i.e. smaller individuals have higher mortality, for all studied species across a wide range of stand ages and forest compositions. My results are in agreement with other studies reporting that higher mortality occurs at the lower end of size (Chen et al. 2008, Kunstler et al. 2009). The effect of relative size on mortality may be explained by the size-dependent resource uptake ability (Brown et al. 2004), resource availability (Weiner 1990, Muller-Landau et al. 2006), external-stress susceptibility (Loehle 1988) and their interactions. In the study area, forest tent caterpillar (*Malacosoma disstria* Hbn.), spruce budworm (*Choristoneura fumiferana* Clem.) and *Armillaria* root disease (*Armillaria* spp.) also appear to be common agents of tree mortality. Browsing by mammals, such as moose (*Alces alces* L.), white-tailed deer (*Odocoileus virginianus* Zimmerman), porcupine (*Erethizon dorsatum* L.) and hares (*Lepus americanus* Erxleben) may also kill small trees.

Also, as I hypothesized, the sensitivity of size-dependent mortality generally decreased with increasing shade tolerance of the studied species. The differences of the size-dependent mortality sensitivity may reflect variations in species' responses to resource limitations and (or) disturbance agents among species. Overall, my findings support that shade-intolerant species require higher light availability to maintain carbon balance (Leverenz 1996). Alternatively, smaller carbon storage in roots and stems (Canham et al. 1999) and lower wood density (Poorter et al. 2010) make shade-intolerant species more susceptible to disturbance agents such as crashing or browsing.

Crowding-induced mortality

My second hypothesis that tree mortality increases with stand basal area is supported by the findings for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana*. My results are consistent with those in temperate forests, i.e. crowding has a positive effect on tree mortality (Dwyer et al. 2010) and a negative effect on growth (Coates et al. 2009). The crowding-induced mortality may reflect competition for below-ground soil resources and above-ground light, and for space both below and above ground (Canham et al. 2004).

The interactions between the relative basal area of the subject tree within a stand and stand basal area in the models for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* suggest that small individuals tend to die due to stand-crowding competition. This finding may be understood as the small individuals receiving less resource in more crowded stands. Given that a tree's crown is scaled with its basal area and more crowded in a stand (Enquist and Niklas 2002), an individual in the understory is expected to receive less light under a denser canopy.

It is not clear why mortality of *Betula papyrifera* decreased with increasing stand basal area. There are two possible explanations. In less crowded stands that are described by stand basal area of the tree layer, higher mortality of *Betula papyrifera* trees was a result of competition with tall shrubs such as beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.), which are most commonly associated with *Betula papyrifera* in North American boreal mixed-wood forests (Chen and Popadiouk 2002, Hart and Chen 2008). Alternatively, since moose and other mammals feed to a large extent on *B.* spp. (Danell et al. 1985), higher mortality of smallsized *Betula papyrifera* trees could be a result of more intense browsing in less crowded stands due to better mobility and higher abundance of edible shrubs.

Species interactions and mortality

The increase of tree mortality of *Populus tremuloides*, *Betula papyrifera* and *Picea mariana* as their conspecific component increases supports my hypothesis that a negative conspecific interaction promotes tree mortality. The negative effects of conspecific neighbours on tree mortality are reported to be an important mechanism to promoting species coexistence and diversity in tropical forests (Janzen 1970, Connell et al. 1984, Comita et al. 2010). The mortality increase in stands with more conspecific individuals may be explained by the following mechanisms. First, intra-specific competition may be stronger than inter-specific competition as a result of possible inter-specific niche separation, e.g. temporal niche separation may occur between *Populus tremuloides* and *Picea mariana* in that the former has leaves only in mid-summer and the latter tends to photosynthesize for six months a year. Second, inter-specific facilitation may occur, e.g. the presence of *Populus tremuloides* can improve the performance of *Picea mariana* by delaying the paludification process and increasing surface soil concentrations of exchangeable cations (Fenton et al. 2005, Legare et al. 2005). Third, Janzen–Connell effects may reduce the performance of individuals through negative plant–soil feedback and above-ground accumulation of species-specific enemies. Although few studies have reported the Janzen–Connell effects in boreal forests, studies conducted in tropical and temperate forests suggest that the below-ground plant–soil feedback is a key driver for coexistence (Comita et al. 2010, Mangan et al. 2010). Regardless of the specific mechanisms evolved, this study demonstrates that individuals in stands with more conspecific neighbours experience higher mortality.

In contrast to my hypothesis, *Pinus banksiana* presented a slight decrease of mortality with increasing ratios of its basal area to stand basal area. Lower mortality has also been found for other species when surrounded by more conspecific individuals (Das et al. 2008). A potential explanation is that faster-growing *Populus tremuloides* over-shades highly shade-intolerant *Pinus banksiana*, leading to higher mortality of *Pinus banksiana*, because *Pinus banksiana* is mostly mixed with *Populus tremuloides* when it is a minor component in my data.

While most studies focus on the negative intra-specific effect on trees at early stages, i.e. seedlings and saplings (Comita et al. 2010), and others indicate that such an effect occurs for all trees (Peters 2003, Gonzalez et al. 2010), my results suggest that these negative effects are stronger for smaller trees of *Populus tremuloides* and *Picea mariana*, indicated by interactions between relative basal area and the ratio of focal species basal area to stand basal area. The results demonstrate that the individuals under stressed conditions have a higher probability of mortality as a result of the negative effects from conspecific neighbours. My results, however, do not show this pattern for *Betula papyrifera*, probably due to its narrow range of rFSBA (i.e. from ~0 to ~0.4).

Age-related mortality

My results support the fourth hypothesis that mortality increases with stand age in boreal forests. It is intuitive that when stands age, larger trees die (Coomes and Allen 2007b), contributing to coarse woody debris (Brassard et al. 2008) and facilitating canopy succession (Taylor and Chen 2011, Chen and Taylor 2012). Age-related mortality is determined by a species' genetics and its interaction with the environment. Since the sites are similar for all studied species, my results appear to reflect both a genetic-driven process and its interaction with disturbance. The increase in the onsets of mortality in these species appears to be consistent with their documented autecology (Burns and Honkala 1990). The presence of disturbance may be the reason for fluctuations of mortality probability against stand age for *Betula papyrifera* and *Picea mariana*, because my data include plots with minor disturbances and these two species are susceptible to forest tent caterpillar and spruce budworm, respectively (Taylor and Chen 2011, Chen and Taylor 2012).

For shallow-rooted *Betula papyrifera*, I found an interactive response of mortality to stand age and stand basal area, i.e. trees in older stands with less stand basal area had a higher mortality rate. This result may be attributable to the windthrow-caused mortality of large individuals in less crowded stands, because windthrow risk is typically higher in less crowded stands (Thorpe et al. 2008).

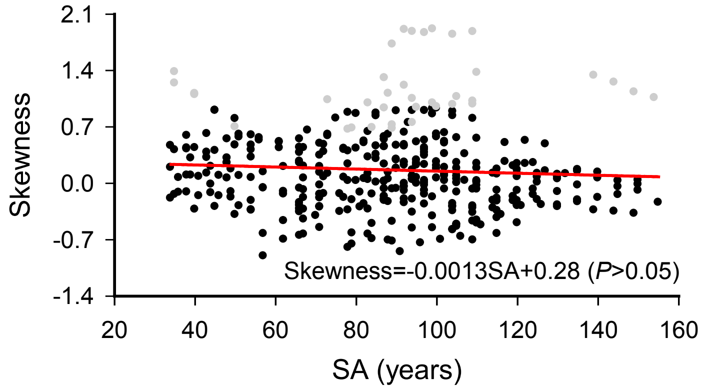
Appendices

Appendix 2. 1. Summary statistics of study plots for the four study species.

Species	Number of plots	Range of the number of measurements	DBH range (cm)	Stand age range (years)
Pinus banksiana	91	2~5	2.0~39.9	34~154
Populus tremuloides	51	2~5	2.0~50.8	34~120
Betula papyrifera	48	2~5	2.0~33.5	34~154
Picea mariana	98	2~5	2.0~33.0	34~155

Appendix 2. 2. DBH distribution for study plots.

The below figure shows that DBH in 92% of the study plots was normally distributed based on the Shapiro-Wilk test. Furthermore, in contrast to the metabolic ecology theory (MET) prediction, i.e., the old forests tend to be equilibrium, the skewness of DBH distribution of my plots did not change with stand age. The solid and hollow circles indicate that the DBH distribution of a measurement passed or failed the Shapiro-Wilk test at a critical α =0.05, respectively.



Appendix 2. 3. An examination of independent influence of DBH on tree mortality. Predictive performance of BRT models with RBA, SBA, FSBA and SA versus those with DBH, SBA, FSBA, SA, and those with DBH, SBA, FSBA, SA, and RBA as explanatory variables.

Tree species	Predictors	Number of trees	CV Predictive error (SE)	CV AUC (SE)
Pinus banksiana	RBA+SBA+FSBA+SA	1750	0.427 (0.005)	0.87 (0.004)
	DBH+SBA+FSBA+SA	3350	0.432 (0.005)	0.86 (0.005)
	RBA +SBA+FSBA+SA+DBH	1750	0.428 (0.006)	0.87 (0.005)
Populus tremuloides	RBA+SBA+FSBA+SA	1350	0.529 (0.010)	0.87 (0.006)
	DBH+SBA+FSBA+SA	1450	0.532 (0.009)	0.86 (0.006)
	RBA +SBA+FSBA+SA+DBH	1150	0.531 (0.011)	0.87 (0.007)
Betula papyrifera	RBA+SBA+FSBA+SA	1150	0.458 (0.009)	0.78 (0.018)
	DBH+SBA+FSBA+SA	1300	0.462 (0.008)	0.78 (0.013)
	RBA +SBA+FSBA+SA+DBH	1250	0.460 (0.011)	0.77 (0.016)
Picea mariana	RBA+SBA+FSBA+SA	3050	0.489 (0.003)	0.80 (0.005)
	DBH+SBA+FSBA+SA	3450	0.493 (0.003)	0.80 (0.004)
	RBA +SBA+FSBA+SA+DBH	3150	0.489 (0.004)	0.80 (0.006)

Abbreviations are: RBA, relative basal area; SBA, stand basal area; FSBA, ratio of focal species basal area to stand basal area; SA, stand age; DBH, diameter at breast-height; CV, cross validation; SE, standard error; AUC, the area under the receiver operating characteristic curve.

Chapter 3. Observations from old forests underestimate climate change effects on tree mortality

Introduction

Observational studies have relied on old forests to quantify temporal trends in background tree mortality, and have shown that tree mortality has increased with recent global warming, increasing atmospheric CO_2, and decreasing water availability in tropical, temperate, and boreal forests (Phillips and Gentry 1994, Phillips et al. 2004, van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Peng et al. 2011). Old forests are assumed to be in an equilibrium state where tree mortality is matched by recruitment, and temporal changes in tree mortality at the forest level due to endogenous processes are assumed to be weak at this stage of stand development (Chen and Popadiouk 2002, Franklin et al. 2002). However, whether there is ever equilibrium is a contentious issue (Connell and Slatyer 1977). Although the effects of competition estimated by temporal changes of stand basal area and stand density on tree mortality have been investigated in some previous studies (van Mantgem et al. 2009, Peng et al. 2011), conspecific negative density-dependence and tree aging could also influence tree dynamics (Luo and Chen 2011, Johnson et al. 2012). Furthermore, the temporal increase of tree mortality could be driven by stand development processes, but not necessarily climate change (Lutz and Halpern 2006, Thorpe and Daniels 2012). Unfortunately, previous studies have used unsuitable statistical methods that marginalize either climate or non-climate drivers for longitudinal data in which these drivers are highly correlated (Brown et al. 2011). Therefore, the relative roles that climate change and stand development processes play on the temporal changes in tree mortality remain uncertain.

Furthermore, climate change-associated tree mortality increases in old forests have been used to represent the tree mortality response of regional forests to climate change (Birdsey and Pan 2011), based on the assumption that effects of climate change on tree mortality are the same for young and old forests. However, this assumption has not been specifically tested. Verification of the assumption is essential for disturbance-driven ecosystems such as boreal forests. Due to high fire frequency, the boreal forests are a mosaic of stands at various developmental stages with old forests accounting for only a small portion of the landscape (Weir et al. 2000, Pan et al. 2011a). With a predicted increase of fire frequency associated with global warming, the mean age of the boreal forests is expected to decrease, as will the portion of old forests (Fauria and Johnson 2008). Thus, understanding how young forests respond to climate change is essential to predicting how boreal forests will respond to future climate change. If tree mortality responses to climate change differ between young and old forests, increased tree mortality based on old forests will be biased for regional forest predictions.

In this chapter, I analyzed tree mortality patterns of boreal tree species in western Canada using 887 permanent sample plots measured between 1958 and 2007. To account for uncertainties in sampling, models, and parameters, I used Bayesian models (Clark 2003, Wikle 2003) to disentangle endogenous (stand development) and exogenous (year, temperature anomaly, or drought) effects on individual tree mortality for five major boreal tree species, *Populus tremuloides* Michx., *Populus balsamifera* L., *Pinus banksiana* Lamb., *Picea mariana* Mill., and *Picea glauca* (Moench) Voss. I tested the assumption that tree mortality increases associated with climate change do not differ with forest age. I also examined whether tree mortality increases are linked to recent regional warming and its negative consequence on water availability. I show that both climate change and forest development processes influence temporal mortality increases, climate change-associated increases are significantly higher in young than old forests, and higher increases in younger forests are a result of their higher sensitivity to regional warming and drought. Furthermore, climate change-associated mortality increases are stronger for moist-habitat adapted *Populus balsamifera* and late-successional *Picea mariana* and *Picea glauca* than *Populus tremuloides* and *Pinus banksiana.*

Method and materials

Study area and the forest inventory data

The study area is located in Alberta and Saskatchewan in western Canada, ranging from 49.01 to 59.73 in latitude and from -101.74 to -119.66 in longitude (Figure 1.1). Elevation ranges from 260 m to 2,073 m above sea level (a.s.l.). Mean annual temperature and mean annual precipitation between 1950 and 2007 varied from -2.38 °C to 4.08 °C and from 365 mm to 1,184 mm, respectively. The major stand-replacing disturbance of the area is wildfire, with a fire return interval (FRI) varying temporally and spatially from 15 to 90 years (Larsen 1997, Weir et al. 2000). A total of 3,006 permanent sampling plots (PSP) were established in the study area mostly during the 1960s and 1970s. Plot sizes varied from 405 m^2 to 8092 m^2. These plots were established in stands (>1 ha in area) that were visually homogeneous in structure and composition and were at least 100 m from any openings to minimize edge effects. The plots were re-measured until 2007 at varying intervals.

In this chapter, I selected PSPs based on the following four criteria: 1) stands originated from a wildfire, where stand age was available, and were not managed nor experienced major disturbances such as fire and/or harvesting since stand establishment, 2) similar to Peng *et al.* (2011) that examined long-term temporal change of tree mortality, I selected plots that had at least three censuses and had been monitored for at least 10 years, 3) all trees within the sample plots, including recruited trees, were clearly marked and their diameters at breast height (DBH) repeatedly measured, and 4) the plot's spatial location was provided so that climate data could be obtained. Stand age for each PSP was determined according to either a known fire event or dendrochronologically at the time of plot establishment by coring a minimum of three dominant/co-dominant trees of each tree species outside the plot. The stand age was the median age of the least shade tolerant tree species in the plot.

Based on the above criteria, 887 plots were selected for analyses (Appendix 3.1). Because Saskatchewan and Alberta use different tree size criteria for monitoring, i.e., ≥7.3 cm and ≥9.7 cm in DBH, respectively, I standardized the data by selecting trees with DBH≥10 cm to eliminate the effect of the different sampling efforts between the two provinces. This process removed small trees that could have died from physical damage caused by understory disturbances such as large mammal browsing and crushing from large trees (Larson and Franklin 2010). For the five study species, there were a total of 140,089 trees measured (mean: 28,018 trees, range: 10,528~51,140 trees for the study species), where 44,450 trees died during the monitoring period. This generated a total of 360,221 observations (Appendix 3.2). The study species vary in shade tolerance and leaf traits. The two *Populus* spp. are shade-intolerant, deciduous broadleaves, while

Pinus banksiana is a shade-intolerant, evergreen conifer. The two *Picea* spp. are shade-tolerant, evergreen conifers.

Explanatory variables

To examine whether long-term tree mortality trends are affected by long-term climate change trends, similar to previous studies (Phillips and Gentry 1994, Phillips et al. 2004, van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Peng et al. 2011, Thorpe and Daniels 2012), I used the middle calendar year of a census period, during which tree mortality measurements were made between two successive censuses, to represent climate change drivers as a whole. To account for the effects of endogenous factors including asymmetric competition, stand crowding, tree ageing, and inter-specific competition on tree mortality, I used the tree's relative basal area (RBA, ratio of subject tree basal area to the mean tree basal area of the stand), stand basal area (SBA), stand age (SA), and the ratio of focal species' basal area to stand basal area (rFSBA), calculated using the preceding measurement of each census period (Luo and Chen 2011).

Climate anomalies were defined as the departure from the long-term climate means (Clark et al. 2011). Since my dependent variable, tree status, was observed at the end of a census period, the departure from the long-term mean for each climate variable was defined as the difference between its mean value over the census period and its long-term mean. The long-term climate mean was calculated based on the 1950-2007 time period, during which plot measurements were taken. Three sets of climate anomalies were calculated: annual temperature anomaly (ATA), annual climate moisture index anomaly (ACMIA), and growing season precipitation anomaly (GPA). The temperature and precipitation data were derived from ClimateWNA software (Wang et al. 2006), which generates scale-free historical climate data for specific locations based on latitude, longitude, and elevation (Mbogga et al. 2009). I derived the scale-free annual climate moisture index (CMI) from BioSIM (Régnière et al. 2012). Annual CMI was the sum of monthly CMIs over 12 month periods from last August 1st to July 31st of the current year (Hogg 1997). The monthly CMI was based on the quantity of monthly precipitation minus monthly potential evapotranspiration (PET), which was computed using a simplified form of the Penman-Monteith equation (Hogg 1997, Hogg et al. 2008). A smaller CMI value indicated a drier condition. The summary statistics for explanatory variables were presented in Appendix 3.3.

Annual mortality probability calculations

I used individual tree mortality analyses, rather than plot-level mortality analyses, to accommodate the individual tree-level variable, RBA, because 1) RBA is the strongest predictor of tree mortality in non-equilibrium boreal forests and 2) its control on tree mortality can change with SBA and rFSBA (Luo and Chen 2011). Similar to previous studies (Dietze and Moorcroft 2011, Hurst et al. 2011), I was interested in estimating annual tree mortality probability where measurement intervals varied. I derived annual mortality probability from tree status as follows.

The survival probability, *S*, of tree *i*, for census period *j* of *t* years, in plot *k* can be expressed as a function of annual survival probability, *s*:

$$S_{ijk} = s_{ijk}^{\;t_{ijk}} \qquad \text{Equation 3.1}$$

Annual mortality probability, $p_{ijk} = 1 - s_{ijk}$ Equation 3.2

The mortality probability for a census period, $P_{ijk} = 1 - S_{ijk}$ Equation 3.3

Lastly, I related a tree's status at the end of the census period (M_{ijk}, alive or dead) to annual mortality probability using Bernoulli likelihood:

$$M_{ijk} \sim \text{Bernoulli}(1 - (1 - p_{ijk})^{t_{ijk}})$$ Equation 3.4

Statistical analyses

For each species, I developed individual tree mortality models using Hierarchical Bayesian logistic regression (HBLogit) with plot identity as a random effect to account for uncertainties potentially affected by different forest characteristics or in different climatic and/or edaphic conditions (Clark 2003, Wikle 2003).

$$\text{logit}(p_{ijk}) = \alpha + \beta \times X_{ijk} + \pi_k \qquad \pi \sim N(0, \sigma_k^2)$$ Equation 3.5

where α and β are the intercept and estimated coefficients; X_{ijk} represents explanatory variables corresponding to tree *i* for census period *j* in plot *k*; the model included a term π_k to describe the random effect of sampling plots. As a rule of thumb, π_k is in normal distribution with a mean of 0.

To examine whether inclusion of endogenous factors alters climate change-associated tree mortality, I compared the year effect between models with and without inclusion of endogenous factors as predictors, i.e., Model 3.1 and Model 3.2, respectively.

$$\text{logit}(p_{ijk}) = \alpha + \beta \times \text{Year}_{ijk} + \pi_k$$ Model 3.1

$$\begin{aligned}\mathrm{logit}(p_{ijk}) = {} & \alpha + f(En) + \beta_{11} \times \mathrm{Year}_{ijk} + \beta_{12} \times \mathrm{Year}_{ijk} \times 0.5^{\mathrm{RBA}_{ijk}} + \beta_{13} \times \mathrm{Year}_{ijk} \times \mathrm{SBA}_{ijk} \\ & + \beta_{14} \times \mathrm{Year}_{ijk} \times \mathrm{SA}_{ijk} + \beta_{15} \times \mathrm{Year}_{ijk} \times \mathrm{rFSBA}_{ijk} + \pi_k\end{aligned}$$

Model 3.2

where $f(En)$ in Model 3.2 was developed based on my previous chapter (Luo and Chen 2011) to account for the endogenous effects on tree mortality:

$$\begin{aligned}f(En) = \mathrm{logit}(p_{ijk}) = {} & \beta_1 \times 0.5^{\mathrm{RBA}_{ijk}} + \beta_2 \times \mathrm{SBA}_{ijk} + \beta_3 \times \mathrm{SA}_{ijk} + \beta_4 \times \mathrm{rFSBA}_{ijk} \\ & + \beta_5 \times 0.5^{\mathrm{RBA}_{ijk}} \times \mathrm{SBA}_{ijk} + \beta_6 \times 0.5^{\mathrm{RBA}_{ijk}} \times \mathrm{SA}_{ijk} + \beta_7 \times 0.5^{\mathrm{RBA}_{ijk}} \times \mathrm{rFSBA}_{ijk} \\ & + \beta_8 \times \mathrm{SBA}_{ijk} \times \mathrm{SA}_{ijk} + \beta_9 \times \mathrm{SBA}_{ijk} \times \mathrm{rFSBA}_{ijk} + \beta_{10} \times \mathrm{SA}_{ijk} \times \mathrm{rFSBA}_{ijk}\end{aligned}$$

Equation 3.6

where βs are the coefficients. I modeled the mortality probability as an exponential function of RBA because my previous results showed that mortality probability decreases exponentially with RBA (Luo and Chen 2011). The Akaike information criterion (AIC) also indicated that the exponential transformation of RBA gave better fits for all species (Appendix 3.4). Furthermore, our previous work (Luo and Chen 2011) showed near-linear mortality trends with tree aging and with stand basal area after taking account of competition and species interaction. Consequently, I modeled mortality probability as a linear function of stand age and stand basal area.

Both Models 3.1 and 3.2 were developed for all plots, young forest plots, and old forest plots, respectively, to examine how the inclusion of endogenous factors affect year effect in these three scenarios. Following Peng *et al.* (2011), I defined that young forests were ≤ 80 years of age and old forests >80 years of age at the first census.

To examine whether increases of mortality could be attributed to regional warming and its negative consequence on water availability, I developed models that replaced year with the climatic variables in Model 3.2, resulting in Model 3.3 and Model 3.4.

$$\begin{aligned}\text{logit}(p_{ijk}) = {} & \alpha + f(En) + \beta_{11} \times \text{ATA}_{ijk} + \beta_{12} \times \text{ATA}_{ijk} \times 0.5^{\text{RBA}_{ijk}} + \beta_{13} \times \text{ATA}_{ijk} \times \text{SBA}_{ijk} \\ & + \beta_{14} \times \text{ATA}_{ijk} \times \text{SA}_{ijk} + \beta_{15} \times \text{ATA}_{ijk} \times \text{rFSBA}_{ijk} + \pi_k\end{aligned}$$

Model 3.3

$$\begin{aligned}\text{logit}(p_{ijk}) = {} & \alpha + f(En) + \beta_{11} \times \text{ACMIA}_{ijk} + \beta_{12} \times \text{ACMIA}_{ijk} \times 0.5^{\text{RBA}_{ijk}} + \beta_{13} \times \text{ACMIA}_{ijk} \times \text{SBA}_{ijk} \\ & + \beta_{14} \times \text{ACMIA}_{ijk} \times \text{SA}_{ijk} + \beta_{15} \times \text{ACMIA}_{ijk} \times \text{rFSBA}_{ijk} + \pi_k\end{aligned}$$

Model 3.4

To examine the temporal trends of endogenous and exogenous factors at the plot level, *Y,* I used the Hierarchical Bayesian linear model (HBL).

$$Y_{jk} = \alpha + \beta \times \text{Year}_{jk} + \pi_k \qquad \pi \sim N(0, \sigma_k^2)$$

Equation 3.7

where Y_{jk} is dependent variable, i.e., endogenous factors and exogenous factors; α and β are intercept and estimated coefficients; Year_{jk} represents middle calendar year at for census period *j* in plot *k*; the model included a term π_k to describe the random effect of sampling plots.

For all analyses, the Bayesian Markov Chain Monte Carlo methods were implemented using *JAGS* (Plummer 2011a) called from R (R Development Core Team 2011) with *rjags* package (Plummer 2011b). All coefficients were assigned non-informative priors. All independent variables were centered in order to reduce their correlations and speed up convergence. For each model, I evaluated convergence by running two independent chains with different initial values and monitoring the Gelman-Rubin statistic (Gelman and Rubin 1992). When convergence was confirmed, an additional 10,000 iterations with thinning of ½ were used to calculate the mean, stand deviation, and 95% credible interval for each coefficient from the posterior distribution.

I developed full models and sequentially removed dimensionless explanatory variables whose posterior 95% credible interval covered 0. The reduced models, assessed by Deviance Information Criterion (DIC), were better than or similar to full models (Appendix 3.5). Consequently, I selected the reduced models as my final models. To assess the adequacy of the final models, I calculated the area under the receiver operating characteristic curve (AUC) based on the mean of each coefficient using *ROCR* package (Sing et al. 2009). A value of AUC > 0.8 indicates that a model has excellent discriminatory power, and a value > 0.7 indicates good discriminatory power (Hosmer and Lemeshow 2000).

Finally, I calculated the mortality sensitivity scores to endogenous factors, exogenous factors, and their interactions as a measure of the influences of these factors on mortality. Similar to Dietze and Moorcroft (2011), I defined sensitivity score on annual mortality probability as the standard deviation of the predicted annual mortality probability for each of the above three groups of factors, holding the other two groups of variables at their mean.

To present how annual mortality probability changes over the study period, I summarized posterior distribution of annual mortality probability (mean and 95% credible interval) using mean of each parameter (β) from the final models. I also calculated the annual fractional change of mortality probability associated with year over the study period using equation exp(β)-1 (van Mantgem et al. 2009), in which β is fitted coefficient for Year.

Results

Effects of year and stand development processes on tree mortality

With all data pooled, the effects of year, used to represent climate change drivers as a whole in both Model 1 and Model 2, were significantly positive for all study species (Table 3.1, Figure 3.1), indicating significant increases of annual mortality probability during the study period (Figure 3.2). The year effects on tree mortality, however, differed between the two models: reduced year effects for *Populus tremuloides*, *Pinus banksiana*, *Picea mariana* and *Picea glauca*, but an increased year effect from *Populus balsamifera* from Model 1 to Model 2 (Figure 3.1a), resulting in different estimates of annual tree mortality probability from the two models (Figure 3.2).

Tree mortality was strongly affected by stand development processes and their interactions with year (Figure 3.1b, and Table A3.6.1 in Appendix 3.6). Year effect decreased significantly with stand age for all study species (Table 3.1). Year effect also increased with stand crowding as measured by stand basal area and in stands with more conspecific individuals for *Picea mariana* and *Picea glauca* (Table 3.1). Tree mortality increases associated with year differed among species with stronger year effects on late-successional *Picea mariana* and *Picea glauca* and moist-habitat adapted *Populus balsamifera* than *Populus tremuloides* and *Pinus banksiana* (Figure 3.1a).

When data were analyzed separately for young forests (initial stand age ≤ 80 years) and old forests (initial stand age > 80 years, same as in Peng et al.(2011)), year effect was consistently higher in young forests than old forests for all species (Figure 3.1a), supporting the strong declining year effect with increasing stand age (Table 3.1). Predicted annual mortality increased by 2.88%, 4.70%, 5.64% and 6.18% per year in young forests, but increased at the lower rates of 1.65%, 2.24%, 3.89% and 4.12% in old forests for *Populus tremuloides*, *Populus balsamifera*, *Picea mariana* and *Picea glauca*, respectively (Appendix 3.7). For drought tolerant *Pinus banksiana*, annual mortality increased by 2.09% per year in young forests, but year had no detectable effect on its mortality in old forests (Appendix 3.7). In both young and old forests, endogenous factors were critical drivers of tree mortality for all study species (Figure 3.1b, and Tables A3.6.2-A3.6.3 in Appendix 3.6).

Table 3. 1. Effect of year and its interactive effects with stand development processes on annual mortality probability. Values are estimated parameters (mean and 95% credible interval in brackets). NS indicates that the corresponding predictor's posterior 95% credible interval covers 0 in the full model and the predictor was removed in the reduced model (see Methods). All the fitted coefficients for reduced Model 3.2 were presented in Table A3.6.1 in Appendix 3.6.

Model	Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Model 3.1	Intercept	-4.03	-3.54	-5.18	-4.94	-5.06
		(-4.10~-3.98)	(-3.63~-3.44)	(-5.37~-5.00)	(-5.08~-4.80)	(-5.17~-4.95)
	Year	2.63	2.64	3.41	4.83	4.47
	($\times 10^{-2}$)	(2.46~2.80)	(2.34~2.95)	(2.59~4.23)	(4.39~5.27)	(4.26~4.67)
	AUC	0.711	0.748	0.768	0.750	0.754
Model 3.2	Intercept	-4.33	-3.67	-5.44	-4.76	-4.86
		(-4.40~-4.27)	(-3.81~-3.59)	(-5.63~-5.25)	(-4.90~-4.62)	(-4.97~-4.75)
	Year	2.42	3.63	1.85	3.83	3.93
	($\times 10^{-2}$)	(2.13~2.71)	(3.24~4.01)	(0.80~2.89)	(3.14~4.49)	(3.55~4.33)
	Year × SA	-4.67	-4.60	-3.40	-3.16	-5.10
	($\times 10^{-4}$)	(-5.54~-3.82)	(-6.06~-3.13)	(-4.63~-2.17)	(-4.41~-1.94)	(-5.85~-4.35)
	Year × SBA	NS	NS	NS	5.46	9.32
	($\times 10^{-4}$)				(1.02~9.97)	(6.85~11.70)
	Year × rFSBA	NS	NS	NS	3.95	6.05
	($\times 10^{-2}$)				(2.20~5.69)	(5.14~7.01)
	AUC	0.812	0.819	0.825	0.777	0.776

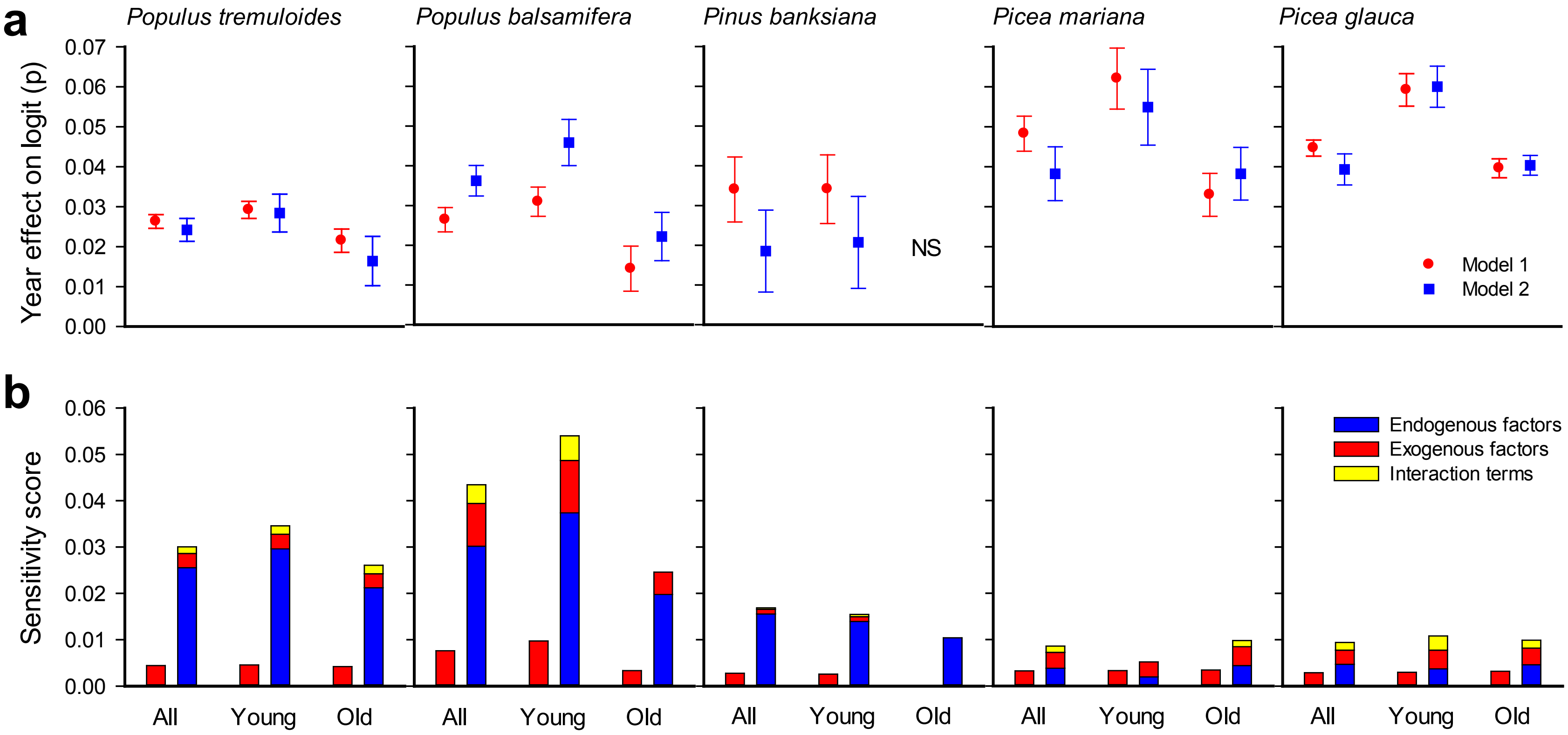


Figure 3. 1. Year effect on annual tree mortality probability and sensitivity scores of predictors. a, Year effect on annual tree mortality probability, logit (p), estimated by Model 3.1 (without endogenous factors as predictors) and Model 3.2 (with endogenous factors as predictors). Models were separately developed all plots (All), young plots (Young, initial stand age ≤ 80 years), and old plots (Old, initial stand age > 80 years). Error bars are 95% credible intervals. b, Sensitivity scores. For each species and age group (All, Young, or Old), sensitivity scores of predictors from Model 3.1 are on the left and Model 3.2 on the right.

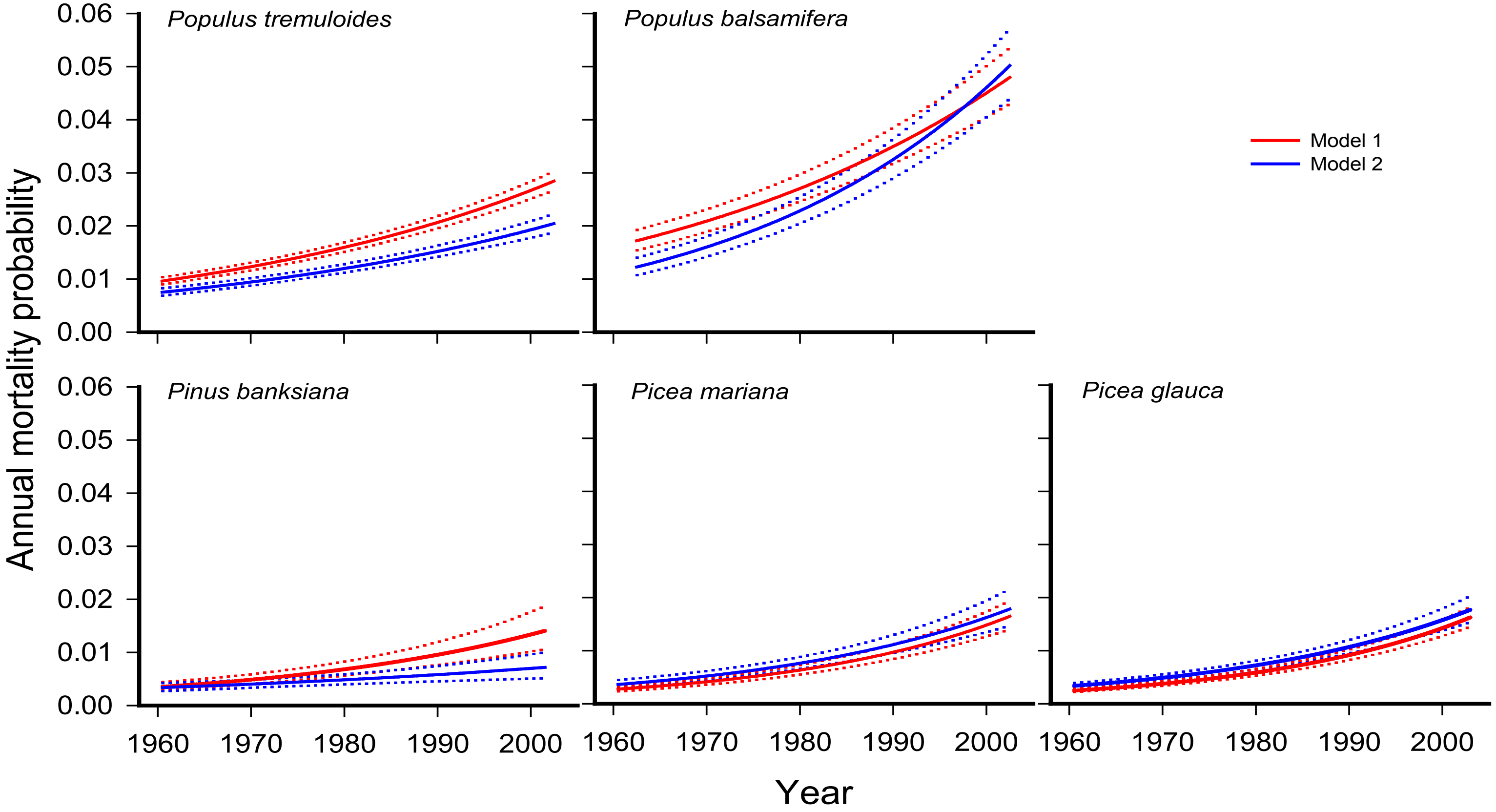


Figure 3. 2. Predicted temporal trends of annual mortality probability associated with calendar year. The predicted means (solid lines) and their 95% credible intervals (dotted lines) of annual mortality probability are derived by using equation exp(β)-1 (van Mantgem et al. 2009), in which β is the fitted Year coefficient from Model 3.1 (red) and Model 3.2 (blue) for each respective species in Table 3.1.

Warming and drought effects on tree mortality

For the study area, annual temperature anomaly (ATA) increased at 0.034 ^{o}C year^{-1}, and annual climate moisture index anomaly (ACMIA) decreased at 0.088 year^{-1}, whereas the growing season precipitation anomaly (GPA) slightly increased at 0.761 mm year^{-1} between 1958 and 2007 (Appendix 3.8). To examine whether increase of mortality could be attributed to regional warming and drought, I developed models that replaced year by these climatic variables (Model 3.3 and Model 3.4). The ATA models showed positive main ATA effects on mortality of all species and higher ATA effects in young than old forests of all species except *Pinus banksiana* (Table 3.2). The ACMIA models indicated negative main ACMIA effects on mortality of all species and greater effects for *Populus balsamifera*, *Picea mariana* and *Picea glauca* than the other two species. Furthermore, the ACMIA effects were stronger in young than old forests for all species except *Pinus banksiana* (Table 3.2).

Table 3. 2. Effect of annual temperature anomaly (ATA) or annual climate moisture index anomaly (ACMIA) and its interactive effects with stand development processes on annual mortality probability. Values are estimated parameters (mean and 95% credible interval in brackets). Full tables for Model 3.3 and Model 3.4 are presented in Tables A3.6.4 and A3.6.5 in Appendix 3.6, respectively.

Model	Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Model 3.3	Intercept	-4.29 (-4.36~-4.23)	-3.91 (-4.03~-3.79)	-5.44 (-5.64~-5.24)	-5.00 (-5.11~-4.89)	-4.90 (-4.98~-4.81)
	ATA ($\times10^{-1}$)	4.67 (4.19~5.15)	5.17 (4.35~6.00)	5.44 (3.35~7.55)	3.97 (3.00~4.90)	5.26 (4.71~5.81)
	ATA × SA ($\times10^{-3}$)	-9.26 (-11.06~-7.53)	-12.80 (-15.84~-9.77)	NS	-4.37 (-6.57~-2.33)	-7.52 (-8.91~-6.17)
	ATA × 0.5^{RBA}	NS	NS	-1.55 (-2.49~-0.59)	NS	NS
	ATA × SBA ($\times10^{-3}$)	NS	NS	NS	NS	7.75 (2.00~13.52)
	ATA × rFSBA ($\times10^{-1}$)	1.88 (0.27~3.47)	NS	NS	NS	9.46 (7.39~11.49)
	AUC	0.801	0.743	0.774	0.745	0.728
Model 3.4	Intercept	-4.30 (-4.37~-4.23)	-3.83 (-3.95~-3.70)	-5.45 (-5.66~-5.24)	-4.61 (-4.79~-4.44)	-4.68 (-4.82~-4.56)

ACMIA	-3.59	-7.27	-1.58	-7.77	-4.44
($\times 10^{-2}$)	(-4.54~-2.64)	(-8.84~-5.70)	(-0.14~-3.02)	(-9.72~-5.83)	(-5.37~-3.48)
ACMIA × SA	1.93	1.99	NS	0.57	1.17
($\times 10^{-3}$)	(1.56~2.29)	(1.39~2.60)		(0.12~1.02)	(0.89~1.46)
ACMIA × 0.5^{RBA}	-8.63	NS	NS	NS	NS
($\times 10^{-2}$)	(-13.09~-4.25)				
ACMIA × SBA	NS	NS	NS	NS	NS
ACMIA × rFSBA	NS	7.33	NS	-12.01	-14.57
($\times 10^{-2}$)		(1.79~12.85)		(-17.81~-6.23)	(-18.41~-10.74)
AUC	0.815	0.798	0.803	0.759	0.783

Discussion

Unlike previous attributions of temporal increases in tree mortality to either climate change (Phillips and Gentry 1994, Phillips et al. 2004, van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Peng et al. 2011) or stand development processes (Luo and Chen 2011, Thorpe and Daniels 2012), by using Bayesian models, I show that both stand development processes and climate change have affected temporal increases in tree mortality. These findings are not likely a result of methodological problems since heterogeneity in sampling strategies had no effect on mortality (Appendix 3.9), though I note that I have not explicitly considered alternate exogenous factors here. Tree mortality associated with year decreased for all species except *P. balsamifera* when stand development factors were included as predictors. The differences in year effect between the models provide support for the notion that studies excluding endogenous factors can potentially produce biased estimates of climate change effects in boreal forests (Brown et al. 2011). The decreased year effect on tree mortality is attributable to stand development processes during the study period. For example, both stand age and stand basal area increased (Appendix 3.10), both of which positively affected tree mortality (Table A3.6.1 in Appendix 3.6). Also, an increase in the conspecific density of shade-tolerant *Picea mariana* and *Picea glauca* (Appendix 3.10), reflecting the nature of secondary succession in boreal forests (Chen and Popadiouk 2002, Chen and Taylor 2012), intensified a negative density dependence effect on these two species (Table 3.1). The increased year effect in moist-habitat adapted *Populus balsamifera* suggests that reduced water availability might have overweighed endogenous effects.

My results show that mortality increases associated with climate change were significantly higher in young than old forests, and the higher increase in younger forests appears to be due to higher mortality sensitivity to recent regional warming and the resulting negative consequence on water availability. This finding indicates that climate change-associated increases in tree mortality would be underestimated if only old forests are used to represent regional forests. Compared with old forests, even-aged young forests established after a stand-replacing disturbance may experience greater competition for space and nutrients among young trees that tend to occupy the same ecological niche (Chen and Popadiouk 2002, Franklin et al. 2002), resulting in them being more vulnerable to external stressors such as climate change-associated drought (Linares et al. 2010, Moreno-Gutierrez et al. 2012). The positive effect of regional warming on mortality could also be attributed to the interdependencies among warming, drought, and forest pests (Allen et al. 2010, McDowell et al. 2011, Anderegg et al. 2012b). In the study area, outbreaks of forest pests could have played a role in the temporal mortality increases (Hogg et al. 2002, Cullingham et al. 2011, Michaelian et al. 2011).

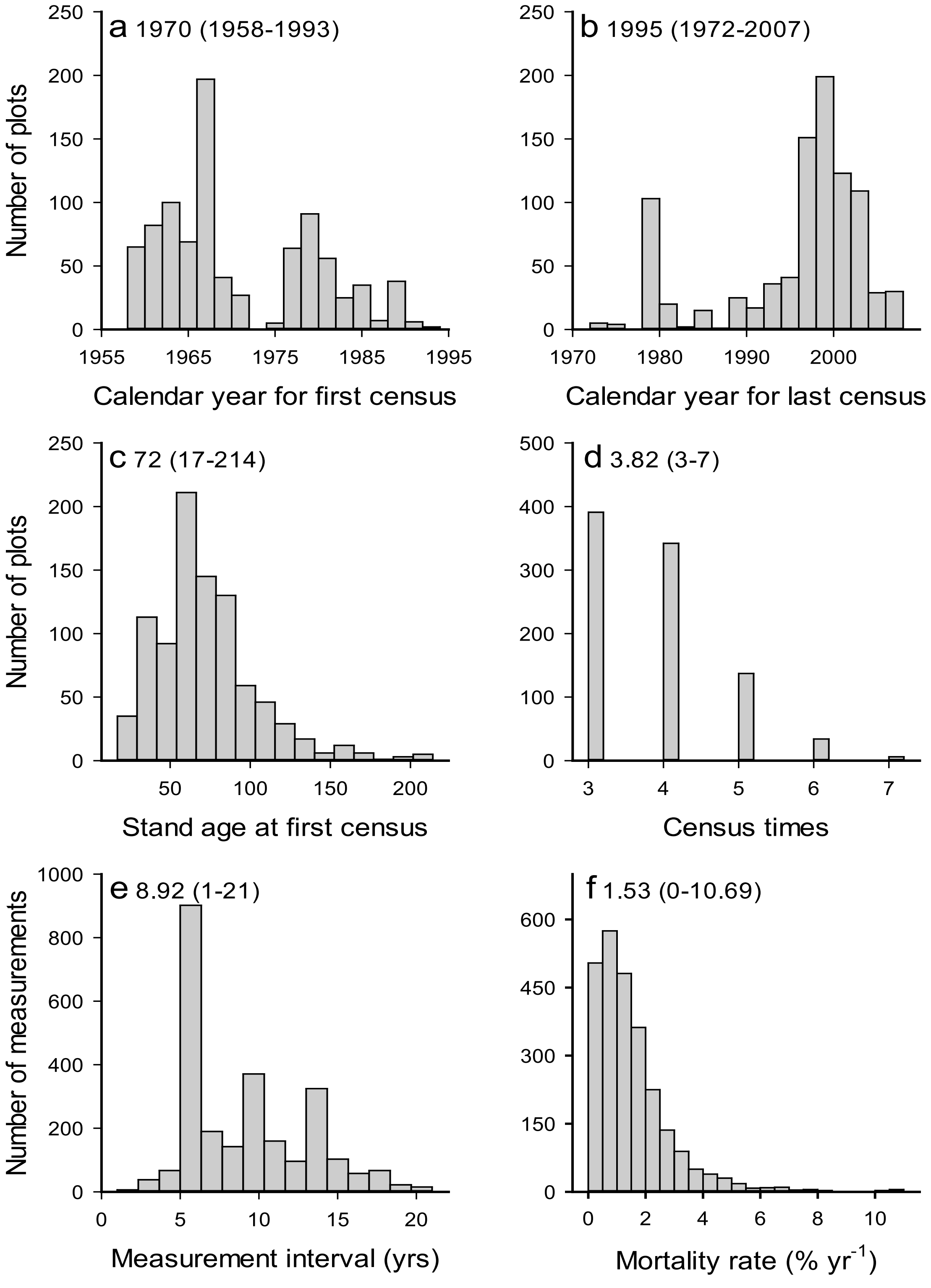
Mortality responses to climate change differed among species, suggesting that the regional forest may be undergoing forest compositional shift that is independent of endogenous forest succession. The highest morality increase in *Populus balsamifera* among pioneer species indicates that reduced water availability by regional warming has the greatest influence on species adapted to moist habitats. The higher mortality increases of late-successional *Picea mariana* and *Picea glauca* than those of early-successional *Populus tremuloides* and *Pinus banksiana* in both young and old forests

(Figures 3.1-3.2) suggest that the regional forest will likely become further dominated by early-successional species if current warming trends continue. The different responses of tree mortality among species, coupled with those by climate change associated fire activities (Larsen 1997, Weir et al. 2000, Fauria and Johnson 2008, Pan et al. 2011a) that promote early-successional species (Ilisson and Chen 2009), may pose a significant conservation challenge for the region under further global warming.

I show evidence that long-term tree mortality trends are influenced by both stand development processes and long-term climate trends, i.e., regional warming and drought. Note that the strength of these drivers on tree mortality differs among species and their influences interact both among endogenous factors and between endogenous and exogenous factors. Because of the higher sensitivity to recent climate change in young than old forests, climate change-associated tree mortality could be underestimated if mortality estimates from old forests are used to represent regional forests. Tree mortality responses to climate change differed among species and these different responses can have strong implications for future forest composition in the western boreal forest.

Appendices

Appendix 3. 1. Descriptions of selected 871 plots by histograms, values were mean with range in the brackets.



Appendix 3. 2. Data description of individual tree mortality analyses.

Species	Number of plots	Number of trees	Number of dead trees	Number of observations
Populus tremuloides	659	51,140	20,636	125,158
Populus balsamifera	444	11,030	5,844	27,472
Pinus banksiana	132	10,528	1,497	26,538
Picea mariana	294	17,456	3,445	42,019
Picea glauca	620	49,935	13,028	139,034
Total	887	140,089	44,450	360,221

Appendix 3. 3. Summary statistics (mean±1 SD and range in brackets) for the explanatory variables.

Species	Year	RBA	SBA (m^2 ha^{-1})	SA (years)	rFSBA	ATA (ºC)	ACMIA
Populus	1983±10	1.09±0.57	36.46±9.34	74.08±26.92	0.69±0.27	0.09±0.45	0.25±2.52
tremuloides	(1961~2003)	(0.06~12.22)	(4.73~90.34)	(18~192)	(0.003~1)	(-1.16~1.21)	(-12.43~10.07)
Populus	1982±10	0.98±0.66	33.79±9.25	77.77±27.82	0.36±0.26	0.08±0.47	0.50±2.57
balsamifera	(1963~2003)	(0.06~11.79)	(5.21~71.85)	(17~184)	(0.001~0.99)	(-1.13~1.19)	(-8.31~10.07)
Pinus	1974±12	1.02±0.40	21.72±7.36	55.16±18.50	0.96±0.11	-0.16±0.52	0.03±2.06
banksiana	(1961~2002)	(0.21~5.76)	(5.28~49.41)	(22~128)	(0.006~1)	(-0.98~1.01)	(-9.48~5.53)
Picea	1983±10	0.83±0.38	36.94±10.94	107.63±36.11	0.49±0.34	0.10±0.51	0.70±2.70
mariana	(1961~2003)	(0.08~11.87)	(4.40~62.86)	(31~243)	(0.001~1)	(-1.16~1.23)	(-9.48~12.33)
Picea	1982±10	1.00±0.72	40.38±8.74	105.35±33.00	0.63±0.25	0.05±0.49	-0.59±2.49
glauca	(1961~2003)	(0.06~10.84)	(5.63~85.76)	(18~243)	(0.001~1)	(-1.13~1.23)	(-12.07~10.07)

Appendix 3. 4. Akaike information criterion (AIC) for the logistic regression models fitted using linear relative basal area (RBA) and exponential-transformed RBA. The AICs for the models with exponentially transformed RBA were smaller than the models with the linear RBA term, indicating that the models using the exponential transformed RBA had a better fit.

Species	Linear	Exponential-transformed
Populus tremuloides	104,785	102,637
Populus balsamifera	27,326	27,162
Pinus banksiana	11,148	11,013
Picea mariana	23,801	23,780
Picea glauca	85,801	85,491

Appendix 3. 5. Deviance Information Criterion (DIC) for the full and reduced models by fitting data to Model 3.2. The reduced models fitted the data better than or same as the full models, indicated by smaller DIC or similar (difference is <5) DIC values of the reduced models.

Species	All		Young		Old	
	Full	Reduced	Full	Reduced	Full	Reduced
Populus tremuloides	88031	88034	60640	60625	27127	27108
Populus balsamifera	22215	22206	15570	15561	6578	6568
Pinus banksiana	9588	9517	8693	8689	813	807
Picea mariana	21207	21208	7559	7558	13625	13621
Picea glauca	73521	73516	22446	22440	51475	51471

Appendix 3. 6. Summary statistics of posterior distribution of reduced Models 3.2-3.4.

Table A3.6.1. Estimated parameters (mean and 95% credible interval in brackets) for both endogenous and exogenous terms in Model 3.2 (see Methods) using all sample plots. NS indicates that the 95% credible interval of the parameter covers 0 for the corresponding predictor. The models predictive performances were evaluated by area under the receiver operating characteristic curve (AUC).

Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Intercept	-4.334	-3.696	-5.437	-4.761	-4.858
	(-4.402~-4.271)	(-3.811~-3.586)	(-5.628~-5.251)	(-4.903~-4.615)	(-4.969~-4.748)
0.5^{RBA}	6.208	4.764	6.272	0.963	1.634
	(6.086~6.329)	(4.552~4.984)	(5.633~6.926)	(0.670~1.255)	(1.535~1.734)
SBA	0.010	0.032	0.095	0.015	0.004
	(0.006~0.013)	(0.025~0.038)	(0.069~0.122)	(0.007~0.023)	(0.001~0.007)
SA	0.013	NS	0.021	0.007	0.008
	(0.010~0.015)		(0.010~0.031)	(0.002~0.012)	(0.004~0.011)
rFSBA	NS	NS	NS	NS	0.723
					(0.528~0.920)
0.5^{RBA} × SBA	0.219	0.133	0.127	0.119	0.096
	(0.206~0.232)	(0.109~0.158)	(0.054~0.200)	(0.092~0.146)	(0.085~0.106)
0.5^{RBA} × SA	-0.056	-0.069	-0.062	-0.015	-0.020
	(-0.061~-0.051)	(-0.077~-0.061)	(-0.092~-0.032)	(-0.023~-0.007)	(-0.023~-0.017)

0.5^{RBA} × rFSBA	3.190	1.307	NS	1.401	0.720
	(2.728~3.666)	(0.577~2.030)		(0.567~2.284)	(0.273~1.171)
SBA × rFSBA	0.015	NS	NS	0.082	0.022
	(0.004~0.025)			(0.061~0.103)	(0.009~0.043)
Year	0.024	0.036	0.019	0.038	0.039
	(0.021~0.027)	(0.032~0.040)	(0.008~0.029)	(0.031~0.045)	(0.035~0.043)
Year × 0.5^{RBA}	NS	NS	NS	NS	NS
Year × SBA	NS	NS	NS	0.546	0.932
($\times 10^{-3}$)				(0.102~0.997)	(0.685~1.170)
Year × SA	-4.669	-4.597	-3.399	-3.158	-5.097
($\times 10^{-4}$)	(-5.542~-3.817)	(-6.060~-3.133)	(-4.625~-2.173)	(-4.406~-1.939)	(-5.850~-4.346)
Year × rFSBA	NS	NS	NS	0.039	0.060
				(0.022~0.057)	(0.051~0.070)
AUC	0.812	0.819	0.825	0.777	0.776

Table A3.6.2. Estimated parameters (mean and 95% credible interval in brackets) for both endogenous and exogenous terms in Model 3.2 for young forests (initial stand age ≤ 80 years).

Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Intercept	-4.446	-3.753	-5.539	-5.211	-5.143
	(-4.528~-4.366)	(-3.877~-3.631)	(-5.732~-5.341)	(-5.455~-4.969)	(-5.331~-4.955)
0.5^{RBA}	6.817	5.730	6.353	1.490	2.045
	(6.667~6.967)	(5.448~6.019)	(5.654~7.057)	(0.958~2.027)	(1.855~2.239)
SBA	0.005	0.042	0.103	0.015	0.021
	(0.000~0.010)	(0.031~0.052)	(0.075~0.134)	(0.001~0.029)	(0.012~0.030)
SA	0.015	NS	0.023	NS	NS
	(0.011~0.019)		(0.011~0.035)		
rFSBA	0.452	NS	NS	1.100	NS
	(0.214~0.694)			(0.490~1.762)	
$0.5^{\mathrm{RBA}} \times$ SBA	0.265	0.226	0.156	NS	0.119
	(0.248~0.283)	(0.192~0.259)	(0.073~0.242)		(0.096~0.143)
$0.5^{\mathrm{RBA}} \times$ SA	-0.057	-0.087	-0.082	NS	NS
	(-0.066~-0.048)	(-0.105~-0.069)	(-0.118~-0.046)		
$0.5^{\mathrm{RBA}} \times$ rFSBA	3.687	3.688	NS	NS	2.286
	(3.056~4.287)	(2.645~4.744)			(1.478~3.063)
SBA × rFSBA	0.029	NS	NS	NS	NS

	(0.014~0.044)				
Year	0.028	0.046	0.021	0.055	0.060
	(0.024~0.033)	(0.040~0.052)	(0.009~0.032)	(0.045~0.064)	(0.055~0.065)
Year × 0.5^{RBA}	-0.028	-0.107	NS	NS	NS
	(-0.043~-0.013)	(-0.134~-0.080)			
Year × SBA	NS	NS	NS	NS	2.345
$(\times 10^{-3})$					(1.511~3.165)
Year × SA	-7.566	-5.762	-7.271	NS	-9.039
$(\times 10^{-4})$	(-9.468~-5.681)	(-8.784~-2.638)	(-13.657~-0.823)		(-12.310~-5.805)
Year × rFSBA	0.029	NS	NS	NS	0.140
	(0.015~0.044)				(0.116~0.165)

Table A3.6.3. Estimated parameters (mean and 95% credible interval in brackets) for both endogenous and exogenous terms in Model 3.2 for old forests (initial stand age > 80 years).

Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Intercept	-3.946	-3.791	-4.895	-4.597	-4.691
	(-4.055~-3.836)	(-3.921~-3.664)	(-5.254~-4.585)	(-4.779~-4.416)	(-4.804~-4.580)
0.5^{RBA}	4.516	2.782	5.944	0.954	1.372
	(4.321~4.708)	(2.424~3.153)	(4.592~7.329)	(0.589~1.317)	(1.263~1.483)
SBA	0.008	0.037	NS	0.018	NS
	(0.003~0.014)	(0.025~0.050)		(0.008~0.027)	
SA	0.016	NS	NS	NS	NS
	(0.010~0.021)				
rFSBA	NS	NS	NS	-0.492	1.192
				(-0.873~-0.116)	(0.967~1.418)
0.5^{RBA} × SBA	0.164	0.083	NS	0.117	0.094
	(0.143~0.185)	(0.041~0.126)		(0.084~0.151)	(0.082~0.106)
0.5^{RBA} × SA	-0.059	-0.061	NS	-0.019	-0.016
	(-0.070~-0.049)	(-0.078~-0.045)		(-0.029~-0.009)	(-0.020~-0.011)
0.5^{RBA} × rFSBA	1.962	NS	NS	1.591	NS
	(1.197~2.704)			(0.600~2.595)	
SBA × rFSBA	0.018	NS	0.146	0.099	0.044

	(0.001~0.036)		(0.062~0.223)	(0.076~0.123)	(0.028~0.061)
Year	0.016	0.022	NS	0.038	0.040
	(0.010~0.023)	(0.016~0.028)		(0.032~0.045)	(0.038~0.043)
Year × SBA	NS	NS	NS	0.844	1.397
(×10^{-3})				(0.310~1.376)	(1.113~1.683)
Year × SA	-6.824	NS	NS	NS	-3.522
(×10^{-4})	(-8.759~-4.922)				(-4.486~-2.541)
Year × rFSBA	NS	NS	NS	0.035	0.051
				(0.017~0.053)	(0.040~0.063)

Table A3.6.4. Estimated parameters (mean and 95% credible interval in brackets) for the effect of annual temperature anomaly (ATA) and the effects of stand development processes on tree mortality in Model 3.3.

Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Intercept	-4.293	-3.905	-5.436	-4.995	-4.896
	(-4.356~-4.233)	(-4.028~-3.787)	(-5.639~-5.242)	(-5.106~-4.887)	(-4.978~-4.813)
0.5^{RBA}	6.316	4.713	6.410	0.866	1.638
	(6.194~6.436)	(4.496~4.926)	(5.757~7.080)	(0.572~1.155)	(1.534~1.738)
SBA	0.018	0.043	0.105	0.029	0.026
	(0.014~0.022)	(0.035~0.051)	(0.076~0.134)	(0.020~0.038)	(0.021~0.030)
SA	0.021	0.005	0.022	0.015	0.017
	(0.019~0.023)	(0.002~0.008)	(0.013~0.030)	(0.012~0.019)	(0.015~0.020)
rFSBA	0.552	-0.730	NS	NS	1.371
	(0.377~0.730)	(-1.162~-0.290)			(1.095~1.638)
0.5^{RBA} × SBA	0.223	0.155	0.097	0.130	0.103
	(0.209~0.237)	(0.129~0.181)	(0.022~0.170)	(0.101~0.158)	(0.093~0.114)
0.5^{RBA} × SA	-0.055	-0.075	-0.052	-0.014	-0.018
	(-0.060~-0.050)	(-0.083~-0.067)	(-0.082~-0.022)	(-0.022~-0.006)	(-0.021~-0.015)
0.5^{RBA} × rFSBA	3.407	1.988	NS	1.760	0.652
	(2.934~3.888)	(1.181~2.808)		(0.896~2.636)	(0.202~1.103)
SBA × SA	NS	NS	NS	NS	NS

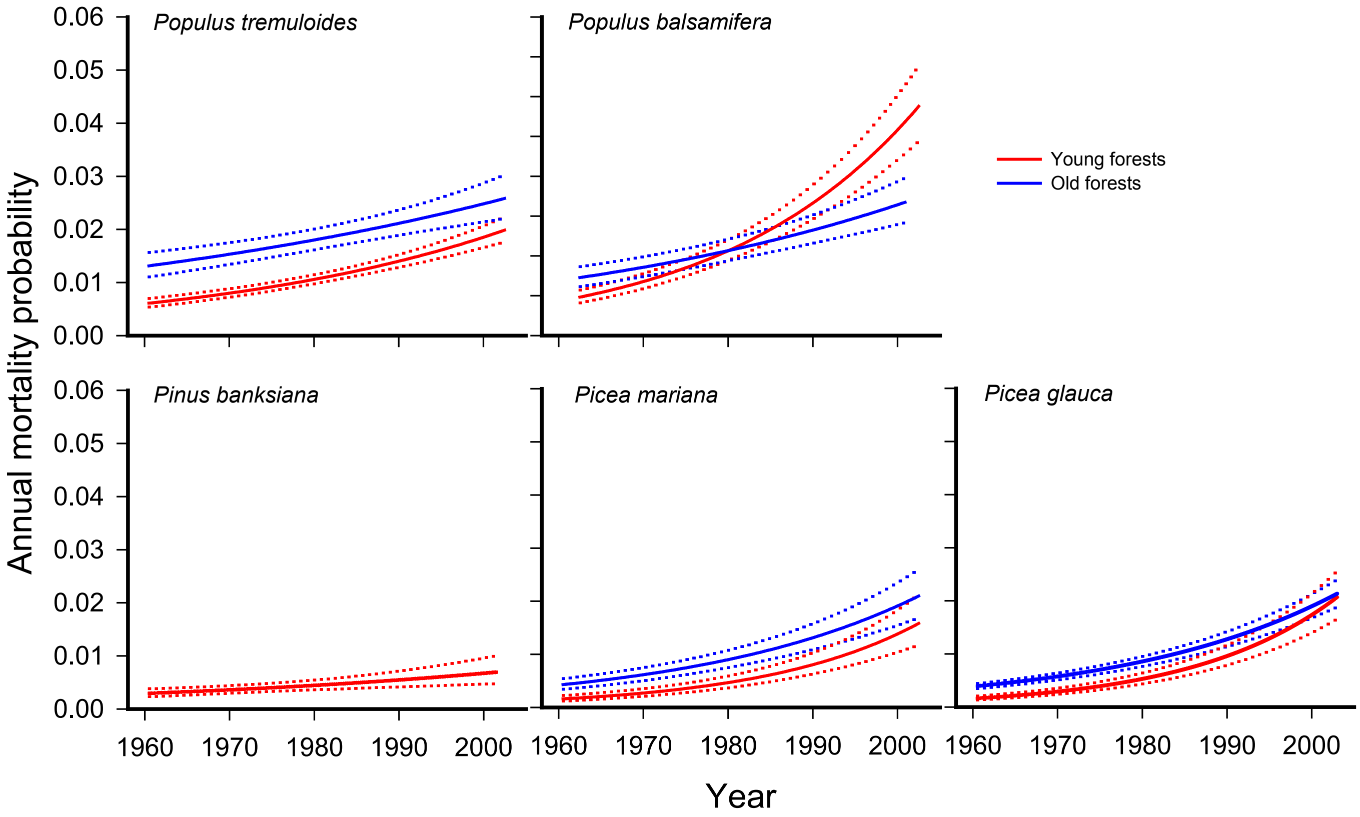
SBA × rFSBA	0.015	NS	-0.002	0.048	0.029
	(0.001~0.029)		(-0.003~-0.001)	(0.024~0.072)	(0.012~0.047)
SA × rFSBA	NS	NS	NS	NS	NS
ATA	0.467	0.517	0.544	0.397	0.526
	(0.419~0.515)	(0.435~0.600)	(0.335~0.755)	(0.300~0.490)	(0.471~0.581)
ATA × 0.5^{RBA}	NS	NS	-1.554	NS	NS
			(-2.494~-0.588)		
ATA × SBA	NS	NS	NS	NS	0.775
(×10^{-2})					(0.200~1.352)
ATA × SA	-9.264	-12.794	-4.689*	-4.437	-7.517
(×10^{-3})	(-11.055~-7.528)	(-15.836~-9.770)	(-14.419~-5.042)	(-6.565~-2.329)	(-8.909~-6.167)
ATA × rFSBA	0.188	NS	NS	NS	0.946
	(0.027~0.347)				(0.739~1.149)

Table A3.6.5. Estimated parameters (mean and 95% credible interval in brackets) for the effect of climate moisture index anomaly (ACMIA) and the effects of stand development processes on tree mortality in Model 3.4.

Term	*Populus tremuloides*	*Populus balsamifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*
Intercept	-4.297	-3.828	-5.453	-4.611	-4.683
	(-4.370~-4.226)	(-3.954~-3.698)	(-5.660~-5.244)	(-4.786~-4.443)	(-4.817~-4.562)
0.5^{RBA}	6.218	4.708	6.264	0.972	1.634
	(6.100~6.340)	(4.489~4.926)	(5.621~6.915)	(0.679~1.277)	(1.535~1.736)
SBA	0.014	0.027	0.112	0.026	0.012
	(0.010~0.017)	(0.020~0.035)	(0.082~0.144)	(0.018~0.034)	(0.009~0.016)
SA	0.026	0.013	0.022	0.016	0.033
	(0.024~0.027)	(0.010~0.017)	(0.013~0.032)	(0.012~0.021)	(0.031~0.035)
rFSBA	0.305	NS	NS	NS	0.666
	(0.140~0.469)				(0.463~0.871)
$0.5^{RBA} \times$ SBA	0.220	0.152	0.124	0.121	0.095
	(0.206~0.233)	(0.126~0.178)	(0.045~0.200)	(0.094~0.149)	(0.084~0.105)
$0.5^{RBA} \times$ SA	-0.054	-0.071	-0.055	-0.016	-0.019
	(-0.058~-0.049)	(-0.079~-0.063)	(-0.087~-0.024)	(-0.024~-0.007)	(-0.022~-0.015)
$0.5^{RBA} \times$ rFSBA	3.196	1.635	NS	1.339	0.600
	(2.725~3.668)	(0.847~2.424)		(0.467~2.226)	(0.154~1.057)

SBA × SA	NS	NS	NS	NS	NS
SBA × rFSBA	0.010	NS	NS	0.085	0.037
	(0.001~0.018)			(0.063~0.107)	(0.023~0.050)
SA × rFSBA	NS	NS	NS	NS	NS
ACMIA	-0.036	-0.073	-0.016	-0.078	-0.044
	(-0.045~-0.026)	(-0.088~-0.057)	(-0.001~-0.031)	(-0.097~-0.058)	(-0.054~-0.035)
ACMIA × 0.5^{RBA}	-0.086	NS	NS	NS	NS
	(-0.131~-0.043)				
ACMIA × SBA	NS	NS	NS	NS	NS
ACMIA × SA	1.926	1.985	NS	0.571	1.173
($\times 10^{-3}$)	(1.560~2.285)	(1.390~2.598)		(0.123~1.017)	(0.889~1.462)
ACMIA × rFSBA	NS	0.073	NS	-0.120	-0.146
		(0.018~0.128)		(-0.178~-0.062)	(-0.184~-0.107)

Appendix 3. 7. Modeled temporal trends of annual mortality probability in young forests (initial stand age ≤ 80 years) and old forests (initial stand age > 80 years).



Appendix 3. 8. Temporal trends of climate variables. The results showed that, over study period, the annual temperature anomaly (ATA, ^{o}C) increased, growing season precipitation anomaly (GPA, mm) also increased, annual climate moisture index anomaly (ACMIA, cm) decreased (Table A3.8.1). The original data points were showed in Figure A3.8.1.

Table A3.8.1. Estimated parameters (mean and 95 credible interval) for year effect on ATA, GPA, and ACMIA.

Climatic variable	β_{year}	
	Mean	95% Credible interval
ATA	0.034	0.033~0.034
GPA	0.761	0.694~0.827
ACMIA	-0.088	-0.097~-0.080

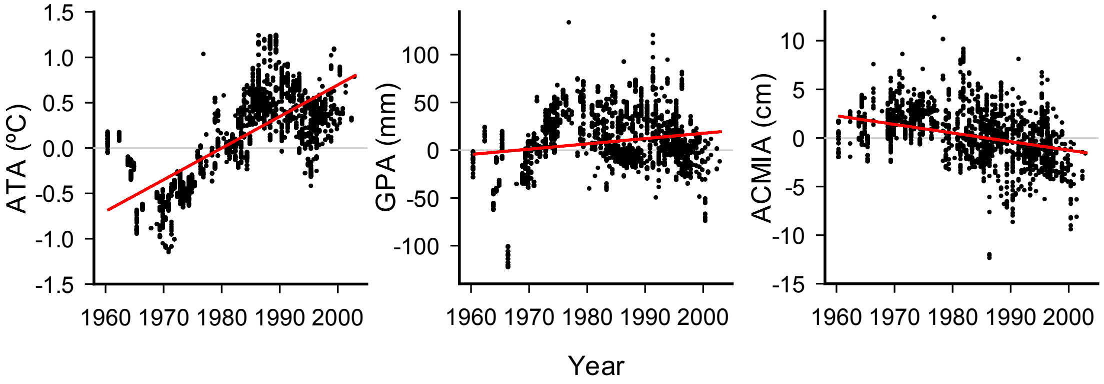


Figure A3.8.1. Original data points (black dots) and fitted trends (red lines) for ATA (^{o}C) (a), GPA (mm) (b), and ACMIA (cm) (c).

Appendix 3. 9. Assessing possible methodological problems

I first examined the spatial auto-correlation and heterogeneity in sampling strategies following the method described by van Mantgem et al. (2009). For all study species, Mantel tests showed no evidence of spatial auto-correlation among the plots for annual mortality probability, annual fractional change of mortality probability, or the effect of plot identity on annual mortality probability (Table A3.9.1). The selected PSPs were located in ecologically heterogeneous regions, and close geographic configuration does not imply similarity in forest characteristics. My result that mortality probability increased more so in young forests than old forests could also be mistaken if the young forest plots were spatially clustered. Thus, I also examined the spatial auto-correlation for initial stand ages. For all study species, the mantel tests showed no evidence of spatial auto-correlation among the plots for initial stand age (Table A3.9.1).

Table A3.9.1. *P* values of Mantel tests for average mortality rate, annual fractional change of mortality rate, residuals of plot identity random effect, and initial stand age.

Species	Average Mortality rate	Annual fractional change of mortality rate	Plot identity effect on annual mortality probability	Initial Stand age
Populus tremuloides	0.68	0.25	0.99	0.13
Populus balsamifera	0.99	0.99	0.35	0.15
Pinus banksiana	0.44	0.46	0.20	0.46
Picea mariana	0.21	0.13	0.30	0.96
Picea glauca	0.41	0.64	0.80	0.67

Note: Spatial autocorrelation among sample plots was tested by plots' geographic locations (latitudes and longitudes).

The linear regressions that related annual mortality fractional change to plot size and average census interval, showed that neither plot size nor average census interval was significantly related to annual mortality fractional change (Figures A3.9.1-2). These results indicate that the variation of mortality changes could not be attributed to plot size heterogeneity or the variation in census intervals.

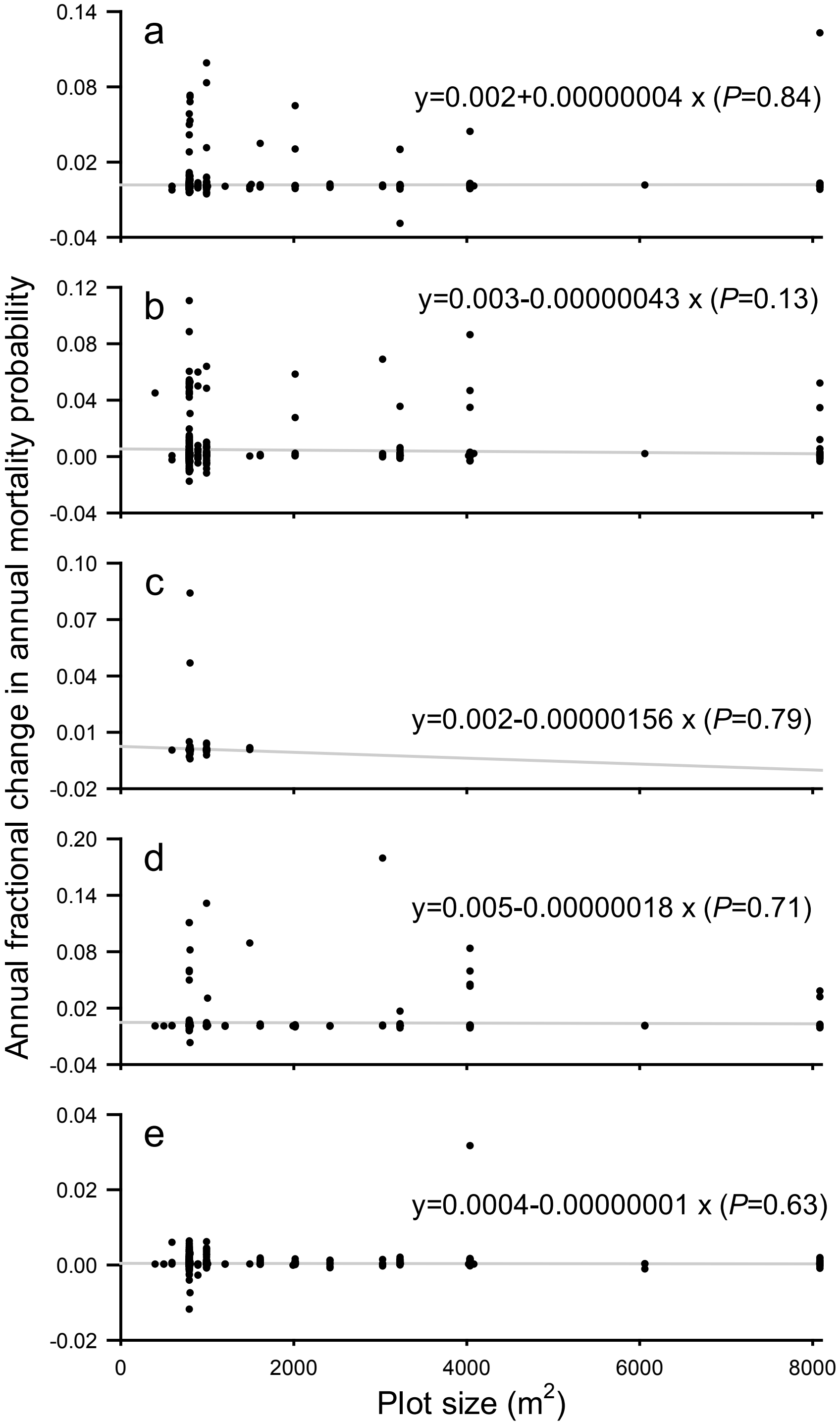


Figure A3.9.1. Modeled annual fractional change in annual mortality probability in relation to plot size for *Populus tremuloides* (a), *Populus balsamifera* (b), *Pinus banksiana* (c), *Picea mariana* (d) and *Picea glauca* (e).

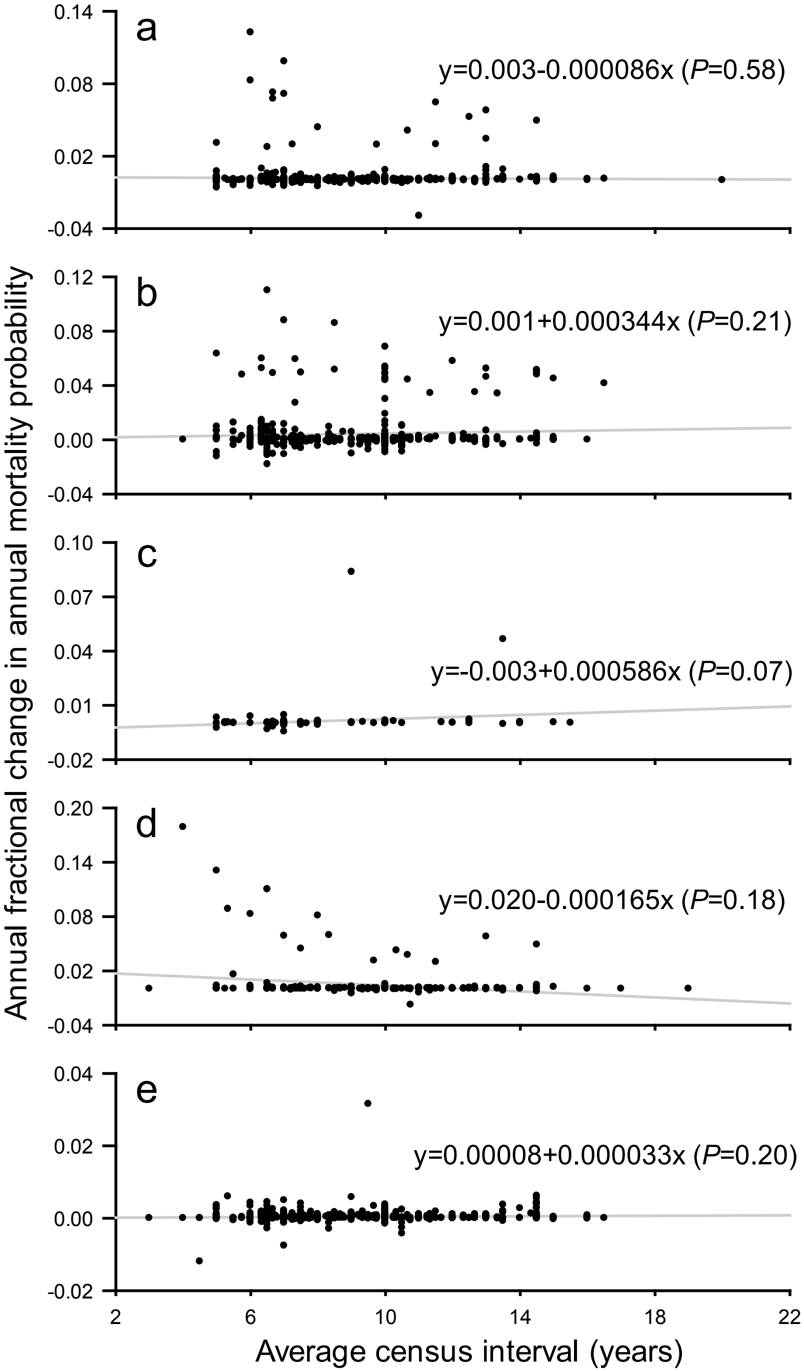


Figure A3.9.2. Modeled annual fractional change in annual mortality probability in relation to plot census interval for *Populus tremuloides* (a), *Populus balsamifera* (b), *Pinus banksiana* (c), *Picea mariana* (d) and *Picea glauca* (e).

Appendix 3. 10. Temporal changes of endogenous factors

Table A3.10.1. Estimated parameters (mean and 95% credible interval in brackets) of year effect on endogenous factors. The results showed that both stand basal area (SBA) and stand age (SA) increased with year; conspecific density (rFSBA) decreased for three shade-intolerant *Populus tremuloides*, *Populus balsamifera*, and *Pinus banksiana*, and increased for two shade-tolerant *Picea mariana* and *Picea glauca*; relative size of individual tree within the stand (RBA) increased for *Populus tremuloides* and *Populus balsamifera*, and decreased for *Picea glauca*.

Species	β_{year} for RBA	β_{year} for SBA	β_{year} for SA	β_{year} for rFSBA
Populus	0.0063	0.14	1.02	-0.0006
tremuloides	(0.0057~0.0069)	(0.12~0.15)	(1.01~1.03)	(-0.0008~-0.0005)
Populus	0.0024	0.14	1.02	-0.0008
balsamifera	(0.0014~0.0034)	(0.12~0.16)	(1.01~1.04)	(-0.0009~-0.0006)
Pinus	-0.0006	0.28	0.81	-0.0005
banksiana	(-0.0015~0.0002)	(0.25~0.32)	(0.78~0.83)	(-0.0007~-0.0002)
Picea	0.0001	0.29	1.01	0.0012
mariana	(-0.0005~0.0005)	(0.27~0.30)	(1.00~1.02)	(0.0011~0.0013)
Picea	-0.0017	0.13	1.03	0.0017
glauca	(-0.0026~-0.0009)	(0.12~0.15)	(1.02~1.04)	(0.0016~0.0018)

Chapter 4. Another mechanism for the temporal increases of tree mortality: intensification of tree-tree competition by recent climate change

Introduction

Temporal increases of tree mortality have been observed in tropical, temperate and boreal forests (Phillips and Gentry 1994, Phillips et al. 2004, van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013) with global implications in forest structure, function, and biosphere-atmosphere interactions (Anderegg et al. 2013). The increased tree mortality has been mainly attributed to global-change-type drought, i.e., increase of water deficit under global warming (Breshears et al. 2005, Breshears et al. 2009). Studies have showed direct processes through hydraulic failure and carbon starvation (Adams et al. 2009, Anderegg et al. 2012b), indirect processes through promoting forest pests outbreaks (Kurz et al. 2008), and interdependent processes among direct processes and indirect processes (McDowell et al. 2011, Gaylord et al. 2013). However, the temporal increase of tree mortality is not necessarily attributable to the global-change-type drought. Increases of tree mortality could also result from intensification of tree-tree competition due to positive climate effects (Phillips et al. 2004). Although this process has been proposed as a potential mechanism of climate change-induced tree mortality (Phillips et al. 2004), no study, so far, has explicitly tested it. Such knowledge is needed to better understand how trees die and to provide better prediction of tree mortality in future climatic scenarios (Anderegg et al. 2012a).

Global warming could affect boreal forests in two ways. On one hand, increases of temperature have a negative effect on boreal forests by increasing drought stress when evaporative demand exceeds water supply, by promoting outbreaks of forest pests, or the combination of both (Barber et al. 2000, Hogg et al. 2008, Kurz et al. 2008, Luo and Chen 2013). On the other hand, in areas where the global-change-type drought is absent, the rising temperature could have positive effects on forests by releasing the soil nutrients and lengthening growing season (Chapin et al. 1993, Myneni et al. 1997, Penuelas et al. 2009). Furthermore, as a major contributor to global warming, an increase in CO_2 could also fertilize the forests (McMahon et al. 2010). Because global-change-type drought is not a worldwide phenomenon (Sheffield et al. 2012), understanding how drought-free forests respond to recent climate changes is paramount to fully appreciate the impact of climate changes on global forests.

At a community level, trees are not isolated from each other. They compete for resources such as soil water and nutrients and light (Weiner 1990, Muller-Landau et al. 2006), and living space (Coates et al. 2009). During these processes, trees could die due to limited supplies (Luo and Chen 2011). The competition effect varies with the identity of its neighbors, generally with stronger negative effect from conspecific neighbors because of possible occupation of the same ecological niche among conspecific individuals, facilitation from interspecific neighbors, and promotion of density-dependent effects (He and Duncan 2000, Condit et al. 2006, Comita et al. 2010, Luo and Chen 2011). One difficulty of plant competition is quantification of competition index, which can be complicated, and sometimes flawed (Weigelt and Jolliffe 2003). A neighborhood analysis is an ideal analytical tool to describe how a tree interacts with its neighbors (Uriarte et al. 2004, Canham et al. 2006, Das et al. 2008, Coates et al. 2009).

In this chapter, I sought to determine 1) whether there was a systematic increase of tree mortality over last three decades in a region without global-change-type drought,

2) what the underlying climate change-associated mechanism would be if the temporal increase of tree mortality had been detected. I specifically tested two hypotheses: 1) tree mortality increases temporally; 2) regional warming has intensified the effect of competition on tree mortality. To achieve this goal, I used 148 long-term measured permanent sampling plots (PSPs) measured from 1986 to 2010 in the Manitoba province of Canada. The study area, unlike western North America, had not experienced drought over the last three decades (Sheffield et al. 2012), providing a unique setting for my purpose. The spatial configuration of each tree has been recorded since the plots were established, making it possible to compile a spatial neighborhood competition index for each tree.

Method and materials

Study area and permanent sampling plot

The study area was located in Manitoba, Canada, ranging from 49°04’ to 56°99’ N in latitude and from 95°30’ to 101°68’W in longitude (Figure 1.1). Mean annual temperature and mean annual precipitation between 1983 and 2010 varied from -3.09 °C to 2.95 °C and from 443 mm to 674 mm, respectively. Elevation ranged from 212 m to 675 m above sea level (a.s.l). Wildfire is the dominant stand-replacing disturbance with a fire return interval varying temporally and spatially from 15 to 90 years (Weir et al. 2000).

Since 1985, there were 371 plots were established in stands (>4 ha in area) that were visually homogeneous in structure and composition and were at least 100 m from any openings to minimise edge effects. The plots were circular with size of 500 m^2, and were re-measured for every 5-year until 2010. In the plots, all trees with height ≥1.5 m had been identified, tagged, and diameter at breast-height (DBH, 1.3 m above root collar) measured. The locations of all trees had been marked by recording the angle from the north and the distance from the plot center. Among these plots, 234 were in naturally-established forests. For these plots, stand ages were determined using dendrochronological methods.

To examine long-term climate change-induced mortality and climate changes-altered effect of competition on tree mortality, I selected the PSPs based on the following three criteria: 1) stands were naturally established with forest age available and were not managed; 2) plots had at least three censuses; 3) plot spatial location was provided so that climate data could be obtained. In total, 148 plots were selected (Figure 1.1). The first census year varied from 1986 to 2000 (mean = 1991); the last census year ranged from 1996 to 2010 (mean = 2008). The monitoring length averaged 16.6 years, ranging from 10 to 20 years. The mean numbers of censuses was 4.3 times, ranging from 3 to 5 times (Appendix 4.1). There were 58,584 trees measured during the monitoring period, with 14,840, 12,913, 941, 22,807, and 969 trees for the major tree species *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera*, *Picea mairana*, *Picea glauca*, respectively (Appendix 4.2).

Explanatory variables

I used the Hegyi competition index (H) to quantify a tree's competitiveness for resources (Hegyi 1974). The index is estimated based on the size of the subject tree, the sizes of neighboring trees and the distances between neighboring trees and the subject tree (Equation 4.1).

$$\mathrm{H}_{ijk}=\sum_{n\neq i}\frac{\mathrm{DBH}_{njk}}{\mathrm{DBH}_{ijk}\times((\mathrm{Distance}_{in})_{jk}+1)} \qquad \text{Equation 4.1}$$

where *i* and *n* are the i^{th} subject tree and its n^{th} surrounding tree. *j* and *k* are the j^{th} census period in k^{th} plot.

Competition from conspecific neighbors to subject tree may be stronger than that from interspecific neighbors because of possibly occupying same ecological niche among conspecific individuals, facilitating from interspecific neighbors, and promoting density-dependent effects (Condit et al. 2006, Comita et al. 2010, Luo and Chen 2011). Therefore, I used the relative conspecific Hegyi index (rH) to account for species interaction. The rH was calculated as the ratio of conspecific Hegyi index to the total Hegyi index (Equation 4.2).

$$\mathrm{rH}_{ijk}=\frac{\sum_{m\neq i}\frac{\mathrm{DBH}_{mjk}}{\mathrm{DBH}_{ijk}\times((\mathrm{Distance}_{im})_{jk}+1)}}{\sum_{n\neq i}\frac{\mathrm{DBH}_{njk}}{\mathrm{DBH}_{ijk}\times((\mathrm{Distance}_{in})_{jk}+1)}} \qquad \text{Equation 4.2}$$

where *i*, *j*, *k*, and *n* were defined as same as in Equation 4.1. *m* was m^{th} conspecific surrounding tree.

Both H and rH were calculated on a tree basis with a radius of 12.6 m. The area corrections were performed if a tree's 12.6 m radius circles lay outside the plot boundaries following Das et al. (2008). Hegyi indexes were weighted by dividing the proportion of shared area to the plot area. H and rH were calculated at the beginning of a census period.

Similar to my previous chapter, to examine the systematic temporal trends of tree mortality, I used the middle calendar year of a census period, i.e., the period between two successive censuses, to represent climate change drivers as a whole (Luo and Chen 2013). I calculated two climate anomalies: annual climate moisture index anomaly (ACMIA) and annual temperature anomaly (ATA). Climate anomalies are defined as the departure of means between two sequential measurements from the long-term climate means (Clark et al. 2011). The long-term climate mean was defined as the average of each climate variable between 1985 and 2010, the period in which the plot measurements were taken. The climate associated with each census period was calculated as the average of climate values during the period. ACMIA was used to verify the study area did not experienced temporal drought. Annual CMI was the sum of monthly CMI over 12 month periods from the previous August 1st to July 31st of the next year (Hogg et al. 2008). The monthly CMI was based on the quantity of monthly precipitation minus monthly potential evapotranspiration (PET), which was computed using a simplified form of the Penman-Monteith equation. A smaller value indicated a drier condition (Hogg et al. 2008). ATA was used to test hypothesis two if the temporal changes of tree mortality were detected. Annual temperature and climate moisture index (CMI) data were derived from BioSIM software (Régnière et al. 2012), which generates historical scale-free climate data for specific locations based on latitude, longitude, and elevation.

Statistical analyses

For each of the five major species, i.e., *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera*, *Picea mairana*, *Picea glauca*, I developed individual tree-based models using Hierarchical Bayesian logistic regression (HBLogit) to detect whether there were temporal increases of tree mortality and whether the regional warming altered tree-tree competition effect on tree mortality (Equations 4.3-4.4).

$$\mathrm{S}_{ijk} \sim \mathrm{Bernulli}(p_{ijk}) \qquad \text{Equation 4.3}$$

$$\begin{aligned} &\mathrm{logit}(p_{ijk}) = \alpha + \beta_m \times (\mathrm{X_m})_{ijk} + \pi_k \\ &\pi_k \sim N(0, \rho_k^2) \end{aligned} \qquad \text{Equation 4.4}$$

where *i*, *j*, *k* are the i^{th} subject tree of j^{th} census period in plot *k*. S is the status of a tree (0: alive, 1: dead) at the end of a census period. *p* is 5-year mortality probability. $\mathrm{X_m}$ and β_m are the m^{th} predictor and its corresponding coefficient. π_k is the random plot effect.

Similar to my previous chapter, I developed a full endogenous base model (FEBM) that included endogenous factors and their two-way interactions (Equation 4.5).

$$\begin{aligned} \mathrm{logit}(p_{ijk}) = \alpha &+ \beta_1 \times \mathrm{H}_{ijk} + \beta_2 \times \mathrm{rH}_{ijk} + \beta_3 \times \mathrm{SA}_{ijk} + \beta_4 \times \mathrm{H}_{ijk} \times \mathrm{rH}_{ijk} \\ &+ \beta_5 \times \mathrm{H}_{ijk} \times \mathrm{SA}_{ijk} + \beta_6 \times \mathrm{rH}_{ijk} \times \mathrm{SA}_{ijk} \end{aligned} \qquad \text{Equation 4.5}$$

For each species, the models were fitted at two steps. Firstly, DIC-based model selection was performed to identify the best endogenous base model (BEBM) from FEBM (Table 1). Next, I expanded BEBM by adding Year and its interactive terms with endogenous factors, i.e., Year×H, Year×rH, Year×SA. DIC-based model selection procedure was performed to determine the best model, which is denoted as BMYear. The threshold of difference in DIC was set as 2 to indicate substantial differences between the two models. To prevent over-fitting, the models with less predictors were selected when the models had similar DICs. The resultant model was used to examine whether there are temporal changes of mortality probability and whether the competition effect on tree mortality changes temporally.

Since I were also interested in the relative importance of endogenous factors and exogenous factors, the mortality sensitivity scores were calculated based on two groups, i.e., endogenous group that contained all the main endogenous factors and their two way interaction, and exogenous group that included year term and its interactive term with the endogenous factor, following the previous studies (Dietze and Moorcroft 2011, Luo and Chen 2013). I defined sensitivity scores on mortality probability as the standard deviation of the predicted mortality probability for each of the above two groups of factors, holding the other two groups of variables at their mean. To present change in mortality for each of the tree species, I calculated annual fractional change of mortality probability using the equation exp(β)-1, in which β is fitted coefficient for Year (van Mantgem et al. 2009, Luo and Chen 2013).

To examine the temporal trends of climatic variables at the plot level, I used the Hierarchical Bayesian linear model (HBL) (Equation 4.6).

$$Y_{jk} = \alpha + \beta \times \mathrm{Year}_{jk} + \pi_k \qquad \pi \sim N(0, \sigma_k^2) \qquad \text{Equation 4.6}$$

where Y_{jk} is climatic variable, i.e., ATA and ACMIA; α and β are intercept and estimated coefficients; Year_{jk} represents middle calendar year at for census period j in plot k; the model included a term π_k to describe the random effect of sampling plots.

To examine whether the regional warming led to temporal changes of mortality probability, I replaced Year with ATA following the same procedures as described in stage 2 of BMYear. The best model for ATA was denoted as BMATA.

For all analyses, the Bayesian Markov Chain Monte Carlo methods were implemented using *JAGS* called from R with *rjags* package (Plummer 2011a, b, R Development Core Team 2011). All independent variables were centred to speed up convergence. For each model, I evaluated convergence by running two independent chains with different initial values and monitoring the Gelman–Rubin statistic. When convergence was confirmed, an additional 10,000 iterations with thinning by half were used to calculate the mean and 95% credible interval for each coefficient from the posterior distribution. For Hierarchical Bayesian logistic regression models, the predictive performances were checked by two ways. Firstly, I provided the area under the receiver operation characteristic curve (AUC). A value of AUC >0.8 suggests excellent predictive power (Hosmer and Lemeshow 2000). Secondly, I binned the data and plotted predicted mortality probability against observed proportion of dead trees.

Results

For all species, the models based only on endogenous factors (FEBMs and BEBMs) performed well to describe mortality probability, as indicated by AUCs, i.e., AUC>=0.77 (Table 4.1). However, inclusions of year and its interactive terms led to better model performances, as indicated by smaller DICs of BMYear (Table 4.1). For all species, endogenous factors explained substantially more variation in tree mortality than exogenous factors did (Figure 4.1). For all species, when the model included the endogenous factors, mortality probability increased over the study period (Table 4.2 and Figure 4.2). Increase of predicted tree mortality was the fastest for *Picea glauca* with annual fractional change of 5.6%, followed by *Populus tremuloides*, *Picea mariana*, *Populus balsamifera*, and *Pinus banksiana* with annual fractional change of 5.3%, 2.7%, 2.6%, and 1.5%, respectively. The competition effects from neighbors decreased and increased with year for *Pinus banksiana* and *Populus tremuloides*, respectively, as indicated by the significant interactive terms between Year and H. The competition effects from conspecific neighbors were intensified over study period for *Pinus banksiana* and *Populus balsamifera*, indicated by the significantly positive interactive term between Year and rH. Temporal increase of mortality was faster in younger forests than that in older forests for *Populus tremuloides*, as indicated by the significantly negative interactive term between Year and SA (Table 4.2). However, for the *Picea mariana* and *Picea glauca*, the interactive term between Year and endogenous factors were not significant predictors in the BMYear models (Table 4.1).

Table 4. 1. Model selection procedure using Deviance Information Criterion (DIC) for each tested species. FEBM, BEBM, BFMYear, and BFMATA are abbreviations for full endogenous base model, best endogenous base model, best model of year, and best model of annual temperature anomaly (ATA), respectively.

Model	Predictors	DIC	ΔDIC	AUC
Pinus banksiana				
FEBM	H + rH + SA + H×rH + H×SA + rH×SA	21737	0	0.86
BEBM	H + rH + SA + H×rH + H×SA + rH×SA	21737	0	0.86
BMYear	BEBM + Year +Year×H + Year×rH	21602	-135	0.87
BMATA	BEBM + ATA + ATA×H + ATA×rH	21674	-63	0.87
Populus tremuloides				
FEBM	H + rH + SA + H×rH + H×SA + rH×SA	27019	2	0.80
BEBM	H + SA + H×rH + H×SA + rH×SA	27017	0	0.80
BMYear	BEBM + Year + Year×H + Year×SA	26444	-573	0.81
BMATA	BEBM + ATA + ATA ×H + ATA ×SA	26801	-216	0.80
Populus balsamifera				
FEBM	H + rH + SA + H×rH + H×SA + rH×SA	1978	-1	0.84
BEBM	H + H×rH + H×SA	1979	0	0.83
BMYear	BEBM + Year + Year×rH	1958	-21	0.84
BMATA	BEBM + ATA×rH	1947	-32	0.84
Picea mariana				
FEBM	H + rH + SA + H×rH + H×SA + rH×SA	23222	1	0.77
BEBM	H + rH + SA + H×rH	23221	0	0.77
BMYear	BEBM + Year	23214	-7	0.77
BMATA	BEBM + ATA +ATA×H + ATA×rH + ATA×SA	23210	-11	0.77
Picea glauca				
FEBM	H + rH + SA + H×rH + H×SA + rH×SA	1068	1	0.79
BEBM	H + rH + SA + H×rH + H×SA	1067	0	0.79
BMYear	BEBM + Year	1061	-6	0.79
BMATA	BEBM + ATA×H	1062	-5	0.79

Table 4. 2. Summaries of posterior distributions of climate variables and its interactive terms with endogenous variables in best model of year (BFMYear), and best model of ATA (BFMATA). NA means not available in the best models.

Terms	*Pinus banksiana*	*Populus tremuloides*	*Populus balsamifera*	*Picea mariana*	*Picea glauca*
BMYear					
Year	1.49	5.17	2.56	2.66	5.45
(×10^{-2})	(0.19~2.79)	(3.05~7.11)	(0.06~5.07)	(1.48~3.86)	(0.73~10.26)
Year×H	-3.77	5.97	NA	NA	NA
(×10^{-4})	(-4.47~-3.07)	(5.34~6.59)			
Year×rH	0.12	NA	0.27	NA	NA
	(0.07~0.16)		(0.15~0.38)		
Year×SA	NA	-2.44	NA	NA	NA
(×10^{-3})		(-2.96~-1.92)			
BMATA					
ATA	0.11	0.25	NA	0.28	NA
	(0.01~0.22)	(0.15~0.35)		(0.16~0.41)	
ATA×H	1.26	4.03	NA	-0.24	3.24
(×10^{-3})	(0.36~2.16)	(3.38~4.68)		(-0.43~-0.05)	(0.82~5.70)
ATA×rH	2.02	NA	3.53	0.57	NA
	(1.53~2.50)		(2.38~4.68)	(0.10~1.03)	
ATA×SA	NA	-1.80	NA	-0.48	NA
(×10^{-3})		(-2.57~-1.01)		(-0.86~-0.10)	

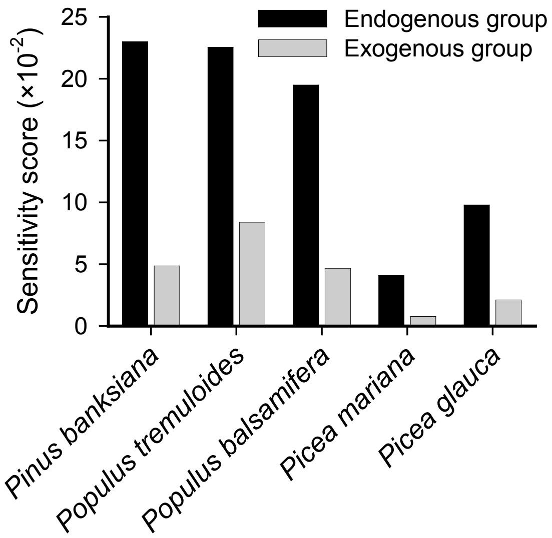


Figure 4. 1. The sensitivity scores for the two predictor groups in best model of Year (BMYear).

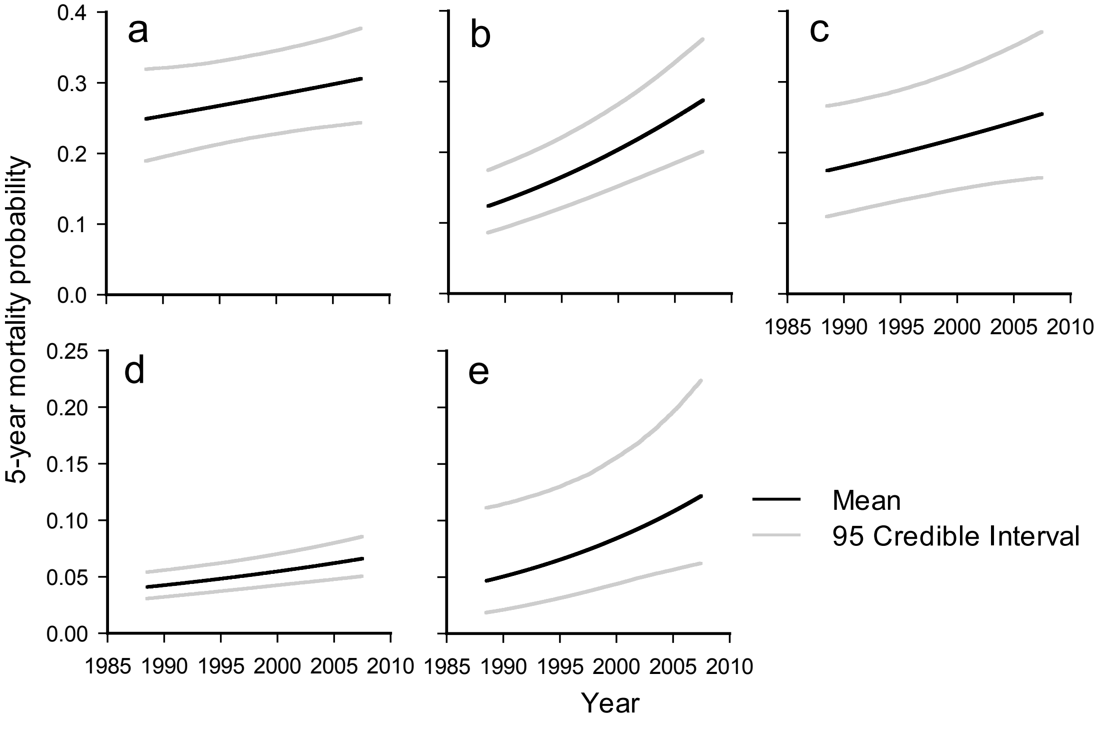


Figure 4. 2. Modeled temporal trend of 5-years' mortality probability for *Pinus banksiana* (a), *Populus tremuloides* (b), *Populus balsamifera* (c), *Picea mariana* (d), and *Picea glauca* (e). The black lines and gray lines were mean and 95% credible interval, respectively.

Over the study period, the ATA, APA, and ACMIA increased by 0.038 °C year^{-1}, 0.332 cm year^{-1} and 0.393 cm year^{-1}, respectively (Figure 4.3). For all the species, models that included ATA gave better fits than BEBMs (Table 4.1). There were overall increases of mortality probability with ATA for *Pinus banksiana*, *Populus tremuloides*, and *Picea mariana* (Table 4.2). The competition effects from neighbors on tree mortality had been intensified by increasing ATA for *Pinus banksiana*, *Populus tremuloides* and *Picea glauca*, but opposite for *Picea mariana*, as indicated by the interactive term between ATA and H (Table 2). For *Pinus banksiana*, *Populus balsamifera* and *Picea mariana*, the competition effects from conspecific neighbors on tree mortality were increased by ATA, as indicated by interactive term between ATA and rH (Table 2).

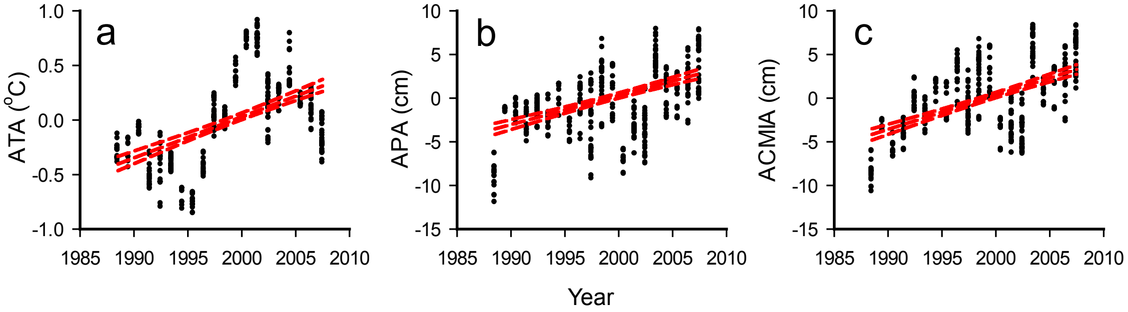


Figure 4. 3. The temporal trend of annual temperature anomaly (ATA, °C) (a), annual precipitation anomaly (APA, cm) (b), and annual climate moisture index anomaly (ACMIA, cm) (c).

Discussion

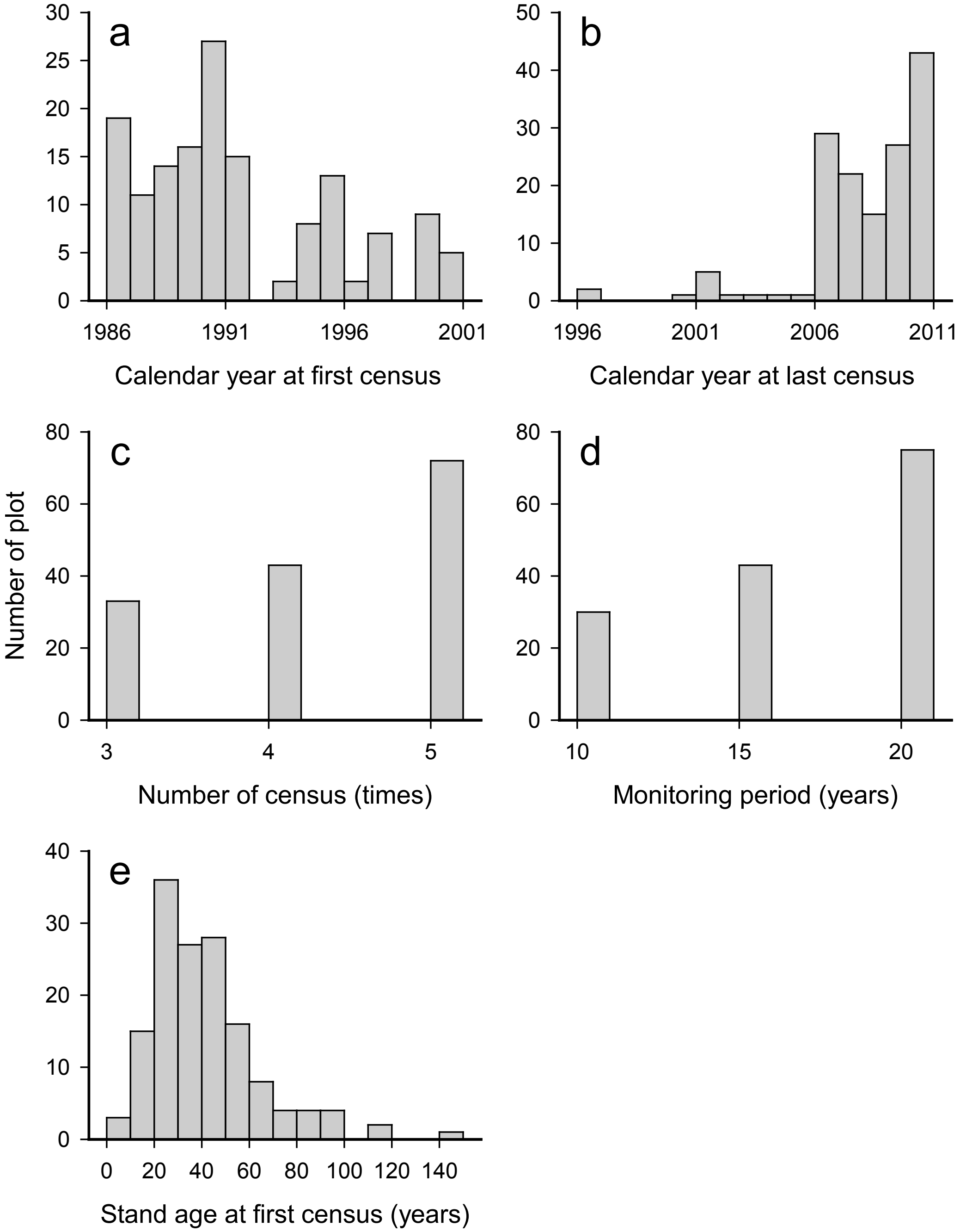
In this study, I found that the tree mortality has increased over last three decades for all the five major tree species, which is in line with previous studies that show the temporal increases of tree mortality (Phillips et al. 2004, van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013). These previous studies suggested the temporal increases of tree mortality are attributable to recent impact of global-change-type droughts on forests across large areas of western North America (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013). However, this interpretation is not applicable to the current study area in Manitoba, where I recorded a significant increase in water availability (i.e., ACMIA) over the period of my analyses. Therefore, the temporal increase of tree mortality in this study is attributable to another mechanism. The neighborhood analyses showed that regional warming had intensified the effects of competition from neighbors on tree mortality, providing evidence that the observed temporal increases of tree mortality were a result of climate-intensified tree-tree competition (Phillips et al. 2004).

My result that regional warming intensified tree-tree competition could be attributed to the positive effects of recent climate change on forests. The study area is located in a cold region where tree growth is presumably often limited by low temperatures. The observed regional warming has likely stimulated tree growth by lengthening growing season and increasing soil nutrient availability (Chapin et al. 1993, Myneni et al. 1997). This, in turn may have increased the tree-tree competition. In this study, I did not relate the temporal increase of tree mortality to temporal increase of atmospheric CO_2 that may also stimulate growth by carbon fertilization (Phillips et al. 2004). The highly correlative nature between temperature and CO_2 suggests that rising CO_2 may have also contributed to temporal increase of tree mortality.

My results are striking for several reasons. Firstly, my results suggest that the temporal increase of tree mortality could be a global phenomenon as a result of global warming. However, the underlying processes are different. In areas where the supply of water does not meet the evaporative demand promoted by warming, temporal increases of tree mortality may have occurred as a result of global-change-type drought (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013). However, in the area where the global-change-type drought is not an issue, the regional warming could kill trees by intensifying competition from their neighbors, as showed in this study. Secondly, my result that the climate change intensified conspecific competition implies that the climate change may have a positive effect to maintain tree species diversity (Condit et al. 2006, Comita et al. 2010). Finally, I reported that the increase rates were higher for *Picea glauca* and *Populus tremuloides* than other three species, suggesting that climate change likely lead to regional species compositional change. However, the regional species compositional change is different from that caused by global-change-type drought, which likely promote the dominance of early-successional species (Luo and Chen 2013).

Appendices

Appendix 4. 1. Histograms of selected 148 plots for calendar year at first census (a), calendar year at last census (b), number of census (c), monitoring period (d), and stand age at first census (e).



Appendix 4. 2. Number of plots, number of trees, and number of observations for all the tree species and five major tree species, *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera*, *Picea mariana*, and *Picea glauca*.

Species	Number of plots	Number of trees		Number of observations
		Live trees	Dead trees	
All tree species	148	39429	19050	153256
Pinus banksiana	81	9406	5329	36495
Populus tremuloides	95	5996	6917	30933
Populus balsamifera	37	305	636	2015
Picea mariana	91	19468	3339	64591
Picea glauca	46	798	171	2213
Tested species percentage		91%	86%	89%

Chapter 5. Widespread carbon sink declines of western boreal forests with climate change

Introduction

Net biomass change of closed-canopy forests is a critical indicator to understanding forest carbon balance (Phillips et al. 1998, Lewis et al. 2009, Phillips et al. 2009, Pan et al. 2011b). Containing nearly half of the global forest ecosystem carbon due to the slow decomposition rate of dead biomass in cold climates, boreal forests play a critical role in the global carbon cycle (Dixon et al. 1994). Compared with spatially extensive observational networks used to estimate net biomass change in tropical and temperate forests (Phillips and Gentry 1994, Phillips et al. 1998, Phillips et al. 2004, Lewis et al. 2009, Phillips et al. 2009, McMahon et al. 2010, Thomas et al. 2010) however, there has been only one recent study reporting net biomass change of old forests (≥80 years old) in Canada, which analyzed 96 sample plots with a total area of approximately 11 ha (Ma et al. 2012). The extent and the degree to which climate change may affect net biomass change remains unclear for the boreal forests due to its diverse types (Gower et al. 2001) and the fact that the majority of the forests are younger than 80 years old due to high frequencies of stand-replacing disturbances (Weir et al. 2000, Magnani et al. 2007).

Net biomass change of closed-canopy forests is the sum of growth of surviving trees, ingrowth from new recruitments, and loss by mortality. Regional warming and drought-associated increases in tree mortality have been widely observed in western North American forests (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013). The increases in tree mortality, however, may not lead to net biomass decline since the growing space and resources released by tree mortality can be utilized by surviving trees and new recruits (Phillips and Gentry 1994, Phillips et al. 2004). Despite persistent increases of global warming (Diffenbaugh and Field 2013) and drought in some terrestrial ecosystems (Sheffield et al. 2012), the systematic trends, which best reflect climate change effects (Parmesan and Yohe 2003, IPCC 2007), in net biomass change associated with warming and drought remain uncertain in natural forests (Chave et al. 2004).

To examine net aboveground biomass change and its systematic trends associated with climate change, I used 871 permanent sampling plots (170.6 ha), monitored between 1958 and 2009 (Appendix 5.1). These plots were established by the Alberta and Saskatchewan governments to monitor growth of closed-canopy forests, using stratified random sampling to cover four forest types and a wide range of forest age classes (ranging from 17 to 210 years old) (Appendix 5.1). Along with the global increase in CO_2 concentration, the region has experienced warming, and droughts (Scheffer et al. 2012, Diffenbaugh and Field 2013), has undergone extensive insect outbreaks (Hogg et al. 2008), but has little nitrogen deposition (Reay et al. 2008). I quantified annual net aboveground biomass change (ΔAGB) as the sum of the changes in growth of surviving trees (ΔAGB_G), ingrowth from recruitment (ΔAGB_I), and loss from mortality (ΔAGB_M). Since observed trends in longitudinal data reflect both endogenous and exogenous processes (Magnani et al. 2007, Brown et al. 2011, Luo and Chen 2013), I used Hierarchical Bayesian models, which are suited for accounting for uncertainties in sampling, models, and parameters associated with observational data

(Clark 2005), to disentangle forest age and climate change effects on ΔAGB and its components.

Method and materials

Study area and the forest inventory data

The study area is located in Alberta and Saskatchewan, Canada, ranging from 49°01’ to 59°44’ N in latitude and from 101°44’ to 119°40’ W in longitude (Figure 1.1). Mean annual temperature and mean annual precipitation between 1950 and 2009 varied from -2.38 °C to 4.08 °C and from 365 mm to 1184 mm, respectively. Elevation ranges from 260 m to 2073 m above sea level (a.s.l). Wildfire is the dominant stand-replacing disturbance with a fire return interval varying temporally and spatially from 15 to 90 years (Weir et al. 2000).

A total of 3006 permanent sampling plots (PSP) were established in the study area mostly during 1960s and 1970s by the Alberta and Saskatchewan provincial governments. The plot sizes vary from 405 m^2 to 8092 m^2. The plots were established in stands (>1 ha in area) that were visually homogeneous in structure and composition and were at least 100 m from any openings to minimise edge effects. The plots were re-measured until 2009 at varying intervals.

To examine long-term changes of aboveground biomass, I selected the PSPs based on the following five criteria: 1) stands originated from a wildfire with forest age available and were not managed; 2) plots had at least three censuses and had been monitored for at least 10 years; 3) All trees within sample plots including recruitment trees were marked and their diameter at breast height (DBH) were measured; 4) plot spatial location was provided so that climate data could be obtained; 5) each plot had at least 30 trees at initial measurement to ensure that the plot represented the sample stand. The last criterion resulted in the exclusion of plots with size <600 m^2. Stand age for each plot was determined according to a known fire or dendrochronologically as the median age of the least shade tolerant species in the plot by coring three dominant/co-dominant trees of each tree species outside the plot at the time of plot establishment. In total, 871 plots (170.6 ha) were selected for analyses with 208,961 trees measured during the monitoring period (Appendix 5.1 and Appendix 5.2). The first census year varied from 1958 to 1993; the last census year ranged from 1972 to 2009. The measurement intervals averaged 9.20 years. The numbers of censuses averaged 3.91 times (Appendix 5.1).

Because each province used different tree size criteria for monitoring, i.e., ≥7.3 cm in DBH in Alberta, ≥9.7cm in DBH in Saskatchewan, respectively, I standardized the data by selecting trees with DBH ≥10 cm to eliminate the effect of the different sampling efforts between the two provinces. Recruitment trees were defined as those reached 10-cm DBH between two successive censuses. A decrease in DBH for a given tree could occur between two successive measurements (Phillips et al. 1998) since DBH could be measured in different directions or due to different levels of tree bark swells and shrinks under different weather conditions when measurements were taken. As such I applied a correction to those cases by interpolating DBH values from the previous and the next measurements (Phillips et al. 1998).

Calculations of annual net aboveground biomass change and its components

I calculated stand-level biomass by summing the biomass of all trees within each sample plot for each census. Individual tree aboveground biomass was estimated by using species-specific DBH-based equations for wood, bark, foliage, and branches, respectively (Lambert et al. 2005). As recommended (Chave et al. 2004), these equations were developed based on 207 to 1534 trees per species with a wide range of sizes, sampled across Canada boreal forests. For less frequently occurring *Pseudotsuga menziesii* Mirb. (437 trees), *Pinus flexilis* James (5 trees), and *Picea engelmannii* Parry ex Engelm. (42 trees), I used the equations of softwood or hardwood to estimate their biomass (Lambert et al. 2005).

I calculated annual net aboveground biomass change (ΔAGB, Mg ha^{-1} yr^{-1}) as the difference of aboveground biomass divided by the number of years between two consecutive censuses. The ΔAGB included biomass gain by the growth of surviving trees (ΔAGB_G), ingrowth by new recruitment trees (ΔAGB_I), and loss due to tree mortality (ΔAGB_M). Similar to studies in tropical forests (Lewis et al. 2009, Phillips et al. 2009), I empirically derived optimum weighting of each observation corresponding to the sampling effort employed (plot size and length of monitoring period), by assessing patterns in the residuals of ΔAGB and its components versus sampling efforts (Appendix 5.3).

Explanatory variables

Similar to previous studies (Phillips et al. 1998, Lewis et al. 2009, Phillips et al. 2009), to examine the systematic temporal trends in ΔAGB and its components, I used the middle calendar year of a census period, i.e., the period between two successive censuses, to represent climate change drivers as a whole (Luo and Chen 2013). I calculated two climate anomalies: annual temperature anomaly (ATA) and annual climate moisture index anomaly (ACMIA). Climate anomalies are defined as the departure of means between two sequential measurements from the long-term climate means (Clark et al. 2011). The long-term climate mean was defined as the average of each climate variable between 1954 and 2009, during which the plot measurements were taken. The climate associated with each census period was calculated as the average of climate values during the period. Annual temperature and climate moisture index (CMI) data were derived from BioSIM software (Régnière et al. 2012), which generates historical scale-free climate data for specific locations based on latitude, longitude, and elevation. Annual CMI was the sum of monthly CMI over 12 month periods from last August 1st to July 31st of current year (Hogg et al. 2008). The monthly CMI was based on the quantity of monthly precipitation minus monthly potential evapotranspiration (PET), which was computed using a simplified form of the Penman-Monteith equation. A smaller value indicated a drier condition (Hogg et al. 2008).

Statistical analyses

To account for uncertainties in sampling, models and parameters, I used the Bayesian Markov Chain Monte Carlo methods with *rjags* package for all analyses (Wikle 2003, Clark 2005, Cressie et al. 2009, Plummer 2011a, b). To estimate the long-term means of ΔAGB and its components, I used:

$$Y_{ij} = \mu + \pi_j \qquad \text{Model 5.1}$$

where Y_{ij} is ΔAGB or its components of plot j for census period i; μ is the long-term mean to be estimated; π_j represents the random effect of sampling plots. As a rule of thumb, π_j is in normal distribution with a mean of 0.

To disentangle the effects of forest development and climate change (Brown et al. 2011), I included forest age and calendar year as predictors:

$$Y_{ij} = \beta_0 + \beta_1 \times \ln(FA_{ij}) + \beta_2 \times Year_{ij} + \pi_j \qquad \text{Model 5.2}$$

where Y_{ij} and π_j are same as in Model 1; β_0, β_1, and β_2 are parameters to be estimated. FA_{ij} is middle forest age of a census period and is transferred by natural logarithms since ΔAGB and forest age relationship is best described by natural log function (Appendix 5.4). The data show a positive collinearity between *FA* and *Year* ($r = 0.16$ or $r^2 = 0.027$). There are three possible approaches to disentangle the joint variations between forest age and climate change effects. The first approach is to simultaneously model forest age and climate change effects without assigning priority. The second is to use residual and sequential regressions by assigning the priority to *FA* and then modeling *Year* effects on the residuals (Graham 2003). The third is to reverse the priority in the second approach. While all three approaches yielded negative parameter values for *FA* and *Year*, the first approach yielded the intermediate parameter values (Appendix 5.5). Because I have no logical or theoretical basis for considering any variable to be prior to any other in terms of a hypothetical causal structure of the data (Cohen and Cohen 1975) and assigning priority to *FA* would marginalize the *Year* effect, and *vice versa* (Brown et al. 2011), I interpreted the results from the simultaneous modeling the effects of *FA* and *Year* (Appendix 5.5).

In model 5.2, $Year_{ij}$ represents systematic climate change drivers including the systematic increase in ATA and decrease in ACMIA. However, the interannual variability of ATA and ACMIA would not be represented by Year. As recommended by Gelman *et al.* (2003), I expanded Model 2 to include ATA and ACMIA as predictors.

$$\begin{aligned} Y_{ij} &= \beta_0 + \beta_1 \times \ln(FA_{ij}) + \beta_2 \times Year_{ij} + \beta_3 \times ATA_{ij} + \beta_4 \times ACMIA_{ij} \\ &\quad + \beta_5 \times Year \times ATA_{ij} + \beta_6 \times Year_{ij} \times ACMIA_{ij} + \beta_7 \times ATA_{ij} \times ACMIA_{ij} + \pi_j \end{aligned}$$

Model 5.3

where Y_{ij}, FA_{ij}, $Year_{ii}$, and π_j are same as in Model 2; ATA_{ij} and $ACMIA_{ij}$ represent the average ATA and ACMIA of a census period, respectively; β_s are parameters to be estimated.

I exhaustively ran all possible models by growing model complexity, starting from the simplest model with forest age as only predictor. I computed Deviance Information Criterion (DIC) and R^2 of all models following the procedures described by Gelman *et al.* (2003) and Gelman and Pardoe (2006), respectively. For all alternative models, *FA* and Year are dominant predictors, accounting for the largest shares in DIC reduction and explained deviance (Appendix 5.6). The models with the smallest DICs increased R^2 by less than 0.02 and reduced DIC by less than 1% from the models with *FA* and Year as predictors (Appendix 5.6). Since models with a small number of predictors can prevent overfitting (Gelman et al. 2003), I focused on the interpretation on the models with *FA* and Year as predictors. To further understand the link between the ΔAGB trends associated with Year and ATA and ACMIA, I reported the models with ATA and ACMIA as predictors. Note that in the ATA and ACMIA models, the variations of ATA and ACMIA included both the systematic trends associated with Year and their interannual variability.

Because forest productivity differs strongly among forest types (Gower et al. 2001) and climate change-associated demographic rates such as tree mortality differs among tree species (Luo and Chen 2013), I examined whether ΔAGB, its components, and their systematic trends differ among the forest types that are classified based on the dominance of tree species with similar leaf traits and successional status by Alberta and Saskatchewan governments. Here forest types are classified based on the proportions of aboveground biomass of species groups at the first census of each sample plot. Deciduous broadleaf forest type (DEC) consisted >75% of aboveground biomass from *Populus tremuloides* Michx., *Populus balsamea* L., and *Betula payrifera* Marsh.; early-successional coniferous forest type (ESC) consisted of >75% of aboveground biomass of *Pinus banksiana* Lamb., *Pinus contorta* Douglas, and *Larix laricina* (Du Roi) K. Koch*;* late-successional conifer forest type (LSC) consisted of 75% of aboveground biomass of *Abies lasiocarpa* (Hooker) Nuttall., *Abies balsamea* (L.) Mill.*, Pseudotsuga menziesii* (Mirb.) Franco*, Picea engelmannii* Parry ex Engelm.*, Picea glauca* (Moench) Voss, and *Picea mariana* Mill.; mixed forest type (MIX) consisted of all stands that did not meet the criteria of the three preceding types.

The age-dependent trends for ΔAGB_G, ΔAG_I, and ΔAG_M, however, differed among forest types (Appendix 5.4). To determine climate change effects, I detrended forest age effects (Brown et al. 2011) by selecting the best fit models among derivative of Monod function (McMahon et al. 2010), Weibull distribution function (He et al. 2012), linear, natural logarithmic, and third-order polynomial models. I then tested climate change effects from the forest age corrected residuals and followed the model selection and diagnosis described above.

The ΔAGB followed normal distributions, while ΔAGB_G, ΔAGB_I and ΔAGB_M were assigned as lognormal distributions as they were skewed to the right. All coefficients were assigned non-informative priors. The sensitivity scores were the slopes of Bayesian linear regressions between dependent variable and each predictor, measuring the changes of dependent variable for per unit change of each predictor (Wolkovich et al. 2012). For all analyses, the Bayesian Markov Chain Monte Carlo methods were implemented using *JAGS* called from R with *rjags* package (Plummer 2011a, b). All independent variables were centred by subtracting mean, to reduce their correlations and speed up convergence. For each model, I evaluated convergence by running two independent chains with different initial values and monitoring the Gelman–Rubin statistic. When convergence was confirmed, an additional 10,000 iterations with thinning of half were used to calculate the mean, s.d. and 95% credible interval for each coefficient from the posterior distribution. Following Gelman et al. (2003), I performed numerical posterior predictive checks on my models by testing the difference between the observed values and the distribution of 10,000 posterior predictions (Appendix 5.7). Analyses were separately performed for all plots and individual forest types.

Assessing possible methodological problems

To make correct inferences about long-term changes in ΔAGB, it is essential to know the uncertainties associated with AGB estimates (Chave et al. 2004). I first examined whether sampling strategies affected forest age-corrected annual changes of ΔAGB and its components. My analyses indicated that the empirical weightings applied to account for sampling efforts produced unbiased estimates of annual changes of ΔAGB

and its components (Appendix 5.8). Second, I examined representativeness of the plot network used the analysis. As recommended (Chave et al. 2004), I examined whether forest age-corrected annual changes of ΔAGB and its components were spatially correlated. The Mantel tests showed no evidence of spatial auto-correlation among the plots (Appendix 5.9). Lastly, to examine whether my use of the Canadian national species-specific tree aboveground biomass equations could have biased my conclusions, I also quantified the annual change in stand basal area and its long-term trends associated with climate change. My analysis shows that both annual net change in stand basal area and ΔAGB had similar responses to climate change, suggesting that my choice of allometric equations does not bias my conclusions (Appendix 5.10).

Results

Annual net aboveground biomass change (ΔAGB), weighted by sampling effort, was 1.11 (95% credible interval (CI), 1.02~1.21) Mg ha^{-1} yr^{-1} between 1958 and 2009 (Figure 5.1). The ΔAGB attributed to growth of surviving trees was 2.33 (CI, 2.27~2.40) Mg ha^{-1} yr^{-1}, ingrowth of new recruitments was 0.19 (CI, 0.17~0.20) Mg ha^{-1} yr^{-1}, and mortality was -1.26 (CI, -1.19~-1.33) Mg ha^{-1} yr^{-1}. ΔAGB decreased with forest age as well as calendar year (Figure 5.2, and Appendix 5.4). After accounting for forest age-associated declines (Appendix 5.6), ΔAGB decreased at -0.031 (CI, -0.037~-0.025) Mg ha^{-1} yr^{-1} yr^{-1}, due to both increased tree mortality and decreased growth of surviving trees, while ingrowth from new recruitments did not change with calendar year (Figure 5.3). The ΔAGB decline represents approximately -2.79% per year, i.e., -0.031 Mg ha^{-1} yr^{-1} yr^{-1} divided by its long-term mean of 1.11 Mg ha^{-1} yr^{-1}, but the relative decline rates increased over time since the denominator continued to decrease.

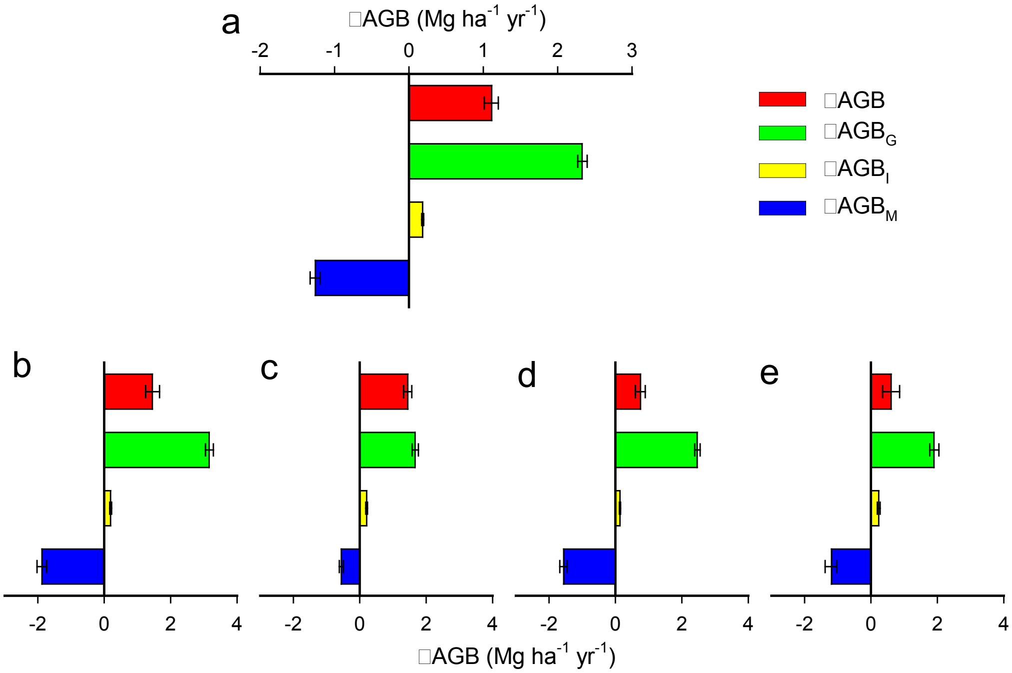


Figure 5. 1. Long-term (1958-2009) annual net aboveground biomass change (ΔAGB) and it components. a, All forest plots. b, Deciduous broadleaf forests. c, Early-successional coniferous forest. d, Mixed forests. e, Late-successional coniferous forests. Values are means and 95% credible intervals weighted by sampling effort (plot size and census-interval length) (see Methods). ΔAGB_G, ΔAGB_I, and ΔAGB_M represent net aboveground biomass change associated with growth of surviving trees, ingrowth from recruitments, and loss through mortality.

Since forest productivity differs strongly among forest types (Gower et al. 2001) and climate change-associated demographic rates such as tree mortality differs among tree species (Luo and Chen 2013), I examined whether ΔAGB, its components, and their systematic trends differ among the forest types, which are classified based on the dominance of tree species with similar leaf traits and successional status by Alberta and Saskatchewan governments. Among forest types, ΔAGB was 1.45 (CI, 1.25~1.67), 1.45 (CI, 1.32~1.57), 0.75 (CI, 0.60~0.90), and 0.61 (CI, 0.35~0.86) Mg ha^{-1} yr^{-1} for deciduous broadleaf, early-successional coniferous, and mixed, and late-successional coniferous forest types, respectively (Figure 5.1). After accounting for negative forest age effects, climate change-associated declines occurred in all forest types with the largest decline in late-successional forests at a rate of -0.074 (CI, -0.093~-0.053) Mg ha^{-1} yr^{-1} yr^{-1}, followed by mixed forests, deciduous broadleaf forests, and earl-successional coniferous forests at -0.040 (CI, -0.051~-0.029), -0.025 (CI, -0.043~-0.006), and -0.022 (CI, -0.029~-0.015) Mg ha^{-1} yr^{-1} yr^{-1}, respectively (Figure 5.3). Both forest age- and climate change-induced declines led to net biomass loss in the late-successional coniferous forests since about 1990 and no biomass gain in mixed forests since 2000, whereas deciduous broadleaf and early-successional coniferous forests retained positive ΔAGB during the study period (Figure 5.2).

During the study period, mean annual temperature increased by 0.031 °C yr^{-1} with a weak decrease in precipitation, resulting in an annual climate moisture index anomaly (ACMIA) decrease of 0.109 cm^{-1} yr^{-1} with calendar year (Figure 5.4). To test whether ATA and ACMIA are the potential drivers for the ΔAGB declines, I examined their associations (Figure 5.4 and Appendix 5.6). The overall changes in forest age-corrected ΔAGB were negatively correlated with ATA due to simultaneous increased mortality and decreased growth of surviving trees with no increase in recruitments; the overall changes were, to a lesser extent, positively related to ACMIA. Analyzed by forest types, the declines of mixed and late-successional coniferous forests were strongly associated with ATA and ACMIA. To a lesser extent, the decline of deciduous broadleaf forests was associated with ATA, but not ACMIA, whereas the decline of early-successional coniferous forests was associated with ACMIA, but not ATA.

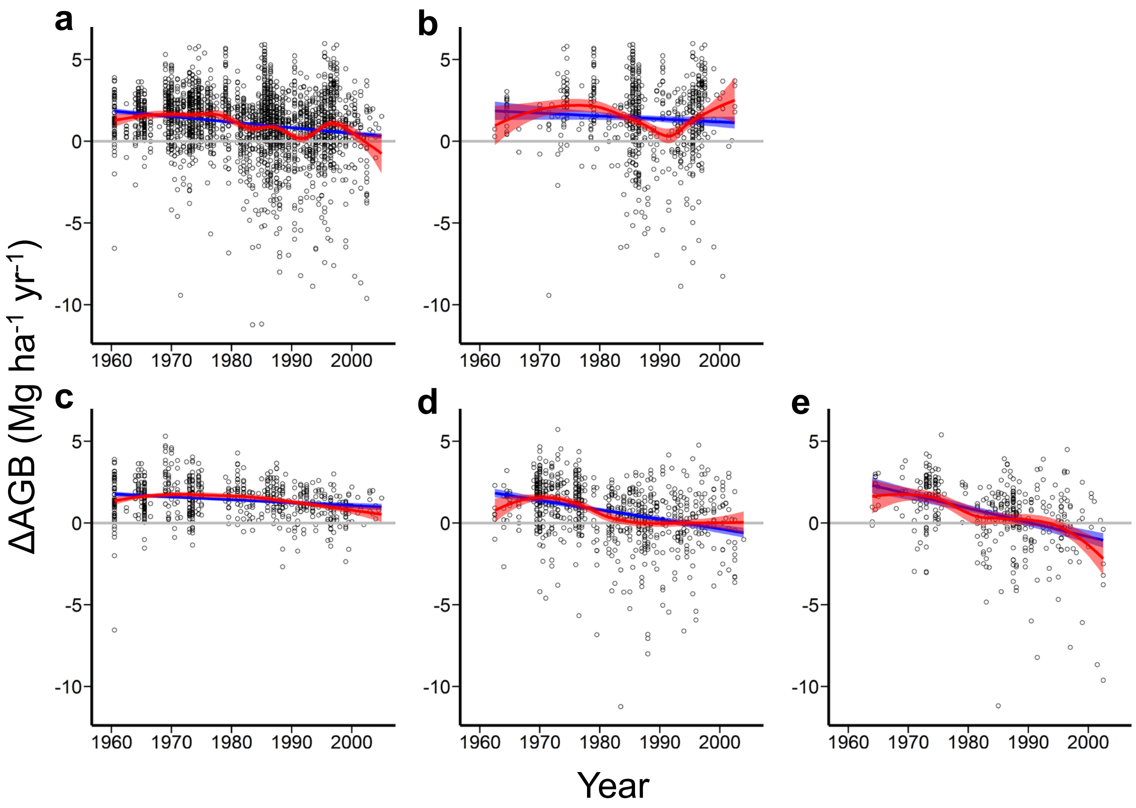


Figure 5. 2. Annual net aboveground biomass change (ΔAGB) in relation to calendar year. a, All forest plots. b, Deciduous broadleaf forests. c, Early-successional coniferous forests. d, Mixed forests. e, Late-successional coniferous forests. Red and blue lines represent linear fit and Loess fit with 95% confidence limits, respectively.

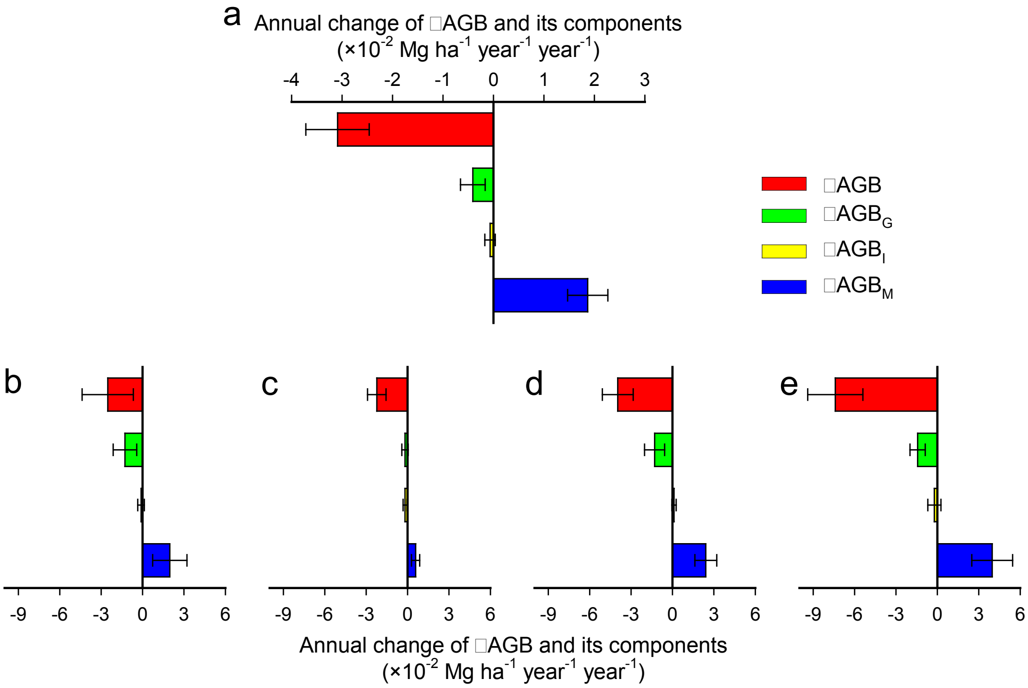


Figure 5. 3. The response of forest age-corrected annual net aboveground biomass change (ΔAGB) and its components to calendar year. a, All forest plots. b, Deciduous broadleaf forests. c, Early-successional coniferous forest. d, Mixed forests. e, Late-successional coniferous forests. The error bars show the 95% credible intervals.

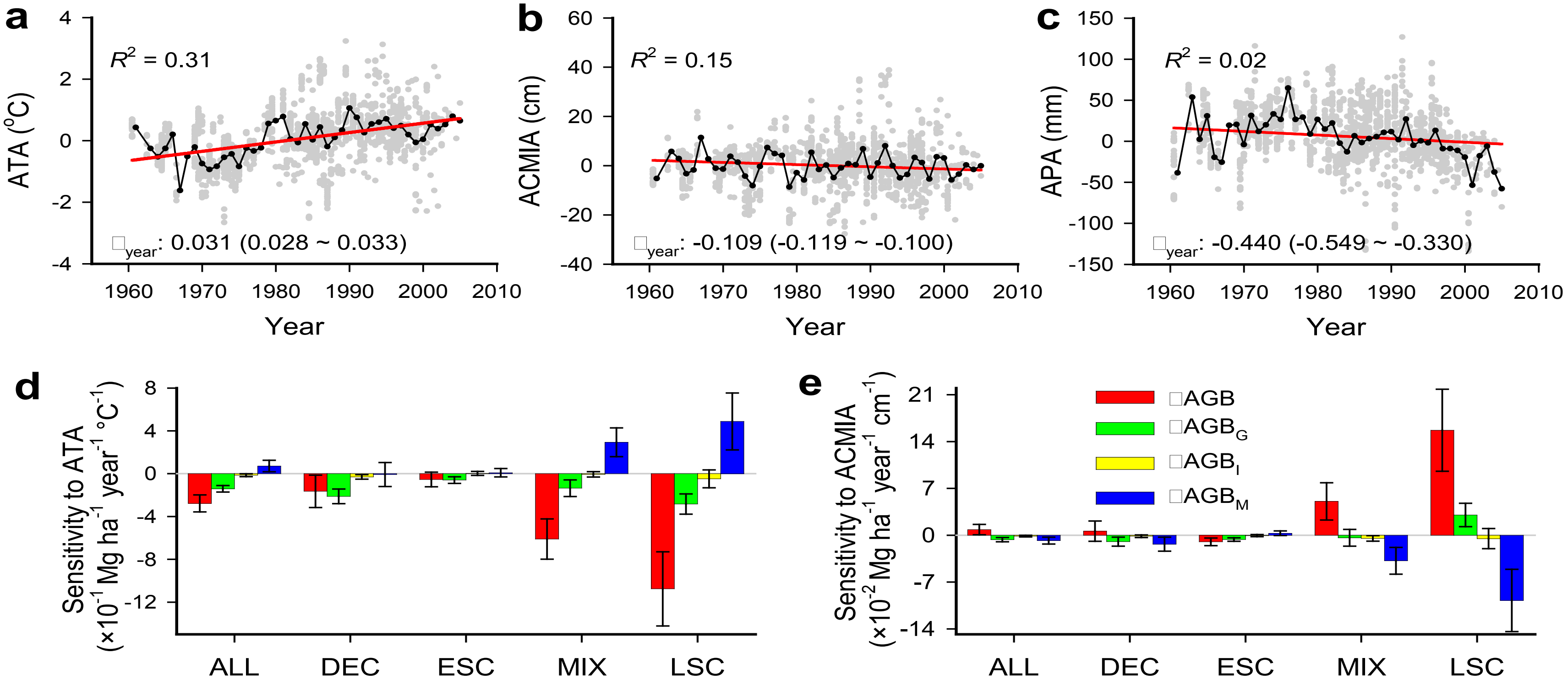


Figure 5. 4. Temporal trends of climatic anomalies and the responses of annual net aboveground biomass change (ΔAGB). a–c, Annual temperature anomaly (ATA), annual climate moisture index anomaly (ACMIA), and Annual precipitation anomaly (APA) with calendar year. The grey dots were the plot-level observations. Black dotted lines were the summarized annual means. Red lines were fitted trends using Hierarchical Bayesian linear model with R^2 and β_{year} mean and its 95% credible intervals. d–e, the sensitivity of forest age- corrected ΔAGB and its components to ATA and ACMIA, respectively.

Discussion

The ΔAGB reported in this study is based on a spatially extensive observational network (170.6 ha) for the closed-canopy boreal forests of diverse types and ages. My estimate of overall mean ΔAGB for the closed-canopy boreal forest is comparable to those reported for tropical old-growth forests on a per unit area basis (Phillips et al. 1998, Lewis et al. 2009, Phillips et al. 2009). Assuming that the sample plots monitored by the provincial governments are representative of the closed canopy forests in the region, these forests have served as a strong aboveground biomass carbon sink over the study period (excluding areas affected by major disturbance such as fire). As expected in boreal and temperate forests (Gower et al. 2001, Magnani et al. 2007), net biomass change decreases with forest age. After accounting for forest age effects, I find that net biomass change declined by -0.031 (CI, -0.037~-0.024) Mg ha^{-1} yr^{-1} yr^{-1}. My estimated decline rate represents approximately 2.79% less net carbon accumulation annually, meaning that over 25 years, the forests will accumulate only half as much carbon, and over 50 years, just a quarter as much. My result shows that the declines in net biomass change did not only result from previously reported climate change-associated increases in tree mortality (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013), but also from reduced growth of surviving trees. However, in contrast to tropical old-growth forests (Phillips and Gentry 1994, Phillips et al. 2004), the increased mortality and reduced growth of surviving trees did not lead to increased recruitment in the western boreal forests.

Among forest types, ΔAGB in deciduous broadleaf and early-succession coniferous forests was twice as much as those in mixed and late-successional coniferous forests (Figure 5.1). The climate change-associated declines in net biomass change did not only occur in previously reported deciduous broadleaf forests (Hogg et al. 2008) and late-successional forests (Ma et al. 2012), but in all forest types. The least decline occurred in early-successional coniferous forests dominated by drought-tolerant *Pinus* spp. The greatest decline was in late-successional coniferous forests dominated by shallow-rooted *Picea* spp. at a rate of -0.074 (CI, -0.093~-0.053) Mg ha^{-1} yr^{-1} yr^{-1}, which is similar to the previously estimated decline rate of old forests in the region (-0.0694 Mg ha^{-1} yr^{-1} yr^{-1}) (Ma et al. 2012). In accordance with my previous analysis of individual tree mortality probability (Luo and Chen 2013), the high mortality loss of biomass in the late-successional forests is a result of the high individual tree mortality probability in *Picea* spp. and their large sizes in the late-successional forests.

The strong associations between the declines in forest age-corrected net biomass change and regional warming between 1958 and 2009 observed in this study provide evidence of long-term systematic climate change effects (Parmesan and Yohe 2003, IPCC 2007) on the western boreal forests. The declines of net biomass change in mixed and late-successional coniferous forests were strongly associated with warming and drought. These results provide stand-level evidence for reduced growth and increased tree mortality of *Picea* spp. associated with warming and drought reported at the individual tree level (Barber et al. 2000, Luo and Chen 2013), suggesting that these climatic changes may have shifted shallow-rooted *Picea* spp. beyond their hydraulic safety margins against injurious levels of drought stress (Choat et al. 2012). These results indicate that the persistent long-term drought that occurred in the western boreal forests during the study period has strong negative effects on *Picea* dominated forests.

The mechanisms associated with the declines in deciduous broadleaf forests and early-successional coniferous forests dominated by deep-rooted *Populus tremuloides* and *Pinus* spp., respectively, are more complex (Anderegg et al. 2012a). A large decline in the early 1990s (Figure 5.2b) followed the warmest year in 1991 (Figure 5.4), contributed to the negative warming effects on net biomass change of the deciduous broadleaf forests (Figure 5.4d). The decline in early-successional coniferous forests, dominated by *Pinus* spp., is positively associated with drought (Figure 5.4). These declines likely resulted from both warming and drought induced hydraulic failures and increased pathogen and insect outbreaks, both of which are positively associated with warm temperatures and droughts in northern latitudes (Logan et al. 2003, Anderegg et al. 2012a).

I present evidence that closed-canopy western boreal forests have served as a carbon sink comparable to old-growth tropical forests on a per unit area basis. Unlike other forests where increased nitrogen deposition and rising atmospheric CO_2 increase forest growth (Magnani et al. 2007, Reay et al. 2008, Lewis et al. 2009, McMahon et al. 2010, Thomas et al. 2010), the carbon sink function of the closed-canopy boreal forests has declined in all forest types, but with different rates. These declines are attributable to long-term persistent warming and drought and their associated pathogens and insect outbreaks. Different sensitivities among forest types to warming and drought indicate that the regional forests have shifted in species composition and will likely become further dominated by early-successional species if current climatic trends continue.

Appendices

Appendix 5. 1. Summary statistics (mean ±1 SD with range in brackets) of the permanent sample plots from Alberta (AB) and Saskatchewan (SK) for all forest plots, Deciduous broadleaf forests (DEC), Early-successional coniferous forests (ESC), Mixed forests (MIX), Late-successional coniferous forests (LSC).

Attribute	All plots	DEC	ESC	MIX	LSC
Plot-based summaries					
Number of plots	871	262	210	260	139
Plot size (m^2)	1958±2107	1461±1890	2011±1862	2399±2400	1994±2085
	(600~8092)	(800~8092)	(800~8092)	(800~8092)	(600~8092)
Number of census	3.91±0.89	3.60±0.85	4.22±0.75	4.04±0.84	3.75±1.01
	(3~8)	(3~8)	(3~7)	(3~7)	(3~6)
Length of monitoring (years)	26.72±10.01	22.40 ±6.79	28.64±11.18	29.39±10.72	26.96±9.23
	(10~48)	(10~48)	(10~47)	(10~48)	(10~44)
Calendar year*	1969.76±8.68	1976.28±6.67	1964.65±8.87	1967.06±6.12	1970.25±8.19
	(1958~1993)	(1960~1993)	(1958~1989)	(1960~1990)	(1960~1990)
Forest age (years)*	71.30 ±28.21	56.14±19.54	60.64±24.92	81.95±21.23	96.07±32.66
	(17~174)	(25~130)	(17~160)	(31~156)	(42~174)
Aboveground biomass (Mg/ha)*	136.46±55.11	149.23±60.28	96.30±44.88	157.21±41.47	134.27±49.19
	(15.12~492.83)	(21.43~492.83)	(15.12~227.87)	(23.20~263.42)	(15.18~242.44)

Number of live trees[*]	205.79±171.03 (33~948)	157.96±138.21 (44~852)	236.11±193.84 (35~948)	227.67±178.29 (39~815)	209.24±158.29 (33~763)
Census period-based summaries[†]					
No. of census period	2531	682	676	791	382
Length of census period (years)	9.20±4.27 (1~29)	8.61±4.35 (1~20)	8.90±3.61 (2~21)	9.66±4.67 (3~29)	9.81±4.19 (1~20)
Forest age (years) [‡]	87.36±32.07 (19.5~205.5)	69.33±22.87 (26.5~157.5)	76.33±28.50 (19.5~169.5)	98.28±24.11 (33.5~165.5)	116.42±36.85 (44.5~205.5)
Year[‡]	1982.78±10.88 (1960.5~2005)	1987.74±8.33 (1962.5~2002.5)	1978.63±12.54 (1960.5~2005)	1981.54±10.21 (1962.5~2004)	1983.83±9.42 (1964~2002.5)
Annual temperature anomaly (°C)	0.06±0.83 (-2.66~3.24)	0.21±0.97 (-2.52~2.65)	0.24±0.95 (-2.66~3.24)	-0.17±0.61 (-1.81~1.51)	-0.04±0.55 (-1.39~1.34)
Annual climate moisture index anomaly (cm)	-0.41±8.39 (-27.69~38.90)	-1.39±10.45 (-23.34~26.82)	-1.93±11.08 (-27.69~38.90)	1.13±3.93 (-13.26~10.73)	0.86±3.17 (-12.38~10.81)
Annual precipitation anomaly (mm)	6.67±30.95 (-133.85~127.08)	2.83±28.51 (-130.50~116.15))	5.66±33.63 (-132.50~127.08)	9.56±32.26 (-133.85~90.49)	9.32±26.34 (-125.50~94.84)

[*] The variables were summarized based on the first census of the plots.

[†] A census period was defined as the period between two successive censuses (see Materials and Methods).

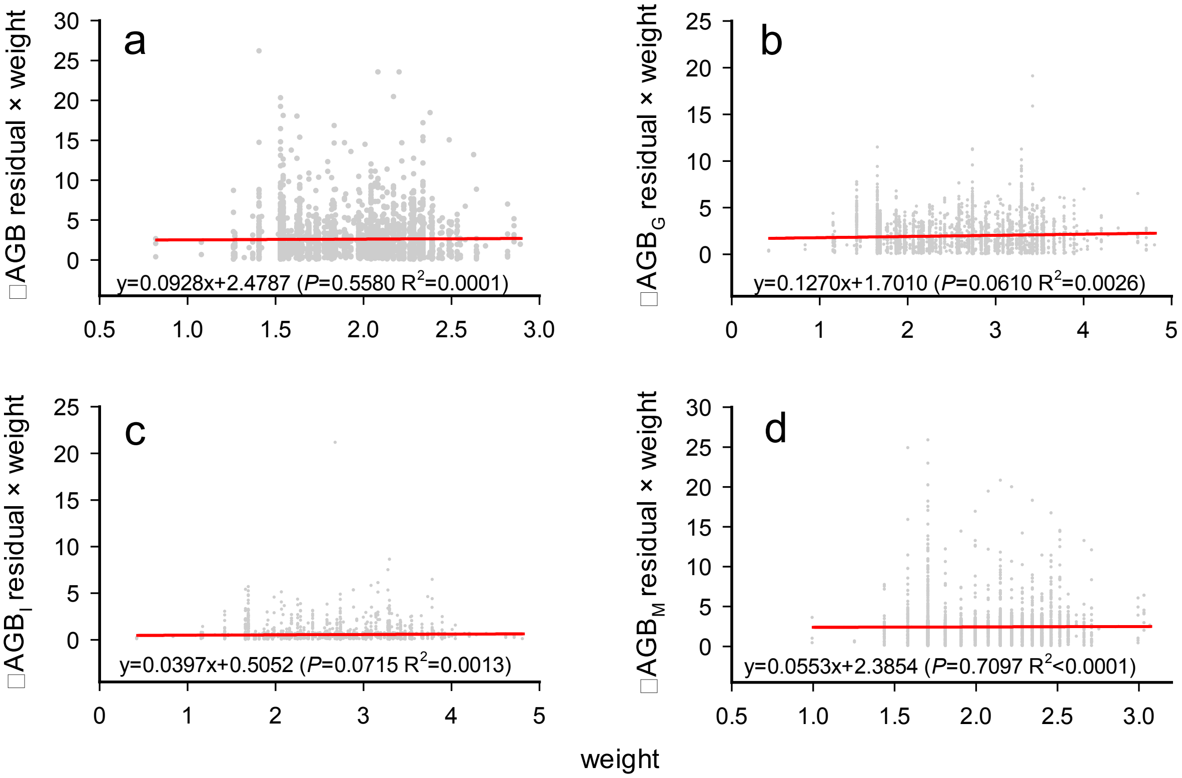
[‡] The variables were defined as the middle point of a census period (see Materials and Methods).

Appendix 5. 2. Definitions of forest type and their brief data descriptions

Forest Type	Definition	N of plots	N of census	N of trees
DEC	Dominated by species among Balsam poplar, Trembling aspen, White birch	262	946	48188
ESC	Dominated by species among Jack pine, Lodgepole pine, Limber pine, White bark pine, Red pine	210	886	59157
LSC	Dominated by species among Balsam fir, Black spruce, Alpine fir, Douglas fir, Englemann spruce, Tamarack, White spruce, Cedar	139	526	34553
MIX	None of above defined species group exceeds 75% in above-ground biomass	260	1057	67063
Total	NA	871	3327	208961

Appendix 5. 3. Determining empirical weightings for net aboveground biomass change (ΔAGB) and its components, i.e., $\Delta\mathrm{AGB}_{\mathrm{G}}$, $\Delta\mathrm{AGB}_{\mathrm{I}}$, $\Delta\mathrm{AGB}_{\mathrm{M}}$.

I proceeded empirical weighting follow previous studies (Lewis et al. 2009, Phillips et al. 2009). The regression lines show no patterns, indicating that the weightings were appropriate. (**a**) Residuals from ΔAGB weighted by plot size^(1/13)+length of measurement intervals^(1/3)-1. (**b**) Residuals from $\mathrm{AGB}_{\mathrm{G}}$ weighted by plot size^(1/3)+length^(1/2)-1. (**c**), Residuals from $\mathrm{AGB}_{\mathrm{I}}$ weighted by plot size^(1/3)+length^(1/2)-1. (**d**) Residuals from $\mathrm{AGB}_{\mathrm{M}}$ weighted by length^(1/3).



Appendix 5. 4. Determining the best functions to describe forest age-dependent responses of ΔAGB and its components

Table A5.4.1. Comparisons of Deviance Information Criterion (DIC) among functions describing forest age-dependent responses of ΔAGB and its components. The functions with smallest DIC value (in bold) indicates the best fit and were used to account for forest age effects.

Data	Y	Derivative Of Monod function	Weibull function	Linear	Log	Third order polynomial
DEC	ΔAGB	2916	2903	2913	**2900**	2901
	ΔAGB_G	NA	2159	2159	**2150**	2152
	ΔAGB_I	NA	NA	-66.37	-98.12	**-195.3**
	ΔAGB_M	NA	NA	2297	**2290**	2658
ESC	ΔAGB	1744	1719	1721	**1719**	1720
	ΔAGB_G	NA	**1080**	1113	1104	1083
	ΔAGB_I	NA	NA	-329.7	-332.2	**-335.9**
	ΔAGB_M	NA	NA	612.1	604.8	**597.5**
MIX	ΔAGB	3056	3021	3014	**2997**	2998
	ΔAGB_G	NA	**1951**	1992	1966	1952
	ΔAGB_I	NA	NA	-618.4	**-628.5**	112
	ΔAGB_M	NA	NA	2362	**2347**	2780
LSC	ΔAGB	1639	1631	1629	**1621**	1622
	ΔAGB_G	NA	835.5	847.9	**835.1**	836
	ΔAGB_I	NA	NA	-83.64	**-84.68**	634
	ΔAGB_M	NA	NA	1077	**1065**	1549

Note: I used the derivative of Monod function and Weibull distribution function to describe ΔAGB following McMahon et al.(2010) and He et al. (2012), respectively, and the Weibull distribution function for ΔAGB_G, these functions are not suitable for other ΔAGB components. The function forms used to determine forest-age responses are:

Derivative of Monod function: $\mathrm{Y} = \dfrac{b_1 \times b_2}{(\mathrm{A} + b_2)^2}$

Weibull distribution function: $Y = b_1 \times (1 + \frac{b_2 \times (\frac{A}{b3})^{b_4} - 1}{\exp(\frac{A}{b_3})})$

Linear model: $Y = b_1 + b_2 \times A$

Log model: $Y = b_1 + b_2 \times \ln(A)$

Third order polynomial: $Y = b_1 + b_2 \times A + b_3 \times A^2 + b_4 \times A^3$

where Y is ΔAGB or its component; A is forest age (years); b_i are parameters to be estimated.

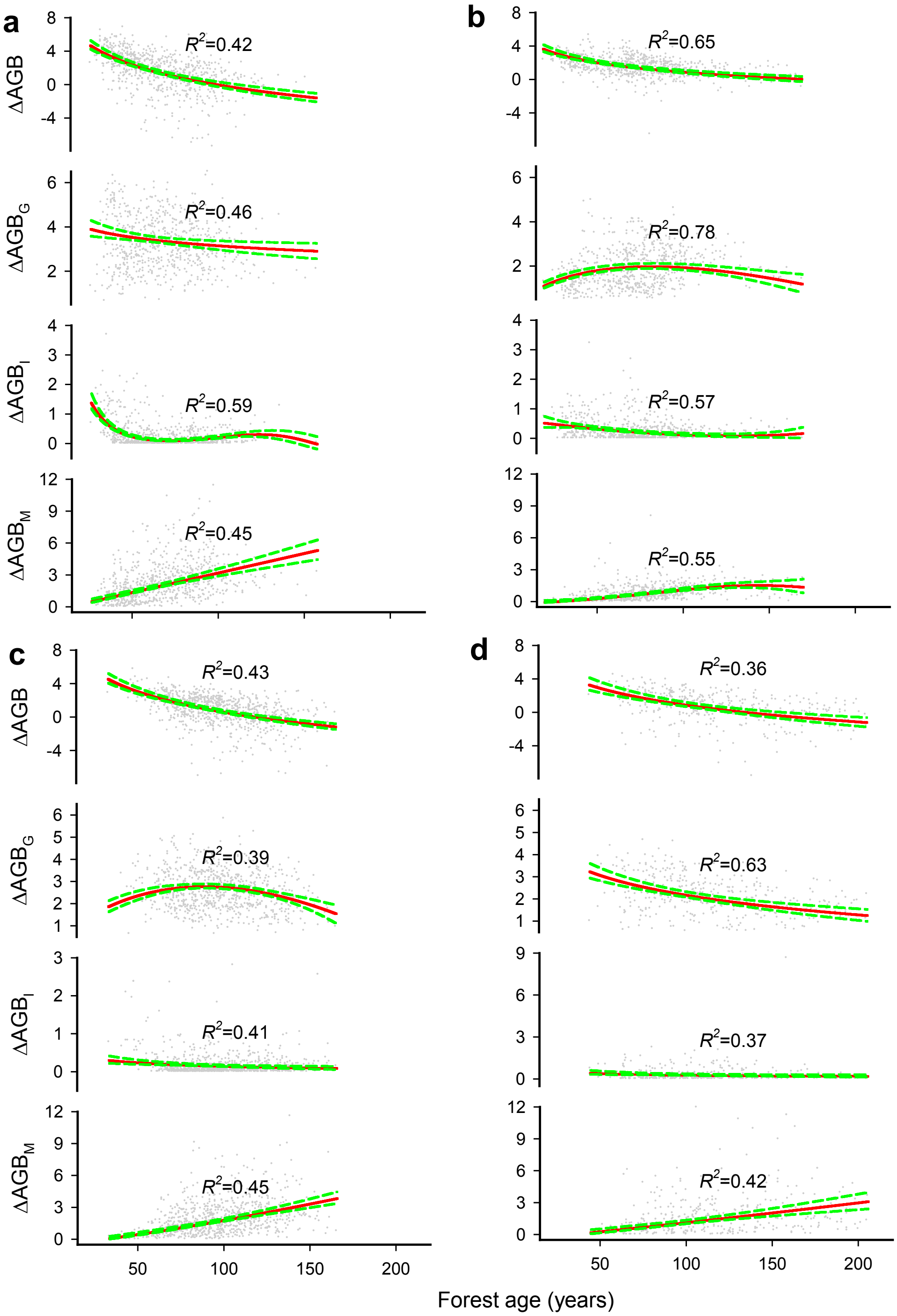


Figure A5.4.1. Fitted forest age-dependent curves of ΔACB and its components. a, Deciduous broadleaf forests (DEC). b, Early-successional coniferous forests (ESC). c, Mixed forests (MIX). d, Late-successional coniferous forests (LSC). The gray dots were the observations. Red lines and broken green lines are the fitted regression and 95% credible intervals, respectively. The functions were determined by the smallest Deviance Information Criterion (DIC) (Table A5.4.1).

Appendix 5. 5. Parameter values estimated from three alternative predictor priority settings in Model 5.2 for annual net biomass change (ΔAGB) of all forest plots and individual forest types.

Forest type	Simultaneous			Priority to Forest Age			Priority to Calendar Year		
	β_0	β_1	β_2 ($\times 10^2$)	β_0	β_1	β_2 ($\times 10^2$)	β_0	β_1	β_2 ($\times 10^2$)
All plots	1.08	-2.25	-3.09	1.07	-2.48	-2.31	1.13	-0.77	-5.27
	(0.99~1.16)	(-2.46~-2.04)	(-3.71~-2.45)	(0.99~1.15)	(-2.70~-2.27)	(-2.81~-1.80)	(1.03~1.23)	(-0.90~-0.64)	(-5.91~-4.61)
DEC	1.42	-3.5	-2.52	1.41	-3.55	-2.24	1.47	-1.5	-5.05
	(1.25~1.59)	(-4.01~-2.98)	(-4.27~-0.56)	(1.24~1.59)	(-4.07~-3.04)	(-3.84~-0.63)	(1.25~1.69)	(-1.86~-1.14)	(-7.04~-3.03)
ESC	1.41	-1.24	-2.23	1.41	-1.69	-0.99	1.44	-0.21	-3.85
	(1.29~1.52)	(-1.56~-0.97)	(-2.88~-1.54)	(1.29~1.53)	(-1.99~-1.41)	(-1.39~-0.59)	(1.30~1.57)	(-0.33~-0.10)	(-4.43~-3.23)
MIX	0.72	-2.85	-3.96	0.72	-3.59	-3.01	0.75	-1.06	-6.68
	(0.59~0.85)	(-3.42~-2.31)	(-5.12~-2.88)	(0.58~0.86)	(-4.12~-3.06)	(-3.65~-2.07)	(0.59~0.92)	(-1.41~-0.72)	(-7.75~-5.59)
LSC	0.55	-2.31	-7.4	0.53	-2.96	-6.4	0.62	-1.11	-9.22
	(0.32~0.76)	(-2.97~-1.6)	(-9.29~-5.29)	(0.29~0.77)	(-3.71~-2.23)	(-8.18~-4.60)	(0.38~0.88)	(-1.60~-0.62)	(-11.22~-7.18)

Appendix 5. 6. Comparisons among alternative models for annual net biomass change (ΔAGB) for all forest plots and individual forest types.

Model[*]	Parameter[†]								R^2	DIC	ΔDIC (%)[‡]
	β_0	β_1	β_2 ($\times 10^2$)	β_3 ($\times 10^1$)	β_4 ($\times 10^2$)	β_5 ($\times 10^2$)	β_6 ($\times 10^3$)	β_7 ($\times 10^2$)			
all plots											
Null	1.07	-2.47							0.468	9780	1.70
	(0.98~1.15)	(-2.69~-2.28)									
A	1.08	-2.25	-3.09						0.507	9640	0.24
	(0.99~1.16)	(-2.46~-2.04)	(-3.71~-2.45)								
B	1.06	-2.47		-2.78					0.502	9709	0.96
	(0.99~1.15)	(-2.69~-2.26)		(-3.58~-1.99)							
C	1.07	-2.5			0.84				0.493	9770	1.59
	(0.99~1.15)	(-2.71~-2.29)			(0.02~1.57)						
D	0.99	-2.37	-2.48	-1.57	0.83	2.34	0.61		0.527	9617	
	(0.90~1.07)	(-2.6~-2.16)	(-3.13~-1.78)	(-2.37~-0.63)	(0.06~1.63)	(1.35~3.17)	(-0.25~1.45)				
DEC											
Null	1.42	-3.5							0.418	2913	1.39
	(1.25~1.58)	(-4.00~-3.00)									
A	1.42	-3.5	-2.52						0.426	2892	0.66
	(1.25~1.59)	(-4.01~-2.98)	(-4.27~-0.56)								
B	1.41	-3.54		-1.65					0.424	2897	0.84
	(1.24~1.57)	(-4.06~-3.04)		(-3.2~-0.18)							

C	1.41	-3.54			0.61			0.423	2907	1.18
	(1.25~1.58)	(-4.06~-3.05)			(-0.78~2.24)					
D	1.29	-3.58	-1.82	-0.43	1.15	2.61	4.74	0.439	2873	
	(1.12~1.49)	(-4.08~-3.09)	(-3.73~0.18)	(-2.1~1.33)	(-0.35~2.77)	(0.35~4.99)	(2.8~6.56)			
ESC										
Null	1.41	-1.69						0.646	1718	5.33
	(1.30~1.52)	(-1.97~-1.39)								
A	1.41	-1.24	-2.23					0.687	1647	0.98
	(1.29~1.52)	(-1.56~-0.97)	(-2.88~-1.54)							
B	1.41	-1.7		-0.54				0.660	1711	4.90
	(1.29~1.52)	(-2.0~-1.42)		(-1.2~0.16)						
C	1.41	-1.71			-0.98			0.673	1694	3.86
	(1.29~1.53)	(-1.99~-1.41)			(-1.52~-0.37)					
D	1.41	-1.27	-2.14		-0.78			0.698	1631	
	(1.29~1.53)	(-1.56~-0.95)	(-2.81~-1.43)		(-1.36~-0.26)					
MIX										
Null	0.72	-3.58						0.433	2997	2.08
	(0.59~0.85)	(-4.07~-3.05)								
A	0.72	-2.85	-3.96					0.479	2943	0.43
	(0.59~0.85)	(-3.42~-2.31)	(-5.12~-2.88)							
B	0.72	-2.96		-6.11				0.456	2952	0.98
	(0.59~0.86)	(-3.5~-2.41)		(-8.02~-4.26)						
C	0.72	-3.54			5.06			0.458	2984	2.94
	(0.58~0.86)	(-4.03~-2.97)			(2.17~7.74)					

D	0.55	-2.9	-2.23	-2.73	4.07	2.52	-4.89	6.7	0.490	2936	
	(0.37~0.73)	(-3.46~-2.35)	(-4.15~-0.22)	(-6.07~0.42)	(0.91~7.14)	(0.08~5.1)	(-9.86~-0.44)	(-1.3~13.0)			
LSC											
Null	0.54	-2.90							0.359	1619	3.92
	(0.33~0.78)	(-3.60~-2.16)									
A	0.55	-2.31	-7.4						0.463	1569	0.71
	(0.32~0.76)	(-2.97~-1.6)	(-9.29~-5.29)								
B	0.53	-2.47		-10.76					0.429	1583	1.60
	(0.28~0.75)	(-3.21~-1.73)		(-14.04~-7.11)							
C	0.54	-2.77			15.69				0.424	1592	2.18
	(0.3~0.78)	(-3.5~-2.09)			(9.52~21.78)						
D	0.62	-2.22	-6.74		8.44				0.468	1558	
	(0.38~0.84)	(-2.89~-1.51)	(-8.94~-4.73)		(2.08~14.56)						

*Null Model has intercept and *ln*(forest age) as predictors; Model A has intercept, *ln*(forest age), and calendar year as predictors; Model B has intercept, *ln*(forest age), and annual temperature anomaly as predictors; Model C has intercept, *ln*(forest age), and annual climate moisture anomaly index as predictors; Model D is the model with the smallest DIC among all possible models (see Material and Methods).

[†] Model parameters are described in Model 5.3 (see Material and Methods).

[‡] ΔDIC (%) is calculated as 100 × (DIC value of the subject model – DIC value of Model D)/DIC value of Model D (%).

Appendix 5. 7. Summary (p value, mean±1 SD) of posterior predictive checks for the fitted models. Distribution of posterior predictions was based on 10,000 simulations. $P > 0.05$ indicates no significant difference between the observed and predicted values.

Forest type	Y	Model[*]			
		A	B	C	D
All plots	ΔAGB	0.35±0.11	0.32±0.13	0.33±0.15	0.37±0.09
	ΔAGB_G	0.12±0.12	0.11±0.10	0.13±0.09	0.15±0.10
	ΔAGB_I	0.18±0.09	0.19±0.09	0.19±0.10	0.22±0.10
	ΔAGB_M	0.20±0.13	0.22±0.09	0.19±0.11	0.24±0.11
DEC	ΔAGB	0.26±0.12	0.24±0.15	0.23±0.13	0.25±0.10
	ΔAGB_G	0.15±0.10	0.14±0.08	0.16±0.11	0.19±0.09
	ΔAGB_I	0.17±0.12	0.13±0.11	0.12±0.09	0.18±0.11
	ΔAGB_M	0.24±0.09	0.32±0.12	0.29±0.12	0.26±0.10
ESC	ΔAGB	0.38±0.11	0.36±0.11	0.37±0.13	0.39±0.09
	ΔAGB_G	0.19±0.12	0.18±0.13	0.17±0.11	0.21±0.10
	ΔAGB_I	0.15±0.10	0.13±0.12	0.11±0.09	0.15±0.10
	ΔAGB_M	0.29±0.13	0.22±0.12	0.24±0.13	0.30±0.12
MIX	ΔAGB	0.30±0.14	0.28±0.11	0.29±0.12	0.31±0.11
	ΔAGB_G	0.16±0.10	0.18±0.13	0.17±0.13	0.17±0.09
	ΔAGB_I	0.20±0.12	0.19±0.11	0.15±0.09	0.21±0.10
	ΔAGB_M	0.30±0.10	0.32±0.10	0.32±0.11	0.33±0.13
LSC	ΔAGB	0.33±0.11	0.30±0.14	0.31±0.13	0.36±0.10
	ΔAGB_G	0.20±0.12	0.18±0.11	0.19±0.11	0.22±0.11
	ΔAGB_I	0.22±0.10	0.20±0.11	0.21±0.09	0.22±0.10
	ΔAGB_M	0.33±0.12	0.30±0.13	0.32±0.12	0.35±0.11

[*] Models A, B, C, and D are described in Appendix 5.6.

Appendix 5. 8. The effects (*P* values) of plot size, census interval, and number of censuses on weighted forest age-corrected annual net biomass change (ΔAGB) and its components.

Sampling attribute	Forest type	Annual change of ΔAGB	Annual change of ΔAGB_G	Annual change of ΔAGB_I	Annual change of ΔAGB_M
Plot size	All plots	0.10	0.48	0.29	0.62
	DEC	0.53	0.42	0.27	0.57
	ESC	0.88	0.23	0.19	0.52
	MIX	0.07	0.71	0.34	0.14
	LSC	0.12	0.69	0.18	0.13
Census interval	All plots	0.16	0.27	0.54	0.18
	DEC	0.29	0.47	0.67	0.56
	ESC	0.28	0.08	0.38	0.97
	MIX	0.28	0.06	0.1	0.06
	LSC	0.16	0.54	0.22	0.16
Number of censuses	All plots	0.07	0.06	0.29	0.97
	DEC	0.97	0.2	0.49	0.16
	ESC	0.09	0.15	0.75	0.25
	MIX	0.10	0.05	0.06	0.51
	LSC	0.20	0.93	0.13	0.21

Appendix 5. 9. *P* values of Mantel tests for annual change of forest age-corrected ΔAGB and its components. Spatial autocorrelation among sampling plots was tested by their geographic locations.

Forest type	Annual change of ΔAGB	Annual change of ΔAGB_G	Annual change of ΔAGB_I	Annual change of ΔAGB_M
All plots	0.64	0.23	0.61	0.21
DEC	0.93	0.09	0.18	0.99
ESC	0.09	0.14	0.41	0.44
MIX	0.64	0.14	0.93	0.86
LSC	0.08	0.42	0.12	0.09

Appendix 5. 10. Parameter values estimated from simultaneously modeling the effects of forest age and calendar year on net change of stand basal area (m^2 ha^{-1} yr^{-1}) for all forest plots and individual forest types**.**

Forest type	β_0	β_1	β_2 ($\times 10^2$)
all plots	0.15	-0.51	-0.87
	(0.13~0.17)	(-0.56~-0.49)	(-1.01~-0.73)
DEC	0.16	-0.81	-0.54
	(0.12~0.20)	(-0.92~-0.70)	(-0.93~-0.14)
ESC	0.28	-0.40	-0.60
	(0.25~0.31)	(-0.48~-0.32)	(-0.77~-0.42)
MIX	0.07	-0.65	-0.90
	(0.04~0.10)	(-0.77~-0.53)	(-1.15~-0.65)
LSC	0.08	-0.51	-1.79
	(0.02~0.14)	(-0.68~-0.33)	(-2.28~-1.31)

Chapter 6. General conclusion

Using datasets from PSPs in central and western Canadian boreal region, which cover a wide range of tree sizes, stand developmental stages and stand compositions, I have examined how endogenous factors affect tree mortality in boreal forests. I have investigated temporal changes of tree mortality and related it to recent climate change. Finally, I have examined the temporal change of aboveground biomass carbon pool in western boreal forests. The findings of this thesis confirm that 1) tree mortality is primarily driven by endogenous factors in boreal forests; 2) recent climate changes also contribute to tree mortality; 3) forest carbon sequestration capacity is altered by climate change-induced tree mortality. A summary of my key findings of this dissertation are as follows:

1. Tree mortality of the four major boreal tree species, i.e., *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*, was strongly dependent on relative size. Species-specific sensitivity to size-dependent mortality was greater in shade-intolerant species than shade-tolerant species. Mortality increased with stand crowding, supporting the notion that crowded stands resulted in on average lower resource availability and consequently higher mortality. Crowding induced mortality was not true for *Betula papyrifera*, which has higher mortality in less crowded stands, suggesting that competition from tall shrubs coupled with browsing from large mammals, might be an alternative cause for mortality. Species interaction can affect mortality either negatively or positively, depending on the traits of the species and its neighbours. Finally, mortality increases with stand age due to tree ageing and its interactions with minor disturbances.

2. Over last fifty years, portions of the boreal forest in Saskatchewan and Alberta have experienced global-change-type drought, as indicated by an increase in annual temperature anomaly and decrease in climate moisture index anomaly. Temporal increases of tree mortality were influenced by stand development processes and global-change-type drought for *Populus tremuloides*, *Populus balsamifera*, *Pinus banksiana*, *Picea mariana*, and *Picea glauca*. The strength of these drivers on tree mortality differs among species and their influences interact both among endogenous factors and between endogenous and exogenous factors. When endogenous factors were factored out, the overall tree mortality increased during the past fifty years for all study species. Both the increased rates of annual mortality probability and the sensitivity of mortality to recent climate trends for the two *Picea spp.* were higher than these for the pioneer species, implying that the regional forest will likely become further dominated by early-successional species in the study area. Climate change-associated increases in tree mortality were significantly higher in young than old forests, suggesting that climate change-associated tree mortality could be underestimated if mortality estimates from old forests are used to represent regional forests
3. Unlike the forests of Saskatchewan and Alberta (Chapter 3), forests of Manitoba have not undergone global-change-type drought, as indicated by increases of both annual temperature anomaly and annual climate moisture index anomaly. However, after partitioning climate change effects from endogenous effects on tree mortality, tree mortality increased over the last three decades for five major tree species *Populus tremuloides*, *Populus balsamifera*, *Pinus banksiana*, *Picea mariana*, and *Picea glauca*. These results suggest that the mechanisms promoting temporal

increases in tree mortality in Manitoba are different from those found in more westerly regions of North America where global-change-type droughts may account for the observed increases in tree mortality. The temporal increase in tree mortality in Manitoba could be attributable to intensification of competition effect on tree mortality due to positive climate change effect such as regional warming as suggested by neighborhood analyses.

4. Over the last fifty years, i.e., from 1958 to 2008, western Canadian boreal forests acted as a carbon sink, with mean net change of annual aboveground biomass (ΔAGB) of 1.11 (95% credible interval (CI), 1.02~1.21) Mg ha^{-1} yr^{-1} regardless of forest types. ΔAGB in deciduous broadleaf and early-succession coniferous forests was higher than those in mixed and late-successional coniferous forests, suggesting stronger carbon storage capacities of deciduous broadleaf and early-succession coniferous forests. Carbon sequestration declined temporally due to both endogenous factors and recent climate changes. After accounting for forest age-dependent decreases, ΔAGB had declined at -0.031 (CI, -0.037~-0.024) Mg ha^{-1} yr^{-1} yr^{-1}. The decline rate was highest in late-successional coniferous forests dominated by shallow-rooted *Picea* spp. at a rate of -0.074 (CI, -0.093~-0.053) Mg ha^{-1} yr^{-1} yr^{-1}. The temporally-reduced biomass carbon sink is likely a result from both warming and drought induced hydraulic failures and increased pathogen and insect outbreaks, both of which are positively associated with warm temperatures and droughts in northern latitudes.

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