SPECIES RELATIVE ABUNDANCE AND ABOVEGROUND BIOMASS

PRODUCTION DRIVEN BY CLIMATE CHANGE AND STAND AGEING

BY

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ABSTRACT

Understanding forest communities' responses to climate change is central to global change ecology research. Access to large data sets from government sources has enabled extensive examinations of the effects of climate change on the boreal forest of Canada. Despite the recent proliferation of studies on boreal forests' responses to climate change, two major facets remain unexamined. First, although it is known that traits and species respond distinctly to climate change, whether these different responses have caused a compositional shift in tree communities is unknown. Second, whether the effects of local soil drainage properties alter the responses to climate change is unknown.

A network of 1,711 permanent sample plots (PSPs) from across Alberta, Saskatchewan, and Manitoba, Canada, was used to determine whether tree community composition has shifted as a result of climate change, while controlling for the effect of endogenous processes related to stand ageing. Over the course of the last half-century, communities have shifted towards a higher prevalence of deciduous broadleaf and early-successional conifers at the expense of late-successional conifers. This shift to more productive species that are less susceptible to climate change has a negative feedback on anthropogenically-induced increases in atmospheric carbon dioxide. The increase in deciduous broadleaf species provides another negative feedback on climate warming through higher albedos and evapotranspiration.

A similar network of 1,324 PSPs from across the three provinces was used to determine if local soil drainage altered the effect of climate change on net aboveground biomass change. Over the course of the study period, the effects of climate change on net aboveground biomass change were more pronouncedly negative for late-successional conifers, and to a lesser extent for deciduous broadleaf species on well drained than

poorly drained sites. However, for drought-tolerant early-successional conifers, the negative effects of climate change were felt stronger on poorly drained than well drained sites.

In summary, climate change has altered community composition in the boreal forest as the responses to climate change have differed with life-history traits and by species. The negative effects of climate change are most detrimental to late-successional conifers on well drained soils. The boreal forest has shifted towards more heavily populated by early-successional conifers on well drained sites, and a mixture of deciduous broadleaf and early-successional conifers on other sites, at the expense of late-successional conifers.

Key words: aboveground production, boreal forest, climate change, community composition, environmental change, global change type drought, local site effects, soil drainage, soil moisture regime

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ACKNOWLEDGEMENTS

NOTE

This is a manuscript-based thesis. The chapters were written to suit the submission requirements of the targeted journals. Formatting and reference styles may differ. Chapters:

2. Searle, Eric B. and Chen, H.Y.H. 2015. Shifts in relative abundance of boreal tree species driven by climate change – (In preparation).

3. Searle, Eric B. and Chen, H.Y.H. 2015. Climate change impacts are dependent on species' life history traits and local site conditions – (In preparation).

CHAPTER ONE: GENERAL INTRODUCTION

Environmental change has affected the boreal forest of western Canada at some of the quickest rates of any terrestrial biome, and is expected to continue to accelerate at unprecedented rates (Diffenbaugh & Field, 2013). Recently, there has been an increased focus on examining how this environmental change has affected the ecosystem functioning of the boreal forest, which stores more carbon than any terrestrial biome (Dixon *et al.*, 1994). Studies point to alarming trends of reduced above-ground biomass accumulation throughout the boreal forest (Ma *et al.*, 2012) and increasing tree mortality rates (Luo & Chen, 2013, Peng *et al.*, 2011). The reason for these trends is still unknown, but most observational studies cite global change-type drought as the cause (Chen & Luo, 2015, Ma *et al.*, 2012, Peng *et al.*, 2011). Global change-type drought occurs when increasing evapotranspiration rates due to a warming climate exceeds available local soil moisture, leading sometimes to drought stress, causing xylem cavitation from breaking of the water column in the tree or carbon starvation from reduced transpiration rates (Allen *et al.*, 2010). However, it is also possible that increased drought stress could lead to higher susceptibility to pests and pathogens (Allen *et al.*, 2010, Suzuki *et al.*, 2014), which are also expected to increase in intensity and extent (Boyd *et al.*, 2013).

Additionally, newer studies have demonstrated that not all forest types respond equally to climate change. For instance, early-successional conifers and broadleaf deciduous stands are less affected by climate change than late-successional conifer stands (Chen & Luo, 2015). Further, drought tolerant species, such as *Pinus contorta*,

may experience increased recruitment under hotter and drier conditions, possibly offsetting the effects of increased mortality (Zhang *et al.*, 2015). Other species, such as *Picea glauca*, are likely to be more negatively affected by environmental change, often seeing reduced growth as well as increased mortality (Barber *et al.*, 2000, Beck *et al.*, 2011b, Luo & Chen, 2013). Despite this recent surge in species-specific and trait-specific examination of demographic rates, no study has yet examined the effects of environmental change on community composition in the boreal forest. If traits and species are in fact responding differently to climate change, then we should be able to detect a significant shift in community composition over the course of the last half-century.

Similar to previous studies in the tropical forests (Brienen *et al.*, 2015, Phillips *et al.*, 2009, Phillips *et al.*, 2004, Phillips *et al.*, 1998), studies examining effects of environmental change on the boreal forest account for plot-specific effects using mixed-effects models (Chen & Luo, 2015, Ma *et al.*, 2012, Zhang *et al.*, 2015). These models allow researchers to account not only for the violation of independence inherent in longitudinal data, but also for plot-specific effects such as initial species composition, local soil properties, and topographic variations (Zuur *et al.*, 2009). While modelling changes in forest productivity in this way is well documented and robust, it does leave some questions unanswered. Specifically, we know that plot-specific features can cause differential responses to environmental change (Brienen *et al.*, 2015), and even in tropical studies these effects are often ignored. However, if the major cause of reduced aboveground productivity in boreal tree species is global change type drought, then we should expect that sites with higher soil moisture or poorer soil drainage, should have

some buffering capacity to mediate the negative effects of environmental change. Additionally, since late-successional conifers have been demonstrated to be more affected by environmental change than early-successional conifers or broadleaf deciduous stands across all soil types (Chen & Luo, 2015), we would expect late-successional conifers to be more negatively affected by climate change on well drained sites than broadleaf deciduous or early-successional conifers on these soil types. Only one study has examined the impact of local site effects on environmental change altered productivity rates across long temporal and large spatial scales although the specific characteristics of the plots that alter environmental change responses were not examined.

Here we use a network of permanent sample plots (PSPs) from across Alberta, Saskatchewan, and Manitoba, Canada, largely located in ecoregions number 88, 90, 139, 148, 149, and 156 (Agriculture and Agri-Food Canada, 2013, Ecological Stratification Working Group, 1995), to examine the effects of environmental change on two aspects of boreal forest ecosystems. First, we use 1,711 plots to examine how environmental change has affected boreal forest community composition (at both the trait and species level) over the past half century. Second, we use 1,324 plots to examine how trait and species aboveground biomass production is altered by environmental change on varying soils.

CHAPTER TWO: SHIFTS IN RELATIVE ABUNDANCE OF BOREAL TREE SPECIES DRIVEN BY CLIMATE CHANGE

Abstract:

Shifts in relative abundance of tree species have profound consequences to ecosystems. How climate change affects background (non-catastrophic) shifts in relative abundance of boreal tree species remains unclear. Using 1,711 plots from western boreal forests of Canada, measured from 1960 to 2013, we show that after accounting for stand age-dependent succession, the relative abundances of six early-successional species, characterized as shade-intolerant, deciduous broadleaf and drought-tolerant evergreen conifers, increased with climate change at the expense of late-successional evergreen conifers. These background shifts may be attributable to rising atmospheric CO_2 concentrations and regional warming favouring fast-growing species. Our results suggest that these shifts may provide a negative feedback on rising atmospheric CO_2 as more productive early-successional species could uptake more atmospheric CO_2 than late-successional conifers. The shift to deciduous broadleaves could also provide a negative feedback to regional warming due to the cooling properties of their high albedos.

Main Text:

Shifts in relative abundance, long before species are threatened by extinction, have profound consequences to ecosystems (Chapin *et al.*, 2000a) by altering ecosystem services (Hooper *et al.*, 2012, Winfree *et al.*, 2015, Zhang *et al.*, 2012), trophic interactions (Blois *et al.*, 2013) and infestation rates of pests and pathogens (Altizer *et al.*, 2013, Boyd *et al.*, 2013). Within the boreal forest in particular, a shift toward deciduous broadleaves may lead to a negative feedback to regional warming due to their higher albedos (Bonan, 2008, Chapin *et al.*, 2000b). Species- and trait-based shifts in relative abundance due to climate change have been documented in old-growth tropical forests (Fauset *et al.*, 2012, Feeley *et al.*, 2011, Laurance *et al.*, 2004), which are otherwise assumed to be at equilibrium (Odum, 1969). In boreal forests, a shift from evergreen conifers to deciduous broadleaves has been inferred from the fact that fire frequency has increased with climate change (Gillett *et al.*, 2004) and that fire promotes broadleaves (Beck *et al.*, 2011b, Chen *et al.*, 2009, Johnstone *et al.*, 2010). With fire return interval, i.e., time in years between two successive fires in a designated area, varying spatially and temporally from approximately 25 to over 600 years in North American boreal forests (Weir *et al.*, 2000), a better understanding of the background (non-catastrophic) shifts in relative abundance of tree species is important to fully appreciate the impacts of climate change on boreal forests. Recent studies based on observations from long-term permanent sample plots in boreal forests have demonstrated differential background responses of growth and mortality rates among tree species and forest types to climate change (Chen & Luo, 2015, Huang *et al.*, 2010, Luo & Chen, 2013, Zhang *et al.*, 2015). However, whether climate change has induced

background shifts in relative abundance of boreal tree species remains poorly understood.

Here we sought to determine whether systematic changes in relative abundances of boreal tree species and life-history traits have occurred in response to climate change in the western boreal forests of Canada, and if so, to identify possible causes of those shifts. The dominant species of the region include deciduous broadleaf *Populus tremuloides* (Michx.)*, Populus balsamifera* (L.), and *Betula papyrifera* (Marshall), early-successional evergreen coniferous *Pinus contorta* (Douglas), *Pinus banksiana* (Lamb.), and *Picea mariana* (Mill.), and late-successional evergreen coniferous *Picea glauca* ((Moench) Voss.) and *Abies balsamea* ((L.) Mill). We used a network of 1,711 permanent plots, spanning the region (Appendix A, Figure 1), measured from 1960 to 2013. These plots varied in size from 202 m^2 to 2023 m^2 (mean = 969 m^2) and years between successive censuses varied from 1 to 29 years (mean = 9.6 years). All plots originated from wildfire, and were located in a wide range of topography, forest types, and stand ages. We quantified relative abundance as the percentage of aboveground biomass and stand basal area by individual tree species or life-history traits at each census of each sample plot. We used calendar year, similar to previous studies in tropical forests (Fauset *et al.*, 2012, Feeley *et al.*, 2011, Laurance *et al.*, 2004), to represent the systematic climate change in our study region. Shifts in relative abundance of tree species are known to occur as forests undergo succession with stand ageing (Connell & Slatyer, 1977). In boreal forests, fast-growing, shade-intolerant *Pinus* spp. and *Populus* spp. are recruited first after a stand-replacing disturbance, and are replaced over time by slow-growing, shade-tolerant species or by fast-growing, shade-intolerant

offspring of the first cohort in large canopy gaps (Bergeron, 2000, Chen & Taylor, 2012, Gutsell & Johnson, 2002). Since relative abundances of individual tree species or life-history traits are strongly associated with stand age, it is essential to account for the effects of stand age while examining potential impacts of climate change on the shifts of tree species or life-history traits (Brown *et al.*, 2011). We used nonlinear mixed effect models to simultaneously test the fixed effects of climate change and stand ageing and random plot effects. All coefficients were estimated by maximum likelihood.

During the study period of 1960 to 2013, relative abundances of all eight major boreal tree species were significantly or marginally affected by stand age and calendar year (Figs. 2-1 & 2-2, Table S2-1). With the effects of stand age accounted for (Fig. 2-2), the relative abundances of *Pinus contorta*, *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera*, and *Picea mariana* increased significantly with calendar year ($P \leq 0.001$), and that of *Populus balsamifera* increased marginally ($P = 0.051$), whereas those of late-successional *Abies balsamea* and *Picea glauca* decreased significantly ($P < 0.001$) (Fig. 2-1). When analysed by life-history traits, the relative abundance of early-successional conifers and that of broadleaves at a lesser extent increased at the cost of late-successional conifers ($P < 0.001$) (Fig. 2-1).
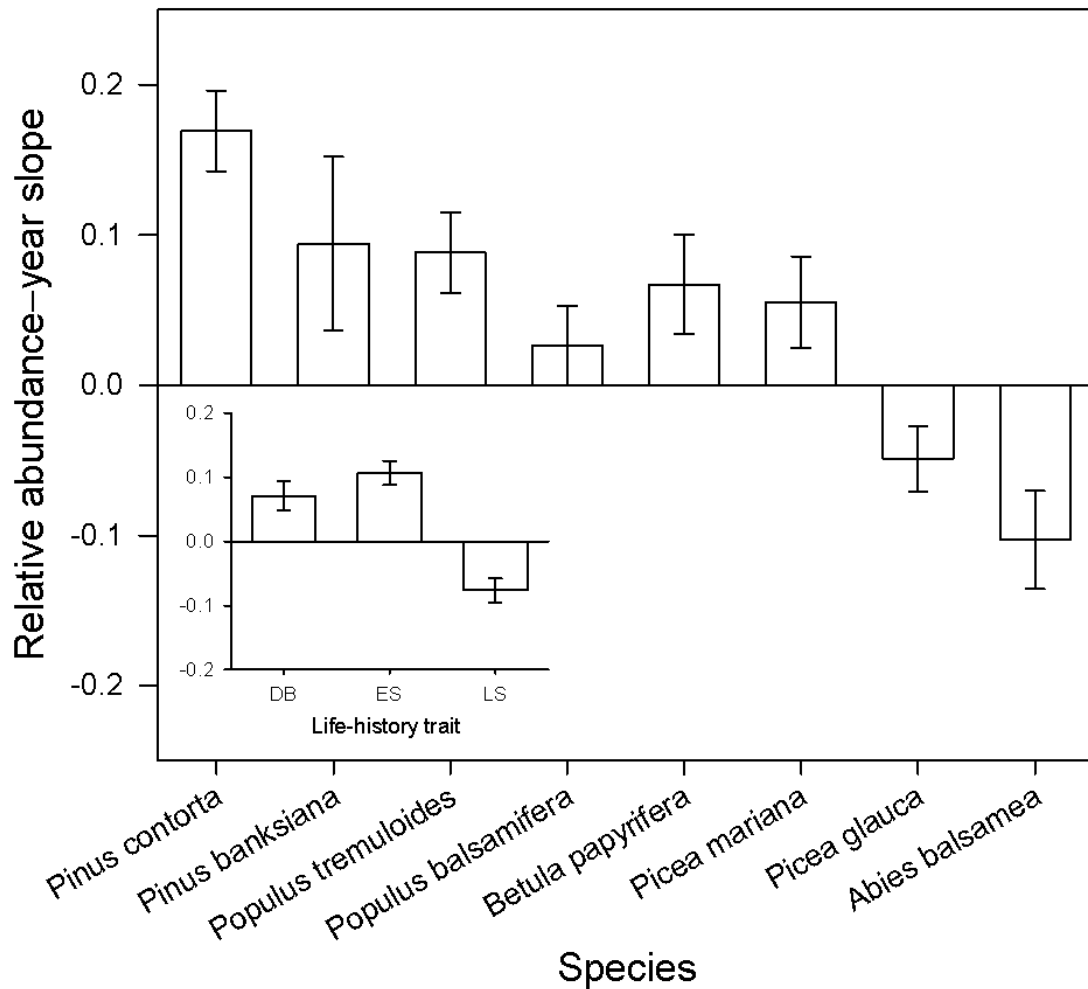
FIGURE 2-1. The slope of standardized relative abundance to calendar year by species and trait. Value are the slope coefficients of calendar year after accounting for the effect of stand age. Error bars are 95% confidence intervals (see Table S2-1). DB, ES, and LS refer to deciduous broadleaf, early-successional conifer, and late-successional conifer respectively. Relative abundance data were scaled, enabling direct comparison among species differencing in abundance.

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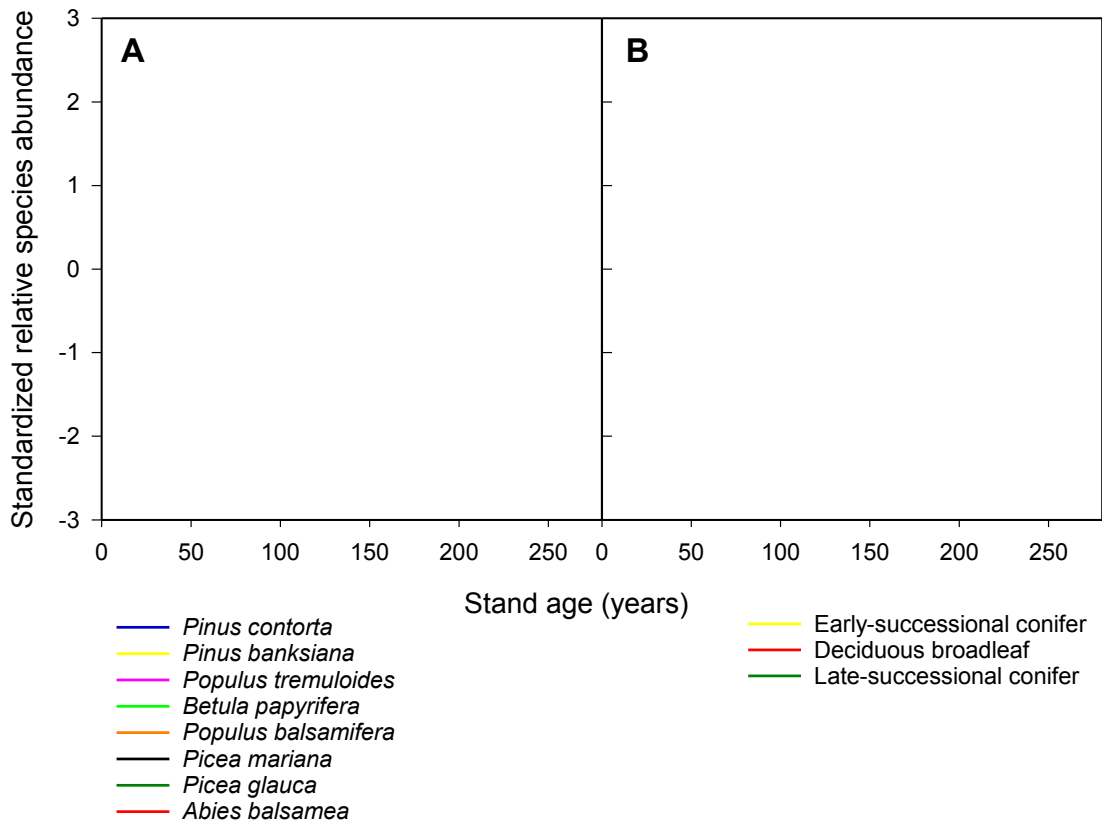
FIGURE 2-2. Changes in standardized relative abundances with stand age. (A) The response of eight major boreal tree species to stand age. (B) The responses to stand age by life-history traits. The model coefficients for the responses of individual species and history traits to stand age were derived from simultaneously accounting for the effect of calendar year (Table S2-1). Each species or life-history trait curve represents the range of observed stand ages.

During the study period, atmospheric CO_2 concentration and mean annual temperature (MAT) increased, while climate moisture index (CMI) decreased (Figs. 2-3A-C, Table S2-3). With the effects of stand age accounted for, the responses of relative abundance of species and life-history traits to atmospheric CO_2 concentration largely mirrored those to calendar year, although notably both relative abundances of *Picea mariana* and *Populus balsamifera* were less associated with CO_2 (Fig. 2-3D.). Relative abundances responded little to MAT and CMI measured at the census year. Removal of

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inter-annual oscillations through the five- and ten-year means revealed stronger associations between relative abundance and MAT (Figs. 2-3E,F). Relative abundance increased significantly for *Populus balsamifera* ($P = 0.005$) and marginally for *Pinus* spp. ($P < 0.08$), while *Betula papyrifera* and *Abies balsamea* decreased with the five-year MAT mean ($P < 0.05$). With MAT averaged over ten years, relative abundance increased for *Pinus contorta* ($P < 0.001$) and marginally for *Populus tremuloides* ($P = 0.063$), while decreasing in *Picea glauca* and *Abies balsamea* ($P \leq 0.001$). Relative abundances by life-history trait did not respond to five-year MAT mean, but, with increasing ten-year MAT mean, they increased in early-successional conifers ($P = 0.002$) and in deciduous broadleaves ($P = 0.068$), and decreased in late-successional conifers ($P < 0.001$). With CMI averaged over five years, relative abundance of *Pinus contorta* increased ($P = 0.001$), while *Picea mariana* decreased ($P < 0.001$) with decreasing CMI. With CMI averaged over ten years, relative abundance of *Betula papyrifera* also increased ($P = 0.025$), while *Populus balsamifera* decreased ($P = 0.004$) with decreasing CMI. Pooled by life-history traits, relative abundances of early-successional conifer increased ($P = 0.022$), while those of late-successional conifers decreased marginally ($P = 0.091$) with decreasing ten-year CMI mean.
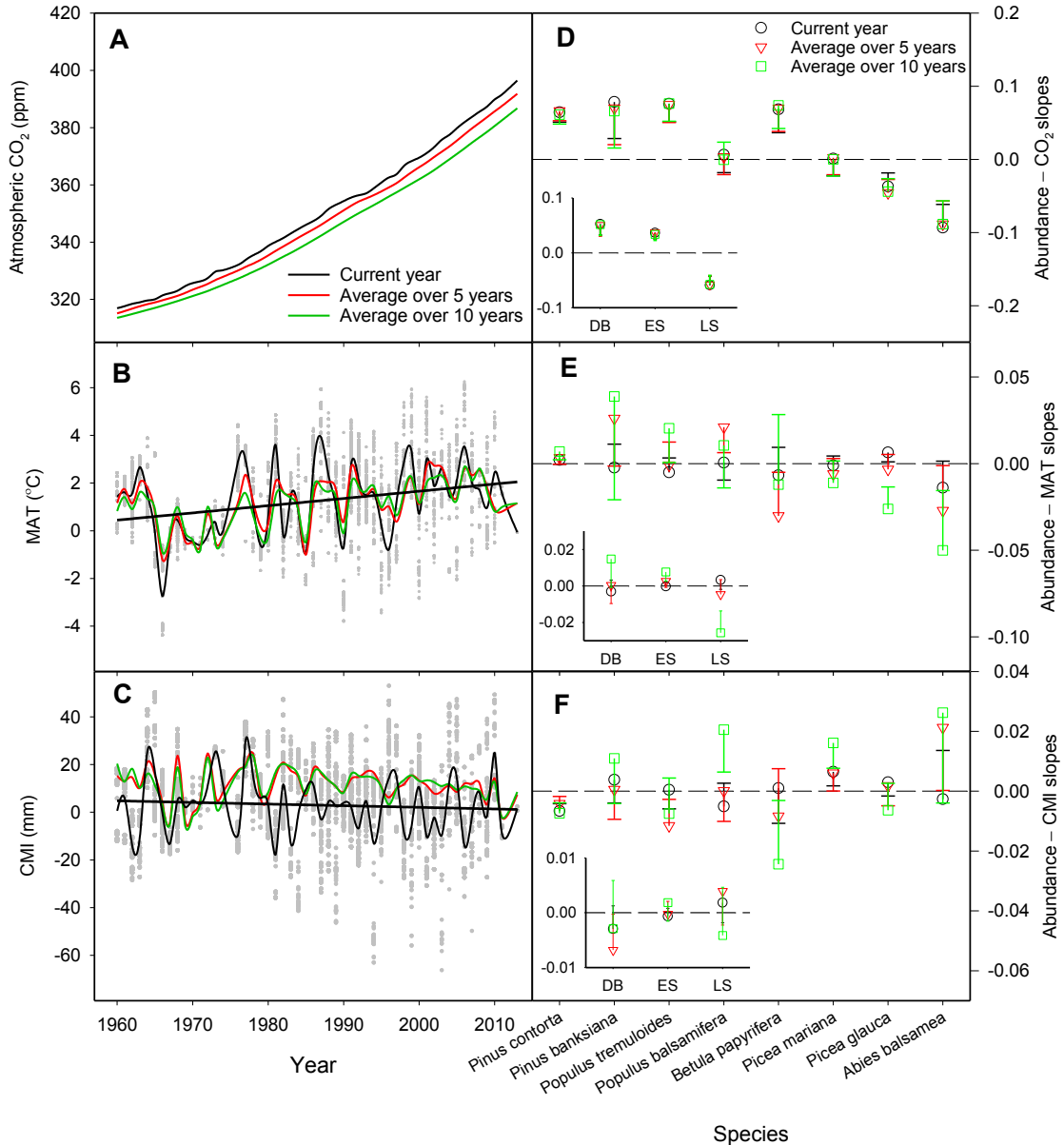
FIGURE 2-3. The changes in climate drivers and the responses of relative abundance. (A-C) Temporal changes in atmospheric CO2, mean annual temperature (MAT) and climate moisture index (CMI). Black lines are the mean observed annual values of the drivers for those plots measured in the corresponding year with a fitted regression. Red and green lines represent the means of the previous five and ten years of the corresponding plot measurement, respectively. (**D-F**) The slope of standardized relative abundance in response to each driver by species and trait. Value are the slope coefficients of each driver after accounting for the effect of stand age. Error bars are 95% confidence intervals (see Table S2-3). DB, ES, and LS refer to deciduous broadleaf, early-successional conifer, and late-successional conifer, respectively.

Unlike in the tropical biome, where stand establishment dates for natural forests are difficult to determine, our plots have undergone documented stand-replacing disturbances, allowing us to explicitly account for age-dependent successional shifts in relative abundance of tree species. After accounting for the effects of stand age, we found that increases in relative abundances of early-successional evergreen conifers and deciduous broadleaves at the expense of late-successional evergreen conifers in the western boreal forests of Canada during the study period. These results extend the previous finding in tropical forests that climate change favours fast-growing shade-intolerant species (Laurance et al., 2004; but see Chave et al., 2008) to boreal forests. Furthermore, similar to tropical regions where long-term droughts have occurred (Fauset *et al.*, 2012, Feeley *et al.*, 2011), drought-tolerant species *Pinus* spp. were more favoured than drought-intolerant *Populus* spp. in our study region where climate moisture availability has decreased temporally.

The exact drivers for the observed long-term, non-catastrophic changes in relative abundance of tree species that are independent of stand age remain inconclusive. Experimental evidence indicates that increasing CO_2 affects species growth rates differentially (Reich *et al.*, 2001) and deciduous species are more favoured under warming (Way & Oren, 2010). The strong associations between changes in relative abundance and CO_2 concentration as well as warming suggest that the observed shifts in relative abundance associated with calendar year may be attributable to temporal increases in CO_2 and warming as well as warming-induced decreasing water availability in the region. Additionally, climate change-associated shifts in trophic interactions

(Blois *et al.*, 2013) and increasing insect outbreaks (Altizer *et al.*, 2013, Boyd *et al.*, 2013) could have contributed to observed shifts in relative abundance of tree species.

This study provides evidence for relative abundance shifts of tree species associated with climate change. This non-catastrophic, succession-independent, relative abundance shift towards early-successional species is likely attributable to a loss in the competitive ability of slow-growing late-successional conifers, resulting from their different responses to climate drivers. This interpretation is consistent with studies demonstrating larger decreases in the above-ground biomass accumulation of late-successional forest types and higher mortality rates in late-successional species than early-successional species (Chen & Luo, 2015, Luo & Chen, 2013, Zhang *et al.*, 2015). The background shifts toward early-successional species, coupled with climate change-associated increases in fire (Gillett *et al.*, 2004) that promote deciduous broadleaves (Beck *et al.*, 2011b, Chen *et al.*, 2009, Johnstone *et al.*, 2010), suggest that the boreal forest has begun to become more heavily dominated by *Populus* spp. and *Pinus* spp. at the expense of late-successional *Picea glauca* and *Abies balsamea*.

The relative abundance shifts could have a negative feedback on rising atmospheric CO_2, as more productive deciduous broadleaf and early-successional coniferous species (Chen & Luo, 2015) could uptake more atmospheric CO_2 than forests dominated by late-successional conifers. Moreover, an increased cover of deciduous broadleaf species may provide a negative feedback to the regional warming due to the cooling properties of their high evapotranspiration rate and albedo (Bonan, 2008, Chapin *et al.*, 2000b). However, the extent of the negative feedback on rising atmospheric CO_2 is limited because warming and associated decreasing water

availability also decrease above-ground net biomass change in forests dominated by broadleaves and early-successional conifers in the study region, just at slower rates than those dominated by late-successional conifers (Chen & Luo, 2015).

Materials and Methods

Study area and long-term repeatedly measured sample plots

Permanent sample plots (PSPs) were established throughout Alberta, Saskatchewan, and Manitoba starting from late 1950s. The PSPs were located in homogenous, well-stocked stands greater than 1 ha in size, at least 100 m from any openings to minimize the impacts of edge effects (Frey, 1981, Vyvere, 2008). A total of 1,711 PSPs were compiled in our study, following the data selection criteria: (*i*) undisturbed PSPs with a known origin date of wildfire, and unmanaged; (*ii*) PSPs with a minimum of three censuses; (*iii*) PSPs with all trees marked and tagged with diameter at breast height (DBH) and species identification tracked accurately over multiple censuses. Each province used different tree size criteria for monitoring, i.e., ≥ 7.3 cm in DBH in Alberta, ≥ 9.2 cm in DBH in Saskatchewan, and all trees ≥ 1.3 m in height in Manitoba.

Plots used in this study varied in size from 202 m^2 to 2023 m^2, and years between successive censuses varied from 1 to 29 years (Table S2-4). Initial censuses were conducted on the 1,711 selected plots from 1960 to 2005, and final censuses were conducted from 1972 to 2013. These plots range in latitude from 49.0° to 59.7° N, in longitude from -119.7° to -95.3° W, and in elevation from 291 to 998 m above sea level (Appendix A Fig. 2-1). Mean annual temperatures ranged from -5.63 to 6.08 °C, and annual precipitation ranged from 278 mm to 995 mm between 1957 and 2014, determined using the BioSIM 10 software (Réginère J, 2012).

Relative abundance

Aboveground biomass for each individual stem at each census for each plot was calculated using species-specific allometric equations (Lambert *et al.*, 2005, Ung *et al.*, 2008). The biomasses of individual stems were summed to total aboveground biomass. Relative abundance was calculated as the proportional biomass of individual tree species or life-history trait group as a fraction of the total biomass at each census for each plot, multiplying by 100. Deciduous broadleaf species included *Populus* spp., *Betula papyrifera*, *Fraxinus* spp., *Ulmus americana*, *Quercus alba*, and *Acer negundo*. Early-successional conifers included *Pinus* spp., *Larix laricina*, and *Picea mariana*, and late-successional conifers included *Abies* spp., *Picea glauca* and *Picea engelmannii*, and *Thuja occidentalis*. Relative abundance was also calculated as a percentage of stand basal area of each species and life-history trait relative to total stand basal area. We calculated relative abundance in four different ways: (1) aboveground biomass including only trees with DBH ≥9.2 cm, (2) aboveground biomass including all measured trees, whose DBH threshed differed among provinces, (3) stand basal area including all trees with DBH ≥9.2 cm, and (4) stand basal area including all measured trees.

Explanatory variables

We used calendar year to represent overall climatic conditions corresponding to each observation of relative abundance. This encompasses not only the systematic increases in atmospheric CO_2 concentration and temperature and a decrease in climate moisture index, but also the changes in other climatic and non-climatic drivers. To understand the influence of climate change drivers on relative abundance, we derived CO_2 measurements from the Mauna Loa Earth System Research Laboratory in Hawaii

(http://www.esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html) and from the Law

Dome DE08 and DE08-2 ice cores

(http://cdiac.ornl.gov/ftp/trends/co2/lawdome.smoothed.yr20). We obtained mean

annual temperature (MAT) for each census for each plot. To assess temporal changes in

climate moisture availability, we calculated climate moisture index (CMI) as the

difference between precipitation and potential evapotranspiration for each month.

Monthly CMI was then summed monthly for an entire calendar year (from January 1st to

December 31st) to obtain annual CMI values (Hogg, 1994) for each census for each plot.

This index has been shown to be a key indicator of growth in boreal *Populus*

tremuloides stands (Hogg *et al.*, 2005), and its inclusion of potential evapotranspiration

gives a rough approximation of global change type drought. Since the changes in

relative abundance may be resulted from accumulative responses to the systematic

changes in growing environment and climate change can be masked by natural

variability on short time scales (Deser *et al.*, 2012), we calculated five- and ten-year

means of climatic drivers including the values at the census year and those of four and

nine years prior to each census for each plot, respectively.

We used stand age to account for stand ageing processes, interpretable as time

since fire, as all selected stands originated from wildfire. Stand age for each PSP was

determined according to the date of a known fire or by coring at least three dominant/co-

dominant trees of each species inside or outside the plot at the time of plot establishment.

When coring was used, the average ring counts of the tree samples for the species with

the oldest age was used to determine time since fire by species-specific relationships

between tree age and time since fire developed for boreal forests (Gutsell & Johnson,

2002, Vasiliauskas & Chen, 2002). No age corrections were applied for trees cored at the root collar. Since there were only four plots with ages greater than 250 years, these plots were assigned a stand age of 250 years.

Data analysis

We tested the effects of climate change and stand age on relative abundance for each species or trait by the following linear mixed effects model:

$$RA_{ij} = \beta_0 + \beta_1 \cdot Y_{ij} + \beta_2 \cdot f(A)_{ij} + \pi_j \qquad (1)$$

where RA_{ij} was relative abundance observed at ith census in jth plot for a given species or trait; Y_{ij} was calendar year corresponding to the species or trait relative abundance observed at ith census in jth plot, $f(A)_{ij}$ was the best fit function for the relationship between relative abundance and stand age (observed at ith census in jth plot) determined by Akaike Information Criterion (Table S2-2); π_j was the random plot error accounting for the random effects of plot size and local site conditions; βs are coefficients to be estimated.

There was a positive collinearity between stand age and calendar year with $r^2 = 0.037$ and 0.031 for all data pooled by species and trait, respectively. The correlation between stand age and calendar year ranged from 0.006 to 0.160 and from 0.022 to 0.053 among species and traits. There are three possible approaches to disentangle joint variation between stand age and calendar effects. The first approach is to simultaneously model forest age and calendar effects without assigning priority. The second is to use residual and sequential regressions by assigning the priority to stand age and then modelling calendar year effects on the residuals. The third is to reverse the priority in the second approach. As we have no logical or theoretical basis for considering any

variable to be prior in terms of a hypothetical causal structure of the data (Cohen & Cohen, 1975), assigning priority to stand age would marginalize the calendar year effect, and *vice versa* (Brown *et al.*, 2011), so we simultaneously modelled the effects of stand age and calendar year (Table S2-1). We fitted a continuous first-order autoregressive structure, since the time between successive censuses varied from measurement to measurement, to account for temporal autocorrelation in the data. All data were scaled, enabling direct comparison between species differencing in abundance (Soudzilovskaia *et al.*, 2013, Zuur *et al.*, 2009).

To understand the role of the individual drivers that may be responsible for observed temporal changes in relative abundance, we replaced *Y* in eqn. 1 by atmospheric CO_2 concentration, MAT, or CMI. Since changes in relative abundance may reflect accumulative responses to climatic drivers, we assessed the response of species and trait relative abundances to CO_2 concentration, MAT, and CMI observed at the year of census, the mean of the previous five years, and the mean of the previous ten years.

To ensure that our results were not influenced by our choice of relative abundance, we conducted analysis based on the four different ways of calculating relative abundance and we found similar results. For simplicity, we presented results for relative abundance based on aboveground biomass including trees with DBH ≥9.2 cm. Analysis was conducted in R 3.2.1, using the *nlme* package. Confidence intervals were determined using a normal approximation to the distribution of the restricted maximum likelihood estimators.

CHAPTER THREE: CLIMATE CHANGE IMPACTS ARE DEPENDENT ON

SPECIES' LIFE HISTORY TRAITS AND LOCAL SITE CONDITIONS

Abstract

While there remains some debate on how climate change will affect the world's forest, there have been recent studies demonstrating climate change-related declines in boreal and tropical forests. Studies conducted in western forests of North America have cited global change-type drought (i.e., demands of increased evapotranspiration exceeding soil water reserves) as the main culprit. If the major cause of the boreal biome's recent loss in productivity is global change-type drought, we should expect poorly drained soils to have a buffer against climate-induced droughts. Here we use a network of 1,341 permanent sampling plots from across Alberta, Saskatchewan, and Manitoba, Canada, measured from 1960 to 2013, to examine whether climate change-induced changes in productivity differ with local soil drainage capacity. We found that poorly drained soils did not have a buffering effect for increases in biomass of deciduous broadleaf and early-successional conifer species, except in *Pinus contorta*. Late successional conifer species, on the other hand, exhibited reduced biomass accumulation, reduced growth, and increased mortality on well drained soils compared with other soil types, showing evidence for a buffering effect of intermediately and poorly drained sites on global change-type drought. This pronounced local site effect may lead to a loss of late-successional conifer species on well drained soils, and a pronounced shift towards deciduous broadleaf, and especially early-successional conifers, on these soils.

Introduction

While positive net biomass change within the world's forests is critical to offsetting global anthropogenic CO_2 emission, recent studies have demonstrated that the rate of positive aboveground biomass change has decreased due to higher biomass loss from mortality than increases in growth in tropical forests (Brienen *et al.*, 2015) or increased biomass loss from mortality accompanying reduced biomass gain from growth in boreal forests (Chen & Luo, 2015, Ma *et al.*, 2012). Increases in tree mortality in tropical forests have been attributed to shortened tree longevity associated with greater climate variability and feedbacks of faster growth on mortality (Brienen *et al.*, 2015). In the boreal and temperate forests, increases in tree mortality (Luo & Chen, 2013, Michaelian *et al.*, 2011, van Mantgem *et al.*, 2009) and decreases in aboveground biomass accumulation (Chen & Luo, 2015, Ma *et al.*, 2012) have been hypothesized to be the result of warming-induced increased demand for evapotranspiration exceeding local water availability (McDowell *et al.*, 2008).

The response of net aboveground biomass change and its mortality and growth components appear strongly spatially variable (Brienen *et al.*, 2015). The variable responses to climate change could result from spatially dependent tree species composition (Chen & Luo, 2015, Coomes *et al.*, 2014) and local site conditions (Brienen *et al.*, 2015). Tree mortality in particular increases more dramatically in late-successional species than drought-tolerant early-successional species in regions with temporally decreasing water availability (Luo & Chen, 2013, van Mantgem *et al.*, 2009). Similarly, tree growth is more sensitive to climate water availability on drier upslope sites compared to moister lowland sites in the southern Appalachian mountain range in

the United States of America (Elliott *et al.*, 2015). If local evapotranspiration exceeding local soil moisture is the cause for increased tree mortality and decreased net aboveground biomass change, sites with rapid soil drainage should be more sensitive to climate change as these sites have less buffering capacity than sites with reduced drainage and better water retention. However, despite the hypothesized linkage between global change-type drought and recent above-ground biomass declines in the boreal forest, there has been no large-scale, long-term, examination of how local soil drainage has affected trait and species response to global-change-type drought.

Here, we use a network of permanent sample plots across western boreal forests of Canada to examine how the response of above-ground biomass accumulation may differ with local site condition across traits and species. In particular, we ask: are species and traits differentially affected by climate change depending on local soil drainage? Since net biomass change within forest ecosystems is strongly age-dependent (Chen & Luo, 2015, Odum, 1969), we examined the responses to climate change by simultaneously accounting for endogenous stand development processes. Stand development processes were accounted for through including a species- or trait-specific function of stand age as a predictor of aboveground biomass accumulation in the statistical analysis.

Methods

Study area and long-term repeatedly measured sample plots

Permanent sample plots (PSPs) were established throughout Alberta, Saskatchewan, and Manitoba starting in 1958. The PSPs were located in homogenous, well-stocked stands greater than 1 ha in size and at least 100 m from any openings to minimize the impacts

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of edge effects. A total of 1,324 PSPs were examined in our study, following the data selection criteria: (*i*) undisturbed PSPs with a known origin date of wildfire, with available soil drainage information, and unmanaged; (*ii*) PSPs with a minimum of three censuses; (*iii*) PSPs with all trees marked and tagged with diameter at breast height (DBH) and species identification tracked accurately over multiple censuses. Each province used different tree size criteria for monitoring, i.e., ≥ 7.3 cm in DBH in Alberta, ≥ 9.2 cm in DBH in Saskatchewan, and all trees ≥ 1.5 cm in DBH in Manitoba.

Plots used in this study varied in size from 202 m^2 to 2,023 m^2, and years between successive censuses varied from 1 to 29 years (Table S3-1). Initial censuses were conducted on the 1,324 selected plots from 1960 to 2005, and final censuses were conducted from 1972 to 2013 (Table S3-1). Selected plots range in latitude from 49.0° to 59.7° N, in longitude from -119.7° to -95.3° W, and in elevation from 291 to 998 m above sea level (Fig. S3-1). Mean annual temperatures ranged spatially and temporally from -5.63 to 6.08 °C, and annual precipitation ranged from 278 mm to 995 mm between 1957 and 2014, determined using the BioSIM 10 software (Réginère J, 2012). The dominant species of the region include deciduous *Populus tremuloides* (Michx.)*, Populus balsamifera* (L.), and *Betula papyrifera* (Marshall) as well as the coniferous *Pinus contorta* (Douglas), *Pinus banksiana* (Lamb.), *Picea mariana* (Mill.), *Abies balsamea* ((L.) Mill) and *Picea glauca* ((Moench) Voss.). Wildfire is the dominant stand-replacing disturbance with a fire return interval varying temporally and spatially from 25 to 645 years (Weir *et al.*, 2000).

Net aboveground biomass change calculations

Aboveground biomass for each individual stem was calculated for individual trees using species-specific allometric equations (Lambert *et al.*, 2005, Ung *et al.*, 2008). The biomasses of individual stems were summed across each trait at each plot to obtain trait-level biomasses, and summed across each species at each plot to obtain species-level biomasses. The annual change in aboveground biomass (ΔAGB) was calculated as the total live biomass at the census minus the total live biomass at the previous census divided by the time between censuses (interval). Annual change in aboveground biomass growth and ingrowth (ΔAGB$_{GI}$) was calculated as the biomass gain of live trees between censuses plus biomass gain from recruited trees divided by the interval. Annual change in aboveground biomass loss due to mortality (ΔAGB$_M$) was calculated as the biomass lost due to mortality divided by the interval. Since the three provinces used different DBH thresholds for measurements, we calculated ΔAGB and its components by including only trees with DBH $\geq$9.2 cm as well as all measured trees. Additionally, we calculated net change in stand basal area by including all trees with DBH $\geq$9.2 cm as well as including all measured trees.

Explanatory variables

We used the mid calendar year of a census period (i.e., if a plot was measured in 1970 and again in 1975, its mid calendar year would be 1972.5) to represent overall climatic conditions during the interval. These conditions encompass not only systematic increases in atmospheric CO_2 concentration and temperature and a decrease in climate moisture index, but also the changes in other climatic and non-climatic drivers. To understand the influence of individual climate change drivers on ΔAGB and its related

components, we derived CO_2 measurements from the Mauna Loa Earth System

Research Laboratory in Hawaii

(http://www.esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html) and from the Law

Dome DE08 and DE08-2 ice cores

(http://cdiac.ornl.gov/ftp/trends/co2/lawdome.smoothed.yr20). We also calculated the

annual temperature anomaly (ATA) for each census, defined as the annual mean annual

temperature of a plot minus the average annual temperature for the plot throughout the

study period. To assess temporal changes in climate moisture availability, we calculated

the annual climate moisture index anomaly (ACMIA). ACMIA is derived from the

climate moisture index: the difference between precipitation and potential

evapotranspiration for a month. Monthly values were then summed monthly for an

entire calendar year (from January 1st to December 31st) to obtain annual climate

moisture index values (Hogg, 1994) for each census for each plot. The anomaly was

then calculated in a similar fashion to ATA. This index has been shown to be a key

indicator of growth in boreal *Populus tremuloides* stands (Hogg *et al.*, 2005), and its

inclusion of potential evapotranspiration gives a rough approximation of global change

type drought. We then calculated the average value of each driver over the census

interval.

Soil drainage class of each plot was categorized into three major groupings: well

drained, moderately drained, and poorly drained. These values correspond to soil

drainage classes of values 1-3, 4 & 5, and 6 & 7 in Alberta and Saskatchewan, and to

soil moisture regime values of 0-3, 4-6, and 7-9 in Manitoba. These values were inferred

from the topographic position of the sample plot, the pore pattern and depth of mineral

soils, and characteristics of the soil profile (Alberta Sustainable Resource Development, 2005, Frey, 1981, Vyvere, 2008).

We used stand age to account for endogenous stand processes, interpretable as time since fire as all selected stands originated from wildfire. Stand age for each PSP was determined according to the date of a known fire or by coring at least three dominant/co-dominant trees of each tree species inside or outside the plot at the time of plot establishment. When coring was used, the average ring counts of the tree samples for the species with the oldest age was used to determine time since fire by species-specific relationships between stand age and time since fire developed for boreal forests (Gutsell & Johnson, 2002, Huang *et al.*, 2009).

Data analysis

We tested the effects of stand age, climate change, and local site conditions on ΔAGB and its components at the trait and species levels by the following linear mixed effects model:

$$(1) \ \Delta\text{AGB}_{ij} = \beta_0 + \beta_1 \cdot f(A_{ij}) + \beta_2 \cdot Y_{ij} + \beta_3 \cdot D_{ij} + \beta_4 \cdot Y_{ij} \times D_j + \beta_5 \cdot L_{ij} + \pi_j$$

where ΔAGB_{ij} was net aboveground biomass change observed at ith census interval in jth plot at the trait or species level (analysis was conducted for each trait and species individually); $f(A)_{ij}$ was the best-fit function between ΔAGB and stand age (observed at ith census interval in jth plot) determined through Akaike Information Criterion (Table S3-2); Y_{ij} was mid-calendar year corresponding to ΔAGB_{ij} observed at ith census interval in jth plot, D_j was the soil drainage class of jth plot and is assumed to not change over multiple censuses; L_{ij} was the length of time in years at ith census interval

in jth plot to account for the effect of sampling heterogeneity on ΔAGB and its components (Talbot *et al.*, 2014). π is the random effect associated with jth plot, which accounts for the effects of plot size and other plot-specific attributes; *β*s are coefficients to be estimated. Since the relationship between stand age and ΔAGB and its components is unknown, we fitted four equations describing the ageing process (linear, quadratic, polynomial, logarithmic) and used Akaike Information Criterion (AIC) analysis to determine the proper descriptive functions (Table S3-2). Traits and species were tested individually, and functions were chosen if their AIC was the lowest by a margin of at least 2.

There was a positive collinearity between stand age and calendar year with r^2 =0.037 and 0.012 for all data pooled species and trait levels, respectively. The correlation between stand age and calendar year ranged from 0.0001 to 0.105 and from 0.002 to 0.027 among species and traits. There are three possible approaches to disentangle joint variation between stand age and calendar effects. The first approach is to simultaneously model forest age and calendar effects without assigning priority. The second is to use residual and sequential regressions by assigning the priority to stand age and then modelling calendar year effects on the residuals. The third is to reverse the priority in the second approach. As we have no logical or theoretical basis for considering any variable to be prior in terms of a hypothetical causal structure of the data (Cohen & Cohen, 1975), assigning priority to stand age would marginalize the calendar year effect, and *vice versa* (Brown *et al.*, 2011), so we simultaneously modelled the effects of stand age and calendar year. All data were scaled, enabling

direct comparison between species differencing in abundance (Soudzilovskaia *et al.*, 2013, Zuur *et al.*, 2009).

To understand the role of the individual climatic drivers that may be responsible for observed temporal changes in ΔAGB and its components, we replaced *Y* in eqn. 1 by y atmospheric carbon dioxide concentration, ATA, and ACMIA. To ensure that our results were not influenced by our choice of biomass versus stand basal area and DBH thresholds, we conducted analysis based on the four different ways of calculating net aboveground biomass or stand basal area change and we found similar results. For simplicity, we presented results for net aboveground biomass change that included trees with DBH ≥9.2 cm.

We used a Bayesian Markov Chain Monte Carlo generalized linear mixed effects model to estimate coefficients in eqn. 1. All continuous predictors were centered to speed convergence. The chain was run for 85000 iterations, with a burn-in of 5000 and a thinning interval of 10, yielding 8000 samples of the posterior distribution. Convergence of the chain was determined through monitoring trace plots, the Gelman-Rubin statistic, and the Raftery-Lewis diagnostic. 95% credible intervals are the upper and lower credible intervals of the posterior distribution for each coefficient. Analysis was conducted in R 3.1.2 (R Development Core Team, 2013), using the *MCMCglmm* package (Hadfield, 2010).

Results

Annual net aboveground biomass (ΔAGB), AGB_{GI} and $ΔAGB_M$ changed significantly at the trait and species levels (Figs. 3-1 & 3-2, Tables S3-3 – S3-5). While there was some difference related to drainage class, it was small compared to overall changes associated

with age (Fig. 3-3). At the species level, all species had distinct curves for all

components. For the most part drainage classes were a smaller portion of overall fits

than the ageing process, although some species were appreciably affected (Tables S3-3

– S3-5).
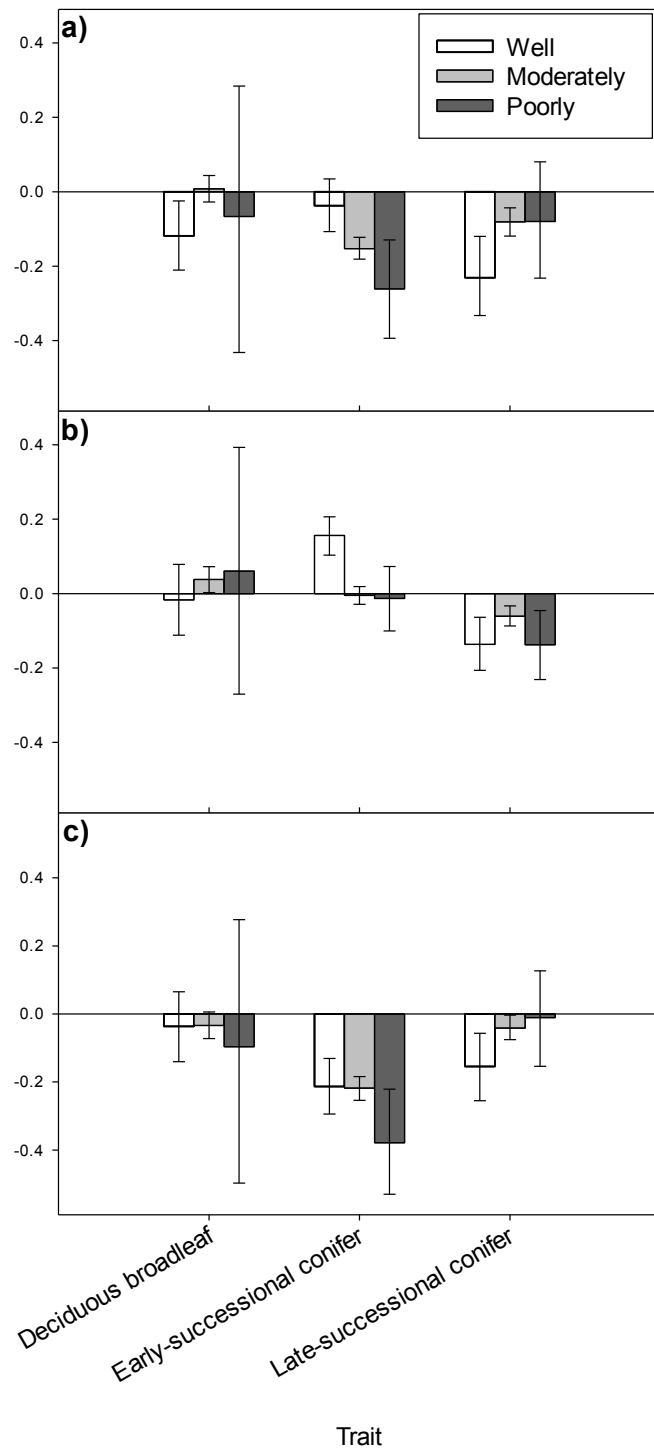
FIGURE 3-1. The slope of ΔAGB and its components by trait and drainage class to calendar year. Each value is the slope coefficient of each driver after accounting for the effect of stand age from the linear mixed effects model, with 95% credible interval.
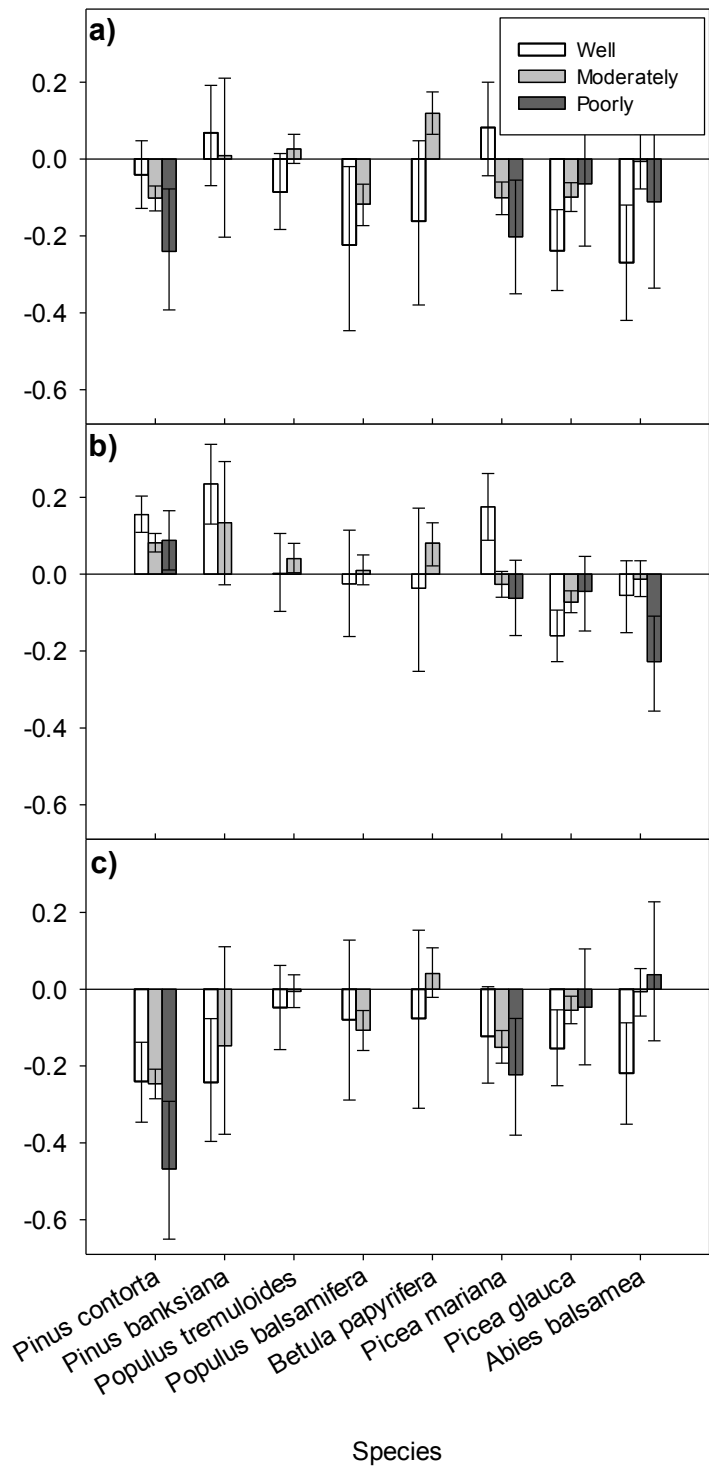
FIGURE 3-2. The slope of ΔAGB and its components by species and drainage class to calendar year. Each value is the slope coefficient of calendar year after accounting for the effect of stand age from the linear mixed effects model, with 95% credible interval.
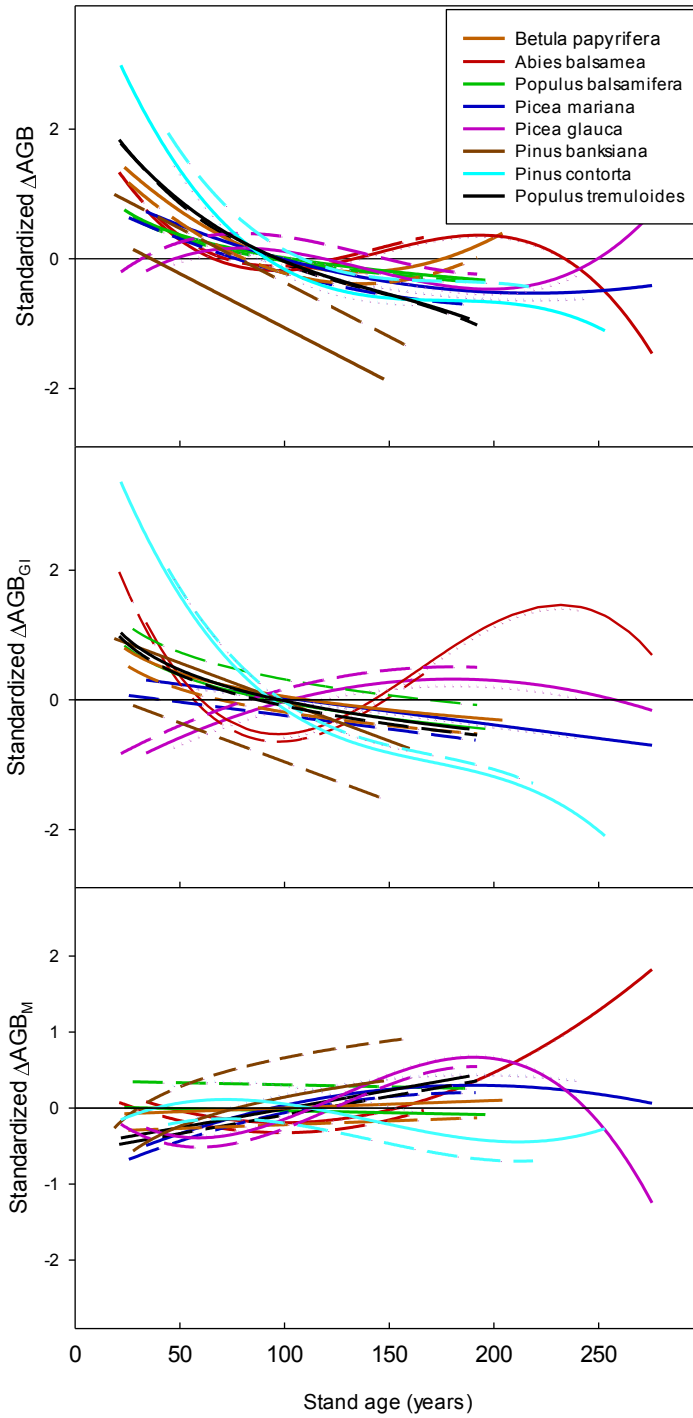
FIGURE 3-3. The effect of ageing and drainage class on standardized ΔAGB and its components at the species level. a) ΔAGB; b) ΔAGBGI; c) ΔAGBM

At the trait level, the response of ΔAGB to calendar year differed significantly with drainage class for all three traits (Tables S3-3 – S3-5). Deciduous broadleaf trees were negatively affected on well drained soils, but not significantly affected on moderately or poorly drained soils (Fig. 4a), although there was no clear effect of drainage class altering those trees' responses of ΔAGB_{GI} and ΔAGB_M to climate change (Figure 3-1b-c). Early-successional conifers were most affected on poorly drained soils, less affected on moderately drained soils, and negligibly affected on well drained soils (Figure 3-1a). This change likely stems from the increased ΔAGB_{GI} on well drained soils and an increase in ΔAGB_M on poorly drained soils with calendar year (Figure 3-1b-c). Finally, late-successional conifers were most negatively affected by calendar year overall, with a significant decrease in ΔAGB on well drained soils. This likely stems from a decrease in ΔAGB_{GI} (also present on poorly drained soils) and increase in ΔAGB_M (Fig. 3-1b-c).

At the species level, ΔAGB of *Pinus contorta*, *Populus balsamifera*, *Picea mariana* and *Picea glauca* decreased, while that of *Betula papyrifera* increased with calendar year (Tables S3-3). The year-related changes in ΔAGB were dependent on soil drainage class. Deciduous broadleaf *Populus balsamifera* and both late-successional conifers *Picea glauca* and *Abies balsamea* were more negatively affected on well drained soils. The late-successional conifers had no appreciable difference in the effect of calendar year between moderately and poorly drained soils (Fig. 3-2a). *Picea mariana* was the only species to experience an increase in ΔAGB on well drained soils (Fig. 3-2a). During the study period, ΔAGB_{GI} of *Pinus* spp., *Populus tremuloides*, and *Betula papyrifera*, whereas that of *Picea glauca* decreased with calendar year (Fig. 3-2b,

Table S3-5). *Pinus contorta* and *Picea mariana* significantly increased their ΔAGB_{GI} on well drained soils compared to moderate and poorly drained soils, whereas *Picea glauca* had a reduced ΔAGB_{GI} on well drained soils (Fig. 3-2b). *Abies balsamea* had no differenece between rates of ΔAGB_{GI} on well and moderately drained soils, but had a significantly reduced rate of ΔAGB_{GI} on poorly drained soils (Fig. 3-2b). ΔAGB_M of *Pinus* spp., *Populus balsamifera*, *Picea mariana*, and *Picea glauca* increased, and *Abies balsamea* also demonstrated an effect of soil drainage class, with increased ΔAGB_M on well drained soils (although *Pinus contorta* had a marginal ($P =0.06$) increase in ΔAGB_M on poorly drained soils) (Fig. 3-2c, Table S3-S7).

Atmospheric CO_2 concentration was highly correlated to calendar year ($r^2=0.99$), and hence, the responses of ΔAGB and its components largely mirrored their responses to calendar year. During the study period, mean annual temperature increased and mean annual precipitation decreased (Fig. 3-4). The responses to ATA were highly similar to those of calendar year, although the magnitudes tended to be muted (Table S3-S6). ACMIA had significant positive effect on ΔAGB_M for early-successional conifers on poorly drained soils, and a significant positive effect on ΔAGB_{GI} for late-successional conifers on poorly drained soils (Table S3-S7).
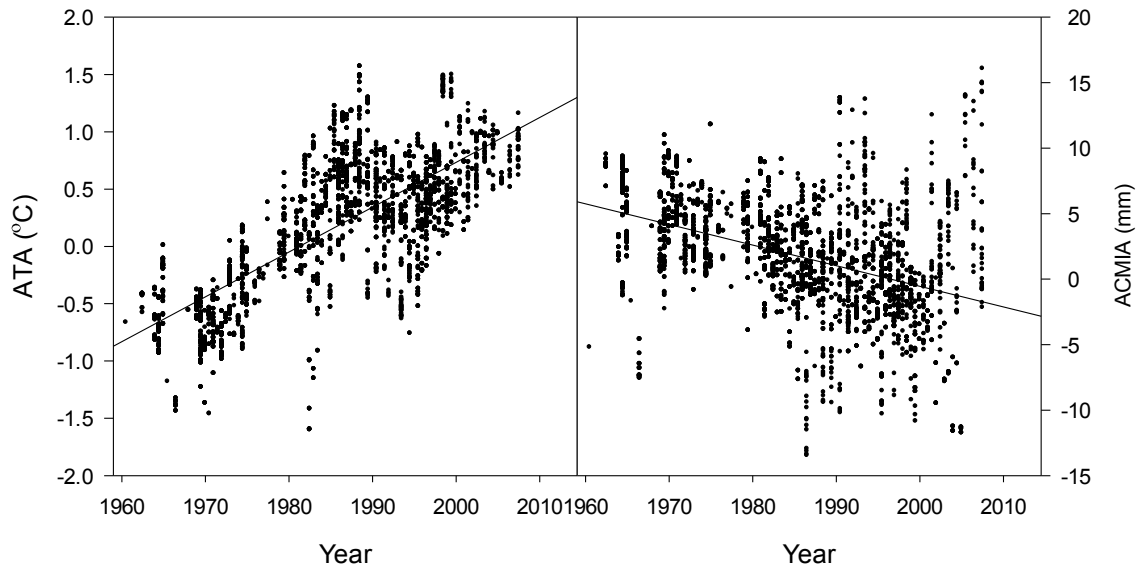
FIGURE 3-4. Trends in climactic drivers over the course of the study period. ATA-Annual temperature anomaly; ACIMA-annual climate moisture anomaly.

Discussion

Similar to previous studies (Chen & Luo, 2015), declines in ΔAGB were observed across all traits. Both deciduous broadleaf and late-successional conifers decreased most significantly on well drained soils, as expected from their relative drought tolerances. Interestingly, deciduous broadleaf trees showed no significant effect of ATA on their ΔAGB and a negative effect of increasing ACMIA on well drained soils, indicating that the negative change in well drained soils may not be directly related to water deficits. For late-successional conifers, well drained soils offered reduced ΔAGB_{GI} and increasing ΔAGB_M, indicating that they have been more negatively affected on these soils, in line with their observed reduction due to global change-type drought (Barber *et al.*, 2000, Beck *et al.*, 2011a, Chen & Luo, 2015). Early-successional conifers, largely characterized as drought-tolerant, were generally

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less affected on well drained soils than on moderately drained soils, demonstrating higher ΔAGB and ΔAGB_{GI} relative to moderate and poorly drained soils.

Deciduous broadleaf species demonstrated little effect of drainage class on climate change effects on ΔAGB and its components. As there is no change in this pattern when examining ACMIA, and since there is extensive literature on *P. tremuloides* recent loss due to climate moisture deficits and droughts (Hogg *et al.*, 2005, Hogg *et al.*, 2008, Michaelian *et al.*, 2011), it seems likely that there is no buffering effect of reduced soil drainage for these species. For *Pinus contorta*, there was a larger reduction in ΔAGB on poorly drained sites than on other sites, largely due to increases in ΔAGB_M. Whether this is due to a direct effect of climate change or an inability of the species to compete with associated species on these soils is unclear. Its increase in ΔAGB on well drained soils suggests this species is able to benefit from competitive release from reductions in late-successional conifers on these soils.

The best evidence for an effect of reduced soil drainage buffering against losses in soil moisture comes from the late-successional conifers. Both *Picea glauca* and *Abies balsamea* lost more biomass on well drained soils compared with all other soils. *Picea glauca*, in particular, has grown significantly slower on well drained soils during the study period. ΔAGB_M was significantly higher on well drained soils for both species. This underperformance on well drained soils is amplified when the systemic increase in ATA is examined and indicates a likely candidate for this loss is global change type drought. While ATA is highly correlated to calendar year, and may encapsulate other changes due to climate, e.g., increasing insect outbreaks (Boyd *et al.*, 2013), previous studies have also specifically linked increasing temperature and a loss in productivity of

Picea glauca (Barber *et al.*, 2000, Beck *et al.*, 2011a). Finally, increasing ACMIA reverses the underperformance of *Picea glauca* leading to no distinction between well drained and moderately drained sites, further indicating a benefit from reduced soil drainage ability to these species. Whether their underperformance is due strictly to drought stress or an inability to allocate the same resources to guarding against infestation during times of lower water availability (McDowell *et al.*, 2008) remains unclear. Given the extent of recent climate change, and its many effects, there are many possibilities, and they are often intertwined (McDowell *et al.*, 2011, Suzuki *et al.*, 2014).

This study provides evidence for some site-dependency in the response of the boreal forest to climate change. While deciduous broadleaf and early-successional conifers show little difference associated with local site condition in their responses to climate change, there is strong evidence for local site condition-dependent responses to climate change in late-successional conifers. A severe reduction in ΔAGB and its components on well drained soils for late successional species over the study period, coupled with a reversal of this effect with increasing ACMIA on *Picea glauca* specifically, provides indirect evidence for an effect of global change-type drought on late-successional conifers. With anticipated increases in global change-type drought in the future, western boreal forest species composition will further change, and the change will depend on local site condition, with deciduous broadleaf and especially early-successional conifer species eventually replacing late-successional species on well drained soils.

CHAPTER FOUR: GENERAL CONCLUSIONS

We sought to answer two specific questions. First, has climate change led to a shift in boreal forest tree composition over the past half century? Second, does local soil drainage mediate the response of aboveground biomass accumulation to environmental change at the life-history trait and species levels? We provide evidence that community composition has shifted across the western boreal forest towards to early-successional conifers and broadleaf deciduous tree species at the expenses of late-successional conifers. Furthermore, these changes in community composition are mirrored by stronger losses in aboveground biomass change in late-successional conifers, particularly on sites with better drainage.

With predicted increases in fire frequency and severity across the western boreal (Flannigan *et al.*, 2009, Gillett *et al.*, 2004) also expected to increase the prevalence of broadleaves (Beck *et al.*, 2011b, Chen *et al.*, 2009, Johnstone *et al.*, 2010), our findings of background increases in these species suggest that the boreal forest could dramatically alter its composition over the next century. The increase in broadleaves might provide a negative feedback to warming due to their higher rates of evapotranspiration and increased albedo (Bonan, 2008, Chapin *et al.*, 2000b). Further studies examining the scaling effects of increased broadleaf coverage on climate forcing are required.

While our findings of late-successional conifers being most affected on well drained soils is likely related to their intolerance to drought and temperature stress (Barber *et al.*, 2000, Beck *et al.*, 2011a), we have no direct evidence in support of this

hypothesis. Further studies are required examining the relative importance of increased nutrient leaching, more pronounced pest and pathogen outbreaks, or global change-type drought on these soils. The provincial forestry branches have accordingly increased their sampling profiles to be able to provide data to examine these effects.

In summary, our studies suggest that climate change will disproportionately negatively affect late-successional conifers over early-successional conifers and deciduous broadleaf species. We provide indirect evidence that late-successional conifers are suffering from the effects of global change type drought, while early-successional conifers and deciduous broadleaf species are relatively better equipped to deal with increasing drought and temperature stress as the boreal forest continues to experience environmental change. Future studies examining the effects of environmental change across wide spatial scales should be cognisant of the ability of local site effects to alter the response of forests to climate change.

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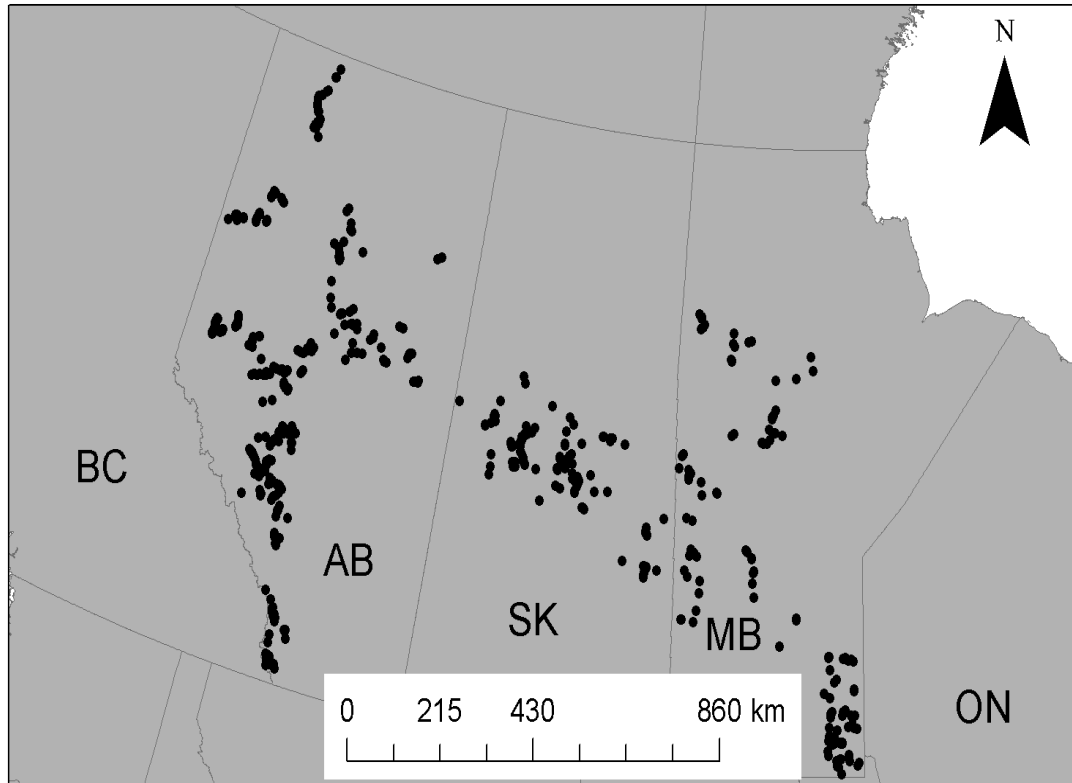
FIGURE S2-1 Map of spatial locations for 1,711 permanent sample plots across Alberta (AB), Saskatchewan (SK), and Manitoba (MB), Canada.

TABLE S2-1 The effects of stand age and calendar year on relative abundance by species and life-history trait. βs are fitted coefficient mean and 95% confident intervals (in brackets) of eqn. 1. A, A^2, A^3 and log(A) are linear, quadratic, cubic and logarithmic terms of stand age (years), respectively. The best relationships between relative abundance and stand age were determined by Akaike Information Criterion (Appendix A Table 2). All βs corresponding to Year are multiplied by 100 to facilitate presentation.

Species/Trait	β_i/F/P	A	A^2	A^3	lnA	Year
Pinus contorta	β_i	-0.52				16.90
		(-0.59,-0.46)				(14.20,19.60)
	F	992.85				152.78
	P	<0.001				<0.001
Pinus banksiana	β_i	-0.34				9.43
		(-0.48,-0.21)				(3.67,15.20)
	F	44.29				10.35
	P	<0.001				0.001
Populus tremuloides	β_i	-0.29	-0.05			8.82
		(-0.35,-0.22)	(-0.07,-0.04)			(6.12,11.50)
	F	83.39	38.49			36.82
	P	<0.001	<0.001			<0.001
Populus balsamifera	β_i				-0.24	2.63
					(-0.30,-0.18)	(-0.01,5.26)
	F				167.50	3.82
	P				<0.001	0.051
Betula papyrifera	β_i				-0.33	6.71
					(-0.41,-0.26)	(3.39,10.00)
	F				87.17	15.72
	P				<0.001	<0.001
Picea mariana	β_i	-0.06	-0.14	0.09		5.53
		(-0.14,0.03)	(-0.17,-0.11)	(0.05,0.12)		(2.47,8.58)
	F	148.11	67.55	24.72		19.36
	P	<0.001	<0.001	<0.001		<0.001
Picea glauca	β_i	0.34	-0.04			-4.90
		(0.28,0.40)	(-0.06,-0.02)			(-7.08,-2.72)
	F	538.43	17.74			16.37
	P	<0.001	<0.001			<0.001
Abies balsamea	β_i	0.52	0.34	-0.18		-10.30
		(0.42,0.62)	(0.29,0.40)	(-0.26,-0.10)		(-13.60,-7.02)
	F	69.91	118.29	19.62		49.05
	P	<0.001	<0.001	<0.001		<0.001

Deciduous broadleaf	β_i	-0.30	-0.02		7.09
		(-0.36,-0.24)	(-0.03,-0.01)		(4.80,9.38)
	F	228.74	9.33		35.62
	P	<0.001	0.002		<0.001
Early-successional conifer	β_i	-0.36	-0.02		10.70
		(-0.42,-0.31)	(-0.03,-0.02)		(8.80,12.50)
	F	343.91	31.39		132.20
	P	<0.001	<0.001		<0.001
Late-successional conifer	β_i	0.46	0.03	-0.06	-7.63
		(0.40,0.52)	(0.01,0.05)	(-0.09,-0.04)	(-9.53,-5.74)
	F	638.77	1.00	20.27	60.57
	P	<0.001	0.318	<0.001	<0.001

TABLE S2-2. Akaike Information Criterion scores for the four functions of stand age

Species/Trait	Linear	Quadratic	Cubic	Logarithmic
Pinus contorta	-2985	-2968	-2978	-2915
Pinus banksiana	-54	-42	-37	-22
Populus tremuloides	2870	2820	2830	2934
Populus balsamifera	1187	1160	1132	1134
Betula papyrifera	1595	1599	1605	1579
Picea mariana	17	-57	-76	-53
Picea glauca	1739	1734	1734	1768
Abies balsamea	1536	1440	1408	1570
Deciduous broadleaf	1734	1711	1721	1814
Early-successional conifer	-5440	-5465	-5457	-5277
Late-successional conifer	951	958	940	1109

The functions used to determine the responses of relative abundance (RA) to stand age (A, years) are:

1) Linear model: $RA = \beta_0 + \beta_1 \times A + \pi$

2) Second order polynomial: $RA = \beta_0 + \beta_1 \times A + \beta_2 \times A^2 + \pi$

3) Third order polynomial: $RA = \beta_0 + \beta_1 \times A + \beta_2 \times A^2 + \beta_3 \times A^3 + \pi$

4) Log model: $RA = \beta_0 + \beta_1 \times \ln(A) + \pi$, β_i are parameters to be estimated, and π is the random plot effect.

1 TABLE S2-3. The effects of atmospheric CO_2 concentration (CO_2), mean annual temperature (MAT), and climate moisture index
2 (CMI) on relative species and trait abundance.

Species/Trait	β_i/F/P	CO_2			MAT			CMI		
		Current	5-yr mean	10-yr mean	Current	5-yr mean	10-yr mean	Current	5-yr mean	10-yr mean
Pinus contorta	β_i	6.45	6.64	6.14	0.20	0.33	0.70	-0.66	-0.42	-0.74
		(5.10,7.79)	(5.30,7.98)	(4.85,7.43)	(-0.03,0.44)	(-0.03,0.70)	(0.22,1.18)	(-0.91,-0.42)	(-0.66,-0.17)	(-1.09,-0.39)
	F	88.54	94.21	86.75	2.80	3.21	8.17	27.36	11.22	17.28
	P	<0.001	<0.001	<0.001	0.094	0.073	0.004	<0.001	0.001	<0.001
Pinus banksiana	β_i	7.85	7.02	6.62	-0.24	2.60	3.87	0.38	0.05	1.10
		(2.87,12.80)	(2.02,12.00)	(1.57,11.70)	(-1.59,1.12)	(-0.14,5.35)	(-2.08,9.82)	(-0.40,1.16)	(-0.94,1.05)	(-0.41,2.61)
	F	9.61	7.60	6.63	0.12	3.47	1.63	0.93	0.01	2.04
	P	0.002	0.006	0.010	0.734	0.063	0.202	0.335	0.916	0.154
Populus tremuloides	β_i	7.60	7.50	7.64	-0.51	-0.09	2.04	0.04	-1.16	-0.75
		(5.14,10.10)	(5.06,9.94)	(5.22,10.00)	(-1.35,0.33)	(-1.42,1.25)	(0.06,4.03)	(-0.59,0.68)	(-2.05,-0.27)	(-1.93,0.44)
	F	29.50	28.55	30.06	1.05	<0.01	3.47	0.18	2.40	<0.01
	P	<0.001	<0.001	<0.001	0.305	0.984	0.063	0.673	0.121	0.949
Populus balsamifera	β_i	0.64	0.35	-0.03	0.06	2.11	1.05	-0.51	0.01	2.05
		(-1.81,3.08)	(-2.08,2.78)	(-2.43,2.37)	(-0.95,1.07)	(0.63,3.58)	(-1.40,3.51)	(-1.29,0.26)	(-1.01,1.03)	(0.64,3.47)
	F	0.26	0.08	<0.01	0.01	7.82	0.71	1.67	<0.01	8.11
	P	0.610	0.775	0.980	0.914	0.005	0.400	0.197	0.983	0.004
Betula papyrifera	β_i	6.85	7.01	7.39	-0.68	-3.02	-1.21	0.10	-0.84	-2.44
		(3.66,10.00)	(3.83,10.20)	(4.24,10.50)	(-2.29,0.94)	(-5.54,-0.50)	(-5.26,2.83)	(-1.07,1.27)	(-2.42,0.75)	(-4.57,-0.31)
	F	17.71	18.72	21.18	0.67	5.54	0.35	0.03	1.07	5.06
	P	<0.001	<0.001	<0.001	0.412	0.019	0.557	0.869	0.301	0.025
Picea mariana	β_i	0.11	0.23	0.03	-0.10	-0.60	-1.11	0.64	0.60	1.61
		(-2.24,2.45)	(-2.10,2.56)	(-2.25,2.31)	(-0.65,0.44)	(-1.49,0.29)	(-2.37,0.15)	(0.18,1.11)	(0.00,1.20)	(0.77,2.46)

Species	Stat									
	F	0.16	0.17	0.53	0.01	1.49	2.34	12.00	16.28	36.16
	P	0.690	0.678	0.469	0.913	0.223	0.127	0.001	<0.001	<0.001
Picea glauca	β_i	-3.71	-4.57	-4.40	0.64	-0.33	-2.62	0.30	0.18	-0.64
		(-5.57,-1.85)	(-6.39,-2.74)	(-6.18,-2.62)	(0.10,1.18)	(-1.20,0.53)	(-3.89,-1.35)	(-0.16,0.76)	(-0.49,0.85)	(-1.53,0.26)
	F	14.80	27.48	26.97	5.74	0.40	17.00	2.09	1.09	0.66
	P	<0.001	<0.001	<0.001	0.017	0.528	<0.001	0.148	0.297	0.415
Abies balsamea	β_i	-9.33	-8.85	-8.83	-1.39	-2.71	-5.01	-0.27	2.12	2.63
		(-12.50,-6.15)	(-12.00,-5.66)	(-12.00,-5.66)	(-2.94,0.15)	(-5.31,-0.12)	(-8.46,-1.55)	(-1.90,1.36)	(0.03,4.22)	(-0.40,5.65)
	F	42.49	38.57	38.05	3.97	7.18	11.07	1.09	0.24	0.02
	P	<0.001	<0.001	<0.001	0.047	0.007	0.001	0.296	0.624	0.883
Deciduous broadleaf	β_i	5.27	5.07	5.16	-0.31	0.04	1.48	-0.30	-0.68	-0.29
		(3.25,7.29)	(3.07,7.07)	(3.20,7.13)	(-0.94,0.32)	(-0.96,1.05)	(-0.07,3.03)	(-0.72,0.12)	(-1.33,-0.03)	(-1.17,0.59)
	F	23.85	22.16	23.59	0.80	0.02	3.34	1.53	2.22	<0.01
	P	<0.001	<0.001	<0.001	0.372	0.883	0.068	0.216	0.136	0.960
Early-successional conifer	β_i	3.66	3.74	3.38	-0.02	0.26	0.77	-0.07	-0.02	0.19
		(2.54,4.79)	(2.61,4.86)	(2.29,4.46)	(-0.24,0.19)	(-0.08,0.61)	(0.27,1.27)	(-0.22,0.08)	(-0.25,0.21)	(-0.16,0.53)
	F	34.29	34.99	29.30	0.01	2.23	9.25	0.26	0.75	5.26
	P	<0.001	<0.001	<0.001	0.910	0.135	0.002	0.612	0.387	0.022
Late-successional conifer	β_i	-5.90	-5.80	-5.74	0.32	-0.46	-2.56	0.18	0.39	-0.41
		(-7.56,-4.25)	(-7.44,-4.16)	(-7.35,-4.13)	(-0.18,0.83)	(-1.27,0.35)	(-3.75,-1.36)	(-0.18,0.55)	(-0.23,1.01)	(-1.29,0.46)
	F	44.12	42.84	43.53	1.63	1.24	16.89	0.39	0.22	2.87
	P	<0.001	<0.001	<0.001	0.202	0.266	<0.001	0.534	0.640	0.091

3

4   Values are derived by modelling individual climatic drivers at different time windows while the effects of stand age are

5   simultaneously accounted for (see Appendix A Table 1 and Methods). All βs are multiplied by 100 to facilitate presentation.

6   TABLE S2-4. Species and trait specific plot characteristics. Where applicable range (~) and averages are presented with ± standard
7   deviation in brackets.

Species/Trait	Census Range (year)	Latitude range (°)	Longitude range (°)	Number of plots	Number of Censuses	Census Interval (years)	Plot size (m²)	Number of stems
Pinus contorta	1960 ~ 2009	49.28 ~ 58.89	-119.45 ~ -114.03	857	4.72 (± 0.82)	10.05 (± 3.56)	930 (± 569)	62 (± 51)
Pinus banksiana	1966 ~ 2010	49.17 ~ 57.21	-115.24 ~ -95.36	151	3.84 (± 0.86)	7.63 (± 4.92)	654 (± 210)	46 (± 39)
Populus tremuloides	1960 ~ 2013	49.04 ~ 59.73	-119.66 ~ -95.31	920	4.38 (± 0.98)	9.81 (± 4.45)	1129 (± 550)	29 (± 34)
Populus balsamifera	1960 ~ 2013	49.20 ~ 59.73	-119.45 – -95.31	488	4.54 (± 1.08)	9.50 (±4.19)	1289 (± 592)	12 (± 19)
Betula papyrifera	1960 ~ 2013	49.24 ~ 59.73	-119.45 ~ -95.31	399	4.44 (±- 1.1)	9.46 (± 4.62)	1209 (± 587)	7 (± 13)
Picea mariana	1960 ~ 2011	49.20 ~ 59.73	-119.39 – -95.36	618	4.53 (± 0.9)	9.80 (± 4.05)	853 (± 519)	24 (± 37)
Picea glauca	1960 ~ 2013	49.20 ~ 59.73	-119.66 ~ -95.36	1077	4.50 (± 1.01)	9.85 (± 4.33)	1092 (± 543)	38 (± 35)
Albies balsamea	1960 ~ 2013	49.20 ~ 58.69	-119.45 ~ -95.36	314	4.75 (± 1.06)	9.06 (± 4.14)	1152 (± 564)	21 (± 24)
Deciduous broadleaf	1960 ~ 2013	49.04 ~ 59.73	-119.66 ~ -95.31	1065	4.36 (± 0.97)	9.67 (± 4.35)	1106 (± 551)	32 (± 39)
Early-Successional conifer	1960 ~ 2011	49.17 ~ 59.73	-119.45 – -95.3	1143	4.56 (± 0.91)	9.58 (± 3.91)	887 (± 533)	65 (± 53)
Late-Successional conifer	1960 ~ 2013	49.20 ~ 59.73	-119.66 – -95.36	1107	4.44 (± 1.04)	9.69 (± 4.26)	1085(± 540)	44 (± 39)

8

TABLE S3-1. Plot characteristics by each level examined. Values are means with standard deviations presented where applicable.

Trait or Species	Drainage class	Initial year	Final year	Number of plots	Number of censuses	Interval (years)	Plot size (m^2)	Number of stems	Above-ground biomass (Mg ha^{-1})	ΔAGB (Mg ha^{-1} yr^{-1})
Broadleaf Deciduous	Well	1961	2010	105	3.61 (±0.54)	7.21 (±3.68)	756.67 (±338.12)	30.97 (±40.98)	45.04 (±47.43)	0.64 (±1.61)
	Moderately	1960	2010	644	3.76 (±0.85)	9.74 (±3.93)	1240.49 (±594.15)	30.54 (±36.54)	61.27 (±56.86)	0.12 (±1.37)
	Poorly	1961	2009	6	3.82 (±0.80)	10.68 (±5.16)	1048.55 (±594.24)	5.34 (±6.48)	8.43 (±16.64)	-0.03 (±0.28)
Early-successional conifer	Well	1958	2010	139	3.77 (±0.59)	7.56 (±3.35)	720.90 (±485.21)	59.68 (±47.03)	76.66 (±51.57)	1.39 (±1.56)
	Moderately	1960	2010	735	3.85 (±0.72)	9.88 (±3.66)	925.43 (±567.45)	63.76 (±48.55)	97.04 (±62.17)	0.81 (±1.28)
	Poorly	1960	2009	32	3.98 (±0.72)	9.51 (±4.11)	723.54 (±349.11)	65.72 (±50.05)	102.53 (±62.88)	0.46 (±1.39)
Late-successional conifer	Well	1961	2010	86	3.76 (±0.76)	8.19 (±3.91)	942.45 (±459.81)	41.55 (±40.37)	68.48 (±59.51)	0.59 (±1.22)
	Moderately	1960	2011	694	3.84 (±0.87)	9.61 (±3.87)	1164.61 (±582.00)	41.33 (±36.93)	72.03 (±63.02)	0.40 (±1.59)
	Poorly	1960	2009	33	4.30 (±0.69)	8.78 (±3.93)	775.64 (±484.96)	42.46 (±37.83)	81.98 (±72.63)	0.24 (±1.16)
Pinus contorta	Well	1961	2009	75	3.92 (±0.59)	9.00 (±3.32)	831.74 (±604.39)	67.19 (±52.26)	90.75 (±48.76)	1.07 (±1.19)
	Moderately	1960	2009	666	3.87 (±0.71)	10.20 (±3.56)	938.70 (±574.02)	59.02 (±45.96)	94.29 (±57.42)	0.69 (±1.16)
	Poorly	1961	2007	23	3.86 (±0.69)	9.67 (±3.58)	574.12 (±185.55)	62.05 (±31.28)	112.00 (±28.06)	0.43 (±1.34)
Pinus banksiana	Well	1958	2010	54	3.64 (±0.53)	5.40 (±1.79)	564.87 (±180.78)	43.89 (±32.45)	56.19 (±45.07)	1.83 (±1.97)

	Moderately	1966	2010	14	3.27 (±0.45)	6.73 (±3.20)	650.26 (±175.63)	23.38 (±31.66)	31.69 (±48.36)	0.58 (±1.19)
Populus tremuloides	Well	1961	2010	94	3.61 (±0.52)	7.63 (±3.94)	770.83 (±307.44)	29.37 (±39.40)	43.30 (±38.59)	0.72 (±1.60)
	Moderately	1960	2011	537	3.81 (±0.89)	9.79 (±3.92)	1290.58 (±594.77)	25.94 (±30.15)	59.56 (±52.03)	0.15 (±1.34)
Populus balsamifera	Well	1961	2010	33	3.42 (±0.58)	6.94 (±3.43)	974.48 (±468.06)	14.80 (±14.76)	31.45 (±46.27)	-0.03 (±0.77)
	Moderately	1960	2011	325	3.96 (±0.96)	9.47 (±3.92)	1430.76 (±604.10)	13.57 (±20.63)	19.49 (±25.91)	0.01 (±0.63)
Betula papyrifera	Well	1966	2010	34	3.48 (±0.50)	6.13 (±2.95)	640.46 (±209.08)	7.54 (±12.55)	6.38 (±8.29)	0.15 (±0.32)
	Moderately	1960	2010	265	3.88 (±0.98)	9.35 (±3.98)	1358.99 (±599.35)	6.99 (±12.40)	7.00 (±11.24)	-0.01 (±0.39)
Picea mariana	Well	1961	2010	50	3.76 (±0.68)	7.79 (±3.64)	883.28 (±598.50)	16.27 (±25.98)	13.48 (±21.40)	0.28 (±0.48)
	Moderately	1960	2011	432	3.83 (±0.70)	9.91 (±3.71)	873.29 (±553.32)	18.26 (±23.06)	21.12 (±28.10)	0.31 (±0.63)
	Poorly	1960	2009	26	4.01 (±0.70)	9.57 (±3.83)	637.71 (±218.36)	27.89 (±41.40)	29.09 (±28.84)	0.26 (±0.60)
Picea glauca	Well	1961	2010	81	3.66 (±0.66)	8.74 (±4.07)	987.28 (±476.12)	33.45 (±31.41)	65.05 (±53.60)	0.56 (±1.16)
	Moderately	1960	2011	695	3.87 (±0.86)	9.65 (±3.88)	1167.28 (±583.03)	34.71 (±32.81)	66.80 (±58.65)	0.35 (±1.51)
	Poorly	1960	2009	30	4.30 (±0.64)	8.97 (±3.93)	791.73 (±531.29)	22.38 (±28.28)	58.18 (±62.06)	0.29 (±0.91)
Abies balsamea	Well	1961	2010	39	3.75 (±0.64)	8.54 (±3.67)	865.64 (±472.18)	16.85 (±18.50)	13.58 (±14.18)	0.09 (±0.84)
	Moderately	1960	2010	201	4.05 (±0.92)	8.80 (±3.73)	1276.29 (±572.97)	21.48 (±23.30)	19.33 (±22.25)	0.04 (±0.75)
	Poorly	1960	2000	17	4.78 (±0.50)	7.66 (±3.42)	981.15 (±589.16)	41.34 (±21.75)	54.30 (±39.78)	-0.01 (±0.99)

TABLE S3-2. Akaike Information Criterion scores for the four functions of stand age.

Model	Stand, Trait, or Species	Linear	Quadratic	Cubic	Logarhitmic
ΔAGB	Deciduous broadleaf	6911	6847	6850	6866
	Early-successional conifer	8247	8050	8054	8099
	Late-successional conifer	8372	8374	8367	8372
	Pinus contorta	7139	6942	6906	6960
	Pinus banksiana	577	579	582	577
	Populus tremuloides	5736	5717	5723	5716
	Populus balsamifera	3721	3718	3721	3716
	Betula papyrifera	2795	2774	2776	2786
	Picea mariana	4700	4684	4686	4691
	Picea glauca	8285	8287	8259	8289
	Abies balsamea	2837	2840	2814	2837
ΔAGB$_{GI}$	Deciduous broadleaf	6898	6900	6906	6894
	Early-successional conifer	6432	6374	6381	6399
	Late-successional conifer	6425	6431	6434	6429
	Pinus contorta	4526	4331	4253	4266
	Pinus banksiana	488	492	488	490
	Populus tremuloides	5823	5824	5828	5817
	Populus balsamifera	2692	2692	2698	2687
	Betula papyrifera	2815	2814	2820	2813
	Picea mariana	3703	3708	3708	3709
	Picea glauca	6489	6474	6480	6480
	Abies balsamea	2109	2103	2014	2138
ΔAGB$_{M}$	Deciduous broadleaf	7350	7341	7341	7344
	Early-successional conifer	9264	9188	9184	9230
	Late-successional conifer	8001	7991	7969	8002
	Pinus contorta	7945	7925	7921	7936

Pinus banksiana	680	675	677	676
Populus tremuloides	6169	6174	6172	6169
Populus balsamifera	3632	3635	3640	3631
Betula papyrifera	3063	3068	3072	3062
Picea mariana	4828	4811	4812	4816
Picea glauca	8104	8066	8024	8091
Abies balsamea	2611	2595	2600	2627

The functions used to determine the responses of relative abundance (RA) to stand age (A, years) are:

1) Linear model: $\Delta AGB = \beta_0 + \beta_1 \times A + \pi$

2) Second order polynomial: $\Delta AGB = \beta_0 + \beta_1 \times A + \beta_2 \times A^2 + \pi$

3) Third order polynomial: $\Delta AGB = \beta_0 + \beta_1 \times A + \beta_2 \times A^2 + \beta_3 \times A^3 + \pi$

4) Log model: $\Delta AGB = \beta_0 + \beta_1 \times \ln(A) + \pi$, β_i are parameters to be estimated, and π is the random plot effect.

TABLE S3-3. The effects of stand age, calendar year, and drainage class on trait and species annual aboveground biomass change.

Trait/Species	F/p	A	A^2	A^3	*ln*A	L	D	Y	Y×D
Deciduous broadleaf	F	397.22	63.42			10.93	3.53	1.36	3.01
	p	<0.001	<0.001			0.001	0.030	0.244	0.049
Early-successional conifer	F	887.43	209.12			3.65	1.28	107.08	6.07
	p	<0.001	<0.001			0.056	0.279	<0.001	0.002
Late-successional conifer	F	39.33	4.75	15.05		1.00	2.22	30.98	3.50
	p	<0.001	0.029	<0.001		0.319	0.109	<0.001	0.030
Pinus contorta	F	866.89	218.69	41.83		4.39	12.40	37.91	2.43
	p	<0.001	<0.001	<0.001		0.036	<0.001	<0.001	0.089
Pinus banksiana	F	31.20				0.00	2.87	1.31	0.36
	p	<0.001				0.995	0.095	0.254	0.549
Populus tremuloides	F				373.03	17.25	0.85	0.01	3.36
	p				<0.001	<0.001	0.357	0.917	0.067
Populus balsamifera	F				41.32	0.59	0.57	27.55	0.73
	p				<0.001	0.444	0.450	<0.001	0.394
Betula papyrifera	F	11.12	35.27			2.48	3.39	10.78	6.82
	p	0.001	<0.001			0.115	0.066	0.001	0.009
Picea mariana	F	134.93	23.19			0.25	0.74	24.70	5.81
	p	<0.001	<0.001			0.616	0.477	<0.001	0.003
Picea glauca	F	65.60	3.74	37.97		0.66	2.91	41.47	3.03
	p	<0.001	0.053	<0.001		0.415	0.055	<0.001	0.049
Abies balsamea	F	0.61	4.19	31.64		0.28	1.40	2.43	4.88
	p	0.436	0.041	<0.001		0.595	0.249	0.119	0.008

TABLE S3-4. The effects of stand age, calendar year, and drainage class on trait and species annual aboveground biomass growth and ingrowth.

Trait/Species	F/p	A	A²	A³	lnA	L	D	Y	Y×D
Deciduous broadleaf	F				90.51	0.53	2.52	2.58	0.59
	p				<0.001	0.465	0.081	0.108	0.553
Early-successional conifer	F	666.79	70.87			1.56	4.40	0.73	17.44
	p	<0.001	<0.001			0.211	0.013	0.392	<0.001
Late-successional conifer	F	77.00				4.51	2.52	24.23	2.94
	p	<0.001				0.034	0.081	<0.001	0.053
Pinus contorta	F	1172.89	230.78	85.62		5.58	1.19	55.62	4.93
	p	<0.001	<0.001	<0.001		0.018	0.305	<0.001	0.007
Pinus banksiana	F	3.30				0.31	3.74	22.59	1.32
	p	0.071				0.576	0.057	<0.001	0.253
Populus tremuloides	F				75.20	0.85	0.70	3.99	0.33
	p				<0.001	0.356	0.404	0.046	0.567
Populus balsamifera	F				42.81	0.07	3.17	0.33	0.21
	p				<0.001	0.785	0.076	0.569	0.647
Betula papyrifera	F				7.40	0.70	2.25	5.72	1.14
	p				0.007	0.405	0.135	0.017	0.286
Picea mariana	F	42.48				6.65	1.49	0.79	11.64
	p	<0.001				0.010	0.225	0.373	<0.001
Picea glauca	F	14.31	23.28			1.69	5.97	28.14	3.60
	p	<0.001	<0.001			0.194	0.003	<0.001	0.028
Abies balsamea	F	79.27	18.36	105.94		1.19	0.46	2.51	5.68
	p	<0.001	<0.001	<0.001		0.276	0.630	0.114	0.004

TABLE S3-5. The effects of stand age, calendar year, and drainage class on trait and species annual aboveground biomass loss due to mortality.

Trait/Species	F/p	A	A²	A³	lnA	L	D	Y	Y×D
Deciduous broadleaf	F	19.55	8.14			17.25	0.96	4.41	0.05
	p	<0.001	0.004			<0.001	0.383	0.036	0.948
Early-successional conifer	F	32.81	80.90	8.46		4.62	18.67	183.74	2.10
	p	<0.001	<0.001	0.004		0.032	<0.001	<0.001	0.122
Late-successional conifer	F	210.94	14.50	34.24		4.89	2.59	13.23	2.85
	p	<0.001	<0.001	<0.001		0.027	0.076	<0.001	0.058
Pinus contorta	F	6.27	24.38	8.57		6.28	15.49	181.79	2.91
	p	0.012	<0.001	0.003		0.012	<0.001	<0.001	0.055
Pinus banksiana	F				11.10	0.22	1.54	11.45	0.83
	p				0.001	0.642	0.220	0.001	0.364
Populus tremuloides	F	37.87				14.45	0.11	0.62	0.43
	p	<0.001				<0.001	0.735	0.431	0.510
Populus balsamifera	F	1.43				0.16	4.59	22.37	0.13
	p	0.233				0.691	0.033	<0.001	0.720
Betula papyrifera	F	1.07				0.01	0.75	2.06	0.92
	p	0.301				0.941	0.388	0.152	0.337
Picea mariana	F	91.83	19.59			6.89	1.23	64.20	0.58
	p	<0.001	<0.001			0.009	0.292	<0.001	0.562
Picea glauca	F	155.07	45.37	53.57		0.98	4.37	17.24	1.45
	p	<0.001	<0.001	<0.001		0.322	0.013	<0.001	0.235
Abies balsamea	F	52.12	26.49			0.80	0.52	1.73	4.15
	p	<0.001	<0.001			0.372	0.595	0.188	0.016

TABLE S3-6. The effects of annual temperature anomaly (ATA) on trait and species annual aboveground biomass change and relative aboveground biomass change and their components.

Stand/Trait/Species	F/p	ΔAGB		ΔAGB_{GI}		ΔAGB_M	
		ATA	ATA ×D	ATA	ATA ×D	ATA	ATA ×D
Deciduous broadleaf	F	3.92	0.06	4.4	0.04	12.48	0
	p	0.048	0.943	0.036	0.962	<0.001	0.996
Early-successional conifer	F	35.01	11.79	21.8	17.99	120.3	4.29
	p	<0.001	<0.001	<0.001	<0.001	<0.001	0.014
Late-successional conifer	F	36.24	0.49	15.66	1.9	13.13	0.91
	p	<0.001	0.611	<0.001	0.149	<0.001	0.403
Pinus contorta	F	8.15	3.67	80.28	3.27	103.71	8.47
	p	0.004	0.026	<0.001	0.038	<0.001	<0.001
Pinus banksiana	F	3.94	2.29	20.19	2.87	5.75	0.14
	p	0.049	0.132	<0.001	0.092	0.018	0.709
Populus tremuloides	F	2.06	0.05	4.07	0.63	6.02	0.55
	p	0.152	0.82	0.044	0.427	0.014	0.458
Populus balsamifera	F	17.41	0.07	0.01	0.15	15.84	1.1
	p	<0.001	0.788	0.943	0.701	<0.001	0.294
Betula papyrifera	F	12.51	3.47	2.82	0.48	3.09	0.49
	p	<0.001	0.063	0.094	0.489	0.079	0.484
Picea mariana	F	21.25	8.35	0.63	13.01	45.58	1.32
	p	<0.001	<0.001	0.427	<0.001	<0.001	0.269
Picea glauca	F	42.98	0.8	13.4	1.84	15.14	0.48
	p	<0.001	0.451	<0.001	0.16	<0.001	0.619

| *Abies balsamea* | F | 2.31 | 4.34 | 2.04 | 1.94 | 0.46 | 4.48 |
| | p | 0.129 | 0.013 | 0.154 | 0.145 | 0.498 | 0.012 |

TABLE S3-7. The effects of annual climate moisture index anomaly (ACMIA) on trait and species annual aboveground biomass change and relative aboveground biomass change and their components.

Stand/Trait/Species	F/p	ΔAGB		ΔAGB_{GI}		ΔAGB_M	
		ACMIA	ACMIA×D	ACMIA	ACMIA×D	ACMIA	ACMIA×D
Deciduous broadleaf	F	2.09	0.39	0.69	0.11	0.2	0.05
	p	0.149	0.676	0.405	0.893	0.651	0.95
Early-successional conifer	F	53.5	3	3.07	0.6	45.7	5.47
	p	<0.001	0.05	0.08	0.547	<0.001	0.004
Late-successional conifer	F	6.79	1.61	24.12	2.31	1.24	1.75
	p	0.009	0.2	<0.001	0.099	0.265	0.174
Pinus contorta	F	18.91	1.41	1.55	4.05	44.61	0.67
	p	<0.001	0.244	0.214	0.017	<0.001	0.51
Pinus banksiana	F	0.91	0.01	2.29	0	3.36	1.92
	p	0.341	0.917	0.132	0.949	0.069	0.167
Populus tremuloides	F	0.06	0.71	0.9	1.03	0.87	0.07
	p	0.813	0.399	0.344	0.309	0.351	0.785
Populus balsamifera	F	26.13	4.33	2.76	4.7	15.07	2.64
	p	<0.001	0.038	0.097	0.03	<0.001	0.105
Betula papyrifera	F	13.86	1.59	2.68	0.5	2.49	0.03
	p	<0.001	0.208	0.102	0.479	0.115	0.862

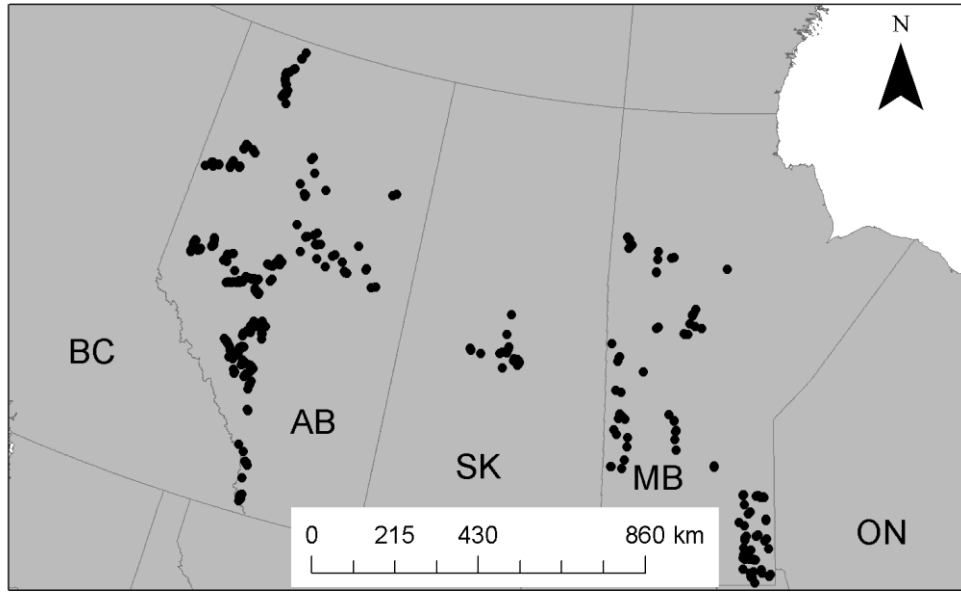|							
Picea mariana	F	33.49	2.5	14.52	3.03	21.34	2.25
	p	<0.001	0.082	<0.001	0.048	<0.001	0.106
Picea glauca	F	11.85	0.08	24.97	0.03	4.04	0.42
	p	0.001	0.922	<0.001	0.975	0.044	0.655
Abies balsamea	F	0.01	3.37	1.89	3.76	0.02	5.11
	p	0.941	0.035	0.169	0.024	0.893	0.006

FIGURE S3-1. Map of permanent sample plot locations from across Alberta, Saskatchewan, and Manitoba, Canada.