University of Alberta

Spatial and Temporal Variations in Tree Growth, Mortality, and Biodiversity in Alberta Forests

by

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ABSTRACT

Understanding the spatial and temporal variation of tree demographic rates and biodiversity is essential for predicting the dynamics of forest ecosystems and their responses to changing environments. This thesis contributes to that understanding through modeling the long-term change in tree growth, mortality, biodiversity and biomass in Alberta forests as specified by the four constituent chapters.

First, using a dataset of half-century observations on 1,680 permanent sample plots in western Canada, I detected a widespread, significant increase in tree mortality but a significant decrease in tree growth. I found that competition was the most important factor responsible for the changes, followed by climate change. This finding challenges previous studies that concluded climate change was the major factor affecting forest dynamics.

Second, I modeled spatial distribution of forest biomass across Alberta by integrating three data sources: 1,968 plots forest inventory data, Lidar data, and land cover, climate and other environmental variables. Total biomass stock in Alberta forests was estimated to be 3.22 petagram. The average biomass density was 80.24 megagram per hectare. Spatial distribution of biomass varied with natural regions, land cover types, and species.

Third, I studied the diversity of breeding birds across 206 sites in Alberta boreal forest and found that temperature, human land cover, and woody plant richness had strong positive correlations with the overall bird richness, while local forest structure and composition were important determinants of bird diversity. The strength and direction of the effects of those variables are guild-specific.

In the last chapter, I integrated taxonomic and phylogenetic diversity to assess the effects of natural and anthropogenic disturbances on plant communities in Alberta. I compared the changes in vascular plant composition along a human disturbance gradient and found high taxonomic diversity at intermediate anthropogenic disturbance levels. I failed to detect significant changes in phylogenetic diversity along disturbance because but richness was not found to significantly correlate with phylogenetic diversity. This result suggested that species turnover may be randomly related to anthropogenic disturbance along the evolutionary tree.

By synthesizing results from direct field measurements and modeling, these chapters together contribute to understanding of ecosystem functioning, community structure, forest dynamics, and biodiversity of Alberta forests in a changing world. This knowledge is essential for sustainable management of Alberta forest ecosystems.

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Chapter 1 General Introduction

1.1 *Biodiversity and Ecosystem Functioning*

Ecosystems support biodiversity and also provide goods and services that are essential to maintaining the well-being of humans. Biodiversity and ecosystem functioning are two essential aspects of sustainable ecosystem management and conservation (de Groot *et al.* 2002). Understanding the factors influencing the patterns, processes, and interactions of biodiversity and ecosystem functioning is one of the main goals of ecology and conservation biology (Hooper *et al.* 2005).

1.2 *Factors Influencing Biodiversity and Ecosystem Functioning*

Changes in biodiversity and ecosystem functioning are caused by multiple, interacting drivers that work over different disturbances, over space and time, and over different taxonomic groups. There are many biotic and abiotic factors which are related to changes in biodiversity and ecosystem functioning. I selected several key drivers of the ecosystem changes, especially for forest ecosystems, to give a short introduction (Figure 1.1).

1) Competition

Competition for foods and resources is one of the universal driving forces of ecosystem assembly. Many ecologists have focused on understanding how competition both within and between species in local communities regulates ecosystem structure and function over space and time. MacArthur's (1958) pioneering work on competition, Huchinson's (1959) work on niches, Paine's

(1966) work on keystone predation, MacArthur and Levins' (1964, 1967) and Tilman's (1982) work on the impact of competition on coexistence are just a few of the influential papers that inspired us to determine to what extent competition influence community structure and ecosystem functioning, and by what mechanisms different species come to dominate communities.

2) *Environmental Variables*

An extensive literature on "species-environment relationship" correlates biological patterns with factors such as elevation, climates, light and soil. Heterogeneous environments are predicted to support more complex and diverse biological assemblages (Kerr & Packer 1997). Changes in habitat configuration and complexity have profound effects on biodiversity, altering the relative abundance and species richness, and have the potential to mediate present and future levels of ecosystem functioning (Balvanera *et al.* 2006; Cardinale *et al.* 2006; Godbold *et al.* 2010).

3) *Evolutionary History of Species*

The role of evolutionary history on constructing plant and animal communities has been recognized since the days of Darwin (Darwin 1859). In the past two decades, the potential effects of historical processes on the distribution and abundance of species has received renewed attention (e.g., Ricklefs 2004; Wiens & Donoghue 2004; Pärtel *et al.* 2008). Instead of only using simple measures of taxonomic diversity (number of species and/or relative abundance) that assume equivalence among species, a number of recent studies have considered two other dimensions of biodiversity, phylogenetic and functional diversity, which are closely related to the evolutionary history of species (Figure 1.2, Swenson 2011). By better understanding these other biodiversity dimensions, we can more effectively detect threats and prioritize species for conservation action, and better understand the patterns and processes related to biodiversity and ecosystem functioning.

4) Climate Change

Climate change in the past century has already had a measurable impact on ecosystems. During the last 100 years, the global mean surface temperature has increased by about 0.6°C, precipitation patterns have changed spatially and temporally, and global average sea level rose between 0.1 and 0.2 meters (Millennium Ecosystem Assessment 2005). Global mean surface temperature is projected to increase from 1990 to 2100 by 1.4-5.8°C. Precipitation patterns are projected to change, leading to an increased incidence in floods and drought (Millennium Ecosystem Assessment 2005).

Observed changes in climate have affected species distributions, population sizes, community structure and composition, and the timing of reproduction or migration events, as well as an increase in the frequency of pest and disease outbreaks, especially in forest ecosystems (Millennium Ecosystem Assessment 2005; Walker *et al.* 1999). Although a lot of studies have worked on the effects of climate change on population and community structures of different ecosystems, we still lack knowledge on the degree to which changes in climate have already affected and continue to affect biodiversity and ecosystem functioning (e.g., biomass and carbon stocks) (Aber *et al.* 2001; Walther *et al.* 2002).

5) Human Disturbance

We live in an era of “anthropocene” (Crutzen & Stoermer 2000), in which human activities have greatly modified the biosphere. Human activities, such as deforestation, forest degradation, environmental pollution, and biological invasions, have changed and continue to change the environment on local and global scales. Many of these alterations are leading to dramatic changes in the biotic structure and composition of ecological communities, either from the loss of species or from the introduction of exotic species. Also, these changes on ecosystems have a strong potential to alter ecosystem properties and the goods and services they provide to humanity (Hooper *et al.* 2005).

6) Spatial and Temporal Impacts

The relative importance of determinants of species diversity and ecosystem functioning varies widely across both space and time. And most related mechanisms are scale-dependent, i.e. they vary with the grain size, spatial extent of the sampling units, and forest successional stages (Levin 1992; Willis & Whittaker 2002). To better understand and evaluate the relative roles of different determinants, one must understand the interactions between the intrinsic scales of heterogeneity within the environment and the scales at which the organism can respond to the heterogeneity (Fahrig 1992).

1.3 The Roles of Boreal Forests in Maintaining Biodiversity and Ecosystem Functioning

The boreal forest biome covers one third of the Earth's forested area and is estimated to store about 22% of all carbon on the earth's land surface (Carlson *et al.* 2009). One recent report from the Canadian Boreal Initiative and the Boreal Songbird Initiative estimates that boreal forest regions store more carbon than any other terrestrial ecosystem, almost twice as much per acre as tropical forests (Carlson *et al.* 2009).

Unfortunately, this region is expected to experience the greatest increase in temperature as a consequence of global warming, and its temperature-limited forests will therefore be most affected (IPCC 2007). The increased CO_2 and temperature are expected to change forest productivity patterns, lengthen growing seasons, alter disturbance regimes, and change patterns of precipitation (Hogg & Hurdle 1995; Monserud *et al.* 2008). And the increased temperature along with prolonged droughts may lead to more intense pest infestations, fires and other environmental stresses that may cause considerable forest degradation and destruction. For example, between 2000 and 2003, harmful forest insect outbreaks in Canada and Siberia affected more than 20 million hectares of boreal forests. Area affected by bark beetles in British Columbia increased during 2002-2003, doubling to 4.2 million hectares (Berg & Henry 2003), from which the expected loss of timber is estimated to be CAN $20 billion. These effects will consequently influence ecological, economic, and cultural sustainability of the region (Bradshaw *et al.* 2009). Thus, it is very important and urgent to study the current and future community structure, biodiversity, functioning and dynamics of the boreal forest in response to human activities and climate change.

1.4 Thesis Outline and Objectives

To address the question of how natural and anthropogenic processes influence biodiversity and ecosystem functions in the boreal forests, I studied the spatial and temporal dynamics of boreal forest biomass and productivity, and the determinants of plant and bird diversity using the data from the ABMI (Alberta Biodiversity Monitoring Institute) program and PSPs (Permanent Sampling Plots) from Western Canada. By synthesizing results from direct field measurements and modeling methods, I studied the processes driving theses changes in the boreal forest and predict how the changes would respond to future climate scenarios and human activities. My Ph.D. thesis consists of four individual research chapters (Chapters 2-5). The major objectives of this work were to:

1) evaluate patterns of change in forest structure and dynamics at various spatial, temporal, and taxonomic levels ***(Chapters 2-5)***;
2) analyze possible causes driving tree growth and mortality ***(Chapter 2)***;
3) map spatial distributions of Alberta forest biomass carbon stock using a combination of forest inventory data and remote sensing data, and investigate the relationships between biomass and biotic and abiotic variables ***(Chapter 3)***;

4) use breeding bird species as an example to assess the relative importance of climate, human disturbance, and other environmental variables on determining biodiversity patterns ***(Chapter 4)***;
5) assess how human disturbance and evolutionary history of vascular plants structure boreal plant community assembly ***(Chapter 5)***.

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Figures

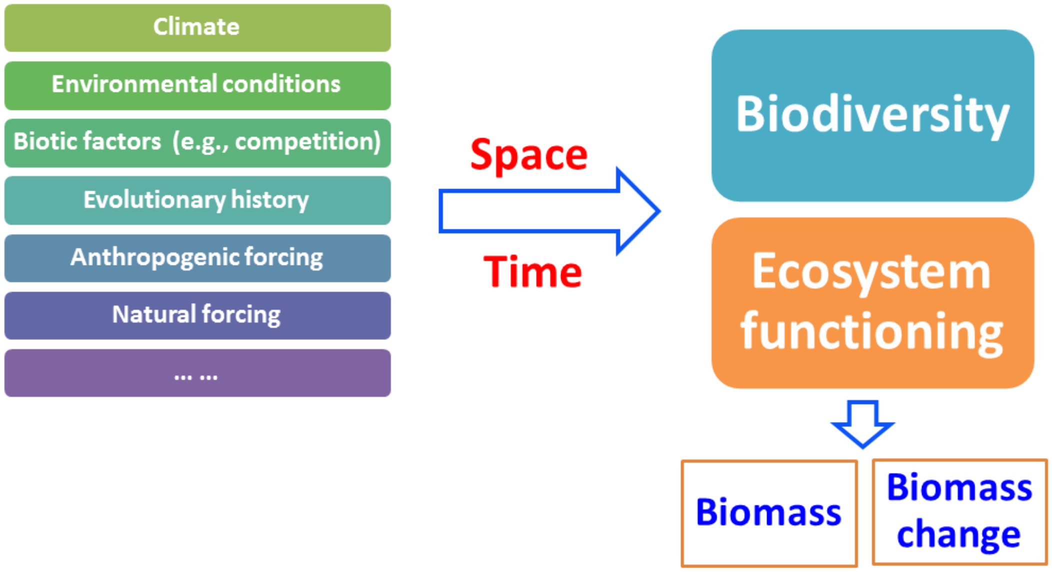

Figure 1.1 Biodiversity and ecosystem functioning

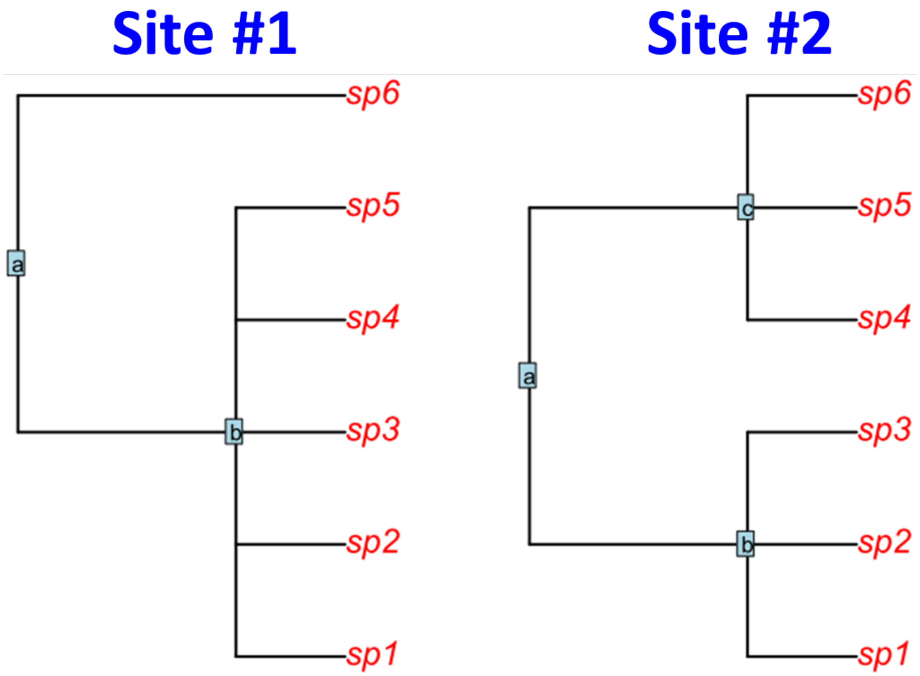

Figure 1.2 An example about how evolutionary history affects community assembly

Chapter 2 Half-century Evidence from Western Canada: Competition and Climate Together Drive Forest Dynamics in High Latitudes

Summary

Long-term demographic changes in tree mortality, growth, and recruitment are the fundamental mechanisms underlying the dynamics of forest stands. They are especially important for understanding the effects of climate change on forest ecosystems. Using a dataset of half-century observations (1958-2009) on 1,680 permanent sample plots in naturally regenerated forests in western Canada, I analyzed the changes in tree mortality, growth, and recruitment at the stand, species, and regional levels for understanding the possible drivers, especially climate and competition, underlying forest dynamics. I found that tree demographic rates changed markedly over the last five decades in western Canada. For all the trees across the plots, I observed a widespread, significant increase in tree mortality but a significant decrease in tree growth over the past five decades. These changes varied greatly, however, across tree size, forest age, ecozones and species. When possible causes of long-term forest dynamics were assessed, competition was the major contributor to changes on tree mortality, growth and recruitment. Regional climate change contributed to tree mortality patterns, but little to tree growth and recruitment, although demographic rates of

different tree species varied considerably in their sensitivity to climate and stand characteristics.

2.1 Introduction

Accurately describing patterns of tree mortality and growth over time and space is critical to understanding forest structure and dynamics and also important for biodiversity conservation and forest management (Franklin *et al.* 1987). Tree mortality and growth, to a great extent, are related to forest turnover (Phillips & Gentry 1994; Clark & Clark 1999), species coexistence (Condit *et al.* 2006; Gilbert *et al.* 2006), carbon and nutrient cycling (Franklin *et al.* 1987; Caspersen *et al.* 2000; McMahon *et al.* 2010), and forest responses to climate change (Feeley *et al.* 2007; van Mantgem *et al.* 2009). However, only a handful of studies have examined long-term changes in tree mortality and growth because of the lack of reliable, long-term datasets. There is also little consensus on forest changes over time and the explanations to the changes. For tree mortality, patterns of widespread increase have been documented in many previous studies in tropical forests (Phillips & Gentry 1994; Lewis *et al.* 2004a; Phillips *et al.* 2004; Laurance *et al.* 2009), temperate forests (van Mantgem & Stephenson 2007; van Mantgem *et al.* 2009; Dietze & Moorcroft 2011), and boreal forests (Michaelian *et al.* 2011; Peng *et al.* 2011), but the explanations to the changes are diverse and contradictory. For tree growth and recruitment, both increased and decreased trends over the last few decades have been documented in tropical forests (Clark *et al.* 2003; Lewis *et al.* 2004a; Feeley *et al.* 2007; Laurance *et al.* 2009), and temperate and boreal forests (McMahon *et al.* 2010; Silva *et al.* 2010; Ma *et al.* 2012).

Plant competition and climate change are considered two major, possible drivers of the changes of tree mortality and growth. Although several recent studies state that climate change on global or regional scales is the major driver of unusual changes of tree mortality and growth recently (Clark *et al.* 2003; Feeley *et al.* 2007; van Mantgem *et al.* 2009; McMahon *et al.* 2010; Peng *et al.* 2011), the roles of tree competition on the changes of demographic rates are often ignored or underestimated. Indeed, the relative contributions of competition and climate change on forest dynamics are rarely evaluated.

Forests in high latitudes account for more than one third of the earth's forested area and have profound influences on global climate change. High-latitude regions are also expected to experience the greatest increase in temperature as a consequence of global warming. Therefore, the forests in high latitudes, which are probably more vulnerable to climate change than those in low latitudes (IPCC 2007), should suffer most under the impacts of current and future climate change. Thus, it is urgent to understand the current and future forest structure, diversity, functioning and dynamics in high-latitude regions. How do forest structure and tree demographic rates change across space and time in these regions? Whether these dynamics are driven by global or regional climate change? If so, what are possible consequences of current and future climate change on long-term forest dynamics? In this study, I addressed these questions by analyzing a dataset collected from five decades of observations on permanent sample plots (PSPs) in undisturbed forest stands in western Canada. I am especially interested in assessing the long-term effects of climate change on high-latitude forests.

2.2 Materials and Methods

Study Area

The study was conducted in fire-originated forests in four provinces of western Canada (49°0’-59°43’N, 95°18’-127°54’W). The study region contains five of Canada’s eleven major forest ecozones.

Data Collection

The network of permanent sample plots (PSPs) in western Canada has maintained more than ten thousand PSPs established and re-censused by the governments and forest industries starting in the 1950s. The PSPs were established over different ecoregions, covering a wide range of densities, stand structures, species composition and site conditions throughout the forested areas. In this study, I limited analyses to the PSPs meeting the following seven criteria (Laurance *et al.* 2009; van Mantgem *et al.* 2009): (1) Only PSPs with no evidence of fire, tree cutting, or other manmade damage in the census periods in order to minimize transient dynamics associated with less severe disturbances; (2) Only PSPs in which the stand ages were larger than 50 years in the initial census, as estimated by counting rings of the largest trees, to minimize transient dynamics associated with stand development and succession; (3) All selected PSPs had at least three complete censuses, a requirement for comparing demographic rates from at least two different time intervals; (4) Only PSP with records of sufficient length (≥10 years of record between their first and last censuses) for detecting possible long-term dynamics; (5) Only trees with ≥ 9 cm DBH were selected for the current analysis to standardize the tree size used in this analysis across the four provinces and also in different census years; (6) Only PSPs with ⩾ 50 trees with ⩾ 9 cm DBH at their first census were assessed to reduce random variation in plot-level demographic rates; (7) Only PSPs with spatial location were selected in order to obtain climatic data for each plot.

Following these criteria, a total of 1,680 PSPs were selected to examine changes in forest structure and demographic rates in western Canada (Figure 2.1, Table 2.1). Plot sizes ranged from 400 m^2 (0.04 ha) to 8,092 m^2 (0.8092 ha) (mean: 0.14 ha). Within each plot, all standing trees with diameter at breast height (DBH) ⩾ 9 cm were tagged, recorded and remeasured at irregular time intervals. Generally, the remeasurement cycle is every 5 years for stands < 80 years old and every 10 years for older stands. The 1,680 PSPs contained 320,878 living trees over the study period. For individual plots, initial census year ranged from 1958 to 1999, and 85% of these plots were established before 1980 (Appendix 2A). Plots have been censused three to eight times (mean: ~3.8 times).

The spatial location of each individual tree was recorded in 143 of the 1,680 PSPs. These 143 PSPs were from Alberta and Manitoba. Each tree in these plots was tagged and mapped. The spatial information of each tree in these plots was used to calculate distance-dependent competition indices to test the contribution of competition on forest dynamics.

Climate Variables

Climate data for the PSPs were derived from the program ClimateWNA v4.62 and ClimatePP v3.21 (Wang *et al.* 2012). These programs use baseline climate data derived from monthly precipitation and temperature grids (Daly *et al.* 2008) based on interpolated climate data from weather stations for the period 1961-1990. Based on input values of longitude, latitude and elevation for the PSPs, the programs can calculate historical monthly, seasonal and annual climate variables for individual years and periods from 1901 to 2009. Details regarding the estimation of derived climate variables can be found in Wang *et al.* (2006). The following climatic variables were selected for initial consideration in the current study: mean warmest month temperature (°C, MWMT), mean coldest month temperature (°C, MCMT), mean annual precipitation (mm, MAP), degree-days above 5°C (DD5), mean annual temperature (MAT), mean annual summer precipitation (MSP), annual mean climate moisture index (CMI), and annual moisture index (AMI).

To test if tree mortality and growth are caused by drought (climatic water deficits), two drought related indices, CMI (the annual climate moisture index) and AMI (Annual moisture index), were also calculated. Monthly CMI values were calculated as monthly precipitation minus PET, where PET is the potential evapotranspiration, which is estimated from maximum monthly temperature (T_{max}), minimum monthly temperature (T_{min}), and elevation (Hogg 1997). Annual CMI was calculated by summing the monthly CMI values from January through December. Positive CMI values indicate relatively moist conditions and negative

CMI values indicate relatively dry conditions. AMI is defined as the ratio of the annual number of degree-days above 5°C to the mean annual precipitation (Rehfeldt *et al.* 2006). Large values of AMI indicate dry conditions due to high heat (thus, high evaporative demand) relative to the available moisture, whereas low values of AMI represent relatively wet conditions.

There was a high degree of intercorrelation among the initially selected climate variables (Appendix 2B). To minimize problems with multicollinearity, I analyzed pair-wised correlations among different climate variables, and selected three variables, MWMT, MWCT and MAP, based on the results of correlations, VIF (variance inflation factor), and biological consideration. Several of the highly correlated climate variables were not used in the models. For example, MAT was highly correlated with MCMT (*Pearson correlation coefficient,* $r = 0.80$), and MWMT was highly correlated with DD5 (*Pearson correlation coefficient,* $r = 0.71$). Also, CMI and AMI were greatly correlated with the MAP (Figure 2.7, *Pearson correlation coefficient,* r = 0.91 and -0.79, respectively). To model the changes in tree demographic rates as a function of climatic variables, I averaged each of these annual climatic variables across all years within each census interval for a given plot.

Competition Measures

To assess the effect of competition on tree growth and mortality, I selected five common competition indices to measure competition at the stand level. Both distance-independent and distance-dependent competition indices were selected. The five competition indices are defined as follows:

1) Stand basal area (BA): I used BA as a surrogate for stand crowding of each plot, since it combines both tree size and density. Stand crowding determines the average resource availability for trees within a stand. Higher stand crowding suggests fewer resources available per individual. BA is considered one of the best competition indices and is widely used in the literature (e.g., van Mantgem *et al.* 2009; Luo & Chen 2011).
2) Basal area of larger trees (BAL): The BAL has been commonly used to capture one-sided (asymmetric) competition in modeling tree growth and mortality. In one-sided competition, larger trees are at a competitive advantage over smaller trees, but smaller neighbors do not affect the growth and survival of larger trees (Cannell *et al.* 1984).
3) Stand density index (SDI): This index, first developed by Reineke (1933), is defined as the degree of crowding within stocked areas. It is a measure of the stocking of a stand of trees based on the number of trees per unit area and the diameter at breast height of the tree of average basal area.

   $$\text{SDI} = N \times \left(\frac{DBH_{mean}}{25.4}\right)^{1.605}$$

   where N represents trees per hectare, and DBH_{mean} represents the quadratic mean diameter by centimeter.
4) The ratio of focal species basal area to stand basal area (RBA): For the analyses at the species level, the effects of species interactions were considered. RBA = BA_i/BA, where BA_i is the basal area of the ith species group, and BA is the stand basal area.

5) Hegyi index (Distance-dependent competition index): In addition to the above distance-independent competition indices, I also assessed how distance-dependent competition index affects the changes of tree demographic rates. Hegyi index takes into account the distances of the competitors (*j*) to the subject tree (*i*) as well as the sizes of the subject tree and its competitors (Hegyi 1974):

   $$H = \sum_{j \neq i} \frac{DBH_j}{DBH_i \times Dist_{ij}}$$

   The index was calculated at the radii of 10 meter and 5 meter. To correct for edge effects, the index was weighted using an area-weighted edge correction (Das *et al.* 2008). For instance, for a subject tree that was within 10 m of the plot edge, its Hegyi index value would be divided by the proportion of a 10 m radius circle that lies inside the plot boundaries. Accoriding to Das *et al.* (2008)’s suggestion, if only 30% of the 10 m radius circle centered around a given tree was within the plot, the raw index value for that tree would be divided by 0.30.

Data Analysis

Changes of tree demographic rates (mortality, growth and recruitment rates) over time were analyzed in the stand-, species- and regional-levels. To assess how changes varied with stand age, I divided the PSPs data into three stand age groups, the plots with the initial stand age 50-80 years (immature forest), 80-120 years (mature forest) and ≥ 120 years (old-growth forest). Also, I divided the PSPs into different groups based on three DBH classes and three elevation gradients to assess how forest structures and demographic rates changed with tree size and plot elevation. Three DBH classes included all trees (DBH ≥ 9 cm), small trees (DBH 9-20 cm) and large trees (DBH ≥ 20 cm). Three elevation gradients included low (< 500 m), middle (500-1000 m) and high (≥ 1000 m) elevations. Possible interactions between competition and climatic variables were also considered. However, these interactions had relatively smaller influences of interactions over changes of tree demographic rates (Figure 2.8), so they were not included in the final models I showed here.

Statistical Models

Linear mixed models (LMM) were used for modelling temporal trends of tree growth on the stand and species levels. Mean annual tree growth rate was calculated as relative annual growth in total basal area at both the stand and species levels, where the growth rate = $\log(BA_{census2})-\log(BA_{census1})]/[time_2-time_1]$, and $time_2$ and $time_1$ are the respective census dates (in years). Absolute annual growth rates in total basal area were also calculated and analysed. I found very similar results from both relative and absolute growth rates, so I only reported the result of relative growth rates. A normal random effect based on plot identity was added to account for differences among study plots.

I used generalized nonlinear mixed models (GNMMs) (van Mantgem *et al.* 2009) to assess trends of tree mortality and recruitment across multiple plots in four provinces and four main ecozones. Mortality and recruitment rates were estimated by annual compounding over the census interval length. All parameters were estimated by maximum likelihood. A normal random effect based on plot identity was added to account for differences among study plots. Specifically, I modelled the rate as a logistic function: $\exp(\beta_0 + \beta_1 t_j + \gamma_i)/(1 + \exp(\beta_0 + \beta_1 t_j + \gamma_i))$, to estimate changes in annual mortality rates, and applied a statistical model to my data where n_{ij} was the number of trees alive at the previous census for the *i*th plot and the *j*th census, and m_{ij} the corresponding count of mortalities:

$m_{ij}|\gamma_i$ ~ Negative binomial with mean $n_{ij}\,p_{ij}$ and variance $n_{ij}\,p_{ij}\left(\dfrac{n_{ij}\,p_{ij} + \alpha^{-1}}{\alpha^{-1}}\right)$

$$p_{ij} = 1 - (1 + \exp(\beta_0 + \beta_1 t_j + \gamma_i))^{-c_j},\ \ \gamma_i \sim N(0, \sigma_\gamma^2)$$

where p_{ij} represents the probability of mortality over the census interval, t_j represents the year of the *j*th census, and *c* represents the census interval length in years. The random parameter (γ_i) follows a normal distribution.

I modeled annual recruitment rates of trees with ≥ 9 cm DBH as $\exp(\beta_0 + \beta_1 t_j + \gamma_i)$ and applied a similar statistical model where r_{ij} is the count of recruits:

$r_{ij}|\gamma_i$ ~ Negative binomial with mean $n_{ij}\,p_{ij}$ and variance $n_{ij}\,p_{ij}\left(\dfrac{n_{ij}\,p_{ij} + \alpha^{-1}}{\alpha^{-1}}\right)$

$$p_{ij} = (1 + \exp(\beta_0 + \beta_1 t_j + \gamma_i))^{c_j} - 1,\ \ \gamma_i \sim N(0, \sigma_\gamma^2)$$

where p_{ij} represents the rate of recruitment over the census interval.

Assessing Possible Drivers of Changes

I sought measurements or indices of endogenous and exogenous factors potentially capable of affecting long-term changes in tree demographic rates (van Mantgem *et al.* 2009). The endogenous factor of the greatest interest was competition within stands. Exogenous factor of interest was changing climate. To test whether there was a relationship between changes in demographic rates and regional climatic variables, I correlated the rates with climatic variables measured over the corresponding census periods.

Relationships between tree growth and possible drivers of changes were estimated using the LMM at both the stand- and species-levels. Relationships between annual mortality and recruitment rates and possible drivers of changes were estimated using the GNMMs at both the stand- and species-levels.

I analyzed the changes of tree demographic rates (mortality, growth and recruitment rates) over time at the stand, species, and regional levels, and assessed how changes varied with stand age, tree size, plot elevation, ecozones, and provinces by dividing these plots into different groups. Two major explanatory variables, competition and regional climate change, were considered in my analyses. For measuring tree competition, I used both distance-independent and distance-dependent indices to test how different measures of competition were related to forest dynamics. For climatic variables, I selected three variables, including mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), and mean annual precipitation (MAP). The possible interactions between competition and climatic variables (Gilman *et al.* 2010) were also considered in my models. I didn’t detect strong interactions between competition and climatic variables (Appendix 2C), so I didn’t show the result here.

2.3 Results

Temporal Changes of Tree Mortality

I observed significant increases in tree mortality in the last five decades (Figure 2.2). Tree mortality increased for all plots combined, for the plots within different successional stages (immature, mature, and old-growth forests), for all four provinces, for four ecozones, for three elevational classes, and for small (DBH 9-20 cm) and large (DBH > 20 cm) trees ($P < 0.0001$, generalized nonlinear mixed model (GNMM)). Among the four provinces, Saskatchewan showed the greatest increases in tree mortality in the last 50 years, and Monitoba recorded a steeper increase over a short period (1986-2009) of record.

Temporal Changes of Tree Growth and Recruitment

Tree relative basal area growth rates of all plots combined declined significantly ($P < 0.001$, linear mixed model (LMM), Figure 2.3). Plots in immature and mature forests also showed decreased tree growth ($P < 0.001$), while the plots in the old-growth forests didn't show significant changes in the recent five decades ($P = 0.0401$). Three of the four provinces, British Columbia, Alberta and Saskatchewan, showed significantly decreased growth ($P < 0.001$), while Manitoba showed no clear trend on tree growth over time ($P < 0.5756$). When I divided the plots into different ecozones, the boreal plain and the montane cordillera showed decreasing growth rates ($P < 0.001$), and the boreal shield and the taiga plain didn't show a clear trend.

In contrast to tree mortality and growth rates, recruitment rates for trees with ≥ 9 cm DBH generally decreased or did not show significant change over time (Figure 2.4). Across all plots, decreasing recruitment rates were detected when all plots were combined ($P < 0.0001$, GNMM). Decreasing recruitment rates were also found in immature ($P < 0.0001$) and mature ($P = 0.0038$) forests, while no significant change in old-growth forests ($P = 0.5074$). Among the four provinces, British Columbia and Manitoba showed decreasing tree recruitment ($P < 0.0011$), while Alberta and Saskatchewan showed no clear change over time. In four ecozones, only the montane cordillera ecozone showed very significant decreasing tree recruitment ($P < 0.0001$).

Species-level Responses on Tree Mortality, Growth and Recruitment

Increasing mortality rates of all trees were also detected at the species level (Figure 2.2). Significantly increasing mortality was found for seven of the nine main tree species in western Canada ($P < 0.0001$, GNMM). Among these tree species, balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), white birch (*Birch papyrifera*), and balsam fir (*Abies balsamea*) showed the highest mortality rates.

At the species level, four conifer species, lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*), showed decreases in growth rates across all plots, while balsam fir showed no clear trend (Figure 2.3).

At the species level, five of the nine tree species, trembling aspen, lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), black spruce and white spruce, showed significantly declined rates in recruitment rates ($P < 0.0001$), balsam fir showed significant increases in recruitment rates ($P = 0.0167$), and jack pine, white birch and balsam poplar show no clear changes in recruitment (Figure 2.4).

Drivers of Temporal Changes on Tree Mortality

To explore possible drivers of the changes of tree demographic rates, I examined correlations of the demographic rates with climatic variables and tree competition. Most climatic variables showed significant changes in the four provinces over the last five decades, although there were strong inter-annual variations (Figure 2.5). MWMT increased in three of four provinces ($P < 0.0004$, LMM), except for British Columbia ($P = 0.1426$, LMM). MCMT appeared to be increasing significantly in the four provinces ($P < 0.0001$, LMM). MAP declined in British Columbia and Alberta ($P < 0.0001$, LMM) and increased in Saskatchewan and Manitoba ($P < 0.0007$, LMM).

For tree mortality, I found consistent, strong effects of competition on changes in mortality over the last five decades (Figure 2.6 and 2.7). In all the analyses across the entire study zone, stand age groups, tree size, provinces, elevations and ecozones, about 80% of 144 analyzed groups showed that tree mortality was significantly positively correlated with stand basal area (a competition index). Two other competition indices, stand density index (SDI) and basal area of larger trees (BAL) were also positively related to tree mortality in most of the analyzed groups. However, for the 143 stem-mapped PSP, distance-dependent competition index (Hegyi index) didn't show strong effects on tree mortality (Figure 2.8).

At the species level, different species varied considerably in their responses to competition and climatic variables (Figure 2.9). For tree mortality, four conifer species (two pines and two spruces) showed strong relationships with stand basal area. Inter-specific competition, measured by relative basal area (RBA), had weak effects on tree mortality for most species. The effects of climatic variables on tree mortality varied widely with species.

Drivers of Temporal Changes on Tree Growth and Recruitment

For tree growth rates, I detected strongly negative relationships with tree competition in over 90% of analyzed groups (Figure 2.6 and 2.7), suggesting that competition was a main factor limiting tree growth. By comparison, all three climate variables showed significant correlations with tree growth in only around 50% of 144 analyzed groups (Figure 2.6). MWMT and MAP had minor effects on tree growth, while MCMT was generally negatively correlated with tree growth in the observed significant groups.

For tree recruitment rates, I also detected strong effects of competition on these rates in almost all analyzed groups (Figure 2.6 and 2.7). The effects of climate variables on tree recruitment were relatively weak. Only MAP showed significant correlations for about 50% of analyzed groups.

At the species level, for tree growth, all nine tree species showed significant correlations with stand-level competition (Figure 2.9). Inter-specific competition had strong effects on tree growth for black spruce, white spruce, balsam fir and Douglas-fir, while the effects of inter-specific competition were weak for other tree species. The effects of climate change on tree growth were weak for all nine tree species.

For species-level tree recruitment, stand basal area showed significant correlations for all nine species (Figure 2.9). Inter-specific competition also had strong limitations on tree recruitment for balsam fir, Douglas-fir, white spruce and white birch. The effects of climate change on tree recruitment were weak for most tree species.

2.4 Discussion

Using a dataset of long-term repeated measurements, covering a wide range of stand types over a large geographical area, I found that forest dynamics changed markedly over the last five decades in high-latitude forests in western Canada. When possible causes of long-term forest dynamics were assessed, I found that competition was the primary driver in determining tree mortality, growth and recruitment dynamics, followed by the regional climate change. Climate was one of the most likely drivers of the changes on tree mortality, but its effects on tree growth and recruitment were limited compared to those of competition.

Recent studies have found increases in the long-term average mortality rate in old-growth forests (Smith *et al.* 2005; van Mantgem & Stephenson 2007; van Mantgem *et al.* 2009). In this study, I found competition indices were significantly correlated with changes in mortality rate. My findings are in accordance with those from other long-term inventory-based mortality studies in temperate forests (Das *et al.* 2008) and boreal forests (Kenkel *et al.* 1997; Luo &

Chen 2011) but was in contrast with studies that suggested competition was not correlated with changes in mortality rate in old-growth temperate forests (van Mantgem *et al.* 2009) and mature boreal forests (Peng *et al.* 2011). These contradictory results are possibly caused by inadequate consideration of tree competition. Both van Mantgem *et al.* (2009) and Peng *et al.* (2011) expressed mortality as a function of only climate variables (i.e., mortality = f(climate variables)). They also used a much smaller dataset (76 plots in van Mantgem *et al.* 2009 and 96 plots in Peng *et al.* 2011) and didn't include any variables directly related to competition into their climate-related models.

For tree mortality, I found strong evidence of climate change resulting in increasing rates of mortality in last five decades (Figure 2.6 and 2.7). Nearly 80% of 144 analyzed groups showed significantly positive correlations between summer temperature (MWMT) and tree mortality. Increased summer temperature may lead to higher respiration costs, higher heat stress (e.g., drought), and higher risk of cavitation (McDowell *et al.* 2008, Allen *et al.* 2010), and thus higher tree mortality rates. This result was similar with previous studies in tropical (Phillips *et al.* 2004; Lewis *et al.* 2004), temperate (van Mantgem *et al.* 2009) and boreal forests (Peng *et al.* 2011). However, it is noteworthy to mention that these previous studies used mean annual temperate (MAT), not MWMT, for their analyses. In my study region, MAT is closely related to MCMT, not MWMT (Appendix 2B). Because of the large differences between summer and winter temperatures in high latitudes, it is better to use these two variables, not the annual average. Winter temperature (MCMT) showed negative correlations with tree mortality, suggesting tree mortality decreased as the winter became warmer. One possible reason is an increase in frost damage in warmer winters (Hänninen 1991).

For precipitation, I didn't detect clear, consistent correlations with tree mortality. Relationships varied greatly in different analyzed groups. Two drought-related indices, annual moisture index (AMI) and annual mean climate moisture index (CMI), were highly related to MAP (Appendix 2B), and they should have the similar trends with MAP. Thus, I found no clear evidence for drought-induced tree mortality in western Canada. However, drought-induced tree mortality was detected in several recent studies in Western Canada (e.g., Hogg *et al.* 2008; Allen *et al.* 2010; Michaelian *et al.* 2011; Ma *et al.* 2012). Further analysis is needed to better understand how drought affects tree mortality in the boreal.

A growing body of scientific literature suggests that western Canada will undergo significant changes over the course of this century as a consequence of global warming. Taking the province Alberta for instance, Barrow and Yu (2005) predicted that, under several climate change scenarios for Alberta, mean annual temperature is expected to rise 3-5^{o}C by the 2050s, with degree-days above 5°C increasing 30-50% and dryness index increasing 20-30%. Thus, regional climate change in western Canada will have major impacts on forest conservation and management. A recent modeling study in managed forests of Canada forecasted that, climate-related increases in fire and insect disturbance are going to turn these forests from a net carbon sink into a net carbon source (Kurz *et al.* 2008).

One possible limitation of this study is that other factors such as time lags, legacy effects, and the potential for ephemeral climate events (e.g. storms or low-temperature anomalies) to have lasting effects, will hinder efforts to link forest dynamics confidently to climate phenomena (Laurance *et* *al.* 2009). Although I only selected the PSPs without large-scale natural or human disturbances, the effects of small-scale disturbances, such as soil water deficit, forest insect outbreaks and diseases, still exist. These effects may have major impacts on tree growth, mortality and recruitment at different stand development stages. Overall, there are many uncertainties in our understanding of forest dynamics under current and future climate change, particularly with regard to possible mechanisms that drive forest dynamics.

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Tables

Table 2.1 Summary of plot characteristics and climate variables in 1,680 permanent sample plots in western Canada

	Basic characteristics of permanent sample plots				**Climatic variables (1958-2009)**		
	No. of Plots	**Census Years**	**Live trees (≥ 9 cm DBH) at the first census**	**Species composition ≥ 10% of trees (the first census)**	**MWMT (℃)**	**MCMT (℃)**	**MAP (mm)**
Total	1680	1958-2009	271809	PL (33%), SW (19%), AW (14%)	15.45±1.86	-12.68±6.33	593.35±185.23
Province							
British Columbia	777	1960-2009	86779	PL (37%), FD (22%), AW (10%)	15.31±1.86	-8.76±4.07	653.03±210.41
Alberta	563	1960-2009	148314	PL (39%), SW (22%), AW (15%), SB (10%)	14.64±1.43	-13.73±5.52	586.46±150.42
Saskatchewan	290	1958-2009	32621	SW (40%), AW (22%), SB (16%), PJ (16%)	17.10±1.14	-20.33±4.15	456.71±64.46
Manitoba	50	1986-2009	4095	SB (40%), PJ (22%), AW (15%)	18.20±1.61	-19.67±4.02	506.23±88.34
Initial stand age group							
50-80 yrs	903	1958-2009	132288	PL (42%), AW (16%), SW (12%)	15.39±1.89	-12.37±6.14	601.70±172.05
80-120 yrs	539	1958-2009	86028	PL (27%), SW (22%), AW (15%), FD (11%)	15.86±1.74	-12.49±6.65	583.88±211.91
≥ 80 yrs	777	1958-2009	139521	SW (27%), PL (25%), AW (13%), SB (12%)	15.52±1.81	-13.03±6.53	583.68±198.97
≥ 120 yrs	238	1960-2009	53493	SW (33%), PL (22%), SB (16%), FB (10%)	14.76±1.73	-14.26±6.08	583.22±166.06
Ecozones							
Boreal Plain	804	1958-2009	166677	PL (32%), SW (24%), AW (17%), SB (13%)	15.68±1.71	-16.16±5.83	526.07±117.99
Montane Cordillera	791	1960-2009	89634	PL (38%), FD (21%), AW (9%)	15.18±1.96	-8.86±4.10	666.62±215.16
Boreal Shield	29	1981-2009	2449	SB (35%), PJ (33%), AW (9%)	18.01±1.79	-20.08±4.53	544.55±85.20
Taiga Plain	29	1966-2004	10049	SW (52%), AW (18%), PL (14%)	15.37±1.50	-20.63±5.75	434.10±104.68

Figures

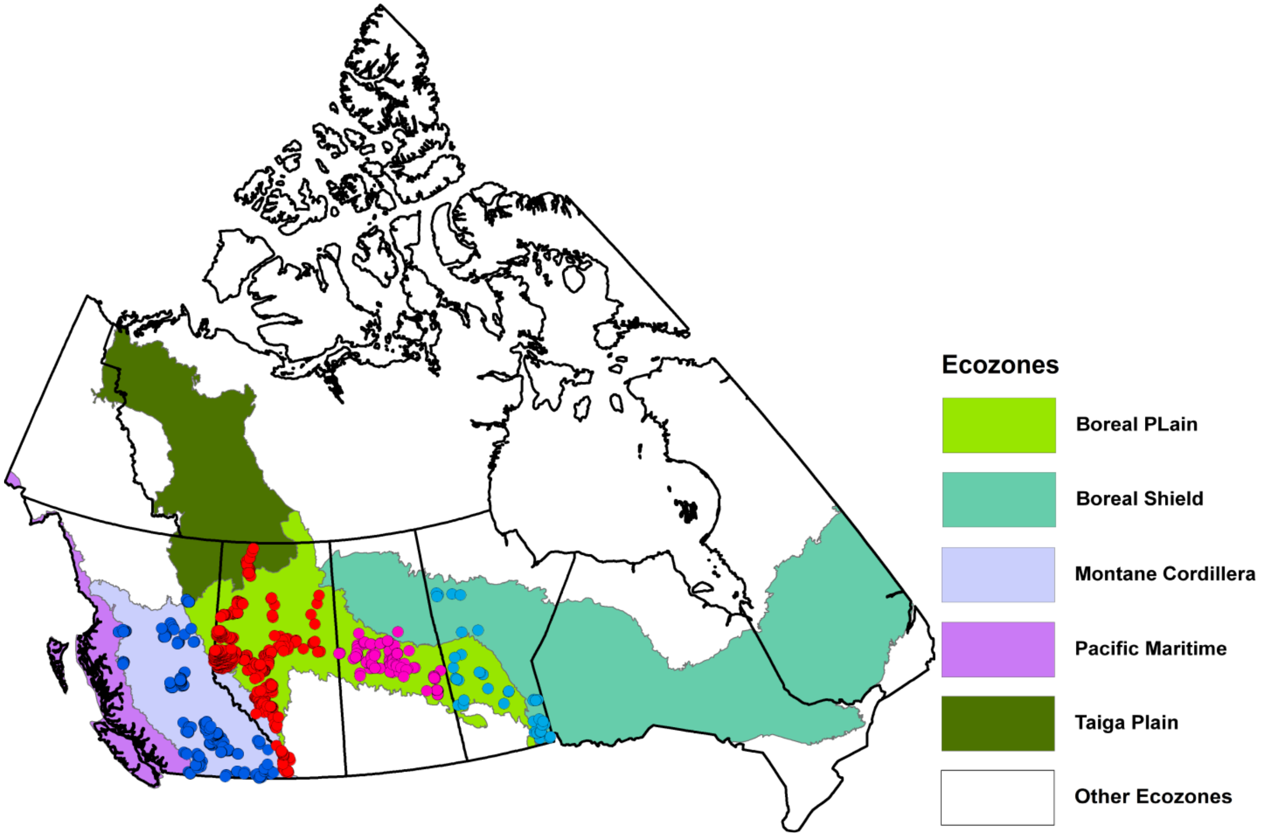


Figure 2.1 Locations of 1,680 permanent sample plots in western Canada

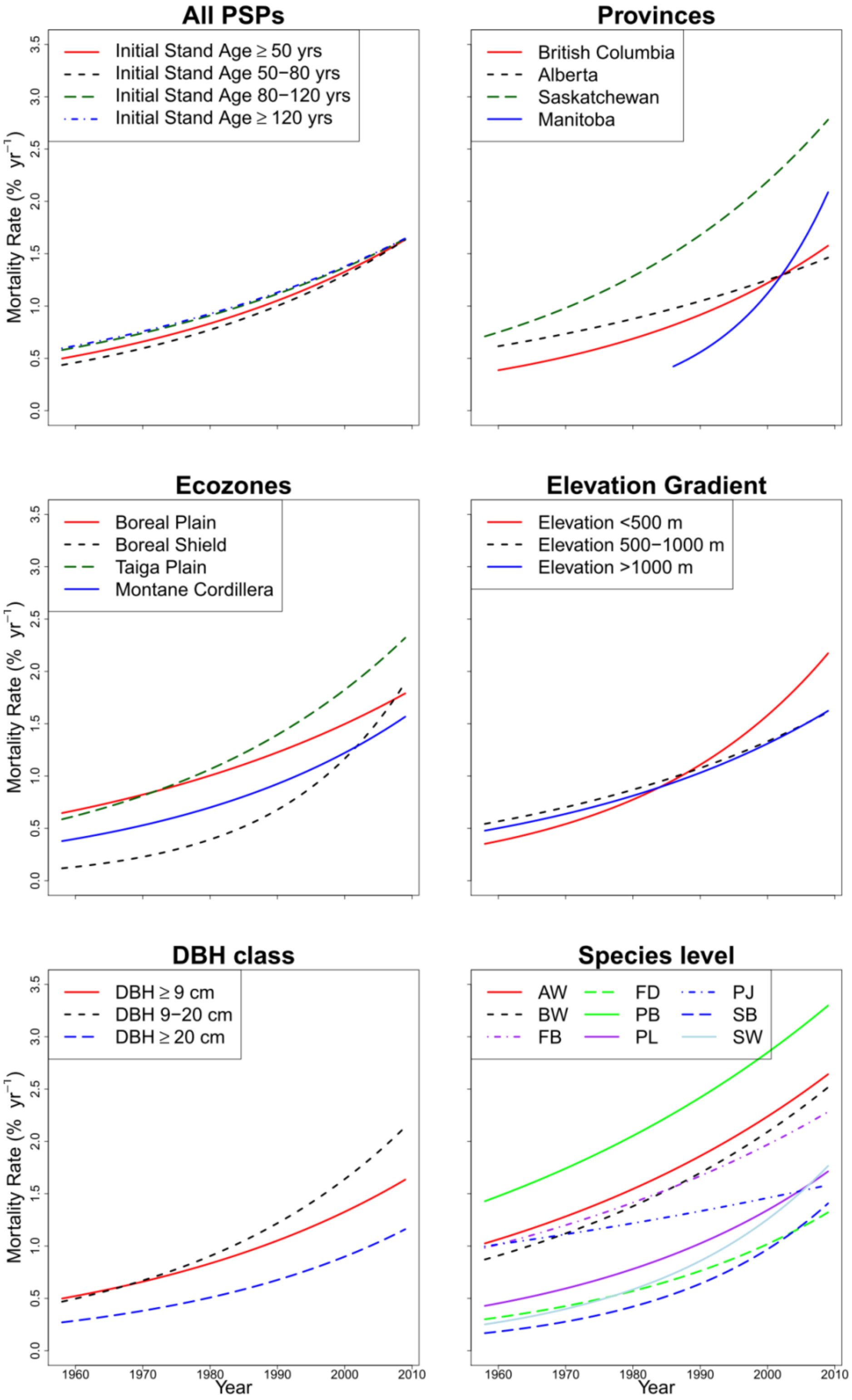


Figure 2.2 Modeled trends (1958-2009) of tree mortality rates

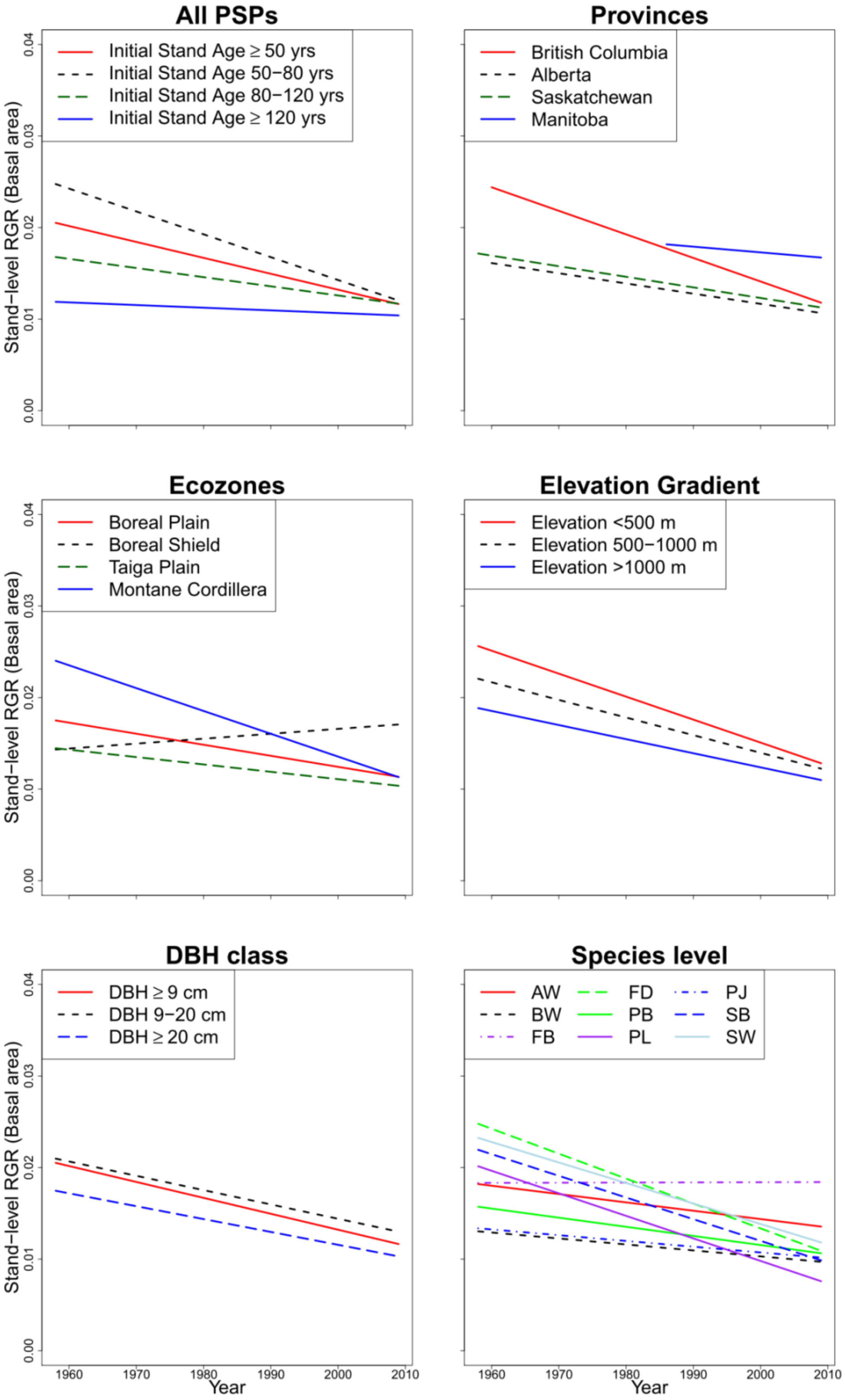


Figure 2.3 Modeled trends (1958-2009) of relative basal area growth rates

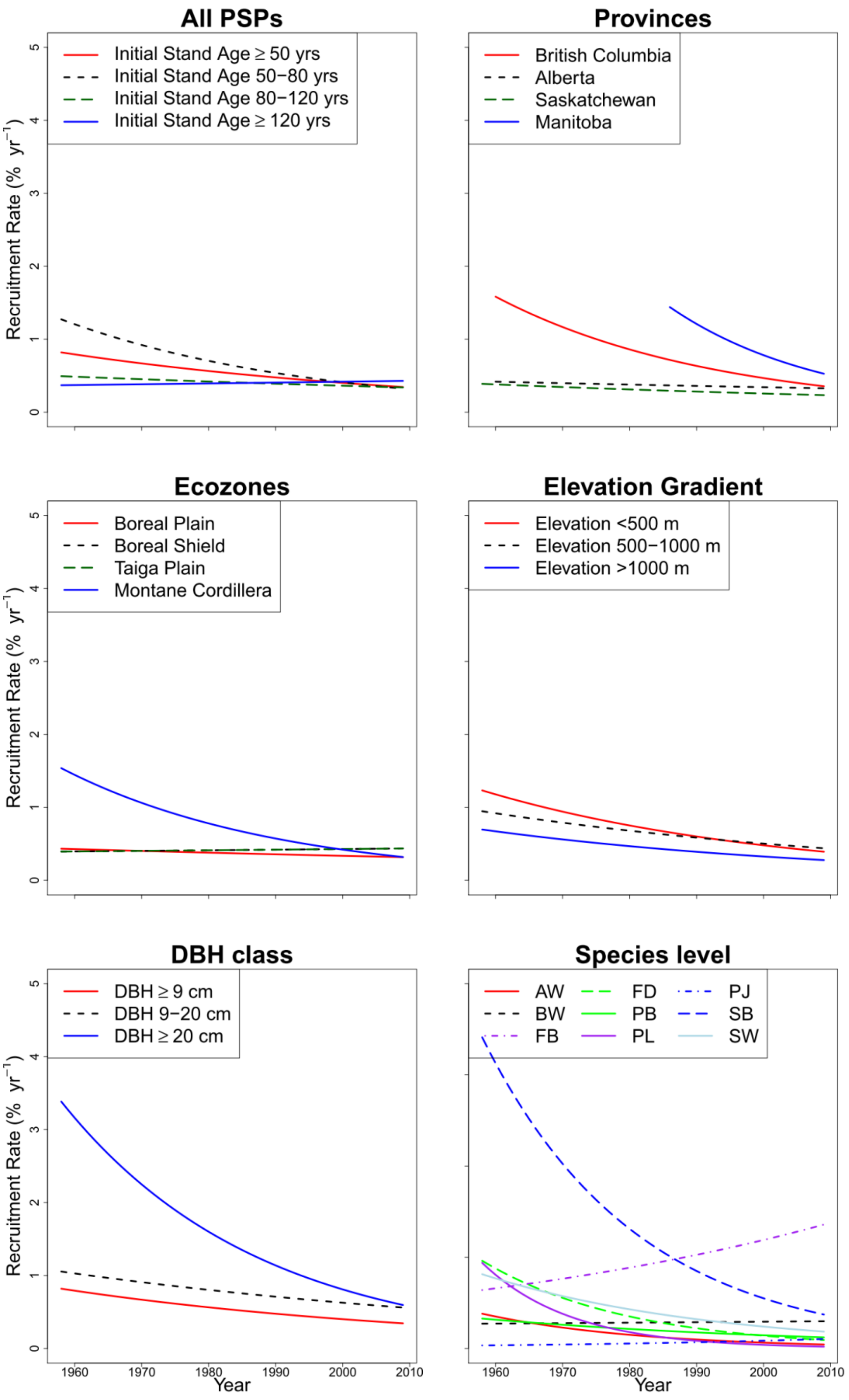


Figure 2.4 Modeled trends (1958-2009) of recruitment rates for trees with ≥ 9 cm DBH

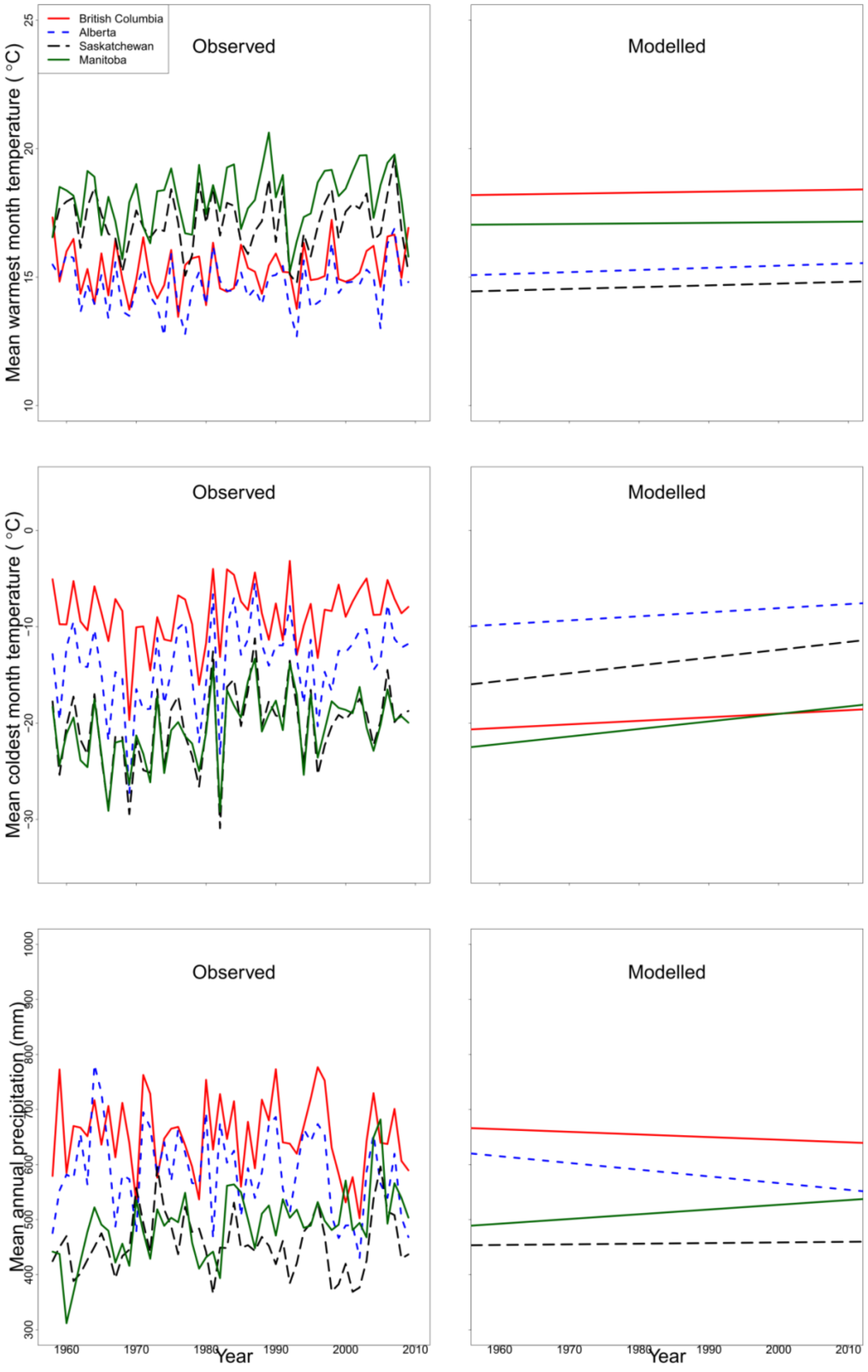


Figure 2.5 Temporal changes of three selected climatic variables (mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), and mean annual precipitation (MAP)) from 1958 to 2009 in forest regions of four provinces in western Canada

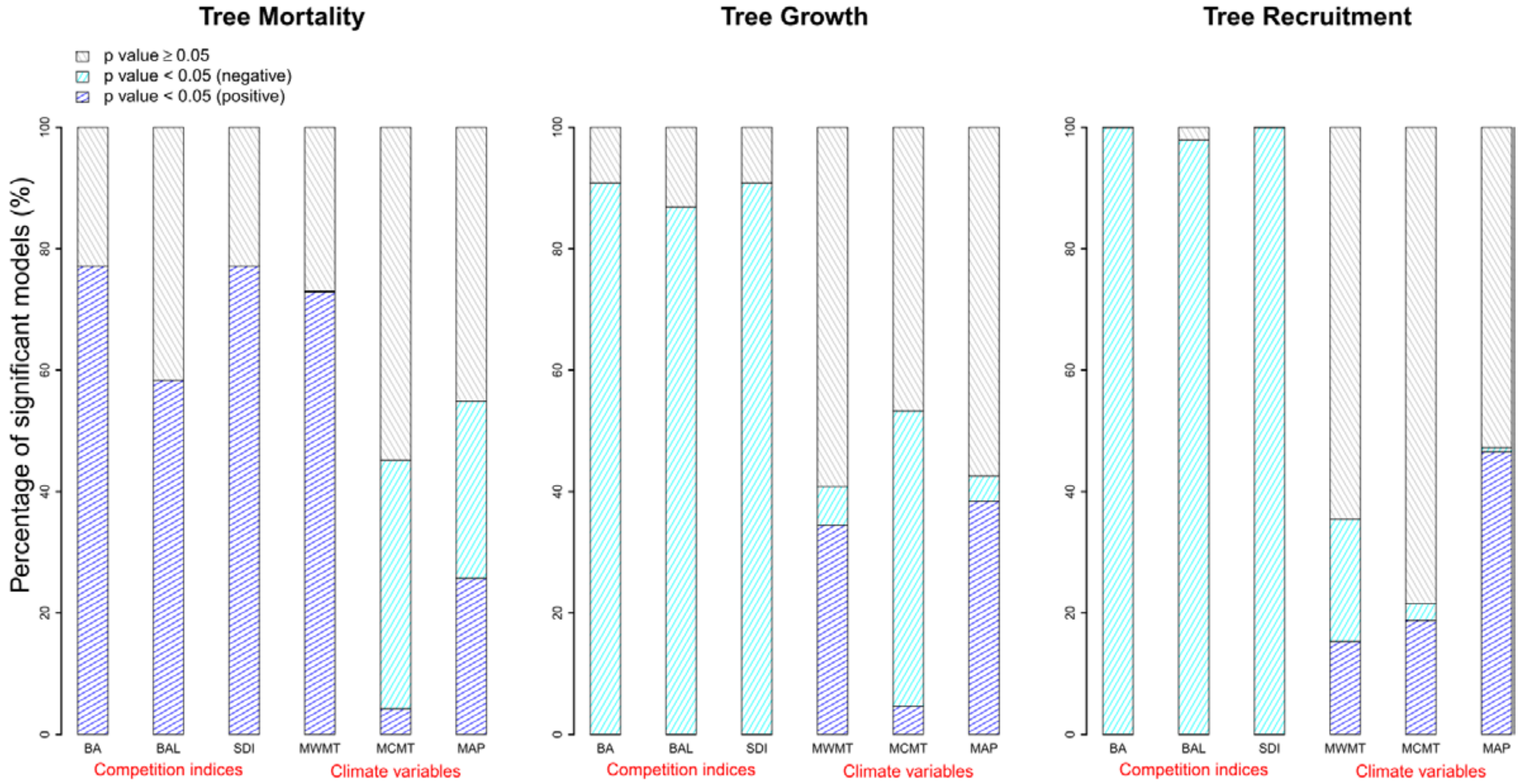


Figure 2.6 Summary of the relationships among tree demographic rates, competition and climate at stand level

***NOTE**:* Only the modeled results with ≥20 plots were included in the summary. BA: stand basal area; BAL: basal area of larger trees; SDI: stand density index; RBA: the ratio of focal species basal area to stand basal area; MWMT: mean warmest month temperature; MCMT: mean coldest month temperature; MAP: mean annual precipitation. Tree recruitment rates were calculated for only trees with DBH ≥9 cm.

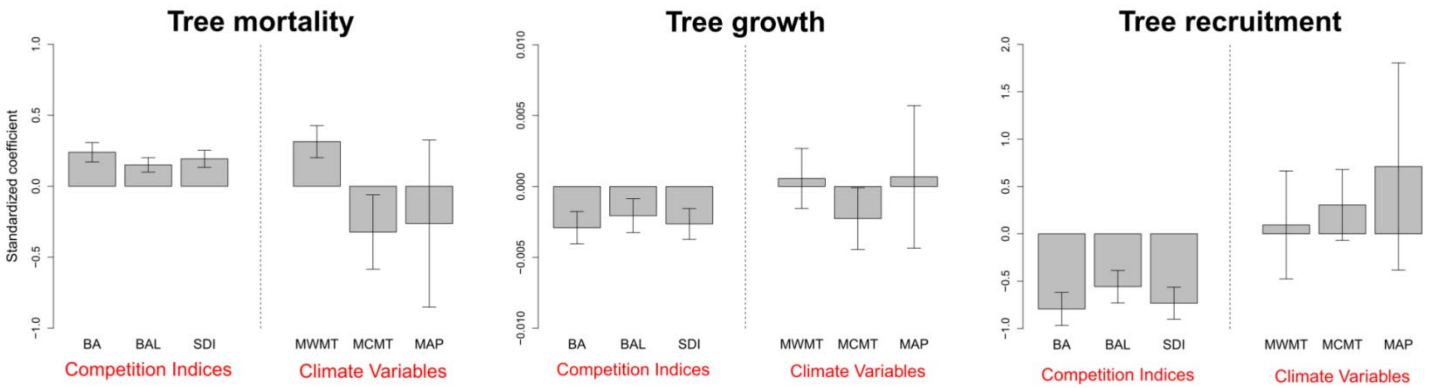


Figure 2.7 Summary of standardized regression coefficients between tree demographic rates with competition indices and climate variables at the stand level

NOTE*:* Other symbols and explanations are as in Figure 2.6.

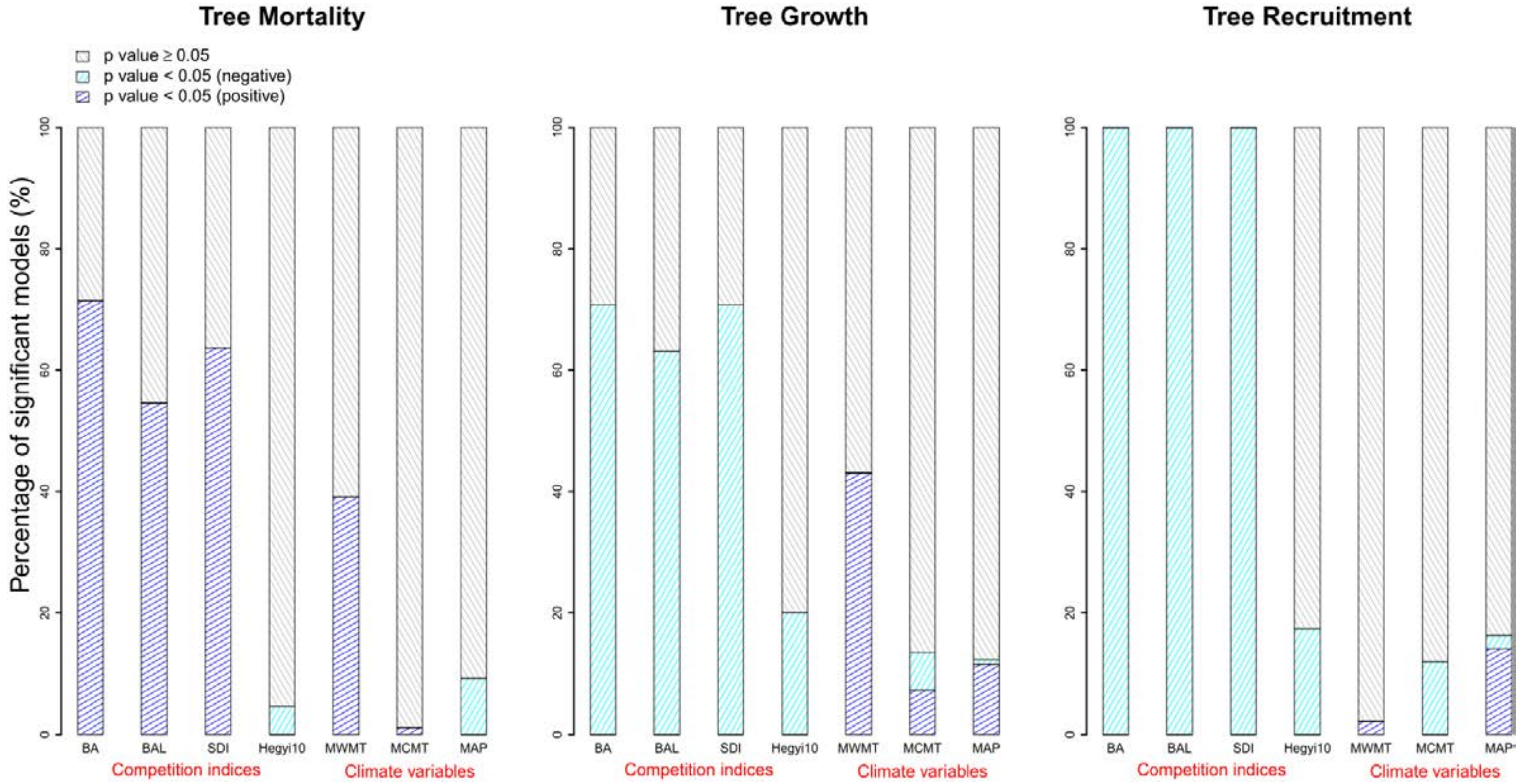


Figure 2.8 Summary of the relationships among tree demographic rates, competition and climate at stand-level for the 143 PSPs with spatial information

***NOTE**:* Only the modeled results with ≥20 plots were included. Other symbols and explanations are as in Figure 2.6.

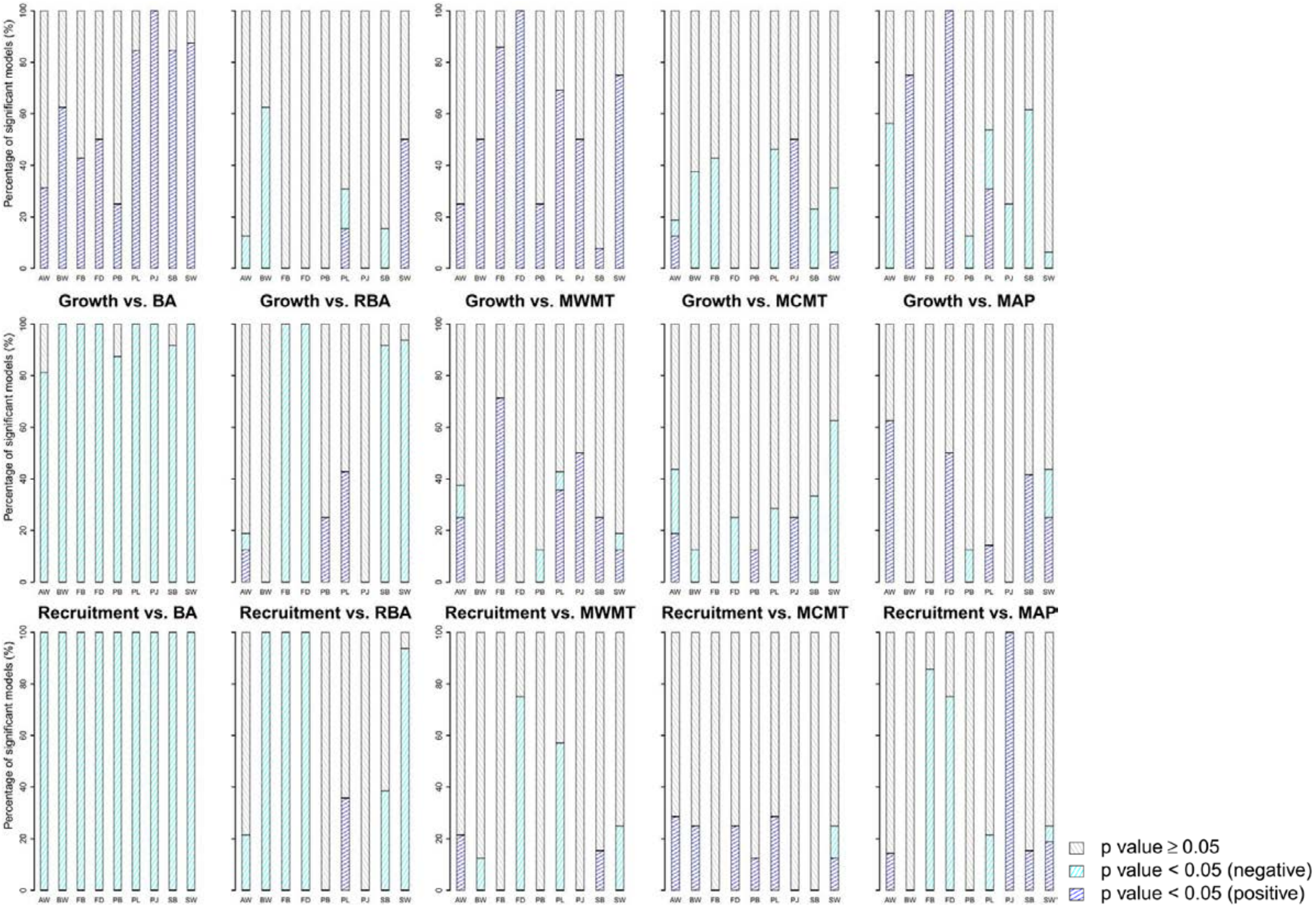
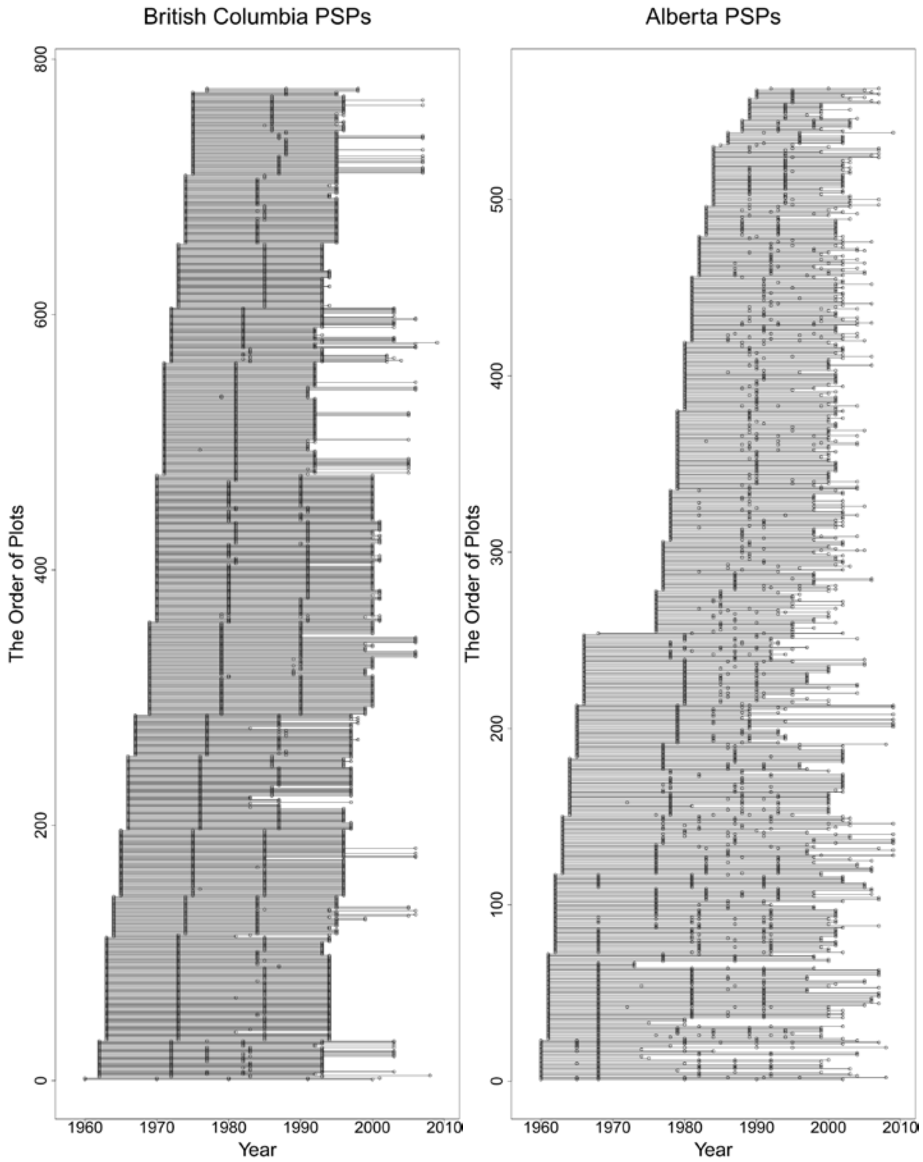


Figure 2.9 Species-level summary of tree demographic rates of 9 tree species over time

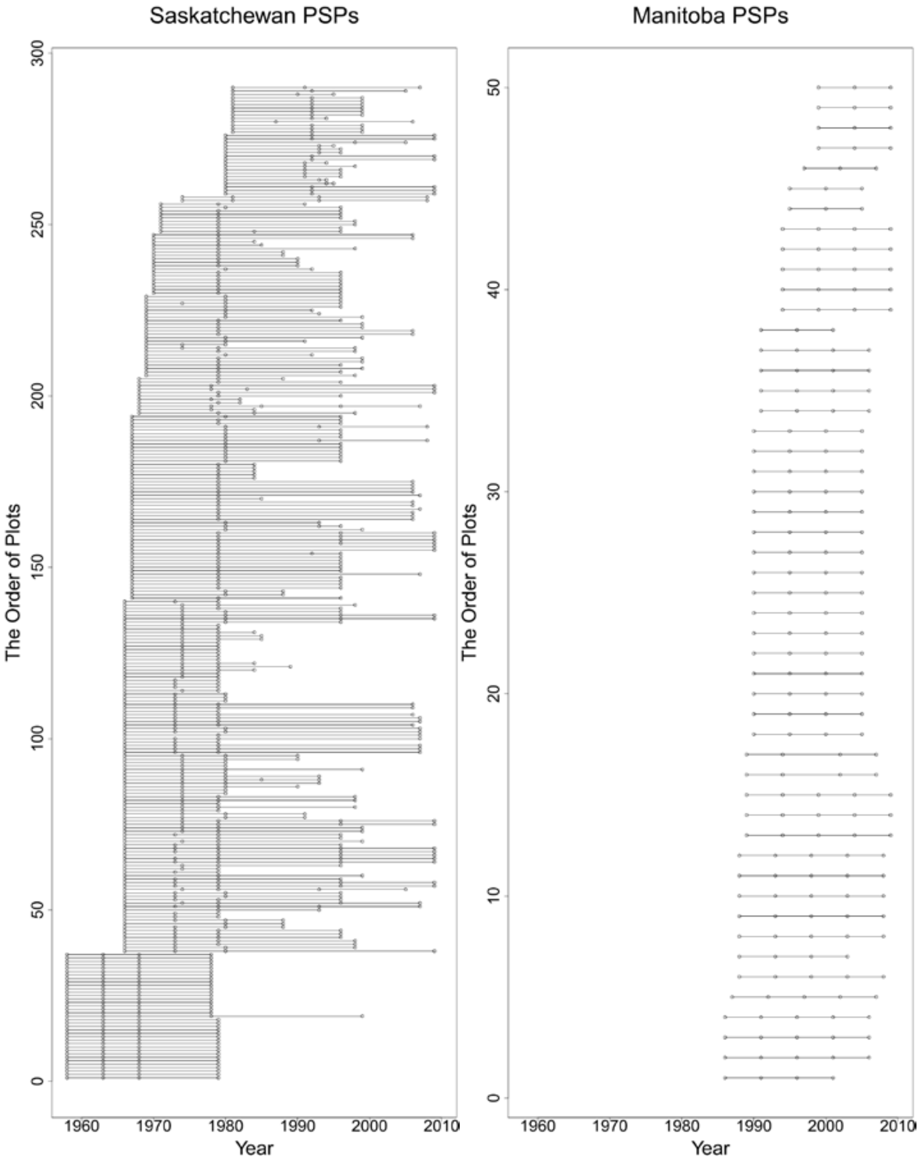
NOTE: These figures are based on the modeled results of 9 main tree species in western Canada. Other symbols and explanations are as in Figure 2.6

Appendix 2A Reporting period of each PSP in four provinces

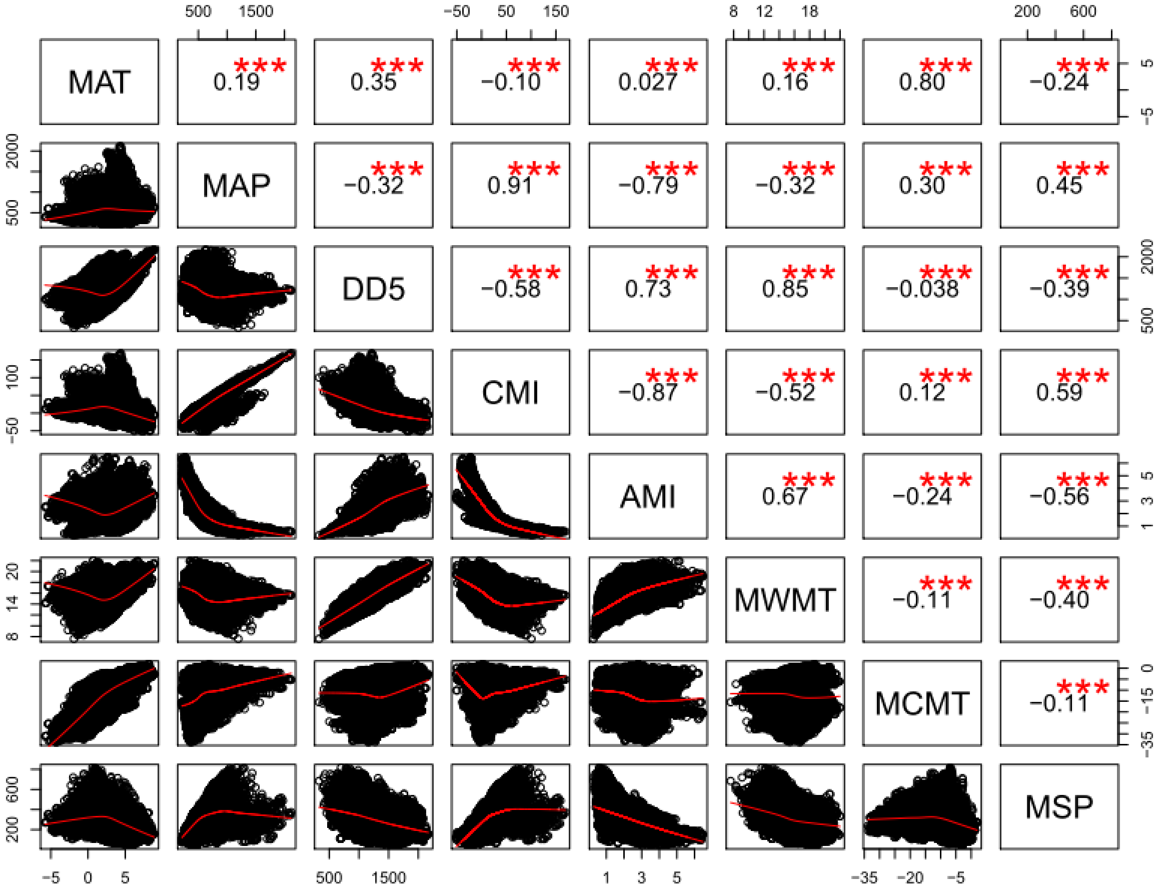


NOTE: Each line stands for one plot, and each point in one line indicates that this plot was censused this year.

Appendix 2A Reporting period of each PSP in four provinces **(Continuted)**

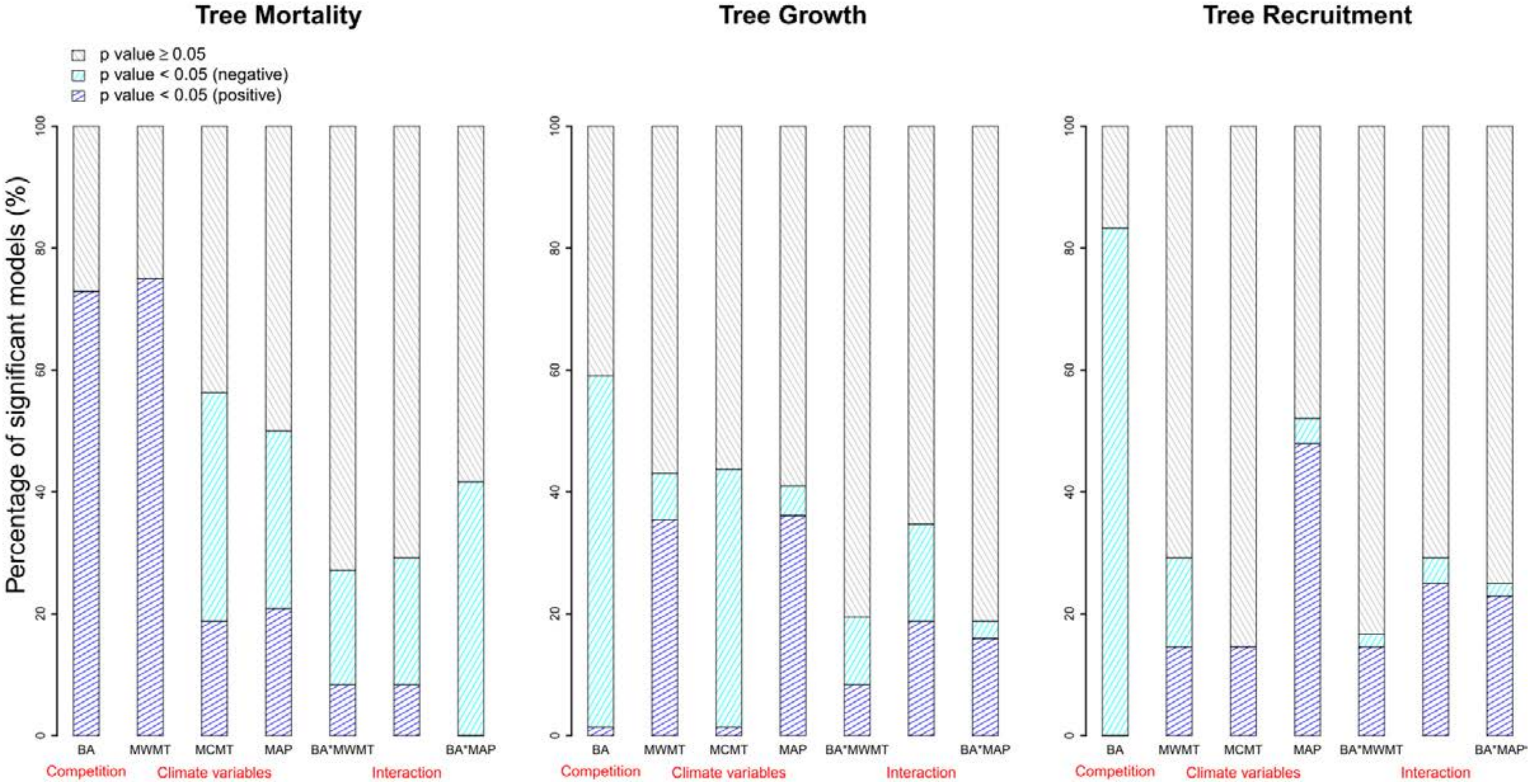


Appendix 2B Pearson correlations of eight climate variables



NOTE: Other symbols and explanations are as in Figure 2.6.

Appendix 2C Summary of the relationships among tree demographic rates, competition and climate at stand-level, accounting for the interactions between competition and climate variables



***NOTE**:* Only the modeled results with ≥20 plots were included in the summary. Other symbols and explanations are as in Figure 2.6.

Chapter 3 Spatial Variations of Alberta forest Biomass[1]

Summary

Uncertainties in the estimation of tree biomass carbon storage across large areas pose challenges for the study of forest carbon cycling at regional and global scales. In this study, I attempted to estimate the present biomass carbon storage in Alberta, Canada, by taking advantage of a spatially explicit dataset derived from a combination of forest inventory data from 1,968 plots and spaceborne light detection and ranging (Lidar) canopy height data. Ten climatic variables together with elevation were used for model development and assessment. Four approaches, including spatial interpolation, non-spatial and spatial regression models, and decision-tree based modelling with random forests algorithm (a machine-learning technique), were compared to find the "best" estimates. I found that the random forests approach provided the best accuracy for biomass estimates. Non-spatial and spatial regression models gave estimates similar to random forests, while spatial interpolation greatly overestimated the biomass storage. Using random forests, total biomass stock in Alberta forests was estimated to be 3.11×10^9 Mg, with the average biomass density of 77.59 Mg ha^{-1}. At the species level, three major tree species, lodgepole pine, trembling aspen and white spruce, stocked about 1.91×10^9 Mg biomass, accounting for 61 % of total estimated biomass. Spatial distribution of biomass varied with natural regions, land cover types, and species. And the relative importance of predictor variables

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[1] *A version of this chapter has been submitted to* ***Biogeosciences****.*

on determining biomass distribution varied with species. This study showed that the combination of ground-based inventory data, spaceborne Lidar data, land cover classification, climatic and environmental variables was an efficient way to estimate the quantity, distribution and variation of forest biomass carbon stocks across large regions.

3.1 Introduction

Forest ecosystems, accounting for over 80% of terrestrial vegetation biomass, play a major role in balancing regional and global carbon (C) budget and analyzing the fate of carbon dioxide produced by the burning of fossil fuels and forest harvesting (Dixon *et al.* 1994; Brown *et al.* 1997; Houghton *et al.* 2009). The accurate estimation of broad-scale biomass C stocks has been a focus of regional and global C cycle studies and has attracted the interest of researchers, forest managers and policy makers over the past half century. A proper assessment of actual and potential roles of forest ecosystems in the global C cycle requires accurate information about carbon storage and change over space and time (Botkin and Simpson, 1990). However, such accurate information has been lacking at regional and global scales.

A number of approaches have been developed to estimate spatial distribution of biomass C stocks, ranging from allometric regression equations or biomass expansion factors (e.g., Brown 1997; Cairns *et al.* 1997; Schroeder *et al.* 1997), local and regional scale forest inventories (Monserud *et al.* 2006; Blackard *et al.* 2008), simulation modelling (Tans *et al.* 1990; Ciais *et al.* 1995), to methods using only remote sensing or combined with inventory data (Hall *et al.* 2011; Myneni *et al.* 2001; Wulder *et al.* 2008; Yemshanov *et al.* 2012). However, the estimates obtained by these different approaches are often inconsistent. For example, Houghton *et al.* (2001) compared several biomass estimates for the Brazilian Amazon forests and found very low agreement across the estimates, with the range ranging from 39 to 93 gigatons (Gt) of carbon. Blackard *et al.* (2008) compared several estimates of C pools in living forest biomass of continental U.S. forests and found that satellite-image based estimation was two times higher than estimates based on inventory data.

Forest ground-based inventory laid out in a statistically sound design is considered to be the optimum approach to accurately and precisely measure forest biomass C stocks (Schroeder *et al.* 1997; Ketterings *et al.* 2001; Brown 2002). However, sampling a sufficient number of trees to represent the size and species distribution in a forest is extremely time-consuming and costly. The task becomes much harder for accurate estimation of biomass C stocks over large areas. For carbon estimation at the regional scale, most researchers tend to measure biomass on a few small, generally non-randomly selected plots, and use various prediction approaches (e.g., spatial interpolation techniques, and regression models), to estimate regional biomass C stocks based on observed values of these small sampling plots. However, inventories based on ground samplings are not free of problems. The first problem is related to the scarcity of ground-based inventory plots (Botkin & Simpson 1990; Wulder *et al.* 2008; Pan *et al.* 2011). The lack of sufficient and high-quality sample plots has been identified as a major barrier to the development of robust biomass estimates and to the subsequent validation of these estimates (Wulder *et al.* 2008). For example, in a recent report about global carbon storage, Pan *et al.* (2011) stated that estimates of C stocks are only limited to the 230 million hectares (Mha) of managed forest in Canada, leaving about 118 Mha of northern forests unaccounted for because of data paucity. The second problem is related to the fact that forest inventories tend to be conducted in forests that are considered to have commercial value, i.e., closed forests, with little regard to the open, drier forests, woodlands, or human-disturbed forests (Botkin & Simpson, 1990; Brown 1997). This biased sampling design usually tends to overestimate biomass C stocks over large areas.

Light Detection And Ranging (Lidar) is perhaps the most promising remote sensing technology for estimating biomass because it directly measures vertical forest structure, such as canopy height and crown dimensions (Simard *et al.* 2011). Generally, Lidar remote sensing has three platforms, including spaceborne, airborne, and ground-based platforms. While airborne or ground-based Lidar methods have been intensely used for biomass-related measurements at the stand level or individual tree level, these methods are only feasible at local or small-regional scales, rarely at larger scales (Popescu *et al.* 2011). The main reason for this restriction is the costs of airborne or ground-based Lidar on data acquisition and analysis are high at large extents (Popescu *et al.* 2011; Saatchi *et al.* 2011). For biomass and carbon estimation at the regional scale, spaceborne Lidar with relatively low cost has some competitive advantages.

The boreal forest, containing large amounts of carbon in its biomass and soils, has been recognized as an important global contributor to the net balance of carbon exchange between the atmosphere and the biosphere (Kurz & Apps 1999; Fyles *et al.* 2002; Pan *et al.* 2011). According to Intergovernmental Panel on Climate Change (IPCC, 2007), climate warming in northern latitudes is occurring almost twice as rapidly as the global average. Climate warming in the boreal may be leading to increases the frequency of wildfires (Harden *et al.* 2000), insect outbreaks (e.g., mountain pine beetle, Kurz *et al.* 2008) and regional drought events (Allen *et al.* 2010), thus influencing carbon stocks and dynamics (Kurz *et al.* 2008; Monserud *et al.* 2006; Pan *et al.* 2011). Since forest biomass is a key biophysical parameter in evaluating and modeling terrestrial carbon stocks and dynamics (Houghton *et al.* 2009), an accurate estimation of regional biomass is important for understanding boreal forests and their responses to climate warming. However, most of the previous studies for biomass estimations in the boreal were limited to the regions with high productivity and little disturbance (Botkin & Simpson 1990). There is a lack of information about biomass in regions under other successional stages and different disturbance extents. In addition, for remote areas in northern boreal regions, few ground inventory data are available.

In this study, I estimated biomass carbon stocks in the forest regions of Alberta, Canada, using recent forest inventory data from different forest monitoring networks and remote sensing data. My inventory data had a large sample size, covered a broad range, and included different disturbance types, stand age groups, and successional stages. My objectives were to: 1) produce a spatially explicit dataset of Alberta forest biomass carbon stocks; 2) quantify the relative contributions of various predictor layers including climate, elevation and canopy height to the biomass carbon stocks; and 3) assess the variability in estimation of biomass carbon stocks using different techniques.

3.2 Materials and Methods

Study area

The Alberta forest region (49°-60°N, 110°-120°W) is an area of about 40.3 million hectares (ha), accounting for about 61% of the total area of the province. It includes four natural regions: Boreal, Foothills, Rocky Mountain and Canadian Shield (Natural Regions Committee 2006). These regions have short summers and long and cold winters. Mean annual temperature ranges from -2.6°C in Canadian Shield to 1.7°C in Foothills (Natural Regions Committee 2006). Mean warmest month temperature ranges from 11.0°C in Rocky Mountain to 16.6°C in Canadian Shield, and mean coldest month temperature ranges from -25.1°C in Canadian Shield to -11.7°C in Rocky Mountain. Precipitation follows a summer-high continental pattern. Mean annual precipitation ranges from 380 mm in Canadian Shield to 798 mm in Rocky Mountain. Elevations range from about 150 m near the Alberta–Northwest Territories border to over 3600 m in Rocky Mountain region. Varying climate and topography in this area produce a wide range of vegetation and serve as habitats to diverse wildlife. In the Boreal natural region, deciduous, mixedwood and coniferous forests are dominant. Aspen (*Populus* *tremuloides*) and balsam poplar (*Populus balsamifera*) are the most common deciduous species, while white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are the dominant conifers. In the Foothills, mixed forests of aspen, lodgepole pine (*Pinus contorta*), white spruce and balsam poplar with variable understories are dominant on average sites at lower elevations, and Lodgepole pine forests with less diverse understories are typical of higher elevations. In the Rocky Mountain, closed coniferous forests are dominant at lower elevations, and open coniferous stands and herbaceous meadows are major vegetation types at higher elevations. In the Canadian Shield, open jack pine, aspen and birch stands occur where the soil is sufficiently deep.

Data source

I combined three different sources of ground-based inventory data for my current study, including 342 permanent sampling plots (PSPs) from Alberta Environment and Sustainable Resource Development (ESRD), 635 PSPs from Weyerhaeuser Canada, 501 PSPs from West Fraser Mill Ltd., and 490 sampling plots from Alberta Biodiversity Monitoring Institute (ABMI). In total, 1,968 plots measured in the period 2000-2012 were selected to estimate current biomass carbon stock in Alberta forest region (Figure 3.1). For the selected plots with more than one census, only the latest inventory data was selected for the current analysis.

Permanent samplings plots (PSPs)

The Alberta PSPs network has maintained more than two thousand PSPs established and re-censused by the government and forest products companies starting from 1950s. Most PSPs were selected in forest regions with high productivity, and these plots were excluded from normal harvesting and other human disturbances. Plot sizes ranged from 400 m^2 (0.04 ha) to 8,092 m^2 (0.81 ha) (mean: 0.12 ha). Within each PSP of ESRD, all living trees and standing dead trees (snags) with tree height ≥ 1.3 m were tagged and recorded. Within each PSP of Weyerhaeuser Canada, all living trees and snags with DBH (diameter at breast height) ≥ 5 cm were measured. Within each PSP of West Fraser, all living trees and snags with DBH ≥ 7 cm were measured. These 1,478 PSPs contained 206,213 living trees and 17,688 snags over the study period.

ABMI sampling plots

ABMI conducts a regional-scale, long-term monitoring program to track biodiversity status and trends in Alberta (http://www.ABMI.ca). ABMI collects information on thousands of terrestrial species and habitat structures at over one thousand sites spaced systematically on a 20-km grid evenly across the entire province. Terrestrial survey sites are established on each grid with a random distance and directional offset of up to 5.5 km from this grid. Different with PSPs network, ABMI sampling plots were relatively randomly distributed in different disturbance types and age groups. The area of each ABMI plot is one hectare (100 m × 100 m). On each site, all trees and snags with ≥ 25 cm DBH in four selected 25 m × 25 m plots, all trees and snags with ≥ 7 cm DBH in four 10 m × 10 m subplots, and all trees and snags in four 5 m × 5 m subplots were measured regardless of size. Totally, 490 sampling plots were included for current work, including 36,059 living trees and 7,046 snags.

Canopy height data from spaceborne Lidar

Spaceborne Lidar top canopy height data for Alberta forest regions were obtained from a global wall-to-wall canopy height map at 1-km spatial resolution (Appendix 3A, Simard *et al.* 2011). This map was produced by using the data acquired by the Geoscience Laser Altimeter System (GLAS), onboard the Ice, Cloud, and land Elevation Satellite (ICESat), in combination with several global ancillary variables, which correspond to climate and vegetation characteristics. These variables included: annual mean precipitation, precipitation seasonality, annual mean temperature, temperature seasonality, elevation, tree cover, and protection status.

Climatic variables

Climate data for Alberta forests were derived from the program CLIMATEWNA 4.70 (Wang *et al.* 2012). This program uses baseline climate data derived from monthly precipitation and temperature grids (Daly *et al.* 2008) based on interpolated climate data from weather stations for the period 1961-1990. The program includes a lapse-rate based down-sampling to 1-km resolution and estimation of biologically relevant climatic variables. Based on input values for longitude and latitude of each inventory plot or each grid, I localized 10 climatic variables using the average values across the last 10 years (2000–2009) to describe local climatic conditions. Ten climatic variables were as follows:

1) MAT: mean annual temperature (°C),
2) MWMT: mean warmest month temperature (°C),
3) MCMT: mean coldest month temperature (°C),

4) MAP : mean annual precipitation (mm),
5) MSP: mean summer (May to Sept.) precipitation (mm),
6) AHM: annual heat: moisture index (MAT+10)/(MAP/1000)),
7) SHM: summer heat: moisture index ((MWMT)/(MSP/1000)),
8) DD0: degree-days below 0°C, chilling degree-days,
9) DD5: degree-days above 5°C, growing degree-days,
10) DI: dryness index (DD5/MAP).

Alberta land cover map

Alberta wall-to-wall land cover map (ABMIw2wLCV2000v2.1) at 30-m spatial resolution was used for identifying forest lands in the study area (Appendix 3B; ABMI 2012). This map is a seamless GIS vector layer with nearly a million polygons describing the spatial distribution of land cover across Alberta, circa 2000, at the 1:125,000 scale. It consists of a mosaic of 977,556 non-overlapping polygons of various sizes, from 0.5 ha to thousands of ha. Each polygon represents a contiguous area relatively homogeneous in terms of land cover. The map is derived by applying a semantic and spatial generalization algorithm to a combination of two pre-existing land-cover products: the Canadian Forest Service's Earth Observation for Sustainable Development (EOSD) map of the forested region, and Agriculture Agri-Food Canada's map of the agricultural zone. This map consists of 11 land cover classes, including waters, snow/ice, rock/rubble, exposed land, developed, shrubland, grassland, agriculture, coniferous forest, broadleaf forest, and mixed forest.

Alberta natural region and subregion classification

To compare how tree biomass carbon stock varies in different forest regions, I used Alberta natural regions (NRs) and natural subregions (NSRs) classification system (Alberta Natural Regions Committee 2006) as the base of comparisons. In Alberta, this system has been used as the provincial natural resource management activities since the 1970s. The current version of this system consists 6 NRs and 21 NSRs. NRs, the largest mapped ecological units in this system, are defined geographically on the basis of landscape patterns, notably vegetation, soils and physiographic features. NSRs, subdivisions of a NR, are generally characterized by vegetation, climate, elevation, and latitudinal or physiographic differences within a given NR.

Data analysis

Estimation of aboveground biomass

Aboveground biomass was estimated for each individual tree in all ground inventory plots using DBH- and height-based biomass allometric equations and tree species-specific parameters provided by Lambert *et al.* (2005) and Ung *et al.* (2008). These equations were derived from thousands of trees sampled across Canada and allow the calculation of tree biomass (foliage, branches, stem bark, and stem wood) based on DBH measurements (for details see Lambert *et al.* 2005 and Ung *et al.* 2008). The form of the allometric equation is as follows:

$$Y = \beta_1 D^{\beta_2} H^{\beta_3} \tag{1}$$

where Y is the biomass component of interest, diameter (D) is measured on each tree, height (H) is measured on a subsample trees in each plot, and β_1, β_2 and β_3

are parameters. The remaining tree heights are estimated from local species-specific height-diameter equations developed by Huang *et al.* (2009).

Total aboveground biomass of each PSP was summed up from all trees in each plot. Total aboveground biomass of each ABMI site was summed up from three parts: the biomass per hectare of trees ≥ 25 cm DBH in the 25 m × 25 m plots, the biomass per hectare of trees 7-25 cm DBH in 10 m × 10 m subplots, and the biomass per hectare of trees < 7 cm DBH in 5 m × 5 m subplots.

Estimation of belowground biomass

Since belowground data were not available from my data, I estimated belowground biomass using the following regression equation developed for boreal forests by Cairns *et al.* (1997):

$$BGB = e^{-1.0587+0.8836\times\ln(AGB)+0.1874} \qquad (2)$$

where *BGB* is the belowground biomass (coarse and fine roots), and *AGB* is the aboveground biomass.

Estimation of debris biomass

My aboveground biomass estimates included standing dead trees. However, there was no inventory data on down and dead woody material (fine and coarse woody debris) on most of the study plots. To estimate debris biomass, I calculated the ratios of above-ground biomass and debris biomass (fine and coarse woody debris) for 90 study sites across Canada forest regions (Shaw *et al.* 2005). I used the average value (5%) of the ratios for current work, so debris biomass was estimated as 5% of aboveground biomass.

Estimation of biomass carbon stock

Estimates of belowground biomass and debris biomass were added to the aboveground estimates to estimate total biomass. Biomass carbon pool was calculated by multiplying a carbon biomass conversion factor of 0.5 to the total biomass (Schlesinger 1997).

Biomass-environment correlations

I used simple Pearson correlations to explore covariation among biomass and 14 variables. Because the presence of spatial autocorrelation in model residuals violates the assumption of data independence (Mauricio Bini *et al.* 2009), Pearson correlations among biomass and biotic and abiotic variables after accounting for spatial autocorrelation were calculated with the R library MODTTEST 1.4 (José Manuel Blanco Moreno, Universitat de Barcelona, Spain, pers. comm.).

Scaling up to the whole region

To get an accurate estimate of biomass distribution, four approaches, including spatial interpolation of direct field measurements, non-spatial regression model, spatial regression model, and decision-tree based modelling with random forests algorithm (RF), were selected for my analysis.

Spatial interpolation methods: The methods have been used for mapping forest variables (e.g. site index, standing volume, above-ground biomass, productivity, etc.) based on forest inventory data where these variables seemingly have spatial autocorrelation (e.g., Dungan 1998; Freeman & Moisen 2007; Viana *et al.* 2012). In this study, I compared several different approaches to find the “best” one for spatial interpolation of tree biomass. These approaches included ordinary kriging (Krige 1951), standardized ordinary cokriging (elevations as the covariate), inverse distance weighting, thin-plate smoothing splines, and partial thin-plate smoothing splines. Cross-validation analysis was used to evaluate effective parameters for these interpolation methods. Results with the highest R^2 in cross-validation analysis were finally selected. Kriging, cokriging and inverse distance weighting were calculated using the geostatistics software GS+ (http://www.gammadesign.com), and thin-plate smoothing splines were calculated using the R package "fields" (Fields Development Team 2006). After producing the biomass map for Alberta region, I used Alberta Natural Region GIS map to mask grassland and parkland regions, and Alberta land cover map to mask the areas with the following land cover classes: waters, snow/ice, rock/rubble, exposed land, shrubland, grassland, and agriculture.

Non-spatial and spatial regression models: Two steps were used to estimate biomass stocks using canopy height data from spaceborne Lidar. First, I used data from the 1,968 forest inventory plots to establish the relationships between total tree biomass and ground-measured top canopy height, climatic variables, elevations, latitudes, and longitudes. Both non-spatial multiple regression models (ordinary least squares, OLS) and spatial linear models [here 'spatial simultaneous autoregressive error models (SARs)'; Kissling & Carl 2008], which allow the inclusion of the residual spatial autocorrelation of the data, were used. Among these predictor variables, some of them were highly correlated. To reduce the risk of multi-collinearity, I used VIF (Variance Inflation Factors) for variable selection. The variables with VIF >10, which represent high collinearity, were removed. The “best” model is selected based on lower AIC (Akaike information criterion) and higher R^2. Second, I applied this selected model to estimate tree biomass density (Mg ha^{-1}) using Lidar canopy height and other environmental variables in each 1 km × 1 km grid in Alberta forest regions. All the analyses were done using R language (R Development Core Team 2013), and SARs were calculated using the R package “spdep” (version 0.5-33).

Decision-tree based modelling with random forests algorithm (RF): The method is an ensemble machine learning technique, where many decision trees are constructed based on random sub-sampling of the given data set (Breiman 2001). As one of tree-based models, RF performs recursive partitioning of data sets, and makes no assumptions regarding the distribution of the input data. RF can capture non-linear relationships between the response variable (tree biomass in my study) and predictor variables (canopy height, climate, and other environmental variable in my study), and can deal with correlated variables while producing a low generalization error (Breiman 2001). In addition, RF can be used to rank the importance of variables in a regression or classification problem in a natural way. In my study, this method was used to detect the relative importance of climate, topography and other environmental variables, and predict the distributions of forest biomass. All analyses were implemented in the R package “randomForest” (Liaw & Wiener 2002).

Model accuracy assessment

Three well-known error statistics were calculated to measure the difference between the observed and predicted forest biomass, including mean absolute error

(MAE), root mean-square error (RMSE), and the normalized root-mean-square error (NRMSE). They are defined as:

$$\text{MAE} = \frac{1}{N}\sum_{i=1}^{N}|PRE_i - OBS_i|$$

$$\text{RMSE} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(PRE_i - OBS_i)^2}$$

$$\text{NRMSE} = 100 \times \frac{RMSE}{OBS_{max} - OBS_{min}}$$

where PRE_i and OBS_i denote the *i*th predicted and observed values, respectively. NRMSE is the RMSE divided by the range of observed values of a variable being predicted. The value is often expressed as a percentage, where lower values indicate less residual variance.

3.3 Results

Biomass variations among forest inventory plots

Direct field measurements yielded an estimate of 172.33±101.23 Mg ha^{-1} for the density of total tree biomass for Alberta forests, with a range from nearly zero to 613.82 Mg ha^{-1} in these inventory plots. For the PSP inventory plots only, the average biomass density estimate was 198.13 Mg ha^{-1}, which is more than double the density of 94.50 Mg ha^{-1} for the ABMI inventory plots ($P < 0.0001$, two-sample *t* test).

For forest inventory plots at the species level, the average biomass density estimates for lodgepole pine, trembling aspen, black spruce and white spruce were 50.86, 44.55, 23.95, and 33.61 Mg ha^{-1}, respectively.

Based on my inventory data, I detected a large variation of total tree biomass along forest stand ages (Fig. 3.2a, b). I classified these plots into four forest age groups (young, immature, mature, and old-growth forests). Old-growth forests (age>120 years) and mature forests (80-120 years) had the highest average tree biomass, 214.32 and 187.96 Mg ha^{-1} respectively. Average biomass density in immature forests (50-80 years) was 121.04 Mg ha^{-1}, and the average in young forests (<50 years) was 63.97 Mg ha^{-1}.

Biomass-environment correlations

The results of Pearson correlations after accounting for spatial autocorrelation showed that total tree biomass of each ground plot was significantly correlated with observed canopy height (correlation coefficient: 0.752; $P < 0.001$; Table 3.1, Figure 3.2c). Elevation also showed significant correlations with total biomass. Among 10 climatic variables, most variables were highly correlated with others. MCMT (mean coldest month temperature) and DD0 (degree-days below 0°C) had relatively high correlations with total tree biomass.

Biomass estimates from four different approaches

I compared the results of four approaches for biomass estimation (Table 3.2, Figure 3.3). The RF approach provided the best accuracy for biomass estimation ($R^2 = 0.62$, $MAE = 48.34$ Mg ha^{-1}, $RMSE = 64.18$ Mg ha^{-1}, $NRMSE = 62.25$ %) (Table 3.2). Non-spatial and spatial regression models performed nearly as well as the RF approach, while spatial interpolation had the poorest estimate (R^2 = 0.29, MAE = 66.77 Mg ha^{-1}, $RMSE$ = 85.08 Mg ha^{-1}, $NRMSE$ = 84.20 %). Total tree biomass estimation from spatial interpolation was 5.07×10^9 Mg, which was much larger than the estimates from spatial regression model (3.01×10^9 Mg) and RF (3.11×10^9 Mg) (Figure 3.3).

Using the RF approach, estimates of total tree biomass across Alberta forest regions was 3.11×10^9 Mg (Table 3.3, Figure 3.3). Average biomass density in each 1 × 1 km grid was 77.59 Mg ha^{-1}. Nearly 25 % of total forest areas had biomass densities between 40-60 Mg ha^{-1}, and around 11 % of total forest areas had biomass densities larger than 150 Mg ha^{-1} (Figure 3.4).

Total tree biomass in the boreal region (RF approach) was about 1.81×10^9 Mg, accounting for 58.17 % of total tree biomass in Alberta forests among the four main natural regions of Alberta (Table 3.3). The estimated biomass was about 0.76×10^9 Mg in the Foothills, 0.50×10^9 Mg in the Rocky Mountain, and 0.03×10^9 Mg in the Canadian Shield. Among the fourteen natural subregions (Table 3.3), Central Mixedwood had the highest total tree biomass (0.91×10^9 Mg), followed by Lower Foothills, Subalpine and Lower Boreal Highlands.

Compared with the average biomass of inventory plots (172.33 Mg ha^{-1}, Table 3.3), Foothills and Rocky Mountain natural regions had higher biomass densities of 192.57 and 190.80 Mg ha^{-1} respectively, than the others. Averages of biomass density also varied greatly in different subregions, from 22.11 Mg ha^{-1} in Boreal Subarctic to 197.01 Mg ha^{-1} in Lower Foothills.

Among three major land cover types in Alberta forests (Appendix 3B), coniferous forests stored 1.57×10^9 Mg biomass, accounting for 50.47 % of total tree biomass in Alberta forests, and broadleaf forests and mixed forests stored 0.84×10^9 and 0.23×10^9 Mg biomass, respectively.

Biomass estimates of major tree species

Three major tree species, lodgepole pine, trembling aspen and white spruce, stocked about 1.91×109 Mg biomass in total, accounting for 61 % of total biomass in Alberta forests (Figure 3.5, Table 3.4). Total biomass of lodgepole pine was 0.76×109 Mg, and 84 % of which is distributed in the Foothills and Rocky Mountain regions. For trembling aspen, total biomass was 0.68×109 Mg, of which 78 % is distributed in the Boreal region. For white spruce, total biomass was 0.47×109 Mg, of which 58 % is distributed in the Boreal region

Variable importance on biomass distribution

Using the RF, I also assessed the importance of various predictor variables on biomass distribution (Figure 3.6). Canopy height, which was directly related to biomass, had major influence on biomass distribution at both stand and species levels. Elevation was also significantly correlated with biomass distribution. Each of the ten climatic variables had relatively weak effects on biomass distribution at the stand level. The three major tree species showed differing relationships with climatic variables. For lodgepole pine, DD0, MCMT and DD5 had stronger impacts on biomass than the other climatic variables. For trembling aspen, four climatic variables related to site dryness, including MAP, MSP, DI and AHM, were much more important than the other climatic variables. For white spruce, MSP and DD5 had slightly stronger effects on biomass than others.

3.4 Discussion

I reported a large-scale spatially explicit dataset for presenting biomass storage in Alberta's forest regions, derived from a combination of forest inventory data from 1,968 plots, spaceborne Lidar data, land cover classification, climate and other environmental variables. Using decision-tree based approach with random forests algorithm, total biomass stock in the study region was estimated to be 3.11×10^9 Mg, which is very close to Bonnor's (1985) estimate (3.15×10^9 Mg) based on volume inventory data (Table 3.5). The average biomass density was 77.59 Mg ha^{-1}, which is close to Bonnor's (1985) estimate (77.52 Mg ha^{-1}). This study showed that the combination of multisource data could be a cost-effective way to estimate the amounts, distributions and variations of biomass carbon stocks across large regions with good accuracy.

Comparison with previous biomass estimations

I summarized previous studies on boreal forest biomass estimation at different spatial extents (Table 3.5). At the global scale, total biomass estimates of boreal forests ranged from 111.32×10^9 Mg (Cao and Woodward 1998) to 176×10^9 Mg (Dixon *et al.* 1994). In Canada forests, total biomass estimates varied from 29.02×10^9 Mg (Kurz and Apps 1999) to 56.34×10^9 Mg (Penner *et al.* 1997). In Alberta forest regions, my estimate (3.11×10^9 Mg) using decision-tree approach was very similar to the estimate of Bonnor (1985), but smaller than the estimate of

Penner *et al.* (1997) (Table 3.5). Compared with other studies, my estimate of mean biomass density was close to several studies at global and regional scales, while it also had a large difference from the estimates of some other studies, such as Dixon *et al.* (1994), Pan *et al.* (2011) and Penner *et al.* (1997) (Table 3.5). Clearly, there are huge disagreements among different estimates, but it is hard to compare them because of different data sources, estimation methodologies, and time periods of data collection.

Compared with previous studies, my current study has several improvements and advantages: 1) multisource data: I combined the data from ground-based inventory, Lidar, land cover, climate and other environmental variables. Many previous studies used only a single data source, and did not consider the role of climate and other variables in their analyses; 2) large, relative unbiased sample plots on forest inventory: the lack of sufficient and unbiased sample plots has been identified as a major barrier to accurately estimate biomass stocks at large area (Botkin & Simpson 1990; Brown 1997; Wulder *et al.* 2008). In the present study, the two different sources of plot data showed significant differences on stand age structure and biomass distribution (Fig. 3.2). The PSP data was derived from undisturbed, relatively productive stands and thus gave much greater average values of biomass density than the ABMI plots, which includes both disturbed and undisturbed sites. Further, the regular distribution of ABMI plots places some of them in peatlands, which generally were avoided in the PSP inventory. Thus, the use of PSP data alone would lead to the overestimation of biomass. In terms of the scope and sample sizes, the data used in this study are more comprehensive and extensive than previous datasets; 3) By combining inventory data and remote sensing data, I provide a cost-effective scheme of mapping biomass stock for provincial- and national-scale assessments.

Comparison of different methods for biomass estimations

Selection of appropriate models plays a central role in estimating biomass and carbon stocks (Fang *et al.* 1998; Saatchi *et al.* 2011). Four different approaches, including spatial interpolation, non-spatial and spatial regression models, and decision-tree based modeling with random forests algorithm (RF), were used to yield an estimate of total tree biomass for my study area. I found that spatial interpolation greatly overestimated total tree biomass, while regression models and RF provided similar estimates with high accuracy. Overestimation by spatial interpolation might be related to the characteristics of the approach itself and the data we use. First, the spatial interpolation approach assumes that spatial distribution of the variable I tried to predict is a spatially continuous surface, and the near points generally receive higher weights than far away points (Krig 1951). This principle can be easily used to the prediction of some climate and topography variables, but, for biomass and carbon, it might not be suitable because the distribution of biomass is discontinuous usually because of different types of natural and anthropogenic disturbances (Appendix 3B). Second, the spatial interpolation approach I used only considered one additional variable, which seriously constricts the ability to accurately predict. Although some techniques have been developed to consider multiple variables into spatial interpolation, they are still not available in most of widely used geostatistics software. Furthermore, for most of the PSP plots placed on upland sites, these are intermixed with a fine-scale mosaic of forested peatlands with much lower biomass.

As a nonparametric approach, RF has shown some outstanding advantages in my study. This is also supported by previous studies for soil mapping (e.g., Grimm *et al.* 2008), biomass mapping in forests (Baccini *et al.* 2004; Neumann *et al.* 2011; Asner *et al.* 2013) and seafloor (Wei *et al.* 2010), and bird distribution modeling (Kreakie *et al.* 2012). The advantages of random forests include: ability of modeling high dimensional non-linear relationships, handling of categorical and continuous predictors, resistance to overfitting, relative robustness with respect to noise features, unbiased measure of error rate, and measures of variable importance (Breiman 2001; Grimm *et al.* 2008**).** Therefore, by combining different predictor variables, this approach has a great potential for improving the estimation of forest biomass at regional and global scales.

Canopy height as an important determinant of biomass distribution

It is well known that canopy height is a critical indicator of forest site quality and growth potential (Kimmins 2004; Fang *et al.* 1998). Also, canopy height is highly related to stand age and forest disturbance, both of which affect directly forest biomass and productivity. Using a large sample of forest inventory data, I detected a significant relationship between biomass and canopy height (Table 3.1, Figure 3.2). The assessment of variable importance using the RF approach also showed that canopy height was the most important variable for determining biomass distribution in my study area (Figure 3.6). However, canopy height has been rarely used in previous estimations of regional-scale biomass and carbon storage, because these data were not available over large areas in the past. The development of remote sensing techniques, especially Lidar, has provided high or medium resolution canopy height products at both regional and global scales (Lefsky *et al.* 2010; Simard *et al.* 2011), and provides an opportunity to obtain more accurate estimates of biomass and carbon storage over large areas. For example, based on 1-km resolution spaceborne Lidar canopy height data (Lefsky *et al.* 2010) and ground inventory data, Saatchi *et al.* (2011) mapped the total biomass carbon stocks in tropical regions across three continents with a forest area of 2.5 billion ha. Therefore, the integration of plot-based measurements of biomass with remotely-sensed observations of canopy height can provide a cost-effective method for large-scale mapping. In addition, the Lidar canopy height data are closely related to logging and fire history, allowing recently logged and burned sites to be more accurately accounted for in biomass carbon estimation.

Biomass-climate relationships

Understanding biomass-climate relationships is important for biomass and carbon mapping under past and current conditions as well as for making future projections under a changing climate. Although climatic variables have been used in biomass estimations, we know relatively little about how climate influences variation in biomass stocks (Stegen *et al.* 2011). In this study, I found that climate explained relatively little of the observed, stand-level variation in Alberta forest biomass (Table 3.1, Figure 3.6), which is consistent with Stegen *et al.* (2011)'s findings on biomass-climate relationships in temperate and tropical forests.

Disturbance regime is likely a better predictor of biomass but these are often difficult to map at regional scales. Because canopy height is strongly influenced by time since the last stand-replacing disturbance (e.g., fire), high-resolution Lidar data can play an important role in estimating biomass and productivity at regional and national scales.

Species-level analysis on biomass-climate relationships showed that tree species respond differently to how climate affects biomass distribution (Figure 3.6). For lodgepole pine, chilling degree-days (DD0), mean coldest month temperature (MCMT) and growing degree-days (DD5) played a more important role than other climatic variables. This strong correlation with degree-days is also supported by previous studies on lodgepole pine site index study in Alberta forests (Monserud *et al.* 2006). For trembling aspen, four drought-related variables (MAP, MSP, DI and AHM) were much more important than other climatic variables, which confirm previous studies about drought-related impacts on aspen stand dynamics (e.g., Hogg *et al.* 2008; Michaelian *et al.* 2011).

Total carbon stocks in Alberta forests

To map total carbon (C) storage of Alberta forests, I also need high quality data on soil C in my study area. Boreal forest ecosystems contain vast C stocks in soil, most of which is found in peatlands and permafrost soils (Deluca and Boisvenue 2012). Soil C in boreal ecosystems has been reported to account for about five times the total C in the standing biomass or about 85 % of the total biome C (Malhi *et al.* 1999). The large-scale estimation of soil C stocks poses many challenges (Liu *et al.* 2013), and was thus not specifically included in the current study. However, using the recent data set of North American soil organic carbon content at 0.25 degree resolution (Liu *et al.* 2013), I estimated the total soil carbon stocks in Alberta's forests to be about 11.8×10^9 Mg, with a high proportion in peatlands (Vitt *et al.* 2000). My estimate of biomass carbon (1.56×10^9 Mg, 50% of total tree biomass) only accounted for 12 % of total carbon stocks (13.36×10^9 Mg), while soil carbon accounted for 88 %. Clearly, more efforts are needed to better understand spatial and temporal variation of biomass and soil carbon stocks in the boreal forest.

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Tables

Table 3.1 Pearson correlations of tree biomass and climatic variables, elevation, and observed canopy height, after accounting for spatial autocorrelation

	ln(Biomass)	Elevation	Canopy height	MAT	MWMT	MCMT	MAP	MSP	AHM	SHM	DD0	DD5
Elevation	0.300***											
Canopy height	0.752***	0.057										
MAT	0.314**	0.341*	0.307***									
MWMT	-0.290**	-0.943***	-0.054	-0.272								
MCMT	0.374**	0.787***	0.230*	0.829***	-0.743***							
MAP	0.276**	0.850***	0.103	0.459**	-0.822***	0.791***						
MSP	0.274**	0.748***	0.150*	0.613***	-0.678***	0.823***	0.832***					
AHM	-0.129*	-0.761***	0.065	0.071	0.788***	-0.414***	-0.831***	-0.604***				
SHM	-0.322**	-0.866***	-0.157	-0.622***	0.828***	-0.896***	-0.877***	-0.950***	0.659***			
DD0	-0.372***	-0.691***	-0.260**	-0.911***	0.636***	-0.981***	-0.721***	-0.796***	0.285**	0.858***		
DD5	-0.189**	-0.898***	0.065	0.044	0.934***	-0.511***	-0.712***	-0.546***	0.854***	0.677***	0.371**	
DI	-0.291**	-0.950***	-0.072	-0.368*	0.951***	-0.797***	-0.924***	-0.815***	0.858***	0.919***	0.704***	0.881***

NOTE: * < 0.05; ** < 0.01; *** < 0.001.

Table 3.2 Validation statistics for four different approaches for total tree biomass estimation

Methods for biomass estimation	**R^2**	**MAE (Mg ha^{-1})**	**RMSE (Mg ha^{-1})**	**NRMSE (%)**
Spatial interpolation	0.29	66.77	85.08	84.20
Non-spatial regression model	0.60	48.38	64.08	63.15
Spatial regression model	0.61	48.39	64.09	63.16
Decision-tree modeling with random forests algorithm	0.62	48.34	64.18	62.25

NOTE: MAE: mean absolute error; RMSE: root mean square error; NRMSE: the normalized root mean square error.

Table 3.3 Total tree biomass estimated by decision-tree based approach in different natural regions and subregions in Alberta forests

Forest regions		**Summary based on 1-km pixels**		**Summary based on forest inventory plots**		
		Total (10^9 Mg)	Percentage (%)	Number of plots	Mean (Mg ha^{-1})	Range (Mg ha^{-1})
Natural regions	Boreal	1.81	58.17	571	126.66	0.01-613.82
	Foothills	0.76	24.56	1137	192.57	0.49-534.08
	Rocky Mountain	0.50	16.16	247	190.80	4.29-423.74
	Canadian Shield	0.03	1.09	13	56.10	8.15-125.16
	Total	3.11	100	1968	172.33	0.01-613.82
Natural subregions	Central Mixedwood	0.91	29.23	349	134.47	0.01-613.82
	Lower Foothills	0.47	15.18	677	197.01	0.49-534.08
	Subalpine	0.36	11.61	216	191.60	4.29-432.74
	Lower Boreal Highlands	0.34	10.94	80	139.48	0.93-486.63
	Dry Mixedwood	0.30	9.70	82	129.97	5.90-335.92
	Upper Foothills	0.29	9.38	460	186.05	1.54-461.15
	Northern Mixedwood	0.12	3.73	20	95.73	4.74-302.41
	Montane	0.11	3.55	30	185.34	51.23-348.82
	Upper Boreal Highlands	0.06	2.00	9	49.01	4.29-158.81
	Athabasca Plain	0.04	1.19	25	35.81	3.19-94.84
	Boreal Subarctic	0.03	1.01	4	22.11	8.85-55.44
	Alpine	0.03	1.00	1	\	\
	Kazan Uplands	0.03	1.09	13	56.10	8.15-125.16
	Peace-Athabasca Delta	0.01	0.36	2	118.63	99.32-137.95

Table 3.4 Total tree biomass of three major tree species estimated by decision-tree based approach

Species	Natural regions	Summary based on 1-km pixels		Summary based on forest inventory plots	
		Total (10^9 Mg)	Percentage (%)	Mean (Mg ha^{-1})	Range (Mg ha^{-1})
Lodgepole pine	Boreal	0.12	15.87	4.56	0.00-224.51
	Foothills	0.33	44.08	64.01	0.00-378.31
	Rocky Mountain	0.30	39.96	100.01	0.00-406.45
	Canadian Shield	0.01	0.06	0.00	0.00-0.00
	Total	0.76	100.00	50.86	0.00-406.45
Aspen	Boreal	0.52	77.53	60.26	0.00-486.02
	Foothills	0.09	13.62	45.31	0.00-497.95
	Rocky Mountain	0.05	6.75	5.70	0.00-217.14
	Canadian Shield	0.01	2.08	26.22	0.00-124.93
	Total	0.68	100.00	44.55	0.00-497.95
White spruce	Boreal	0.27	58.11	29.69	0.00-389.88
	Foothills	0.10	21.32	33.01	0.00-360.92
	Rocky Mountain	0.09	18.34	46.20	0.00-406.45
	Canadian Shield	0.01	2.20	19.86	0.00-111.75
	Total	0.47	100.00	33.61	0.00-389.88

Table 3.5 Biomass estimations in previous studies

Reference	Study Area	Area (Mha)	Methodology or data source	Total tree biomass (10^9 Mg)	Mean Biomass density (Mg ha^{-1})
Dixon *et al.* 1994	Boreal forests (Global)	1372	Inventory data (1987-1990)	176	128
Cao & Woodward 1998	Boreal forests (Global)	1210	Predicted from a global carbon model (1990s)	111.32	92
Jarvis *et al.* 2001	Boreal forests (Global)	1381	Inventory data (1990s)	114.99	83
Myneni *et al.* 2001	Northern forests (Global)	1419.9	Remote sensing (NDVI; 1995-1999)	121.44	85.82
Pan et al 2011	Boreal forests (Global)	1135	Inventory data & statistical or process models (2007)	140	123.35
Bonnor 1985	Canadian forests	440.7	Volume Inventory data (1981)	35.48	80.24
Dixon *et al.* 1994	Canadian forests	436	Inventory data (1987-1990)	24	56
Penner *et al.* 1997	Canadian forests	440.7	Volume Inventory data (1991)	56.34	127.84
Kurz & Apps 1999	Canadian forests	404.2	Inventory data (1990s)	29.02	71.8
Pan et al 2011	Canadian forests	229.4	Inventory data & statistical or process models (2007)	38	165.65
Myneni *et al.* 2001	Canadian forests	239.5	Remote sensing (NDVI; 1995-1999)	21.12	88.18
Liski & Kauppi 2000	Canadian forests	244.6	Inventory data (mid-1990s)	23.78	97.22
Penner *et al.* 1997	Alberta forests	40.3	Volume Inventory data (1991)	4.28	106.08
Bonnor 1985	Alberta forests	40.3	Volume Inventory data (1981)	3.15	77.52
This study	Alberta forests	40.3	Inventory data (2000-2012) & Lidar canopy height data (2006)	**3.11**	**77.59**

NOTE: For the studies with aboveground biomass data only, belowground biomass is assumed to be 0.36 of the aboveground biomass (Jarvis *et al.* 2001).

Figures

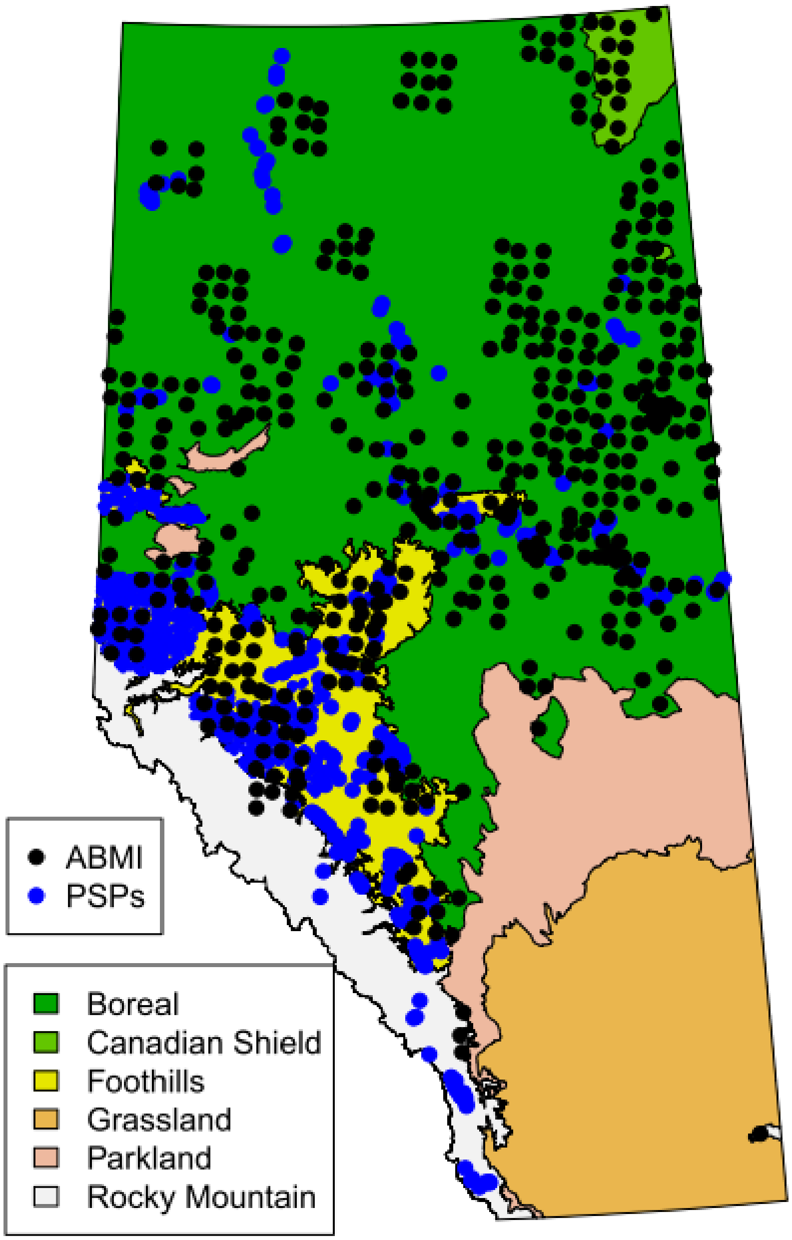


Figure 3.1 Spatial distribution of 1,968 ground-based inventory plots in Alberta forests, Canada

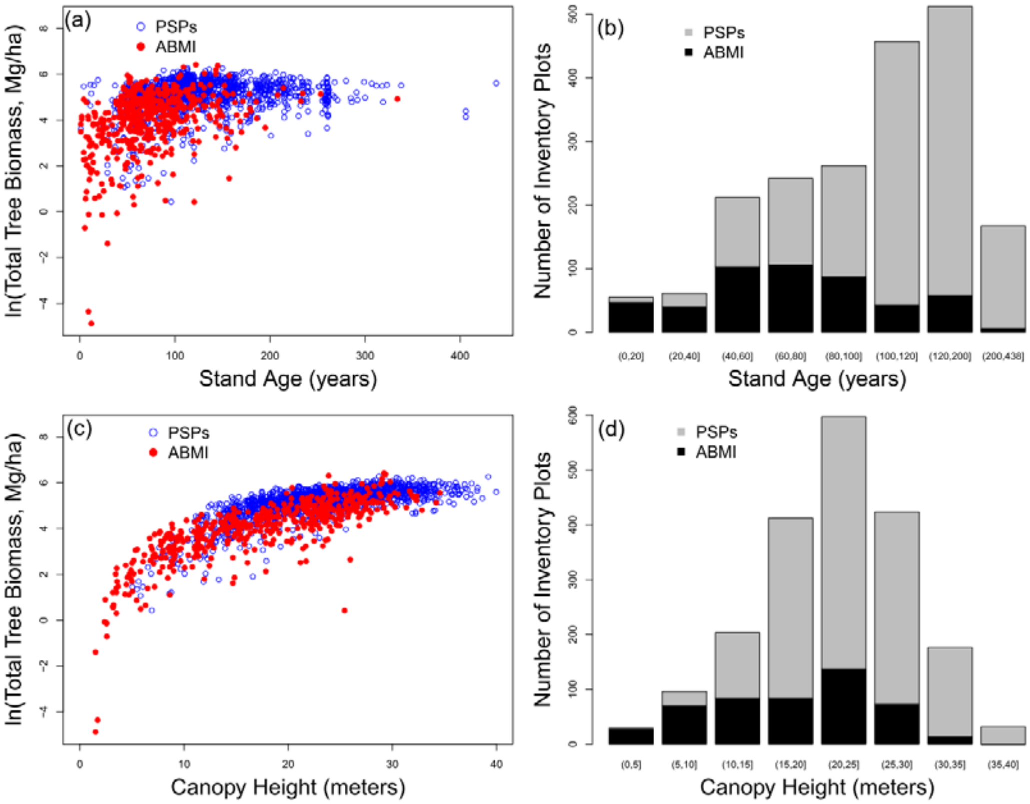


Figure 3.2 Total tree biomass versus canopy height and stand age of 1,968 ground-based inventory plots

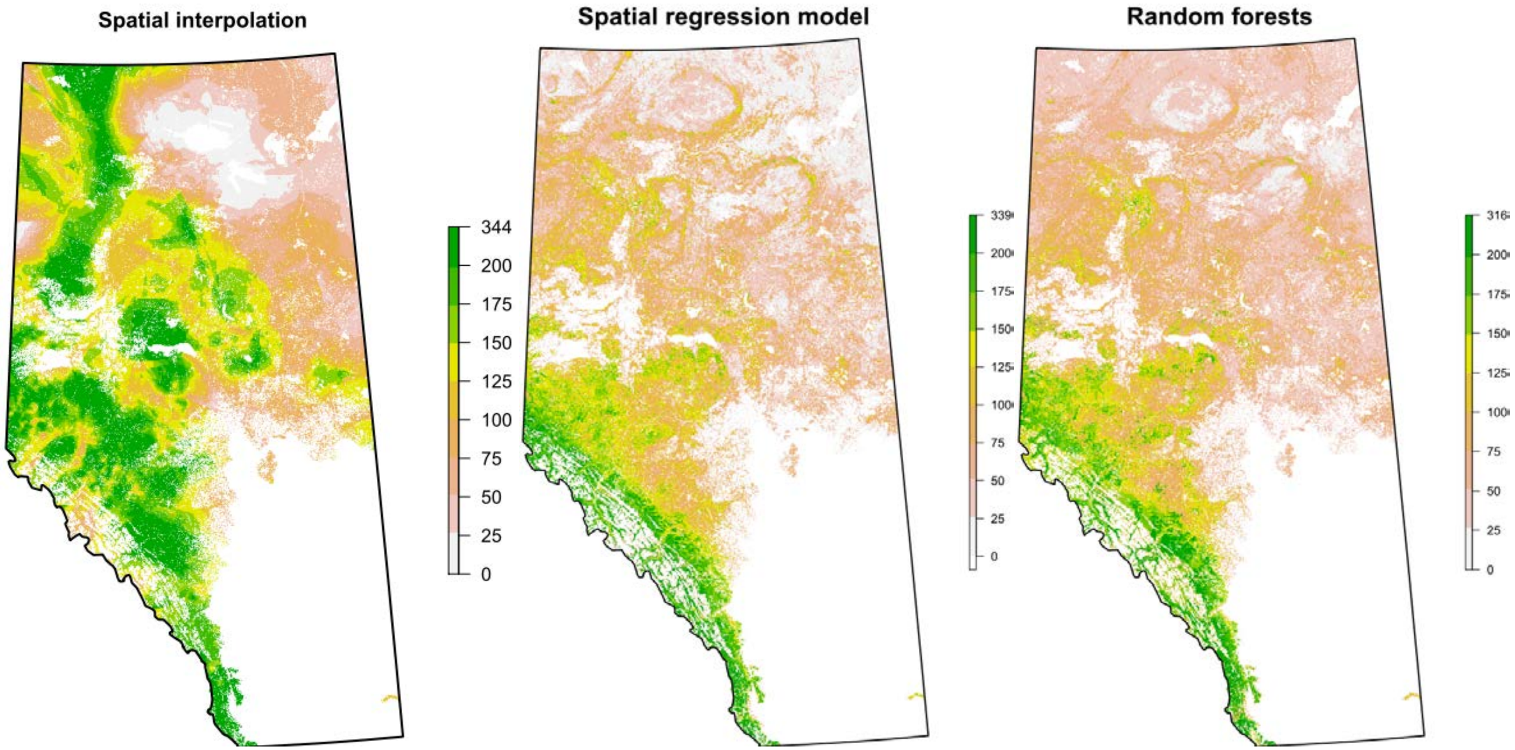


Figure 3.3 The estimates of total biomass density (Mg ha^{-1}) using spatial interpolation, multiple regression model, and decision-tree based modeling with random forests algorithm (Projection: UTM zone=11; spatial resolution: 1-km)

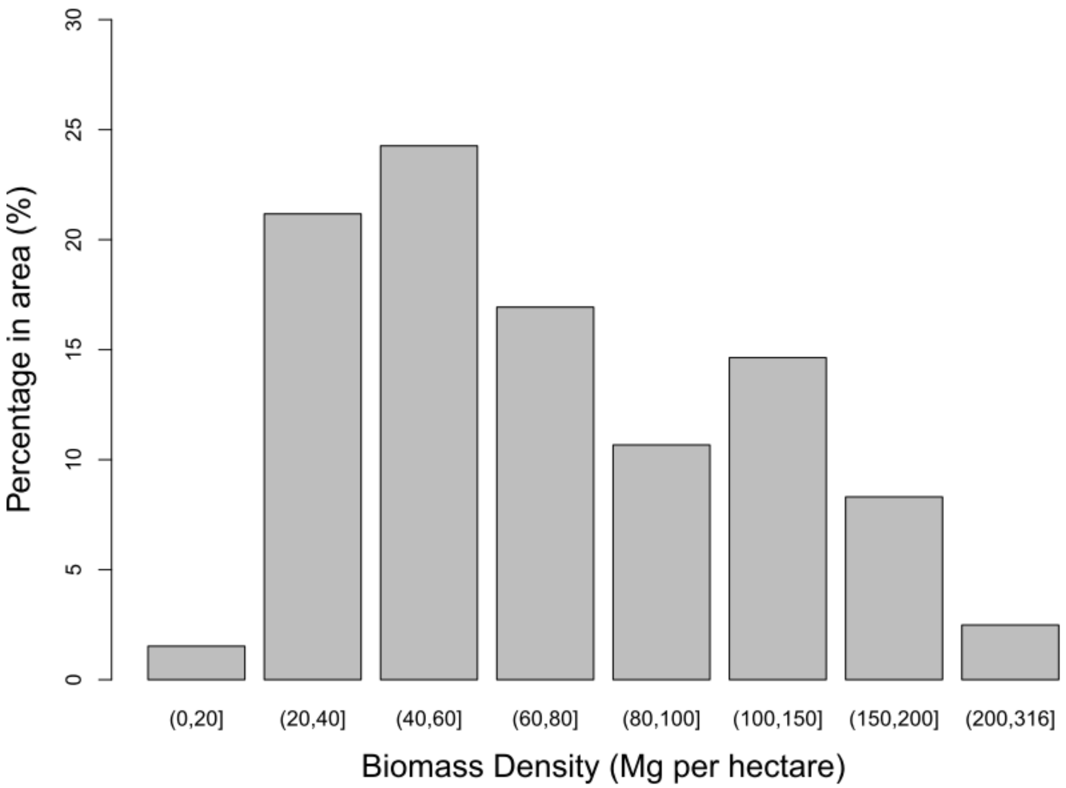


Figure 3.4 Histogram of forest biomass density based on the estimate of decision-tree based modeling

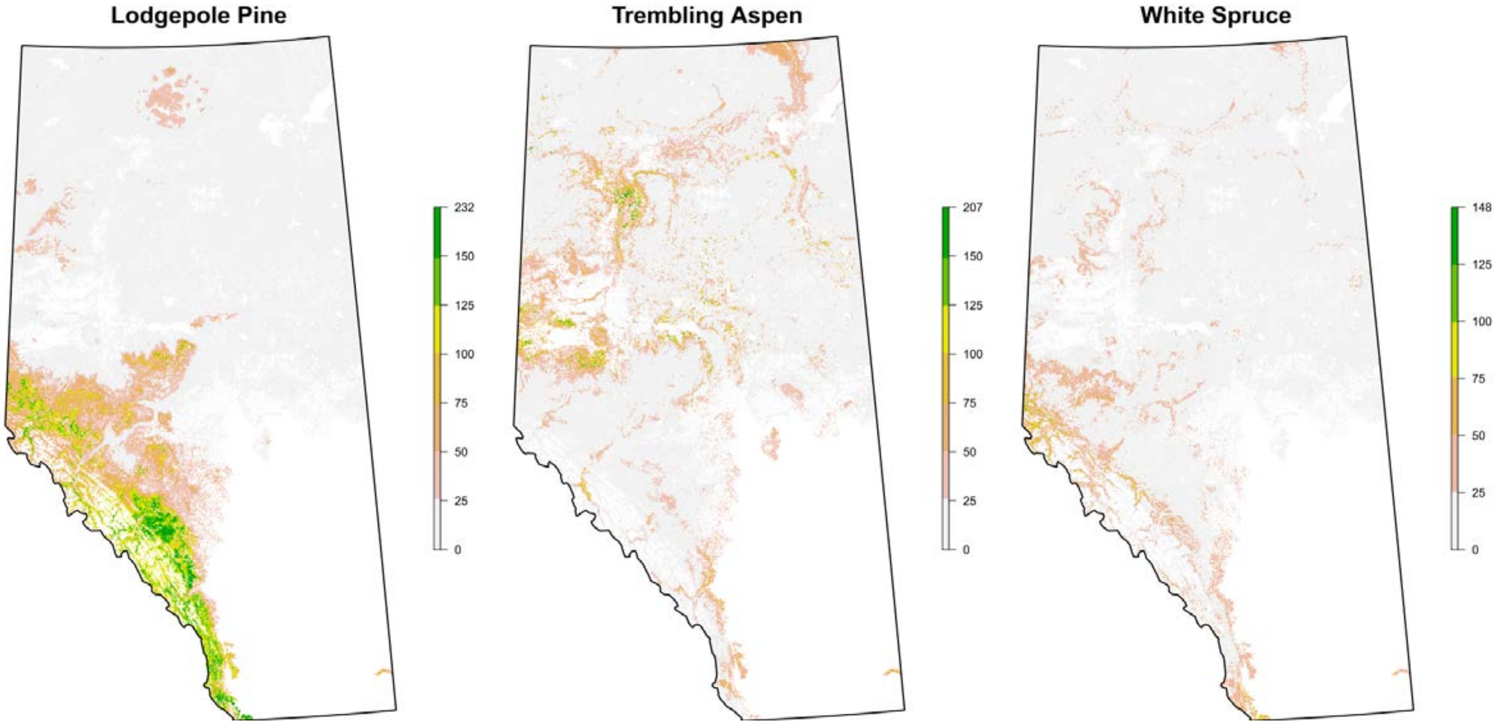


Figure 3.5 Total tree biomass density (Mg ha^{-1}) of three major tree species based on decision-tree based modeling (Projection: UTM zone=11; spatial resolution: 1-km)

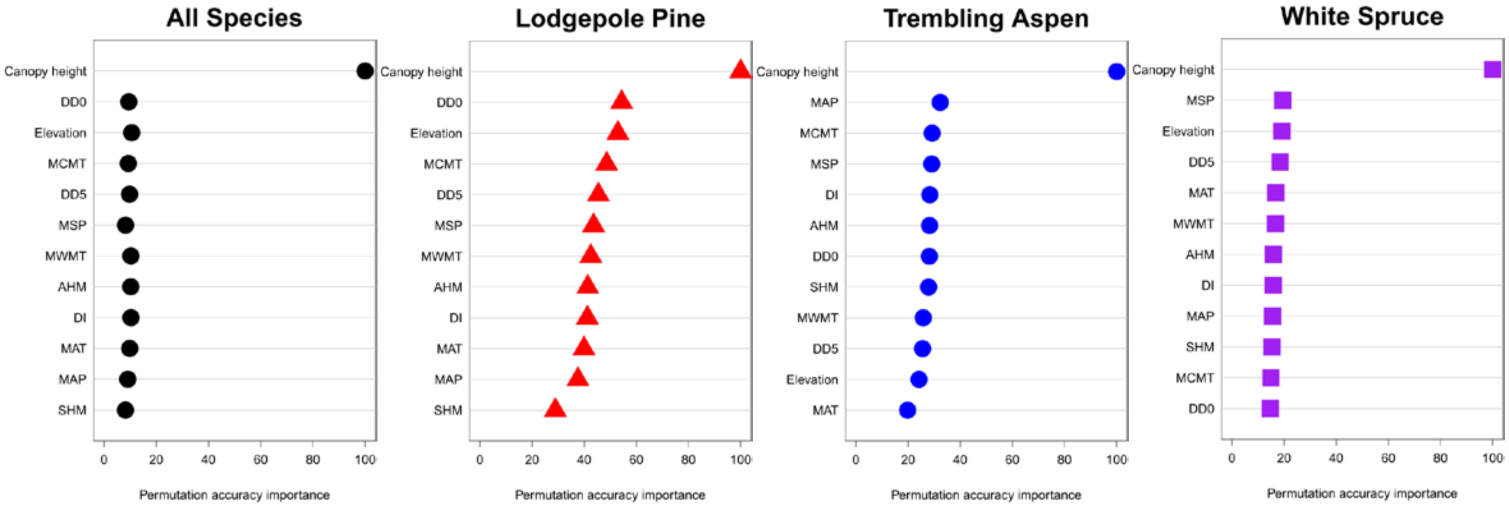
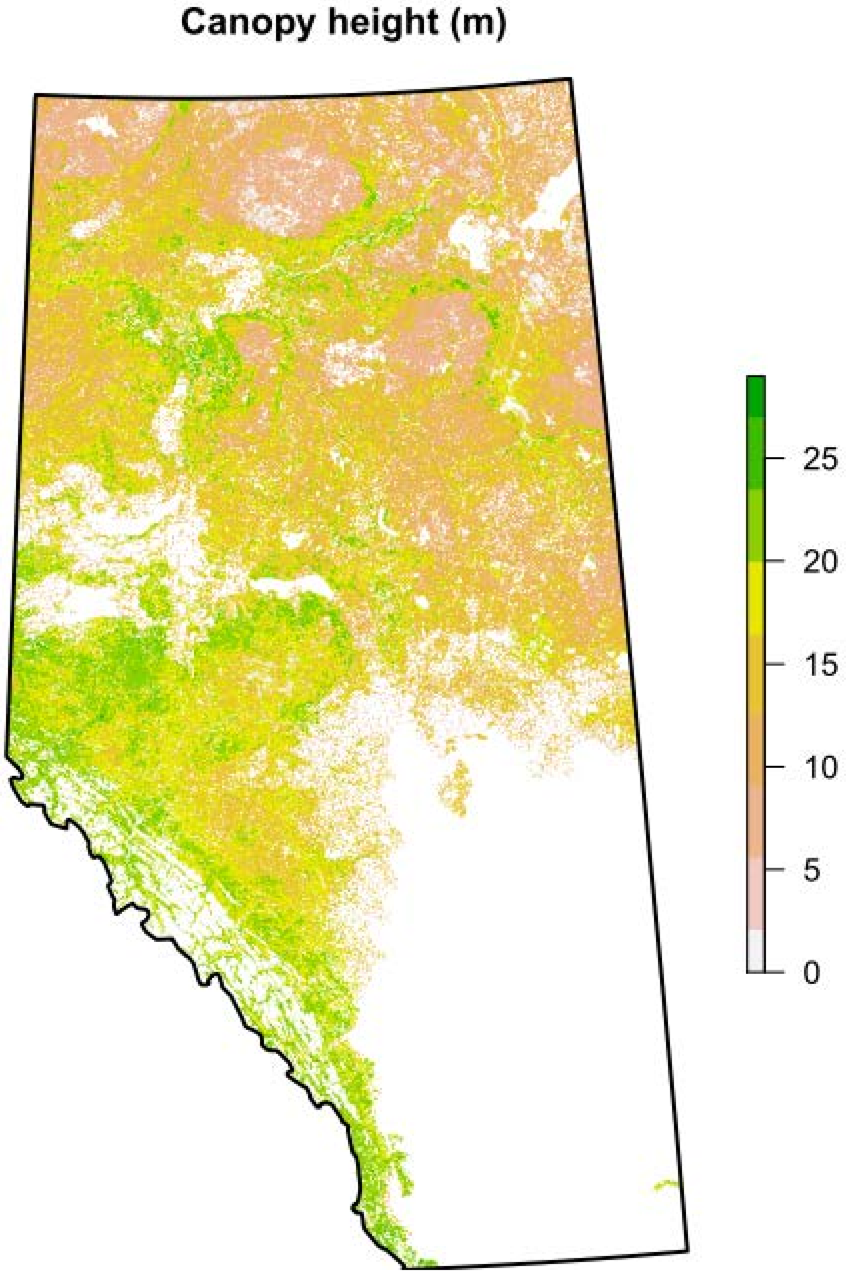


Figure 3.6 Relative variable importance of biomass predictions by decision-tree based modeling

NOTE: Variable importance is measured in mean decrease in accuracy, which is the decrease in accuracy of a classification after the variable has been randomly permuted. A higher mean decrease in accuracy means the variable contributes more to the accuracy of the classification.

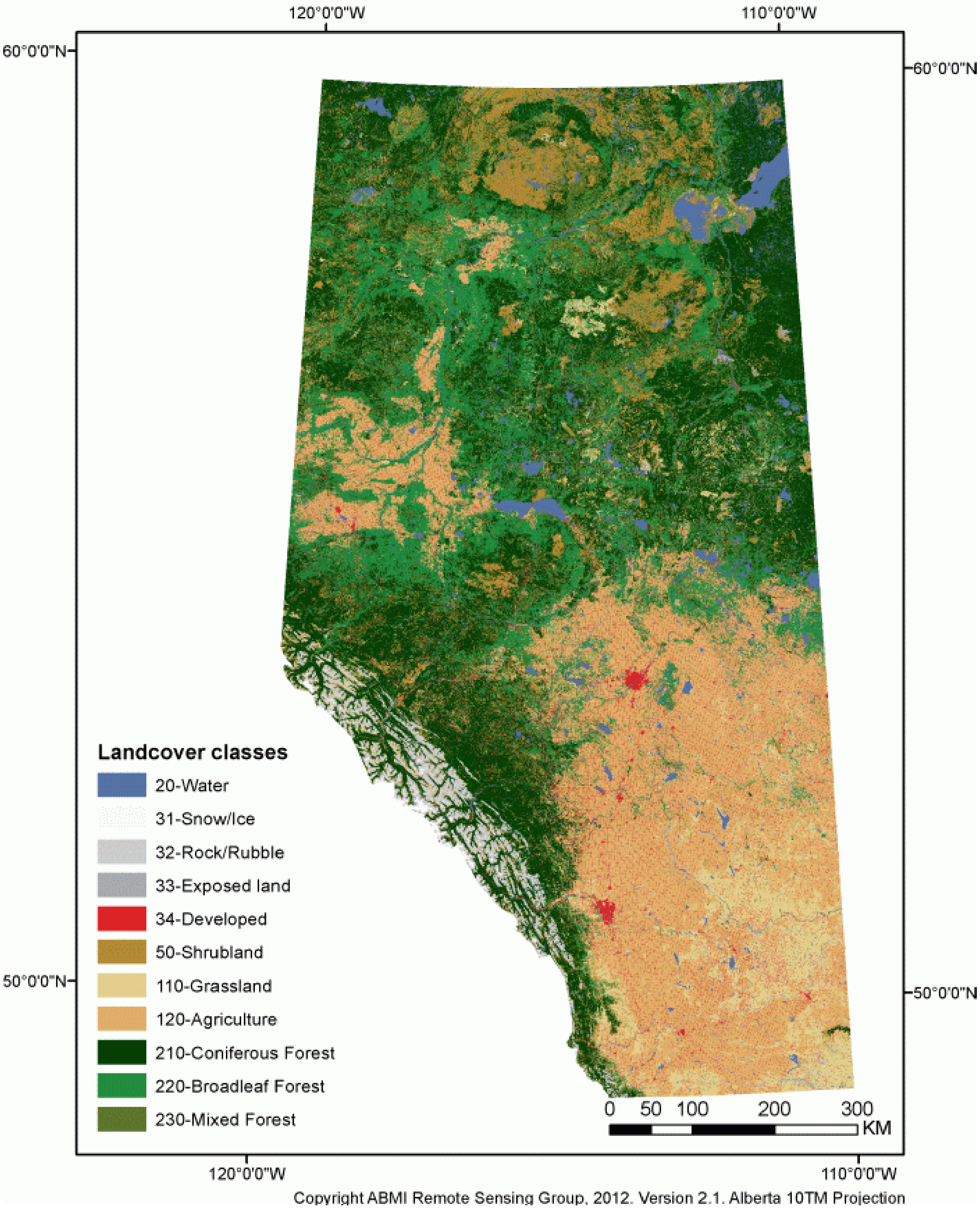
Appendix 3A Canopy height map from space-borne Lidar

Projection: UTM zone=11; spatial resolution: 1-km.



Appendix 3B Alberta wall-to-wall land cover map

(Source: www.ABMI.ca)



Copyright ABMI Remote Sensing Group, 2012. Version 2.1. Alberta 10TM Projection

Chapter 4 Local Forest Structure, Climate and Human Disturbance Determine Regional Distribution of Boreal Bird Species Richness in Alberta[2]

Summary

Aim: It is challenging to disentangle how local habitat structure, climate, and human disturbance interplay to determine broad-scale variation of species richness. Here, I separated various measures of local forest structure and composition, abiotic factors, and human land cover that constrain species richness of bird guilds in the boreal forest.

Methods: Data on breeding birds, habitat structure, climate and human footprints in 206 sites were sampled, with each site centered on an area of 1-ha in size. The 206 sites cover a large geographical extent with the distance of approximately 1000 km between the most distant sites. Bird guild species richness was modeled as a function of forest structure and composition (woody plant richness, forest biomass, number of vegetation layers, canopy openness), abiotic environment (temperature, precipitation, elevation), and percentage area of human land cover. I classified bird species into different guilds based on dietary preference, habitat specialization and migratory status, and used structural equations to quantify the effects and strengths of predictor variables.

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[2] A version of this chapter has been published in ***JOURNAL OF BIOGEOGRAPHY***. DOI: 10.1111/jbi.12063.

Results: I found that temperature, low levels of human land cover, woody plant richness and number of vegetation layers had strong positive correlations with overall bird species richness in the boreal forest. Moreover, local forest structure and composition showed a pronounced variation in its relationships with species richness of different guilds. Insectivores, old-growth forest specialists, forest generalists, long-distance migrants and winter residents showed strong positive correlations with woody plant richness, whereas old-growth forest specialists and winter residents were strongly related to forest biomass. The number of vegetation layers was positively related to species richness of most guilds, whereas the response to canopy openness was most pronounced for old-growth forest specialists and winter residents (being negatively correlated).

Main conclusions: In addition to climate and human disturbance, local forest structure and composition are important determinants to broad-scale variations in bird species richness in boreal forest. However, the strength and direction (positive/negative) of determinants is guild-specific, suggesting a strong functional component to community structure.

4.1 Introduction

Understanding the mechanisms and determinants of species diversity patterns is of central interest in ecology and biogeography. For birds and other terrestrial vertebrates, geographical variation in species richness across broad spatial extents is related to abiotic and biotic variables, including climate and energy availability (Wright 1983; Currie 1991; Hawkins *et al.* 2003; Hurlbert & Haskell 2003;

Hansen *et al.* 2011), habitat heterogeneity (Kerr & Packer 1997), food resources (Kissling *et al.* 2007), and human disturbance (Lepczyk *et al.* 2008; Devictor *et al.* 2008; Desrochers *et al.* 2011). At local spatial scales, the importance of habitat conditions and vegetation structural complexity has long been emphasized (MacArthur & MacArthur 1961). However, the relative importance of determinants of species richness varies widely, possibly because mechanisms are scale-dependent, i.e. they vary with the grain size and spatial extent of the sampling units (Levin 1992; Willis & Whittaker 2002; Qian & Kissling 2010). While climatic variables have been widely examined as determinants of species richness across scales, the importance and scale-dependence of biotic drivers remains less clear (Field *et al.* 2009).

Variation and scale-dependence in the relative importance of broad-scale biotic determinants of species richness is reflected in contradictory findings of plant–bird richness analyses. For example, in North American forests, James & Wamer (1982) showed a positive relationship between woody plant and bird richness using local bird census data, while Currie (1991) found that birds showed weak associations with tree species richness when using coarse-grained grid cells. One possible reason for these inconsistencies is that detailed and accurate information on several key variables (e.g. plant species distributions and vegetation structure) is incomplete (Willson & Comet 1996). Also, spatial scale (i.e. the spatial grain or resolution of analysis units) matters (Willis & Whittaker 2002; Qian & Kissling 2010). At local spatial scales, i.e. within habitat patches (Willis & Whittaker 2002) or at grain sizes < 10 km^2 (Field *et al.* 2009), previous studies have looked into determinants of forest bird species richness at one or a few study sites, while analyses of local (i.e. fine-grained) data across broad-scale gradients have been scarce. In contrast, most studies on large-scale patterns of bird species richness have used coarse grain sizes (e.g. 50 km × 50 km grid cells) for which the quantification of local habitat structure and composition is largely overlooked. Hence, it remains essential to link local-scale observations across large geographical extents for understanding bird diversity across scales. Few studies have analysed local-scale forest bird data across such broad spatial extents with the aim of testing the relative importance of local habitat structure and composition versus broad-scale environmental gradients.

To improve our understanding of species richness patterns it is important to quantify whether, and to what extent, determinants vary with specific traits or natural history characteristics of species (Carnicer & Díaz-Delgado 2008; Kissling *et al.* 2012). Bird-specific traits, such as dietary preference, habitat specialization and migratory behaviour, constrain demographic dynamics and population parameters and thus influence species distributions and richness variation across large geographical extents (Carnicer *et al.* 2012). For example, the dietary preference of a bird species represents a fundamental aspect of its ecological niche, and determines a species' functional role in an ecosystem (Kissling *et al.* 2012). Similarly, the degree of habitat specialization can strongly constrain the presence/absence and abundance of bird species along broad-scale environmental gradients (Devictor *et al.* 2008). While some previous broad-scale studies have examined the relative importance of predictor variables for species richness of some selected guilds (e.g. dietary guilds: Kissling *et al.* 2012), comprehensive assessments of those determinants for various bird guilds across broad geographical extents are rare.

In this study, I used a spatially fine-grained (< 1 km^2 resolution) data set covering a large geographical extent (almost 1000 km between the most distant sites) to analyse biotic and abiotic determinants of spatial variation in bird species richness across the boreal forest in Alberta, Canada. The boreal forest is the largest terrestrial biome in the world, containing about one third of the Earth's forest. Birds are the richest vertebrate taxon in the forest, comprising approximately 75% of all terrestrial vertebrate species (Niemi *et al.* 1998). In contrast to tropical and temperate forests, the proportion of migratory bird species generally exceeds that of permanent residents (Niemi *et al.* 1998). However, our understanding of the determinants of boreal bird species diversity is still limited in comparison with that of other forest ecosystems (Cumming *et al.* 2010), largely owing to the limited availability of comparable data for bird species and the shortage of standard sampling techniques in the boreal region. I examined bird species richness in relation to abiotic environment (temperature, precipitation and elevation), human land cover, and local forest structure and composition (woody plant richness, forest biomass, number of vegetation layers and canopy openness), and classified bird species into different guilds based on dietary preference, habitat specialization and migratory status. I was specifically interested to test how the relationships between bird species richness and biotic and abiotic variables vary among guilds, and how various measures of local forest structure and composition are related to guild species richness after statistically accounting for abiotic environmental determinants across a large spatial extent.

4.2 *Materials and Methods*

Study Sites

The study was conducted at 206 sites in the boreal forest region in Alberta, Canada (Figure 4.1), and included all the boreal forest sites maintained by the Alberta Biodiversity Monitoring Institute (ABMI). ABMI conducts a broad-scale, long-term monitoring programme on tracking biodiversity status and trends in Alberta (http://www.ABMI.ca). The boreal region has short summers (only 1 or 2 months have average daily temperatures exceeding 15 ^{o}C) and long and cold winters (average daily temperatures are below –10 ^{o}C for 4 months or more) (Natural Regions Committee 2006). Precipitation follows a summer-high continental pattern, with peak rainfall occurring in July and about 60–70% of the annual precipitation falling between April and August. Elevations range from about 150 m near the Alberta–Northwest Territories border to over 1100 m near the Alberta–British Columbia border. As the largest natural region in Alberta, this region has vast deciduous, mixedwood, and coniferous forests interspersed with extensive wetlands. Due to varying climate and topography in this area, tree species composition and structure vary greatly across the study area. Main tree species include aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*).

Data Collection

I recorded the presence of breeding birds and characterized the abiotic environment, human land cover, and several measures of local forest structure and composition for each of the study sites. Predictor variables used have previously been shown to influence bird species richness at various spatial scales (MacArthur & MacArthur, 1961; Cody, 1985; Hawkins *et al.* 2003; Kissling *et al.* 2008, 2012). Descriptive statistics of those variables across my study sites are provided in Table 4.1.

Breeding birds were surveyed at nine point count stations at each ABMI site during the breeding season (June) in the years 2003–2010. Point count stations were arranged in a gridded pattern with one point count station located at the centre and the remaining stations located 300 m apart surrounding the centre. An omnidirectional microphone (Compression Zone Microphone, developed by River Forks Research Corporation, Chilliwack, BC, Canada) was used to digitally record singing birds for 10 minutes at each of the nine stations. All audio recordings were later interpreted by a single expert in a standardized laboratory setting. I used the number of recorded bird species to indicate species richness at each site.

To characterize the abiotic environment, I included mean annual temperature (TEMP, related to ambient energy), mean annual precipitation (PREC, related to water availability), and absolute elevation (ELEV, characterizing topography) (Table 4.1). Climate data for the temperature and precipitation variables were derived from the program CLIMATEAB 3.22 (Wang *et* *al.* 2006). This program uses baseline climate data derived from monthly precipitation and temperature grids (Daly *et al.* 2008) based on interpolated climate data from weather stations for the period 1961–1990 (only for USA and Canada). The program includes a lapse-rate based down-sampling to 1-km resolution and estimation of biologically relevant climate variables (Wang *et al.* 2006). Based on input values for longitude and latitude of each ABMI site, I localized the annual climate variables (PREC and TEMP) from the last 10 years (2000–2009) and then used the average values across the 10 years to describe local climatic conditions of each site. ELEV was extracted from Alberta Digital Elevation (DEM) data with the resolution of 100 m for each site.

To characterize the influence of human disturbance (HUMAN) on bird species richness I used land cover data derived from manually interpreting aerial photography of photoscale 1:30,000 and SPOT satellite imagery within 500 m distance from the centre of each ABMI site. Land cover types considered to characterize strong human influence on forest bird species richness included agriculture, forest harvesting, roads, and urban and industrial areas. The percentage area of these land cover types within a 500 m radius from the centre of each site was used to quantify human influence.

I derived four variables to describe local forest structure and composition for birds at my study sites (Table 4.1). Woody plant richness (WOODY) was surveyed within a 1-ha (hectare) square plot (100 m × 100 m) in the centre of each ABMI site. The plot was divided into four 0.25-ha subplots, and all vascular plants were surveyed during July for each subplot using 20-minute area-restricted searches. I only included the number of woody plant species (trees and shrubs) as they are the most important plant species to characterize bird habitat in forested ecosystems (Cody 1985).

As a second habitat variable, I quantified stand biomass (BIOMASS) in the 1-ha plot at each site. BIOMASS reflects the accumulative effect of past growth of trees (Elo *et al.* 2012) with larger BIOMASS possibly implying a higher production rate of many critical resources for birds, such as invertebrate prey, seeds and other plant food resources, cover from predators, as well as nesting and roosting sites. All trees with ≥ 25 cm diameter at breast height (d.b.h.) in 25 m × 25 m plots, all trees with ≥ 7 cm d.b.h. in 10 m × 10 m subplots, and all trees regardless of size in 5 m × 5 m subplots were measured for d.b.h.. Above-ground biomass was then estimated for each site using d.b.h.-based biomass equations and tree species-specific parameters as provided by Lambert *et al.* (2005) and Ung *et al.* (2008). These equations were derived from thousands of trees sampled across Canada and allow the calculation of tree biomass (foliage, branches, stem bark, and stem wood) based on d.b.h. measurements (for details see Lambert *et al.* 2005 and Ung *et al.* 2008). Total biomass of each site was summed up from three parts: the biomass per hectare of trees with ≥ 25 cm d.b.h. in 25 m × 25 m plots, the biomass per hectare of trees with 7–25 cm d.b.h. in 10 m × 10 m subplots, and the biomass ha^{-1} of trees with < 7 cm d.b.h. in 5 m × 5 m subplots.

As a third habitat variable I included the number of vegetation layers (LAYERS) as recorded in a 150 m radius around each bird point count station at each ABMI site. A total of five vegetation layers were distinguished: veteran layer (defined as the layer of trees older than the rest of the stand and usually a remnant from a previous forest), dominant canopy layer, suppressed canopy layer, upper shrub layer (> 1.3 m), and lower shrub layer (< 1.3 m). I determined the number of vegetation layers for each point count station and then used the average values of the nine point count stations as the number of vegetation layers at each site.

As a fourth measure of bird habitat structure, I included canopy openness (CANOPY) estimated with a spherical (concave) densitometer held at elbow height (i.e. with arm bent at a right angle). Canopy openness was measured at eight locations per site (two readings at each of the four 10 m × 10 m quadrats). I calculated the average canopy openness at each site by averaging values of the four quadrants: values for canopy openness ranged from 0 (closed canopy) to 96 (high canopy openness).

Bird Guild Classification

I classified all bird species (BIRDS) into functional groups (termed ‘guilds’ here) according to their dietary preferences, habitat specialization, and migratory status. Similar to previous publications (Carnicer & Díaz-Delgado 2008; Kissling *et al.* 2012), species were classified according to the major fraction of their diet. Dietary guilds were distinguished following their major food types during the breeding season (De Graaf *et al.* 1985; Canadian Wildlife Service 2005): (1) insectivores (Diet_INS, feeding predominantly on insects); (2) omnivores (Diet_OMN, feeding on both animals and plants); and (3) carnivores (Diet_CARN, feeding predominantly on vertebrates). Nine species (‘not classified’ in Appendix 4A) were not included because they belonged to other dietary guilds (e.g. granivores, piscivores, frugivores) for which sample sizes were too small for my analysis. Habitat guilds were distinguished based on species' preferences and dependence on forest habitat (ABMI, 2009): (1) old-growth forest specialists (Hab_FORSPEC, defined as species which depend on forests older than 80 years for living/reproduction during the breeding season and have higher densities in old-growth forests than in other vegetation types); (2) forest generalists (Hab_FORGEN, defined as species depending on forests for living/reproduction and having higher densities in forest than in other vegetation types, but excluding Hab_FORSPEC); (3) habitat generalists [Hab_GENERAL, defined as species inhabiting various habitat types during the breeding season, but excluding (1) and (2)]. Finally I distinguished migratory guilds depending on the migratory behaviour of species (Godfrey, 1986; Canadian Wildlife Service, 2005; ABMI, 2009): (1) long-distance migrants (Mig_LONG, i.e. neotropical migrants defined as birds breeding in North America during the spring and early summer but spending the winter in Mexico, the Caribbean, and Central and South America); (2) short-distance migrants (Mig_SHORT defined as birds that migrate to southern Canada, coastal Canada, or the USA for the winter); and (3) winter residents (Mig_RESI defined as birds remaining in Alberta during the winter). Species that did not fit into a guild category were excluded from guild-specific analyses.

Statistical Analysis

I first used simple Pearson correlations to explore covariation among variables (Table 4.2). I then used structural equation models (SEMs) (Grace 2006) to investigate direct and indirect effects of abiotic environment, human land cover, and local forest structure and composition on species richness of terrestrial breeding birds and of dietary, habitat and migratory guilds. SEMs allow partitioning of the correlations between predictor and response variables into direct and indirect effects and thus enable the evaluation of hypothesized causal relationships in data sets with more than one dependent variable and effects of dependent variables on one another (Grace 2006). Based on previous analyses of broad-scale patterns of bird and vertebrate species richness (e.g. Kissling *et al.* 2007, 2008; Qian & Kissling 2010), I designed a set of SEMs with the aim of specifically assessing the relative importance of local forest structure and composition (and environmental and human determinants) on terrestrial bird and guild species richness across my study sites. I developed four a priori theoretical SEMs (Figure 4.5) with abiotic environmental variables (TEMP, PREC, ELEV), human land cover (HUMAN), and the four measures of forest structure and composition (WOODY, BIOMASS, LAYERS, CANOPY). The structures of the four a priori SEMs were the same except for the local forest structure variable which was substituted in each model (Figure 4.5). This was carried out to specifically test the influence of different forest structure and composition variables on bird richness. To test how abiotic environment, human land cover, and local forest structure and composition influence the species richness of guilds, I used the same a priori theoretical SEM structure (Figure 4.5), but interchanged BIRDS with the respective guild richness variable (Diet_INS, Diet_OMN, Diet_CARN, Hab_FORSPEC, Hab_FORGEN, Hab_GENERAL, Mig_LONG, Mig_SHORT, or Mig_RESI; see Figures 4.6-4.9).

To develop the final SEMs, I started with the initial a priori SEMs and then evaluated their residual correlations, modification indices, and model fits when implementing them for a specific bird guild. Missing paths were identified from large residuals and high modification indices and subsequently accounted for by adding error covariances between pairs of variables. This was repeated until satisfactory measures of model fit were obtained. I used the chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit. The following criteria were used to indicate SEMs with a satisfactory fit: (1) P-values of chi-square tests > 0.05; (2) lower 90% confidence intervals of RMSEA < 0.05; and (3) CFIs > 0.90. In a final step, I deleted non-significant paths (with $P > 0.05$) in SEMs with satisfactory model fit and reassessed model fits. All final SEMs had P-values of chi-square tests > 0.1, lower 90% confidence intervals of RMSEA equal to 0, and CFIs > 0.98.

Because the presence of spatial autocorrelation in model residuals violates the assumption of data independence, I additionally assessed to what extent residual spatial autocorrelation exists and whether its inclusion would change the relative importance and statistical significance of explanatory variables (Mauricio Bini *et al.* 2009). To assess spatial autocorrelation I calculated Moran's I values on the residuals of non-spatial multiple regression models (ordinary least squares, OLS) using the same variables as in the SEMs (i.e. abiotic environment, human land cover and forest structure and composition as predictors, and bird richness as the response), and then fitted spatial linear models [here ‘spatial simultaneous autoregressive error models (SARs)’; Kissling & Carl 2008], which allow the inclusion of the residual spatial autocorrelation of the data. I then compared the relative importance of predictor variables from OLS models with those of SARs by calculating the standardized partial regression coefficients of all predictor variables (cf. Kissling *et al.* 2008). For the non-spatial (OLS) models, these standardized partial regression coefficients are equivalent to the direct effects on species richness in my SEMs.

All statistical analyses were carried out using R 2.15.0 software (R Development Core Team 2012). Pearson correlation coefficients after accounting for spatial autocorrelation were calculated with the R library MODTTEST 1.4 (José Manuel Blanco Moreno, Universitat de Barcelona, Catalonia, Spain, pers. comm.), the SEMs were calculated with the R library LAVAAN 0.4-13, and Moran’s *I* values and SARs were calculated using the R library SPDEP 0.5-33. The spatial weight matrices of the SARs and the Moran’s *I* values were calculated with the nearest neighbour and a row-standardized coding style (Kissling & Carl 2008). To improve normality and linearity in my models, I log-transformed species richness of overall birds and bird guilds, TEMP, PREC and WOODY, and square-root-transformed ELEV, HUMAN, BIOMASS and CANOPY for all statistical analyses.

4.3 Results

Geographical Variation of Bird Species Richness and Environments

A total of 134 breeding bird species were recorded across the 206 boreal sites (Figure 4.1, Appendix 4A). Overall bird species richness per site ranged from 10 to 55, with an average of nearly 29 species per site (Table 4.1) and about 80% of the sites having > 20 species (Figure 4.1). Species richness of guilds per site ranged from 0 to 35 species (Table 4.1), with only two guilds (Diet_CARN and Hab_GENERAL) having less than 20 species. Spatial patterns of species richness of some guilds (e.g. Diet_INS, Diet_OMNI, Hab_FORGEN) were similar to overall bird richness whereas most other guilds showed idiosyncratic patterns (Figure 4.10). Abiotic environmental conditions across my study sites were characterized by a mean TEMP of *c.* 1 °C, almost 440 mm PREC, and a mean absolute ELEV of *c.* 590 m (Table 4.1). However, there was a clear spatial trend in TEMP and PREC decreasing from the south to the north (Figure 4.11). On average, human-modified land cover types covered about 8% of the 500 m radius centred at the site (Table 4.1), but peaked at some sites with HUMAN > 70% (Figure 4.11). Measures of forest structure and composition also showed large variations across sites (Figure 4.11) with on average; 18 woody plant species, a stand biomass of about 86 Mg/ha, 3.5 vegetation layers and a canopy openness of 46% (Table 4.1).

Determinants of Overall Bird Species Richness

I examined the direct and indirect effects of predictor variables on overall bird species richness using four SEMs (Figure 4.2a–d). In all SEMs, TEMP had the strongest direct (and positive) correlation with BIRDS among all predictor variables followed by HUMAN (positive effect) and ELEV (negative effect) (Figure 4.3). The correlation between PREC and BIRDS was statistically not significant and thus removed in the final SEMs (Figure 4.2). Among the four forest structure variables, WOODY showed the strongest (positive) effect followed by LAYERS (positive), with BIOMASS and CANOPY being unimportant for BIRDS in the boreal forest (Figure 4.2a–d, 4.3). Overall, the results for the overall bird species richness supported my hypotheses except for HUMAN, BIOMASS and CANOPY. The effect of HUMAN was positive (instead of negative) and the strength of BIOMASS and CANOPY was much less pronounced than expected.

Determinants of Guild Species Richness

Simple Pearson correlations between guild species richness and my predictor variables indicated large variations in the correlations between them (Table 4.3). SEM models with guild species richness similar in structure to those of BIRDS confirmed this variation of guild-specific responses (Figure 4.6-3.9). Overall, the direction of the relations between guild richness and abiotic environment (TEMP, PREC, ELEV) and HUMAN were similar to those of BIRDS in most cases although the strength of the correlations varied markedly among guilds (Figure 4.4). For instance, TEMP was markedly related to species richness of most guilds, PREC had weak or no effects on all guilds, ELEV showed the strongest (negative) correlation on long-distance migrants, and HUMAN showed strong positive correlations on most guilds (except carnivores).

Local forest structure and composition variables also showed a pronounced variation in their relationships with species richness of the various bird guilds (Figure 4.4). Insectivores, old-growth forest specialists, forest generalists, long-distance migrants and winter residents showed strong positive correlations with WOODY, whereas old-growth forest specialists and winter residents were also strongly related to BIOMASS as well (Figure 4.4). LAYERS showed positive correlations with almost all guilds (except carnivores and short-distance migrants), whereas the correlations with CANOPY varied markedly among guilds, with old-growth forest specialists being most strongly negatively related (Figure 4.4). Overall, these results supported the idea that bird guilds with different dietary, habitat and migratory preferences showed differential or contrasting responses to environmental and habitat structure conditions.

Effects of Spatial Autocorrelation

Some of the non-spatial multiple (OLS) regression models (equivalent to the SEMs) showed a statistically significant spatial autocorrelation structure in model residuals (Table 4.3). When spatial regression models (SARs) were used, the spatial autocorrelation structures in species richness were removed as indicated by non-significant Moran's *I* values (Table 4.3). In almost all cases, the relative importance and ranks of predictor variables, based on standardized partial regression coefficients, did not change between spatial and non-spatial models (Table 4.3). Therefore, the effects of spatial autocorrelation on the results of my analyses were negligible.

4.4 Discussion

My analyses clearly showed that bird species richness patterns in the boreal forest are related to a combination of climate, human land cover, and local forest structure and composition. The importance of these determinants varies markedly among guilds. For instance, my results suggest that some determinants (e.g. forest biomass and canopy openness) are guild-specific, whereas other determinants (e.g. temperature, elevation, and human land cover) have similar effects across most guilds. This indicates that the overall response of bird community composition to biotic and abiotic drivers is guild-specific, suggesting a strong differentiation in behaviour of the guilds and their varied adaptation to different habitats; there is no unified mechanism linking these drivers with species richness.

Among predictor variables, mean annual temperature (TEMP) was found to be a key determinant of bird species richness in the boreal forest across guilds (Figures 4.3, 4.4, 4.6-4.9). These results support the ambient energy hypothesis (Wright 1983; Hawkins *et al.* 2003) and suggest that bird diversity at high latitudes is directly controlled via an effect of ambient energy [e.g. temperature or potential evapotranspiration (PET)] at the individual organism level (Currie 1991; Hawkins *et al.* 2003). This effect could be mediated via the physiological tolerances of individual species (Hawkins *et al.* 2003), via an increase of bird population growth and reproduction at high temperatures (Hawkins *et al.* 2003), or via accelerated evolutionary rates over evolutionary time-scales (Gillman *et al.* 2012). For some guilds (e.g. winter residents) the direct effects of temperature on species distributions might be even more pronounced if seasonal climatic extremes (e.g. severe winter conditions) are directly considered (Carrascal *et al.* 2012). Overall, the strong direct effects of temperature on bird richness of almost all guilds indicate that variation in guild species richness in the boreal forest is strongly temperature dependent. This suggests that future climate change (i.e. rising temperatures) is likely to have strong effects on bird guild species richness in the boreal forest. Compared with other terrestrial ecosystems in the tropics, subtropics, and temperate zones, the boreal forest is expected to experience the greatest increase in temperature (Houghton *et al.* 1996), which may result in pervasive impacts on temperature-dependent bird distributions (Hitch & Leberg 2007; Brotons & Jiguet 2010). In contrast, the direct effect of precipitation in my models was less pronounced (Figures 4.3, 4.4, 4.6-4.9), indicating that climate change in relation to temperature could be more important for boreal bird diversity than precipitation changes. However, future precipitation changes could also act indirectly on bird diversity, e.g. via woody plant richness and forest biomass, and such indirect effects could even occur with strong time-lags (Kissling *et al.* 2010), making precise predictions of future bird species composition and diversity challenging.

Bird species richness was strongly affected by the footprint of human disturbance, as measured by the percentage of agriculture, forest harvesting, roads, and urban and industrial areas in the surroundings. For almost all guilds, species richness increased with increasing human influence. One possible explanation of this positive (rather than negative) relationship in my study is that most of my study sites have relatively low levels of human land cover (Table 4.1, Figure 4.10). For instance, 78% of study sites have less than 10% human land cover and 86% of sites have less than 20% human land cover. At such low levels of human disturbance, it is possible that an increase in habitat heterogeneity is positively related to bird species richness. For instance, analyses of northern temperate forest landscapes across Ontario, Canada, show that almost half of the natural land cover can be converted to human-dominated forms before avian richness started to decline (Desrochers *et al.* 2011), although the abundance of individual species populations can be negatively affected by low levels of anthropogenic land cover (Lepczyk *et al.* 2008). Another possible explanation of this positive relationship is that human settlements may provide additional food resources for birds (Marzluff 2001). Also, it is possible that bird species may select environments that are similar to those of humans (Hansen *et al.* 2011).

In addition to broad-scale climatic gradients and human influence via land cover, local forest structure and composition emerged as an important driver of breeding bird species richness in the boreal forest. I detected a strong and positive relationship between woody plant richness and overall bird richness, supporting previous findings of local (i.e. fine-grained) studies from North America (James & Wamer 1982) and western Canada (Hobson & Bayne 2000) and results from broad-scale (i.e. coarse-grained) studies from China (Qian & Kissling 2010) and Kenya (Kissling *et al.* 2008). However, there were pronounced differences between bird guilds in the magnitude of responses to plant richness. Among dietary guilds, insectivores showed a much stronger association with WOODY than omnivores and carnivores, possibly because there is a larger number and higher abundance of insect species with increasing plant species richness (Danks & Foottit 1989; Blondel *et al.* 1991). Among habitat and migratory guilds, WOODY showed stronger effects on old-growth forest specialists, forest generalists, long-distance migrants and residents than on habitat generalists and short-distance migrants, respectively. Diverse food supplies and more nesting habitats for birds in the forests with high woody plant richness might be the main reason for these positive relationships.

Direct effects of stand biomass on overall bird species richness and most guilds (except old-growth forest specialists and residents) were weak in my study (Figures 4.3, 4.4), suggesting that stand biomass does not limit bird species diversity in the boreal forest of Alberta. These findings appear in contrast to several other studies which find strong effects of stand biomass on species richness of birds (Mitchell *et al.* 2001; Honkanen *et al.* 2010; Elo *et al.* 2012), but are not inconsistent when analysed on the basis of guilds. For guild-specific analyses, I found that stand biomass is a strong determinant of bird species richness of old-growth forest specialists and residents, being even stronger than temperature (Figure 4.4). These results are in line with those of Honkanen *et al.* (2010) who found that species richness of old-growth forest specialists and residents in boreal forests of Finland is strongly related to total volume and total growth of trees (compare my results with their results for ‘observed species richness’; Honkanen *et al.* 2010, their Tables 4 and 5). Old-growth forest specialists and residents are further strongly related to woody plant richness (positive), the number of vegetation layers (positive), and canopy openness (negative), suggesting that both guilds predominantly occur in closed and locally undisturbed forests.

The number of vegetation layers and canopy openness played a less important role in determining overall bird species richness although their relative importance was pronounced for some guilds (Figure 4.4). Species richness of old-growth forest specialists and forest generalists was most strongly (and positively) related to the number of layers, suggesting that those guilds strongly depend on the vertical structure and diversity of forest habitat (*sensu* MacArthur & MacArthur 1961). In contrast, canopy openness had a relatively strong negative effect on old-growth forest specialists and residents, especially when compared with the other direct effects in these SEMs (Figure 4.9). This highlights that these guilds depend on dense wood stands with little disturbance at a local scale. A possible mechanism could be that structural diversity provides a larger array of nesting locations and increases nesting success by reducing the ability of predators to find nests (Cody 1985). Overall, these results highlight the importance of vegetation structural diversity at a local scale for maintaining variation in bird richness across large spatial extents.

My findings have wide implications for the prediction of bird community composition, for biodiversity conservation, and forest management. First, my study highlights the importance of local forest structure and composition (i.e. woody plant richness, forest biomass, number of vegetation layers, and canopy openness) in complementing climate and land cover as determinants of bird species diversity across large spatial extents. This means that local influences (e.g. via forest management regimes) can substantially affect bird community composition and species richness distribution in addition to, or in conjunction with, broad-scale trends in climate and human disturbance. Second, my study further highlights the importance of spatially fine-grained data for assessing and measuring the relative effects of biotic versus abiotic determinants of species richness across large spatial extents, which might otherwise not be revealed (Field *et al.* 2009). In contrast to many previous macroecological studies, my analysis at $< 1\ \text{km}^2$ grain size shows that the effect of local habitat structure is readily detectable across large geographical extents.

In conclusion, my findings emphasize that biotic and abiotic determinants of bird species richness depend on local and regional factors and the life history traits of species. Thus, guidelines for biodiversity conservation and forest management should pay attention to the combined influence of local and regional factors, and to the specific requirements of diverse bird guilds. Beyond diet, habitat preference and migratory behaviour, other traits related to demographic rates, natal and breeding dispersal, competitive abilities or predator avoidance may also need consideration (Blaum *et al.* 2011; Carnicer *et al.* 2012). We see great potential for better understanding and predicting spatial variation in bird species richness and community composition by using data on species' traits and life history and by measuring local conditions across large geographical extents.

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Tables

Table 4.1 Descriptive statistics of abiotic environment, human land cover, local forest structure and composition, and bird guild species richness in the 206 study sites in Alberta

Variables	Abbreviation	Total	Mean	SD	Range
Abiotic environment					
Mean annual temperature (°C)	TEMP	-	0.95	1.06	-1.75–3.35
Mean annual precipitation (mm/yr)	PREC	-	440.35	40.60	296.10–529.00
Elevation above sea level (m)	ELEV	-	593.04	155.25	192.20–1190.50
Human land cover					
Percent human land cover types (%)	HUMAN	-	7.89	13.25	0.00–74.47
Local forest structure and composition					
Woody plant richness (no. of species)	WOODY	101	17.55	6.28	3–36
Stand biomass (Mg/hectare)	BIOMASS	-	85.95	90.74	0.01–480.05
Number of vegetation layers	LAYERS	-	3.52	0.61	0.67–4.56
Canopy openness (%)	CANOPY	-	46.08	26.30	1–96
Overall bird species richness					
All birds (no. of species)	BIRDS	134	28.43	9.85	10–55
Dietary guild richness					
Insectivore (no. of species)	Diet_INS	72	15.85	6.26	4–35
Omnivore (no. of species)	Diet_OMN	42	11.50	3.96	3–22
Carnivore (no. of species)	Diet_CARN	12	0.15	0.41	0–3
Habitat guild richness					
Old-growth forest specialist (no. of species)	Hab_FORSPEC	37	10.10	4.07	2–22
Forest generalist (no. of species)	Hab_FORGEN	43	11.46	4.25	3–24
Habitat generalist (no. of species)	Hab_GENERAL	17	2.10	1.66	0–8
Migratory guild richness					
Long-distance migrants (no. of species)	Mig_LONG	54	12.14	5.19	1–27
Short-distance migrants (no. of species)	Mig_SHORT	53	11.91	4.16	4–27
Winter residents (no. of species)	Mig_RESI	26	4.37	2.31	0–12

***NOTE**:* Mean ± standard deviation (SD) are given. Total numbers are only available for species richness data.

Table 4.2 Pearson correlation coefficients among bird guild species richness, abiotic environment, human land cover and local forest structure

Variables	BIRDS	**Dietary guilds**			**Habitat guilds**			**Migratory guilds**		
		Diet_INS	Diet_OMN	Diet_CARN	Hab_FORSPEC	Hab_FORGEN	Hab_GENERAL	Mig_LONG	Mig_SHORT	Mig_RESI
Abiotic environment										
TEMP	0.516***	0.469***	0.477***	0.125	0.388***	0.461***	0.415***	0.455***	0.475***	0.263*
PREC	0.212*	0.23**	0.128	0.04	0.177*	0.196*	0.077	0.153	0.269**	0.133
ELEV	0.166	0.172	0.145	-0.01	0.116	0.152	0.111	0.077	0.28**	0.086
Human land cover										
HUMAN	0.451***	0.388***	0.469***	0.066	0.286***	0.392***	0.397***	0.362***	0.443***	0.244**
Local forest structure										
WOODY	0.315***	0.395***	0.197*	0.087	0.418***	0.366***	0.123	0.347***	0.131	0.329***
BIOMASS	0.062	0.161*	-0.043	-0.15*	0.34***	0.048	-0.031	0.102	-0.127	0.296***
LAYERS	0.109	0.153*	0.081	-0.156*	0.204**	0.187**	0.07	0.148*	-0.012	0.157*
CANOPY	-0.084	-0.187*	0.002	0.111	-0.311***	-0.16*	-0.011	-0.17*	0.158*	-0.245**

***NOTE**:* Bird species richness, WOODY, TEMP, and PREC were log-transformed, while ELEV, HUMAN, BIOMASS, CANOPY, GPP and GPPJune were square-root-transformed. P-values were calculated after accounting for spatial autocorrelation using Dutilleul (1993)’s method: ****P* < 0.001; ***P* < 0.01; **P* < 0.05.

Table 4.3 Standardized partial regression coefficients from non-spatial (ordinary least squares, OLS) and spatial (spatial linear models, SLM) regression models with species richness for all birds and bird guilds as a response variables, and abiotic environment, human land cover and local forest structure as predictor variables

(a) Models with woody plant richness (WOODY)

Variables	**All**		**Dietary guilds**						**Habitat guilds**						**Migratory guilds**					
	BIRDS		Diet_INS		Diet_OMN		Diet_CARN		Hab_FORSPEC		Hab_FORGEN		Hab_GENERAL		Mig_LONG		Mig_SHORT		Mig_RESI	
	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
WOODY	0.238	0.249	0.345	0.403	0.118	0.128	\	\	0.378	0.378	0.299	0.304	\	\	0.283	0.291	\	\	0.293	0.296
TEMP	0.459	0.458	0.371	109.796	0.412	0.407	0.125	0.124	0.410	0.412	0.407	0.409	0.380	0.391	0.465	0.470	0.344	0.337	0.171	0.167
PREC	\	\	0.203	-0.003	\	\	\	\	\	\	\	\	\	\	-0.250	-0.265	\	\	\	\
ELEV	-0.179	-0.189	-0.269	0.493	-0.186	-0.188	\	\	-0.125	-0.130	-0.153	-0.158	-0.182	-0.180	\	\	0.283	0.283	\	\
HUMAN	0.264	0.262	0.210	0.403	0.324	0.316	\	\	\	\	0.214	0.212	0.280	0.242	0.190	0.188	\	\	0.125	0.126
Model R^2	0.401	0.409	0.392	109.796	0.345	0.348	0.016	0.020	0.302	0.313	0.358	0.360	0.249	0.267	0.359	0.370	0.289	0.291	0.172	0.193
Model AIC	44.482	44.578	110.643	-0.003	42.844	44.028	27.160	28.468	133.367	133.122	77.545	78.868	296.107	294.367	183.257	182.690	61.396	62.829	232.283	230.411
Errors Moran's *I*	0.114	0.001	0.142*	0.493	0.073	0.003	0.075	-0.003	0.125	-0.005	0.070	-0.002	0.156*	-0.003	0.134	-0.006	0.063	0.002	0.165*	-0.007

***NOTE**:* R^2, coefficient of determination; AIC, Akaike information criterion; Moran's *I*, measure of residual spatial autocorrelation (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Values from OLS analyses are identical to direct effects in structural equation models.

Table 4.3 Continuted-1

(b) Models with stand biomass (BIOMASS)

Variables	**All**		**Dietary guilds**						**Habitat guilds**						**Migratory guilds**					
	BIRDS		Diet_INS		Diet_OMN		Diet_CARN		Hab_FORSPEC		Hab_FORGEN		Hab_GENERAL		Mig_LONG		Mig_SHORT		Mig_RESI	
	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
PRODUC	\	\	0.007	0.007	\	\	-0.160	-0.159	0.336	0.326	\	\	\	\	\	\	-0.139	-0.138	0.296	0.311
TEMP	0.476	0.475	0.414	0.417	0.420	0.417	0.138	0.136	0.356	0.355	0.429	0.429	0.380	0.391	0.485	0.488	0.362	0.357	0.151	0.142
PREC	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
ELEV	-0.180	-0.186	-0.140	-0.147	-0.187	-0.188	\	\	-0.159	-0.160	-0.155	-0.158	-0.182	-0.180	-0.252	-0.262	\	\	\	\
HUMAN	0.289	0.286	0.252	0.249	0.336	0.331	\	\	0.194	0.194	0.245	0.241	0.280	0.242	0.220	0.215	0.266	0.265	0.192	0.194
Model R^2	0.346	0.350	0.293	0.299	0.331	0.332	0.041	0.045	0.289	0.294	0.270	0.273	0.249	0.267	0.281	0.291	0.307	0.310	0.174	0.207
Model AIC	60.712	61.671	139.787	140.490	45.065	46.735	23.731	25.200	139.257	140.218	101.907	103.359	296.107	294.367	205.065	204.950	57.864	59.405	231.658	227.513
Errors Moran's *I*	0.086	-0.001	0.096	-0.004	0.047	0.001	0.066	-0.003	0.085	-0.001	0.063	-0.002	0.156*	-0.003	0.122	-0.004	0.057	0.001	0.208**	-0.009

(c) Models with the number of vegetation layers (LAYERS)

Variables	**All**		**Dietary guilds**						**Habitat guilds**						**Migratory guilds**					
	BIRDS		Diet_INS		Diet_OMN		Diet_CARN		Hab_FORSPEC		Hab_FORGEN		Hab_GENERAL		Mig_LONG		Mig_SHORT		Mig_RESI	
	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
LAYERS	0.143	0.152	0.194	0.198	0.120	0.128	-0.155	-0.155	0.233	0.238	0.220	0.225	0.121	0.135	0.165	0.166	\	\	0.187	0.207
TEMP	0.457	0.456	0.352	0.351	0.403	0.399	0.124	0.123	0.306	0.305	0.398	0.402	0.376	0.382	0.462	0.469	0.344	0.337	0.175	0.172
PREC	\	\	\	\	\	\	\	\	\	\	\	\	-0.183	-0.179	\	\	\	\	\	\
ELEV	-0.164	-0.173	\	\	-0.173	-0.175	\	\	\	\	-0.129	-0.137	\	\	-0.232	-0.247	\	\	\	\
HUMAN	0.315	0.312	0.254	0.253	0.358	0.351	\	\	0.179	0.182	0.284	0.281	0.285	0.251	0.249	0.245	0.283	0.283	0.191	0.191
Model R^2	0.366	0.373	0.294	0.306	0.345	0.348	0.040	0.044	0.218	0.242	0.316	0.321	0.263	0.284	0.307	0.317	0.289	0.291	0.122	0.156
Model AIC	56.412	56.639	137.520	136.781	42.748	43.926	24.045	25.415	157.035	154.220	90.368	91.228	294.100	291.745	199.425	199.148	61.396	62.829	244.262	240.376
Errors Moran's *I*	0.113	-0.002	0.143	-0.005	0.074	0.001	0.072	-0.002	0.183*	-0.005	0.091	-0.002	0.170*	-0.005	0.127	-0.004	0.063	0.002	0.204**	-0.018

Table 4.3 Continuted-2

(d) Models with canopy openness (CANOPY)

Variables	**All**		**Dietary guilds**						**Habitat guilds**						**Migratory guilds**					
	BIRDS		Diet_INS		Diet_OMN		Diet_CARN		Hab_FORSPEC		Hab_FORGEN		Hab_GENERAL		Mig_LONG		Mig_SHORT		Mig_RESI	
	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
CANOPY	\	\	-0.146	-0.135	\	\	0.128	0.131	-0.278	-0.263	-0.109	-0.108	\	\	\	\	0.202	0.204	-0.227	-0.239
TEMP	0.476	0.475	0.345	0.345	0.420	0.417	0.141	0.140	0.282	0.280	0.406	0.407	0.383	0.387	0.485	0.488	0.375	0.369	0.156	0.146
PREC	\	\	\	\	\	\	\	\	\	\	\	\	-0.178	-0.171	\	\	\	\	\	\
ELEV	-0.180	-0.186	\	\	-0.187	-0.188	\	\	\	\	-0.143	-0.147	\	\	-0.252	-0.262	\	\	\	\
HUMAN	0.289	0.286	0.228	0.228	0.336	0.331	\	\	0.156	0.160	0.252	0.250	0.261	0.230	0.220	0.215	0.268	0.265	0.172	0.176
Model R^2	0.346	0.350	0.278	0.284	0.331	0.332	0.032	0.037	0.240	0.250	0.282	0.284	0.249	0.266	0.281	0.291	0.329	0.332	0.139	0.170
Model AIC	60.712	61.671	142.003	142.751	45.065	46.735	25.751	26.890	150.931	151.094	100.597	102.103	296.055	294.689	205.065	204.950	51.421	52.679	240.320	236.771
Errors Moran's I	0.086	-0.001	0.095	-0.003	0.047	0.001	0.084	-0.003	0.111	0.000	0.060	-0.002	0.149*	-0.002	0.122	-0.004	0.073	0.001	0.195**	-0.007

Figures

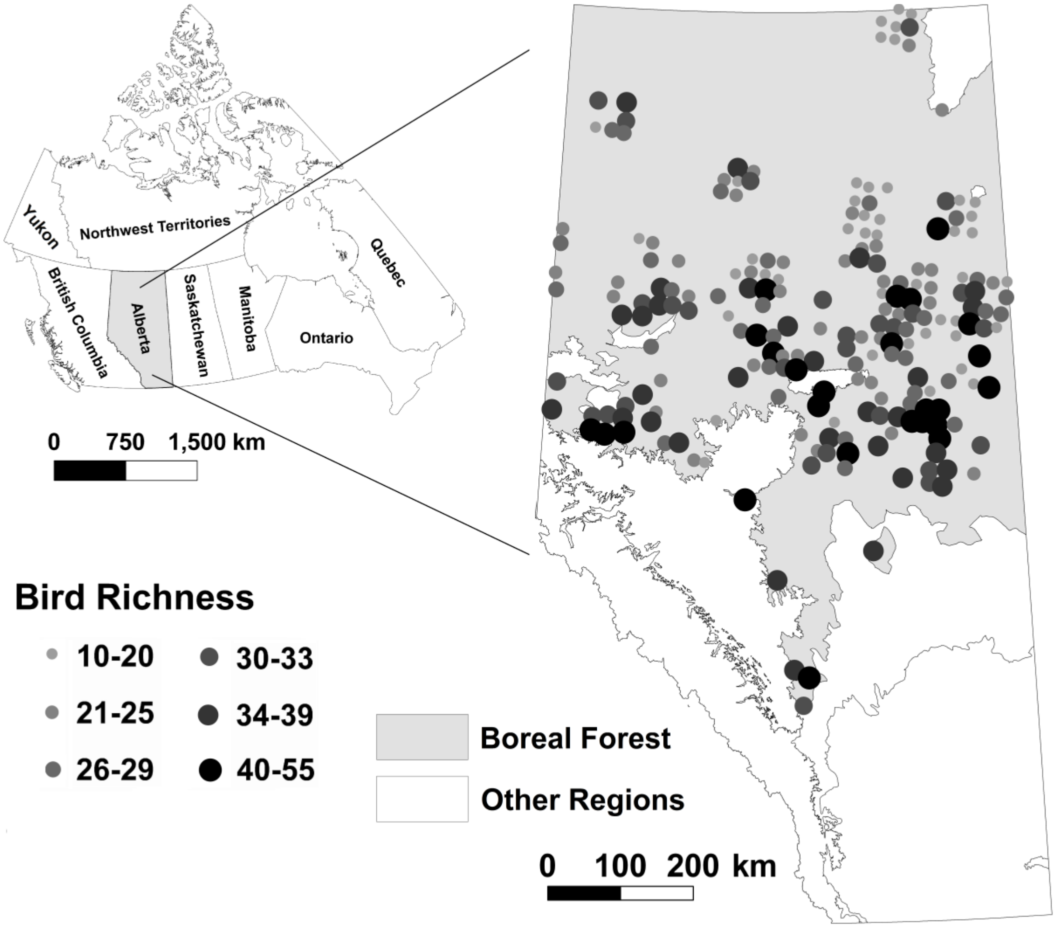
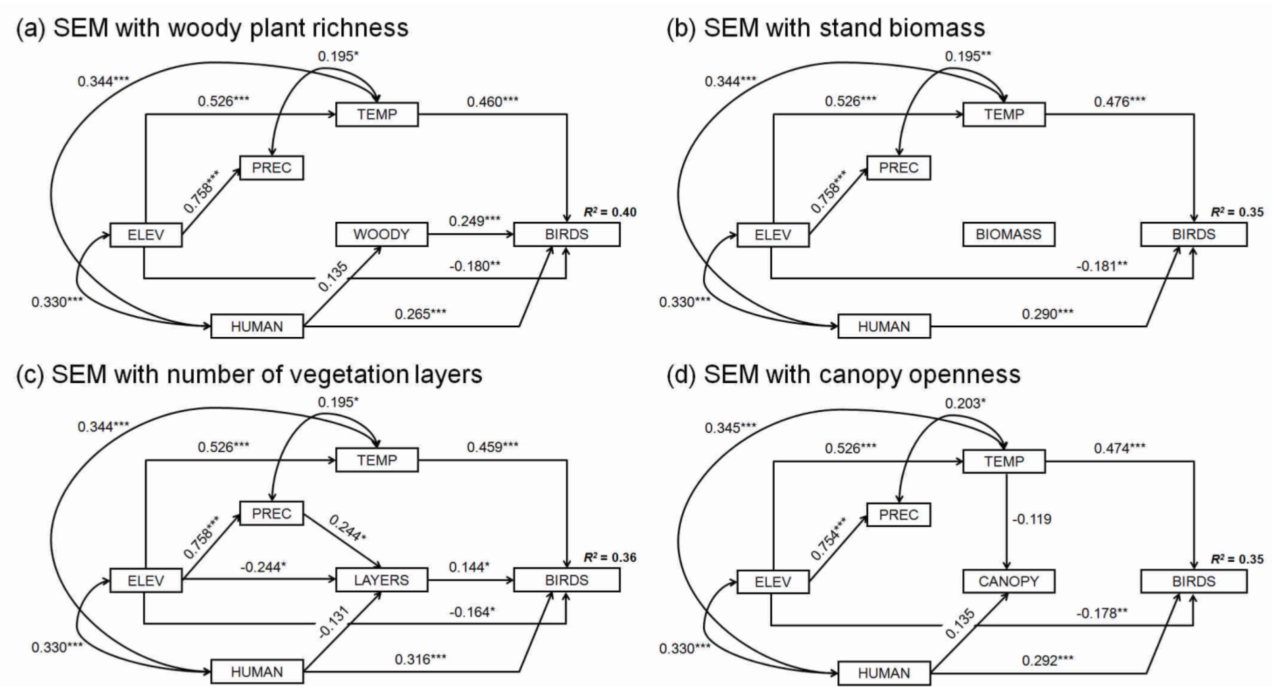


Figure 4.1 The distribution of the 206 study sites and their breeding bird species richness across the boreal forest in Alberta

***NOTE**:* Quantile classification was used for species richness, and NAD83 (North American Datum of 1983) for map projection.



(a) SEM with woody plant richness

(b) SEM with stand biomass

(c) SEM with number of vegetation layers

(d) SEM with canopy openness

Figure 4.2 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover, and local forest structure and composition on overall bird species richness

NOTE*:* Measures of local forest structure and composition include: (a) woody plant species richness, (b) stand biomass, (c) number of vegetation layers, and (d) canopy openness. A priori structure of all four SEMs was initially the same (see Figure 4.5), but that non-significant paths were removed and missing error covariances (curved arrows) added to improve model fits. Straight arrows illustrated standardized path coefficients and their significance levels (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Abbreviations of variables are explained in Table 4.1.

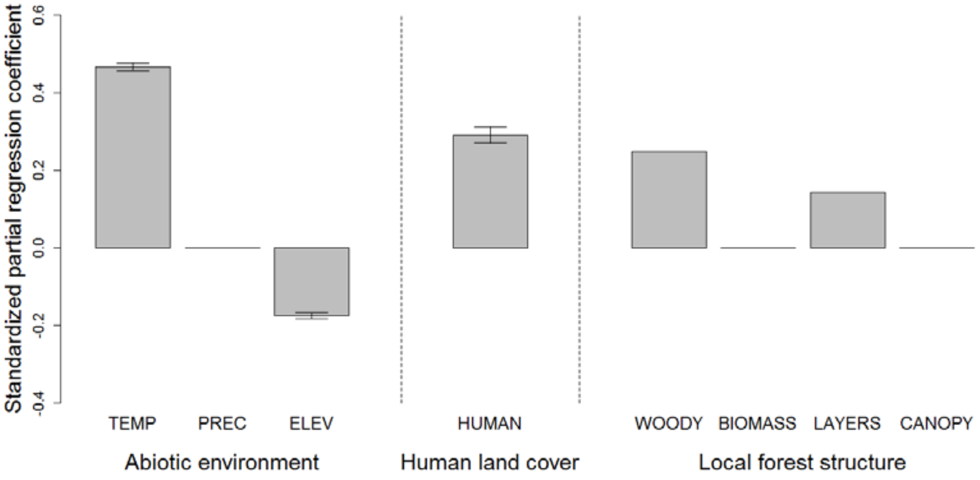


Figure 4.3 Direct effects of abiotic environment, human land cover and local forest structure and composition on species richness of all birds, as derived from structural equation models (SEMs).

***NOTE**:* Mean ± SD is given for standardized path coefficients of environmental and human predictor variables across four SEMs (Figure 4.2a–d). For local forest structure variables only one standardized path coefficient is available (cf. Figure 4.2). Abbreviations of variables are explained in Table 4.1. Other symbols and explanations are as in Figure 4.2.

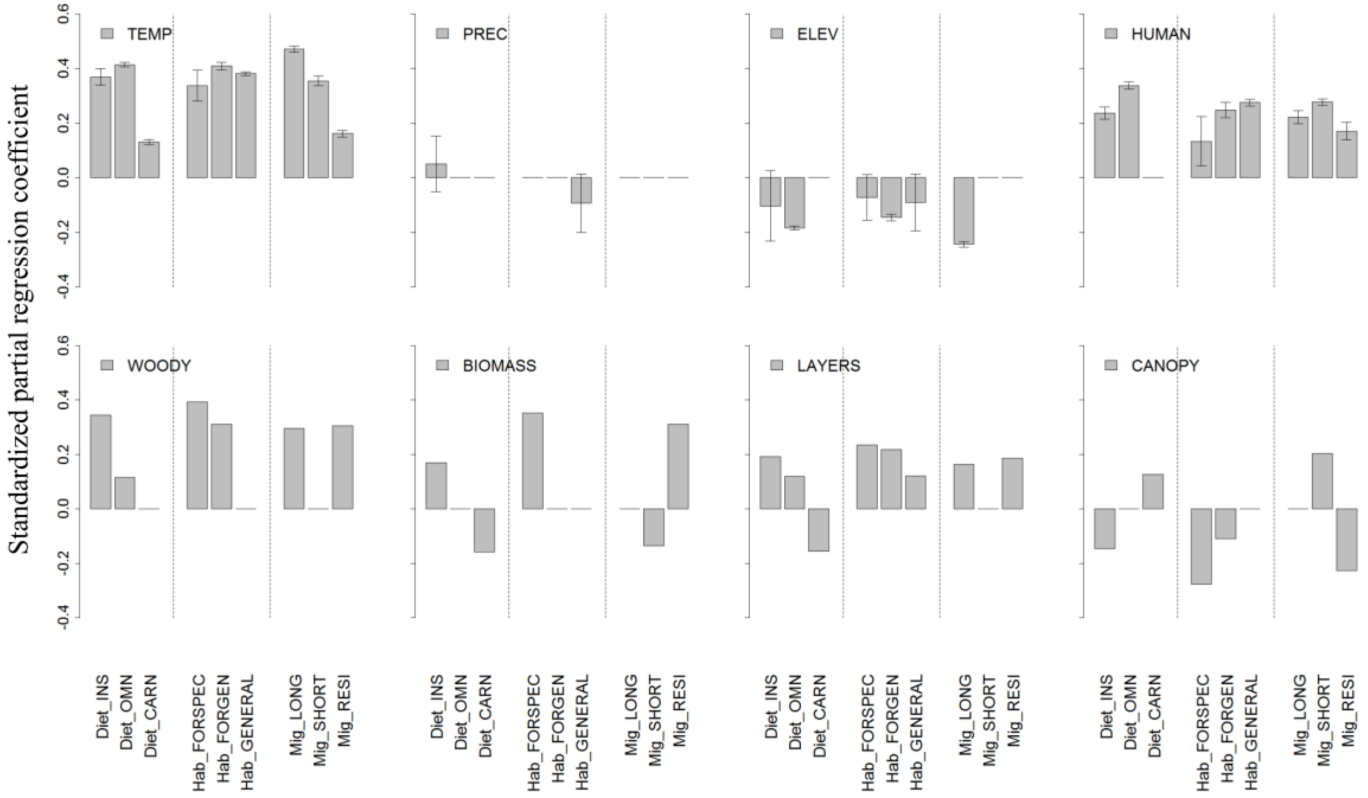
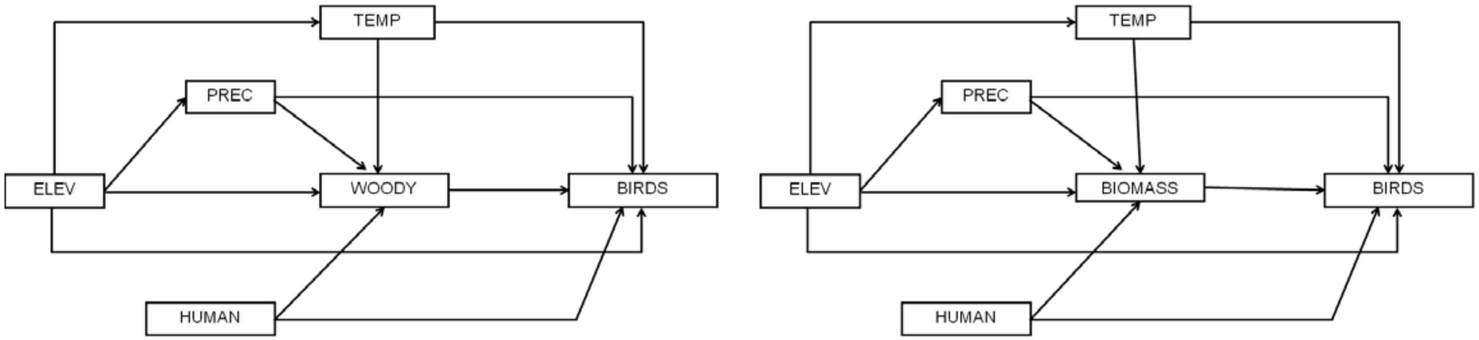
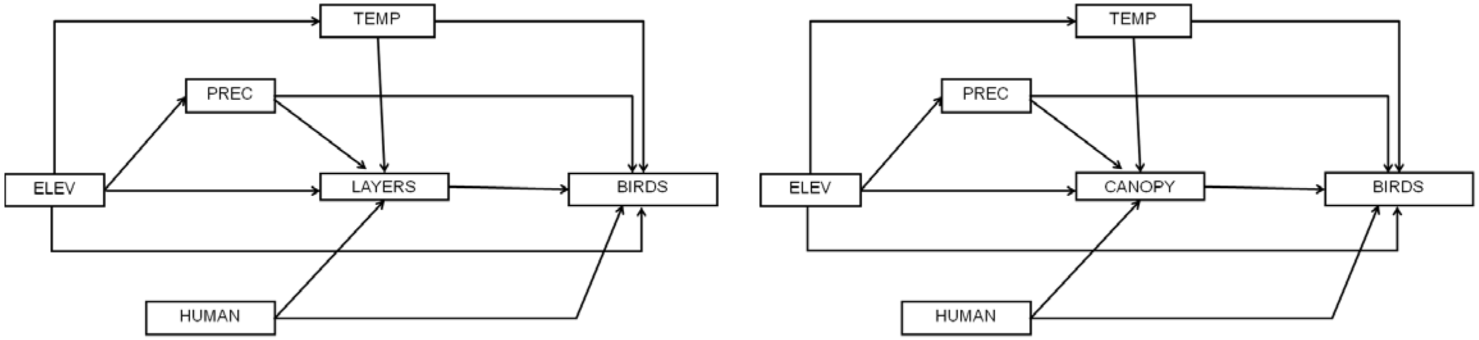


Figure 4.4 Direct effects of abiotic environment, human land cover, and local forest structure and composition on bird species richness of dietary, habitat, and migratory guilds

NOTE*:* Standardized path coefficients are derived from structural equation models (SEMs) similar to those in Figure 4.2 where the species richness of birds was replaced by the species richness of guilds (see Figures 4.6–4.9). Other symbols and explanations are as in Figure 4.3.


(a) SEM with woody plant richness

(b) SEM with stand biomass


(c) SEM with number of vegetation layers

(d) SEM with canopy openness

Figure 4.5 Four a priori theoretical structural equation models (SEMs) to detect possible influences of (a) woody plant richness, (b) biomass, (c) vegetation layers, and (d) canopy openness on bird richness

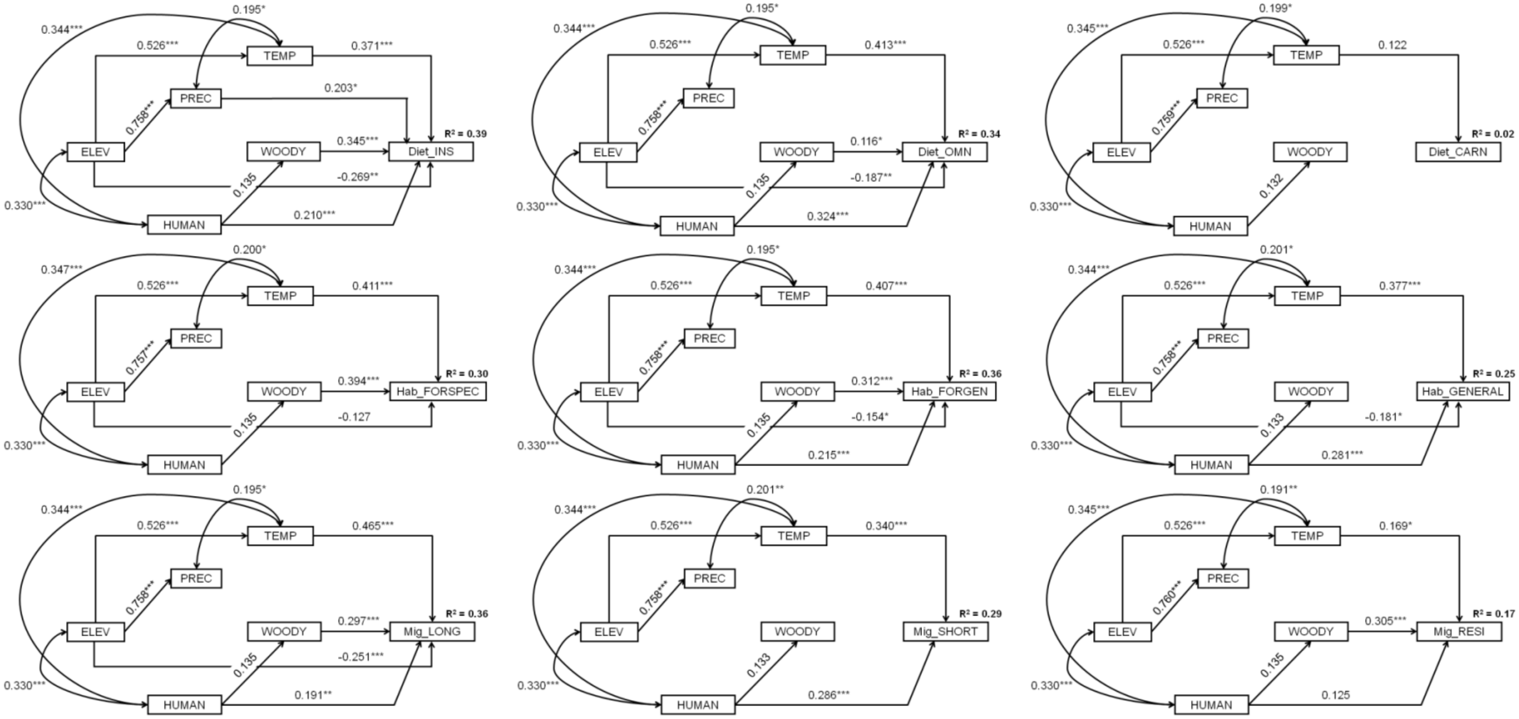


Figure 4.6 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover and woody plant richness on bird guild richness

NOTE*:* Illustrated are standardized partial regression coefficients and their significance levels *(*P < 0.05, **P < 0.01, ***P < 0.001).* For abbreviation of variables see Table 4.1 in the main text. Other symbols and explanations are the same as for Figure 4.2 in the main text.

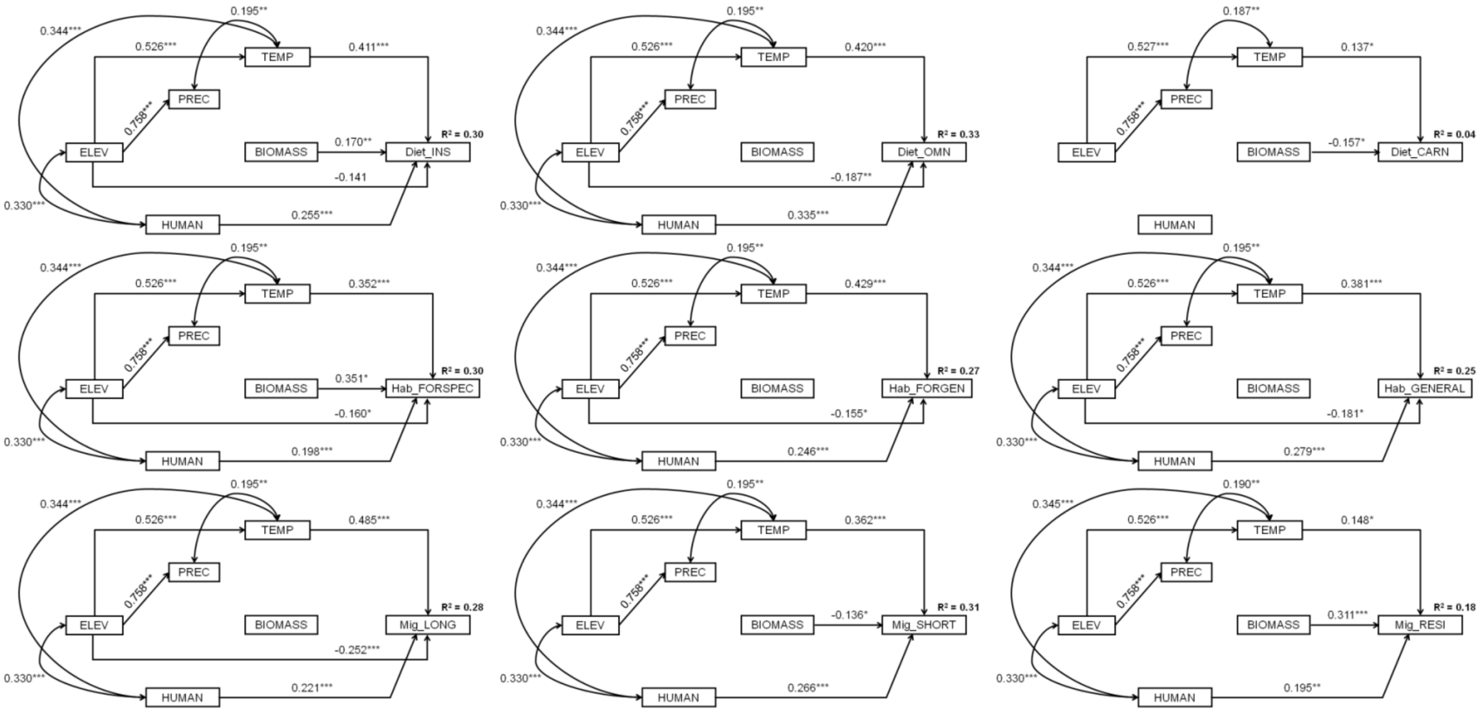


Figure 4.7 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover and stand biomass on bird guild richness

NOTE*:* For abbreviation of variables see Table 4.1 in the main text. Other symbols and explanations are the same as for Figure 4.5.

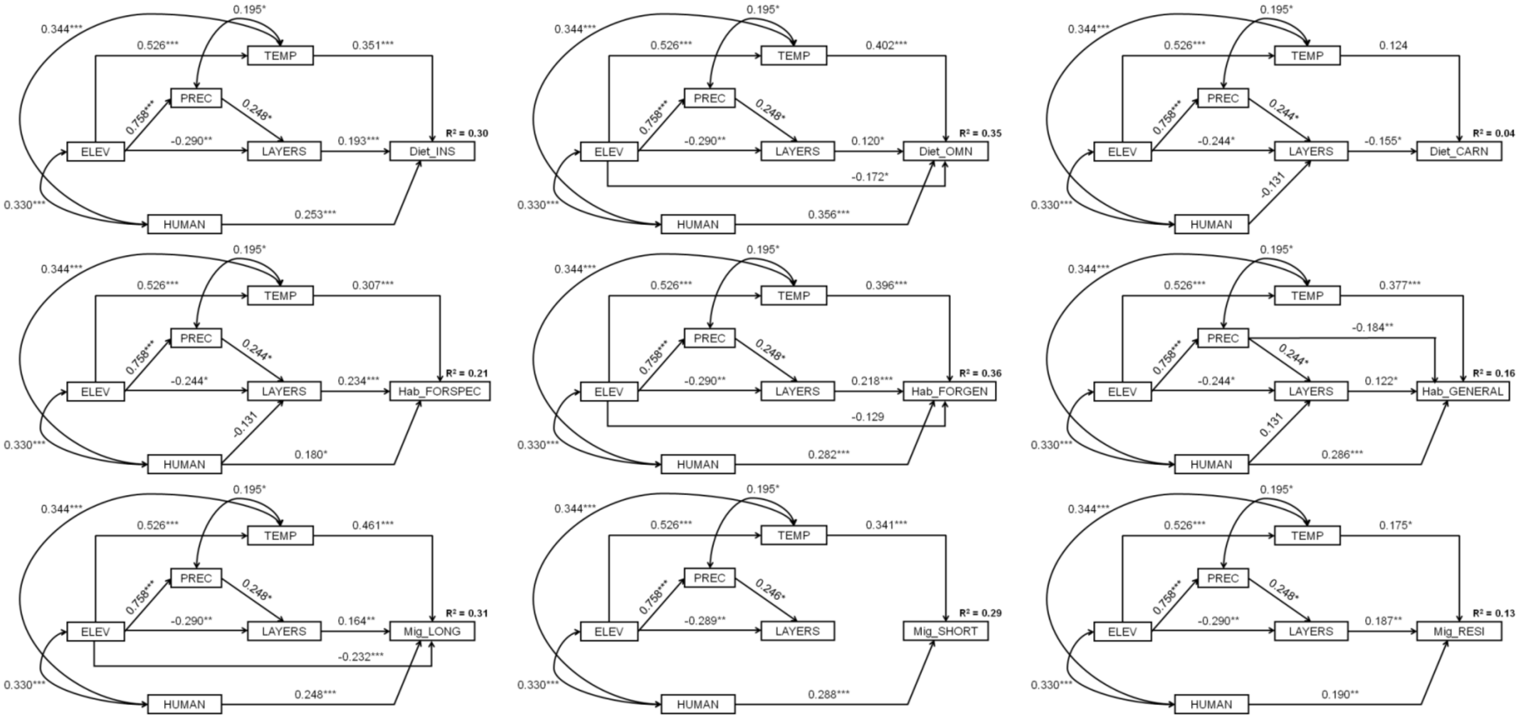


Figure 4.8 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover and number of vegetation layers on bird guild richness

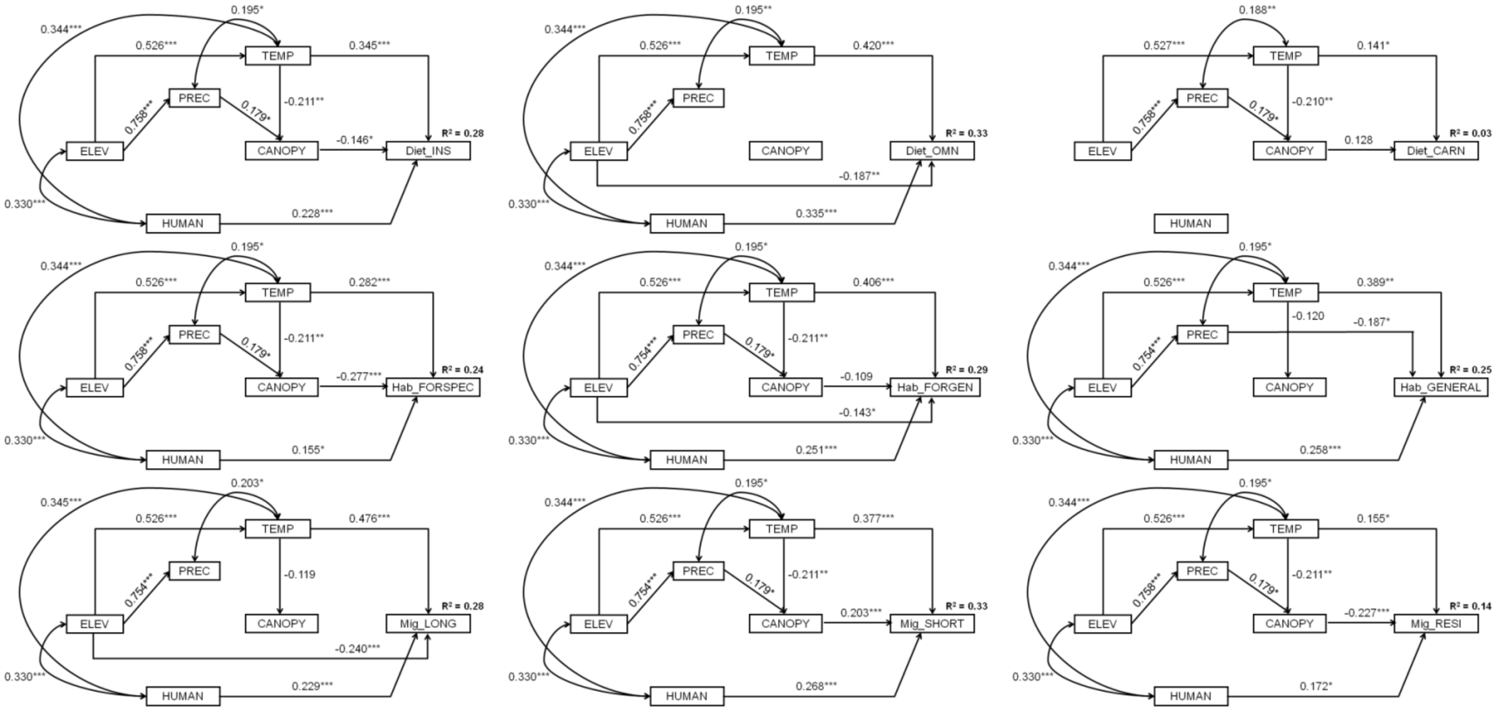


Figure 4.9 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover and canopy openness on bird guild richness

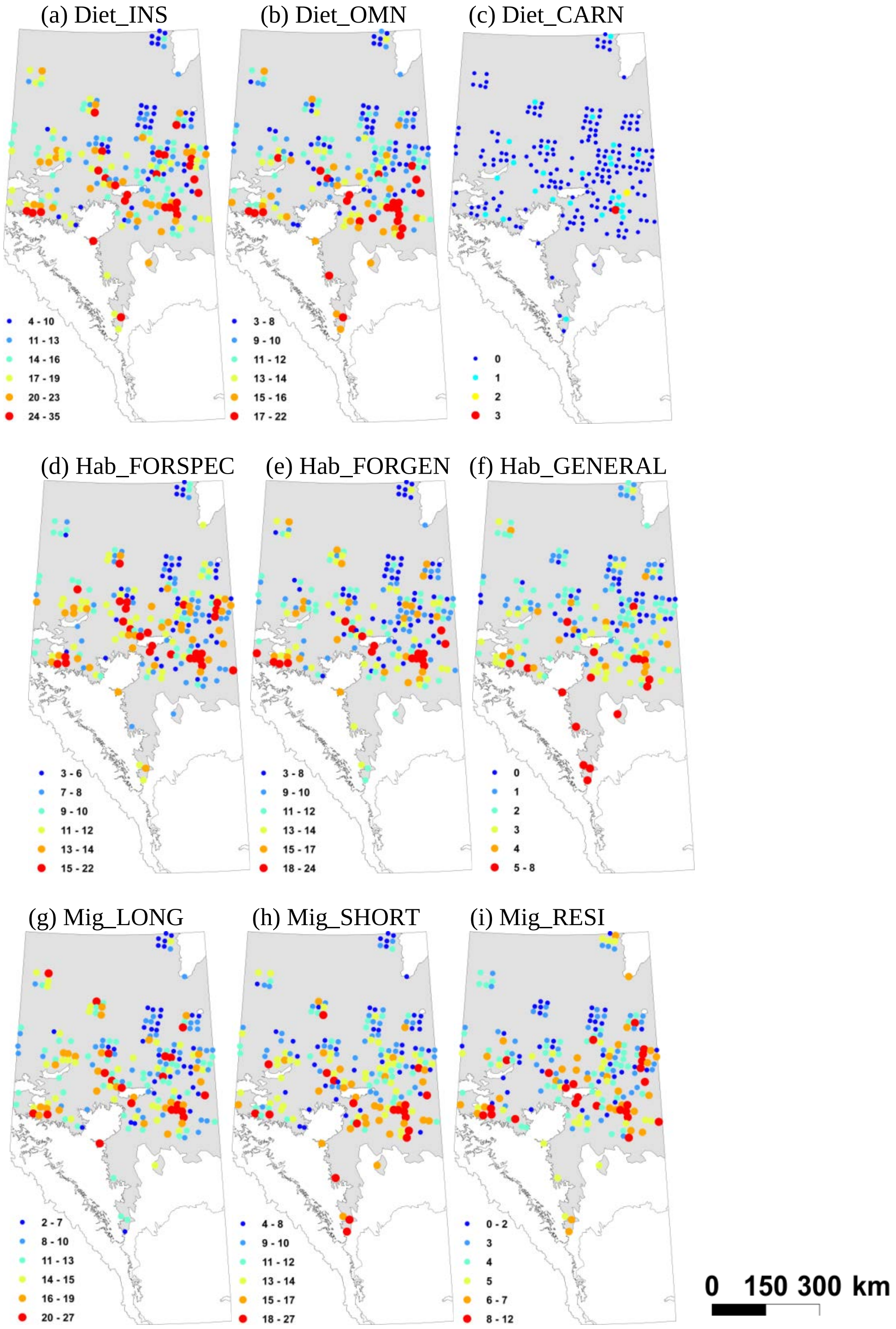


Figure 4.10 Spatial patterns of bird species richness in the boreal forest of Alberta for different dietary guilds (upper row), habitat guilds (middle row), and migratory guilds (lower row)

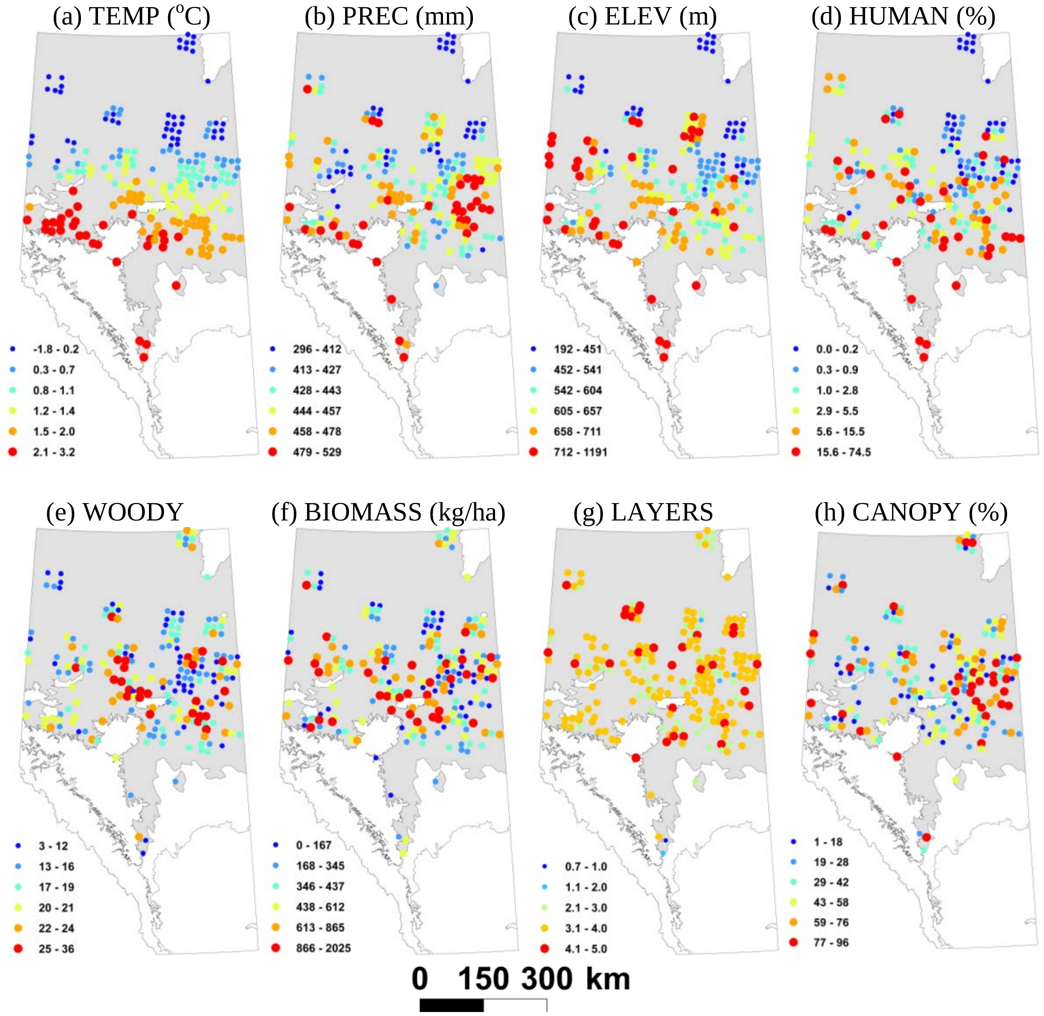


Figure 4.11 Spatial patterns of abiotic environment, human land cover and local forest structure across the boreal forest of Alberta

Appendix 4A *Species List of Breeding Birds in the Boreal Forest of Alberta*

NOTE: INS: Insectivore; OMN: Omnivore; CARN: Carnivore; FORSPEC: Old-growth Forest Specialist; FORGEN: Forest Generalist; GENERAL: Habitat Generalist; LONG: Long-distance migrants; SHORT: Short-distance migrants; RESI: Winter residents; NC: Not classified.

Scientific name	Common name	Family	Dietary guild	Habitat guild	Migratory guild
Buteo platypterus	Broad-winged hawk	Accipitridae	CARN	FORSPEC	LONG
Accipiter gentilis	Northern goshawk	Accipitridae	CARN	FORGEN	RESI
Circus cyaneus	Northern harrier	Accipitridae	CARN	NC	SHORT
Buteo jamaicensis	Red-tailed hawk	Accipitridae	CARN	GENERAL	SHORT
Accipiter striatus	Sharp-shinned hawk	Accipitridae	CARN	FORGEN	SHORT
Eremophila alpestris	Horned lark	Alaudidae	OMN	NC	SHORT
Ceryle alcyon	Belted kingfisher	Alcedinidae	NC	NC	SHORT
Bombycilla garrulus	Bohemian waxwing	Bombycillidae	NC	FORGEN	SHORT
Bombycilla cedrorum	Cedar waxwing	Bombycillidae	INS	FORGEN	SHORT
Chordeiles minor	Common nighthawk	Caprimulgidae	INS	GENERAL	LONG
Pheucticus ludovicianus	Rose-breasted grosbeak	Cardinalidae	OMN	FORSPEC	LONG
Piranga ludoviciana	Western tanager	Cardinalidae	OMN	FORSPEC	LONG
Certhia americana	Brown creeper	Certhiidae	INS	FORSPEC	RESI
Charadrius vociferus	Killdeer	Charadriidae	INS	NC	SHORT
Zenaida macroura	Mourning dove	Columbidae	NC	GENERAL	SHORT
Corvus brachyrhynchos	American crow	Corvidae	OMN	GENERAL	SHORT
Pica hudsonia	Black-billed magpie	Corvidae	INS	GENERAL	RESI
Cyanocitta cristata	Blue jay	Corvidae	OMN	FORGEN	RESI
Corvus corax	Common raven	Corvidae	OMN	GENERAL	RESI
Perisoreus canadensis	Gray jay	Corvidae	OMN	FORGEN	RESI
Spizella breweri	Brewer's sparrow	Emberizidae	INS	NC	LONG
Spizella passerina	Chipping sparrow	Emberizidae	OMN	FORGEN	SHORT
Spizella pallida	Clay-colored sparrow	Emberizidae	OMN	NC	LONG
Junco hyemalis	Dark-eyed junco	Emberizidae	OMN	FORGEN	SHORT
Passerella iliaca	Fox sparrow	Emberizidae	OMN	FORGEN	SHORT
Chondestes grammacus	Lark sparrow	Emberizidae	OMN	NC	SHORT
Ammodramus leconteii	Le Conte's sparrow	Emberizidae	OMN	NC	SHORT
Melospiza lincolnii	Lincoln's sparrow	Emberizidae	OMN	NC	SHORT
Ammodramus nelsoni	Nelson's sharp-tailed sparrow	Emberizidae	OMN	NC	SHORT
Passerculus sandwichensis	Savannah sparrow	Emberizidae	OMN	NC	SHORT
Melospiza melodia	Song sparrow	Emberizidae	OMN	FORGEN	SHORT
Melospiza georgiana	Swamp sparrow	Emberizidae	OMN	NC	SHORT
Zonotrichia albicollis	White-throated sparrow	Emberizidae	OMN	FORGEN	SHORT
Zonotrichia leucophrys	White-crowned sparrow	Emberizidae	OMN	NC	SHORT

Appendix 4A Continued-1

Scientific name	Common name	Family	Dietary guild	Habitat guild	Migratory guild
Pooecetes gramineus	Vesper sparrow	Emberizidae	OMN	NC	SHORT
Falco sparverius	American kestrel	Falconidae	INS	FORGEN	LONG
Falco columbarius	Merlin	Falconidae	CARN	GENERAL	SHORT
Carduelis tristis	American goldfinch	Fringillidae	OMN	NC	SHORT
Coccothraustes vespertinus	Evening grosbeak	Fringillidae	OMN	FORSPEC	RESI
Carduelis pinus	Pine siskin	Fringillidae	OMN	FORSPEC	SHORT
Carpodacus purpureus	Purple finch	Fringillidae	NC	FORSPEC	SHORT
Loxia curvirostra	Red crossbill	Fringillidae	OMN	FORSPEC	RESI
Loxia leucoptera	White-winged crossbill	Fringillidae	OMN	FORSPEC	RESI
Riparia riparia	Bank swallow	Hirundinidae	INS	NC	LONG
Hirundo rustica	Barn swallow	Hirundinidae	INS	GENERAL	LONG
Petrochelidon pyrrhonota	Cliff swallow	Hirundinidae	INS	NC	LONG
Stelgidopteryx serripennis	Northern rough-winged swallow	Hirundinidae	INS	NC	LONG
Tachycineta bicolor	Tree swallow	Hirundinidae	INS	FORGEN	LONG
Tachycineta thalassina	Violet-green swallow	Hirundinidae	INS	FORGEN	LONG
Icterus galbula	Baltimore oriole	Icteridae	OMN	FORSPEC	LONG
Euphagus cyanocephalus	Brewer's blackbird	Icteridae	OMN	GENERAL	SHORT
Molothrus ater	Brown-headed cowbird	Icteridae	OMN	FORGEN	SHORT
Quiscalus quiscula	Common grackle	Icteridae	OMN	FORGEN	SHORT
Agelaius phoeniceus	Red-winged blackbird	Icteridae	OMN	NC	SHORT
Euphagus carolinus	Rusty blackbird	Icteridae	INS	NC	SHORT
Sturnella neglecta	Western meadowlark	Icteridae	INS	NC	SHORT
Xanthocephalus xanthocephalus	Yellow-headed blackbird	Icteridae	OMN	NC	LONG
Chlidonias niger	Black tern	Laridae	INS	NC	LONG
Dumetella carolinensis	Gray catbird	Mimidae	OMN	FORGEN	SHORT
Anthus rubescens	American pipit	Motacillidae	INS	NC	SHORT
Anthus spragueii	Sprague's pipit	Motacillidae	INS	NC	SHORT
Poecile atricapillus	Black-capped chickadee	Paridae	INS	GENERAL	RESI
Poecile hudsonica	Boreal chickadee	Paridae	INS	FORSPEC	RESI
Poecile gambeli	Mountain chickadee	Paridae	INS	FORGEN	RESI
Setophaga ruticilla	American redstart	Parulidae	INS	FORGEN	LONG
Dendroica castanea	Bay-breasted warbler	Parulidae	INS	FORSPEC	LONG
Mniotilta varia	Black and white warbler	Parulidae	INS	FORGEN	LONG
Dendroica striata	Blackpoll warbler	Parulidae	INS	FORSPEC	LONG
Dendroica virens	Black-throated green warbler	Parulidae	INS	FORSPEC	LONG
Wilsonia canadensis	Canada warbler	Parulidae	INS	FORGEN	LONG
Dendroica tigrina	Cape May warbler	Parulidae	INS	FORSPEC	LONG
Dendroica pensylvanica	Chestnut-sided warbler	Parulidae	INS	FORGEN	LONG

Appendix 4A Continued-2

Scientific name	Common name	Family	Dietary guild	Habitat guild	Migratory guild
Geothlypis trichas	Common yellowthroat	Parulidae	INS	NC	SHORT
Oporornis agilis	Connecticut warbler	Parulidae	INS	FORGEN	LONG
Dendroica magnolia	Magnolia warbler	Parulidae	INS	FORSPEC	LONG
Oporornis philadelphia	Mourning warbler	Parulidae	INS	FORGEN	LONG
Seiurus noveboracensis	Northern waterthrush	Parulidae	INS	FORSPEC	LONG
Vermivora celata	Orange-crowned warbler	Parulidae	INS	FORGEN	SHORT
Seiurus aurocapilla	Ovenbird	Parulidae	INS	FORGEN	LONG
Dendroica palmarum	Palm warbler	Parulidae	INS	NC	LONG
Vermivora peregrina	Tennessee warbler	Parulidae	INS	FORGEN	LONG
Wilsonia pusilla	Wilson's warbler	Parulidae	INS	FORGEN	LONG
Dendroica petechia	Yellow warbler	Parulidae	INS	FORGEN	LONG
Dendroica coronata	Yellow-rumped warbler	Parulidae	INS	FORSPEC	SHORT
Passer domesticus	House sparrow	Passeridae	NC	NC	RESI
Bonasa umbellus	Ruffed grouse	Phasianidae	OMN	FORGEN	RESI
Picoides arcticus	Black-backed woodpecker	Picidae	INS	FORGEN	RESI
Picoides pubescens	Downy woodpecker	Picidae	INS	FORGEN	RESI
Picoides villosus	Hairy woodpecker	Picidae	INS	FORSPEC	RESI
Colaptes auratus	Northern flicker	Picidae	INS	FORGEN	SHORT
Dryocopus pileatus	Pileated woodpecker	Picidae	INS	FORSPEC	RESI
Picoides tridactylus	Three-toed woodpecker	Picidae	INS	FORGEN	RESI
Sphyrapicus varius	Yellow-bellied sapsucker	Picidae	OMN	FORSPEC	SHORT
Coturnicops noveboracensis	Yellow rail	Rallidae	OMN	NC	SHORT
Regulus satrapa	Golden-crowned kinglet	Regulidae	INS	FORSPEC	SHORT
Regulus calendula	Ruby-crowned kinglet	Regulidae	INS	FORSPEC	SHORT
Tringa melanoleuca	Greater yellowlegs	Scolopacidae	NC	NC	LONG
Tringa flavipes	Lesser yellowlegs	Scolopacidae	INS	NC	LONG
Numenius americanus	Long-billed curlew	Scolopacidae	OMN	NC	LONG
Tringa solitaria	Solitary sandpiper	Scolopacidae	INS	NC	LONG
Actitis macularius	Spotted sandpiper	Scolopacidae	INS	GENERAL	LONG
Gallinago delicata	Wilson's snipe	Scolopacidae	NC	NC	LONG
Gallinago gallinago	Wilson's (common) snipe	Scolopacidae	NC	NC	LONG
Sitta canadensis	Red-breasted nuthatch	Sittidae	INS	FORSPEC	RESI
Sitta carolinensis	White-breasted nuthatch	Sittidae	INS	FORSPEC	RESI
Strix varia	Barred owl	Strigidae	CARN	FORSPEC	RESI
Aegolius funereus	Boreal owl	Strigidae	CARN	FORSPEC	RESI
Strix nebulosa	Great gray owl	Strigidae	CARN	FORSPEC	RESI
Bubo virginianus	Great horned owl	Strigidae	CARN	FORSPEC	RESI
Surnia ulula	Northern hawk owl	Strigidae	CARN	FORGEN	RESI

Appendix 4A Continued-3

Scientific name	Common name	Family	Dietary guild	Habitat guild	Migratory guild
Sturnus vulgaris	European starling	Sturnidae	OMN	GENERAL	SHORT
Archilochus colubris	Ruby-throated hummingbird	Trochilidae	OMN	GENERAL	LONG
Troglodytes aedon	House wren	Troglodytidae	INS	GENERAL	LONG
Cistothorus palustris	Wren	Troglodytidae	INS	NC	SHORT
Troglodytes troglodytes	Winter wren	Troglodytidae	INS	FORSPEC	SHORT
Turdus migratorius	American robin	Turdidae	OMN	GENERAL	SHORT
Catharus guttatus	Hermit thrush	Turdidae	INS	FORGEN	SHORT
Sialia currucoides	Mountain bluebird	Turdidae	INS	FORGEN	SHORT
Catharus ustulatus	Swainson's thrush	Turdidae	OMN	FORSPEC	LONG
Ixoreus naevius	Varied thrush	Turdidae	INS	FORSPEC	SHORT
Catharus fuscescens	Veery	Turdidae	OMN	FORGEN	LONG
Empidonax alnorum	Alder flycatcher	Tyrannidae	INS	FORGEN	LONG
Empidonax occidentalis	Cordilleran flycatcher	Tyrannidae	INS	FORGEN	LONG
Tyrannus tyrannus	Eastern kingbird	Tyrannidae	INS	GENERAL	LONG
Empidonax hammondii	Hammond's flycatcher	Tyrannidae	INS	FORSPEC	LONG
Empidonax minimus	Least flycatcher	Tyrannidae	INS	FORSPEC	LONG
Contopus cooperi	Olive-sided flycatcher	Tyrannidae	INS	FORGEN	LONG
Contopus sordidulus	Western wood pewee	Tyrannidae	INS	FORSPEC	LONG
Empidonax flaviventris	Yellow-bellied flycatcher	Tyrannidae	INS	NC	LONG
Sayornis phoebe	Eastern phoebe	Tyrannidae	INS	FORGEN	SHORT
Tyto alba	Barn owl	Tytonidae	CARN	GENERAL	SHORT
Vireo solitarius	Blue-headed vireo	Vireonidae	INS	FORSPEC	SHORT
Vireo olivaceus	Red-eyed vireo	Vireonidae	INS	FORGEN	LONG
Vireo gilvus	Warbling vireo	Vireonidae	INS	FORSPEC	LONG

Chapter 5 Does Disturbance Regime Change Community Assembly of Angiosperm Plant Communities in the Boreal Forest?[3]

Summary

Aims: To examine if and how species and phylogenetic diversity changes in relation to disturbance, I conducted a review of ecological literature testing the consistency of the relationship between phylogenetic diversity and disturbance, and compared taxonomic groups, type of disturbance, and ecosystem/habitat context. I provide a case study of the phylogenetic diversity-disturbance relationship in angiosperm plant communities of a boreal forest region, comparing with types of natural and anthropogenic disturbances and plant growth forms.

Methods: Using a large-scale sampling plot network along a complete (0-100%) anthropogenic disturbance gradient in the boreal biome, I compared the changes of angiosperm plant community structure and composition across plots. I estimated natural disturbance with historical records of major fires. I then calculated phylogenetic diversity indices and determined species richness in order to compare linear and polynomial trends along disturbance gradients. I also compared the changes of community structure for different types of anthropogenic disturbances, and examined how the relationships between species

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[3] *A version of this chapter has been accepted by* ***Journal of Plant Ecology***.

and phylogenetic diversity and disturbance regimes vary among three different life forms (i.e., forbs, graminoids and woody plants).

Results: Phylogenetic diversity was inconsistently related to disturbance in previous studies, regardless of taxon, disturbance type, or ecosystem context. In the understudied boreal ecosystem, angiosperm plant communities varied greatly in species richness and phylogenetic diversity along anthropogenic disturbance gradients, and among different disturbance types. In general, a quadratic curve described the relationship between species richness and anthropogenic disturbance, with the highest richness at intermediate anthropogenic disturbance levels. However, phylogenetic diversity was not related to disturbance in any consistent manner and species richness was not correlated with phylogenetic diversity. Phylogenetic relatedness was also inconsistent across plant growth forms and different anthropogenic disturbance types. Unlike the inconsistent patterns observed with anthropogenic disturbance, community assembly among localities varying in time since natural disturbance exhibited a distinct signature of phylogenetic relatedness, although those trends varied among plant growth forms.

5.1 Introduction

Disturbances by natural processes and human influence are perhaps the most dramatic factors shaping ecological communities. Changes in biodiversity due to human activities have been much more rapid over the last half century than at any time in human history (Millennium Ecosystem Assessment 2005). Habitat loss due to land-use change, considered as one of the most important drivers of biodiversity changes (Millennium Ecosystem Assessment 2005), can drive native species to local extinction and facilitate spread of alien species (Winter *et al.* 2009). Taken together, these environmental changes affect many aspects of biodiversity, but it remains unclear if these aspects are impacted in similar ways.

Biodiversity assessments which have been based on the number of species and/or their relative abundance often provide little indication of spatial and temporal changes of community structure in fragmented landscapes (Swenson 2011). Such assessments rarely take into account evolutionary information, yet conservation biologists advise that species which are most distinct in their evolutionary history should be of greater priority for preservation (Winter *et al.* 2013). We lack a strong understanding of different effects of disturbance on species of different evolutionary histories. A fundamental question is: 'does disturbance randomly change the composition and evolutionary relatedness among species, or are some evolutionary lineages disproportionately affected by disturbance?' To better understand and predict human-driven changes in biodiversity, we need to consider a wider array of components of biodiversity, especially evolutionary relatedness, helping guide conservation efforts and natural resource management.

Recognition of the sensitivity to anthropogenic disturbance of diversity at higher levels of taxonomy than species is not new. For example, Warwick and Clarke (1995) showed that taxonomic distinctness decreased with anthropogenic stress in marine communities, and that taxonomic changes were more sensitive to disturbance than was species diversity. More recently, the importance of the evolutionary history (phylogeny) of species on assessing changes of biodiversity and community structure has gained increased recognition and attention (HilleRisLambers *et al.* 2012; Mouillot *et al.* 2013; Swenson 2011; Webb *et al.* 2002; Winter *et al.* 2009). These recent studies have been facilitated by new and more efficient methods enabling phylogenetic tree construction which consider not only taxonomic relationships, but also evolutionary branch lengths. Increased interest in phylogenetic community structure is due in part to the prospect that a phylogeny reflects the processes controlling community assembly across ecological and evolutionary time scales and may shed light on our understanding about species assembly (Webb *et al.* 2002). Generally, habitat and land-use change is expected to drive non-random changes in biodiversity among branches of a phylogenetic tree, disproportionately affecting some lineages more than others (Mace *et al.* 2003). Disturbance is thought to reduce the impact of interspecific competition through local extinction of disturbance-vulnerable species and can change local habitat conditions, which may lead to environmental filtering of species in community assembly with increasing disturbance (Winter *et al.* 2009). Disturbance may therefore result in communities that are composed of species more phenotypically similar to each other, due to sharing of traits which confer a benefit in disturbed environments, such as growth form and shade tolerance (Bernhardt-Römermann *et al.* 2011; Helmus *et al.* 2010; Knapp *et al.* 2008; Lavorel *et al.* 1997). This non-random change in community composition can be observed as increased trait similarity (or trait clustering). If species with more similar traits are more likely to be more phylogenetically related, then I expect species to be more phylogenetically clustered in disturbed communities. I define phylogenetic clustering as greater similarity in evolutionary relatedness than expected by chance. If the changes are random, phylogenetic structure of disturbed communities should show no difference compared with undisturbed ones. This hypothesis relies on two major assumptions: first, “trait clustering” when traits are more similar among species in disturbed environments, and second “trait conservatism”, when species which are more phenotypically similar are also more phylogenetically similar, as would result from the conservation of traits through evolutionary lineages.

Despite rarely addressing these assumptions, a number of recent studies have empirically investigated whether disturbance results in phylogenetic clustering (Table 5.1). To assess the generality of phylogenetic structure following disturbance, I reviewed the recent literature exploring impacts of natural or anthropogenic disturbances on phylogenetic dispersion to determine if field evidence supports the prediction that disturbed communities exhibit increased phylogenetic clustering of species (Table 5.1). I made several observations. First, the results of these previous studies are inconsistent; communities are sometimes but not always phylogenetically clustered following disturbance. For example, Dinnage (2009) found that disturbed sites were more clustered than expected in an old field system, indicating strong influence by environmental filtering. Letcher (2010) found strong phylogenetic overdispersion at multiple scales during tropical forest succession, which they attributed to competitive exclusion. Arroyo-Rodríguez *et al.* (2012) detected very weak changes in the phylogenetic diversity in fragmented rain forests. These mixed results may arise from differences in habitat conditions, species groups, traits, and spatial scales of each study (HilleRisLambers *et al.* 2012). Or they may result from violation of the trait clustering and trait conservatism assumptions discussed above. Second, many previous studies were limited in data quantity and/or quality. Some studies were limited by small sample sizes; those based on inventory data usually had fewer than one hundred samples (Table 5.1). Other studies observed incomplete disturbance gradients, risking missing levels of disturbance at which effects might be observed. Similarly, disturbance was often classified very coarsely. Third, most previous studies focus on tropical forest ecosystems (Table 5.1) and few studies have examined temperate or boreal regions. Temperate and boreal regions experience intense human activities and land use changes, and have evolved with frequent stand replacing natural disturbances like fire and insect outbreaks in contrast to gap-replacement regimes underlying many typical of topical forest systems. Importantly, temperate and boreal ecosystems contain relatively fewer species, so their response to disturbance may differ from species-rich tropical forests.

In response to this relative dearth of studies of the phylogenetic diversity-disturbance relationship in the boreal region, the remainder of my current study empirically evaluates phylogenetic and community structure of a boreal forest ecoregion. The boreal forest is one of the largest forest ecosystems on the planet, containing about one third of the Earth's forest and storing ~22 percent of the total carbon stored on the earth’s land surface (Watson *et al.* 2000). However, the boreal forest is facing a series of threats from urbanization, industrial development and global climate change. In this study, I used a dataset with a fine spatial grain (< 1 km^2 resolution) but large regional extent which described human land use change on boreal plant biodiversity in Alberta, Canada. I examined how taxonomic and phylogenetic diversity of angiosperm plant communities changed in relation to different levels and types of natural and anthropogenic disturbance. Specifically, I addressed the following questions: 1) Does disturbance result in community assemblages of more closely related species? 2) How do species and phylogenetic diversity change with varying disturbance, and are changes in phylogenetic diversity similar to those of species diversity? 3) Do species and phylogenetic diversity relate similarly to anthropogenic (land use) versus natural (primarily fire) disturbance? 4) How does phylogenetic diversity vary with anthropogenic disturbance extent, permanence, and among land-use types? 5) Are the relationships between phylogenetic diversity and anthropogenic disturbance consistent among species' growth forms?

5.2 Materials and Methods

Study Sites

The study included 301 sites from boreal ecoregion in Alberta, Canada (Figure 5.1), with data provided by Alberta Biodiversity Monitoring Institute (ABMI). ABMI conducts a broad-scale, long-term programme monitoring biodiversity status and trends in Alberta (http://www.ABMI.ca). The area of boreal ecoregion of Alberta is about 381,047 km^2, an area comparable to Germany. This ecoregion has short summers (only 1 or 2 months have average daily temperatures exceeding 15 ^{o}C) and long and cold winters (average daily temperatures are below -10 ^{o}C for 4 months or more) (Natural Regions Committee 2006). Precipitation follows a summer-high continental pattern, with peak rainfalls occurring in July and about 60-70% of the annual precipitation falling between April and August. Elevations range from about 150 m near the Alberta-Northwest Territories border to over 1100 m near the Alberta-British Columbia border. As the largest natural region in Alberta, this region has vast deciduous, mixedwood, and coniferous forests interspersed with extensive wetlands. Due to varying climate and topography in this area, tree species composition and structure vary greatly across the study area. Main tree species include aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Natural Regions Committee 2006).

Plant Diversity Data

In each of the 301 ABMI sites, vascular plants were surveyed within a 1-ha square plot that was centered on a permanent ABMI site marker. The 1-ha plot was flagged into four 0.25-ha sub-plots, and vascular plants were surveyed during July for each sub-plot using area-restricted, 20-minute searches to find as many species as possible. At each site, the presence-absence of vascular plants was recorded. Species not identified in the field were collected for expert identification in the laboratory.

Anthropogenic Disturbance Data

To characterize the influence of anthropogenic disturbance on plant species richness, I used land cover data derived from manually interpreting aerial photography of photoscale 1:30,000 and SPOT satellite imagery within 150 m distance from the center of each ABMI site. Total anthropogenic disturbance of each site was estimated by the percentage area of anthropogenic disturbance within the 150 m radius circle. Recent studies based the same data have shown that the relationship between vascular plant richness and human footprint was the strongest at this scale (Mayor *et al.* 2012; Mayor 2013). Disturbance extents ranged from 0 to 100% disturbed in my study sites.

I also divided anthropogenic disturbance into different disturbance types in order to determine how different types of disturbance influence plant community structure (Table 5.2). There are three major disturbance categories in this study (Mayor *et al.* 2012), including perpetual disturbance (virtually permanent landscape changes), temporary disturbance (dynamic and successional changes in species composition following initial disturbance), and no anthropogenic disturbance (total anthropogenic disturbance equal to 0). To evaluate the influences of different disturbance types on plant diversity, I divided perpetual disturbance into three groups (agriculture, urban and industry, and hard linear features), and temporary disturbance into two groups (forestry and soft linear features) (Table 5.2).

Natural Successional Stages in Boreal Forests

To assess how plant community structure changes along forest succession following natural disturbance, I selected all the ABMI sites without any anthropogenic disturbance and divided these into five successional age categories based on stand age data of each site (Table 5.2). These five age classes included stand age 0-20 years, 20-50 years, 50-80 years, 80-120 years, and ≥120 years. Stand age of each site was estimated based on the tree increment core age data of dominant trees.

Phylogenetic Structure Analysis

I first produced a full species list of 585 angiosperm plant based on APG III (Angiosperm Phylogeny Group 2009) classification, and classified species by genus and family. I then used the program Phylomatic to construct a plant community species pool onto a dated version of megatree of Davies *et al.* (2004) (davies2004.bl.new; available at https://github.com/camwebb/tree-of-trees/tree/master/megatrees_other) (Webb *et al.* 2008). Branch lengths were estimated with the BLADJ algorithm to reduce variance between branch lengths by evenly spacing nodes of unknown ages. I excluded non-angiosperm taxa in my analyses because a reliable phylogenetic supertree including both angiosperms and non-angiosperm vascular plants is not available currently (e.g., Ding *et al.* 2012; Letcher 2010). In addition, considering possible influence of alien plants on community phylogenetic structure, I did two sets of analyses: one with native species only and the other with both native and alien species. Only the results of the native species analysis were provided in the main text, while the results of all plant species were included as supplementary information (Appendix 5A-5D).

Based on the phylogeny tree of the angiosperm species in my study region (Figure 5.2), I calculated the net relatedness index (NRI) for each site to quantify the degree of phylogenetic relatedness among species within the site. NRI is a standardized measure of mean pairwise distance (MPD), which measures the average pair-wise phylogenetic distance between species in a sample. Observed values of MPD are compared to null distributions generated by creating communities of identical size by random draws from the source pool. NRI is calculated as follows (Webb 2000; Webb *et al.* 2002):

$$NRI = -1 \times \frac{MPD_{obs} - MPD_{rnd}}{sdMPD_{rnd}}$$

where MPD_{obs} is the observed MPD, MPD_{rnd} is the expected MPD from a set of randomized samples, and sdMPD_{rnd} is the standard deviation of the MPD of the randomized samples. Values of NRI close to zero indicate random phylogenetic structure, positive values phylogenetic clustering, and negative values phylogenetic evenness (overdispersion) (Webb 2000).

MPD and NRI of each site were calculated using the "*COMSTRUCT*" function of Phylocom 4.2. For calculating NRI, I randomly generated 9,999 null communities using null model 2 of Phylocom 4.2. In this model, the number of taxa in the sample is kept constant, and the taxa used in randomizations are a random draw from the regional phylogeny pool (Webb *et al.* 2008). The null model assumes that all species of the pool are equally able to colonize any site within the study area and has the advantage of maintaining the species richness within communities.

Previous studies have shown that plant growth form tends to be well related with response to disturbance (Lavorel *et al.* 1997). To assess how phylogenetic diversity varies with plant life forms (forbs, graminoids, and woody plants) against disturbance, I constructed a phylogeny tree for each life form group and calculated MPD and NRI using the phylogeny pool of each life form. The classification of plant life forms was based on the USDA PLANTS database (http://plants.usda.gov/growth_habits_def.html).

Statistical Analysis

To detect the trends of species richness and phylogenetic diversity along a disturbance gradient, I performed regression analyses using linear, quadratic, and cubic models. The best-fit model was selected using AIC (Akaike information criterion).

I used one-way analyses of variance (ANOVA) to examine differences of species richness and phylogenetic diversity indices among different anthropogenic disturbance types and natural successional age categories. Tukey-Kramer HSD (honestly significant difference in post hoc comparisons) tests were used a posteriori to find means that are significantly different from each other. These analyses were performed with the software R, version 2.15.2 (R Development Core Team 2012).

5.3 Results

Taxonomic and Phylogenetic Diversity of Plant Communities

I recorded a total of 585 angiosperm plant species belonging to 71 families and 244 genera. Native plant species richness averaged 39 per site in 301 study sites, ranging from 2 to 102 (Figure 5.1a). Large variations were also detected at genus and family levels. There were on average 30 genera, ranging from 2 to 68 per site, and 18 families, ranging from 1 to 29 per site. Considering three life form groups, the average of plant richness of forbs, graminoids and woody plants were 20.3, 6.2 and 14.2, respectively.

Estimated ages of angiosperm families in my study varied greatly (Figure 5.2), ranging from 36.69 to 154.26 million years. Compared with species richness (Figure 5.1a), net relatedness index (NRI) showed a pervasive clustering pattern (Figure 5.1b): 78.7 % of sites were significantly phylogenetically clustered (NRI larger than 1.96). Significant phylogenetic clustering patterns were also found for 121 forb assemblages, 34 graminoid assemblages and 15 woody plant assemblages. Patterns of phylogenetic overdispersion (NRI smaller than -1.96) were not found for all plant species combined and three life-form groups.

Taxonomic and Phylogenetic Diversity along Anthropogenic Disturbance gradient

Along a full range (0-100%) of anthropogenic disturbance, species richness of all native plants fit the cubic model bettern than the other two types of models ($R^2 = 0.182$, $P < 0.001$, Figure 5.3a), peaking at intermediate disturbance. However, the phylogenetic index NRI did not correlate with the anthropogenic disturbance gradient (linear model: $R^2 = 0.020$, $P = 0.117$), although most sites showed phylogenetic clustering patterns (Figure 5.3e).

Considering the three life forms (Figure 5.3b-d), both forbs and graminoids had more species under intermediate disturbance levels than other levels (forbs: quadratic model, $R^2 = 0.096$, $P < 0.001$; graminoids: cubic model, $R^2 = 0.265$, $P < 0.001$), but woody plants didn’t show a clear trend along the disturbance gradient (quadratic model: $R^2 = 0.025$, $P = 0.027$). Compared with these species richness patterns, phylogenetic diversity of three life forms showed differences across the disturbance gradients. For forbs (Figure 5.3f), NRI peaked at intermediate disturbance, with phylogenetic clustering patterns observed for most sites (quadratic model: $R^2 = 0.104$, $P < 0.001$). For graminoids (Figure 5.3g) and woody plants (Figure 5.3h), there was no significant difference of NRI along the disturbance gradient.

Species richness varied according to anthropogenic disturbance classification. For perpetual disturbance (Figure 5.4a), the sites at intermediate disturbance levels had significantly more species than those in other disturbance levels (quadratic model: $R^2 = 0.511$, $P < 0.001$). For temporary disturbance (Figure 5.4b), the sites with low anthropogenic disturbance had relatively less species than those in other levels (quadratic model: $R^2 = 0.139$, $P < 0.001$). For phylogenetic diversity (Figure 5.4c-d), differences of NRI along the disturbance gradient were not significant for both major disturbance categories. When I divided each major disturbance category into life-form groups (Appendix 5B), for species richness, I detected significant differences for each group along the disturbance gradient, except for woody plants under temporary disturbance. In contrast, for NRI, I did not find clear differences for each group at either disturbance types, except for forbs under temporary disturbance.

Taxonomic and Phylogenetic Diversity under Different Anthropogenic Disturbance Types

Comparing native species richness under different anthropogenic disturbance types (Figure 5.5a), urban and industrial sites (UrbInd) had higher species richness on average than other sites (one-way ANOVA: $F_{4, 144} = 5.84$, $P < 0.001$), and agriculture sites (Agri) had fewer species than others. All five disturbance types showed phylogenetic clustering patterns according to the values of NRI (Figure 5.5b), but the differences among these disturbance types were relatively small (Figure 5.5b).

However, when I analyzed diversity patterns according to life-form groups, different patterns were detected (Figure 5.5c-f). For species richness (Figure 5.5c, 5.5e and 5.5g), urban and industrial sites had significantly more forbs and graminoids, but less woody plants, than other disturbance types. Forestry (For) and soft-linear (SoftLin) sites had more woody plants but fewer graminoids than others. Values of NRI in urban and industrial sites were higher for forbs, but lower for graminoids, than others (Figure 5.5d, 5.5f and 5.5h). Values of NRI in forestry sites had large NRI for forbs, close-to-zero NRI for graminoids, and negative NRI for woody plants. Values of NRI in soft-linear sites had similar but weaker trends with those in forestry sites.

Taxonomic and Phylogenetic Diversity along Natural Succession

Comparing species richness of 122 sites with only natural disturbance (Figure 5.6a, 5.6c, 5.6e and 5.6h), I did not detect any significant change in richness along natural succession (one-way ANOVAs; All plants: $F_{4, 117} = 1.75$, $P = 0.143$; Forb: $F_{4, 117} = 1.73$, $P = 0.149$; Graminoid: $F_{4, 94} = 0.56$, $P = 0.693$; Woody plant: $F_{4, 117} = 1.60$, $P = 0.178$).

Values of NRI for all plants combined also didn't show a large difference in the five age classes (one-way ANOVAs: $F_{4, 117} = 1.16$, $P = 0.334$) (Figure 5.6b). However, large differences of NRI were detected when dividing angiosperm species into three life form groups. For forbs, young forests (age 0-20 years) had the largest NRI on average, while NRI of forbs in old-growth forests (age ≥120 years) was close to zero (Figure 5.6d). For graminoids, young forests (age 0-20 years) had negative NRI, while other age classes had positive NRI (Figure 5.6f). For woody plants, old-growth forests and young forests (age 0-20 years) had positive values of NRI on average, although values of NRI showed large variations in each age class (Figure 5.6h).

5.4 Discussion

Phylogenetic diversity is important for conservation due to its intrinsic value as natural heritage and evolutionary history, as a proxy for functional diversity, and as an indicator of future evolutionary potential (Winters *et al.* 2013). However, it is unclear how phylogenetic diversity is impacted by anthropogenic disturbance or if such changes are comparable to observed impacts on more commonly investigated aspects of biodiversity like species richness. Contrary to theoretical expectations, phylogenetic diversity among species of boreal angiosperm plants was generally unrelated to anthropogenic disturbance. Most recent studies follow Webb (2000) in hypothesizing phylogenetic similarity should increase with anthropogenic disturbance, with species more closely related than in undisturbed communities. This hypothesis is however based on the prediction that disturbance inflicts an environmental filter on species based on their functional traits, thereby filtering phylogenies (Ding *et al.* 2012; Helmus *et al.* 2010). This assumes that traits are phylogenetically conserved, such that more closely related species are more functionally similar in their traits (Webb 2000). However, I did not detect significant changes in phylogenetic diversity along the anthropogenic disturbance gradient in the boreal forest region (Figure 5.3 and 5.4). This finding indicates that changes in species composition in boreal angiosperm assemblages associated with disturbance may occur randomly throughout the phylogenetic tree (Arroyo-Rodríguez *et al.* 2012).

Studies of phylogenetic diversity and disturbance have provided mixed results (Table 5.1). My meta-analysis revealed that two studies in tropical forests (Arroyo-Rodríguez *et al.* 2012; Santos *et al.* 2010) and one study in alpine meadows (Yang *et al.* 2012) showed no evidence supporting disturbance-induced changes on phylogenetic diversity, while increasing phylogenetic clustering patterns along disturbance were detected in several other studies, e.g., Ding *et al.* (2012) and Verdú and Pausas (2007) in tropical forests, Dinnage (2009) in temperate forests, and Brunbjerg *et al.* (2012) in coastal dunes. Overall, these findings refute the universality of reduced phylogenetic diversity following disturbance; disturbed communities are more likely to be composed of more closely related species than more distantly related species, but the most common conclusion was no effect of disturbance on phylogenetic diversity. The inconsistent relationship may be related to differences in trait conservatism across systems (Arroyo-Rodríguez *et al.* 2012; Cahill *et al.* 2008).

Phylogenetic diversity was also generally unrelated to species richness, and this lack of relationship was observed regardless of whether anthropogenic disturbance was considered. My findings challenge the use of species richness as a proxy for other levels of diversity. I anticipated that phylogenetic diversity and species richness would be positively correlated because unrelated species are less likely to exhibit strong competition, but that hypothesis assumes that more closely related species have more similar niches, because niches are phylogenetically conserved. My result has varying support among previous studies. For example, Williams & Gaston (1994) and Balmford *et al.* (1996) found that family richness was a good predictor of species richness. Maherali & Klironomos (2007) found that fungal communities of more distantly related species retained more species in experimental trials, a pattern of phylogenetic overdispersion which they attributed to reduced competition among phenotypically dissimilar species. By contrast, Forest *et al.* (2007) found plant genus richness and phylogenetic diversity were so dissimilarly distributed in the Cape of South Africa that different reserve networks would result from decisions based on one or the other exclusively. I suggest that correspondence between species and phylogenetic diversities is too inconsistent across studies to assume that they are linked with each other. Indeed, the underlying assumption that niches are phylogenetically conserved is debatable, and under considerable scrutiny. For example, Devictor *et al.* (2010) found the distributions of taxonomic, phylogenetic and functional diversities were related but varied spatially and were poor surrogates for one another.

Unlike phylogenetic diversity, species richness was related to disturbance. The relationship was quadratic with maximum richness of the curve at moderate levels of disturbance, fitting the intermediate disturbance hypothesis. This hypothesis is generally based on the idea that a trade-off in species life history traits prohibits species with poor colonization traits (such as seed number) at high disturbance, excludes less competitive species in older undisturbed communities, but allows a mix of both groups of species at intermediate disturbance (Connell 1978). Mayor *et al.* (2012) explored this relationship further with these boreal plant communities.

As with anthropogenic disturbance, phylogenetic diversity was also generally unrelated to time since natural disturbance (Figure 5.6). When divided into different life forms, differences in phylogenetic diversity among successional stages were observed, but these patterns were inconsistent among forbs, graminoids, and woody plants. Previous studies of phylogenetic community structure and forest succession found varying results (Table 5.1). In tropical forest trees (Letcher *et al.* 2012, Norden *et al.* 2012) and Mediterranean woody plants (Verdú *et al.* 2009), phylogenetic relatedness declined as succession proceeded following natural disturbance. I suggest that phylogenetic relatedness sometimes varies with natural succession, but these trends vary among taxonomic groups. The link between phylogenetic diversity and natural disturbance relies similarly on the assumptions discussed for anthropogenic disturbance.

The phylogenetic diversity-disturbance relationship also depended on types of disturbance (Figure 5.5). Among all observed boreal angiosperm species, phylogenetic diversity was related neither to permanent nor temporary disturbance. When life forms were analyzed individually, phylogenetic relatedness of woody angiosperms increased with perpetual anthropogenic disturbance, but decreased with temporary disturbance. This may suggest that perpetual disturbance effectively removes niche space (and geographic space), while temporary disturbance can increase environmental heterogeneity.

The lack of relationship between phylogenetic diversity and anthropogenic disturbance was inconsistent among species groups varying in growth form. For a subset of observed species, forbs, phylogenetic diversity did fit a quadratic relationship to anthropogenic disturbance (Figure 5.3f). This relationship was similar in shape to the species richness of forbs relative to disturbance (Figure 5.3b). It is unclear why forbs showed a different pattern than other growth forms like graminoids or woody plants. Loss of statistical power due to a smaller sample of species seems unlikely because the richness-disturbance relationship of each growth form showed significant quadratic relationships.

Although phylogenetic diversity varied little along the disturbance gradient, I did observe significant phylogenetic clustering in most communities. This low phylogenetic diversity was consistent among nearly all levels of ecological organization and types of anthropogenic disturbance (Figure 5.1b and 5.3b), indicating that closely related species tend to co-occur in the boreal forest. This pattern may suggest that abiotic filtering plays a substantial role on governing boreal plant community assembly at the regional scale (Webb 2000), regardless of disturbance. However, this finding also relies on previously discussed and debatable assumption that filtering acted on traits that are conserved throughout lineages. Consistent with my study, Vamosi *et al.* (2009) found that 23 of 39 studies (59%) reported phylogenetic clustering in a meta-analysis of undisturbed ecosystems.

Although Canada's boreal forest is still relatively intact, the forest is under ever-increasing pressure from forestry, mining, urbanization, and oil and gas development, and only 10 percent of the forest has been protected to date, far less than what is scientifically recognized as necessary to sustain the ecosystem over time (Noss *et al.* 2012). This situation raises several controversial questions about boreal forest conservation. First, does conservation of areas high in species richness also result in conservation of other aspects of biodiversity, particularly phylogenetic diversity? My findings suggest that species richness is a poor proxy for phylogenetic diversity and I suggest that conservation and management strategies should consider multiple aspects of biodiversity (Mouillot *et al.* 2013; Winter *et al.* 2013). Second, do different levels and types of disturbance influence the changes of species richness and phylogenetic relatedness in the similar way? My results suggest species richness and phylogenetic relatedness respond to different types of disturbance in different ways.

My study provides the first evidence on how phylogenetic structures of boreal angiosperm plant communities change with different levels and types of disturbance over a large region. Yet our understanding of plant community assembly is still limited. Phylogenetic analysis can facilitate more informed conservation planning, but their utility is limited by the limited resolution of phylogenetic trees (Letcher 2010; Swenson 2009). Improved technologies and analytical methods promise more reliable results. Second, a better understanding of functional trait diversity is needed to empower interpretations of phylogenetic diversity. Previous studies have showed that phylogenetic structure can be a poor predictor of the dispersion of functional traits (e.g., Ding *et al.* 2012; Newbold *et al.* 2012). My results based on life form groups of plant species also support this conclusion. Integrating phylogenetic and trait-based approaches will be greatly helpful for our understanding of community assembly (Mouillot *et al.* 2013). Third, abundance data should be included in the analysis of community structure. Norden *et al.* (2012) analyzed the changes of tree community structure along succession using both species abundance data and species occurrence data, and found that abundance data showed a much stronger signal than occurrence data. In addition, detailed information on disturbance intensity and frequency is required for a better understanding on this topic.

In general, I suggest that the hypothesized link between phylogenetic diversity and disturbance is circumstantial and based on the assumption of trait conservatism which is in turn inconsistently supported. To progress, ecology needs both better theoretical foundations for the phylogenetic diversity-disturbance relationship and additional observational and experimental evidence to evaluate them.

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Tables

Table 5.1 Summary of previous studies related to phylogenetic diversity and disturbance

Ecosystem types	**Habitat type**	**Type of study**	**Source**	**Number of sites**	**Groups by disturbance or succession**	**Taxon**	**Dispersion (phylogenetic clustering/evenness)**
Tropical forest	Neotropical forests	Phylogeny	Letcher *et al.* 2012	64	Five successional age categories	Tree species	Decline in phylogenetic relatedness during succession
Tropical forest	Atlantic rainforest (Brazil)	Phylogeny	Santos *et al.* 2010	75	Old-growth, forest edge, secondary forest	Tree species	No evidence supporting fragmentation-induced clustering or evenness
Tropical forest	Lowland forests (Costa Rica)	Phylogeny	Norden *et al.* 2012	6	Succession over time	Tree species	Relatedness decreases during succession based on abundance data, but no trend based on species occurrence.
Tropical forest	Neotropical rain forests (Mexico)	Phylogeny	Arroyo-Rodríguez *et al.* 2012	45	Different deforestation levels	Tree species	Few and very weak changes
Tropical forest	Lowland rain forest (New Guinean)	Phylogeny	Whitfeld *et al.* 2012	19	Succession	Tree species	Clustering in secondary forests; evenness in primary forests
Tropical forest	Tropical rain forest (China)	Phylogeny and traits	Ding *et al.* 2012	18	Disturbed *vs.* undisturbed	Tree species	Clustering in the highly disturbed lowland sites; evenness in other forest types
Tropical forest	Tropical successional communities (Mexico)	Traits	Lebrija-Trejos *et al.* 2010	18	Formerly corn fields with different abandonment times *vs.* a mature forest	Tree species	Clustering
Tropical forest	Old-growth and secondary forests (Costa Rica)	Phylogeny	Letcher 2010	30	Five successional age categories	Vascular plants	Strong phylogenetic evenness at multiple scales

Table 5.1 Continued-1

Ecosystem types	Habitat type	Type of study	Source	Number of sites	Groups by disturbance or succession	Taxon	Dispersion (phylogenetic clustering/evenness)
Tropical forest	Mediterranean plant communities (Spain)	Phylogeny	Verdú *et al.* 2009	149	Post-fire succession	Woody plants	A random pattern in the pioneer stage, evenness in intermediate phases, and a random structure in the late stages
Tropical forest	Mediterranean plant communities (Spain)	Phylogeny and traits	Verdú and Pausas 2007	9	Different fire histories	Woody plants	Clustering in high fire frequency sites; evenness in low fire frequency sites
Tropical forest	Tropical and subtropical rain forests (Australia)	Phylogeny and traits	Kooyman *et al.* 2011	596	Historic disturbance (climatic oscillations) vs. long-term stable (refugial) locations	Woody plants	More clustering patterns along historic disturbance gradient than those in long-term stable locations
Tropical forest	Tropical and sub-tropical forests	Phylogeny and traits	Newbold *et al.* 2012	24	Urbanization gradient	Birds	Species responses to land use depended on their traits
Temperate forest	Disturbed old fields (Canada)	Phylogeny	Dinnage 2009	38	Disturbed *vs.* undisturbed	Herbs	Clustering in disturbed sites; evenness in undisturbed sites
Urban ecosystem	Italy; temperate biome	Phylogeny	Ricotta *et al.* 2008	15	Urbanized areas	Vascular plants	Clustering
Urban ecosystem	Germany; temperate biome	Phylogeny and traits	Knapp *et al.* 2008	1736 grids	Urbanized areas, agricultural, semi-natural areas	Vascular plants	Clustering in urban areas; phylogenetic diversity didn't reflect their high species richness
Urban ecosystem	Household yard (USA)	Phylogeny and traits	Knapp *et al.* 2012	137	Urbanization gradient	Vascular plants	Phylogenetic diversity didn’t change with housing density; clustering in yards compared with natural areas

Table 5.1 Continued-2

Ecosystem types	Habitat type	Type of study	Source	Number of sites	Groups by disturbance or succession	Taxon	Dispersion (phylogenetic clustering/evenness)
Aquatic ecosystem	Aquatic beetle communities (Segura Basin); Mediterranean biome	Phylogeny	Abellán *et al.* 2006	422	Freshwaters *vs.* saline-waters	Aquatic beetles	Taxonomic distinctness measures were apparently less sensitive to the effects of anthropogenic impact than species richness
Coastal dunes	Denmark	Phylogeny and traits	Brunbjerg *et al.* 2012	2702	Fixed herb dunes, fixed dune heath, and dune slack	Vascular plants	Clustering in disturbed sites
Grassland	Alpine meadows (China); tundra biome	Phylogeny and traits	Yang *et al.* 2012	32	Land use (fertilization and grazing)	Grass	No evidence of clustering in relation to intensified land use
Zooplankton communities	USA and Canada); temperate biome	Phylogeny and traits	Helmus *et al.* 2010	34	Disturbed *vs.* undisturbed	Zooplankton	Clustering in disturbed sites regardless of disturbance type

Table 5.2 Classification of disturbance types in my study sites

Major Disturbance Category	Disturbance Types	Description	Number of Sites
Perpetual disturbance	Agriculture	Pasture and croplands	24
	Urban & Industry	Urban and rural settlements, coal and mineral surface minds, oil sands development and others	12
	Hard Linear	Linear features that are paved or gravel (logging roads, railways)	4
Temporary disturbance	Forestry	Forestry harvesting areas	25
	Soft Linear	Linear features that are grass or natural vegetation after disturbance (cutlines, pipelines)	84
No anthropogenic disturbance	Age 0-20	Stand age <20 years (young forest)	11
	Age 20-50	Stand age 20-50 years (young forest)	19
	Age 50-80	Stand age 50-80 years (immature forest)	44
	Age 80-120	Stand age 80-120 years (mature forest)	25
	Age ≥120	Stand age ≥120 years (old-growth forest)	23

Figures

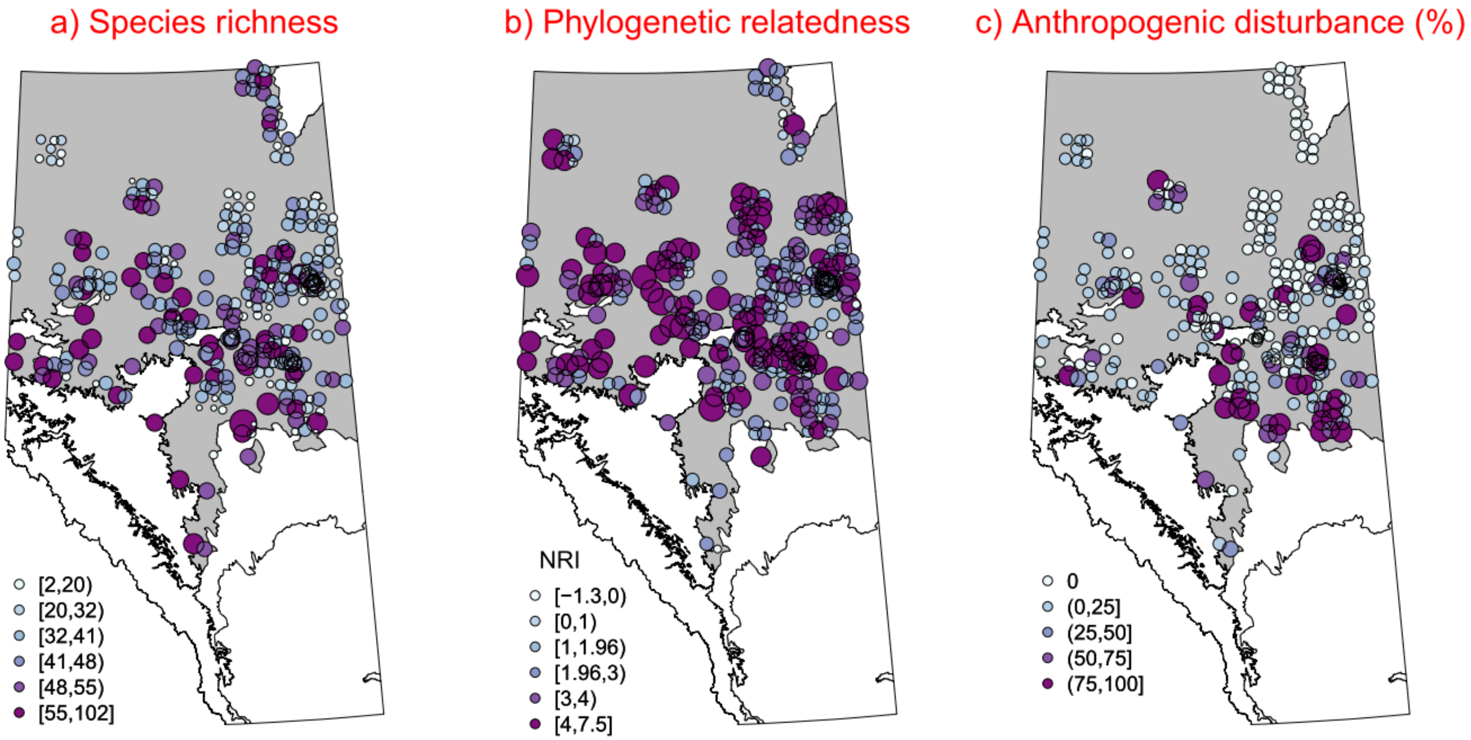


Figure 5.1 Spatial distribution of native angiosperm plant species richness, phylogenetic relatedness (NRI) and anthropogenic disturbance extents in the boreal ecoregion of Alberta

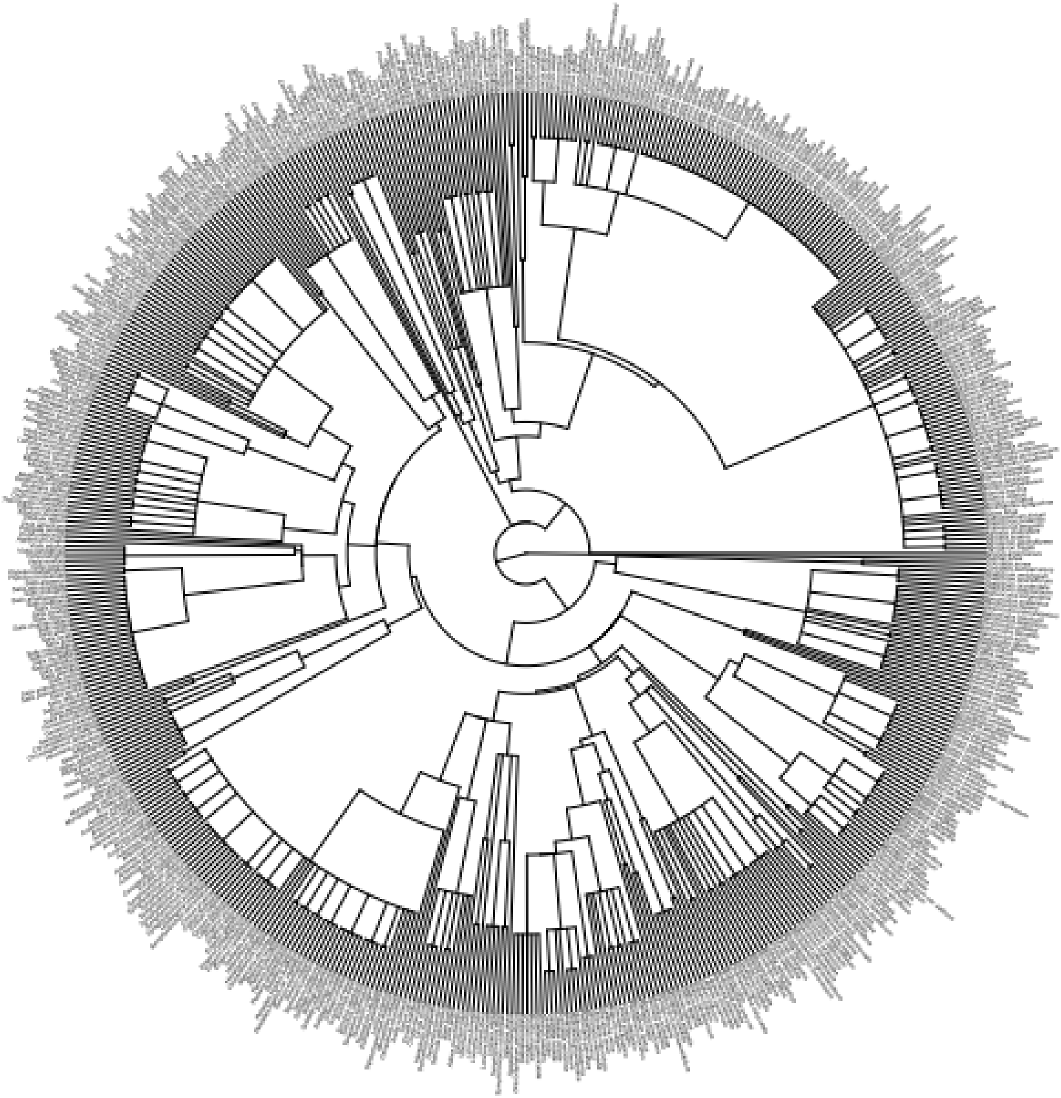


Figure 5.2 Phylogenetic tree of 585 angiosperm plant species in Alberta boreal forests

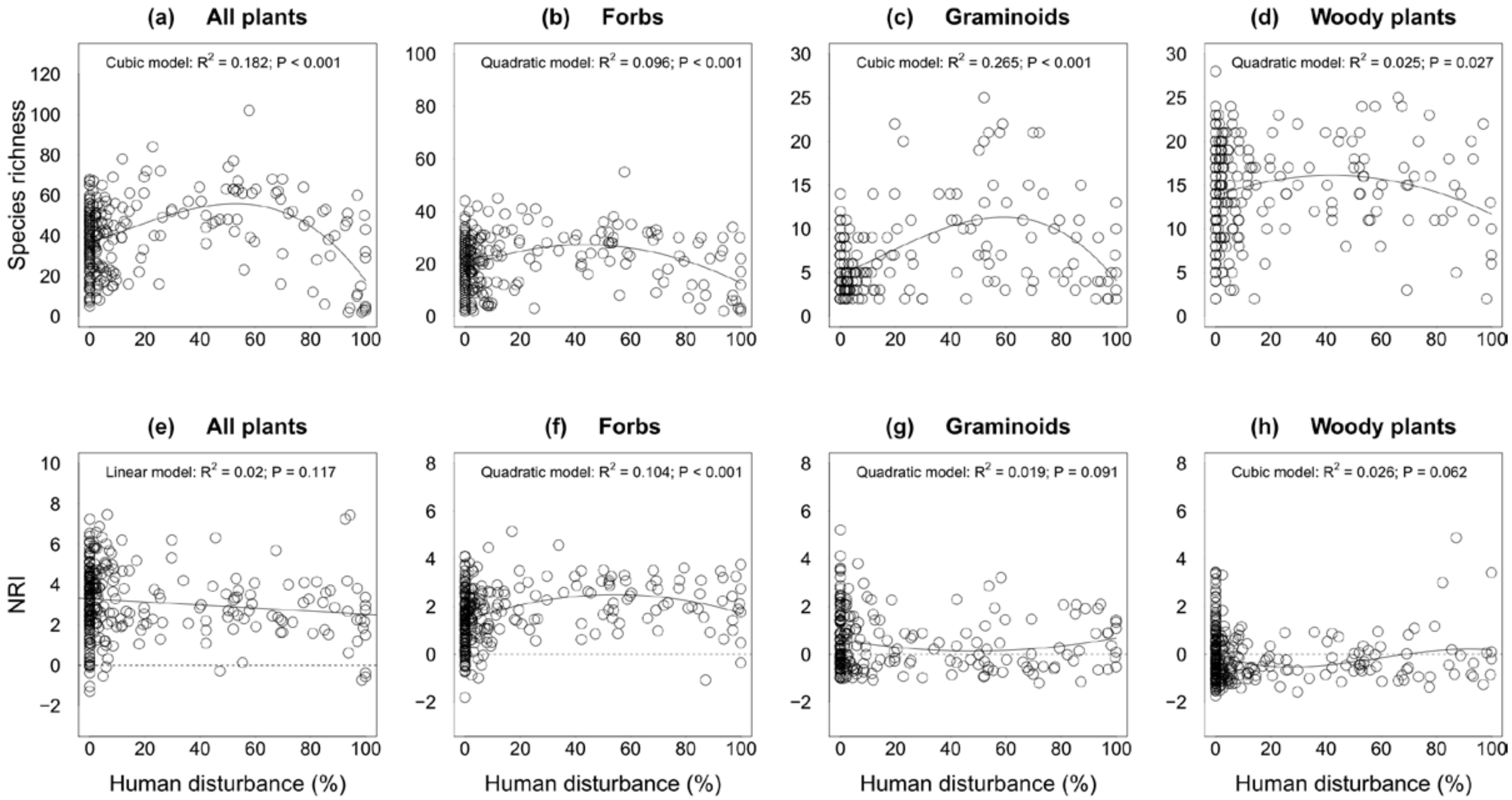


Figure 5.3 Changes of native angiosperm plant richness and NRI under total anthropogenic disturbance gradient

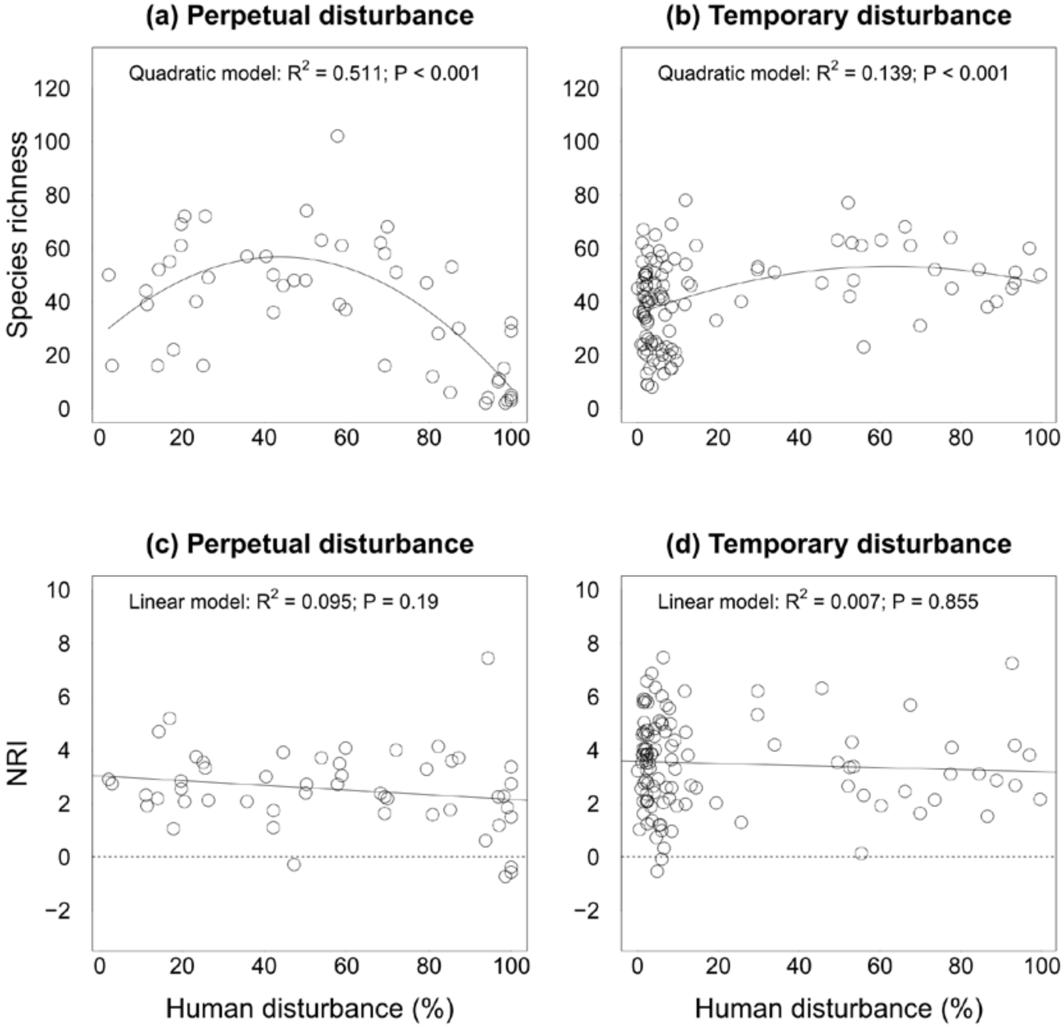


Figure 5.4 Changes of native plant species richness and NRI under two major anthropogenic disturbance categories

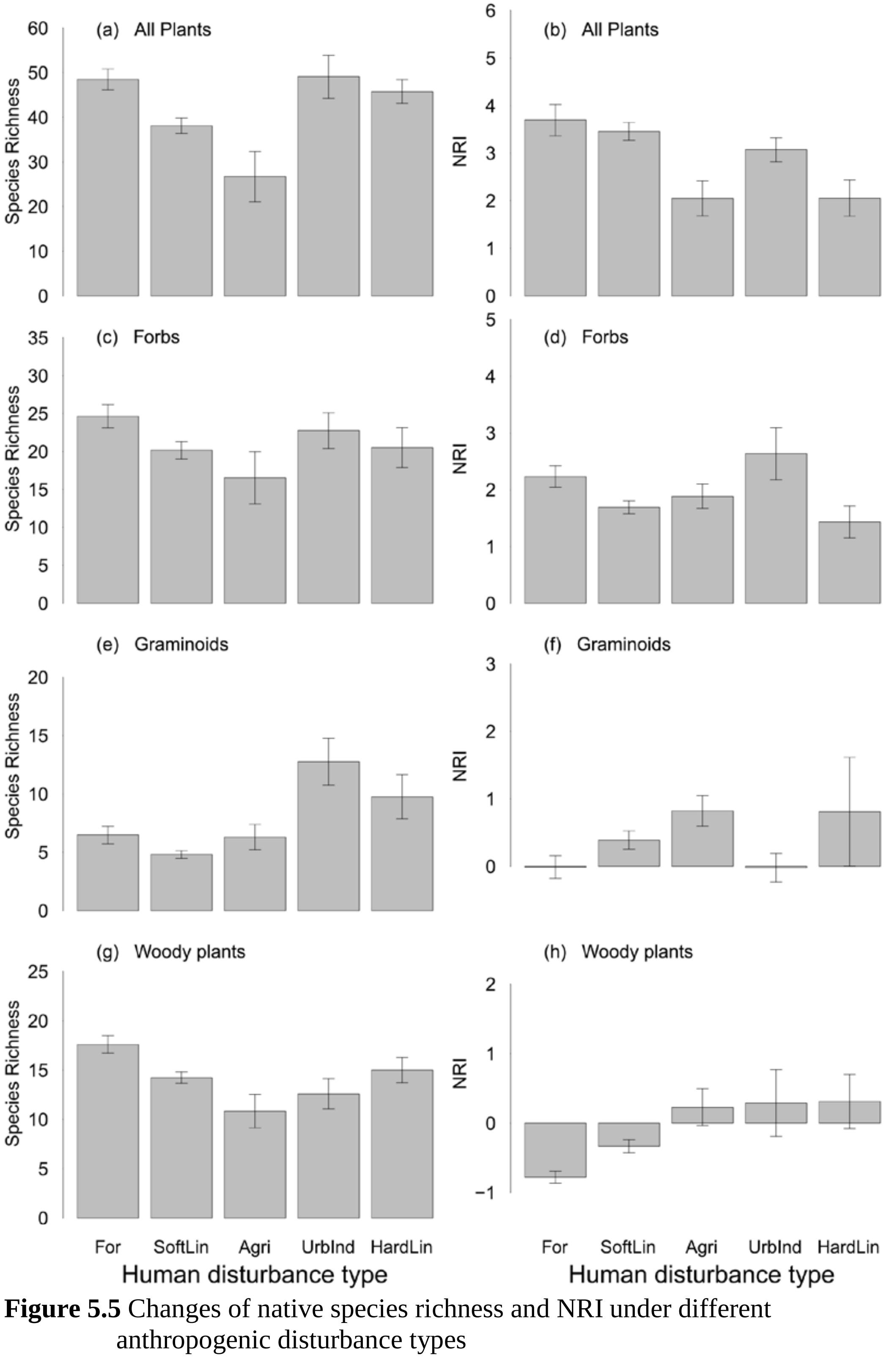


Figure 5.5 Changes of native species richness and NRI under different anthropogenic disturbance types

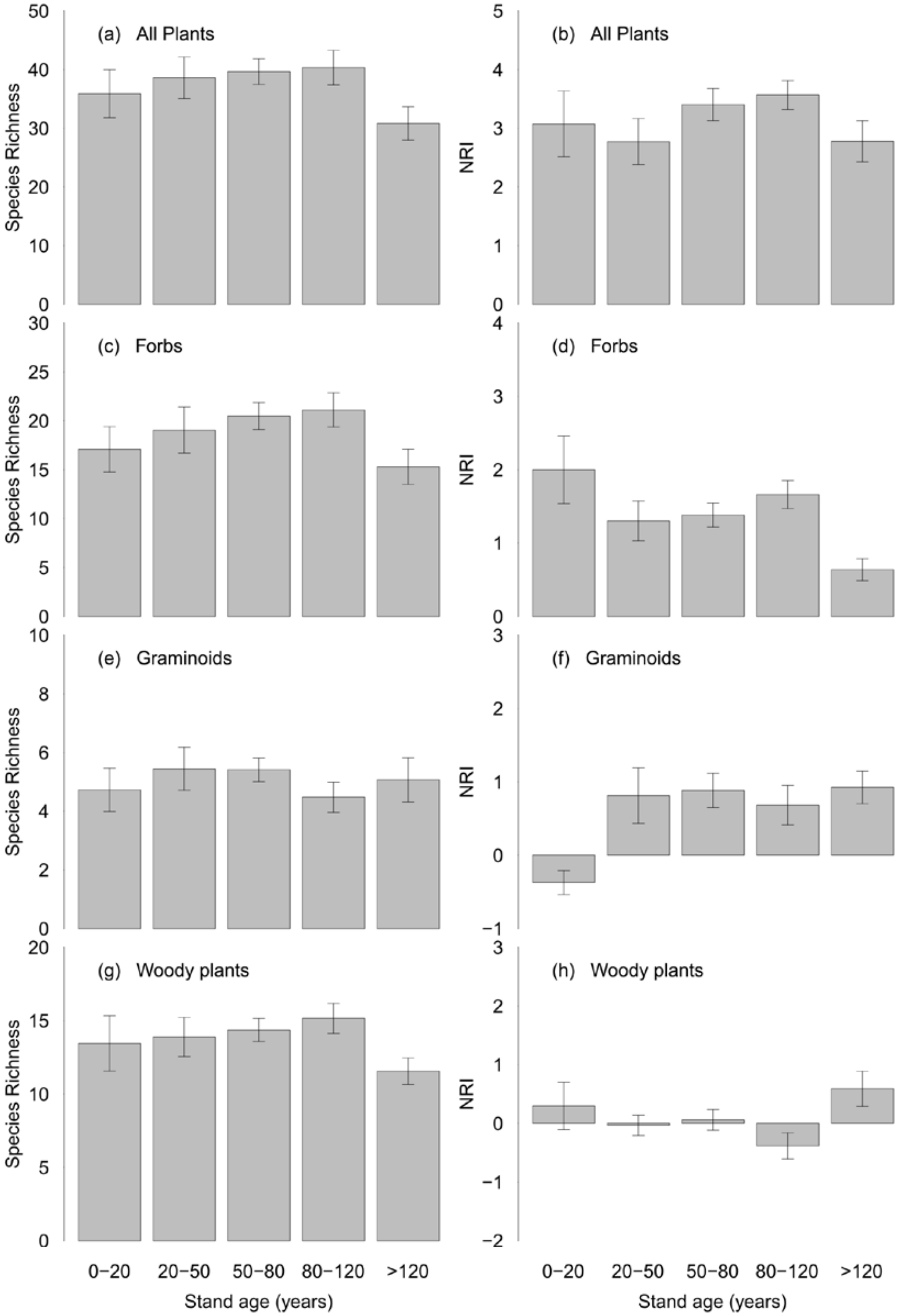


Figure 5.6 Changes of native species richness and NRI along natural succession for study sites with only natural disturbance

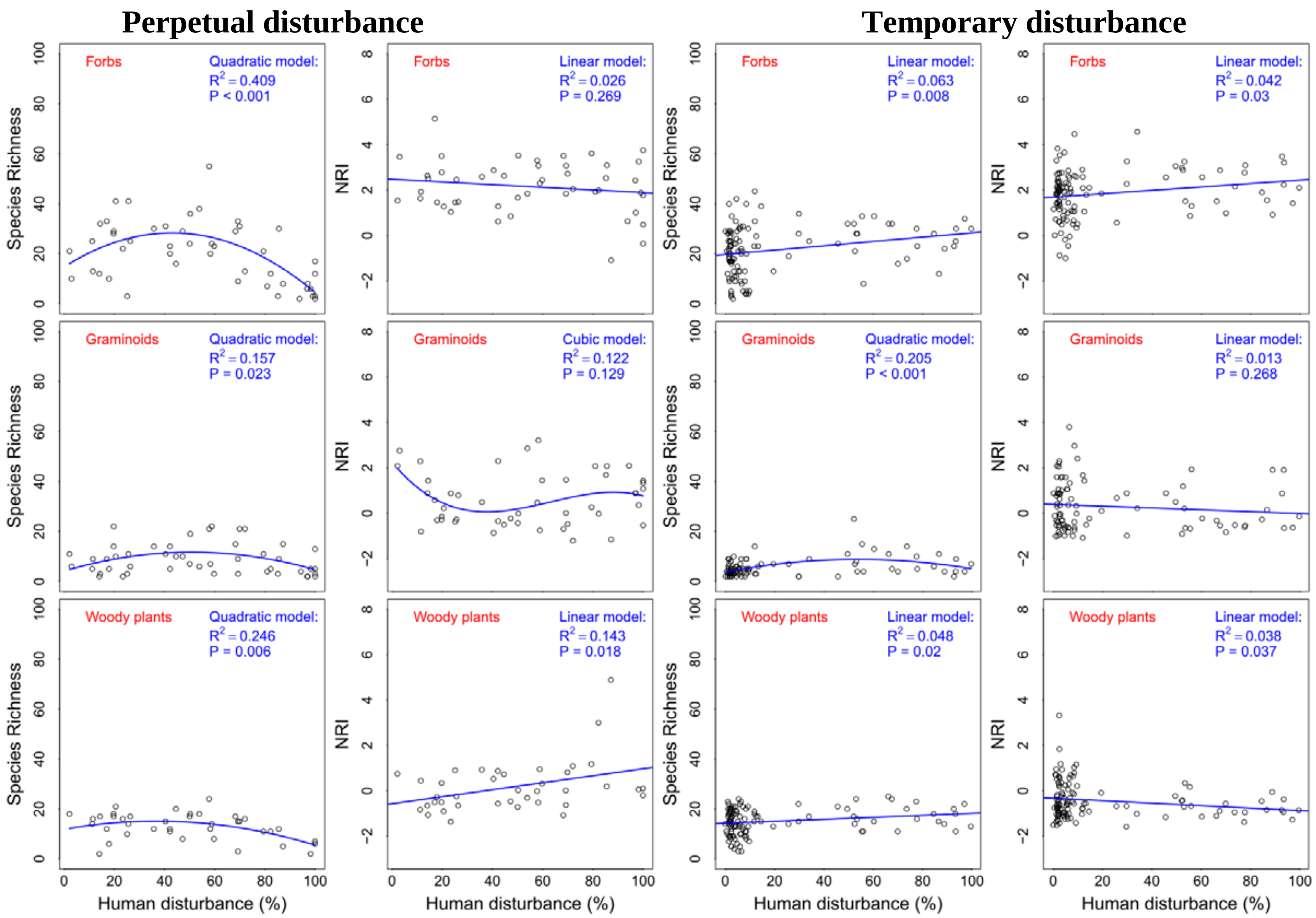
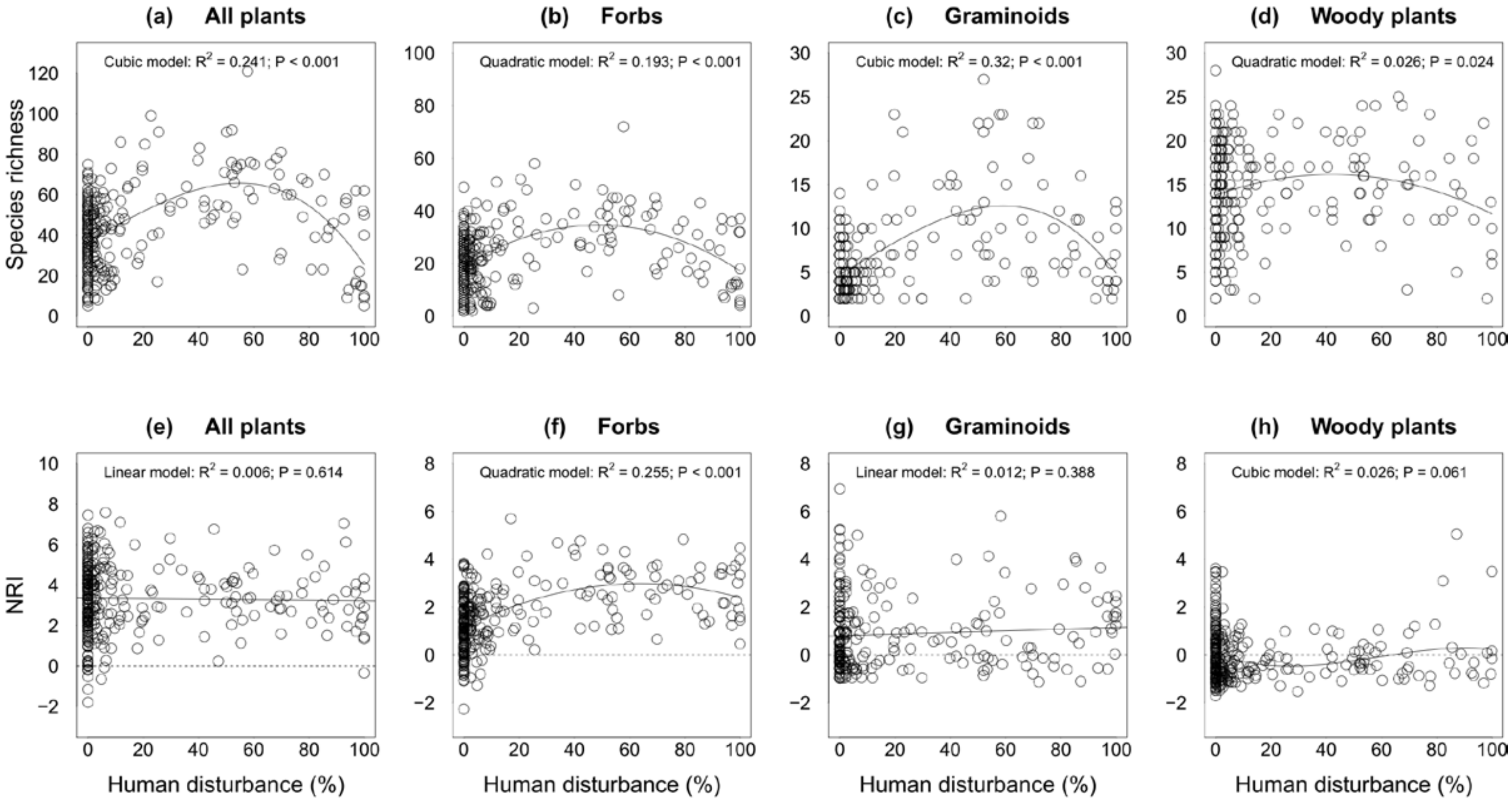
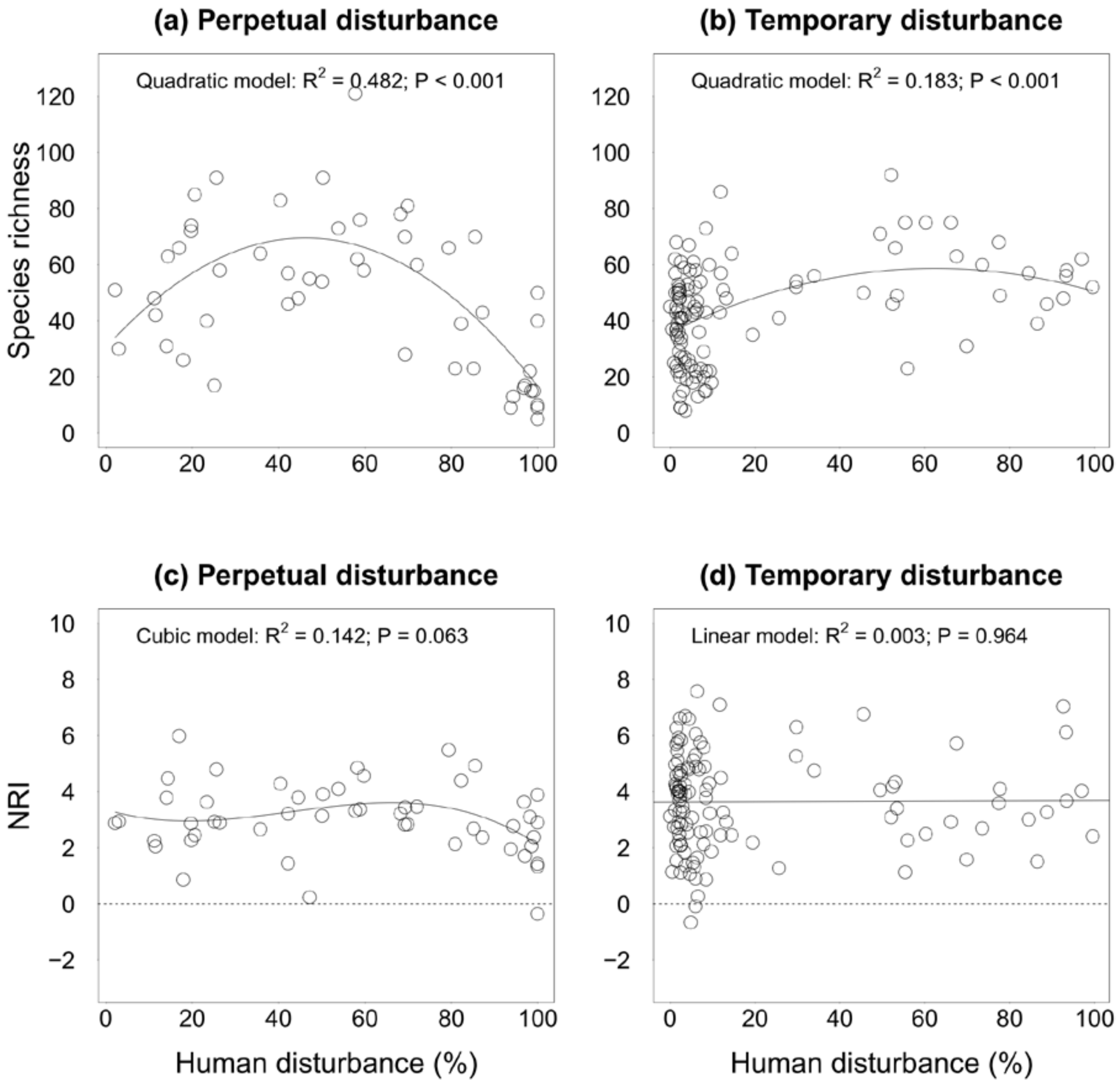


Figure 5.7 Changes of native species richness and NRI of different life forms under two major anthropogenic disturbance categories

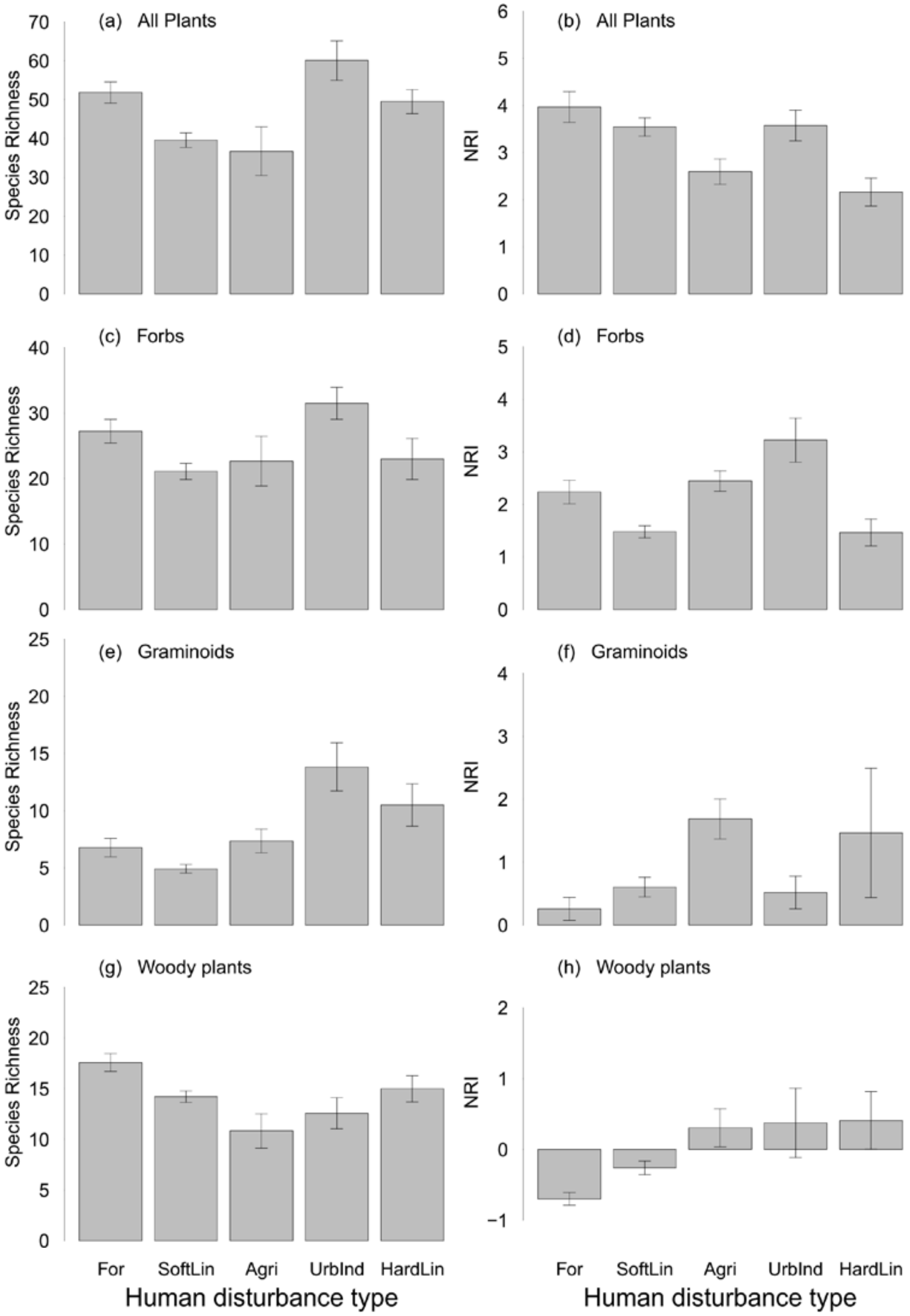
***Appendix 5A** Changes of angiosperm plant richness and NRI under total anthropogenic disturbance gradient*



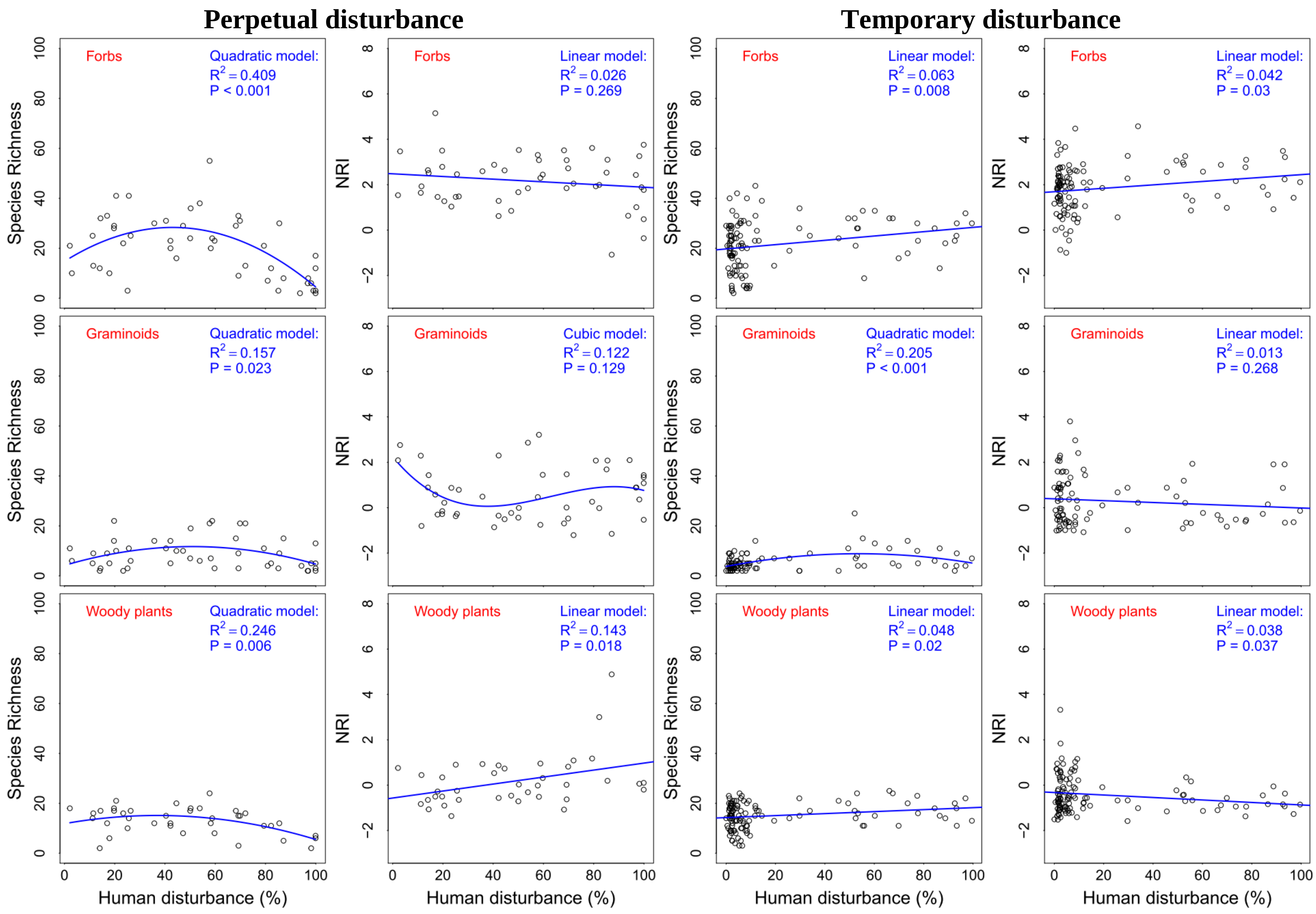
Appendix 5B *Changes of angiosperm plant richness and NRI under two major anthropogenic disturbance categories*



Appendix 5C *Changes of angiosperm plant richness and NRI under different anthropogenic disturbance types*



Appendix 5D *Changes of angiosperm plant richness and NRI of different life forms under two major anthropogenic disturbance categories*



Chapter 6 General Discussion and Conclusions

6.1 *Research Summary*

The scope of my thesis was to evaluate how the patterns and processes of biodiversity and ecosystem functioning change with climate, environments, natural and anthropogenic disturbances, evolutionary history of species, and biotic factors. By using a long-term and large amount of data sets from variable sources and novel methods and approaches, I came to the following key conclusions:

1) In Chapter 2, using five decades of forest inventory data in western Canada, I systematically evaluated the relative roles of tree competition and climate change on affecting tree growth, mortality, and recruitment. I observed a widespread, significant increase in tree mortality but a significant decrease in tree growth. When possible causes were assessed, competition was clearly the major contributor to all the changes. Climate change contributed greatly to tree mortality, but little to tree growth and recruitment. Meantime, these changes varied greatly across tree size, forest age, ecozones and species.
2) In Chapter 3, I reported a spatially explicit dataset for present biomass carbon storage in Alberta forests, derived from a combination of forest inventory data, spaceborne Lidar data, land cover, climate and environmental variables. Total biomass stock was estimated to be 3.11×10^9 Mg. Average biomass density was 77.59 Mg ha^{-1}. Three major tree species, lodgepole pine, trembling aspen and white spruce, stocked

about 1.91×10^9 Mg biomass totally, accounting for 61% of total estimated biomass. Spatial distribution of biomass varied with natural regions, land cover types and species.

3) In Chapter 4, using breeding bird species as an example, I highlighted the critical roles of local habit structure (vegetation layers, canopy height, etc.) on determining broad-scale bird diversity patterns, which has been largely overlooked in many previous studies. Also, I emphasized the importance of considering life-history traits (guilds) into bird diversity assessment and conservation.
4) In Chapter 5, I assessed the roles of evolutionary history in structuring boreal plant communities. As far as I am aware, this is the first study to directly address this question in boreal plant communities. In most cases, I observed high species richness at intermediate anthropogenic disturbance levels, but richness did not correlate with phylogenetic diversity. And I failed to detect significant changes in phylogenetic diversity with disturbance, indicating that species turnover may relate to anthropogenic disturbance randomly or uniformly throughout the phylogenetic tree in boreal plant assemblages.

6.2 Management and Conservation Implications

My thesis research should have important implications to forest management and biodiversity conservation in the boreal forests, including:

1) **Drivers of tree growth and death**: I provided a synthetic understanding of the relative influences of climate change and competition on forest dynamics (Chapter 2). The results will help scientists, forest managers and policy makers better understand the long-term effects of climate change on forest productivity, and thus guide conservation practices and sustainable forest management and maximize conservation and cost-efficiency.
2) **Benchmark map of Alberta forest biomass carbon stocks**: I provided a spatially explicit biomass map for current Alberta forest (Chapter 3). This information could be used as a baseline data for evaluating how much Alberta contributes to regional and global carbon storage and for predicting how Alberta will response to changing climate and increasing human activities in the future. Also, I concluded that spaceborne Lidar can be used to estimate broad-scale biomass. By combining with inventory data, climate, environmental variables, we can estimate biomass storage and changes in a cost-effective way.
3) **Biodiversity assessment**: My results provided a comprehensive biodiversity assessment for both plants and birds in the boreal (Chapters 4 & 5). The assessment considered evolutionary history and life-history characterises of species and quantified the values of their addition to traditional biodiversity assessments and conservation decisions (Zhang *et al.* 2014). These results will inform approaches of boreal forest biodiversity conservation including protected areas planning and management, inputs into the Land-Use Framework and biodiversity policy.

4) **Life-history & biodiversity conservation**: My results highlight the importance of life-history characteristics on biodiversity conservation, and evaluate how different life-history strategies respond to different disturbance types and extents (Chapters 4 & 5). These results assist us in determining which life-history characteristics are relatively sensitive to changing environments (Zhang *et al.* 2013, 2014). This information can be used in multi-species assessments and recovery.

5) **Human disturbance *vs.* biodiversity and ecosystem functioning**: Chapters 4 and 5 contribute to this issue. For birds and vascular plants in the boreal, both human disturbance types and extents have great impacts on constructing community assembly.

6.3 Limitations and Recommendations for Future Research

The present research resulted in a better understanding of patterns and underlying processes of biodiversity and ecosystem functioning in Alberta boreal forest region, but has also lead to several limitations.

In the second chapter about long-term forest dynamics, there are at least three specific limitations to this study. First, due to the different field survey protocols in different provinces and during different time periods, the analyses were only focus on individual trees with DBH larger than 9 cm. We don’t know how tree seedling and saplings response to changing biotic and abiotic environments in the last five decades. Second, my analyses only focus on the plots with stand age larger than 50 years to reduce the difficulty to explain my results.

However, it could be interesting to look at how young forests response to climate change and plant competition. Luo & Chen (2013) analyzed tree mortality patterns in 887 PSPs in Western Canada, and found that climate change-associated increases were significantly higher in young than old forests, and higher increases in younger forests were a result of their higher sensitivity to regional warming and drought. Third, I didn’t find a clear signal of drought-induced tree mortality, while the effects of drought on tree mortality were detected in other studies in Alberta aspen forests (Hogg *et al.* 2008; Michaelian *et al.* 2011). One possible reason is that I used the averages of climatic variables during each census interval, which might hide the possible effects of drought on tree mortality. And I didn’t consider lagged effects of drought in this chapter (e.g., Bigler *et al.* 2007). Clearly, further studies are needed to better consider these limitations.

In the third chapter about biomass mapping, one possible limitation is the quality of spaceborne Lidar canopy height data. One recent study by Bolton *et al.* (2013) addressed this question by comparing canopy height data from spaceborne Lidar and 34 Lidar transects of small-footprint airborne Lidar data across Canada’s boreal forests. They found the global GLAS-derived product (Simard *et al.* 2011), which I used for this chapter, was in closer agreement with airborne Lidar-derived height estimates ($RMSE$ = 3.9 m in all ecozones; $RMSE$ = 4.39 m in Boreal Plains) (Bolton *et al.* 2013). In addition, it could be interesting to investigate the agreement among ground inventory data, airborne Lidar, and spaceborne Lidar in a relatively small area.

In the fourth chapter about Alberta breeding bird distribution, human disturbance was qualified by the percentage area of land cover types within a 500 m radius from the centre of each site. The results only based on this measurement raise some possible issues. Further studies are needed to focus on how different human or natural disturbance types, combining with abiotic and biotic factors, constrain species richness of bird and other taxa, such as vascular plants, mosses, lichens and mites. Those data sets are also publicly available from ABMI (http://www.ABMI.ca).

In the fifth chapter about phylogenetic diversity and disturbance, I have the same limitation on human disturbance data. In addition, the utility of phylogenetic analysis is limited by the limited resolution of phylogenetic trees (Letcher 2010; Swenson 2009). Improved technologies and analytical methods will promise more reliable results. Also, functional trait data will empower interpretations of my phylogenetic diversity results. Integrating phylogenetic and trait-based approaches will be greatly helpful for our understanding of community assembly (Mouillot *et al.* 2013).

Finally, there are a lot of questions related to biodiversity conservation and forest management we could address from my study and huge amounts of data I presented. I anticipate my thesis to be a starting point for more comprehensive examinations of related questions.

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