Bottom-up controls of flammability in the Canadian boreal forest at multiple temporal and spatial scales

by

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Abstract

Wildfires are the most common disturbances occurring in the Canadian boreal forests. Their incidence and characteristics are controlled by different factors at different temporal and spatial scales. At every scale, vegetation is an essential factor fueling fires. Despite its importance, some aspects of vegetation flammability in a biological context remain poorly understood. In this work, I explore the role of vegetation as a bottom-up control of fire and its interaction with climate at different spatial and temporal scales, in the Canadian Boreal Forest.

First, I examined the flammability of living jack pine (*Pinus banksiana* Lamb.) needles as characterized by their physicochemical features (moisture, chemical, and form) as a function of leaf age and time of the growing season. I measured their curvature, form coefficient, surface-area-to-volume ratio and calculated their content of carbon, nitrogen, starch, sugars, lipids and terpenes. I employed a modified cone calorimeter and open flame to measure their ignitability, combustibility, sustainability, and consumability of the pine needles. The results indicated that needles under a year old are the least flammable; they were rounder, more voluminous, with higher moisture and nitrogen content. One- and two-year-old needles are more ignitable, combustible, and consumable; they are drier, more curved, thinner, longer, and contain more carbon and terpenes than younger needles. Regardless of age, needles release more energy during the first half of the growing season (June-July) when starch and lipids are at their highest concentrations. Overall, the results suggest that needle moisture content by itself had a minor influence on their flammability compared to their form and chemical content.

Second, I built a model to estimate the development and potential regeneration failure of a conifer forest under scenarios of vegetation resistance to reburn and climate change. Young forests are less likely to reburn, mainly due to fuel limitations, and they have the potential to reduce fire activity. On the other hand, climate change enhances fire activity through increasing temperatures, droughts, and the frequency of extreme fire events. To evaluate the effect of resistance and climate change on age structure and forest loss, I built a state-and-transition model parametrized with a Markov Chain Model. The model structure was based on 157 years of fire history in a conifer-dominated forest in northern Quebec. I created scenarios from the combination of different levels of resistance to burning and climatic change, plus two behaviors of interannual variation (irregular vs smooth). After forecasting for 50 years, I found that: 1) the youngest forests increase in frequency, while older ones disappear for short periods. 2) resistance to reburn varies latitudinally affecting the degree of forest loss, 3) forest loss without reburning resistance would be two times higher, 4) reburning resistance may counteract the effects of the projected climate change reducing forest loss from 1.5 to two times, but 5) occasional events of extreme fire conducting conditions may overwhelm this resistance. This study emphasizes the significance of incorporating the negative feedback from vegetation on fire occurrence to enhance the accuracy of estimating the future of the boreal forest.

Finally, I assessed the impact of human influence on the fire regime in two areas of the boreal forest in north Alberta. Humans do not only alter the number of fires and area burned directly by setting fires, but they also suppress them. Indirectly, humans intentionally modify the landscape as a preventive measure, or unintentionally through other activities (e.g., agriculture, urban development, forest harvesting). To determine the type and extent of these changes on the fire regime, I compared trends and cyclical patterns of fire activity of two areas with contrasting human influence from 1970 to 2015 (Wood Buffalo National Park and Lower Athabasca Plains) and examined their climate-fire associations. Human influence affects fire activity by 1) limiting area burned and reversing the increase in the number of fires caused by climate change, 2) shifting the peak of fire activity from the summer to the spring, 3) modifying the association between fire and climate, and 4) shortening the cyclical patterns of fires. In conclusion, humans have altered the temporal and spatial patterns of fire activity creating a novel fire regime in areas under their influence.

Preface

This thesis is the original work of Rodrigo Tzunun Campos Ruiz, who conducted the research led by Professor Emeritus Michael Flannigan, at the University of Alberta, Department of Renewable Resources, and Research Scientist Marc-André Parisien, at the Canadian Forest Service, Northern Forestry Centre. The research was a collaboration under the Canadian Partnership for Wildland Fire Science. Rodrigo Tzunun Campos Ruiz performed the literature review, designed the methods, processed all data, and interpreted the results. Data collection was mainly performed by Rodrigo Tzunun Campos Ruiz and different collaborators on each chapter.

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Chapter 3 is currently unpublished. Rodrigo Tzunun Campos Ruiz performed the design, data analysis and composition. M.-A. Parisien and Mike Flannigan contributed to the manuscript inputs and edits. M.-A. Parisien contributed with the concept formation. Data was provided by Professor Dominique Arsenault at the Université du Québec à Rimouski, Jesse Héon, at the

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Table of contents

ABSTRACT……………………………………………………………………………….……..… ii

PREFACE…………………………………………………………………………….………... v

ACKNOWLEDGEMENTS…………………………………………………….………… vii

TABLE OF CONTENTS……………………………………………………………….. xi

LIST OF TABLES………………………………………………………….………….. xiii

LIST OF FIGURES…………………………………………………….….……….... xvi

1 INTRODUCTION 1

1.1 BACKGROUND 1
1.2 CONTROLS OF FIRE 1
1.3 FLAMMABILITY 2
1.4 PARADIGMS IN FIRE RESEARCH 3
1.5 RESEARCH JUSTIFICATION AND OBJECTIVES 4
1.6 REFERENCES 7

2 PHYSICOCHEMICAL CHARACTERISTICS CONTROLLING THE FLAMMABILITY OF LIVE *PINUS BANKSIANA* NEEDLES IN CENTRAL ALBERTA, CANADA 19

2.1 ABSTRACT 19
2.2 INTRODUCTION 19
2.3 METHODS 22
  2.3.1 Sample collection 23
  2.3.2 Flammability tests 24
  2.3.3 Moisture content 25
  2.3.4 Form analysis 25
  2.3.5 Chemical analysis 27
  2.3.6 Statistical analysis 27
2.4 RESULTS 29
  2.4.1 Flammability 29
  2.4.2 Foliar moisture content, form, and chemical content 31
  2.4.3 Needle age and month of collection 35
  2.4.4 Form and chemical characteristics 37
2.5 DISCUSSION 40
2.6 CONCLUSIONS 45
2.7 ACKNOWLEDGEMENTS 45
2.8 REFERENCES 46

3 STAND RESISTANCE TO REBURN MODERATES THE POTENTIAL FOR REGENERATION FAILURE IN THE NORTHEASTERN CANADIAN BOREAL FOREST…... 62

3.1 INTRODUCTION 62

3.2 METHODS 65

3.2.1 Study site and data collection 66

3.2.2 The model 69

3.2.3 Burning resistance 73

3.2.4 Simulating regeneration failure 75

3.2.5 Simulating climate change effects 78

3.2.6 Simulating variations over time 78

3.2.7 Scenarios 81

3.3 RESULTS 83

3.4 DISCUSSION AND CONCLUSIONS 90

3.5 ACKNOWLEDGEMENTS 96

3.6 REFERENCES 96

4 TEMPORAL PATTERNS OF WILDFIRE ACTIVITY IN AREAS OF CONTRASTING HUMAN INFLUENCE IN THE CANADIAN BOREAL FOREST 112

4.1 ABSTRACT 112

4.2 INTRODUCTION 113

4.3 MATERIALS AND METHODS 116

4.3.1 Study Areas 116

4.3.2 Fire Variables 120

4.3.3 Fire-Climate Variables 120

4.3.4 Statistical Analysis 121

4.4 RESULTS 125

4.5 DISCUSSION 129

4.6 CONCLUSIONS 134

4.7 ACKNOWLEDGEMENTS 135

4.8 AUTHOR CONTRIBUTIONS 136

4.9 CONFLICTS OF INTEREST 136

4.10 REFERENCES 136

5 CONCLUSIONS 149

BIBLIOGRAPHY 152

APPENDIX 198

List of tables

Table 2.1 Flammability parameters and their associated variables obtained from the cone calorimeter.... 25

Table 2.2 Biometric variables of jack pine needles 26

Table 2.3 Repeated measures correlation coefficients (r_{rm}, *d. f.* = 87, top-right) and their respective *p*-values (bottom-left) for the variables of flammability, form, and chemical content. Bold numbers indicate significant correlations ($p<0.05$). Acronyms: IGT, ignition time, HRR, peak heat release rate, EHC, effective heat of combustion and MLR, average mass loss rate. Other letters represent: FMC, foliar moisture content, CRV, curvature, FCO, form coefficient, AVR, surface-area-to-volume ratio, N, nitrogen, C, carbon, SS, soluble sugars, ST, starch, LI, lipids and TE, terpenes. 34

Table 3.1 Estimated Beta distribution parameters by MEM (Moment Matching Estimation) for the burning probability of each state and transect section. Random draws from a Beta distribution with these parameters were used for the inhomogenous (time-varying) Markov Model scenarios. Baseline conditions (without climatic override) reflect historical patterns of fire occurrence, while climatic override assumes a higher probability of fires (x1.5). 80

Table 3.2 Scenarios to predict age structure and forest loss resulting from the combination of different properties of time variation, burning resistance, and climatic overrides. Time variation refers to constant (homogeneous: **H**) versus changing (inhomogeneous: **I**) burning probabilities over time. Burning resistance refers to variations of resistance between forest states (**R**) versus the assumption that no such distinction exists (**E**). Climatic change represents a higher (×1.5) burning probability (**C**), which is the expected increase of fire occurrence under climate change in the area of study (see text for details)........ 82

Table 4.1 Area occupied or modified by the leading human activities in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP).. 118

Table 4.2 Climate variables and Fire Weather Index System codes and indices used (Modified from Van Wagner, 1987)... 121

Table 4.3 Theil-Sen slope values (*β*) and significance by a random-phase Mann-Kendall trend test (* ≤0.05, ** ≤0.005) for the fire-climate variables in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Values were calculated from annual time series. 127

Table 4.4 Correlation coefficients for the number of fires (upper-right) and area burned (lower left, shaded) of the fire activity time series in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Significance was calculated by a random-phase test (* ≤0.05, ** ≤0.005). Letters following area name indicate ignition cause: Lightning (L) and human (H). 127

Table 4.5 Kendall-correlation coefficients for the relationship between the number of fires and area burned with fire-climate time series at lag 0 (i.e., current year) in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Significance was calculated using a random-phase test (* ≤0.05, ** ≤0.005). 128

Table A1 Monthly weather data for temperature and precipitation for the sampling period of the study. Maximum and minimum temperatures indicate extremes. Source: Edmonton Woodbend weather station (ID: 1872), Alberta, located at 1.65 km from the study site. 198

Table A2 Detailed methods for the extraction and calculation of the chemical composition of jack pine needles 200

Table A3 Results for the repeated measures ANOVA for the effects of the month of collection and needle's age on jack pine needles' flammable characteristics (*n* = 96). Transformations (if any) are indicated in parenthesis under the variable name, and *p*-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate.. 201

Table A4 Results for the repeated measures ANOVA for the effects of month of collection and age of the needle on the foliar moisture content and form characteristics of jack pine needles (*n*=96). Transformations (if any) are indicated in parentheses under the variable name, and *p*-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate 202

Table A5 Results for the repeated measures ANOVA for the effects of month of collection and age of the needle on jack pine needles' chemical characteristics (*n*=96). Transformations are indicated in parenthesis under the variable name, and *p*-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate. 203

Table A6 Correlation coefficients of the NMDS variables with their ordination axes, and the result of the premutation test. Coefficients (*r*) indicate the correlation of each variable with the ordination axes. 204

Table A7 Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and log-likelihood values for the Markov Chain Model fitting of the stand age state sequences derived from the fire scar history of the cells in the north and south portions of the transect (N equals the number of plots). We used the function *fitMarkovChain* (package "clickstream" in R), specifying the quadratic/Lagrange approach (Scholz, 2016). 206

Table A8 Predicted proportional forest loss (NF) by the Homogeneous and In-Homogeneous MCM (x̄ ± SD) scenarios after 50 years. Scenarios simulate reburn resistance under historical climatic conditions (**R**) and with climatic change (**RC**) and lack of burning resistance without (**E**) and with climatic change (**EC**). 207

Table A9 Fire statistics in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP) from 1970 to 2015. Letters L and H indicate lightning and human-caused fires respectively. 209

List of figures

Figure 2.1 Non-metric multidimensional scaling of jack pine needles (stress=0.05) with 95% confidence ellipses for the age factor. Different colors indicate sample age and different shapes the month of the collection. The strength of the relationship between variables is reflected by the arrow's length, whereas their direction indicates their type: positive for the same direction, negative for opposite directions. Bold letters highlight the flammability parameters: IGT, ignition time, HRR, peak heat release rate, EHC, effective heat of combustion and MLR, average mass loss rate. Other letters represent: FMC, foliar moisture content, CRV, curvature, FCO, form coefficient, AVR, surface-area-to-volume ratio, N, nitrogen, C, carbon, SS, soluble sugars, ST, starch, LI, lipids and TE, terpenes. 31

Figure 2.2 Variance partitioning for each component of flammability of jack pine needles. Non-overlapped areas represent the unique variation explained by each variable (MC) or set of variables (chemistry and form). The significant differences of the unique variance explained are marked with an asterisk. Overlapped areas indicate common variance explained. 32

Figure 2.3 Flammable characteristics of jack pine needles by age (zero, one, and two-year-old) and month (June, July, August, September): a) Time to ignition, b) peak rate of heat release, c) effective heat of combustion, and d) average mass loss rate. Points represent the mean, and whiskers the bootstrapped standard error. 36

Figure 2.4 Plots for the foliar moisture content and form characteristics of jack pine needles by age (zero, one or two-year-old) and months (June, July, August, September): a) moisture content, b) curvature, c) form coefficient, and d) surface-area-to-volume ratio. Points represent the mean, and whiskers the bootstrapped standard error. 38

Figure 2.5 Plots for the chemical concentrations of jack pine needles by age (zero, one or two-year-old) and months (June, July, August, September): a) carbon, b) nitrogen, c) starch, d) soluble sugars, e) lipids, and f) terpenes. Points represent the mean, and whiskers the bootstrapped standard error. 39

Figure 3.1. Map of the study area in the province of Quebec, Canada. The two transects are shown in purple (north) and green (south). 66

Figure 3.2. A state-and-transition diagram representing a discrete-time "birth and disaster" Markov chain model. The model is specified by a transition matrix (**A**) and an initial condition for each state, which are ratios of each stand age class (i.e., initial cohort, $\boldsymbol{x}_1$). The squares denote the states (s) that transit at discrete intervals (m). Arrows indicate three different kinds of transitions: growth (g) or transition from a state to a successive one, permanence (r) on the same state, and fire events (f) or resetting process, which is the transition from any state to the first one. A cell at a state s_m can transit (grow) to s_{m+1} with a probability of g_m, remain in the same state with a probability of r_m or burn with a probability of f_m, which would make it transit to the initial state. 70

Figure 3.3. State-and-transition diagrams for the six-state baseline model with the observed forest dynamics for the north and south portions of the transect. Boxes indicate forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and arrows the transitions between them with their corresponding probabilities. Transitions represent growth (transition to the following stage), stasis (permanence in the same stage) and fire (i.e., burning; transition to the initial stage resetting the process)... 72

Figure 3.4. Frequency of fire events at each age state (S0, <1 year; S1, 1-20 years old; S2, 21-40 years old; S3, 41-60 years old; S4, 61-80 years old and S5, >80 years old) obtained from the fire history of each transect segment. The lower section represents the proportional contribution of each state to the χ^2 test of dependency (residuals). The bigger the absolute value, the most different it is from the expected value and the most influence on the age-fire dependence. 74

Figure 3.5. State-and-transition diagrams for seven-state models employed to project forest dynamics for the north and south portions of the transect. Boxes indicate forest states (NF, non-forested; S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and arrows the transitions between them with their corresponding probabilities. Transitions represent growth (transition to the following stage; g), stasis (permanence in the same stage; r), fire (burning; transition to the initial stage resetting the process; $fm_{>1}$), regeneration failure (transition to non-forest state; f_1) and recovery (transition from the non-forest state to S1). 77

Figure 3.6. Steady-state distribution resulting from the baseline model for the north and south transect. Different colors indicate different states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.). It is the potential forest states' long-term proportion at equilibrium and the result from the baseline (historical) forest dynamics: with reburn resistance and without regeneration failure, climatic change or interannual variability. 84

Figure 3.7. Projections of the homogeneous Markov chain model (time-constant) scenarios for fifty years. Different colors indicate six sequential forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and one resulting from regeneration failure (NF). Scenarios simulate reburn resistance under historical climatic conditions (**HR**) and with climatic override (**HRC**) and lack of burning resistance without (**HE**) and with climatic override (**HEC**). 86

Figure 3.8. Examples of single projections for each inhomogenous (time-varying) Markov chain model scenarios. Different colors indicate six forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and one resulting from regeneration failure (NF). Scenarios simulate reburn resistance under historical climatic conditions without (**IR**) and with climatic override (**IRC**) and lack of burning resistance without (**IE**) and with climatic override (**IEC**). 87

Figure 3.9. Predicted age distribution ($\bar{x}$ ± SD) and forest loss (NF) by the inhomogeneous MCM after 50 years under the different scenarios tested. Scenarios simulate reburn resistance under historical climatic

conditions (**IR**) and with climatic override (**IRC**) and lack of burning resistance without (I**E**) and with climatic override (**IEC**) (replications = 1000). 88

Figure 3.10. Cumulative projected potential conifer regeneration failure (non-forested frequency) for 50 years by the Homogenous (time-constant: **H**, top) and the inhomogeneous Markov Chain Models (time-varying: **IH**, bottom) under the different scenarios tested. Scenarios simulate reburn resistance under historical climatic conditions (**R**) and with climatic change (**RC**) and the lack of burning resistance without (**E**) and with climatic change (**EC**). 89

Figure 4.1. Maps showing (a) the location of the areas of interest (53.63◦ N, 110◦ W, 60.70◦ N, 115.60◦ W):Wood Buffalo National Park, which occupies a portion of Alberta (AB) and Northwest Territories (NT), and Lower Athabasca Plains, which borders with the province of Saskatchewan (SK), (b) Human infrastructure cover (30-metre-resolution, Landsat; Alberta Biodiversity Monitoring Institute, 2012), (c) Area burned from 1970–2015 (one-kilometer resolution), (d) Land cover (Global Land Cover Characterization Project, one-kilometer resolution, AVHRR; (US Geological Survey, 2014)), € Elevation, (f) Mean annual temperature, (g) Mean annual precipitation, and (h) Mean climate moisture index (precipitation minus potential evapotranspiration, mm, 1◦ latitude by 1 longitude resolution; Wang et al., 2012). 117

Figure 4.2. Number of fires and area burned in Wood Buffalo National Park and Lower Athabasca Plains by season (spring, summer, and fall) and cause of ignition (lightning or human). Information based on fires ≥10 ha from 1970–2015. 119

Figure 4.3. Time series representing the number of fires (upper) and area burned (lower) for the period 1970-2015 in Wood Buffalo National Park and Lower Athabasca Plains. Thin solid lines indicate raw time series, dotted lines, the non-linear trend extracted by Singular Spectrum Analysis, and solid straight lines, the significant linear trends obtained by Mann-Kendall trend test. Different colors indicate the cause of ignition. Theil-Sen's slopes (β) and trend significance by Mann-Kendall are shown. 126

Figure 4.4. Periodicities (i.e., duration of oscillations) of the fire activity and fire-climate variables, calculated for the cyclical components found in the time series. Size and color of the points indicate the variance explained by the eigenvectors from which the oscillations were extracted during SSA. Shading corresponds to the “typical” climatic teleconnection domains: Quasi-Biennial Oscillation (2–2.5 years, dark grey), El Niño Southern Oscillation (2.5–8 years, moderate grey), and a quasi-decadal oscillation (9–13 years, light grey). 130

Figure A1. Modified setup for the cone calorimeter flammability testing.......... 198

Figure A2. Determination for ignition time (IT) was assessed visually and confirmed with the heat differential heat release rate curve. IT matches the first, and usually the highest peak of HRR. 199

Figure A3. Historical stand age distribution from the north and south sections of the transect for the period of 1940 to 2013. S0 represents a fire record; the rest, age states S1: 1-20, S2: 21-40, S3: 41-60, S4:61-80, S5: >80 years.......... 205

Figure A4. Shannon entropy index for the forest age distribution from 1840 to 2013. Values closer to one indicate high diversity, while closer to zero indicates low diversity of age states.......... 205

Figure A5. Historical frequencies (probabilities) for the processes of burning, stasis and growth by age state in yellow, green and blue, respectively. 206

Figure A6. Example of the Cullen and Frey graph to determine the optimal probability distribution for the observed values based on their kurtosis and skewness. The bootstrapped values come from random samples of the data. Empirical distributions are listed in the top-right corner. In this example, the data fits a beta distribution. This graph is obtained with the *descdist* function from the fitdistr package in R. The output of this function is accompanied by the values of the mean, standard deviation, skewness, and kurtosis. Additionally, to confirm the result, accompanying functions can be used to compare empirical and theorical histogram of densities, q-q plots, cumulative density functions and p-p plots.......... 208

Figure A7. Autocorrelation plots for the number of fires and area burned time series in Wood Buffalo National Park and Lower Athabasca Plains. 210

Figure A8. Autocorrelation plots for the weather and fire weather time series in Wood Buffalo National Park and Lower Athabasca Plains. 211

Figure A9. An example of decomposition by SSA for temperature time series in LAP, showing its additive components: trend, cycles (oscillations) and residuals (white noise, random). In this case, the trend is upward non-monotonic and each cycle has a distinctive periodicity of 5.8, 3.7 and 9.5 years respectively. 212

1 Introduction

1.1 Background

Wildland fire is a persistent and ubiquitous phenomenon that regulates the structure and function of many ecosystems on Earth (Bond & Keeley, 2005; Bowman et al., 2009; Pyne, 2007; Whelan, 1995). Nowadays, wildfires are recognized as fundamental ecological processes in many ecosystems worldwide and as providers of ecosystem services by contributing to biodiversity (He *et al*., 2019; Pausas & Keeley, 2019). In the boreal ecosystem, a wildfire is a recurrent event that has become indispensable for its maintenance.

1.2 Controls of fire

Wildland fires' characteristics result from the interaction of many factors occurring at different spatial and temporal scales. At a fine spatial scale (plant and plant parts) and short time frame (seconds to days), a flame during combustion is mainly controlled by the presence of oxygen, a heat source, and biomass (compounds to particles). In contrast, a wildfire is regulated by weather, topography, and the fuel complex at intermediate spatial and temporal scales (landscape, from hours to weeks). At broader temporal (years to centuries) and spatial scales (landscape to global), a fire regime is controlled by climate and vegetation types (Castro Rego et al., 2021; Heyerdahl et al., 2001; Moritz et al., 2011; Parisien et al., 2011a; Parisien et al., 2011b). Fire regimes are defined as distinctive patterns of frequency, intensity, severity, extent, seasonality, type (surface, crown, ground) and ignition type. However, individual fires are usually classified by their severity (.., tree mortality) as stand-replacing or stand-thinning fires (Agee, 1998).

The factors regulating fire are also categorized as top-down and bottom up-controls, according to their uniformity and range of influence. Top-down controls, such as weather and climate are the ones with significant impact over large areas. In contrast, bottom-up controls, such as topography (e.g., edaphic factors, microclimate and elevation) and vegetation (live, dead, and decomposing plant biomass) have a more localized and heterogeneous effect (Loudermilk et al., 2022; Parks et al., 2012; Peters et al., 2004).

The role of vegetation characteristics and the extent at which they affect forest fires is receiving increasing attention in the past few decades. Considering vegetation as merely fuel disregards the inherent properties of vegetation, its responses to its environment and history and consequently, and its variation in flammability. Therefore, an enhanced understanding of the patterns of fire activity at different spatial and temporal scales requires studying the mechanisms and extent to which bottom-up controls modulate fire activity (Finney et al., 2013; Loudermilk et al., 2022; Schwilk, 2015).

1.3 Flammability

Plants have been tightly linked to fires since their appearance in terrestrial ecosystems ~420Mya because they constitute and provide the fuel necessary for fires to occur (Pausas & Moreira, 2012; Scott & Glasspool, 2006). Vegetation constitutes the potential energy stored by plants during photosynthesis in the form of carbon-based compounds and is a source of energy during fires (McKenzie et al., 2011). Vegetation's capacity to burn and release this energy is called flammability. Flammability is a multi-faceted vegetation property comprising several parameters that vary according to the spatio-temporal scale of interest (Prior et al., 2018).

At fine spatial and temporal scales, flammability encompasses four parameters: ignitability (ability to catch fire), combustibility (the rate of energy release), sustainability (duration of combustion and amount of energy released), and consumability (velocity of solid conversion to gases and portion of consumed fuel). These parameters measured in laboratory settings can approximate field measurements of fire behaviour, including the probability of ignition and rate of spread, flame residence time, fireline intensity (along with energy release), and fuel consumption, respectively. At broader spatial scales, those parameters roughly correspond to the number of fires, fire size, area burned, fire severity and intensity, which results from the ability of vegetation to ignite and sustain spread (Anderson, 1970; Martin et al., 1993; Prior et al., 2018; Prior et al., 2017; White & Zipperer, 2010).

Vegetation characteristics regulate flammability parameters. Stand flammability varies with age, density and configuration (e.g., time since fire, the relative abundance of plant life forms, canopy height and bulk density, tree continuity). At finer spatial and short temporal scales, plants or plant part flammability depends on their chemical, shape, and structural features (e.g., starch and oil content, surface area to volume ratio, leaf age, density and arrangement in twigs and branches). At larger spatial and temporal scales, the fire regime is constrained by vegetation age and types (e.g., conifer, grasslands, mixedwood) and its heterogeneity. All these factors interact with top-down controls, creating very complex combustion patterns, fire behaviour and activity.

1.4 Paradigms in fire research

Modern fire research tends to integrate the biological, physical and cultural paradigms to study the impacts of top-down and bottom-up factors on fire regime (Pyne, 2007). The biological paradigm considers fires as an expression of living organisms' biochemical processes, a physical paradigm that focuses on management, firefighting, and protection of values, and a cultural paradigm that relates the complex historical human interaction with fire. Each paradigm has been used with some success in its specific fields, but integrating fire's biological, physical, and human aspects is yet to be developed.

By building a solid biological theoretical basis on vegetation dynamics we may be able improve our understanding on fire flammability and fire regimes. Vegetation dynamics include plants' physiological and phenological aspects, and at broader spatial and temporal scales, their history and properties as biological entities (i.e*.,* communities). These additions would potentially increase (or confirm) the reliability of current fire behaviour models and forecasting abilities to predict the ecological effects of fire (Finney et al., 2013; Mitchell et al., 2009; Pausas & Moreira, 2012; Schwilk & Caprio, 2011; Schwilk, 2015; Varner et al., 2015)

1.5 Research justification and objectives

The present work explores the influence of bottom-up and top-down controls of fire on the flammability of the Canadian boreal forest at multiple temporal and spatial scales. Each chapter sets a specific temporal and spatial scale to answer particular questions about the factors controlling combustion, fire occurrence and fire activity in the boreal ecosystem. This involves the application of the appropriate techniques, parameters and analysis. At the same time, each chapter also contributes to fill the gap in knowledge at each scale.

According to earlier research, the main driver in the flammability of dead and live vegetation is moisture content, a variable that has been widely employed to build models of fire behaviour (Alexander & Cruz, 2012; Byram, 1959; McAllister et al., 2012; Philpot, 1970; Pyne et al., 1996; Rothermel, 1983; Simms & Law, 1967). However, recent evidence points out that other foliar characteristics, such as form and chemical content, may also have an essential role in their flammable aspects in laboratory settings (Jolly et al., 2012; Jolly & Johnson, 2018; McAllister et al., 2012; Page et al., 2012; Pickett et al., 2010; Popović et al., 2021; Weise et al., 2005) and fire behaviour modelling (Alexander & Cruz, 2013; Grootemaat et al., 2017; Jolly et al., 2016; Schwilk & Caprio, 2011; Torero & Simeoni, 2010). In most cases, evidence was peripheral to their primary objective, and standardized techniques to measure flammability parameters were lacking. Moreover, most samples consisted of dead plant parts, even though living foliage is a significant source of fuel for high-intensity crown fires, the most common in the boreal forest (de Groot et al., 2013). To fill these gaps, in Chapter two, I designed an experiment to test the influence of living vegetation properties at a particle level (i.e*.,* needles) on flammability.

To assess the relative contribution of moisture content and physical and chemical features of needles to their flammability, I determined their association with the flammable characteristics of *Pinus banksiana* Lamb. living needles in a laboratory setting. These physicochemical features are derived from different ages and development stages of needles from trees growing in central Alberta, Canada. Unlike other research focusing on only one flammability parameter, I considered needle ignitability, combustibility, sustainability and consumability to obtain a more comprehensive outlook of the impact of ten physicochemical variables.

Young forests in many North American ecosystems, including the Canadian boreal forest, exhibit lower flammability than older ones of the same type. These forests show fewer and smaller fires in the first 50 years since the last fire. This has reduced their burn rates (percent of annual area burned) up to half of older forests (Beverly, 2017; Collins et al., 2009; Erni et al., 2018; Héon et al., 2014; Parks et al., 2015). However, the same young forests are the most sensitive to vegetation conversion through short interval reburns during abnormal climate change conditions (Coop et al., 2020). To this day, the degree to which resistance to burning can counteract conversion or forest loss due to climate change remains uncertain.

In the third Chapter, I address this issue by building a Markov Chain Model (MCM) based on almost 160 years of fire history in a *P. banksiana* Lamb. and *Picea mariana* (Mill.)

forest in northeast Quebec. MCMs are widely used in ecosystem modelling (Balzter, 2000; Daniel et al., 2016; Isagi & Nakagoshi, 1990; Liénard & Strigul, 2016; Usher, 1981). A model to forecast forest conditions at this scale would require a large number of variables (i.e., climatic and vegetation characteristics). Alternatively, our approach uses a "data-driven" model that depends on the historical patterns of fire occurrence, and it can be modified using fewer parameters to simulate particular conditions of interest. This model captures historically observed burning resistance (lower flammability) in young stands and latitude variation. To determine if reburn resistance could reduce climate change effects, I simulated the response of the forest age composition and potential forest loss to higher fire probability. Moreover, I simulated the response assuming no resistance exists to estimate the extent of the influence of reburn resistance. Finally, I incorporated uncertainty by inducing stochastic variations of fire probability over time to increase realism.

The controls of fire have been altered by human activities for millennia and are reflected in fire activity. Directly, humans affect fire activity by increasing the number of ignitions, lengthening the fire season, and implementing fire management measures (Balch *et al*., 2017). Indirectly, humans affect fire activity by changing landscape flammability through modifications to the arrangement, continuity, amount, structure, and distribution of vegetation. Exacerbated by climate change, these modifications alter the severity, likelihood, size, frequency and intensity of fires (Bowman et al., 2011; Castro Rego et al., 2021; Gustafson et al., 2004; Hanes et al., 2019; Krawchuk & Cumming, 2011; Marlon et al., 2008; Parisien et al., 2006; Wang et al., 2015; Whitman et al., 2022). The alteration is such that fire-climate relationships have been disrupted in some ecosystems, including the boreal forest (Brotons et al., 2013; Chavardès et al., 2018; Higuera et al., 2015).

In Chapter three, to assess human influence over fire activity I analyzed the temporal patterns of the number of fires and area burned for almost five decades in the Albertan boreal forest. I compared the fire activity of two adjacent areas with similar topography and climate but contrasting human influence: Wood Buffalo National Park and Lower Athabasca Plains. I examined the trends and cyclical patterns of fire activity, tested their relationships with fire-climate variables (e.g., Fire Weather Index System codes and indices), and compared the results between the areas.

The present dissertation consists in three stand-alone chapters, which can be read individually. Chapters two and four are published and formatted in the respective journal styles: *International Journal of Wildland Fire* and *Forests*. Chapter three is not published yet at this time, and Chapter five summarizes the significant findings of all of them.

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2 Physicochemical characteristics controlling the flammability of live *Pinus banksiana* needles in central Alberta, Canada

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2.1 Abstract

Background. Few studies have focused on the integral assessment of live fuel flammability in the boreal forest. Aims. We aimed to examine the flammability of living needles of jack pine (*Pinus banksiana*) as characterised by their form, moisture and chemical content at different ages and times of the year. Methods. With a calorimeter and open flame, we estimated needle ignitability, consumption rate, maximum speed and amount of energy released. We measured their form, moisture and chemical content. Key results. Needle form has a major effect on ignitability, whereas chemical composition primarily influences the amount and rate of energy release. Needles <1 year old are the least flammable; they are rounder and voluminous, with higher moisture and nitrogen content. Needles ≥1 year old are more flammable; they are drier, more curved, thinner, longer, and contain more carbon and terpenes. Needles release more energy during the early growing season, when starch and lipids are at their peak concentrations. Conclusions. Moisture content is not the major factor affecting the flammability of jack pine live needles; physicochemical changes specific to age and month of collection are the most influential factors. Implications. Assessing the multi-faceted properties of live fuels flammability will help to comprehend stand- and landscape-scale fire behaviour.

2.2 Introduction

Research on the flammability of fuels has been a priority for understanding forest fire behaviour for decades (Bond & van Wilgen, 1996). Although tree crowns represent a significant source of fuel for high-intensity crown fires (the most prevalent fire type occurring in the Canadian boreal forest; de Groot et al., 2013), much of this research has focused on downed woody debris and litter. Conversely, the flammability of the living fraction of the boreal vegetation remains relatively understudied (Rivera et al., 2012; Finney et al., 2013).

The spatial and temporal context determine the assessment of forest flammability. At the particle scale (i.e., leaves, twigs, and small branches) and short periods (seconds), flammability encompasses four parameters: ignitability (ability to catch fire); combustibility (the rate of energy release); sustainability (fuel capacity to maintain flaming combustion, and the amount of energy released); and consumability (velocity of solid fuel conversion into gases) (Anderson, 1970; Martin et al., 1993). At this scale, it is possible to quantify flammability in laboratory settings accurately, but not without limitations; flammability studies are very diverse in terms of techniques, equipment, fuel units and flammable parameters considered (Popović et al., 2021), which makes generalisations and comparisons challenging.

Foliar moisture persists as the primary perceived driver of forest flammability because of water's strong physicochemical properties: high specific heat and high thermal conductivity. Consequently, water-rich fuels require larger amounts of energy during the preheating stage, so that water can evaporate and dissipate before they can burn. Additionally, water's diffusivity as aerosol or steam reduces the immediate oxygen availability necessary for combustion (Byram, 1959; Simms & Law, 1967; Philpot, 1970; Rothermel, 1972; Pyne et al., 1996). Based on its known physicochemical properties and estimation simplicity, foliar moisture remains the cornerstone factor for forest fire modelling (Rothermel, 1972; Van Wagner, 1977; Alexander & Cruz, 2012; McAllister et al., 2012). The high amount of moisture in living fuels led us to assume that they would burn similarly to dead fuels containing substantial moisture. In contrast to dead duels, living fuels can ignite before their moisture is expelled entirely (Pickett et al.,

2010) and sustain and spread fire at foliar moisture contents >100% (Weise et al., 2005), whereas dead fuels hardly ignite or spread fire at moisture content content >35% (Hawley, 1926).

Dead fuels are functionally, physically, and chemically different from living fuels; therefore, their flammability differs. Dead fuels water dynamics follow relatively simple physical water absorption and evaporation principles, so they are more susceptible to the influence of weather. On the other hand, water uptake and losses by plants occur by evapotranspiration, a complex process involving their phenology, immediate environment, a multitude of interacting structures, chemical compounds, and other physical phenomena (Johnson, 1966). Moreover, water in plant tissues acts as a solvent, providing colligative properties (Burgan, 1979; Bloom et al., 1985; Raven, 1998; Pyne, 2007; Finney et al., 2013). Thus, understanding the physiological role and dynamics of water in plants helps understand their flammability.

Although multiple studies identify foliar moisture as the primary driver of flammability, their results also suggest interactions with organic compounds. Chemical components that function as structure (e.g., cellulose), defence (e.g., waxes, oils, and terpenes in the resin), and energy storage (e.g., fats and starch) are highly flammable (Carson & Mumford, 1994), with the potential to enhance the flammability of the leaves. Despite results describing the potential effects of the chemical composition of leaves since the past century (Hubert, 1932; Johnson, 1966; Philpot & Mutch, 1971), the study of flammability has, for decades, been predominantly focused on moisture content. More recently, researchers have turned to study how the chemical composition of leaves affect flammability, including fats (van Wilgen, et al., 1990), terpenes and other volatile organic volatiles (Owens et al., 1998; Behm et al., 2004; de Lillis et al., 2009; Della Rocca et al., 2017; Romero et al., 2019; Ganteaume et al., 2021; Guerrero et al., 2021), sugars, starch, and assortments of these compounds (Jolly et al., 2012; McAllister et al., 2012;

Page et al., 2012). Moreover, the shape and size of leaves regulate the heat transfer process and kinetics of combustion at the particle scale (Kanury, 1994; McAllister et al., 2012; Naresh et al., 2018). Besides foliar moisture content, many morphological and chemical traits have been identified to affect flammability. However, an integral assessment of these characteristics related to the boreal tree's phenology is lacking. This study aims to examine the flammability changes of living needles of jack pine (*Pinus banksiana* Lamb) ensuing from different developmental stages and needle ages during the growing season in central Alberta, Canada. We selected this species due to its abundance, proclivity to wildfires, and its role in the study of forest fire behaviour and ecology in Canada to develop the Canadian Forest Fire Rating System (Heinselman, 1973; Little 1979; Van Wagner, 1987; Gauthier et al., 1993; Farrar, 1995). In particular, we aimed to:

1. Assess the relative contributions of living needle form, moisture and chemical content to their ignitability, combustibility, sustainability and consumability;
2. Identify the variables of needle form, moisture and chemical that drive the different aspects of flammability; and
3. Recognise the temporal patterns of needle flammability, form, moisture and chemical content during the growing season and according to their age.

2.3 Methods

To investigate the role of moisture content and jack pine living needles' morphological and chemical characteristics on their flammability, we studied three different needle ages collected monthly during the growing season in Alberta, Canada. We employed a modified cone calorimeter with an open flame as the heat source and obtained the needles' flammable characteristics: ignitability, combustibility, sustainability and consumability.

2.3.1 Sample collection

We collected needles from eight jack pine trees at the natural area of the University of Alberta Botanic Garden (Alberta, Canada, 53°24′07.1″N 113°45′14.6″W) between 1100 and 1400 hours each month, from June to September 2015. To reduce the environmental humidity influence on the needles, we sampled the trees on days with no rain over the previous 3 days. This site belongs to the Boreal Mixedwood ecological area, where jack pine is abundant in dry sandy soils (Beckingham & Archibald, 1996). From June to September 2015, the average temperature and total precipitation normals in this area were greater for daily average temperature (14.8°C) and lower for total precipitation (221 mm) than the climate normals (1981–2010; 14.0°C and 303 mm; Appendix Table A1, Government of Canada, 2019). This period overlaps with the highest wildfire activity in Alberta, also referred to as 'fire season' (1 March–31 October), which exhibits a peak of number of fires during the summer (specially June and July; Campos-Ruiz et al., 2018).

We prepared the samples for flammability and biometrical analysis (form, and chemical) in the laboratory. For each monthly sample, we clipped three twigs from the middle section of the crown in the south-facing side of the same trees. We stored them in sealed plastic bags and transported them inside a cooler with icepacks to the laboratory, where we kept them in a fridge at 4°C. The needles were manually detached from the twigs and, based on their distance from the distal point of the twig, separated them according to their age: 0 years old or new (newly emerged during the current year), 1 year old, or 2 years old. We obtained 96 stacks of pine needles (samples) from the combination of three needle ages (new, 1 year old, 2 years old), 4 months (June–September), and eight tree replicates. We divided each sample into three subsamples destined for flammability, chemical and morphological analysis.

2.3.2 Flammability tests

We subjected the first set of subsamples (~4 g or 50 needles each) to an oxygen consumption calorimetry experiment employing a modified mass loss cone calorimeter (Mass Loss Calorimeter ISO 13927, Fire Testing Technology, East Grinstead, West Sussex, UK) at the Protective Clothing and Equipment Research Facility of the University of Alberta, Edmonton. The cone calorimeter measures heat release (EHC), heat release rate (HRR), and gravimetric changes of a sample exposed to a constant heat flux (Babrauskas, 1984). The heat source is usually a radiant heater with the shape of a cone positioned over the sample. Instead, we opted for a more realistic setup where we exposed the samples to the radiation and convection of a flame instead of a radiator.

We employed an open methane burner (10 × 10 cm) set at a constant flow of 9 L per min (Melnik et al., 2022; Appendix Fig. A1). We estimated the time to ignition (IGT) as the time elapsed between the burner start and the observation of a flaming reaction of the sample. This time was later confirmed with the heat release rate output from the sample (Appendix Fig. A2). We subtracted the contribution of the flame from the output to obtain the differential heat release rate (i.e., the difference between measurements with and without a sample, hereafter HRR) and the effective heat of combustion based on the total heat release (EHC; Table 2.1). We placed each subsample uniformly on a metallic mesh holder (10 × 10 cm) at 5 cm over the burner and exposed it to the flame for at least 80 s when the whole sample was consumed entirely. We interpreted the outputs in terms of flammability components: time to ignition (ignitability); peak heat release rate (combustibility); effective heat of combustion (sustainability); and the average rate of mass loss (consumability; Table 2.1).

Table 2.1 Flammability parameters and their associated variables obtained from the cone calorimeter

Parameter	**Variable**	**Abbreviation**	**Calculation**	**Units**
Ignitability	Time to ignition	IGT	The time to ignition after being exposed to the flame. Visual assessment and confirmation with the HRR curve. Short TI means greater ignitability	s
Combustibility	Peak heat release rate	HRR	The maximum value of the velocity of energy release	kW m^{-2}
Sustainability	Effective heat of combustion	EHC	The amount of energy released at 80 s, normalized by the initial sample mass	kJ g^{-1}
Consumability	Average mass loss rate	MLR	The slope of the mass loss per unit of time	g s^{-1}

2.3.3 Moisture content

We calculated the foliar moisture content (FMC, dry-based %) from the form subsamples by weighing the needles before and after drying them in a convection oven at 75°C for 48 h (Table 2.2).

2.3.4 Form analysis

We measured form characteristics from the second set of subsamples by scanning 20 needles per treatment combination and replicate (age × month × tree) and processed the images with the WINSEEDLE software (Reagent Instruments Incorporated, Quebec, QC, Canada). We obtained the sample averages (per needle) curvature and form coefficient and calculated the surface-area-to-volume ratio by assuming the volume of a hemi-ellipsoid and adjusting the projected area to a hemi-surface leaf area (Table 2.2; Bond-Lamberty et al., 2003).

Table 2.2 Biometric variables of jack pine needles

Parameter	Variable	Acronym	Calculation / Method	Units
Moisture content	Foliar Moisture content	FMC	Dry basis gravimetric moisture content (Fresh weight - Dry weight)/ Dry weight * 100	%
Morphological	Curvature	CRV	D/L, where D is the perpendicular distance from the center of the needle at the maximum straight width to the straight length and L is the straight length. Higher values represent more curvature.	-
	Form coefficient	FCO	4πA/P, where A is the area and P is the perimeter. A value of 1 defines a perfect circle and 0 a filiform object.	
	Surface-area-to-volume ratio	AVR	A/V, where A is the surface area and V is the volume. Estimation from the hemi-surface leaf area and three-dimensional model assuming a hemi-ellipsoid shape.	mm^{-1}
Chemical	Nitrogen	N	Determined by combustion and elemental analyzer (Costech 4010 with EAS Clarity data collection software).	%
	Carbon	C		%
	Soluble sugars	SS	Determined calorimetrically (Thermo Scientific Evolution 300 UV/Vis spectrometer) after extraction by using an anthrone reagent. Enzymatic conversion to glucose was performed for starch.	%
	Starch	ST		%
	Lipids	LI	Extraction with hexane solvent and extraction and determination with a gas chromatography spectrometer (Agilent Masshunter 7890/5975C and NIST2014 spectral database).	%
	Terpenes	TE		%

2.3.5 Chemical analysis

We kept the third set of subsamples frozen at −25°C and sent in a cooler with dry ice to the Chemistry Services Laboratory (Victoria, BC, Canada) of Natural Resources Canada for chemical analysis. The analysis included the most abundant, functionally relevant and high energy components of needles: total nitrogen, carbon, non-structural carbon (NSC's: starch and soluble sugars), lipids, and terpenes (Table 2.2. Detailed methods of extraction and measure in Appendix Table A2).

2.3.6 Statistical analysis

The experiment was based on a repeated-measures factorial design to test the effects of age (three levels: 0, 1 and 2 years old) and month (June, July, August, and September) on their flammability, foliar moisture content, form, and chemical makeup of the needles. First, to explore and visualise the similarity between samples and possible relationships between flammability and biometric variables, we used a non-metric multidimensional scaling (NMDS) procedure. Second, to confirm the significance of the sample groupings observed with the NMDS, we used its scores to test for differences between ages and months of sampling with a permutational Multivariate Analysis of Variance (MANOVA) for repeated measures. Third, we calculated the relative contributions of moisture content, form and chemical content on flammability through variance partitioning, based on the NMDS output. Fourth, we ran correlations for repeated measures to confirm associations between flammability and biometric variables. Finally, we tested the effect of needle age and month of collection on each flammability and physicochemical variable, employing a repeated-measures analysis of variance (rmANOVA) and pairwise comparisons.

We calculated the distances between observations with Bray–Curtis dissimilarities (*distance* function, ecodist package in R; Goslee & Urban, 2007; R Development Core Team, 2016), ordinated those observations via the *nmds* function (vegan package in R; R Development Core Team, 2016; Oksanen et al., 2020), and grouped them by age with 95% confidence limit ellipses. To test whether age and month were significant, we employed the scores derived from the NMDS (two-dimensional) and used a permutational MANOVA for repeated measures (*MANOVA* function in the MANOVA.RM package for R; Friedrich et al., 2018). The power to detect significant differences among treatments by MANOVA was 0.72 ($\alpha = 0.05$, n =96) (G*Power software; Faul et al., 2007). This value, which ranges from zero to one, reflects the capability to find differences between treatments based on alpha, the magnitude of expected change (medium in this case), the number of samples, the number of treatments, and the number of repeated measurements.

Next, we performed a variation partitioning procedure to determine the relative and combined explanatory power of moisture content and grouped morphological and chemical characteristics on each flammability component. We employed the *varpart* function from the vegan R package using the grouped variables in Table 2.2. Finally, we used distance-based redundancy analysis (dbRDA) to assess the significance of the unique variation explained by each of the three groups.

We used repeated-measures correlation tests (RMCOR) and NMDS to find potential relationships between flammability variables with chemical and form features. RMCORR calculates correlation coefficients (r_{rm}) in repeated measures (within-subjects) designs without averaging the repeated measures that may obscure meaningful relationships. The resulting coefficient delivers the same interpretation as a Pearson correlation coefficient, with the advantage of having higher degrees of freedom and power than averaged data analysed with traditional correlation techniques. Additionally, in RMCOR, the effect size is calculated with bootstrapping to estimate the parameters' accuracy; thus, non-normally distributed data were supported. We calculated the correlations between variables using the *rmcorr* function in R (rmcorr package; Bakdash & Marusich, 2017).

We tested the effect of needle age and month of collection on flammability, morphological, and chemical variables with rmANOVA. We checked the normality data and residuals for each variable. If any of the assumptions for this test were violated, we transformed the data (log, root squared, or logit transform) before the analysis. We performed the rmANOVA (specifying for repeated measures on the subjects), Tukey multiple comparisons test, and grouping. These tests were performed with the functions *aov*, *lsmeans*, and *cdl* in base R, lsmeans, and multcomp packages; (Hothorn, 2008; Lenth, 2016). We adjusted *p*-values through false discovery rate methods to control type I errors (Benjamini and Hochberg, 2000).

2.4 Results

2.4.1 Flammability

Younger needles, especially in the earlier growing season, were significantly different from older ones based on their flammability, FMC (foliar moisture content) and biometric variables, which results in distinct grouping in the NMDS (Fig. 2.1). Biometrical variables (form and chemical composition) explained most of the variance of each flammability component, but FMC explained the least (Fig. 2.2). The older needles (1 and 2 years old) had higher HRR (heat release rates) and MLR (mass loss rates) and lower IGT (ignition times) than new (0 years old) needles (Figs 2.1, 2.3a, b, d). We observed significantly higher EHC (effective heat of combustion) during the first half than the second half of the growing season, regardless of age (Fig. 2.3c). We found multiple significant correlations between IGT, HRR, EHC and MLR with the needles' physical and chemical characteristics, such as foliar moisture content, form coefficient, curvature, surface-to- volume ratio, nitrogen, carbon and terpenes. Only EHC showed correlations with lipids and starch (Table 2.3). In general, age and month of collection had a significant effect on live needle flammability, their moisture content, form and chemical composition (Appendix Tables A3–A5).

The resulting NMDS showed that new needles formed a distinct group almost independently from the rest of the data during June and July, but overlapped in August and September with the oldest age groups. At least one group resulting from age and month of collection in the NMDS (new leaves in June and July; Fig. 2.1) was statistically different from the rest (rmMANOVA, $p = 0.001$, month $p = 0.001$, number of permutations = 999). The first axis reflects significant age differences, with variations in IGT, HRR, and MLR associated with FMC, FCO, CRV, AVR, N, C, and TE content. In contrast, the second axis reflects the month of collection and variations in EHC associated with ST and LI. All variables, except for SS, were significantly correlated to the ordination axes (Appendix Table A6). The NMDS had a stress value of 0.05, which is an excellent representation of the data in two dimensions (Clarke, 1993; Fig. 2.1, Appendix Table A6).

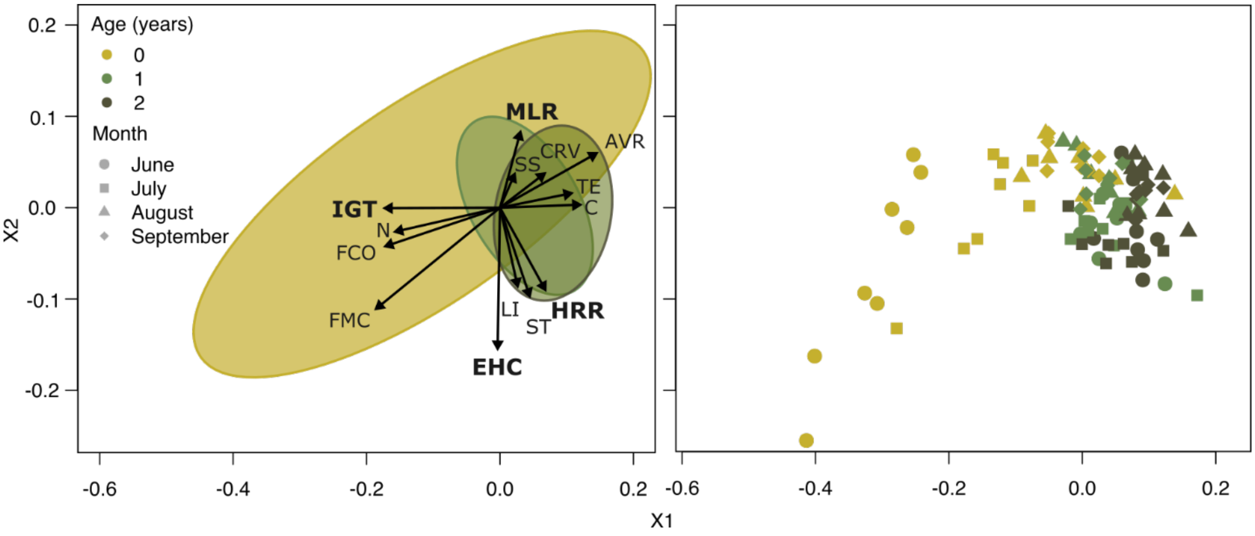

Figure 2.1 Non-metric multidimensional scaling of jack pine needles (stress=0.05) with 95% confidence ellipses for the age factor. Different colors indicate sample age and different shapes the month of the collection. The strength of the relationship between variables is reflected by the arrow's length, whereas their direction indicates their type: positive for the same direction, negative for opposite directions. Bold letters highlight the flammability parameters: IGT, ignition time, HRR, peak heat release rate, EHC, effective heat of combustion and MLR, average mass loss rate. Other letters represent: FMC, foliar moisture content, CRV, curvature, FCO, form coefficient, AVR, surface-area-to-volume ratio, N, nitrogen, C, carbon, SS, soluble sugars, ST, starch, LI, lipids and TE, terpenes.

2.4.2 Foliar moisture content, form, and chemical content

The contribution of foliar moisture content to flammability variance was minor compared with form and chemical composition. According to the variation partitioning, FMC only accounts for 1% or less of each component of flammability's unique variance, whereas form and chemistry explain larger amounts (Fig. 2.2). Needle form, chemistry, and FMC explained 71% of IGT variance together. Although FMC, form and chemistry explained 45% (1 + 3+ 3 + 38), 65% (12 + 3 + 38 + 12) and 54% (1 + 3+ 12 + 38) of IGT variance respectively, a large percentage (38%) was explained simultaneously by the three sets of variables (shared or redundant). FMC and chemistry only explain 1%, whereas form explains 12% uniquely (Fig. 2.2a).

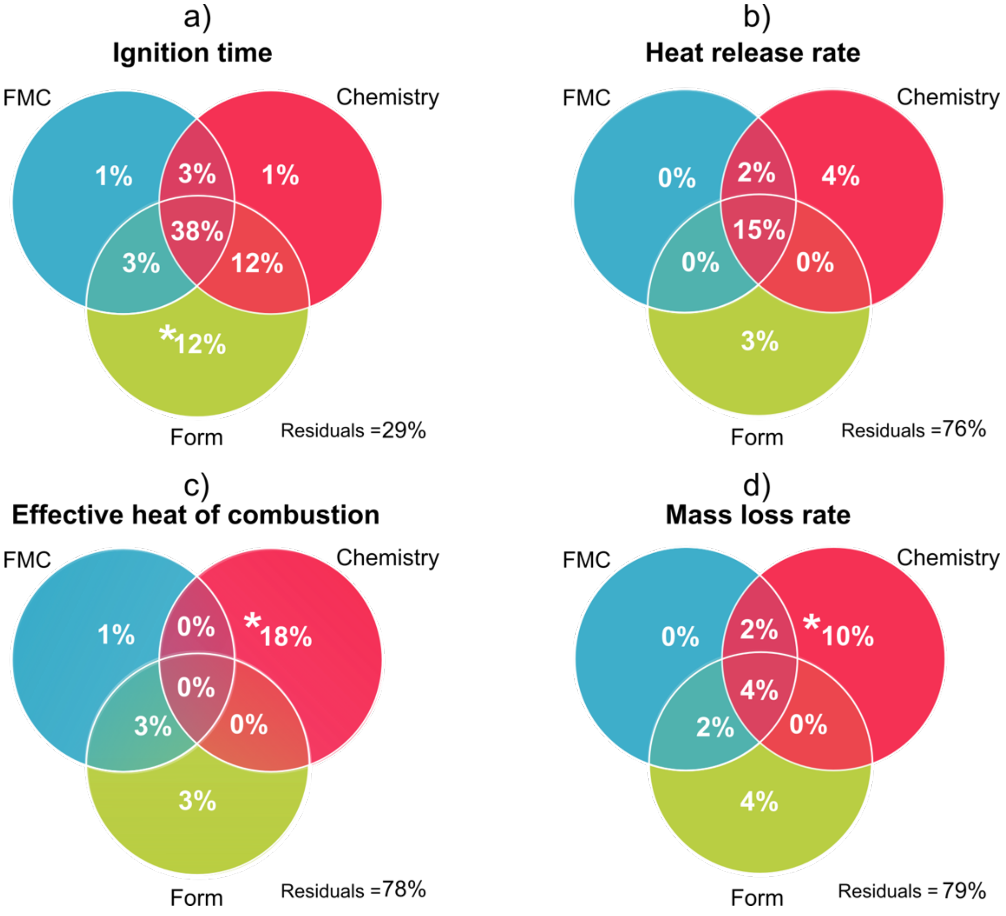

Figure 2.2 Variance partitioning for each component of flammability of jack pine needles. Non-overlapped areas represent the unique variation explained by each variable (MC) or set of variables (chemistry and form). The significant differences of the unique variance explained are marked with an asterisk. Overlapped areas indicate common variance explained.

Chemical composition explained most of the HRR variance, shared and unique. Chemistry, form, and FMC explained 21, 18 and 17% of HRR variance respectively, but uniquely they each explained <4%. In total all variable sets explained 24% of HRR variance, from which 15% was shared (Fig. 2.2b). Chemistry also explained most of EHC and MLR variance (shared: 18 and 16%, uniquely 18 and 10%). Form and FMC explained the least variance for EHC and MLR (shared <8%, unique <4%; Fig. 2.2c, d). It is important to note that EHC variance explained by chemistry did not overlap (i.e., it is not redundant). Residuals for

HRR, EHC and MLR ranged from 76 to 79% suggesting that other variables not included in our study may explain more of their variance.

Flammability components were correlated with most of the needles' tested morphological and chemical characteristics. IGT had a strong negative correlation with AVR ratio ($r_{rm} = -0.42$, *d.f.* = 87, $p < 0.001$) and positive with FMC, FCO, N and LI content ($r_{rm} \leq 0.25$; Table 2.3). Then, the more ignitable needles (i.e., low IGT) had higher AVR, were narrower, longer, drier, and had less N and LI. Peak HRR exhibited negative correlations with MC, FCO, N, but positive C, TE, and CRV (all with $r_{rm} \geq 0.22$; Table 2.3). EHC was positively correlated to starch ($r_{rm} = 0.33$, *d.f.* = 87, $p < 0.01$) and lipid content ($r_{rm} = 0.31$, *d.f.* = 87, $p < 0.01$). MLR had positive correlations with CRV, C, and TE content (Table 2.3), which means that needles consumed faster by fire were curvier and had more carbon and terpenes.

Table 2.3 Repeated measures correlation coefficients (r_{rm}, *d. f.* = 87, top-right) and their respective *p*-values (bottom-left) for the variables of flammability, form, and chemical content. Bold numbers indicate significant correlations ($p<0.05$). Acronyms: IGT, ignition time, HRR, peak heat release rate, EHC, effective heat of combustion and MLR, average mass loss rate. Other letters represent: FMC, foliar moisture content, CRV, curvature, FCO, form coefficient, AVR, surface-area-to-volume ratio, N, nitrogen, C, carbon, SS, soluble sugars, ST, starch, LI, lipids and TE, terpenes.

Variable	**IGT**	**HRR**	**EHC**	**MLR**	**FMC**	**FCO**	**CRV**	**AVR**	**C**	**ST**	**SS**	**N**	**LI**	**TE**
IGT	-	**-0.30**	**0.32**	-0.19	**0.72**	**0.76**	**-0.31**	**-0.83**	**-0.43**	-0.18	-0.13	**0.81**	0.00	**-0.51**
HRR	**0.00**	-	**0.25**	**0.29**	**-0.35**	**-0.41**	**0.30**	**0.27**	**0.35**	-0.01	0.02	**-0.37**	-0.06	**0.41**
EHC	**0.00**	**0.02**	-	-0.17	0.20	**0.23**	-0.10	**-0.31**	-0.15	**0.27**	-0.49	0.16	**0.31**	-0.14
MLR	0.07	**0.01**	0.11	-	**-0.30**	**-0.34**	**0.35**	**0.23**	**0.23**	0.02	0.13	-0.16	-0.08	**0.28**
FMC	**0.00**	**0.00**	0.07	**0.00**	-	**0.74**	**-0.38**	**-0.74**	**-0.44**	**-0.25**	-0.14	**0.72**	-0.11	**-0.45**
FCO	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	-	**-0.49**	**-0.81**	**-0.34**	**-0.36**	-0.11	**0.81**	-0.17	**-0.48**
CRV	**0.00**	**0.00**	0.37	**0.00**	**0.00**	**0.00**	-	**0.34**	0.19	0.17	0.09	**-0.34**	0.01	**0.27**
AVR	**0.00**	**0.01**	**0.00**	**0.03**	**0.00**	**0.00**	**0.00**	-	**0.34**	0.15	0.06	**-0.84**	0.02	**0.40**
C	**0.00**	**0.00**	0.15	**0.03**	**0.00**	**0.00**	0.08	**0.00**	-	-0.08	0.13	**-0.23**	-0.09	**0.41**
ST	0.09	0.93	**0.01**	0.83	**0.02**	**0.00**	0.12	0.14	0.48	-	0.07	**-0.28**	**0.70**	0.07
SS	0.25	0.87	0.64	0.21	0.19	0.31	0.42	0.55	0.23	0.54	-	-0.10	0.00	**0.28**
N	**0.00**	**0.00**	0.12	0.13	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.01**	0.34	-	-0.06	**-0.34**
LI	0.96	0.57	**0.00**	0.44	0.29	0.11	0.93	0.87	0.40	**0.00**	0.99	0.58	-	-0.05
TE	**0.00**	**0.00**	0.19	**0.01**	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	0.49	**0.01**	**0.00**	0.67	-

2.4.3 Needle age and month of collection

Old needles ignited significantly faster than new ones (rmANOVA, *F* = 45.69, *d.f.* = 2, $p < 0.001$) in the first 2 months of collection (rmANOVA, *F* = 36.24, *d.f.* = 3, $p < 0.001$), but especially in June (rmANOVA, F = 28.21, *d.f.* = 6, $p < 0.001$; Appendix Table A3). It took up to 49.60 s (x̄ , s.e. = 3.69) for the 0-year-old needles to ignite in June, whereas it occurred in less than 22 s for the 1- and 2-year-old needles (Fig. 2.3a). Differences in ignitability due to age disappeared in August when all needles ignited under 16 s. The highest HRR was found in 1- and 2-year-old needles (rmANOVA, *F* = 16.19, *d.f.* = 2, $p < 0.001$), especially 2-year-old needles in July (x̄ = 130 kW m−2, s.e. = 10.41), and the lowest in 0-year-old needles in June (x̄ = 63.10 kW m−2, s.e. = 3.10). HRR was the lowest for all needle ages in June but reached their maximum value at different months: 1-and 2-year-old needles in July, and 0-year-old needles in August. Thus, month (rmANOVA, *F* = 11.23, *d.f.* = 3, $p < 0.001$) and interaction (rmANOVA, F = 2.80, *d.f.* = 6, $p < 0.05$) also had a significant effect on HRR; Fig. 2.3b, Appendix Table A3).

The EHC was similar between needle ages (0, 1, and 2 years old) but varied depending on the month of collection (rmANOVA, *F* = 13.26, *d.f.* = 3, $p < 0.05$; Fig. 2.3c, Appendix Table A3). During June and July, needles released almost three times more energy (x̄ = 11.30 kJ g−1, s.e. = 2.00) than in August and September (x̄ = 4.40 kJ g−1, s.e. = 1.05).

The amount of FMC was higher in 0-year-old than 1and 2-year-old needles, mainly during the first 2 months of collection (Fig. 2.4a). New needles exhibited a maximum FMC of 295% (x̄ , e.e. = 35.7) in June and dropped to 129% in September (x̄ , e.e. = 4.51), a level similar to older needles (~100%). FMC of needles, then, was significantly affected by age (*F* = 94.47, *d.f.* = 2, $p < 0.001$), month of collection (*F* = 12.13, *d.f.* = 3, $p < 0.001$), and interaction (*F* = 13.99, *d.f.* = 6, $p < 0.001$).

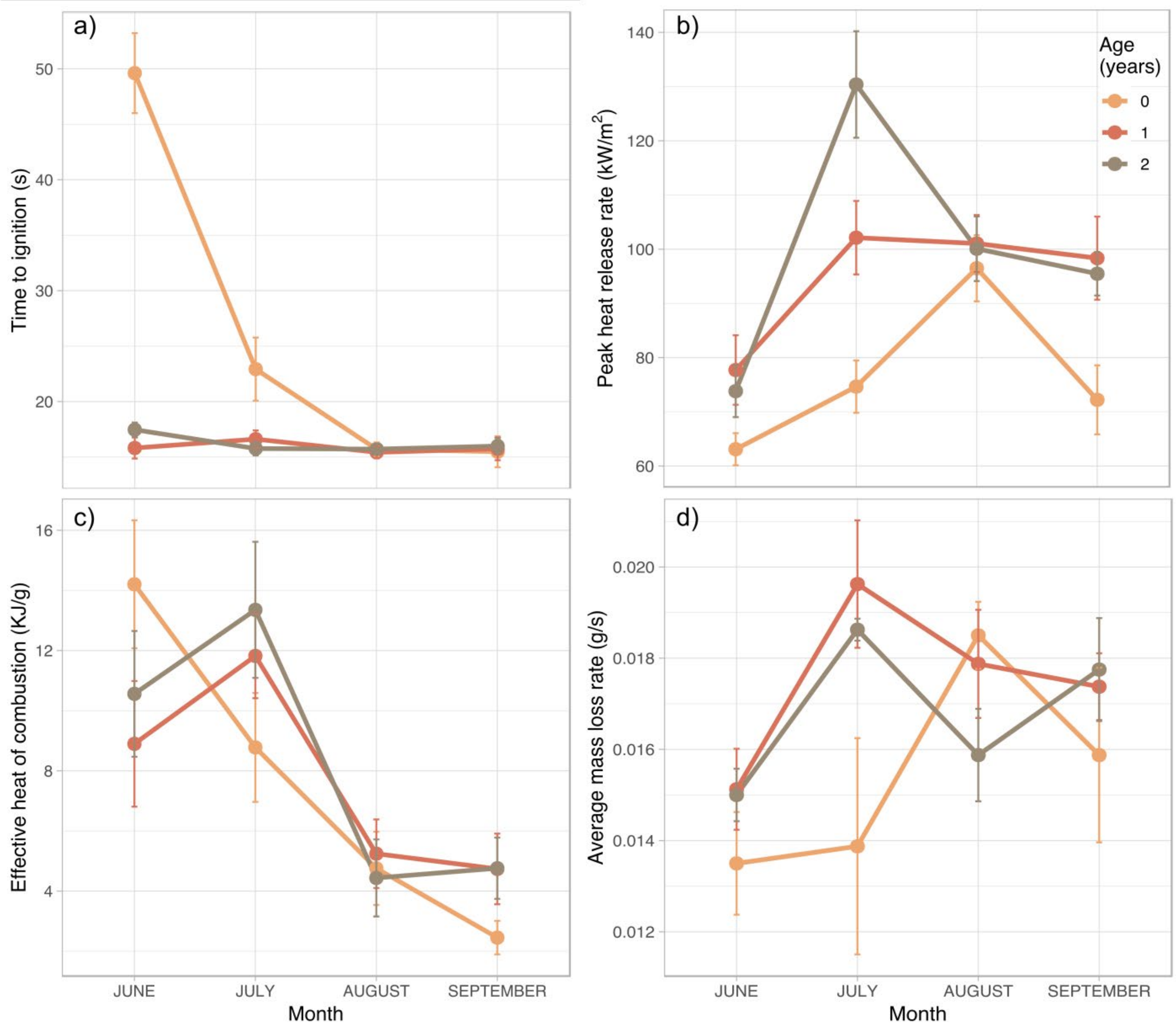

Figure 2.3 Flammable characteristics of jack pine needles by age (zero, one, and two-year-old) and month (June, July, August, September): a) Time to ignition, b) peak rate of heat release, c) effective heat of combustion, and d) average mass loss rate. Points represent the mean, and whiskers the bootstrapped standard error.

2.4.4 Form and chemical characteristics

Age and month significantly affected the needles' form (Fig. 2.4, Appendix Table A4). New needles (0 years old in June) showed low curvature ($\bar{x}$ = 0.30, s.e. = 0.002), high form coefficients ($\bar{x}$ = 0.26, s.e. = 0.01) and low area- to-volume ratio ($\bar{x}$ = 6.36, s.e. = 0.33), whereas the opposite was observed in older ones (Fig. 2.4b–d). Chemical content varied according to age and month of collection (Fig. 2.5, Appendix Table A5). Needles' growth during the growing season and years led to increases in carbon and terpene content but a reduction of lipids (Fig. 2.5a, e, f). We identified 50 different terpenes (36 monoterpenes, 12 sesquiterpenes and two diterpenes). The most abundant were α-pinene, β-phellandrene, borneol acetate, β-pinene, camphene, β-myrcene, 3-carene, linalool, germacrene D-4-ol, myrtenyl acetate, (+)-R-limonene and phytol. Starch content in older needles decreased over the months, eventually matching new leaves (from 7 to ~0.21%; Fig. 2.5c). Lipids fell consistently for needles of all ages as the growing season advanced (Fig. 2.5e), soluble sugars had a pattern of highs and lows (Fig. 2.5d), and nitrogen decreased drastically in 0-year-old needles after June, matching the other needle ages. At the end of the growing season (September), the needles' chemical characteristics were similar regardless of age.

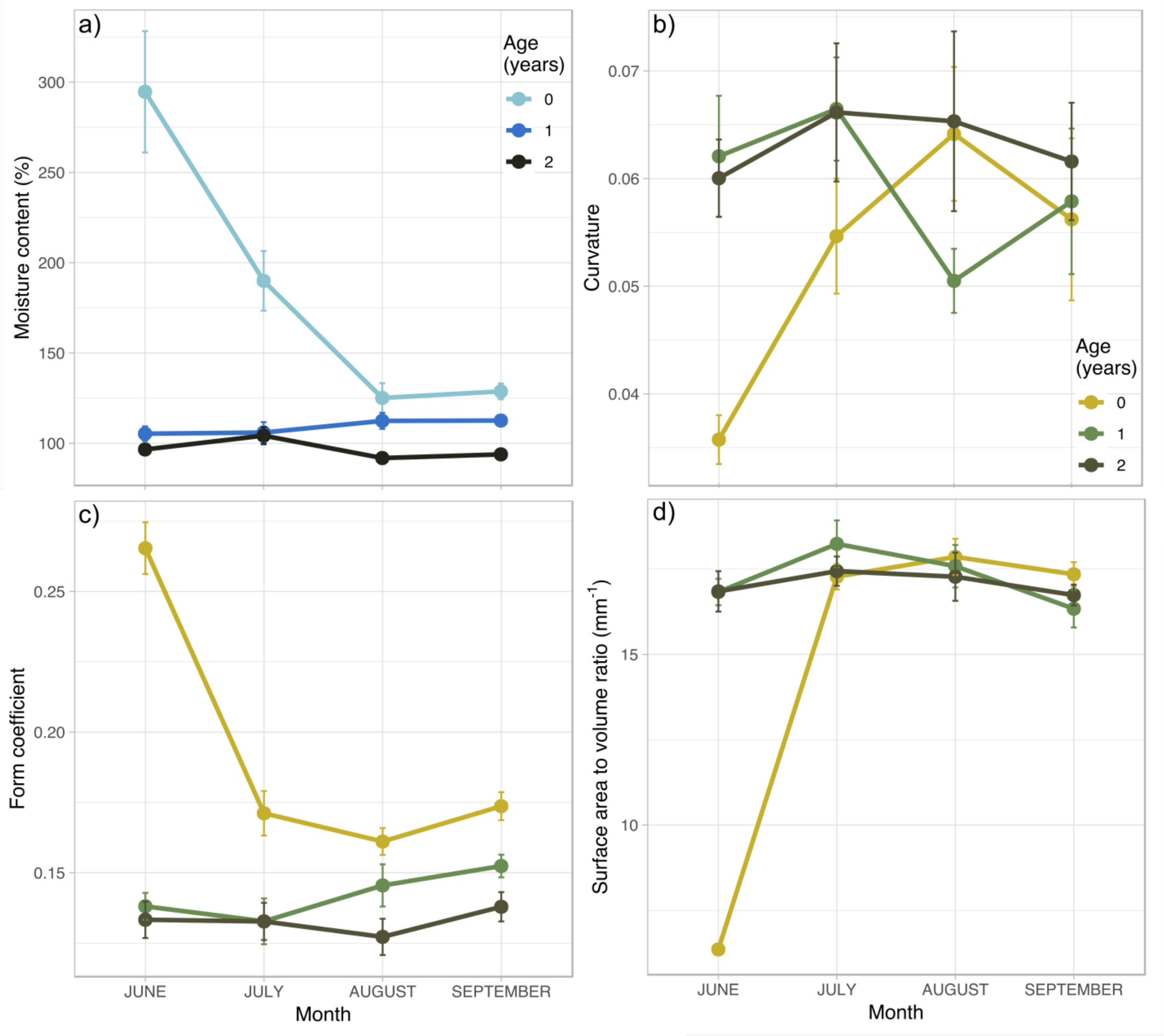

Figure 2.4 Plots for the foliar moisture content and form characteristics of jack pine needles by age (zero, one or two-year-old) and months (June, July, August, September): a) moisture content, b) curvature, c) form coefficient, and d) surface-area-to-volume ratio. Points represent the mean, and whiskers the bootstrapped standard error.

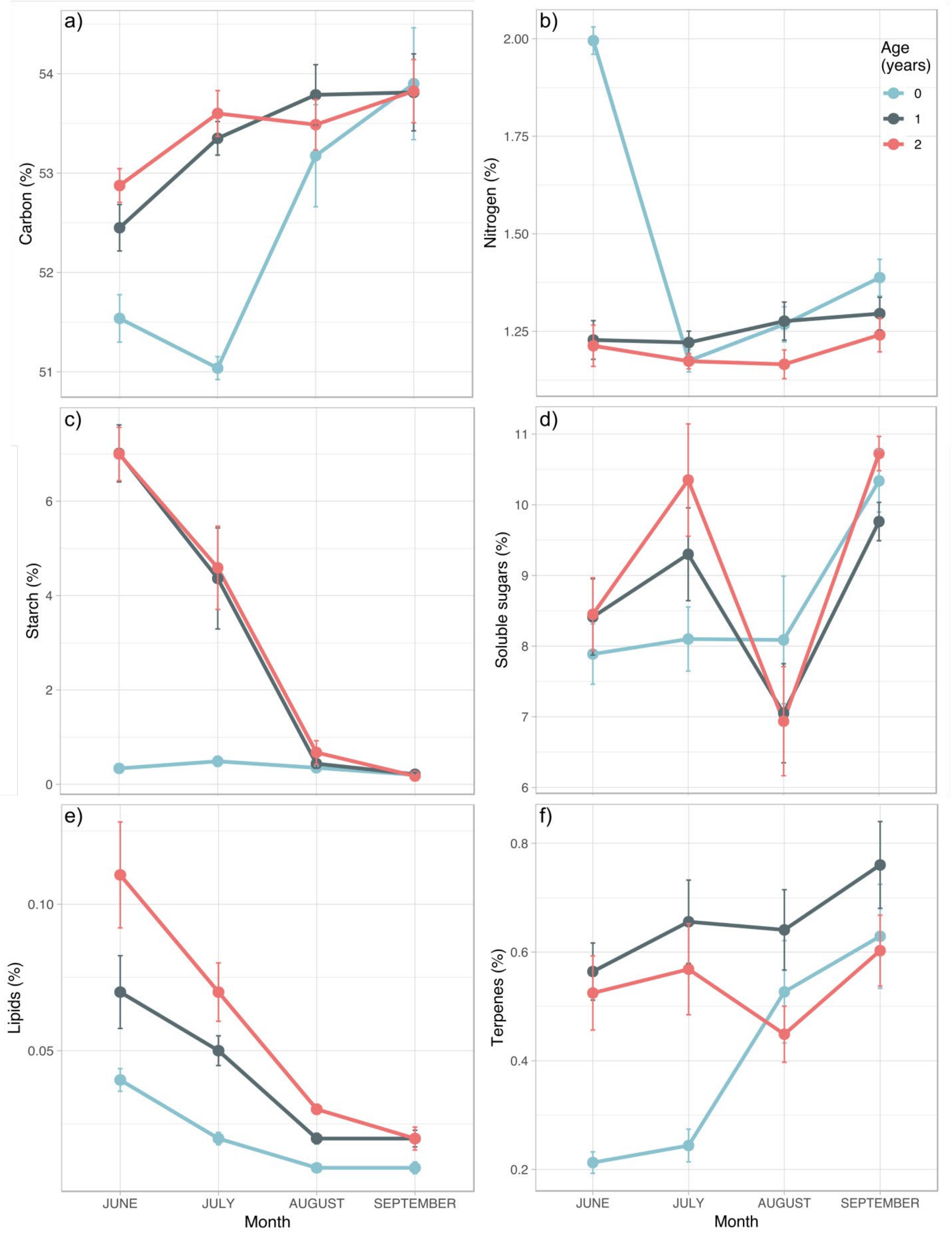

Figure 2.5 Plots for the chemical concentrations of jack pine needles by age (zero, one or two-year-old) and months (June, July, August, September): a) carbon, b) nitrogen, c) starch, d) soluble sugars, e) lipids, and f) terpenes. Points represent the mean, and whiskers the bootstrapped standard error.

2.5 Discussion

Ignitability, combustibility, sustainability and consumability reach their maximum at different times of the year and vary with needle age, matching both natural developmental and seasonal stages of jack pine needles. Needles ignite and release energy faster at maturity, which is also when they are no longer significantly different physically or chemically. However, the total energy released responds to the shift of needle chemical composition between the early and late growing seasons regardless of their developmental stage. During the early season (i.e., June and July), the energy is three times the amount released later (e.g., August and September), a difference similar in magnitude between living and dry, dead needles of *Pinus halepensis* (~10 kJ g^{-1}; Jervis & Rein, 2016). These results suggest there is an intrinsic potential for more intense crown fires in the early fire season, which is also the period with the region's highest number of forest fires. However, weather and topography also modulate fire intensity at larger spatial scales. Nevertheless, although more research is needed to study the interactions between live foliage flammability and larger-scale factors, our findings highlight the importance of flammability studies of living foliage in a biological context.

The form and chemical content of jack pine needles had a more substantial effect on flammability than foliar moisture content. We observed the lowest ignitability and combustibility at higher FMC, consistent with similar experiments testing conifers and broadleaved species (Etlinger & Beall, 2004; Weise et al., 2005; Jervis & Rein, 2016). However, despite their significant correlations with FMC, two observations showed that FMC was not the only factor driving flammability. First, needle ignition occurred before their desiccation (also described by Pickett et al., 2010), contradicting the traditional combustion progression (Byram, 1959). Second, the combustibility does not precisely track the monthly patterns of needle moisture content (cf. Philpot & Mutch, 1971). In fact, FMC in living conifer needles could contribute to the sudden release of droplets (micro-explosions) mixed with volatile compounds that can heat and ignite adjacent needles (Darwish Ahmad et al., 2021; Fazeli et al., 2022). Previous studies also acknowledged that plant leaf form and chemical content also affect flammability (Philpot & Mutch, 1971; Weise et al., 2005; Jolly et al., 2012, 2016; McAllister et al., 2012; Jervis & Rein, 2016). However, our analysis further allowed us to discern the precise magnitude of influence exerted by each set of variables on flammability and indicated a more minor role of FMC than we were expecting. These results suggest that under the conditions of a high- intensity crown fire, the effect of moisture content may be considered negligible on ignitability and combustibility (Weise et al., 2005; Fletcher et al., 2007; Alexander & Cruz, 2013), or limited to ignitability (Ganteaume 2018) and the peak rate of energy release. This low contribution of FMC to flammable characteristics may explain the lack (or undetectable role) of this variable in crown fire behaviour models (Van Wagner, 1998; Cruz et al., 2005; Rossa and Fernandes, 2018). Given the preponderance of high-intensity crown fires in the Canadian boreal forest, performing more experiments on a broader scale and a larger number of species will help us determine the extent and type of influence FMC exerts on the flammability of living foliage of trees.

Moisture content may indirectly influence ignitability by modifying the form of jack pine needles. Needles with high moisture content are more voluminous and rounder, which increases their thermal capacity and delays ignition. This observation is similar to that of Jolly et al., (2016), who also noted delayed ignitability at higher needle mass and density, which in turn was associated with higher FMC and starch contents in red and jack pine. Such associations might also explain the high redundancy of variance explained by FMC and form. The tight association between form and ignitability has allowed researchers to rate different species by their fire hazard, and to develop fire spread and severity prediction models based solely on leaf form traits (Montgomery & Cheo, 1971; Papió & Trabaud, 1990; Weise et al., 2005; Murray et al., 2013, 2020; Shen & Fletcher, 2015).

The chemical composition of jack pine needles is the main factor determining sustainability and consumability and has a minor role in combustibility and ignitability. High needle carbon content boosts ignitability, combustibility and consumability. Carbon increment in new needles reflects the rise of lignin and cellulose, which form structural tissues (*sensu lato* structural carbon; Kozlowski et al., 1991). Although they reduce flaming times and energy release in lodgepole pine (*Pinus contorta* Dougl.) dry needles (Page et al., 2012), lignin is a source of high energy in the combustion of wood (White, 1987). More importantly, non-structural carbon like starch and lipids are strongly associated with needle sustainability. These high-energy compounds observed in many conifers, are more abundant during shoot expansion in the early growing season, (Little, 1970; Fischer & Höll, 1991; Mandre et al., 2002; Hoch et al., 2003; Schoonmaker, 2013) when their high concentrations may increase needles' flammable characteristics (Philpot & Mutch, 1971; Page et al., 2012; Jolly et al., 2016). This implies that jack pine needles have the potential to burn more intensely during the first half of the fire season.

Terpenes tend to get immobilised in the needle tissues over time in the resin canals (Langenheim, 1994), increasing the flammability of older leaves. In our study, they enhanced the consumability, combustibility and ignitability of living jack pine needles due to their inherent high heating value, low ignition temperature (flashpoint), and low ignitable concentration (lower flammability limit; Carson & Mumford, 1994). In several species, a significant relationship exists between some terpenes and ignitability (de Lillis et al., 2009; Pausas et al., 2016; Romero et al., 2019; Della Rocca et al., 2020; Guerrero et al., 2021), combustibility (Dewhirst et al., 2020), and consumability of foliage (Owens et al., 1998). Moreover, terpene content can explain the high percentages of variance with respect to flammability (19–24%; Della Rocca et al., 2017). However, their role depends on the flammability parameter studied, their type (number of isoprene units and associated functional groups in their structure), season and developmental stage (Della Rocca et al., 2017; Dewhirst et al., 2020; Ganteaume et al., 2021).

In the present study, the most abundant terpenes in jack pine needles are monoterpenes, which also play a significant role in the flammability of living foliage of *Globularia alypum* and *Rosmarinus officinalis* (Alessio et al., 2008; Pausas et al., 2016), 13 species of pines (including *P. banksiana*; Dewhirst et al., 2020), and several Mediterranean conifer species (Della Rocca et al., 2017; Ganteaume et al., 2021). Needles emit terpenes and other volatile organic compounds when exposed to heat (Greenberg et al., 2006), which may have accelerated and caused ignition prior to needle desiccation in our samples (Darwish Ahmad et al., 2021; Fazeli et al., 2022). We identified terpenes in our samples that are considered highly flammable (e.g., α-pinene; Raman et al., 2016), and others that are recognised as suppressors of flammable properties (e.g., β-pinene and α-humulene; Ganteaume et al., 2021) in other studies. Nevertheless, the suppressing or enhancing role of individual terpenes on flammability was beyond the scope of the present work.

Both N and FMC are abundant in jack pine needles during shoot expansion due to the high physiological activity involving multiple proteins, enzymes, amino acids, and nucleic acids (Kramer & Kozlowski, 1979; Vose & Ryan, 2002). At this stage, needles are less ignitable and combustible than at later stages, but distinguishing the role between N or FMC cannot be asserted entirely. On the other hand, when only considering older needles, higher N concentrations might reflect different N fractions such as volatile flavonoids and phenolic precursors of lignin (Zakzeski et al., 2010), with highly flammable properties such as piperidines (Patnaik, 2007; Virjamo & Julkunen-Tiitto, 2016). Further research is necessary to assert the role of more specific compounds in the flammability of jack pine needles.

Although small-scale controlled experiments have been considered limited in their ability to explain field fire behaviour (Fernandes & Cruz, 2012), the results obtained from them are valuable to cement our understanding of underlying factors influencing combustion. This information can potentially be used to improve mechanistic-based models of fire behaviour involving crown fire initiation, rate of spread, and energy release. These experiments have facilitated the rating of vegetation into flammable categories (Papió & Trabaud, 1990; Dimitrakopoulos & Papaioannou, 2001; Weise et al., 2005), the management of the wildland–urban interface (White & Zipperer, 2010; Simeoni et al., 2012; Ganteaume, 2018; Krix et al., 2019; Murray et al., 2020), explained fire activity patterns at continental scales (Prior et al., 2017), and even allowed for interpretation of paleological reconstruction of fire activity (Belcher, 2016). Furthermore, needle form and chemical characteristics in the foliage and litter bed have been employed to explain and develop fire spread and severity models (Schwilk & Caprio, 2011; Torero & Simeoni, 2010; Jolly et al., 2016; Grootemaat et al., 2017). Understanding leaf-level flammability has utilitarian applications in fire management.

Additional physical traits of jack pine trees should also be considered to explain their flammability at a landscape scale. Needle position, distribution and density in twigs and branches, needle age relative proportion, and crown architecture (e.g., height, bulk, and density) all modify the air/fuel mix in the crown and canopy, which has an important influence on landscape flammability (Rothermel, 1972; Van Wagner, 1977; Bond & Midgley, 1995; Agee, 1996; Schwilk, 2003). For example, aggregated narrow, long needles provide high air circulation, enhancing their ignitability and combustibility, compared with shorter, wider needles that form more compact foliage (Scarff & Westoby, 2006; Kane et al., 2008; Cornwell et al., 2015; Schwilk, 2015). On the other hand, narrow needles spaced on the twigs, like spruce, are highly ignitable, but the same needles generate a very compact fuel bed with low ignitable potential (Ganteaume, 2018). More research is required at different spatial scales to discern the influence of chemical and physical traits on fire behaviour as additional tree features could enhance or counteract the effect of needle flammability.

2.6 Conclusions

Far from behaving as a simple high moisture fuel, the flammability of living foliage is astoundingly intricate due to the complex relationships among the variables typical of living systems. We were able to experimentally determine the significance of living needle traits and their natural variation over the growing season on different flammable characteristics. Surprisingly, foliar moisture was not the primary driver of needle flammability, as is commonly assumed. Needle form significantly affected ignitability, whereas chemical composition affected combustibility and consumability. Our results suggest indirect effects of moisture content on flammability through form and chemical composition, but the nature of these interactions is still misunderstood. We advise studying vegetation fuels with an ecological approach, which will benefit wildland fire research and help us to understand the processes at finer spatial scales and improve fire behaviour modelling.

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3 Stand resistance to reburn moderates the potential for regeneration failure in the northeastern Canadian boreal forest.

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3.1 Introduction

Recent climatic fluctuations causing warmer and drier conditions have promoted more frequent and severe fires in many areas of the Canadian boreal forest (Hanes et al., 2019; Jain et al., 2022; Price et al., 2013), pushing its resilience capacity (ability to recover its composition and structure after a disturbance) to its limit. As a result, extensive areas of the boreal forest have undergone profound changes in their average forest age (Kuuluvainen & Gauthier, 2018), regeneration density (Pinno et al., 2013), and shifting to alternate vegetation communities, including vegetation conversion and regeneration failure (Baltzer et al., 2021; Hart et al., 2019; Whitman et al., 2019). However, the fate of the boreal forest depends on the species involved and the degree of the fire regime disruptions.

The boreal forest fire regime is typically characterized by infrequent, high-intensity and stand-replacing wildfires (i.e., prompting forest renewal; Amiro et al., 2001; Weber & Stocks, 1998), resulting from the interactions between climate, vegetation and topography. Climate, classified as a top-down control of fire, strongly regulates fire occurrence at large spatial and temporal scales. At the same time, vegetation and topography, also known as bottom-up controls, operate at a finer scale modifying the spatiotemporal patterns of fire (McKenzie et al., 2011; Parks et al., 2012). Vegetation is highly variable in space and time, producing unexpected fire patterns that cannot be explained by top-down factors alone. For example, wildfires in the

Canadian boreal forest show a substantial proclivity to burn conifer forests over any other vegetation type, as well as forest stands older than 30 years (Bernier et al., 2016).

The persistence of conifer forests relies upon their remarkable capacity to regenerate in post-fire environments. Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* Mill.) dominate most of the boreal treed area in Canada (Canada's National Forest Inventory, 2021). These species form highly flammable landscapes due to foliage form, chemical composition and arrangement, crown architecture, and density (Arseneault, 2001a; Campos-Ruiz et al., 2022; Stocks et al., 2004; Thompson et al., 2017; Van Wagner, 1977, 1983). These species bear serotinous cones that store seeds (i.e., aerial seed bank) and protect them from the lethal heat produced during a fire. The heat triggers cone opening, releasing the stored seeds in the post-fire environment. Cone serotiny is an advantageous trait that allows jack pine and black spruce to self-replace from low-frequency stand-replacing fires (Greene et al., 1999; Groot & Bothwell, 2004). However, their regeneration is compromised when fire frequency increases. Short fire intervals (< 30 years) are likely to cause regeneration failure (Buma et al., 2013; Gauthier et al., 1996; Hart et al., 2019; Lavoie & Sirois, 1998) due to insufficient seed storage in the aerial seed bank ("immaturity risk" *sensu* Ne'eman et al., 1999). In this case, conifer regeneration failure would mean the loss of their pre-fire dominance over other vegetation types (Stevens-Rumann et al., 2022).

Young forests are the most susceptible to experience regeneration failure, but are also less likely to burn than older ones. This property constitutes a negative vegetation feedback to recurrent fire events and a critical bottom-up control of the fire regime. In the boreal forest, the reburn limitation lasts up to 50 years after a fire event (Bernier et al., 2016; Erni et al., 2017; M. Girardin et al., 2017; Héon et al., 2014). It is associated with fewer ignitions and low spread capability (Beverly, 2017), mainly due to fuel scarcity (Bernier et al., 2016; Thompson et al., 2017). Without reburn resistance, burning rates (percent of annual area burned) in northern Quebec would have been almost two times greater than those observed and five times less likely to burn than older ones (Erni et al., 2017). Lower probability of fire occurrence soon after fire events is not exclusive to the boreal forest, as it has also been documented in other ecosystems in the western U.S. with a limitation ranging from six to 18 years following a fire (Collins et al., 2009; Parks et al., 2015).

Reburn resistance may counteract the effects of climate change. Higher temperature and more intense drought associated with climate change have increased fire frequency and incidence of extreme fire-weather events across Canada (Flannigan et al., 2013; Hanes et al., 2019; Stocks et al., 2001; Wang et al., 2017; Wotton et al., 2010). However, vegetation resistance to reburn at early stages might limit the excessive fire activity caused by climate change (Girardin et al., 2013). On the other hand, shorter fire intervals may overwhelm age-dependent resistance, allowing reburning almost independently of the time since the last fire (Erni et al., 2017; Parks et al., 2018) and subsequently reducing forest resilience (Erni et al., 2017; Hayes & Buma, 2021; Whitman et al., 2019). In the worst-case scenario, frequent reburns, combined with drought, have been reported to cause deficient or total regeneration failure in intervals under ~17 years in Alberta (Whitman et al., 2019).

The combined effect of climate change and burning resistance on regeneration success is still uncertain. Several climate-based models have been designed to project forest growth and future burn rates under different climate change scenarios and fire severity and harvesting levels. Yet, only some of those models consider the negative vegetation feedback provided by reburn resistance in young forest stands (Balshi et al., 2009; Bergeron et al., 2004, 2006; Girardin et al., 2013; Splawinski et al., 2019), leading to overestimation of future fire activity (Boulanger et al., 2014; Girardin et al., 2017).

In this paper, we project future forest age composition and the potential forest loss by simulating different reburning resistance levels, climate-induced changes in fire, and variability of fire activity within and beyond historical ranges. To do so, we employ a Markov chain model, a relatively simple, area-free (not spatially explicit and spatially independent), data-driven model based on two centuries of fire-history data in northern Quebec. We recreate various scenarios by modifying the fire probabilities ascribed to different stages of forest development to answer the following questions: What are the expected forest age distributions and potential conifer regeneration failures if 1) the natural resistance to re-burn would not exist? (i.e., resistance vs. no resistance), 2) novel conditions of climate change reduce fire return intervals? (i.e., shorter vs longer historical fire intervals), 3) interannual variations of burning probability are incorporated? (i.e., time-constant vs time-varying fire probabilities).

3.2 Methods

We built a state-and-transition model parametrized as a discrete time Markov chain model to estimate stand-level dynamics in the boreal forest of northwestern Quebec, Canada, for 50 years into the future since 2013. The baseline model was based on a 174-year fire history reconstructed from tree rings and fire scars from Héon et al. (2014) and Erni et al. (2017). We established specific model parameters to simulate different levels of reburn resistance, climatic change effects, and interannual burning variations. These modifications allowed us to estimate the future stand age composition and potential forest loss due to successional failure.

3.2.1 Study site and data collection

Fire history from 1800 to 2013 was reconstructed from a 340 km-long transect extending across a conifer-dominated area in east Quebec (Fig. 3.1). The transect is in a relatively homogeneous area, consisting of gentle hills and depressions with a vegetation cover dominated by black spruce (*Picea mariana* Mill.; 56%) and jack pine (*Pinus banksiana* Lamb., 43%) (Beaudoin et al., 2022). The non-forested area consists of open peatlands and water bodies, including numerous rivers draining into James Bay. The inhabiting conifer species bear traits that enhance the flammability of the landscape and successfully recolonize the burned landscape. After a fire event, these species can regenerate from seeds stored in serotinous or semi-serotinous cones (Buma et al., 2013; Gauthier et al., 1993; Greene & Johnson, 1999; de Groot & Bothwell, 2004).

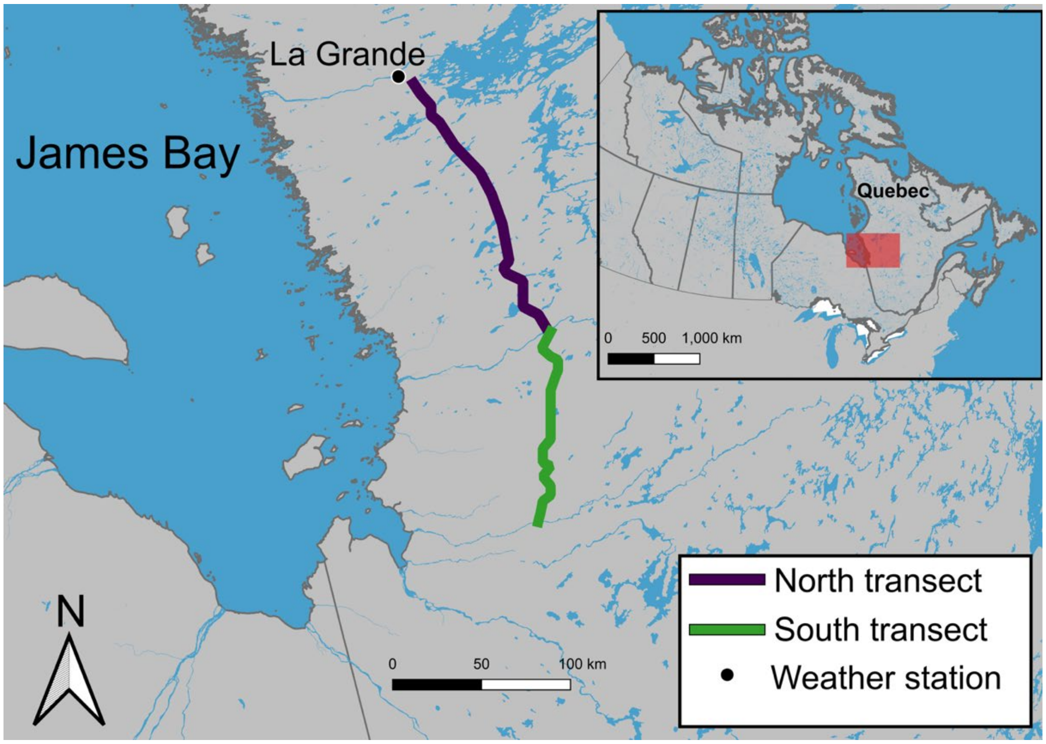


Figure 3.1. Map of the study area in the province of Quebec, Canada. The two transects are shown in purple (north) and green (south).

The area is subject to minimal fire suppression and logging activities. North and south transects are located in the Taiga Shield East and the Hudson Plains ecozones, respectively (Boulanger et al., 2012; Ecological Stratification Working Group, 1995), and are classified under the Eastern and Western James Bay Fire Regime Zone (Bernier et al., 2016). The sections were also identified based on differences in fire sizes, intervals, and species abundance. Each section contains 75 and 93 cells of 2 km^2, north and south, respectively.

Fire history for each cell was reconstructed from fire scars of the available stems. Cells were surveyed exhaustively to find at least three stems (trees, snags, or woody debris) per cell exhibiting fire scars. Groups of stems were located in unburned patches or edges of stand-replacing fires, and localized surface fires, which are usually associated with topographic features that limit fire spread, such as water bodies, peatlands, and exposed bedrocks. The selected cell size ensured a reliable recording of fire history for the last 200 to 300 years. Five additional procedures were carried out in order to improve registry quality: First, large stems with multiple scars were preferred over smaller stems. Second, grouped stems were preferred over isolated stems to be able to confirm fire scars (duplicates). Third, in case no duplicates were found inside the cell, they were searched at no more than 500 outside the cell. Fourth, the first tree ring from jack pine stems (indicating an establishment date) was used to confirm fires, specially at short interval events. And fifth, an index of fire discontinuity was calculated to consider fires occurring at the same year as separate events (i.e., burned segments 10 km apart) (Héon et al., 2014).

A total of 1834 fire scars were dated from cross-sections of the stems considering light rings for validation, correcting for a time lag in first tree rings, and employing a master chronology for dead or suppressed tree samples. Establishment dates (n = 1363) were estimated using the tree pith close to the root collar. In total, 2062 stems were sampled, and 3197 fire dates were detected (Erni et al., 2017; Héon et al., 2014) (Fig. A3 and A4). We used data from 1840 to 2013, to increase the accuracy of fire history. We recreated fire history represented as 168 binary sequences (fire or no-fire year; denoted as one or zero) corresponding to each surveyed cell, over 174 years. Then, each no-fire year was assigned a value equivalent to the time (year) since fire (TSF). The year of fire occurrence was designated as year zero. Then we classified each year into six categories (forest states), that indicate a forest age interval: S0 (<1 year or year exhibiting a fire), S1 (1-20 years old), S2 (21-40 years old), S3 (41-60 years old), S4 (61-80 years old), and S5 (>80 years old). We discretized forest development (i.e., classification into states) because forest development occurs over large time scales, and consequently, model complexity was reduced (Strigul et al., 2012). Therefore, we adopted an approach similar to Héon et al. (2014) and Strigul et al. (2012) to define state interval durations (~20 years), which also allowed us to represent the forest states resistant to reburn. This approximation of forest age assumes that every fire registered was stand-replacing (Pan et al., 2010). As a result, we obtained 168 sequences, representing surveyed each cell, summarizing annual state changes over 174 years.

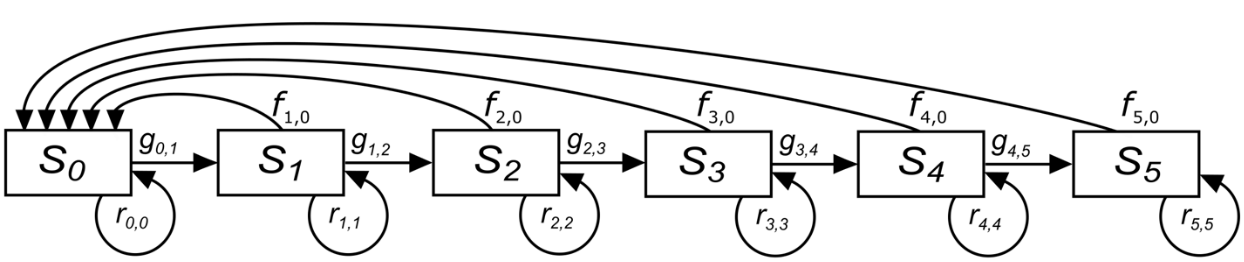
Changes or transitions between forest states were summarized into a transition matrix, the “heart” of the model. We tallied changes of states from one year to the next and summarized them in a raw tally matrix (6x6). Then, each element of the raw tally matrix indicated the number of times a cell changed from one state to the another every year. The tally matrix was converted into a transition matrix (a.k.a. Markov matrix, probability matrix; Balzter 2000; Haefner 2005; Grinstead and Snell 2006; Gagniuc 2017), by turning each of its elements into proportions or frequencies. The frequencies were the relative times each transition took place in the sequences, and in the model, they were interpreted as probabilities to transit to other states. For example, if a transition from S1 to S0 occurred *x* times, and S1 transitioned *y* times, the frequency would be *x*/*y*.

For this end, we employed the functions *seqtrate* and *seqdec* in the 'TraMineR' package in R (Gabadinho et al., 2015) and obtained a transition matrix for the north and south portions of the transect.

3.2.2 The model

We represented the cells history as a state-and-transition model (STM) and parametrized it as a discrete-time Markov chain model (MCM) using the transition matrices as inputs. STMs are conceptual representations of the dynamics of a system usually employed to characterize and simulate non-linear changes (as arrows) between discrete vegetation states (as boxes), which could be a product of succession, disturbances, and management practices (Bestelmeyer et al., 2003; Brice et al., 2020; Stringham et al., 2003; Stringham & Krueger, 2001; Thompson, 2013; Westoby et al., 1989). Furthermore, an MCM framework provides an estimated sequence of events though projections. The method is relatively simple, offers high flexibility to simulate different scenarios and requires a relatively low number of parameters. Projections by MCMs assume spatial independence and, in the case of first-order MCMs (Appendix Table A7), assumes that the future state of the system ($\boldsymbol{x}_{t+1}$) relies only on the current state ($\boldsymbol{x}_t$) (Balzter, 2000; Urban & Wallin, 2017). This means the system is "memoryless," or in other words: "the future, given the present, is independent of the past" (Dobrow, 2016).

Our baseline model consists of six consecutive forest age states (S0, < one year; S1, 1-20 years old; S2, 21-40 years old; S3, 41-60 years old; S4, 61-80 years old and S5, >80 years old) transitioning to each other through three different processes contained in the transition matrix: growth (*g*) or transition to an older state, permanence (*r*) or remaining in the current state, and fire (burning, *f*), transition triggered by fire occurrence which resets the process of forest development (Fig. 3.2, 3.3 and S5). Transitions occur successively in discrete (equal) annual time steps, following a fixed set of probabilities (time-homogeneous). This way, the model conforms to a "birth and disaster Markov chain" (Strigul et al., 2012).



$$\mathbf{A} = \begin{bmatrix} r_{0,0} & g_{0,1} & 0 & \cdots & \ldots & 0 \\ f_{1,0} & r_{1,1} & g_{1,2} & 0 & \ldots & 0 \\ f_{2,0} & 0 & r_{2,2} & g_{2,3} & 0 & 0 \\ f_{3,0} & \vdots & 0 & r_{3,3} & g_{3,4} & 0 \\ f_{4,0} & \vdots & \vdots & 0 & r_{4,4} & g_{4,5} \\ f_{5,0} & 0 & 0 & 0 & 0 & r_{5,5} \end{bmatrix}$$

$$\boldsymbol{x_1} = [s_1 \quad s_2 \quad s_3 \quad s_4 \quad s_5]$$

Figure 3.2. A state-and-transition diagram representing a discrete-time "birth and disaster" Markov chain model. The model is specified by a transition matrix (**A**) and an initial condition for each state, which are ratios of each stand age class (i.e., initial cohort, $\boldsymbol{x}_1$). The squares denote the states (*s*) that transit at discrete intervals (*m*). Arrows indicate three different kinds of transitions: growth (*g*) or transition from a state to a successive one, permanence (*r*) on the same state, and fire events (*f*) or resetting process, which is the transition from any state to the first one. A cell at a state s_m can transit (grow) to s_{m+1} with a probability of

g_m, remain in the same state with a probability of r_m or burn with a probability of f_m, which would make it transit to the initial state.

We projected each stage's proportional number of cells (*i. e.,* cohort projection) by multiplying the transitions matrix ($\mathbf{A}$) by an initial state distribution ($\boldsymbol{x}_t$) to obtain the subsequent age distribution:

$$\boldsymbol{x}_{t+1} = \boldsymbol{x}_t \cdot \mathbf{A}$$

In this case, we repeated the process for 50 time-steps (thus projecting the following 50 years) using the 2013 state distribution ($\boldsymbol{x}_1$; the last recorded year in the dataset) as the starting point. This way we obtained the relative amount of each forest state from 2014 to 2063. Additionally, to obtain the general tendency of the projections, we calculated the stable state distribution (aka steady-state distribution), which is the convergence point in MCM projections where the distributions no longer change. We used R software to generate the projections (R Core Team, 2008) and the function *steadyState* to determine the stable states of the model ('markovchain' R package; Spedicato et al., 2016). A compiled version of the script can be found in the link provided in the supplementary material section (page 213).

The baseline model was verified and validated by comparing test-run results with the dataset used to construct the model. We followed the method proposed by Urban and Wallin (2017) and Haefner (2005); verification was performed by testing our model against the data used to build it. We ran the baseline model and used 1840s state distribution to initialize the projection for 174 years. The result was compared to the 2010-2013 period (average). For the model validation, we tested the model against a portion of the data not used to build it (i.e., independent). We created a model with a transition matrix built from data from 1840 to 2003.

Then we projected the 2003 state distribution for ten years and compared it to the 2010-2013 period. We chose to compare the outputs of the verification and validation processes with a period of time (2010-2013) instead of just the last year (2013) because 2013 was an unprecedented fire year that may not represent the whole fire history of the area of study (Héon et al., 2014). The result of validation and verification procedures did not exactly reproduce the 2010-2013 average state distributions, but it produced very similar results, suggesting that the model can produce a reasonable representation of the actual system.

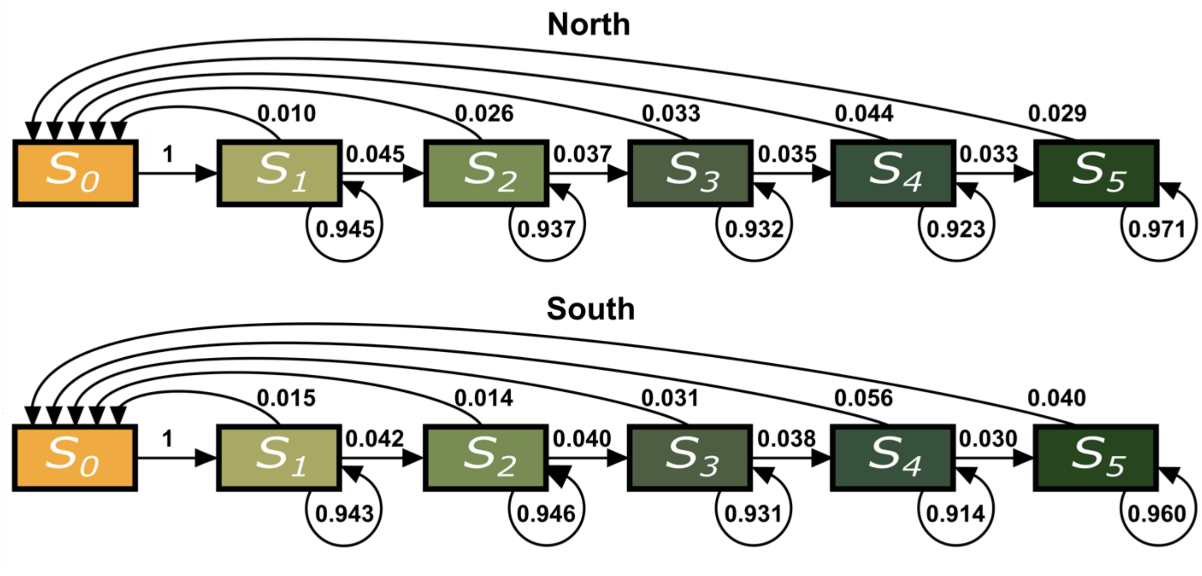


Figure 3.3. State-and-transition diagrams for the six-state baseline model with the observed forest dynamics for the north and south portions of the transect. Boxes indicate forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and arrows the transitions between them with their corresponding probabilities. Transitions represent growth (transition to the following stage), stasis (permanence in the same stage) and fire (i.e., burning; transition to the initial stage resetting the process).

3.2.3 Burning resistance

The baseline model reflects reburn resistance inherently because each state exhibits different burning probabilities. In the north transect section, young stands (S1: 1-20 years old) show burning probabilities five times lower than 40- and 80-year-old stands (S3 and S4, Figures 3.3 and 3.4), followed by a slight decrease in the oldest stage. In the south section, resistance extends to 40 years (S1 and S2), but at a minor degree than the north section (1.2 to 4 times lower than older stands, Fig. 3.4).

We found a significant dependency between fire occurrence and stand age by comparing the number of the observed and expected fire events in the states 1 to 5 (whole transect: $\chi^2=142.33$, $d.f.= 4$, $p<0.001$, north: $\chi^2=81.33$, $d.f.= 4$, $p<0.001$, and south: $\chi^2=79.15$, $d.f.= 4$, $p<0.001$). Additionally, the analysis of the residuals of the χ^2 tests (standardized difference between the observed and expected values) indicated that the dependency between fire probability and age is mainly driven by the negative influence of the youngest states (S1:<20 y. o.). This influence is more evident in the north (S1) compared to the south (S1 and S2; Fig. 3.4). We used the *chisq* test function from the base R software (R Core Team, 2008).

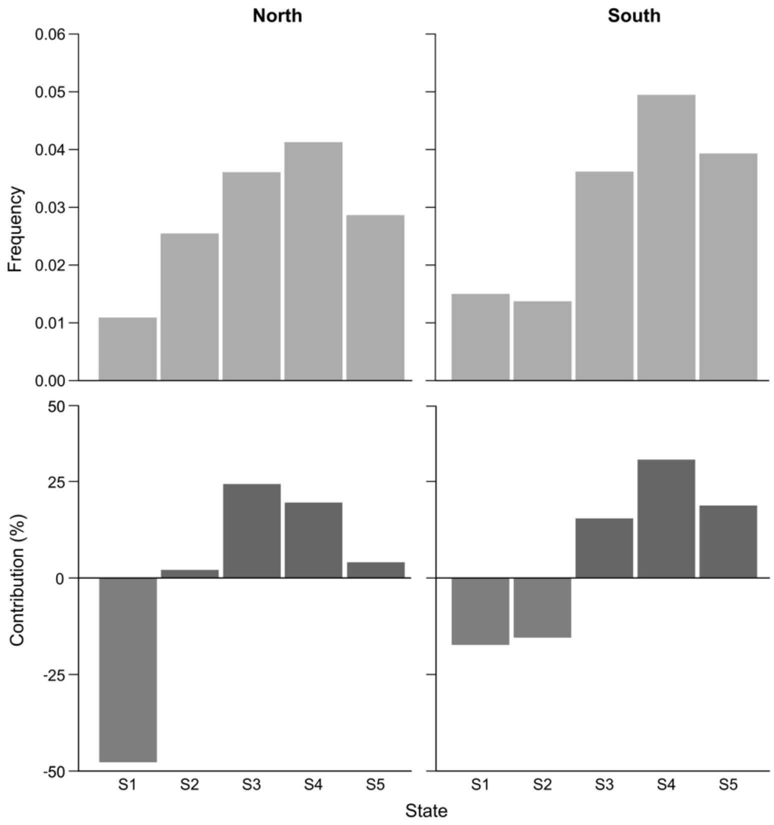


Figure 3.4. Frequency of fire events at each age state (S0, <1 year; S1, 1-20 years old; S2, 21-40 years old; S3, 41-60 years old; S4, 61-80 years old and S5, >80 years old) obtained from the fire history of each transect segment. The lower section represents the proportional contribution of each state to the χ^2 test of dependency (residuals). The bigger the absolute value, the most different it is from the expected value and the most influence on the age-fire dependence.

To compare age-dependent against age-independent burn probabilities, we set equal burning probabilities for every state (mean *f* probability) in the transition matrices. We compared age-dependent resistance scenarios (indicated with an "**R**" on the scenario's name: **HR**, **HRC**, **IR**, **IRC**) against scenarios lacking resistance (equal resistance denoted with an "**E**": **HE**, **HEC**, **IE**, **IEC**; Table 3.2).

3.2.4 Simulating regeneration failure

We considered the possibility of a non-forested stage resulting from regeneration failure in all the simulated scenarios. Regeneration failure is the inability of a forest to replace itself after a fire, resulting in a post-fire condition dissimilar to the pre-fire one (Coop et al., 2020; Stevens-Rumann et al., 2022). Regeneration failure is common in young stands where there isn't a significant aerial seed bank able to guarantee recolonization, suggesting a minimum (threshold) age at which a forest can regenerate after a fire. Although we cannot recognize forest loss in the history of the studied transects before 2013, it has been documented in many boreal forest areas under short-interval burning. This phenomenon has been observed in forests dominated by black spruce and jack pine as the total or nearly total disappearance of the dominant tree species for several years after a fire (Greene & Johnson, 1999; Hart et al., 2019; Pinno et al., 2013; Whitman et al., 2019), or switching to alternative vegetation types (e.g., *Populus tremuloides*-dominated forest; Johnstone and Chapin 2006, or an open canopy lichen woodland; Arseneault, 2001a; Girard et al., 2008; Portier et al., 2016).

Failed and poor regeneration is associated with wildfire occurrence in boreal conifer communities in stands <20 to 30 y. o. (Brown & Johnstone, 2012; Johnstone & Chapin, 2006; Pinno & Errington, 2016; Whitman et al., 2019). However, different thresholds and variability exist depending on the dominant species and location; black spruce requires a longer time after a fire (50-60 years) to accumulate sufficient aerial seed bank to regenerate (Buma et al., 2013; Gauthier et al., 1996; Hart et al., 2019; Lavoie & Sirois, 1998). In contrast, jack pine (the most abundant species in our study area) only requires 10-20 years (Briand et al., 2015; Cayford & McRae, 1983; Greene & Johnson, 1999). We employ regeneration failure thresholds similar to other models for jack pine and spruce forest, based on aerial seed bank maturity, which ranges from 10 to 30 years (Cyr et al., 2022; Splawinski et al., 2019).

We added a non-forested state (*NF*) resulting from regeneration failure. For simplification, this state may include any transition to a non-conifer-dominated state (non-forest, open lichen woodland, or deciduous vegetation dominance). The transition to this state also represents a short interval-reburning because it only occurs at the S1 stage (<20 y. o, Fig. 3.5), which according to the literature and other modelling implementations, may likely lead to regeneration failure. We also used the probability of escaping from the non-forested state from Hart et al. (2019). In other words, in our model, every time there is a fire in a stand under 20 y. o., it will transit to the non-forest stage (S1 to NF), and recovery (escape) will happen at a low probability (NF to S1 = 0.003).

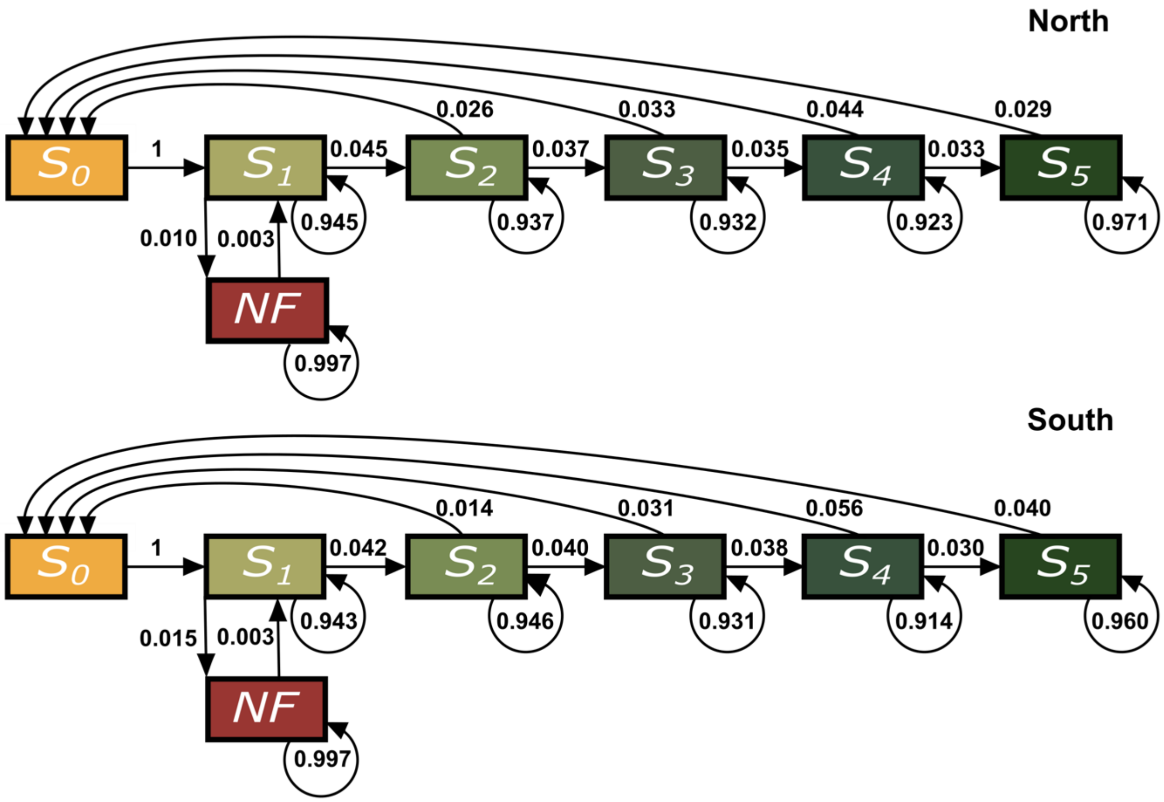


Figure 3.5. State-and-transition diagrams for seven-state models employed to project forest dynamics for the north and south portions of the transect. Boxes indicate forest states (NF, non-forested; S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and arrows the transitions between them with their corresponding probabilities. Transitions represent growth (transition to the following stage; *g*), stasis (permanence in the same stage; *r*), fire (burning; transition to the initial stage resetting the process; $fm_{>1}$), regeneration failure (transition to non-forest state; f_1) and recovery (transition from the non-forest state to S1).

3.2.5 Simulating climate change effects

We created climate change scenarios to account for its higher burning probabilities. For these scenarios, we increased the burning probabilities (*f*) in the transition matrix by a factor of 1.5, which is a moderate increase considering that projections of fire activity in other areas may reach a two- to three-fold increase by the end of this century. Anticipated increases in the Eastern James Bay HFR (homogeneous fire regime) zone, which contains our study area, ranged from 1.3 to two times between 2011 and 2040 (Boulanger et al., 2013, 2014; Hanes et al., 2019). Different from other areas of the boreal forest, the increase in fire activity as a product of the rise in temperatures, may be hindered by a gradual and slight increase in precipitation in our study area (Price et al., 2013). Scenarios simulating climate change are denoted with a "**C**" at the end of their name: **HRC**, **HEC**, **IRC**, **IEC** (Table 3.2).

When climate change is combined with a lack of reburn resistance, we obtain scenarios simulating a climatic override. Complete override scenarios contemplate the possibility of high burn probabilities regardless of stand age due to extreme climatic conditions. These scenarios simulate an overwhelmed resistance to reburn (all states have the same probability of burning and burn 1.5 times more: **HEC**, **IEC**) (Table 3.2). Climatic override scenarios stem from observations during the 2013 Eastmain fire that occurred in the study area, which burned stands as young as eight years old (Erni et al., 2017). Climatic overrides have also been observed in some fuel-limited areas of western U.S. (Abatzoglou et al., 2021).

3.2.6 Simulating variations over time

The baseline model is a time-invariant MCM: transition probabilities do not change over time, a property called homogeneity. Although informative, time homogenous Markov chain models (HMCM) may not be considered realistic enough to represent the dynamics of biological systems (Binkley, 1980; Boyd, 1998; Daniel et al., 2017; Isagi & Nakagoshi, 1990), but can be modified to encompass variations from real-world data as a time-inhomogeneous MCMs. To account for these variations, we calculated a transition matrix for every year in our dataset (N=156) and fit a distribution model for the burning probabilities. We found that burning probabilities follow a beta distribution, a particular case of the Weibull distribution used previously to characterize fire interval distributions (Baker, 1989).

The beta distribution can be described by two shape parameters, α and β, which we estimated and used to randomly draw new burning probabilities (f) for each forecasted year. We employed the *descdists* and *fitdist* functions from the ‘fitdistrplus’ R package to determine the distribution type (Cullen and Frey graph, Fig. A6) and calculate its parameters (α, β, mean, and variance) through the "moment matching" method (Table 3.1). Then, we used the *rbeta* function in base R to generate random numbers under the beta distribution with the parameters α and β, mean and variance calculated per each state. Those numbers defined the probabilities of fire for the 50 years predicted. This process resulted in 50 transition matrices instead of only one used in the HMCMs. We projected the initial distribution in the same fashion as the HMCM but employed one of the 50 matrices for each projected year. We repeated the process to obtain 1000 projections per scenario, from which we calculated each state's mean and standard deviation at $t = 50$ (the year 2062). We incorporated uncertainty into the model by employing the intrinsic variations of fire probability over time.

For the scenarios with burning resistance (**IR**), we used parameters specific to each state. Whereas, for the equally resistant forest state scenarios (no resistance; **IE**), we used the overall parameters for all stages (Table 3.1). The climatic override simulation was achieved by recalculating the shape parameters of the beta distribution through a modified fire probability mean (f ×1.5) and the same standard deviation (Equations A1 and A2; Table 3.1). Time constant or homogeneous scenarios are denoted with an "**H**" (**HR**, **HRC**, **HE**, **HEC**) and time-varying or inhomogeneous with an "**I**" (**IR**, **IRC**, **IE** and **IEC**).

Table 3.1 Estimated beta distribution parameters by MEM (Moment Matching Estimation) for the burning probability of each state and transect section. Random draws from a beta distribution with these parameters were used for the inhomogenous (time-varying) Markov model scenarios. Baseline conditions (without climatic override) reflect historical patterns of fire occurrence, while climatic override assumes a higher probability of fires (x1.5).

Climatic override	**Burning probability**	**North**				**South**			
		μ	σ^2	α	β	μ	σ^2	α	β
No	S1	0.019	0.010	0.0151	0.7719	0.012	0.002	0.047	3.915
	S2	0.021	0.010	0.0238	1.0646	0.016	0.004	0.044	2.568
	S3	0.025	0.012	0.0265	1.0142	0.029	0.015	0.023	0.775
	S4	0.020	0.010	0.0167	0.8147	0.040	0.027	0.017	0.419
	S5	0.022	0.008	0.0290	1.2848	0.028	0.011	0.036	1.254
	Overall	0.021	0.010	0.0218	0.9827	0.025	0.012	0.025	0.959
Yes	S1	0.028	0.010	0.048	1.673	0.018	0.002	0.141	7.696
	S2	0.031	0.010	0.062	1.941	0.024	0.004	0.116	4.739
	S3	0.037	0.012	0.072	1.896	0.043	0.015	0.074	1.668
	S4	0.030	0.010	0.057	1.852	0.060	0.027	0.064	1.009
	S5	0.033	0.008	0.098	2.890	0.042	0.011	0.111	2.546
	Overall	0.031	0.010	0.060	1.941	0.037	0.012	0.072	1.896

3.2.7 Scenarios

In total, we simulated eight scenarios for the north and south transects. The scenarios result from the combination of different properties of the model: time variation, burning resistance, and climatic override. **HR**: Homogeneous with early state burning resistance, **HRC**: Homogenous, with early state burning resistance and climate change, **HE**: Homogeneous without burning resistance, **HEC**: Homogeneous, without burning resistance and climatic change (climatic override), **IR**: Inhomogenous with early state burning resistance, **IRC**: Inhomogenous with early state burning resistance and climatic change, **IE**: Inhomogenous without burning resistance and **IEC**: Inhomogenous without burning resistance and climatic change (climatic override) (Table 3.2).

We simulate fire intervals shorter than the historical reference in scenarios without resistance (**E**) and under climatic change effects (**C**). This is because these scenarios increase the burning probabilities of all the states, including the youngest one (S1). If the earliest stage has increased burning probabilities, it will be more likely to burn, thus, increasing the likelihood of short-interval reburning. As a result, the maximum probability of short-fire interval occurs in scenarios with both **E** and **C**, where the burning probability of the youngest state (S1) is as much as the older states (S2 to S6), and where climate change increases its likelihood to burn 1.5 times more. We compared the scenarios outputs after 50 time-steps (years, 1962): the final stand age distribution (frequency of each age state) and the accumulated non-forested state. Frequencies were interpreted as percentages for simplicity.

Table 3.2 Scenarios to predict age structure and forest loss resulting from the combination of different properties of time variation, burning resistance, and climatic overrides. Time variation refers to constant (homogeneous: **H**) versus changing (inhomogeneous: **I**) burning probabilities over time. Burning resistance refers to variations of resistance between forest states (**R**) versus the assumption that no such distinction exists (**E**). Climatic change represents a higher (×1.5) burning probability (**C**), which is the expected increase of fire occurrence under climate change in the area of study (see text for details).

Time-varying	Burning resistance	Climatic change	Scenario
No (**H**)	Yes (**R**)	No	**HR**
		Yes (**C**)	**HRC**
	No (**E**)	No	**HE**
		Yes (**C**)	**HEC***
Yes (**I**)	Yes (**R**)	No	**IR**
		Yes (**C**)	**IRC**
	No (**E**)	No	**IE**
		Yes (**C**)	**IEC***

H: homogeneous (time constant *f* probabilities), **I**: in-homogeneous (time-varying *f* probabilities), **R**: Age-dependent burning resistance ($f_1 \neq f_2 \neq \ldots f_5$), **E**: equal (without) burning resistance ($f_1 = f_2 = \ldots f_5$), and **C**: climatic change ($(f_1, f_2 \ldots f_5) \times 1.5$). Reburn resistance overridden by extreme climate change events are indicated with an asterisk.

3.3 Results

Our predictions indicate a general pattern of high representation of young states and lower of older ones in all scenarios. Regeneration failure leading to forest loss ranged greatly between scenarios as a function of reburn resistance (**E** vs **R** scenarios), latitude (north vs south sections), climate change (with and without **C** scenarios) and variations of burning probability over time (**H** vs **IH** models). After 50 years, less forest would be lost under baseline (historical) conditions (reburn resistance **R** scenarios: 15 - 34 %), while much more would be lost under conditions of a complete climate change override (no reburn resistance and complete climatic override, **EC**: 35-62%). Interannual variation (**IH** models) caused abrupt "jumps" in the patterns of the non-forested state over the years, causing sudden rises in the frequency of the NF and temporary depletions of the most flammable forest states. The scenarios for the north section of the transect exhibited more restrained changes under all the simulations compared to the south section. We estimated the highest forest loss in the scenarios with a complete climatic override (no resistance and increased probability of fire) in the south section. Meanwhile, the scenario with reburn resistance without climatic override (resistance and historical burning probability) exhibited minor forest loss in the north section.

Homogenous model projections, such as the baseline ones, were characterized by the smooth and gradual trajectories of their states. The baseline model's steady state distribution was very similar between sections, showing a high representation of younger states (S1: 40%) and a gradually declining representation of older ones (S5: 7%, Fig. 3.6). This distribution reflects the inherent tendency set by the historical dynamics of the studied stands (growth, stasis, and fire probability) and is consistent in every scenario tested (Figs. 3.7, 3.8 and 3.9).

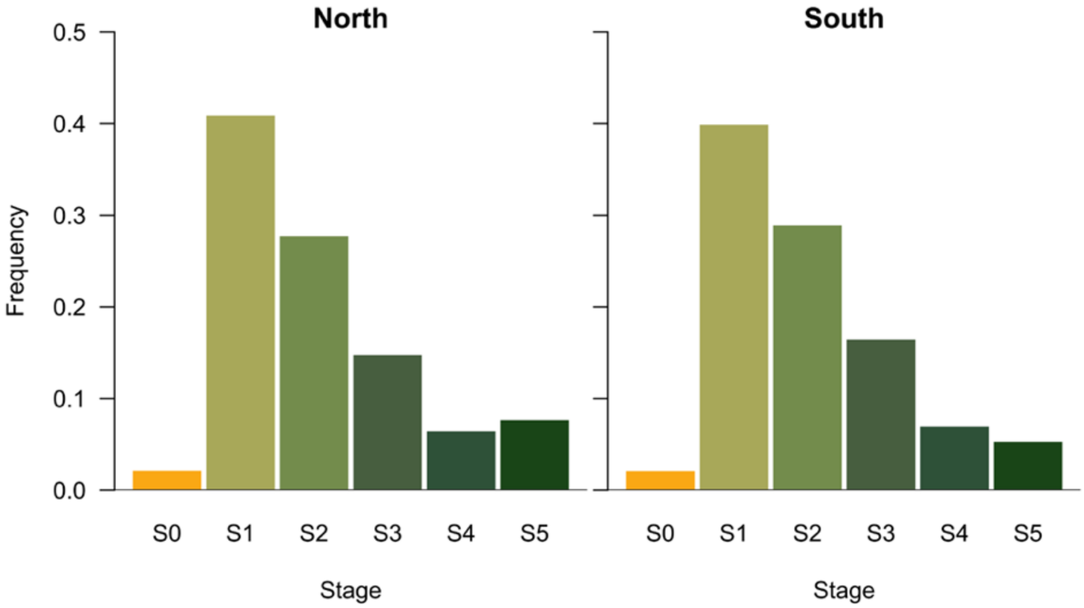


Figure 3.6. Steady-state distribution resulting from the baseline model for the north and south transect. Different colors indicate different states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.). It is the potential forest states' long-term proportion at equilibrium and the result from the baseline (historical) forest dynamics: with reburn resistance and without regeneration failure, climatic change or interannual variability.

The accumulation of the non-forested state resulted from the increased fire frequency, its interannual variability, and the lack of reburn resistance enhanced by latitude. Scenarios with burning resistance (**R**) predicted the least amount of forest loss. Regeneration failure ranged from 15 to 37 % in scenarios with burning resistance at early states (**HR** north and **HRC** south, respectively; Figs. 3.7 and 3.10), while without it, failure would reach 24 to 62 % (**IE** north, **HEC** south; Figs. 3.7, 3.9 and 3.10; Table A8). Differences in fire resistance between the transect sections (Fig. 3.4) led to slightly higher forest loss in the south (21 to 62 %) than in north scenarios (15 to 50 %; Figs. 3.7, 3.9 and 3.10; Table A8).

As expected, climatic change (i.e., increase of burning probabilities or fire frequency; **C** scenario) increased forest loss to almost the same extent as the simulated burning probability increase (~1.5). However, the effect of climatic override on forest loss varies according to resistance and interannual variability. Resistance in scenarios with a climatic change (i.e., **RC**) reduced forest loss from 1.6 (72% to 37%, **HRC** and **HEC** south) to up to 2 times (50 to 25 %, **HEC** and **HRC** north).

Interannual variation of fire probability simulated by the IHMCMs, produced abrupt patterns of change in the age distribution and forest loss in all scenarios (Fig. 3.8), mimicking the historical patterns observed in the previous 157 years (Fig. A3). Compared to HMCMs, IHMCM scenarios estimate similar results to the HMCMs (Fig. 3.10) but with slightly lower overall values of forest loss (Figs. 3.9 and 3.10; Table A8).

Reburn resistance in IHMCM scenarios (**IR**) reduced forest loss 1.2 to 1.7 times in the north and south transects, respectively. In contrast, climate change scenarios (**IRC** and **IEC**) increased forest loss between 1.4 and 1.7 times (north and south). Unexpectedly, reburn resistance in the north transect did not reduce forest loss under climate change conditions (**IRC**, Fig. 3.10). But, although **IRC** and **IEC** north scenarios estimate a similar forest loss (34 and 35 %; Fig. 3.9 and 3.10; Table A8), values in **IEC** remained very low compared to their south and HMCM counterparts.

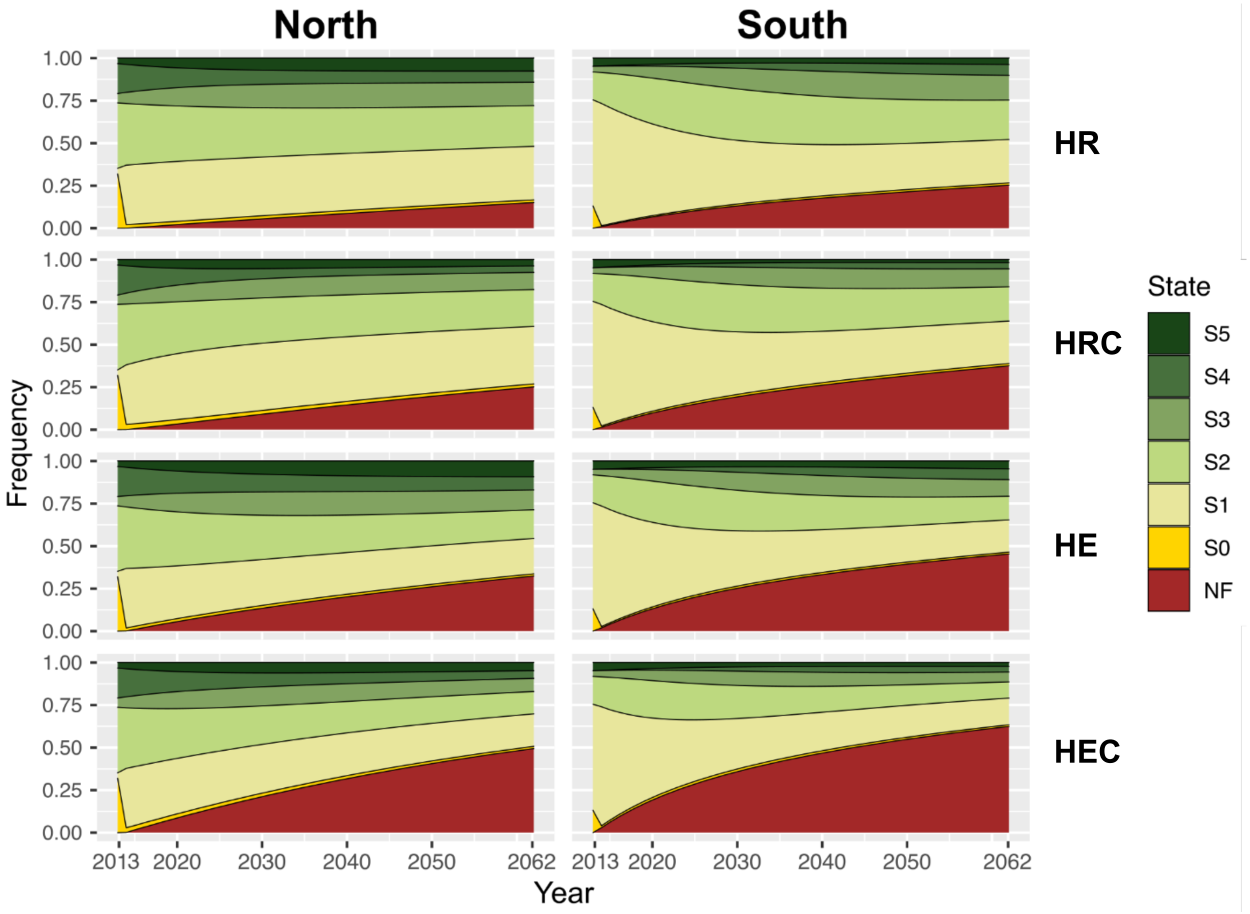


Figure 3.7. Projections of the homogeneous Markov chain model (time-constant) scenarios for fifty years. Different colors indicate six sequential forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and one resulting from regeneration failure (NF). Scenarios simulate reburn resistance under historical climatic conditions (**HR**) and with climatic override (**HRC**) and lack of burning resistance without (**HE**) and with climatic override (**HEC**).

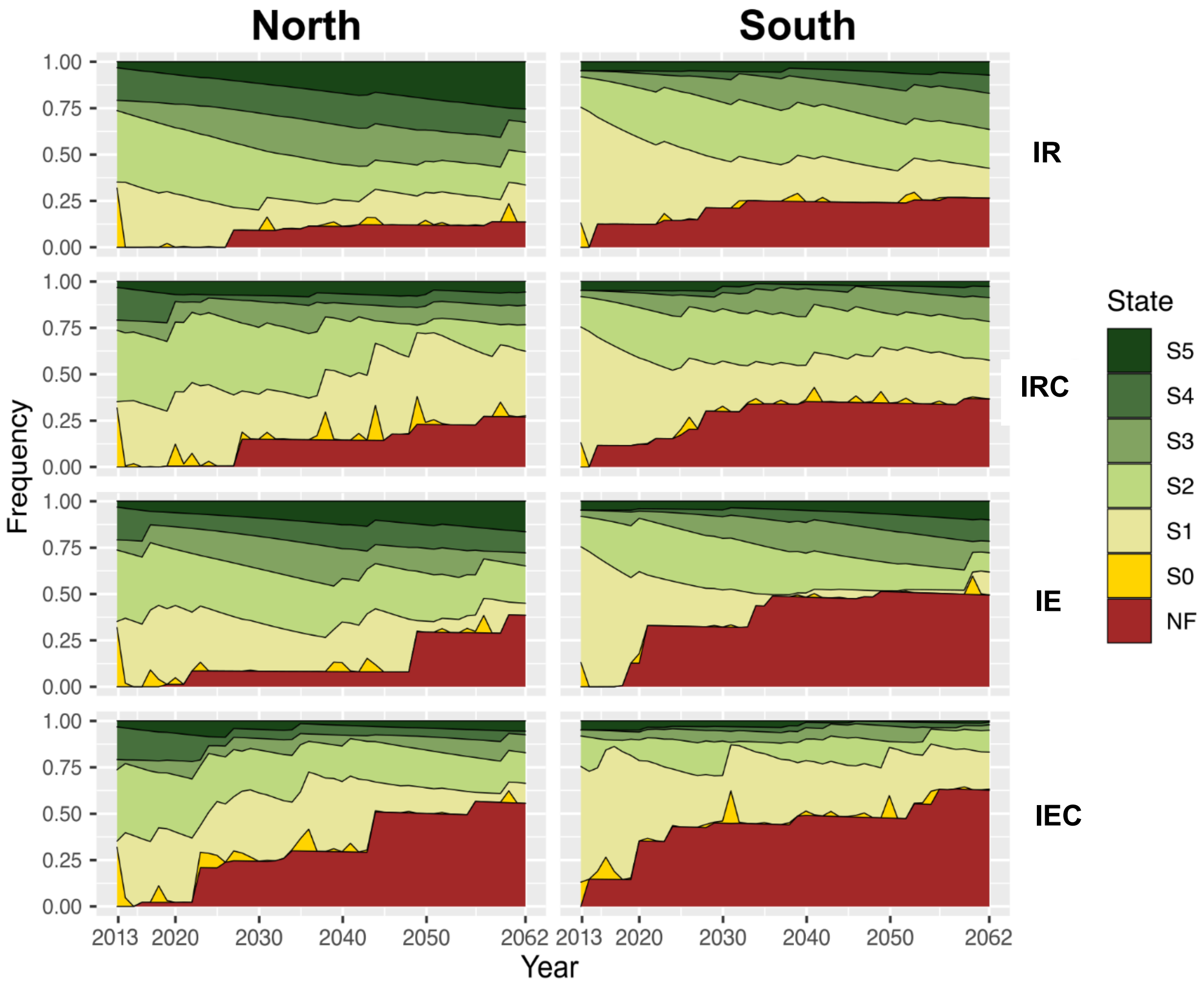


Figure 3.8. Examples of single projections for each inhomogenous (time-varying) Markov chain model scenarios. Different colors indicate six forest states (S0, <1 year; S1, 1-20 y. o.; S2, 21-40 y. o.; S3, 41-60 y. o.; S4, 61-80 y. o. and S5, >80 y. o.) and one resulting from regeneration failure (NF). Scenarios simulate reburn resistance under historical climatic conditions without (**IR**) and with climatic override (**IRC**) and lack of burning resistance without (**IE**) and with climatic override (**IEC**).

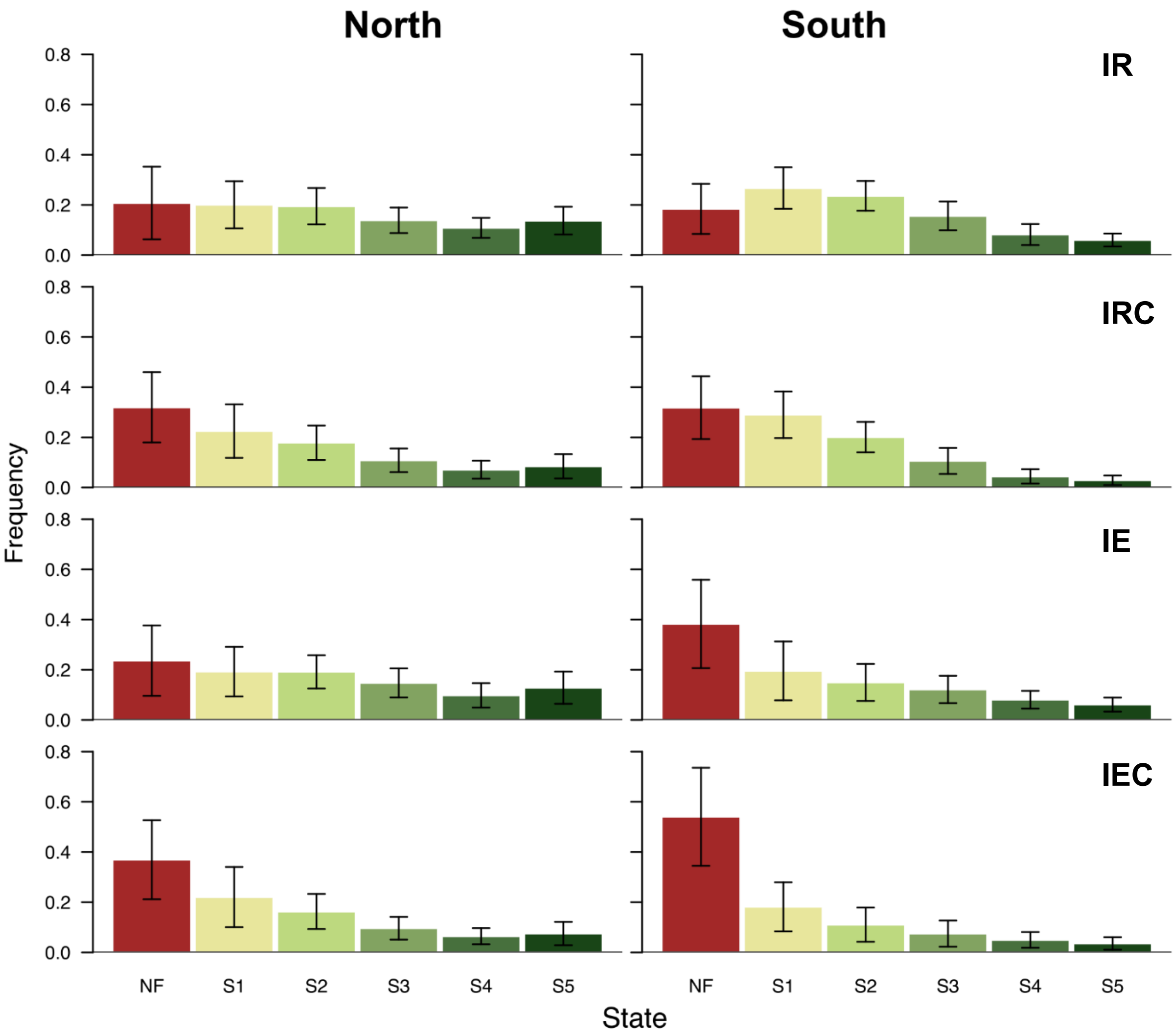


Figure 3.9. Predicted age distribution (x̄ ± SD) and forest loss (NF) by the inhomogeneous MCM after 50 years under the different scenarios tested. Scenarios simulate reburn resistance under historical climatic conditions (**IR**) and with climatic override (**IRC**) and lack of burning resistance without (**IE**) and with climatic override (**IEC**) (replications = 1000).

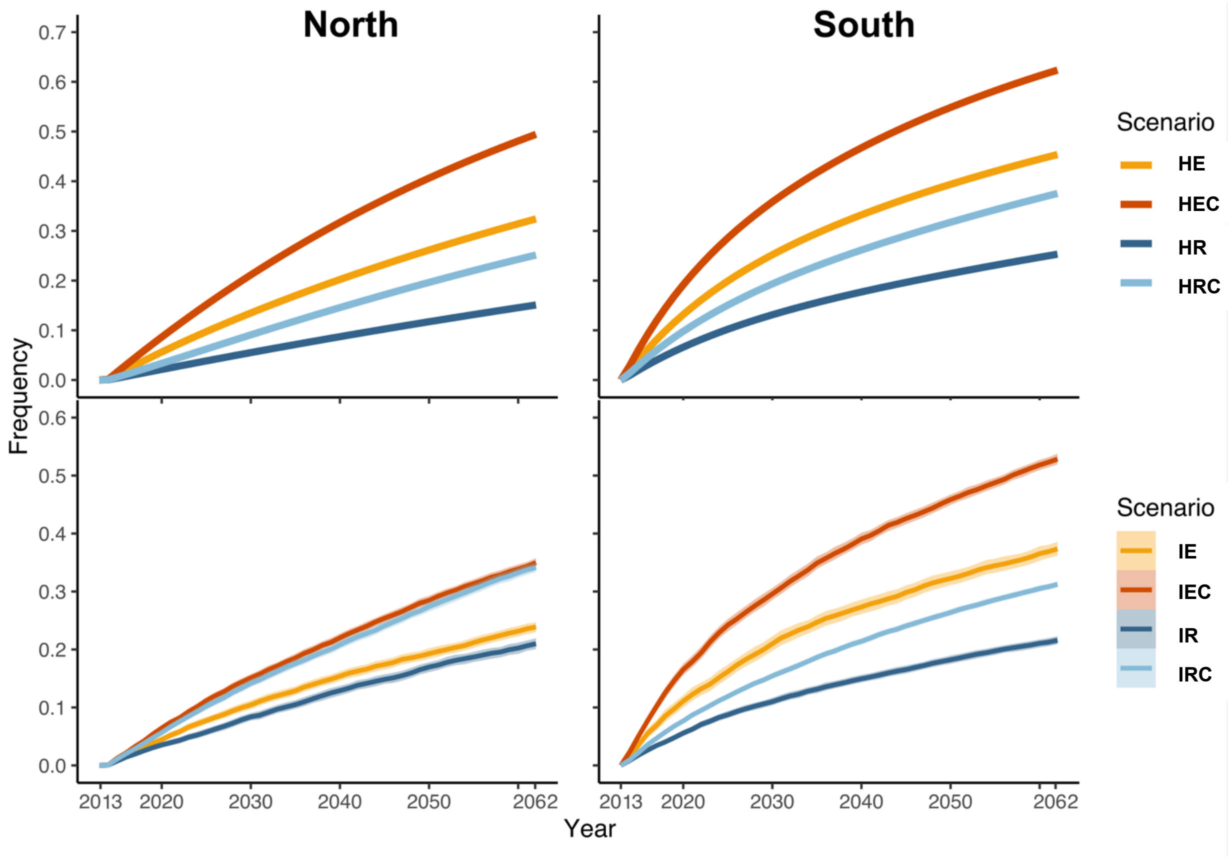


Figure 3.10. Cumulative projected potential conifer regeneration failure (non-forested frequency) for 50 years by the Homogenous (time-constant: **H**, top) and the inhomogeneous Markov Chain Models (time-varying: **IH**, bottom) under the different scenarios tested. Scenarios simulate reburn resistance under historical climatic conditions (**R**) and with climatic change (**RC**) and the lack of burning resistance without (**E**) and with climatic change (**EC**).

3.4 Discussion and conclusions

Our results highlight the relevant role of forest reburn resistance in structuring the forest age distribution and controlling potential regeneration failure. Moreover, we reaffirm the importance of the earliest stages of forest development (1-20 years old) in assuming two virtually opposing roles: significantly reducing the probability of new fires and becoming unforested upon reburning. This means that even small changes affecting this state can produce significant changes in the forest dynamics; such is the case for increased fire frequency (i.e., shorter intervals) caused by climate change and increased probability of regeneration failure.

Our results indicate a prevalence of the youngest forests over older ones in all scenarios. This pattern is caused by positive feedback, where more fires in mature stands also produce more young forests (Baker, 1989; Van Wagner, 1978). However, we could also distinguish substantial fluctuations in young forest proportion in time-varying scenarios (inhomogeneous MCMs) and the persistence of older forests. Overrepresentation of young forests over older ones may impact the overall diversity by reducing habitat availability of late-successional organisms (Hanski, 2000; Kuuluvainen & Gauthier, 2018) and delaying harvesting times (Cyr et al., 2009, 2022). Yet, the continuous growth of the forest (transitions from one state to the next) and the heterogeneity of the landscape and local climate may allow the preservation of a diverse forest age mosaic. Instead, forest loss and vegetation shifts pose a greater risk to organisms endemic to the boreal conifer community.

Despite their low frequency, the oldest forests (S5: >80 years) persist in every scenario. But their apparent lower flammability doesn't agree with the fact that these forests usually hold a more abundant and flammable black spruce component, and that fuel wouldn't be a limiting factor in a forest at that age (Bernier et al., 2016; Thompson et al., 2017). Instead, their persistence may be a result of the continuous contribution from previous states by growing (*g* transitions), the presence of water bodies and peatlands (Ali et al., 2009; Erni et al., 2017; Nielsen et al., 2016), saturation by low flammable coarse woody debris (Kitzberger et al., 2012) or the dominance of local weather over the fuel controlling fire (Ali et al., 2009; Bessie & Johnson, 1995; Parks et al., 2018). So far, the apparent resistance (low burning probability) in old stands is not further supported in the boreal forest literature (Bernier et al., 2016; Beverly, 2017; Hart et al., 2019; Ratz, 1995). Nevertheless, forests over 80 years old exhibit a relatively lower burning likelihood for our study area to contribute to their persistence, although not as low as observed in younger stands.

Conifer forest loss was restrained by resistance to reburn in the early stages of forest development (**R** scenarios). Burning probability in young forests (S1) can be four times lower than in mature stands. Our results show a potential loss of 30 to 50 % of the forest without resistance by 2062 (**E** and **C** scenarios, Figs. 3.7, 3.9 and 3.10). The time extent (time since fire) and strength of reburn resistance (10 to 20 years and 3-4 times lower burning probability relative to older forests) are comparable to other studies in the boreal conifer ecosystem (Bernier et al., 2016; Buma et al., 2022). Because vegetation negative feedbacks produce such a substantial effect on forest dynamics in the boreal ecosystem, it is fundamental to consider the extent, the strength, and spatial variation of the reburning resistance to avoid overestimations of fire activity, forest loss and vegetation shifts (Boulanger et al., 2014, 2017).

Weaker reburn resistance caused higher regeneration failure predictions in the south than in the north transect. Although reburn resistance in the south transect lasts longer (40 years) than in the north (20 years), it is relatively weaker and did not offset the high fire probabilities in older stages, especially in climate change scenarios (**C**). Moreover, reburn resistance in the study area is not static; burning resistance was greater (lower burn rates and shorter intervals) in the north transect between 1840 and 1910 than after 1910. The difference in reburn resistance might be associated with vegetation cover or, most likely, local climatic differences (Ali et al., 2009; Parks et al., 2018).

Our estimations of forest loss are consistent with a study near our study area for a similar period by Splawinski et al. (2019) under the current fire regime (15-25% vs 18% respectively) and under climate change (25 to 60% vs 66%). These similarities may be due to using the same criteria to simulate regeneration failure and climate change. Both studies establish a threshold age before forest maturity has been attained (i.e., insufficient aerial seed bank to recolonize); thus, regeneration failure is more likely. Both employed the HFR zones to determine the most likely increase in fire activity. Besides that, the models broadly differ in structure, mechanisms at play and number of parameters used. This means that even by using a simpler model but selecting the appropriate key parameters, we can still generate helpful predictions of forest dynamics.

By incorporating uncertainty, we captured the abrupt changes in age state distribution and regeneration failure caused by non-gradual events of fire occurrence. This behavior in the boreal forest history deviates from the previously accepted negative exponential stand-age distribution (*cf.* Van Wagner 1978). Instead of a relatively stable distribution and gradual changes over time, the age distribution is very dynamic, and its variability should be considered in simulation models (Armstrong, 1999; Boychuk & Perera, 1997; Daniel et al., 2017; Stralberg et al., 2018; Van Wagner, 1978).

Fluctuating climate change may overcome the effects of reburn resistance. Climatic change scenarios in the north transect yielded almost identical forest loss after 50 years (34-35%). This suggests that the negative feedback from vegetation is sensitive to sudden and extreme shifts in climatic controls. This phenomenon was documented in previous studies in the boreal forest (Buma et al., 2022; Hart et al., 2019), whose results also pointed out that resistance in young stands cannot completely counteract the increase of fire probability due to climate change. However, forest loss in these scenarios was considerably lower compared to the south transect (31-52%, respectively), indicating that, although the limit of resistance was reached in the north, another mechanism might exist restraining forest loss. Further study is needed to understand the complexity of the relationship between biotic feedback and extreme fluctuations caused by climate change.

Topographic features also play an essential role in regulating fire activity in the area and determining vegetation composition. Proximity or presence of water bodies (e.g., lakes, rivers, bogs) are other bottom-up controls limiting burning probabilities because they act as fire breaks and "sinks." Water bodies favour the regeneration and permanence of black spruce by increasing fire intervals and excluding species intolerant to poorly-drained soils (i.e., jack pine; Ali et al., 2009; Baltzer et al., 2021; Le Goff & Sirois, 2004; Parisien & Sirois, 2003). Untangling the relative role of water bodies with fuel limitation and flammability needs to be addressed to understand the mechanisms of bottom-up controls of fire. However, this subject is beyond the scope of this work.

The present model does not contemplate the expansion of the conifer forest to other areas or shifts. Although we predict an increasing accumulation of non-conifer forests, it only implies local extinction. However, the conifer forest persistence at larger spatial scales may also rely on their capacity to expand to other areas (Baltzer et al., 2021). Jack pine expansion is also associated with a decline of back spruce at higher fire frequency, but our model does not assess this process explicitly. We can just assume that higher fire frequency (short-interval fires) leads to the dominance of jack pine in the simulated scenarios.

Additionally, any type of vegetation different from the conifer forest (e.g., open lichen woodlands, mixedwoods or aspen-dominated communities) was assigned to the non-forested category. Although this generalization allowed us to simplify the model, we cannot wholly assess the potential magnitude of total forest loss (i.e., lack of the tree component). To include shifts to other vegetation types, we may also need to consider fire severity, as this factor can determine the following vegetation type after conifer regeneration failure (Arseneault, 2001b; Miquelajauregui et al., 2016). Further research in the study area and modifications to the model would help us specify the conifer forest's fate (replacement by other vegetation types or desertification).

Estimations of regeneration failure by time-varying models (inhomogeneous MCMs) are lower than the expected ones in HMCMs. This might be a consequence of the model fitting method selected. The "Moment Matching Estimation" method is commonly used to calculate the beta distributions parameters and was used instead of the "Maximum Likelihood Estimation" because of its capacity to deal with values equal to 0 and 1 but tends to under-estimate parameters in skewed data (Delignette-Muller & Dutang, 2015). Nevertheless, using alternative parametrizations for the beta distribution, employing different parameter estimation techniques, or even empirical distributions may improve future model applications.

Future model implementations would improve the climate change scenarios. In this version, we increased the observed fire probability 1.5 times for the whole projected period, similar to Splawinski et al. (2019). However, we might adopt an approach of a linear increase of fire probability until reaching the expected overall increase (Cyr et al., 2022), or simply by calculating and following the trends of fire events recorded in our database. Hence, we would refine the effect of climate change on the model.

The baseline model design may unintentionally delay the forest loss. The structure of the model considers that, every time a fire occurs, the forest will transit to a temporary non-forest state (S0). This might invertedly add one extra year to the fire cycle. The next version of the model will deal with this inaccuracy. Moreover, we will consider employing one-year interval forest states. This will reduce errors in the projection interpretation, and, although the great increase of forest states would be more computationally demanding, current technology and software implementations would allow us to run new projections effortlessly.

Despite these limitations, MCMs remain relatively simple and flexible models that can be easily modified and expanded. Moreover, the possibility of graphical representation (state and transition diagrams) improves the understanding of the processes modelled on it. MCMs are also area free, meaning that the projected states' trajectories are independent of each other. Consequently, contagion and synchronicity of extreme fire events are not explicitly assessed. For example, the Eastman fire in 1983 burned young stands (<20 years old) adjacent to more flammable older ones under extreme weather conditions. Despite these shortcomings, MCM's results can be interpreted as areas, computing time is very short, and improvements to include area-related parameters are possible.

Our model helped to elucidate the potential effects of climate change and resistance to reburning on the future age distribution and regeneration failure by maximizing the application of the long fire history recorded in the study area. With this information, we built a model based on fire activity temporal patterns without inputting multiple variables. Hence, employing a Markov model framework shows excellent potential to recreate novel scenarios by modifying or adding a few parameters. By doing so, we will understand how vegetation dynamics and properties interact with future climate and fire activity variations.

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4 Temporal Patterns of Wildfire Activity in Areas of Contrasting Human Influence in the Canadian Boreal Forest

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4.1 Abstract

The influence of humans on the boreal forest has altered the temporal and spatial patterns of wildfire activity through modification of the physical environment and through fire management for the protection of human and economic values. Wildfires are actively suppressed in areas with higher human influence, but, paradoxically, these areas have more numerous ignitions than low-impact ones because of the high rates of human-ignited fires, especially during the springtime. The aim of this study is to evaluate how humans have altered the temporal patterns of wildfire activity in the Canadian boreal forest by comparing two adjacent areas of low and high human influence, respectively: Wood Buffalo National Park (WBNP) and the Lower Athabasca Plains (LAP). We carried out Singular Spectrum Analysis to identify trends and cycles in wildfires from 1970 to 2015 for the two areas and examined their association with climate conditions. We found human influence to be reflected in wildfire activity in multiple ways: (1) by dampening (i.e., for area burned)—and even reversing (i.e., for the number of fires)—the increasing trends of fire activity usually associated with drier and warmer conditions; (2) by shifting the peak of fire activity from the summer to the spring; (3) by altering the fire-climate association; and (4) by exhibiting more recurrent (<8 year periodicities) cyclical patterns of fire activity than WBNP (>9 years).

4.2 Introduction

Wildfire is a critical phenomenon maintaining the ecological processes and integrity of the Canadian boreal forest (Weber & Stocks, 1998). Although most fire regimes in Canada are characterized by infrequent, high-intensity, extensive fires occurring mostly between May and August, there is great variability in the components of the fire regime across spatial and temporal scales(Stocks et al., 2002). Understanding the spatio-temporal patterns of fire occurrence and area burned is thus of foremost interest in Canada in ecological, social, and economic terms. Wildland fires burn on average between 1 to 3 million ha annually in Canada, affecting biological diversity (Bergeron et al., 2002; Johnstone, 2006), ecological services (Amiro et al., 2001; Kurz & Apps, 1999), and forest resources (Martell, 1994), and require costly fire management strategies for infrastructure and community protection (Bowman et al., 2011; Hope et al., 2016).

Fire activity, which is usually measured as the number of fires and the total area burned, is driven by weather, climate (Flannigan & Wotton, 2001; Weber & Flannigan, 1997), vegetation type (Cumming, 2001; Krawchuk & Cumming, 2011), topography, human activities (Bowman et al., 2011; Gralewicz et al., 2012b; Podur, 2001), and complex interactions among these factors. Globally, wildfire dynamics have been altered by human activities for millennia through people setting (accidental or deliberate) ignitions that add to the ones caused naturally by lightning, and by modifying the landscape through their activities, increasing access to wildlands, and by altering the arrangement, continuity, amount, structure, and distribution of fuels (i.e., flammable biomass). These changes, combined with climate change, have modified the components of the fire regime: severity, likelihood, seasonality, size, frequency, and intensity of fires (Flannigan et al., 2013; Gustafson et al., 2004; Krawchuk & Cumming, 2011; Marlon et al., 2008; M. Parisien et al., 2006; Pechony & Shindell, 2010).

Evidence suggests that fire suppression practices also have an important effect on the fire–weather relationship, potentially undermining the reliability of weather-based predictions. Current ignition rates in France, for example, are not as high as they were during the pre-suppression period, even under similar weather conditions (Ruffault & Mouillot, 2015). Fire regimes in Catalonia, Spain, cannot be efficiently predicted unless fire suppression activities, in addition to climatic variables, are taken into account (Brotons et al., 2013). In the U.S. Rocky Mountains, alternating periods of fire–climate relationship strength were reported for the past century, suggesting that the interaction of climatic and non-climatic factors, such as fire suppression, is highly complex and needs to be assessed to improve our understanding of fire activity (Higuera et al., 2015).

Over the last century, fire management activities in the Canadian boreal forest have shaped fire activity through aggressive suppression efforts and preventive measures. However, fire management has not been uniform over space and time because deploying resources to prevent and attack fires involves balancing potential economic, social, and ecological impacts, which can sometimes be conflicting (Cumming, 2005; Magnussen & Taylor, 2012; Martell & Sun, 2008; Murphy, 1985). To better reflect regional priorities, most of Alberta's forested land surface has been divided into ten Wildfire Management Areas (Alberta Agriculture and Forestry, 2017) that are managed by the provincial government. Fire management in Alberta has increased the containment (i.e., extinguishment before they reach 2 ha in size) of fires from 75% in 1998 to 93% in 2015 (Alberta Environment and Parks, 2015). Regardless of technological advances and preventive measures, large fire events still occur in Alberta. Such is the case of the Horse River fire in Fort McMurray, Alberta (spring 2016; 580,633 ha burned), which caused the evacuation of 80,000 people and was the costliest natural disaster in Canada, with an estimated damage worth of CAN$10.9 billion (Alam et al., 2016; KPMG, 2017). In contrast, National Parks within Alberta are not included in the provincial Wildfire Management Areas because the administration falls under federal jurisdiction. In these parks, unlike the rest of forested Alberta, the ecological role of fires is favored and wildfires are only suppressed when they pose a risk to surrounding inhabited areas, park infrastructure and areas containing rare natural resources (Parks Canada Agency, 2017).

Although it is well recognized that human influence can alter fire activity in the boreal forest, the magnitude and direction of recent changes remain largely undocumented. The main goal of this study is to assess how human influence has affected the fire regime of two contrasting areas in the Canadian boreal forest over the past few decades. To achieve this goal, we analyzed the changes in the number of fires and area burned (fire activity) over time and their relationships with climate in two contiguous regions of Alberta with contrasting human influence (fire management and human land use). First, to establish whether fire activity has changed in each region, we analyzed annual trends of the number of fires and area burned, from 1970 to 2015, and compared them while distinguishing natural from anthropogenic fires. Secondly, to determine if the fire–climate relationships remain coherent despite the dissimilar human influence, we compared these relationships between regions. Finally, to better understand the correlations between fire activity and climate, we characterized the cyclical patterns of the number of fires, area burned, and climate, and compared them between regions in terms of the duration of their periodicities.

4.3 Materials and Methods

4.3.1 Study Areas

We chose two adjacent study regions located in the northeastern corner of the province of Alberta and a southern portion of Northwest Territories, Canada, that differ in their level of human influence, including wildfire management (Fig. 4.1): Wood Buffalo National Park (WBNP, 4.3 Mha) and the Lower Athabasca Plains (LAP, 7.9 Mha). Both regions are located within the Boreal Forest Natural Region (BFNR), which covers approximately 58% of Alberta. The topography is mostly flat to gently hilly, and the vegetation is represented by four dominant types: upland deciduous, coniferous, mixed forests, and wetlands. The most common tree species found are black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*P. glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* (Michx.)), balsam poplar (*P. balsamifera* L.), and eastern larch (*Larix laricina* (Du Roi) K. Koch) (Natural Regions Committee., 2006).

Although WBNP and LAP are very similar in terms of topography and vegetation composition, they are subjected to contrasting levels of human influence. Established in 1922, WBNP is a UNESCO (United Nations Educational, Scientific and Cultural Organization) world heritage site where the human influence is remarkably low; less than one percent of its area has been modified by human activities, which mainly consist of two roads (Table 4.1, Fig. 4.1b). In contrast, LAP has almost 10 percent of its area destined to agriculture, tree harvesting, oil-and-gas exploration, and other rural and industrial activities. Comparatively, LAP also possesses a more extensive road network and more human settlements (Table 4.1, Fig. 4.1b) (Alberta Biodiversity Monitoring Institute, 2012; Natural Regions Committee., 2006). Despite belonging to the same land management unit, we excluded the portion of LAP located on the north side of

Lake Athabasca, because it is located in the Canadian Shield, which represents a topo-edaphic setting that differs substantially from the rest of the study area and WBNP, both located in the Boreal Plain.

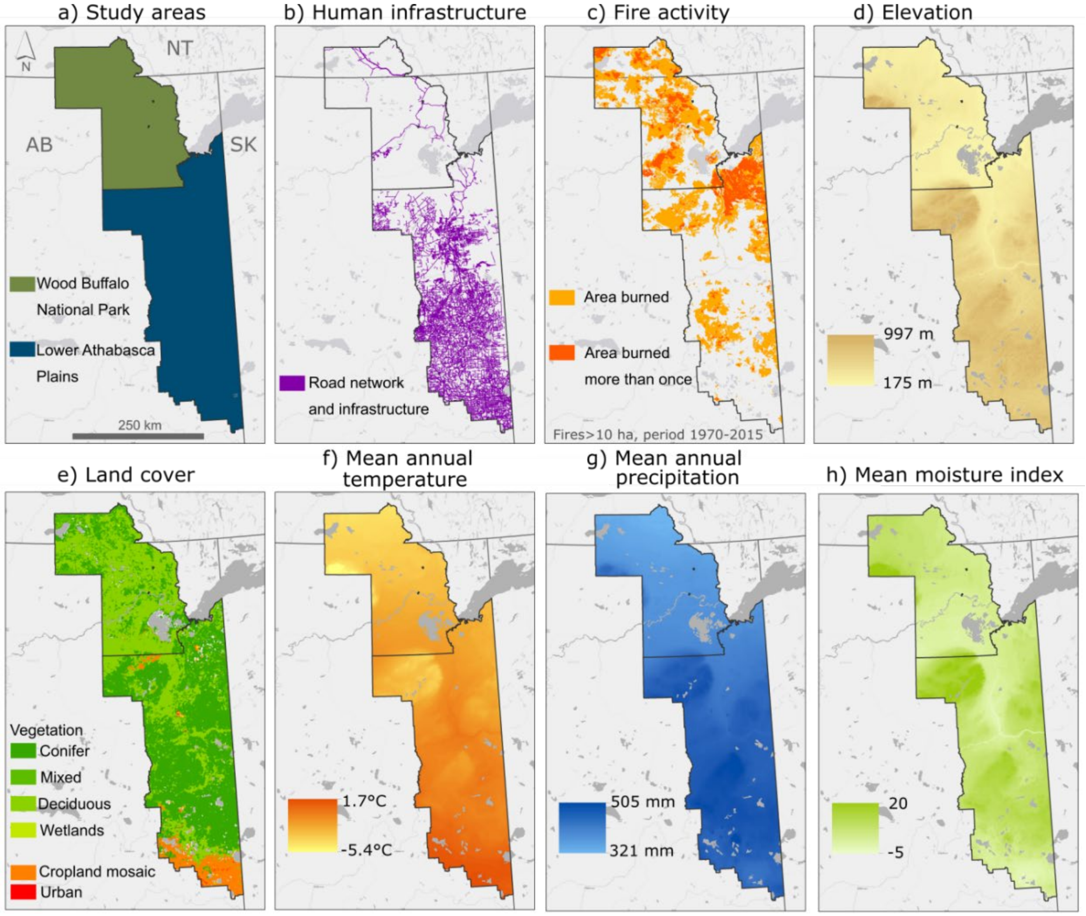

Figure 4.1. Maps showing (a) the location of the areas of interest (53.63◦ N, 110◦ W, 60.70◦ N, 115.60◦ W):Wood Buffalo National Park, which occupies a portion of Alberta (AB) and Northwest Territories (NT), and Lower Athabasca Plains, which borders with the province of Saskatchewan (SK), (b) Human infrastructure cover (30-metre-resolution, Landsat; Alberta Biodiversity Monitoring Institute, 2012), (c) Area burned from 1970–2015 (one-kilometer resolution), (d) Land cover (Global Land Cover Characterization Project, one-kilometer resolution, AVHRR; (US Geological Survey, 2014)), € Elevation, (f) Mean annual temperature, (g) Mean annual precipitation, and (h) Mean climate moisture index (precipitation minus potential evapotranspiration, mm, 1◦ latitude by 1 longitude resolution; Wang et al., 2012).

Table 4.1 Area occupied or modified by the leading human activities in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP).

Region	**WBNP Area kha**	**(%)**	**LAP Area kha**	**(%)**
Total	4266	(100)	7932	(100)
Cultivation	0		134.80	(3.16)
Harvested (cut blocks)	0		111.33	(2.61)
Mining	0		32.42	(0.76)
Seismic lines	0		29.86	(0.70)
Industrial-rural	0		23.90	(0.56)
Roads and vegetated margins	0.85	(0.02)	15.36	(0.36)
Urban	0		2.58	(0.06)
Total human-modified area	0.85	(0.02)	350.25	(8.21)

Fire management also differs between these regions. Fire management in the Canadian National Parks has undergone some changes since their establishment. Due to the increase of visitors in 1945, Parks Canada opted for a “protection” plan, resulting in fire suppression efforts aiming for fire exclusion. Later, in 1986, Parks Canada switched their policies to “management” phase. Management policies included the recognition of wildfires as intrinsic ecological processes (i.e., complete exclusion was not necessary), and active management (i.e., prescribed burning). The later phase intended to restore what was considered the “natural” fire regime (Woodley, 1995). The intensity and temporality of the application of these policies have varied between national parks in the Canadian territory. Nevertheless, lightning-caused fires in WBNP are not actively suppressed, only monitored, unless they are caused by humans and pose an imminent threat to infrastructure within the park or neighbouring communities, leaving wildfires to fulfill their “natural” role. In contrast, LAP includes the community of Fort McMurray and most of the Lac La Biche Alberta Wildfire Management areas, where there is a strict policy to suppress and prevent fires. On average, during the period 1970–2015, lightning-caused fires in WBNP are larger than the ones in LAP (Table A9), whereas anthropogenic ones are larger in LAP. Human contribution to area burned is so prominent in LAP that the area burned by human-caused fires exceeds the area burned by lightning-caused fires in this region (Table A9). Summer is the season with the highest fire activity (number of fires and area burned; Fig. 4.2) in both regions, but the human contribution to fires is considerably higher during the spring in LAP than in WBNP.

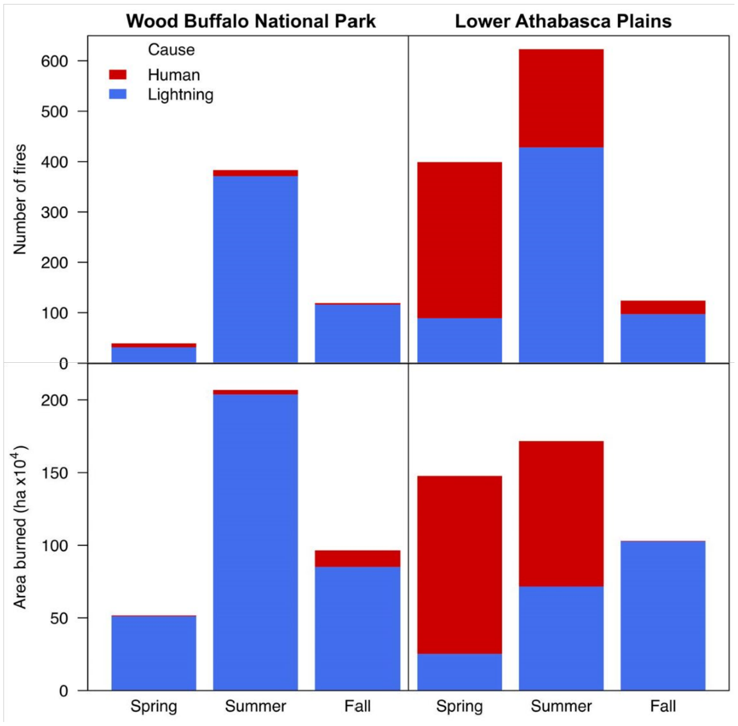

Figure 4.2. Number of fires and area burned in Wood Buffalo National Park and Lower Athabasca Plains by season (spring, summer, and fall) and cause of ignition (lightning or human). Information based on fires ≥10 ha from 1970–2015.

4.3.2 Fire Variables

We obtained the historical fire records from the Canadian National Fire Database (Canadian Forest Service, 2016) from which we derived the number of fires and area burned (ha) during the fire season (March 1 to October 31) (Forest and Prairie Protection Act, 2000) for the period 1970–2015. Although the database extends earlier than 1970, the analysis was limited to this time period because the data recording and methods of detection during the contemporary era were more reliable and consistent than those of the earlier period (Armstrong, 1999; Cumming, 2005; Murphy, 1985). In addition, we only included fires ≥10 ha because they are less likely to go undetected or unreported than fires <10 ha. The fires were stratified by area (WBNP or LAP) and by cause (human or lightning: H or L) and summarized into annual time series using the total number of fires and total area burned (log transformed) during the fire season.

4.3.3 Fire-Climate Variables

In order to uncover possible relationships with the fire activity variables (area burned and number of fires), we built mean annual time series of climate and fire danger indexes from the Canadian Fire Weather Index System (FWIS; Van Wagner, 1987) during the fire season (March 1 to October 31, Table 4.2). We used the records from 17 weather stations located in WBNP and 53 in LAP for the period 1970–2015 (Natural Resources Canada; Canadian Forest Service, 2016). Climate variables include annual means of temperature (°C), relative humidity (%), wind speed (km/h), and 24-h precipitation (mm), as well as codes and indices from the FWIS (Van Wagner, 1987): Fine Fuel Moisture Code (FFMC), Duff Moisture Content (DMC), Drought Code (DC), Initial Spread Index (ISI), Buildup Index (BUI), Fire Weather Index (FWI), and Daily Severity Rating (DSR). Indices and codes were calculated daily based on noon local standard time (LST) weather variables (temperature, humidity and wind-speed), and the FWIS moisture codes were also calculated based on wind-speed and precipitation from the previous day (Table 4.2).

Table 4.2 Climate variables and Fire Weather Index System codes and indices used (Modified from Van Wagner, 1987).

Acronym	Name	Units	Description
TEMP	Temperature	°C	A measure of heat present in the air
PRECIP	Precipitation	mm	A form of water, such as rain, snow etc. that condenses from the atmosphere and fall to the Earth
RH	Relative Humidity	%	Amount of water vapor present in air
WINS	Wind Speed	km/h	Velocity of air flow
FFMC	Fine Fuel Moisture Code	unitless	Moisture contained in the upper soil layer (litter and fine fuels)
DMC	Duff Moisture Code	unitless	Moisture for the loose organic layers of the soil, including medium-sized woody debris
DC	Drought Code	unitless	Moisture in deep compacted organic layer and large woody debris
ISI	Initial Spread Index	unitless	The expected rate of spread based on FFMC and wind speed
BUI	Buildup Index	unitless	Proxy for the fuel load available for combustion. Based on DMC and DC
FWI	Fire Weather Index	unitless	Reflects fire intensity and fire danger in forested areas. Based on ISI and BUI
DSR	Daily Severity Rating	unitless	Exponential transformation of FWI indicating severe conditions when DSR >2

4.3.4 Statistical Analysis

We searched for linear trends in the time series to identify overall changes in the number of fires and area burned during the 1970–2015 period. By decomposing the time series, we were able to separate them into their additive components: non-linear trend, oscillations (cyclical), and white noise. The non-linear trend was subtracted from the original time series as a “pre-whitening” step, which reduces the occlusion of the remaining components; in this way, we were able to identify oscillation frequencies and calculate their periodicities (years between peaks). Finally, we ran correlation tests between the fire-climate and fire activity time series in order to identify potential relationships between them. If a relationship was identified, we described its nature (positive, negative), strength, and periodicity (through their regular oscillations). All analyses were performed using R (R Development Core Team, 2016).

4.3.4.1 Linear Trend Detection

We tested the time series for autocorrelation processes, after which we ran a phase-randomized version of the Mann-Kendall trend test (slope different from 0: $p \leq 0.05$, H_0: $\beta_1 = \beta_2$, H_a: $\beta_1 6{=}\beta_2$) to find a significant linear trend. The Theil-Sen slope method was employed to calculate the slope value (β) (Mann, 1945, Sen, 1968, Jain 2017).

Some time series showed autocorrelation processes (aka. "red noise"), for which the magnitude and order were calculated. This was achieved by means of the autocorrelation and partial autocorrelation functions using the *Acf* function of the forecast *R* package (Hyndman & Khandakar, 2008) (Figs. A7 and A8). We found autocorrelation processes in the number of fires and area burned for both lightning-caused fires (first order autoregressive model, AR1 = 0.34) and human-caused fires (autoregressive-moving-average model, ARMA (3, 0), $p = 0.42$) in WBNP. In LAP, only area burned by human-caused fires and the total (L+H) showed ARMA (6, 0) autocorrelation. To account for the serial correlation, we employed a phase-randomization method for the hypothesis testing of the trend, which is suitable for non-normal, autocorrelated data, and is robust against outliers (i.e., influential or extreme data). This method consists of the creation of surrogate time series (randomized versions of the original) to create a distribution which is then compared to the original time series to determine its significance. By doing so, we avoided spurious regressions due to the lack of error independence and unequal variances (Crawley, 2013; Fox & Weisberg, 2011; Metcalfe & Cowpertwait, 2009) and obtained a robust estimate of parameters of the regression by bootstrapping (Harrell, 2015). We employed the *MKcorr.test* function contained in the MKCorr R package (Jain, 2017).

4.3.4.2 Time Series Decomposition

Next, we separated the time series (number of fires, area burned, climate and FWIS indices) into their additive components: non-linear trend, oscillations (regular cycles), and white noise (random signal; see example in Fig. A9) by using an iterative Singular Spectrum Analysis (SSA; Golyandina & Korobeynikov, 2014) included in the Rssa package (Golyandina et al., 2014) in R. SSA is an adaptive non-parametric method ideal for short, noisy time series. This method does not require a priori knowledge of the model to be fitted (e.g., linearity, normality, and stationarity of the residuals, or the number and value of the contained periodicities), making it an advantageous technique to explore and analyze data when the parameters are unknown.

The separation of the components was achieved by running the decomposition process twice (hence the term “iterative”): first, we ran the analysis to extract the non-linear trend and, second, we subtracted this trend (detrending) from the original time series and ran the decomposition process again to extract the oscillatory (cyclical) components. This step also reduces the red noise significantly, so that the oscillations detected are unlikely to be autocorrelation processes (Yue & Wang, 2002). Each iteration requires “windows” (adjacent values) of different lengths (number of values) to establish the resolution and minimum periodicity to detect. We used a small window (L = 12 years) to extract the non-linear trend, and a larger window (L = 24 years) on the detrended time series to extract the cyclical components (Golyandina & Korobeynikov, 2014). We calculated the periodicities of the cyclical components originating from the eigenvectors that explained most variance (>20%) according to the SSA. This was achieved through the Estimation of Signal Parameters via Rotational Invariance Techniques (ESPRIT; Roy & Kailath, 1989) using the function *parestimate* in the Rssa package and confirmed with the spectrum (*mvspec* function, astsa package; Stoffer, 2016). As a result, we obtained a new set of time series produced for the two study areas (WBNP and LAP), the three ignition causes (lightning, human, lightning + human), the two fire variables (number of fires and area burned), the eleven fire-climate variables, and the two SSA derived outputs (one non-linear-trend and one detrended time series). Non-linear trends, unlike linear ones, may show changes over time according to different rates that might not be detected with the Mann-Kendall test, but they may still represent a relevant pattern in the time series.

4.3.4.3 Cross-Correlations of Time Series

In order to evaluate the correlations of fire activity time series between areas and fire activity series with fire-climate variables, we calculated the Kendall rank correlation coefficients and their significance from the detrended time series. We carried out correlations for two different time lags (zero and one year) to test for current and delayed effects of climate on fire, respectively.

We used a non-parametric "randomized-phase surrogate" technique for significance testing to reduce type-1 errors. This test employs the Fourier transform to generate a large number of random time series (called surrogates) with the same spectral properties as one of original (and thus, the same autocorrelation, if present) but with random phases. Then, the correlation between the two original time series is compared to a distribution of correlations produced by the surrogate series to obtain the statistical significance (Baddouh et al., 2016;

Ebisuzaki & Ebisuzaki, 1997). This analysis was performed using the *surrogateCor* function contained in the package astrochron (Meyers, 2014) in R with 2000 random surrogate series.

4.4 Results

Fire activity from 1970 to 2015 has increased in WBNP in both the number of fires ($\beta = 0.30$, $p < 0.01$, Fig. 4.3a) and area burned ($\beta = 0.14$, $p < 0.01$, Fig. 4.3c), while in LAP, there is a statistically significant decrease in the number of fires ($\beta = -0.21$, $p = 0.01$, Fig. 4.3b), and no overall change in area burned ($\beta = 0.02$, $p > 0.05$; Fig. 4.3d). Lightning-caused fires were responsible for raising the number of fires in WBNP ($\beta = 0.28$, $p < 0.05$), whereas anthropogenic fires remained low ($\beta = 0$, $p > 0.05$) and their area burned unchanged ($\beta = 0$, $p > 0.05$; Fig. 4.3a, c). Fire activity in WBNP exhibited nonlinear trends, indicating that the increase was faster during the second half of the time period than the first half. Although the non-linear trends suggest a decline in the number of fires caused by lightning or humans in LAP, neither of them was statistically significant ($\beta = 0$, $p > 0.05$ and $\beta = -0.9$, $p > 0.05$ respectively), but their sum (L + H) was (Fig. 4.3b).

In general, a warming and drying climate trend was found over the 46 years studied in both WBNP and LAP, with faster changes in WBNP (Table 4.3). Most of the fire-climate time series showed some change (linear trend) over the same period that would lead to an increased wildfire activity, but this is only observed in WBNP. In general, for both WBNP and LAP, we found a declining trend in PRECIP, RH, and WINS, and an increasing trend for FFMC, DMC, DC, and BUI. Only ISI did not change overall in any of the areas. Although we did not find a linear trend for temperature in LAP, the non-linear trend extracted by SSA does show an increase (Fig. A9), as well as for FWI and DSR in WBNP. The most drastic increase in both areas was observed in the Drought Code, which indicates moisture deficits in the deeper soil levels (Table 4.3).

Cross-correlations of detrended time series between regions indicated a similar pattern of fire activity regardless of the differences in human influence. Lightning-caused fire time series correlations (for both number of fires and area burned) showed the highest coefficients, whereas human-caused fires showed the lowest (Table 4.4).

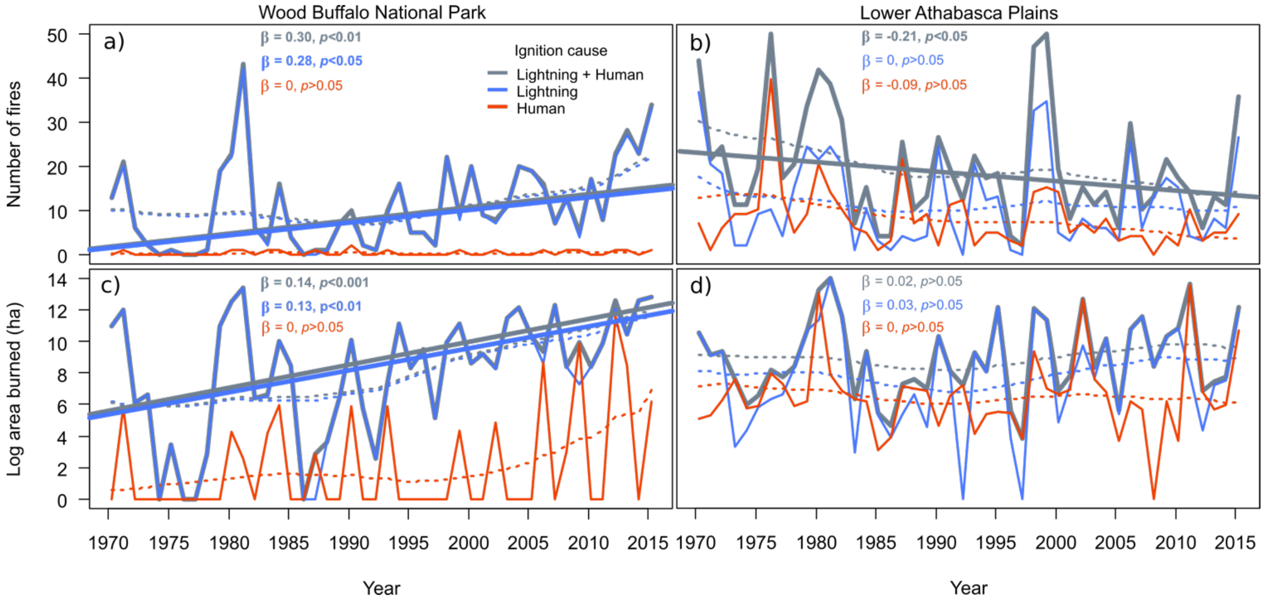

Figure 4.3. Time series representing the number of fires (upper) and area burned (lower) for the period 1970-2015 in Wood Buffalo National Park and Lower Athabasca Plains. Thin solid lines indicate raw time series, dotted lines, the non-linear trend extracted by Singular Spectrum Analysis, and solid straight lines, the significant linear trends obtained by Mann-Kendall trend test. Different colors indicate the cause of ignition. Theil-Sen's slopes (β) and trend significance by Mann-Kendall are shown.

Table 4.3 Theil-Sen slope values (β) and significance by a random-phase Mann-Kendall trend test (* ≤0.05, ** ≤0.005) for the fire-climate variables in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Values were calculated from annual time series.

Acronym	**Name**	**WBNP**	**LAP**
TEMP	Temperature	0.03**	0.01
PRECIP	Precipitation	<–0.01*	–0.01 **
RH	Relative Humidity	–0.15**	–0.06 **
WINS	Wind Speed	–0.10**	–0.03 *
FFMC	Fine Fuel Moisture Code	0.07*	0.07 **
DMC	Duff Moisture Code	0.30**	0.23 **
DC	Drought Code	2.83**	3.23 **
ISI	Initial Spread Index	0	0
BUI	Buildup Index	0.44**	0.42 **
FWI	Fire Weather Index	0.04	0.06 **
DSR	Daily Severity Rating	0.02	0.02 *

Table 4.4 Correlation coefficients for the number of fires (upper-right) and area burned (lower left, shaded) of the fire activity time series in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Significance was calculated by a random-phase test (* ≤0.05, ** ≤0.005). Letters following area name indicate ignition cause: Lightning (L) and human (H).

Region		**WBNP**			**LAP**		
	Cause	**L + H**	**L**	**H**	**L + H**	**L**	**H**
WBNP	**L + H**	1	0.96 **	0.17 *	0.31 **	0.36 **	0.08
	L	0.94 **	1	0.13	0.30 **	0.35 **	0.09
	H	0.09	0.04	1	0.18	0.24 *	−0.07
LAP	**L + H**	0.26 *	0.25 *	0.10	1	0.68 **	0.37 **
	L	0.33 **	0.32 **	0.09	0.76 **	1	0.06
	H	−0.01	−0.01	0	0.29 *	0.09	1

Although the association of fire activity with fire climate was similar in both regions (we observed significant correlations with similar coefficient values for both the number of fires and area burned time series; Table 4.5), we noted that: (1) mean annual temperature was only correlated with lightning-caused fires in WBNP and human-caused fires and area burned in LAP, (2) low mean annual precipitation was associated with high lightning-caused fire activity but not human-caused fires in both areas, (3) human-caused fires in WBNP do not have any association with fire-climate, and (4) lightning-caused fires only correlated with temperature and relative humidity in WBNP. We only found three one-year lagged correlations: between the number of human-caused fires in LAP with wind speed ($\tau = -0.30$, $p < 0.005$), and area burned by lightning ignitions with precipitation in WBNP ($\tau = -0.26$, $p < 0.05$) and temperature in LAP ($\tau = 0.29$, $p < 0.005$).

Table 4.5 Kendall-correlation coefficients for the relationship between the number of fires and area burned with fire-climate time series at lag 0 (i.e., current year) in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP). Significance was calculated using a random-phase test (* ≤0.05, ** ≤0.005).

	Number of Fires						**Area Burned**					
Region	**WBNP**			**LAP**			**WBNP**			**LAP**		
Ignition cause	**L + H**	**L**	**H**	**L + H**	**L**	**H**	**L + H**	**L**	**H**	**L + H**	**L**	**H**
Temperature	0.20 *	0.19 *	0.17	0.20	0.12	0.23 *	0.07	0.07	0.1	0.10	0.09	0.17 *
Precipitation	−0.29 *	−0.27 *	−0.02	−0.22 *	−0.21 *	−0.14	−0.23 *	−0.25 *	0.07	−0.20 *	−0.21 *	−0.14
Relative humidity	−0.24 *	−0.23 *	−0.05	−0.20	−0.13	−0.18 *	−0.21	−0.22 *	−0.03	−0.27 *	−0.24 *	−0.22 *
Wind speed	−0.14	−0.15	−0.05	−0.18	−0.07	−0.2 *	−0.27	−0.23	−0.09	−0.02	−0.01	−0.12
FFMC	0.26 *	0.24 *	0.1	0.23 *	0.22 *	0.15	0.20	0.20 *	0.05	0.29 *	0.27 *	0.19 *
DMC	0.33 *	0.32 **	−0.01	0.27 *	0.03 *	0.21 *	0.37 **	0.40 **	−0.06	0.40 **	0.34 **	0.30 **
DC	0.34	0.34 **	0.04	0.23 *	0.25 *	0.18 *	0.36 *	0.40 **	−0.02	0.24 *	0.26 **	0.27 *
BUI	0.20 *	0.35 **	0	0.30 *	0.26 *	0.2 *	0.37 **	0.40 **	−0.03	0.40 **	0.35 **	0.30 *
ISI	0.21 *	0.20 *	0.10	0.28 *	0.30 *	0.1	0.23 *	0.26 *	0.07	0.40 **	0.32 **	0.21 *
FWI	0.30 *	0.30 *	0.06	0.31 *	0.30 *	0.16	0.36 **	0.40 **	0.01	0.44 **	0.36 **	0.30 **
DSR	0.28 *	0.26 *	0.01	0.34 **	0.30 **	0.20	0.37 **	0.40 **	0.02	0.44 **	0.35 **	0.31 **

Fire activity in WBNP was characterized by longer and more acute periodicities than the ones found in LAP. We observed that the number of fires and area burned by lightning in WBNP showed strong activity peaks every ~12 years, whereas in LAP, weaker oscillations (i.e., under eight years) were most frequent. Anthropogenic ignitions in both areas mostly displayed high frequency (short periods) oscillations (~3–6 years); however, area burned by humans also showed strong oscillations every ~11 years (Fig. 4.4).

4.5 Discussion

Human activities have been continuously altering the dynamics of the boreal forest in Alberta over the past few decades, and have generated recognizable spatial and temporal patterns of wildfire activity. In the 1970–2015 period, we found increasing fire-conducive climatic trends in both study areas that were reflected in occurrence and area burned increases only in the region with the lowest human interference (WBNP), which agrees with findings reported across Canada (Girardin, 2007; Jolly et al., 2015; Tymstra et al., 2007). In contrast, we observed a dampening effect of fire activity in the region with the most human impact (LAP), resulting in a decline in the number of fires and no overall change (no trend) in the area burned. Previous studies also suggest that although area burned has increased due to the changing climate in the boreal forest, this is not necessarily the case in areas of higher human influence (Parisien et al., 2016; Robinne et al., 2016).

The main causes limiting the potential area burned under high human influence are: (1) the strong prevention and fire suppression policies, (2) improved accessibility, (3) the location of the human ignitions (i.e., closer to human infrastructures), and (4) land-use change. The first cause is a consequence of two of the objectives of fire suppression in Alberta: reducing the

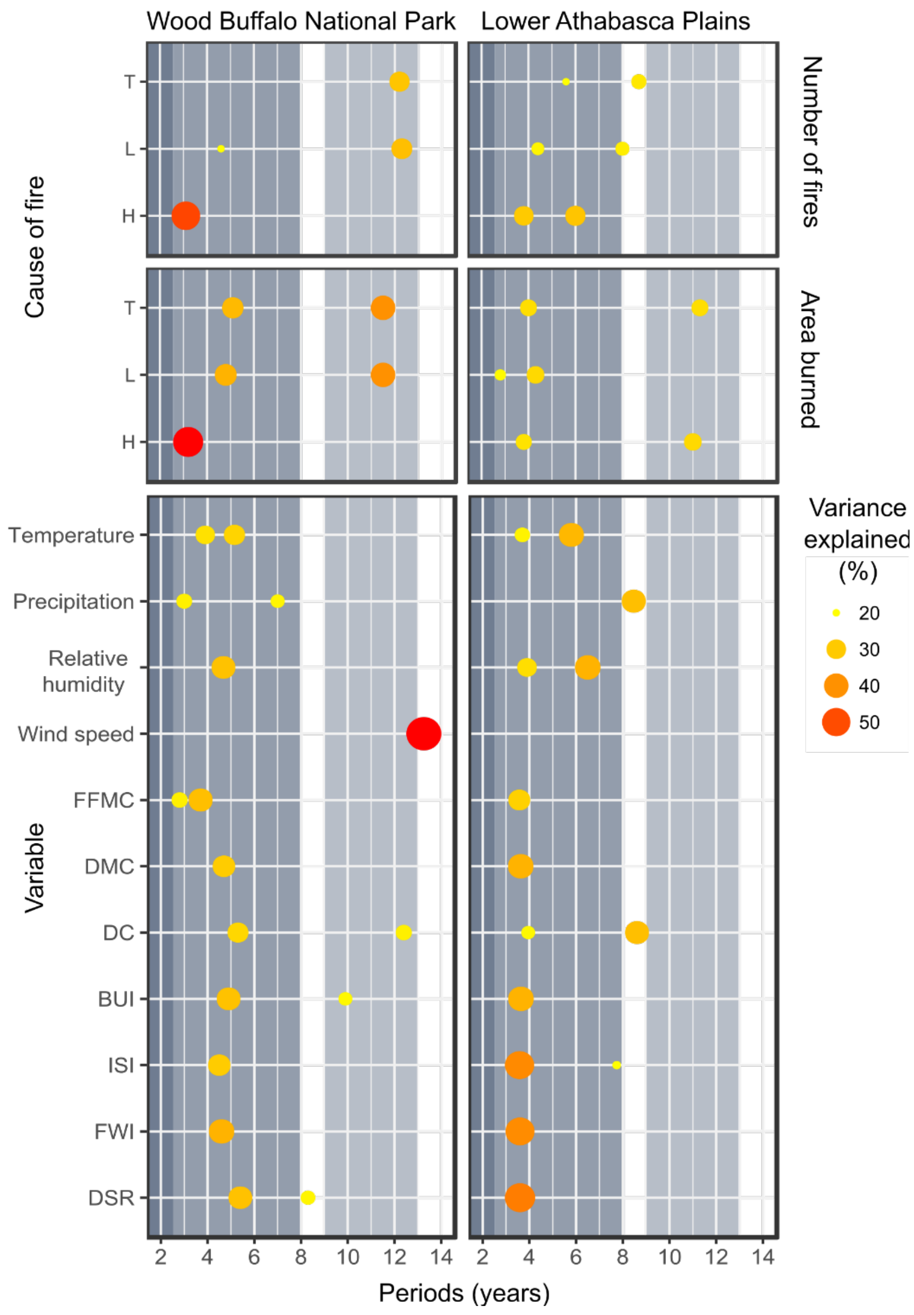

Figure 4.4. Periodicities (i.e., duration of oscillations) of the fire activity and fire-climate variables, calculated for the cyclical components found in the time series. Size and color of the points indicate the variance explained by the eigenvectors from which the oscillations were extracted during SSA. Shading corresponds to the "typical" climatic teleconnection domains: Quasi-Biennial Oscillation (2–2.5 years, dark grey), El Niño Southern Oscillation (2.5–8 years, moderate grey), and a quasi-decadal oscillation (9–13 years, light grey).

spread of fires before 10 AM of the following day and preventing them from attaining 2 ha in size (Alberta Agriculture and Forestry, 2017), which results in fewer escaped fires (i.e., defined here as fires ≥10 ha). In addition, the widespread road network facilitates access for fire-management activities to take place. Although human ignitions might increase over time, they also tend to cluster in the wildland-urban interface (WUI; Gralewicz et al., 2012a; Robinne et al., 2016), where fire detection and initial attack are more efficient, impeding their further growth in spite of fire-prone weather conditions. Finally, conversion of forested areas to agricultural, urban, and petrochemical mining land uses has altered the vegetation's structure and composition. These changes, in turn, have impacted the burn rates and ignition likelihood, and the increased fragmentation has reduced vegetation continuity, countering potential area burned (Gralewicz et al., 2012b; Krawchuk et al., 2006; M.-A. Parisien et al., 2011; Podur et al., 2002; Ryu et al., 2006).

Wildfire suppression practices, in conjunction with other human-induced changes, have the potential to not just slow down, but also to reverse trends in fire activity; hence, non-climatic factors have the potential to alter fire-climate relationships. Such cases have been reported in France, where recent fire activity stopped tracking climatic trends and decreased along with major changes in fire suppression policy (Fréjaville & Curt, 2017; Ruffault & Mouillot, 2015), and in South Africa, where land-use changes mediated the relationship between climate and area burned (Archibald et al., 2009).

The impact on fire regime by historical changes in wildfire management in WBNP are relatively minor compared to the compound changes observed in LAP. Fire management policies in WBNP evolved from exclusion in the 40´s to mostly monitoring in the 80´s (Woodley, 1995). In contrast, in LAP, the effort to suppress all fires has continuously increased over time as human activities continue to develop and extend in the area. The effect of fire management policy changes on fire activity within areas is beyond the scope of this study. However, our results properly show the differences in fire activity between areas of contrasting human influence over almost half a century.

Unlike trends, overall annual fluctuation patterns of wildfire activity exhibited some similarities between regions, regardless of the level of human influence. This is because climate and lightning still persist as dominant factors regulating the totality of fire activity in the boreal forest (Erni et al., 2017; Veraverbeke et al., 2017; Wang & Anderson, 2011). We further support this observation, given that wildfire activity was similarly related to climate in both regions. In general, peaks of fire activity tracked a drier and warmer climate in both areas. We also found that temperature and relative humidity did not correlate to the number of lightning-caused fires in LAP, whereas they did in WBNP, suggesting that non-climatic factors (i.e., fire management, land-use change, road density) might have interfered with those relationships (Arienti et al., 2009; Ruffault & Mouillot, 2015).

Anthropogenic fire activity is associated with the same climatic variables as lightning-caused fire activity, with only very few exceptions. Most notably, we observed a lack of association between anthropogenic fires and precipitation that might indicate that more of these fires may occur in years with higher soil moisture conditions than lightning-caused fires. This observation has also been reported before in the U.S. (Balch et al., 2017), where the authors concluded that anthropogenic ignitions can occur in a broader range of moisture environments than lightning-caused fires, thereby resulting in a wider wildfire “niche”. In addition, the shift of the peak of anthropogenic fire activity from the summer to the spring, accompanied by a longer fire season length (Albert-Green et al., 2013; Balch et al., 2017; Flannigan et al., 2013; Wang et al., 2015), might have caused anthropogenic and lightning fires associated with different climatic conditions within the year. This means that even if precipitation was higher overall during the year, the actual precipitation events might have been clustered to only the season where they could limit lightning-caused fires (summer), but not anthropogenic fires (spring).

We found periodicities that suggest a match with different teleconnections' oscillatory patterns. Large-scale climatic patterns (teleconnections) and their interactions influence weather and local climate, and consequently, fire activity in Canada (Fauria & Johnson, 2006; Mori, 2011). Wildfire cycles under higher human influence (LAP), as well as most fire-climate periodicities, were predominantly characterized by shorter periods (<8 years) compared to longer periods under low human influence (WBNP; >9 years).

The short periodicities of fire activity under high human influence suggest a higher susceptibility to Quasi-biennial and el Niño Southern Oscillations (QBO and ENSO, 2–2.5 and 2.5–8 years), whereas under lower human influence (WBNP), they seem to respond to ENSO and a quasi-decadal oscillation (Pacific Decadal Oscillation + sunspot cycle, 9–13 years) (Bridgman et al., 2006). We also found traces of larger oscillations in WBNP (<15 years, not shown) that are usually associated with the PDO and IPO (Pacific Decadal and Pacific Interdecadal Oscillations), but due to the short time series we used, the signals were weak and possibly spurious. The absence of long fire-climate periodicities explaining area burned by humans in LAP at 10–12 years, might be a result of coinciding peaks of short oscillations of different periodicity that may create longer, stronger oscillations. These kinds of interactions have been documented for longer-term climatic patterns, when negative phases of ENSO and PDO concur with positive AMO phase, increasing the occurrence of fires in Colorado (Schoennagel et al., 2007), or when positive ENSO and PDO phases coincide in the Rocky

Mountains (Schoennagel et al., 2005) in the U.S. In order to support these partial observations, future research with longer, seasonal time series are required.

The creation of Wood Buffalo National Park almost a century ago gave us the opportunity to compare this area of very low human impact with the adjacent area under a strong anthropogenic transformation in the same ecological region, avoiding the conflation of human influence with other factors. Furthermore, we used a temporal and spatial extent that allowed us to distinguish more directly the effect of human influence on fire activity in the short term (years to decades) (Gralewicz et al., 2012a; Tymstra et al., 2007; Y. Wang & Anderson, 2011), which generates useful information for land managers. Understanding the temporal patterns of fire activity helps fire management agencies assign and efficiently distribute material and human resources to fight and prevent fires. For example, in the province of Alberta, increasing attention is being given to the earliest part of the fire season (i.e., spring), when numerous human ignitions often coincide with the early onset of warm weather due to a lengthening of the fire season that has resulted in large and destructive wildfires (e.g., the Fort McMurray fire of 2016) (Pickell et al., 2017).

4.6 Conclusions

Over the 46-year period studied (1970–2015), we observed how wildfire activity patterns in the boreal forest have been shaped by the continuously increasing influence of humans, potentially creating a novel fire regime through the modification of the seasonality, size, and frequency of fires. In our area of study, under high human influence, fire activity (area burned and number of fires) peaks in the spring instead of the summer, burning rates are lower, on average, and fewer fires over 10 ha occur than in the more natural area. Analyses used mostly non-parametric statistical techniques that are suitable for the highly variable and stochastic nature of the data.

We showed how human influence affects fire activity by changing its trends and cyclical patterns, and how anthropogenic wildfire activity generates temporal patterns and associations with climate distinctive (albeit similar) from those associated with lightning wildfire activity. In general, although northern Alberta is subjected to drier and warmer climatic conditions, in areas of a high anthropogenic footprint, human influence appears to dampen and reverse the expected fire activity trends and affect the cyclical nature of fire occurrence. These rapid changes pose a new set of challenges for managers and researchers who try to understand and predict the impact of altered fire regimes on the diversity, structure, and future fire activity of a boreal forest. Our results further emphasize the importance of explicitly incorporating the multi-faceted human impact to improve our understanding of fire activity, how it is affecting the fire regime at different spatial and temporal scales, and to produce more accurate predictive models of fire activity.

4.7 Acknowledgements

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4.8 Author contributions

M.D.F. conceived the original idea and supervised this project. R.C.-R. designed and performed the data analysis; R.C.-R. and M.-A.P. interpreted the results and wrote the paper.

4.9 Conflicts of Interest

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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5 Conclusions

The present research emphasizes vegetation's active and dynamic role as a bottom-up control, modifying fire in the boreal forest. Each chapter of this dissertation addressed the importance of vegetation controls on flammability at different spatial and temporal scales, from single leaves to anthropogenic landscapes, where I highlight the active role of plants in fire activity.

At a fine spatial and temporal scale, we showed how *Pinus banksiana* L. (jack pine) needle traits, determined by physiology and phenology, affect their flammability in Chapter 1 Needle age was related to most of the changes observed in their flammability. At the end of the growing season, older needles that are at least one year old ignited, released energy, and got consumed faster than their younger counterparts. Higher flammability was linked to older needles' longer shapes, larger surface area to volume ratios, higher amounts of carbon and terpenes, and lower amounts of moisture content and nitrogen. However, regardless of age, needles released the largest amount of energy in the early months of the growing season when they contained greater concentrations of high-energy compounds (starch and lipids).

Surprisingly, moisture content was not the main factor controlling the flammability of jack pine needles. Although high moisture content was associated with low flammability, its influence was relatively minor. In other words, variance in form and chemical content explained more variance on ignitability, combustibility, sustainability and consumability than moisture content. On the other hand, moisture content may have indirectly affected flammability by modifying the needles' form and interacting with chemical components, which alter their properties.

Forest stand age, at broader spatial and temporal scales, also regulates forest flammability. Because younger forests are less likely to reburn, they create a negative feedback or resistance that reduces overall fire activity. In Chapter 3, this characteristic was incorporated in a Markov chain model, based on historical fire activity patterns in northern Quebec, providing a tool to better understand forest dynamics. The simulated scenarios not only confirmed the regulating effect of reburn resistance, but also that it holds the potential to moderate forest loss under climate change conditions. Model predictions showed that without reburn resistance forest loss would be ~2 times more likely. Additionally, resistance may reduce forest loss due to climate change by half. Although resistance to reburn may not completely counteract climate change effects, it would still moderate its effects in the forecasted 50-year period in Quebec. The result emphasizes the significance of vegetation as a bottom-up control of fire in near-pristine conditions. However, the increasing human influence affecting large portions of the boreal forest, has created divergent patterns of fire activity that differ from historical ones.

Human influence has modified fire activity in boreal forest in Alberta, creating a novel fire regime. Chapter 4 of this thesis explores the impact of human activities on fire activity in northern Alberta between 1970 and 2015. Two adjacent areas with contrasting human influence allowed us to study the extent of human impact on fire activity: an area with a minimal human influence, Wood Buffalo National Park (WBNP), and Lower Athabasca Plains (LAP), which is subject to strong firefighting effort, more human-caused ignitions, higher road connectivity, and more altered landscapes by harvesting, agriculture, livestock farming and oil exploitation.
The results of this chapter indicate that human activities are switching the seasonality, dampening annual trends of number of fires and area burned, altering the relationship between climate and fire, and reducing the cyclical patterns of fire activity. Under higher human influence

(LAP), number of fires and area burned by humans have increased during the spring, surpassing those caused by lightning during the same season. At lower human influence (WBP) there is an increasing trend in the number of fires and area burned concurrent with expected increases due to climate change. In contrast, in LAP, the number of fires decreased, and area burned remained unchanged. These trends may reflect the strong fire suppression, land-use change, and clustering of human-caused fires near populated areas in LAP. Preventive measures in LAP, more vigilant surveillance, and high road connectivity enhance suppression activities that protect valuable resources and human lives, allowing easier access to fire-fighting resources than in WBNP.

Human influence has also changed the climate-fire relationship. Correlations between fire-related variables and fire activity are different between areas of study and between causes of fire (human vs. lightning-caused fires). Moreover, cyclical fire activity patterns in LAP resemble short-cycle teleconnection oscillations, while those in WBNP are more akin to longer-cycle oscillations, which links human fire activity to higher frequency climatic patterns. The new conditions associated with the human footprint will require managers to adapt continuously to Alberta's novel patterns of fire activity.

The present dissertation dealt with the complex bidirectional relationship between vegetation and wildfires at different scales. By setting the most appropriate parameters and techniques for each temporal and spatial scale, I addressed various questions about vegetation's influence on fire. It was evident through this work that the nature of the vegetation-climate-fire relationship is non-linear and non-stationary, exposing the complexity of wildland fires research. Directing our attention to understand plants' inherent physiological traits and phenology as individuals and their distribution, structure, periodicities, and interactions as communities can shed light on their intricate relationships with wildfires.

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Appendix

Table A1 Monthly weather data for temperature and precipitation for the sampling period of the study. Maximum and minimum temperatures indicate extremes. Source: Edmonton Woodbend weather station (ID: 1872), Alberta, located at 1.65 km from the study site.

Month	Maximum temperature (C°)	Minimum temperature (C°)	Mean temperature (C°)	Precipitation (mm)
June	32.5	3	15	36
July	33.5	4	18.2	80.2
August	30	1	15.8	28
September	26	-2.5	9.7	76.3

Figure A1. Modified setup for the cone calorimeter flammability testing.

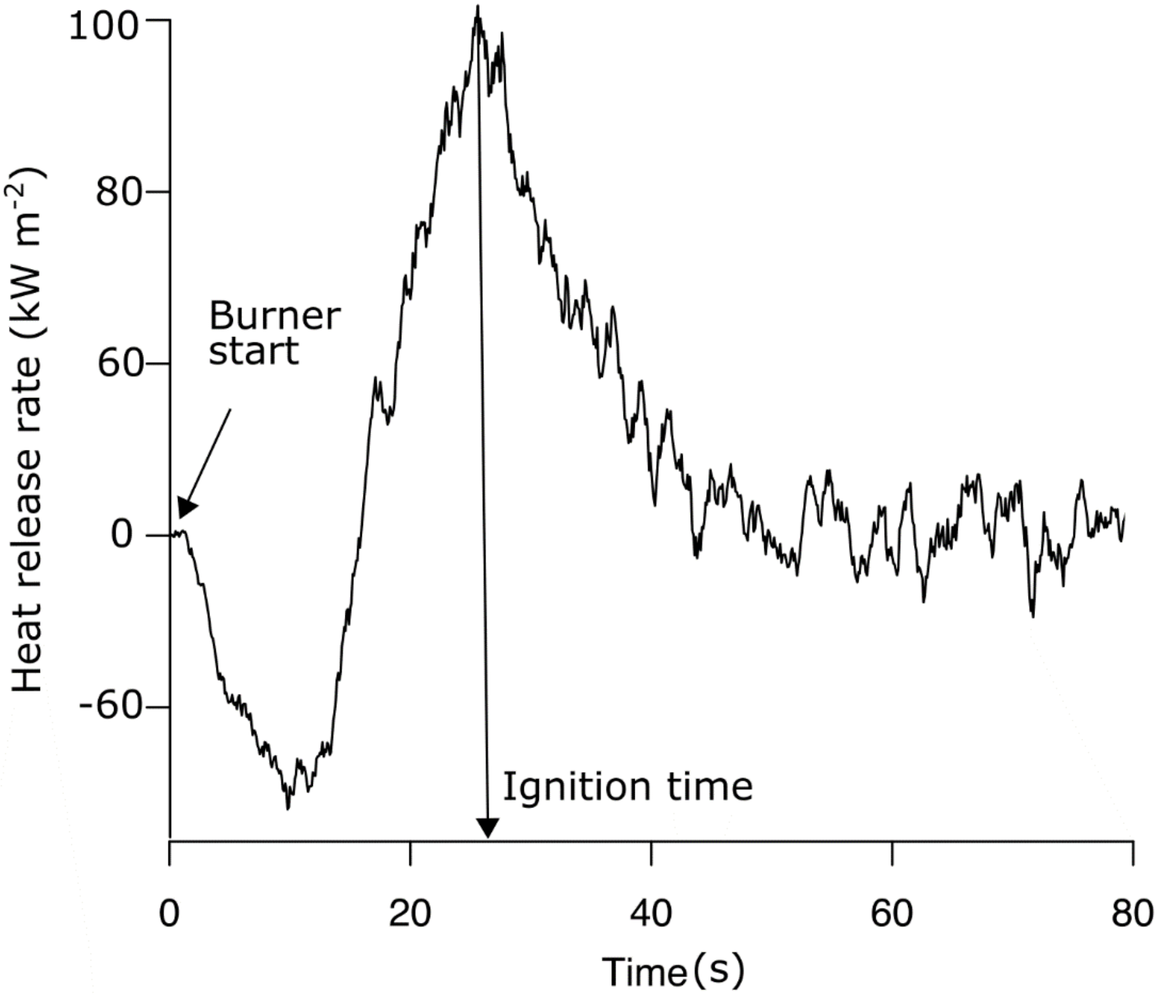

Figure A2. Determination for ignition time (IT) was assessed visually and confirmed with the heat differential heat release rate curve. IT matches the first, and usually the highest peak of HRR.

Table A2 Detailed methods for the extraction and calculation of the chemical composition of jack pine needles

Compound/ element		Extraction	Equipment
Nitrogen	N	Samples were oven-dried at 70ºC and finely ground. Then, they were subject to oxygen-rich combustion to produce carbon dioxide and nitrogen gas (CO_2, N_2) that can be quantified.	Costech 4010 calorimeter and EAS Clarity data collection software
Carbon	C		
Soluble sugars	SS	Samples were oven-dried and finely milled. Then, hot ethanol was used to separate the sugars from the rest of the tissues, and an anthrone/sulphuric acid reagent was added	Determined calorimetrically (Thermo Scientific Evolution 300 UV/Vis spectrometer) using the anthrone reagent
Starch	ST	After removing soluble sugars, the sample is boiled to gelatinize the starch, and then the starch is hydrolyzed into glucose using an amyloglucosidase enzyme.	Determination of glucose by calorimetry (Thermo Scientific Evolution 300 UV/Vis spectrometer)
Lipids	LI	Samples were frozen with liquid nitrogen and ground. An hexan solvent was added and the mix was later filtered to analyze. The total lipid content does not include terpenes.	Agilent Masshunter 7890/5975C gas chromatography spectrometer and NIST2014 spectral database
Terpenes	TE		

Table A3 Results for the repeated measures ANOVA for the effects of the month of collection and needle's age on jack pine needles' flammable characteristics ($n = 96$). Transformations (if any) are indicated in parenthesis under the variable name, and p-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate

Variable	**Factor**	***F* (3,2,6)**	***p***
	Flammability		
Ignition time (Squared root)	Month	36.24	**<0.001**
	Age	45.70	**<0.001**
	Month × Age	28.21	**<0.001**
Peak heat release rate (log)	Month	11.23	**<0.001**
	Age	16.19	**<0.001**
	Month × Age	2.80	**0.02**
Effective heat of combustion	Month	13.26	**<0.001**
	Age	0.21	0.80
	Month × Age	1.64	0.16
Average mass loss rate	Month	2.55	0.09
	Age	3.01	0.07
	Month × Age	1.98	0.09

Table A4 Results for the repeated measures ANOVA for the effects of month of collection and age of the needle on the foliar moisture content and form characteristics of jack pine needles (*n*=96). Transformations (if any) are indicated in parentheses under the variable name, and *p*-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate

Variable	**Factor**	***F* (3,2,6)**	***P***
	Moisture content		
Moisture content (log)	Month	12.13	**<0.001**
	Age	94.50	**<0.001**
	Month × Age	14	**<0.001**
	Morphology		
Curvature	Month	1.30	0.20
	Age	4	**<0.01**
	Month × Age	2.60	**<0.05**
Form coefficient (logit)	Month	9.54	**<0.001**
	Age	149.35	**<0.001**
	Month × Age	22.42	**<0.001**
Surface area to volume ratio	Month	57.43	**<0.001**
	Age	54.42	**<0.001**
	Month × Age	66	**<0.001**

Table A5 Results for the repeated measures ANOVA for the effects of month of collection and age of the needle on jack pine needles' chemical characteristics (*n*=96). Transformations are indicated in parenthesis under the variable name, and *p*-values <0.05 are shown in bold. The *p-value* was adjusted for the false discovery rate.

Variable	**Factor**	***F* (3,2,6)**	***P***
	Chemistry		
Carbon (logit)	Month	14.3	**<0.001**
	Age	10.34	**<0.001**
	Month × Age	3.32	**<0.05**
Nitrogen (logit)	Month	16	**<0.001**
	Age	61.21	**<0.001**
	Month × Age	34.75	**<0.001**
Starch (logit)	Month	71	**<0.001**
	Age	61.40	**<0.001**
	Month × Age	20.32	**<0.001**
Soluble sugars (logit)	Month	4.60	**<0.05**
	Age	1	0.38
	Month × Age	2.55	**<0.05**
Lipids (logit)	Month	26.22	**<0.001**
	Age	64.40	**<0.001**
	Month × Age	3.72	**<0.05**
Terpenes (logit)	Month	4.80	**<0.05**
	Age	32.43	**<0.001**
	Month × Age	5.86	**<0.001**

Table A6 Correlation coefficients of the NMDS variables with their ordination axes, and the result of the premutation test. Coefficients (*r*) indicate the correlation of each variable with the ordination axes.

Variable	**Acronym**	**Axis 1 (x axis)**	**Axis 2 (y axis)**	***r***	***p***
Ignition time	IGT	-0.98	0.19	0.76	0.01
Heat release rate	HRR	0.50	-0.86	0.46	0.01
Effective heat of combustion	EHC	-0.21	-0.97	0.63	0.01
Mass loss rate	MLR	0.52	0.85	0.37	0.01
Foliar moisture content	FMC	-0.92	-0.37	0.96	0.01
Form coefficient	FCO	-0.86	0.50	0.78	0.01
Curvature	CRV	0.92	0.37	0.32	0.03
Surface-area-to-volume ratio	SVR	0.98	0.19	0.68	0.01
carbon	C	0.99	-0.02	0.52	0.01
Starch	ST	0.16	-0.98	0.56	0.01
Soluble sugars	SS	0.79	0.61	0.16	0.32
Nitrogen	N	-0.94	0.33	0.69	0.01
Lipids	LI	0.06	-0.99	0.47	0.01
Terpenes	TE	0.99	0	0.46	0.01

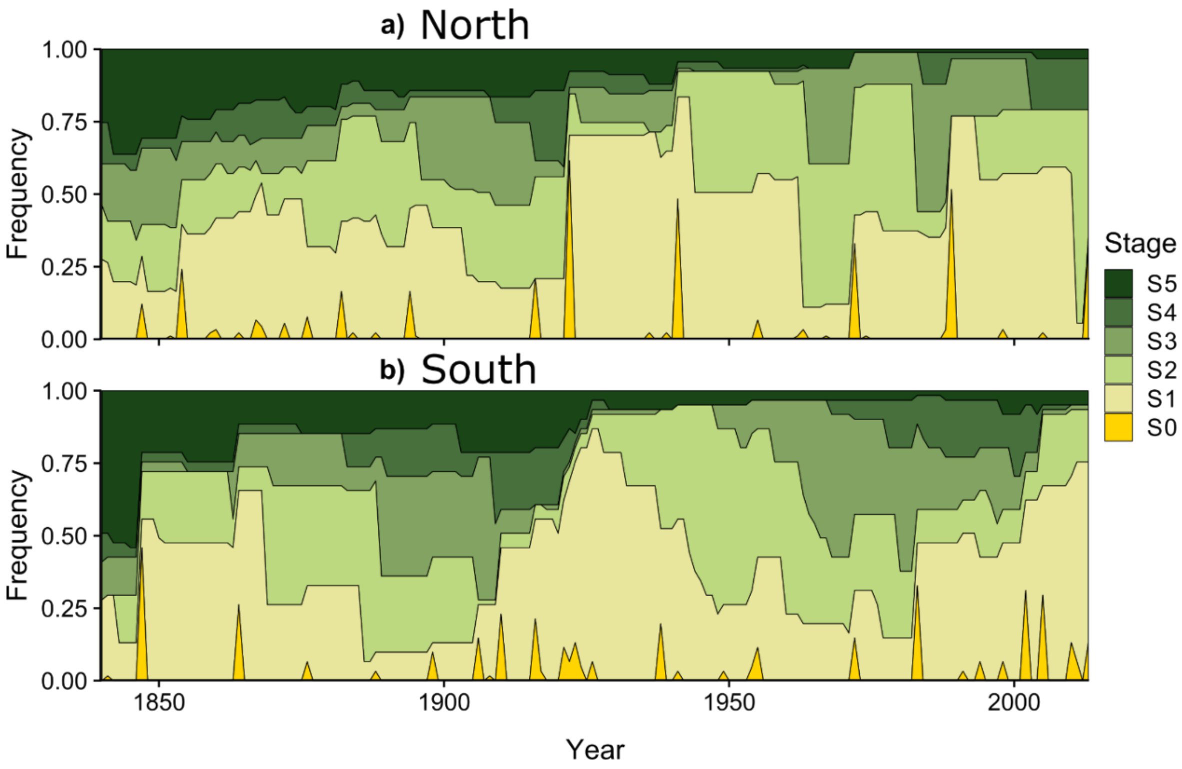

Figure A3. Historical stand age distribution from the north and south sections of the transect for the period of 1940 to 2013. S0 represents a fire record; the rest, age states S1: 1-20, S2: 21-40, S3: 41-60, S4:61-80, S5: >80 years.

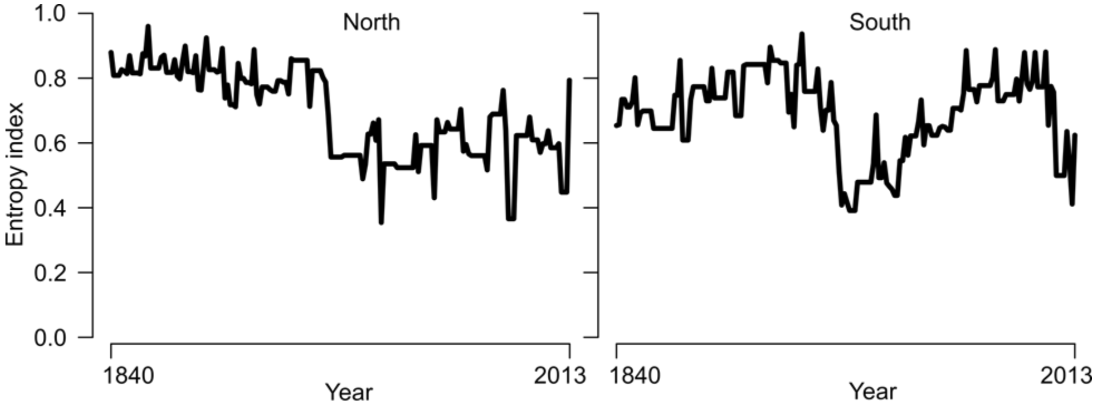

Figure A4. Shannon entropy index for the forest age distribution from 1840 to 2013. Values closer to one indicate high diversity, while closer to zero indicates low diversity of age states.

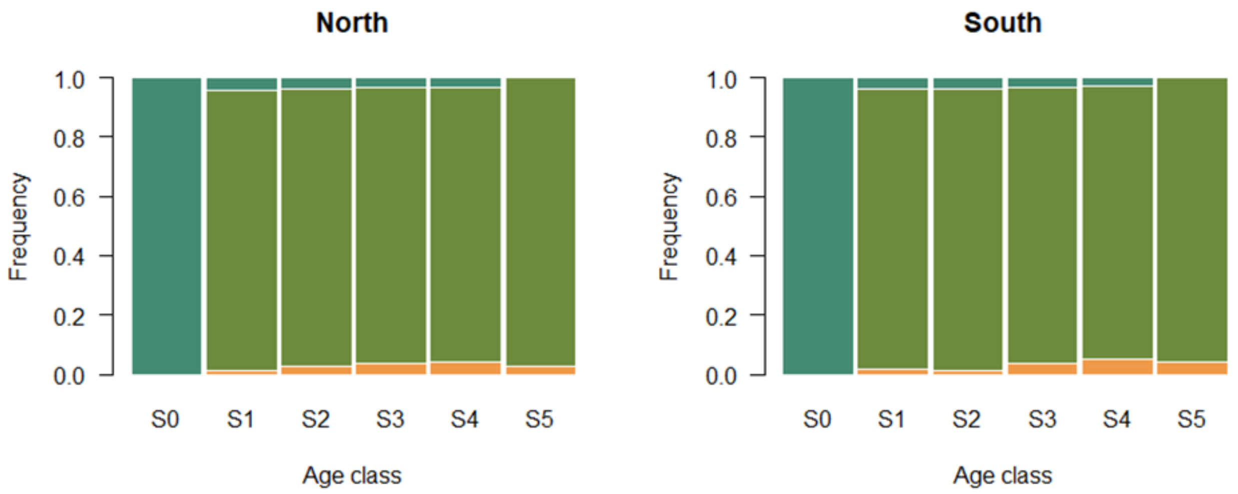

Figure A5. Historical frequencies (probabilities) for the processes of burning, stasis and growth by age state in yellow, green and blue, respectively.

Table A7 Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and log-likelihood values for the Markov Chain Model fitting of the stand age state sequences derived from the fire scar history of the cells in the north and south portions of the transect (N equals the number of plots). We used the function *fitMarkovChain* (package "clickstream" in R), specifying the quadratic/Lagrange approach (Scholz, 2016).

	North (N=15834)			South (N=10614)		
Order	AIC	BIC	log-likelihood	AIC	BIC	log-likelihood
1	7745.64	7799.33	-3865.82	5220.43	5271.32	-3865.82
2	7759.64	7867.02	-3865.82	5234.43	5336.21	-3865.82
3	7773.64	7934.71	-3865.82	5248.43	5401.10	-3865.82
4	7787.64	8002.40	-3865.82	5262.43	5465.99	-3865.82
5	7801.64	8070.09	-3865.82	5276.43	5530.88	-3865.82

Equation A1. Calculation of the α parameter of the Beta distribution from the mean (μ) and variance (σ) of the data.

$$\alpha = \left(\frac{1-\mu}{\sigma^2} - \frac{1}{\mu}\right)\mu^2$$

Equation A2. Calculation of the β parameter of the Beta distribution from the mean (μ) and variance (σ) of the data.

$$\beta = \alpha\left(\frac{1}{\mu} - 1\right)$$

Table A8 Predicted proportional forest loss (NF) by the Homogeneous and In-Homogeneous MCM (x̄ ± SD) scenarios after 50 years. Scenarios simulate reburn resistance under historical climatic conditions (**R**) and with climatic change (**RC**) and lack of burning resistance without (**E**) and with climatic change (**EC**).

Scenario	**North**	**South**
HR	0.150	0.253
HRC	0.251	0.375
HE	0.324	0.453
HEC	0.494	0.623
IR	0.209 ± 0.152	0.215 ± 0.111
IRC	0.341 ± 0.136	0.312 ± 0.086
IE	0.238 ± 0.142	0.373 ± 0.187
IEC	0.349 ± 0.124	0.528 ± 0.139

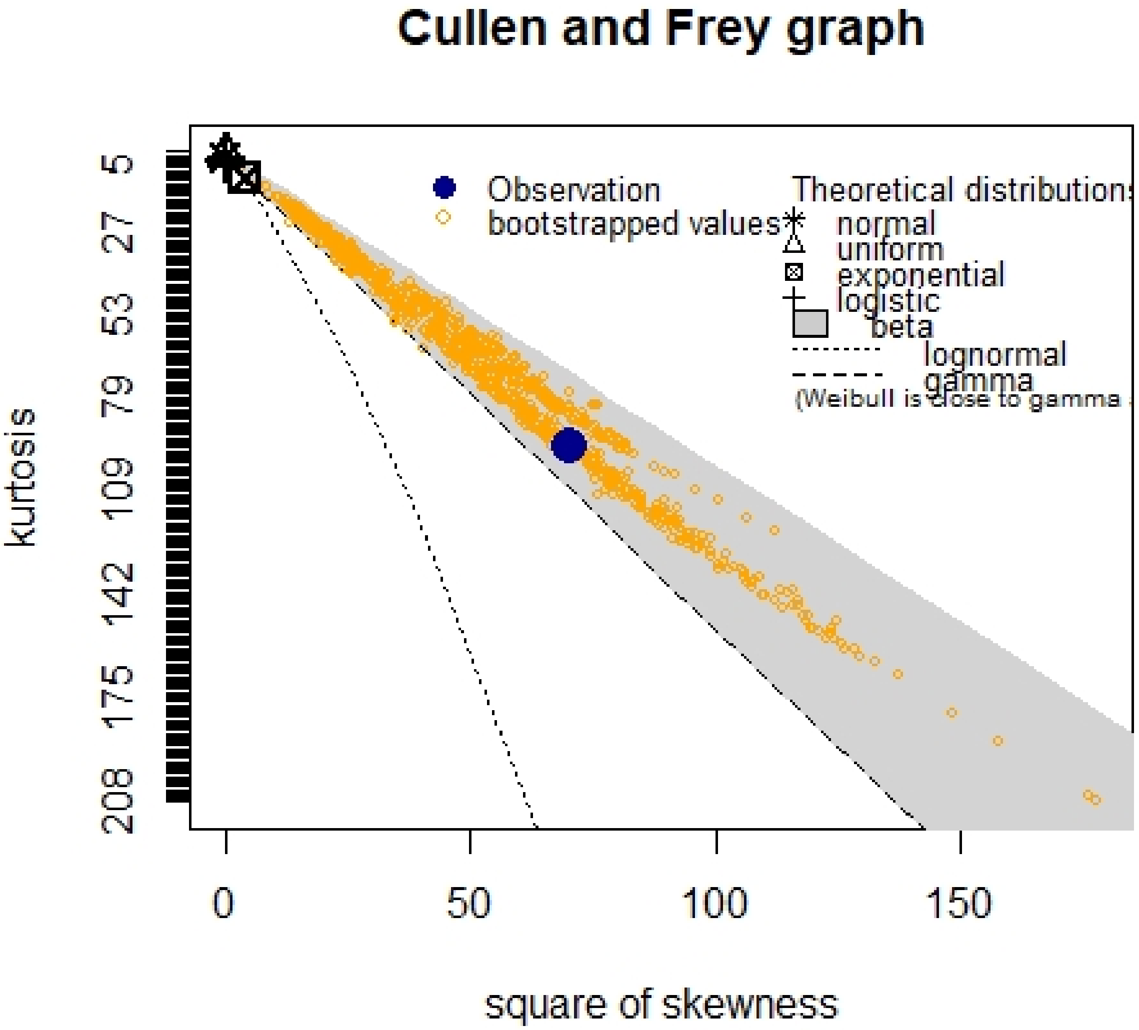

Figure A6. Example of the Cullen and Frey graph to determine the optimal probability distribution for the observed values based on their kurtosis and skewness. The bootstrapped values come from random samples of the data. Empirical distributions are listed in the top-right corner. In this example, the data fits a beta distribution. This graph is obtained with the *descdist* function from the fitdistr package in R. The output of this function is accompanied by the values of the mean, standard deviation, skewness, and kurtosis. Additionally, to confirm the result, accompanying functions can be used to compare empirical and theorical histogram of densities, q-q plots, cumulative density functions and p-p plots.

Table A9 Fire statistics in Wood Buffalo National Park (WBNP) and Lower Athabasca Plains (LAP) from 1970 to 2015. Letters L and H indicate lightning and human-caused fires respectively.

Region	**WBNP**			**LAP**		
Cause	**L+H**	**L**	**H**	**L+H**	**L**	**H**
Number of fires	541 (100%)	518 (95.75%)	23 (4.25%)	1146 (100%)	614 (53.60%)	532 (46.40%)
Proportional number of fires (fires per 100kha)	12.70	12.14	0.54	14.44	7.74	6.70
Area Burned (ha x10^4)	355.08 (100%)	339.87 (95.70%)	15.21 (4.30%)	422.39* (100%)	199.56 (47.25%)	222.83 (52.75%)
Mean fire size (ha)	7,332.51	6,978.90	353.60	7,384.40	4,411.42	2,972.98

Note: Information shown here is for fires ≥10 ha. Based on the National Fire Database.

*The Horse River fire (Fort McMurray) in 2016, increased this value by 13% in just one year.

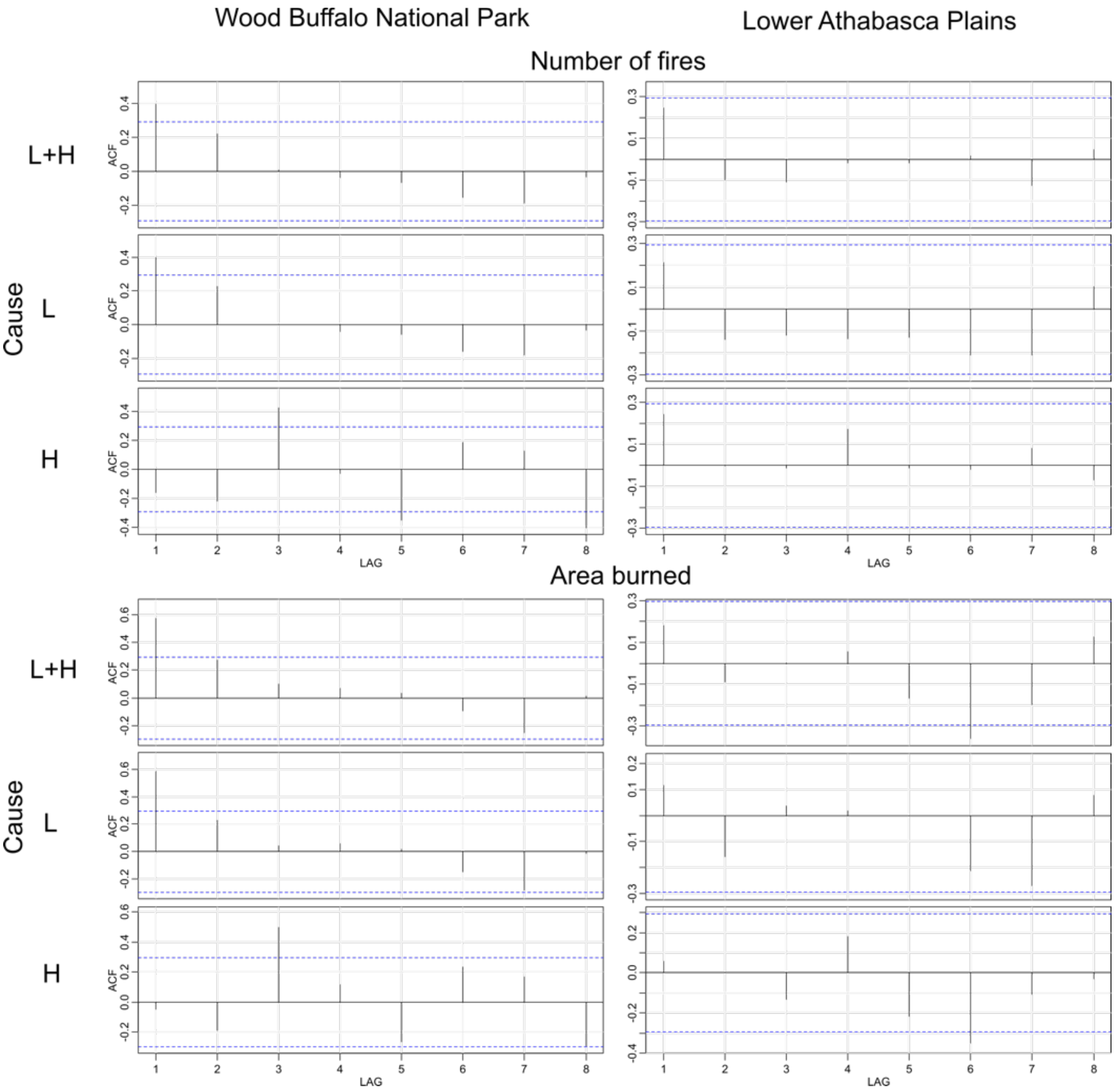

Figure A7. Autocorrelation plots for the number of fires and area burned time series in Wood Buffalo National Park and Lower Athabasca Plains.

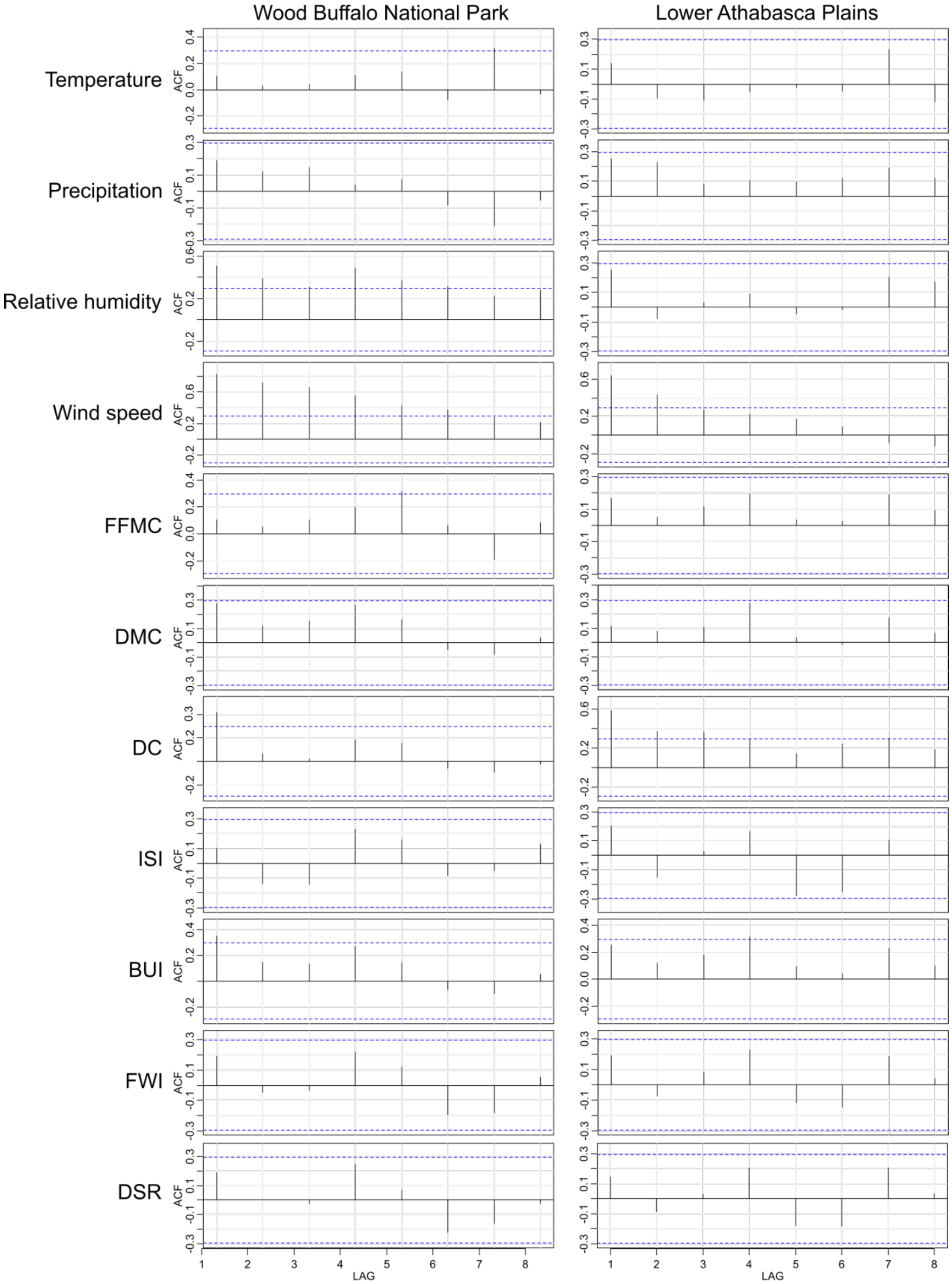

Figure A8. Autocorrelation plots for the weather and fire weather time series in Wood Buffalo National Park and Lower Athabasca Plains.

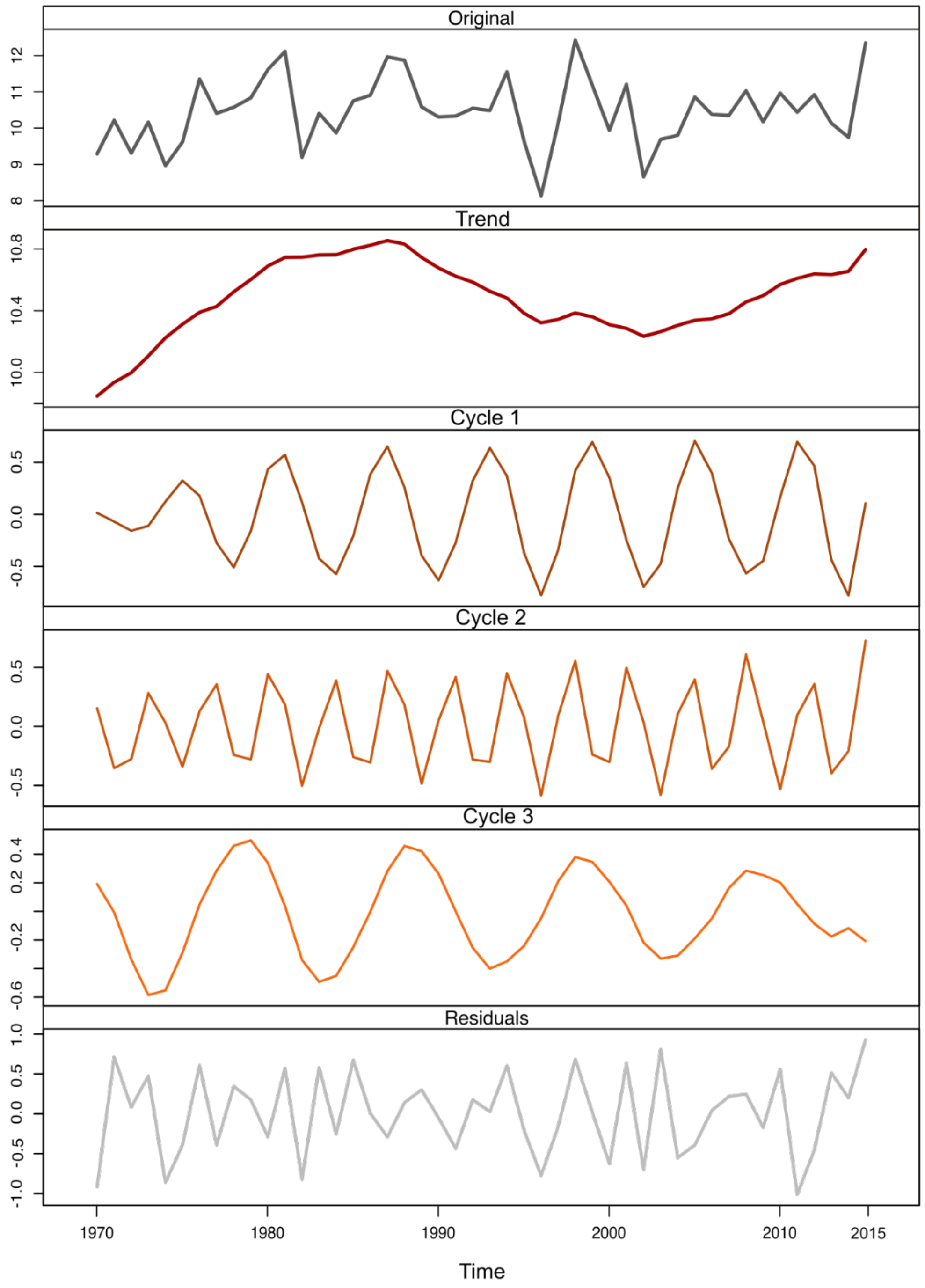

Figure A9. An example of decomposition by SSA for temperature time series in LAP, showing its additive components: trend, cycles (oscillations) and residuals (white noise, random). In this case, the trend is upward non-monotonic and each cycle has a distinctive periodicity of 5.8, 3.7 and 9.5 years respectively.

Scripts for chapter 3:

https://drive.google.com/file/d/1OPPoiaWUdpfgZId_Rh6U5Pa0D_Bp7TfO/view?usp=sharing

https://drive.google.com/file/d/14rX5Hlez84pps7pEWg0jkD6QEltaJ8cw/view?usp=sharing

The scripts can also be provided upon reasonable request by email: rcampos@ualberta.ca