A HYBRID MODELING APPROACH TO SIMULATING PAST-CENTURY UNDERSTORY SOLAR IRRADIATION IN ALBERTA, CANADA

by

Adam Michael Erickson

B.A., University of Puget Sound, 2004

M.C.R.P., University of Oregon, 2011

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

August 2017

© Adam Michael Erickson, 2017

Abstract

In western Canada, the effects of warming and increasing human activity may alter the structure, composition, and function of forests, producing quantitatively and qualitatively different understory light conditions. While difficult to measure directly, process-based models may facilitate inference of historical forest states. Yet, existing models are limited in the dynamics they represent. A promising new approach in hybrid modeling, first demonstrated here, is the fusion of machine learning and process-based models to simulate pattern-based processes. The objective of this dissertation was to simulate the effects of past-century climate and fire conditions on understory global solar irradiation trajectories across a 25.2 million ha landscape in Alberta, Canada. The LANDIS-II forest landscape model was applied to simulate past-century changes to competition, fire, and regeneration. Simulated tree species and age maps were classified into landcover types. A regression model of canopy light transmission as a function of landcover and site index showed good fit with field observations ($R^2 = 0.94$) and was applied to a classification of LANDIS-II outputs. Canopy light transmission was multiplied by mean annual bare-earth global solar irradiation to produce understory light maps. Empirical and semimechanistic fire models were also applied. A variant of stochastic gradient descent was applied for parameter optimization, improving fire model performance ($\overline{R^2} = 0.96$; $\overline{\Delta R^2} = +0.14$). Simulations showed a mild decline in forested area across the 1923-2012 period, attributable to a velocity of warming three times faster than migration. Migration was primarily controlled by fire and secondarily by regeneration. Simulated understory light levels declined across the period due to reduced mortality rates, preceding a likely long-term increase in light attributable to reduced regeneration rates. The key innovations of this work are as follows: characterization of humandominated fire regimes in western Alberta (Chapter 4); advancement of the TACA-GEM regeneration model (Chapter 5); development of an algorithm for fire model parameter optimization (Chapter 6); development of new LiDAR models of canopy light transmission (Chapter 7); demonstration of a new hybrid modeling approach to simulating pattern-based processes, applied to understory light (Chapter 8); demonstration of long-term climatic regulation of understory solar irradiation through forest regeneration (Chapter 8).

Lay Summary

This work seeks to understand the effects of warming and increased human activity on forests in western Alberta over the past century. The research relies on an advanced class of models known as hybrid models, which combine different model architectures together in a single model. Hybrid models are used for two reasons: (1) to enable large-scale simulations; (2) to model pattern-based processes poorly represented by physical models. Historical data on climate, fire, species traits, and forest cover were used for parameterization. An analysis of historical fires showed that humans now cause most fires and have shifted the fire regime toward more frequent and smaller fires. Model results suggest that the rate of forest recovery may be outpaced by disturbance. Model results also suggest that reduced mortality may decrease understory light in the short-term while inhibiting species from tracking warming. This has the potential to produce broad forest change over time.

Preface

This dissertation contains elements of six scientific papers of which I am the lead author, presented in five chapters, as Chapter 3 contains content from two papers. The initial project was proposed by Dr. Nicholas Coops, in collaboration with Gordon Stenhouse of Foothills Research Institute. In Chapters 4 and 5, Dr. Craig Nitschke of University of Melbourne designed the Tree and Climate Assessment Germination and Establishment Model (TACA-GEM) and provided tree species parameters. Dr. Steven Cumming assisted in interpreting TACA-GEM model results. Dr. Robert Scheller of Portland State University led development of the LANDIS-II model. Drs. Andreas Hamann and Laura Gray of University of Alberta provided modeled tree species distributions. Drs. Sally Aitken, Robert Guy, and Scott Nielsen provided valuable manuscript edits and feedback along the way. Foothills Research Institute provided airborne LiDAR data on behalf of Hinton Wood Products. I located parameterization data, conducted the simulations, built statistical models, performed analyses, and led authorship of the manuscripts. In Chapter 3, I detail novel fire regime changes under Anthropocene conditions in Alberta in comparison with national trends. In Chapter 4, I develop new soil and daily weather parameterization methods for TACA-GEM applicable across Canada. In Chapter 5, I develop a new method for efficient parameter optimization with forest fire models, solving a longstanding modeling challenge. I also develop LANDIS-II parameterization methods for Alberta, Canada. The simulation results shed light on a recently observed, but poorly understood, decline in forested area for some regions of the western U.S. and Canada. In Chapter 6, I develop two new airborne LiDAR metrics of canopy light transmission. This work is the first, to my knowledge, to quantify the effects of common fisheye lens geometry models on the estimation of canopy light transmission using

V

LiDAR data. I also develop a 2-D vertically layered variant of the spike-free canopy height model algorithm of Khosravipour, Skidmore, and Isenburg (2016). In Chapter 7, I develop a method of combining empirical regression models of canopy light transmission with LANDIS-II simulation outputs. This work is also the first, to my knowledge, to combine machine learning with a dynamic vegetation model.

Versions of Chapters 3 and 5 are in review. Versions of Chapters 6 and 7, as well as an expanded version of Chapter 3, are in preparation for submission. A version of Chapter 4 is published in the following, re-printed here with the consent of the publisher:

• Erickson, A., Nitschke, C., Coops, N., Cumming, S., Stenhouse, G. (2015) Past-century decline in forest regeneration potential across a latitudinal and elevational gradient in Canada. *Ecological Modelling*. 313, 94-102.

Table of Contents

Abstract	ii
Lay Summary	iv
Preface	V
Table of Contents	vii
List of Tables	xii
List of Figures	xiii
List of Symbols	xvi
List of Abbreviations	xix
Acknowledgements	xxiii
Dedication	xxiv
Chapter 1: Introduction	1
1.1 Global Change and Forest Ecosystems	1
1.2 Global Change in Forests of Canada	2
1.3 Global Change in Boreal and Montane Forests of Alberta	4
1.4 Understory Plants and Canopy Light Transmission	7
1.5 Dynamically Simulating Understory Solar Irradiation	
1.5.1 Hybrid Models of Forest Ecosystems	
1.5.2 Airborne Laser Scanning Models of Canopy Light Transmission	14
1.6 Research Overview	16
Chapter 2: Model Data and Descriptions	20
2.1 Introduction	20 vii

2.2	Fire	e History Data	20
2.3	Tre	e Regeneration Model	21
2.3.	.1	Model Description	22
2.3.	.2	Data Requirements	25
2.3	.3	Daily Weather	25
2.3.	.4	Soil Textural Classes	26
2.3.	.5	Species Biophysical Attributes	28
2.4	LA	NDIS-II Forest Landscape Model	34
2.4.	.1	Model Description	34
2.4.	.2	Data Requirements	38
2.4	.3	Model Core	41
2.4	.4	Base Fire	44
2.4.	.5	Dynamic Fuels and Fire System	44
2.5	Air	borne Laser Scanning Data	46
Chapter	r 3: P	ast-century Fire Regimes of Western Alberta, Canada	48
3.1	Intr	oduction	48
3.2	Me	thods	52
3.3	Res	ults	55
3.4	Dis	cussion	70
3.5	Lin	nitations	81
Chapter	r 4: T	ree Species Regeneration Modeling	83
4.1	Intr	oduction	83
4.2	Met	thods	85
			viii

4.3	Results	
4.4	Discussion	
4.5	Limitations	
Chapter	5: Forest Landscape Modeling	
5.1	Introduction	
5.2	Methods	
5.2.	1 Historical Fire Regimes	
5.2.	2 Model Scenarios	
5.3	Results	
5.4	Discussion	
5.5	Limitations	
Chapter	6: Airborne Laser Scanning Models of Canopy Light Transmission	125
6.1	Introduction	
6.2	Methods	
6.2.	1 Pre-processing	
6.2.	2 Spike-free Canopy Height Model Algorithm	
6.2.	3 Hemispherical Voronoi Gap Fraction	
6.2.	4 Point-density Normalized Gap Fraction	
6.2.	5 Comparison with Other ALS LiDAR Metrics	
6.3	Results	
6.3.	1 ALS Estimates of ACC and P_o	
6.3.	2 Point-density Normalized Canopy Gap Fraction	
6.3.	3 Spike-free Canopy Height Model	
		ix

6.3.	4 Tree and Crown Metrics	158
6.4	Discussion	
6.5	Limitations	
Chapter	7: Simulation of Understory Global Solar Irradiation	166
7.1	Introduction	
7.2	Methods	
7.2.	1 Data	
7.2.	2 Linear and Machine Learning Regression Models of <i>P</i> _o	
7.2.	3 Landcover Classification of LANDIS-II Species-age Cohorts	
7.2.	4 Bare-earth Global Solar Irradiation Model	
7.3	Results	
7.3.	1 Simulation of P_o and I_u with Model Fusion	177
7.4	Discussion	
7.5	Limitations	
Chapter	8: Conclusion	
8.1	Limitations	
8.2	Research Contributions	
8.3	Areas of Future Research	199
Referen	ces	207
Appendi	ix A: Statistical Analysis of Historical Fire Regimes	272
Appendi	ix B: ALS Models of ACC and VCC	277
Appendi	ix C: Random Forest Algorithm	
Appendi	ix D: ABMI Landcover 2010 Classification Scheme and Algorithm	
		Х

Appendix E: Bare-earth Global Solar Irradiation Algorithm	286
Appendix F: Validation of TACA-GEM with Permanent Sample Plot Data	290

List of Tables

Table 2.1 Soil texture and latitudinal parameters used with TACA-GEM version 4.4	
Table 2.2 Source of tree species parameters used in the TACA model	
Table 2.3 TACA-EM parameters used in the LANDIS-II simulations	
Table 2.4 Tree species biophysical parameters used in TACA-GEM	
Table 2.5 Sources of life history attribute species parameters used in LANDIS-II	
Table 2.6 Tree species life history attributes used in LANDIS-II simulations	
Table 3.1 Fire regime statistics by period for the western Alberta study area	57
Table 3.2 Fire regime change by season	61
Table 3.3 Fire seasonality	61
Table 5.1 Simulation scenario codes based on model configuration and period	106
Table 5.2 Simulated and observed fire time-series statistics	110
Table 6.1 Understory light metrics calculated in this study	
Table 6.2 Additional VCC metrics	
Table 6.3 Comparison of top three univariate ALS models (<i>VCC_{fci}</i> ; <i>VCC_{ir}</i> ; <i>VCC_{ir}</i>) with	<i>P_{pdn}</i> 155
Table 6.4 Comparison of height-to-crown-area model results	159
Table 7.1 Multiple linear regression model	174
Table D.1 ABMI Landcover 2010 classification scheme	
Table F.1 Linear models of total understory regeneration change by height class	

List of Figures

Figure 1.1 Study area in western Alberta, Canada	. 4
Figure 2.1 TACA-GEM model diagram (Erickson <i>et al.</i> , 2015)	24
Figure 2.2 Alberta study area overlaid on NASA SRTM version 2	27
Figure 3.1 Mean annual trends for fires in the Alberta study area, 1919 to 2012	56
Figure 3.2 Fire adjacency to roads by cause overlaid on SRTM 90 m elevation data	59
Figure 3.3 Decadal area burned by fire source for the Alberta study area	60
Figure 3.4 2-D kernel density estimation for fire frequency by ordinal date and year	62
Figure 3.5 Mean annual trends for fires Canada-wide, 1919 to 2012	63
Figure 3.6 Fire regime change-point segmentation using the binary segmentation algorithm	65
Figure 3.7 Fire regime patterns nationwide and Alberta study area changes in seasonality	66
Figure 3.8 Monthly and daily patterns of fire frequency, mean fire size, and total area burned.	69
Figure 3.9 Fire statistics by reported detection source Canada-wide	75
Figure 4.1 TACA-GEM parameterization scheme for Canada	86
Figure 4.2 Modeled mean change in species regeneration across regions for the full period	88
Figure 4.3 Mean change in species regeneration probability, 1923-1952 to 1983-2012 period	89
Figure 4.4 Regeneration probability boxplots	93
Figure 5.1 Model parameterization, fusion, and optimization of TACA-EM and LANDIS-II 10	03
Figure 5.2 Historical fire statistics by region and time period	08
Figure 5.3 Simulated annual fire regimes by period and scenario	11
Figure 5.4 Simulated annual total forested area (sum of 1 ha pixels) by year and scenario 1	13
Figure 5.5 Simulated annual individual and ensemble model results for scenarios and species 1	14
Х	.111

Figure 5.6 Simulated annual incremental change in species abundance by scenario 117
Figure 5.7 Mean annual simulated forest change 118
Figure 6.1 Univariate linear model angular canopy closure (ACC) model R^2 by metric
Figure 6.2 Change to univariate linear ACC model R^2 by metric due to filtering disturbances. 150
Figure 6.3 Example LiDAR plot process colored by point height 152
Figure 6.4 Example LiDAR plot demonstrating each of the hemispherical lens geometries 153
Figure 6.5 Metrics based on Monsi & Saeki (1953) and the Beer-Lambert Law 156
Figure 6.6 ALS canopy height models for an example site, 1 m resolution
Figure 6.7 Empirical height-to-crown-area linear models
Figure 6.8 Individual tree crown detection for an example ALS plot
Figure 7.1 Predictor variable maps for the study area
Figure 7.2 Random Forest variable importance used for initial feature selection 175
Figure 7.3 Random Forest model out-of-bag MSE by the number of trees parameter 176
Figure 7.4 Modeling of mean landscape full-spectrum understory solar irradiation (Iu) 178
Figure 7.5 Mean understory solar irradiation (Iu) across all simulation years by scenario 180
Figure 7.6 Change in understory solar irradiation (Iu) by simulation year and scenario
Figure A.1 Model fit for log-transformed fire sizes Canada-wide
Figure A.2 Anderson-Darling Weibull parameter estimation for fire sizes Canada-wide 274
Figure A.3 Mixed Gaussian model probability density of log-transformed fire size, Alberta 275
Figure A.4 Fire size distribution
Figure B.1 Pearson's correlation coefficient (r) for convex spherical densioneter measurements
and hemispherical Voronoi gap fraction (<i>P</i> _{hv})
Figure B.2 Pearson's correlation coefficient (r) for ground measurements and ALS metrics 279
xiv

Figure B.4 <i>VCC_{fci}</i> model fit for all 950 ground ACC measurement plots	. 279
Figure B.5 Models of P_{pdn} and ground ACC measurements	. 280
Figure B.6 Individual tree segmentation using three-dimensional α-shapes	. 281
Figure F.1 Changes in regeneration and observation frequency over time in SDS plot data	. 292
Figure F.2 Box plots of mean tree age and height for all age classes	. 293
Figure F.3 Regeneration changes in the PSP data by year	. 295
Figure F.4 Plots for understory and overstory angular canopy closure (ACC) class, mean site	tree
age, and mean tree height by year for PSP data	. 297
Figure F.5 Correlations between height classes, total regeneration, and year (r)	. 299
Figure F.6 Changes to regeneration by height class in the PSP data	. 300
Figure F.7 Frequency of height class 1 regeneration by tree height and age	. 301

List of Symbols

$A_{Sector(i,j)}$	Area of hemisphere sector <i>i</i> , <i>j</i>
$A_{Hemisphere}$	Area of hemisphere
A^2	Anderson-Darling statistic
ACC_{hv}	Hemispherical Voronoi angular canopy closure
ACC_{pdn}	Point-density normalized angular canopy closure
$C_{returns(i,j)}$	Point set within polar and azimuthal sector <i>i</i> , <i>j</i>
<i>C-7</i>	FBP System Ponderosa pine and Douglas fir fuel class
CHM _{fpf}	Fast-pit-free canopy height model
CL	Clay-Loam soil textural class
C_x, C_y	Principal distances along the <i>x</i> , <i>y</i> plane
D	Hartigan's dip test
$D_{FirstReturns}$	Point density of first returns on the <i>x</i> , <i>y</i> plane
DD_{canopy}	Distance and direction to nearest canopy pixel
DD _{crown}	Distance and direction to nearest detected crown pixel
VCC _{aci}	Above-height cover index
VCC_{bl}	Beer's Law-modified intensity-return ratio
VCC _{cv}	Cartesian Voronoi vertical canopy cover
VCC _{fci}	First-echo cover index
VCC _{fr}	Canopy-to-total-first-return ratio
VCC _{ir}	Intensity-return ratio

VCC_p	Canopy-to-total-pixel ratio
VCC _r	Canopy-to-total-return ratio
<i>VCC</i> _{sci}	Solberg's cover index
F	F-test statistic
G	Leaf angle distribution; Basal area
I _u	Understory solar irradiation
ITC_{mw}	Variable-radius moving window individual tree crown detection
<i>ITC_{wat}</i>	Watershed segmentation individual tree crown detection
K-L	Kullback-Leibler divergence
K-S	Kolmogorov-Smirnov statistic
L	Leaf area index
L_e	Effective leaf area index
<i>M-1/M-2</i>	FBP System Boreal Mixedwood fuels classes
$n_{FirstReturns(i,j)}$	Number of first returns in hemisphere sector <i>i</i> , <i>j</i>
<i>p50</i>	Leaf water potential at 50% loss of hydraulic conductivity
arphi	Azimuth angle
P_o	Canopy gap fraction
P_{hv}	Hemispherical Voronoi gap fraction
P_{pdn}	Point-density normalized gap fraction
r	Radial distance; Pearson's correlation coefficient
R	Radius of a sphere or hemisphere
$r * \theta$	Radial projection function

R^2	Coefficient of determination
ρ	Spearman's rank correlation coefficient
SiCL	Silt-Clay-Loam soil textural class
t	<i>t</i> -test statistic
Т	Canopy light transmission
θ	Zenith or polar angle
W	Wilks-Shapiro test statistic
W^t	Weight matrix
х'Н, у'Н	Principal point coordinates for point x, y
x'i, x'j	Image sensor coordinates for point <i>i</i> , <i>j</i>
$X^{\!\scriptscriptstyle W}$	Three-dimensional point coordinates
α_i	Barycentric coordinate <i>i</i>
Δx ', Δy '	Camera distortion model
heta _{returns i}	Zenith angle point subset
ϕ returns j	Azimuth angle point subset
$\overline{\omega}$	Cramér-Von Mises statistic
$arOmega_{app}$	Apparent clumping index

List of Abbreviations

ACC	Angular canopy closure
AGL	Above ground level
AIC	Akaike information criterion
ALS	Airborne LASER scanning
ALTM	Airborne LASER terrain mapper
ANOVA	Analysis of variance
ASPRS	American Society of Photogrammetry and Remote Sensing
ASWC	Available soil water capacity
BEHAVE	Fire behavior prediction and fuel modeling system
BIC	Bayesian information criterion
BRDF	Bidirectional reflectance distribution function
CESM1	Community earth system model, version one
СНМ	Canopy height model
ClimateNA	Climate North America
CNN	Convolutional neural network
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
COTS	Consumer-off-the-shelf
ED	Ecosystem demography model
EM	Expectation-maximization algorithm
EMD	Earth mover's distance (Wasserstein metric)

ENVI-IDL	Environment for visualizing images – interactive data language
Envisat-MERIS	Environment satellite – medium resolution imaging spectrometer
fAPAR	Fraction of absorbed photosynthetically active radiation
FARSITE	Fire area simulator
FBP System	Fire behavior prediction system
FIRETEC	Transport model for prediction of wildfire behavior
FMC	Foliar moisture content
FORÊT	Forests of eastern Tennessee model
FPGA	Field-programmable gated array
FRP	Fire rotation period
FWI	Fire weather index
GAN	Generative adversarial network
GCI	Grassland curing index
GDD	Growing degree days
GHCN-D	Global historical climatology network – daily
GIS	Geographic information system
GPGPU	General purpose graphics processing unit
GPS-INS	Global positioning system – inertial navigation system
HESFIRE	Human-earth system fire model
HIGRAD	High resolution model for strong gradient applications
ITC	Individual tree crown
JABOWA	Janak, Botkin, and Wallace model

LAI	Leaf area index
LANDIS-II	Landscape disturbance and succession model version two
LANDSIM	Landscape simulator
LAS	LASER file format
LASER	Light amplification by stimulated emission of radiation
LAStools	LAS file processing tools by Martin Isenburg
LFDB	Large fire database
LiDAR	Light detection and ranging
LMG	Lindemann, Merenda and Gold statistic
LSTM	Long short-term memory
MCMC	Markov-chain Monte Carlo simulation
MFRI	Mean fire return interval
MODIS	Moderate resolution imaging spectroradiometer
MODIS HS	MODIS hotspot product
NASA	National Aeronautical and Space Agency
NDVI	Normalized Difference Vegetation Index
NFDB	National fire database
NIR _V	Near-infrared reflectance of vegetation
NOAA	National Oceanic and Atmospheric Administration
NSR	Natural subregions of Alberta
PAR	Photosynthetically active radiation
PMVD	Proportion marginal variance decomposition

PnET	Photosynthetic evapotranspiration model
PPFD	Photosynthetic photon flux density
R	The R programming language
RADAR	Radio detection and ranging
RMSE	Root-mean-square error
RNN	Recurrent neural network
rOpenSci	R Open Science Foundation
SAR	Synthetic aperture RADAR
SIF	Solar-induced fluorescence
NSDB-SLC	National soil database – Soil landscapes of Canada
SORTIE-PPA	SORTIE perfect plasticity approximation
SRTM	Shuttle RADAR topography mission
TACA-EM	Tree and climate assessment – Establishment model
TACA-GEM	Tree and climate assessment – Germination and establishment model
TIN	Triangulated irregular network
TLP	Turgor loss point
TLS	Terrestrial LASER scanning
USGS	United States Geological Survey
VCC	Vertical canopy cover
WRF-Fire	Weather research and forecasting – fire model
ZELIG	ZELIG stand simulator model
ZELIG++	ZELIG stand simulator model, C++ version

Acknowledgements

This research was generously funded through Foothills Research Institute's Grizzly Bear Program and an NSERC grant to Dr. Nicholas Coops. Foothills Research Institute provided the collection performed by Aerial Imaging.

I would like to thank Dr. Nicholas Coops for his generous support over the past three years. I also thank my committee members, Drs. Sally Aitken, Robert Guy, and Scott Nielsen, for their informative questions, support, and counsel. I am very grateful to Drs. Craig Nitschke of University of Melbourne and Patrick Waeber of ETH Zürich for providing guidance on TACA-GEM. I am also grateful to Drs. Robert Scheller of North Carolina State University and Matthew Duveneck of Harvard University for their guidance on LANDIS-II.

I thank Dr. Brian Sturtevant and Brian Miranda of the USDA Forest Service, Cordy Tymstra, Ralph Wright, and Bob Mazurik at Government of Alberta, and, Drs. Brad Hawkes and Marc-Andre Parisien at Natural Resources Canada, for providing guidance on the application of forest fire models. I also thank Dr. Steven Cumming of Laval University for his valuable insights on model design. Finally, I thank Drs. George Church of Harvard University, Timothy Lu of MIT, Steven Strauss of Oregon State University, and Harris Wang of Princeton for their conversations on extending process-based vegetation models into the era of next-generation sequencing, precise gene editing, and synthetic ecology. Most of all, I thank my family for giving me the opportunity to pursue a dream.

Dedication

This work is dedicated to the memory of my friend, collaborator, and a source of inspiration, Dr. Thomas Hilker. This work is also dedicated to all who have endured hardship to advance our scientific understanding of the world, as the path to discovery is often a rocky road. I am most inspired by the work of Alan Turing, who pioneered new fields long before their time. Turing's last works provide a glimpse into today's deepening union of computing, biology, and artificial intelligence. I also dedicate this work to the memory of John von Neumann and Stanislaw Ulam, whose cellular automata and Monte Carlo methods developed at Los Alamos are the basis of forest landscape and classical fire models. Furthermore, I am inspired by the pioneering transdisciplinary research of C.S. Holling, Daniel Botkin, Richard Rothermel, Masami Monsi, Toshiro Saeki, Greg Asner, John Gamon, my supervisor, Nicholas Coops, and many others that brought a first-principles approach to ecology. Mathematicians prove concepts, engineers build them, and ecologists use them to reduce a forest of complexity.

Chapter 1: Introduction

1.1 Global Change and Forest Ecosystems

Forests are essential to biodiversity and provide many ecosystem services for the world's growing population (Costanza *et al.*, 1997, 2006; Rockström *et al.*, 2009). Given the persistence of Anthropocene trends, the future of the world's forests remains uncertain (Magnani *et al.*, 2007; Bonan, 2008; Houghton *et al.*, 2012; Worrall *et al.*, 2013). Despite recent policy-related gains in regions such as China (Viña *et al.*, 2016), the global land area occupied by forests is at a historic low, with a net loss of ~7 to 11 million km² of forestland over the past 300 years (Ramankutty & Foley, 1999; Foley *et al.*, 2005; World Resources Institute, 2014).

Larger losses are estimated over greater timescales, in connection with agricultural land clearing (Ruddiman, 2003). The global rate of deforestation is likely increasing, with only Asia and North America experiencing recent net gains in forestland (Rudel *et al.*, 2005; Lindquist *et al.*, 2012). Meanwhile, the rate of forest loss surged in Canada and Russia for the 2011-2013 period, primarily attributable to forest fires, accounting for 34% of global forest loss (World Resources Institute, 2014). Many existing forests are managed forests, which lack the structural and functional attributes of primary forests (Nepstad *et al.*, 1999; Chazdon, 2008). Large trees have declined in frequency (Lindenmayer *et al.*, 2014), notable for their carbon storage (Luyssaert *et al.*, 2008; Stephenson *et al.*, 2014) and habitat provisions (Franklin *et al.*, 1981; Hansen *et al.*, 1991).

Despite evidence of a recent increase in forest net primary production (Cao & Woodward, 1998; Bonan, 2008; Keenan *et al.*, 2014), a long-term decline is evidenced by net annual deforestation rates ranging from 5.2 million hectares (Food and Agrigulture Organization of the United Nations, 2010) to 13.5 million hectares (Lindquist *et al.*, 2012). Globally, forest carbon emissions are estimated to outweigh carbon sequestration five-to-one (Potter, 1999; Mason Earles *et al.*, 2012). An increased rate of soil respiration at high latitudes, attributable to enhanced microbial activity under warming, may further amplify carbon emissions beyond the predictions of existing models (Karhu *et al.*, 2014).

Warming directly impacts the cryosphere, with reduced surface albedo due to snowmelt providing an additional warming feedback (Perovich *et al.*, 2007; Lee *et al.*, 2011). Snowpack reductions also stress freshwater and estuarine ecosystems while increasing the incidence of drought and wildfire (Knowles, 2002; Westerling *et al.*, 2006; Abatzoglou & Williams, 2016). Higher rates of global tree mortality have been attributed to drought under existing levels of warming (Allen *et al.*, 2010; Anderegg *et al.*, 2013). Global forest fire activity has similarly increased, due to higher fuel severity under warming (Abatzoglou & Williams, 2016). Critically, climatic changes to germination and establishment may prevent some forests from regenerating following disturbance (Nitschke & Innes, 2008; Worrall *et al.*, 2013).

1.2 Global Change in Forests of Canada

Canada is home to 9% of the world's forests, 93% of which are publicly owned (Gillis *et al.*, 2005). Due to the relative intactness of its forests, despite accelerated fire-induced forest loss in the 2011-2013 period (World Resources Institute, 2014), scientific inquiry in Canada focuses

less on land-use conversion and more on structural and functional aspects (Chen *et al.*, 2003). Canada experienced nominal deforestation over the past three centuries, losing ~5% of its forests to land-use conversion (Ramankutty & Foley, 1999). Yet, a low rate of land-use conversion obscures the extent of human influence. Over 67% of Canada's forestland is managed (Power & Gillis, 2006; Canadian Forest Service, 2013b), including forestland managed for any type of use (e.g., conservation, economic, or recreation) per Section 3.1.2.1 of the Good Practice Guidance for Land-use and Land-use Change in Forestry (Intergovernmental Panel on Climate Change, 2003). Less than 0.3% of Canada's 347 million ha of forestland is harvested annually, while 7% was disturbed by fire or insects in 2014 (Natural Resources Canada, 2016). Similar to other regions, Canada's forests are further impacted by indirect anthropogenic effects, such as warming, hydrological cycle change, CO₂ fertilization, and nitrogen deposition, which may also alter the evolutionary trajectory of these forests.

The evolution of boreal forests, as a class of species interaction network (Proulx *et al.*, 2005; Peralta, 2016), was shaped by climate and fire, and fire remains the most prominent disturbance type (Rowe & Scotter, 1973). Wildfires were historically climatic and indigenous in cause, with lightning strikes and controlled burning providing major sources of ignition (Wright & Bailey, 1982; Baker, 2012). Early European settlers viewed fire as destructive to timber resources and property, motivating a policy of fire suppression that may reshape vegetation communities (Bond *et al.*, 2005; Thorpe & Daniels, 2012). While harvest patterns emulating natural disturbance regimes have undergone extensive research (Work *et al.*, 2004), existing methods cannot replicate important physiological interactions with fire. The importance of these interactions is evidenced by the initial evolution of pyrogenic traits in boreal genera such as *Pinus* beginning over 100 million years ago (He *et al.*, 2012).

1.3 Global Change in Boreal and Montane Forests of Alberta

This dissertation focuses on the Rocky Mountain foothills region of Alberta. To incorporate neighborhood effects, the 25.2-million-hectare western Alberta study area boundary of the Foothills Research Institute's Grizzly Bear Program was utilized for Alberta (Figure 1.1).



Figure 1.1 Study area in western Alberta, Canada, overlaid on Canadian Forest Service boreal forest classes in NAD83 Lambert conformal conic coordinates with WGS84 graticules; Alaska displays the contiguity of boreal fires

The western Alberta study area is characterized by a strong elevational gradient and a related transition between montane Cordilleran forests in the southwest and boreal forests in the northeast, with the Great Plains (Canadian Prairies) beginning in the southeast (Natural Regions Committee, 2006). Mean elevations for biogeoclimatic regions range from 525 meters to 2,350 meters, while the latitudinal maxima range from 49° to 58° (Natural Regions Committee, 2006). Tree species diversity is lower here than in temperate and tropical zones, with only seventeen common species from six genera: *Pinus, Picea, Populus, Betula, Larix,* and *Abies*. About a third of species occur in the boreal, with approximately two-thirds in the foothills and montane regions. High-elevation areas (above 1,900 m) beyond the tree line are comprised of alpine meadows, exposed rock, snow, and glaciers (Natural Regions Committee, 2006).

Regional temperature and precipitation patterns reflect elevational and latitudinal gradients. While higher elevations and latitudes produce cooler temperatures, precipitation patterns are strongly influenced by local topography (Natural Regions Committee, 2006). Regions containing the shortest fire rotation periods, such as the boreal lowlands and plains, occur at lower elevations where precipitation is lowest and temperate extremes are highest, adjacent to more productive highlands (Natural Regions Committee, 2006). The foothills region is characterized by the most precipitation and the most productive forests, supporting an active timber industry.

The Cordilleran ice sheet covered the region during the Last Glacial Maximum, producing an abundance of well-drained upland soils. Parent materials are morainal and glacio-lacustrine in origin, with gray Luvisols and black Chernozems the most abundant soil types. Luvisols are more common in wetter regions, such as the boreal, while Chernozems are common in drier

regions. Soils in the eastern Albertan plains contain a relative abundance of sand and silt, attributable to aeolian deposition (Natural Regions Committee, 2006).

Many plants in the study area evolved competitive mechanisms not only to survive, but to thrive, following high-severity wildfires (Schwilk & Ackerly, 2001). While quaking aspen (*Populus tremuloides* Michaux) may act as a fuel break, resprouting vegetatively post-fire as a pioneer species (United States Forest Service, 2013), jack pine (*Pinus banksiana* Lambert) and lodgepole pine (*Pinus contorta* Douglas) are also pioneer species that rely on fire, but through cone serotiny (Burns & Honkala, 1990; Farrar, 1995b). In the absence of fire, these species may decline in abundance (Thorpe & Daniels, 2012).

The foothills region is characterized by relatively homogeneous stands of lodgepole pine, the result of large historical fires (Tande & Tande, 1979; Arno, 1980; Lotan & Perry, 1983; Critchfield, 1985). Lodgepole pine thrives on cool, dry sites and is estimated to have the widest range of environmental tolerances of any conifer in North America (Burns & Honkala, 1990). Alberta lodgepole pine are associated with glacial till, rather than alluvial soils or lacustrine deposits common in some parts of their range (Burns & Honkala, 1990). Other common tree species here include Engelmann spruce (*Picea engelmannii* Parry ex Engelmann), subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), and balsam fir (*Abies balsamea* (Linnaeus) Miller). Quaking aspen is the most abundant deciduous species (Nielsen *et al.*, 2009).

Intensive extractive industrial activity has occurred in the foothills region in recent decades, as Alberta experienced population and economic growth (Nielsen *et al.*, 2009). Over the past forty years, forest harvest levels in Alberta increased four-fold (Canadian Forest Service, 2013a). Other regional extractive activities that affect forests include oil and gas exploration (e.g. seismic lines and well sites), and mining. The western Alberta study area is also home to iconic National Parks – Banff, Jasper, and Waterton Lakes – that comprise 23% of the 132,076 km² brown bear core conservation area, within the study area (Nielsen 2009). These National Parks have attracted an unprecedented number of recreationists in recent years. In total, the number of people accessing Alberta's forests is estimated to be at an all-time high (Bourbonnais *et al.*, 2013; Fortin *et al.*, 2016).

Effective fire suppression may alter forest composition. Due to fewer large fires in recent decades, Alberta's lodgepole pine stands have transitioned toward a species composition of black spruce (*Picea mariana* Miller) and white spruce (*Picea glau*ca (Moench) Voss) (Thorpe & Daniels, 2012). A diminished rate of burning may also reduce gross primary production for *Pinus* and *Populus* species through demographic change (Fahey & Knight, 1986; Magnani *et al.*, 2007). Such strong demographic changes were recently shown for the region (Zhang *et al.*, 2015), including reduced growth and recruitment rates.

1.4 Understory Plants and Canopy Light Transmission

Photosynthetically active radiation is a key limiting factor of regeneration and productivity for understory plants (Monsi & Saeki, 2005). Models of understory plant distribution and abundance remain limited by uncertainties surrounding the understory light environment, a function of difficult-to-model succession and disturbance processes. Traditional statistical models and machine learning approaches are a modern application of the static Hutchinsonian niche, performing well at coarse scales, but lacking dynamic processes needed to predict fine-scale patterns (Araújo & Peterson, 2012). Unlike climatic and edaphic variables that may hold for broad scales, light transmission is a function of leaf properties and forest gaps resulting from fine-scale mortality and regeneration patterns (Beaudet & Messier, 2002). Directly simulating salient processes of forest dynamics represents a promising approach to modeling the understory light environment.

1.5 Dynamically Simulating Understory Solar Irradiation

I hypothesized that past-century changes to fire disturbance and regeneration have had a significant effect on the long-term (50-year) trajectory of understory solar irradiation, ignoring changes to harvest levels. Accordingly, the purpose of this thesis was to quantify the effects of past-century changes in climate and fire regimes on understory solar irradiation in western Alberta, Canada, as a proxy for understory vegetation production potential. First, past-century changes to fire regimes were assessed. Next, climatic changes to tree regeneration potential were modeled. The results were used as inputs in forest landscape simulations to assess the effects of past-century changes to disturbance and regeneration on understory solar irradiation. The simulations were conducted across a 25.2 million ha forested landscape at 1 ha spatial resolution and annual temporal resolution across a fifty-year period. A hybrid modeling approach is provided with global change and biodiversity conservation applications.

Full-spectrum understory solar irradiation was dynamically simulated for four historical scenarios by combining process-based models of succession, disturbance, and regeneration with a regression model of canopy light transmission. The regression model utilizes site index values

and simulated changes to landcover to predict canopy light transmission. For forest site index, Canada Land Inventory values were used to capture the long-term productive capacity of sites. Site index differs from spectral photosynthesis metrics such as NDVI, SIF, and NIR_V (Badgley *et al.*, 2017), as it represents the integral rather than instantaneous photosynthetic capacity. Site index encapsulates centennial-scale variation in soils, climate, and drainage (Knight, 1967). Thus, I infer that site index exerts great influence on canopy light transmission. Resulting maps of canopy light transmission for each time-step were multiplied by bare-earth solar irradiation model outputs to predict mean annual stand-scale understory irradiation (\overline{W} ha⁻¹ yr⁻¹). This allows representation of local understory light patterns produced by forest dynamics and local topographic conditions at the landscape scale. This work was conducted in seven components, each corresponding to a chapter:

- Chapter 2: Model design and parameterization data
- Chapter 3: Analysis of fire regimes over the past century in Alberta and Canada
- Chapter 4: Modeling tree species regeneration responses to past-century climate change
- Chapter 5: Simulating forest ecosystems under past-century climate and fire conditions
- Chapter 6: Models of canopy light transmission from convex spherical densiometer measurements and airborne laser scanning metrics
- Chapter 7: Solar radiation modeling and fusion of linear and machine learning models of canopy light transmission
- Chapter 8: Dynamic simulation of understory solar irradiation at the landscape scale over the past century

In the following section, I provide an overview of the hybrid modeling approach developed in this research.

1.5.1 Hybrid Models of Forest Ecosystems

Forest ecosystems contain nonlinear dynamics from organismal to landscape scales that can be conceptualized as complex adaptive systems (Levin, 1998). The collective behavior of low-level individual agents produces high-level self-organization and emergence (Grimm et al., 2005; Levin, 2005). Due to their non-linear nature, simulating complex systems poses unique conceptual and computational challenges. Despite the advent of network-based models, under current computational and model design constraints, hybrid models that are both process-based and stochastic are perhaps best-suited to represent the 'unavoidable criticality' of biological systems (Bak et al., 1989; Mora & Bialek, 2011). This is due in part to the current immaturity of ecological network models, which typically lack multiple interaction types (Pilosof et al., 2017), species traits, agent-based interactions (Ings *et al.*, 2009), and dispersal dynamics that may govern the formation of ecological networks (Thompson & Gonzalez, 2017). Nevertheless, the goal with both models is often the same: to locate a system state within the phase space, which may attract toward criticality (Mora & Bialek, 2011). By focusing on salient dynamics, hybrid models have a limited parameter space, reduced dimensionality, and a computationally efficient design, in comparison to physical individual-based models.

Forest landscape models blend the functionality of empirical growth-and-yield models with physical gap models in a hybrid model design (Bugmann, 2001; Kimmins *et al.*, 2010). Based on the theory of forest dynamics (Shugart, 1984), stand-resolution and landscape-scale assumptions

are used to identify salient processes and reduce model complexity, enabling spatiotemporally explicit simulations across millions of interacting stands. Computational efficiency is achieved with two-dimensional cellular automata well suited to massively parallel high-performance computing systems, including general-purpose graphics processing units (GPGPUs) and heterogeneous CPU-GPU architectures.

An influx of remote sensing and ground network data combined with increased computational resources provide an opportunity to improve model parameterization, design, and implementation. While some recent modeling approaches are semi-empirical, relying on ground-satellite data assimilation to parameterize and constrain physical models (Quaife *et al.*, 2008; Mandel *et al.*, 2009), these models, as with current dynamic global vegetation models, lack important spatial, successional, and evolutionary dynamics. Future work may blend forest dynamics and physical processes through data assimilation in new hybrid model architectures. New models may rely on deep learning for modeling complex spatiotemporal patterns, such as wildfire spread and forest growth, trained on spaceborne remote sensing time-series. For such applications, generative adversarial networks hold particular promise (Goodfellow *et al.*, 2014a).

Forest landscape models simulate dynamic changes in the composition, structure, and function of forests, typically at a species taxonomic resolution, based on classical Linnaean taxonomic classification schemes rather than modern genomics data. Forest dynamics thought to be most impacted by global change are the focus of this thesis. In the foothills region of Alberta, anthropogenic changes to climate and fire are two such dynamics. Warming is predicted to alter the mortality and establishment rates of trees (Brubaker, 1986; Allen *et al.*, 2010; Luo & Chen,

2013), which may explain a recently observed demographic shift in Alberta's forests (Zhang *et al.*, 2015). While regeneration rates are likely to decline in some areas, a number of models predict that fire frequency, size, intensity, and thus tree mortality rates (severity), will likely increase under warming (Flannigan *et al.*, 2001; Ali *et al.*, 2012; de Groot *et al.*, 2013). The combined effect of these dynamics is the subject of this research, focusing on potential impacts to understory irradiation, which is an important predictor of understory plant productivity.

In northern forests, fire and climate mediate the pace of forest compositional change through the effects of growth and mortality events on successional pathways (Gavin *et al.*, 2013). Changes to light availability may regulate the capacity of understory plants to respond to climatic change through migration by altering the likelihood of successful germination and establishment. While previous modeling efforts represent many of these dynamics individually, statically (e.g., bioclimatic envelope models), or mechanistically (e.g., gap models), there is a need to simulate the interaction of these processes at the landscape scale under global change conditions. This interaction may serve to amplify or attenuate forest compositional, structural, and functional changes to forests in the coming decades (Nilsson & Wardle, 2005; Hart & Chen, 2006; Gracia *et al.*, 2007; Smith, 2011; Wing *et al.*, 2012).

An appropriate forest landscape model should incorporate salient spatial and aspatial dynamics of succession and disturbance, including ageing, competition, dispersal, mortality, regeneration, and fire spread. Such a model should incorporate physiological changes to germination and establishment, based on soil attributes in relation to the timing of seasonal weather events and species-specific tolerances. The model should represent fire ignition, initiation, and fuels- and
weather-modified spread rates, in accordance with observations. The model will need to simulate changes to understory light conditions, directly or indirectly. Based on the above model selection criteria, LANDIS-II (Landscape Disturbance and Succession model, variant II, version 6.0) was parameterized, optimized, and used to simulate forest processes in western Alberta.

The LANDIS family of models, including LANDIS-II (Scheller *et al.*, 2007; Sturtevant *et al.*, 2009) and LANDIS PRO (Wang *et al.*, 2013, 2014b), following the original LANDIS work (He & Mladenoff, 1999; He *et al.*, 1999; Mladenoff & He, 1999; Sturtevant *et al.*, 2004; Yang *et al.*, 2004), is unique in its ability to represent stochastic, mechanistic, logical, and probabilistic processes through a number of user-provided extensions in an open-source software framework. Of these models, LANDIS-II has the most active user community and provides the most user-developed sub-models. LANDIS-II and other cellular automaton-based hybrid models extend from empirical growth-and-yield equations, mechanistic gap models, and classical fire models (Scheller *et al.*, 2007).

To reduce components of stand competition to a network of logical operations, LANDIS-II incorporates ecological succession through species life history strategies. For model initialization, LANDIS-II requires parameters for tree species life history attributes, tree species distributions, landcover classes, age classes, biogeoclimatic regions, regeneration probabilities, and, optionally, disturbance regimes. Of these parameters, regeneration probabilities are frequently the most difficult to attain. These values are typically imported from a separate ecophysiological model of planet regeneration, such as PnET-II (Aber & Federer, 1992; Aber *et*

al., 1995, 1997; Gustafson *et al.*, 2014) or TACA-GEM (Nitschke & Innes, 2008; Mok *et al.*, 2012; Erickson *et al.*, 2015).

Combined with the latest ecophysiological regeneration models, such as the updated TACA-GEM model presented herein (Chapter 4), LANDIS-II can simulate forest dynamics at a stand resolution and landscape scale. A hybrid modeling approach provides greater representation of salient dynamics than models that rely purely on correlative relationships, lending to a theoretically greater ability to extrapolate beyond past conditions. LANDIS-II is designed to model at the species taxonomic resolution, necessary given evidence of historical no-analogue species assemblages (Urban *et al.*, 2011). Details on the design of TACA-GEM and LANDIS-II are provided in Chapter 2.

1.5.2 Airborne Laser Scanning Models of Canopy Light Transmission

The distribution and intensity of understory light provides a physical control on the establishment and production of understory plants (Hart & Chen, 2006). Along with soils, understory light is a major source of uncertainty in modeling understory plant distributions. Understory light is a product of solar radiation propagation, transmittance, reflectance, and extinction within forest canopies (Ligot *et al.*, 2014). In boreal forests, understory light is primarily a function of canopy light transmission resulting from structural and compositional forest conditions related to climate and fire history (Gavin *et al.*, 2013). Tree canopy properties that vary with stand composition (e.g., leaf area index, leaf angle distribution, canopy bulk density, leaf chemistry) play an important role in controlling the quantity and quality of understory light (Niinemets, 2010a; Ishii *et al.*, 2012; Niinemets *et al.*, 2015).

Following a landmark study in ecophysiology (Monsi & Saeki, 1953, 2005), a suite of methods exist to estimate canopy light transmission. Here, I develop models of canopy light transmission from convex spherical densiometer measurements and airborne laser scanning data. New methods are provided for mapping and simulating changes to canopy light transmission across forested landscapes. While previous studies model canopy light transmission using 3-D forest growth models and ray-tracing (Casella, 2008; Lintunen *et al.*, 2013), such gap model simulations are difficult to extend beyond the stand scale.

In recent years, a number of studies have utilized light-detection-and-ranging (LiDAR) for mapping understory light conditions. With airborne laser scanning (ALS), off-nadir scan angle pulse penetration used to represent angular canopy closure and on-nadir pulse penetration used to represent vertical canopy cover (Korhonen & Morsdorf, 2014). LiDAR systems can be singlereturn, multiple-return, or full-waveform digitizing systems. Typical ALS systems for terrestrial applications consist of a 1064 nm near-infrared neodymium-doped yttrium aluminum garnet (Nd:YAG) LASER source, avalanche photodiode detector with telescopic receiving optics, oscillating mirror or rotating polygon scanning device, precision inertial measurement unit (IMU) and global positioning system (GPS) receiver, and data recording device, mounted in an aircraft system (Baltsavias, 1999; Wehr & Lohr, 1999). Precise localization of points is achieved with IMU-GPS sensor fusion, typically using a variant of the Extended Kalman Filter (Caron *et al.*, 2006). Sorties are flown at a velocity, altitude, and side-lap designed to reach a given target point density with even sampling.

Compared to ground-based approaches, ALS methods provide more robust and efficient estimation of canopy light transmission at broader scales (Lieffers *et al.*, 1999). ALS methods of estimating light transmission in forests are rooted in geometry (Alexander *et al.*, 2013), statistics (Morsdorf *et al.*, 2006), the physical Beer-Lambert Law (Hopkinson & Chasmer, 2009), or a combination of the three, as exhibited by gap fraction, leaf-area index, and canopy light transmission (Richardson *et al.*, 2009; Korhonen & Morsdorf, 2014). By characterizing canopy light transmission for different forest types and stages of development along productivity gradients, and connecting these values to dynamically simulated forest attributes and a bare-earth solar irradiation model, it may be possible to forecast changes to understory solar irradiation and thus plant productivity. While machine learning provides a promising approach of connecting empirical measurements to dynamic vegetation model, linear regression may be sufficient. In order to integrate remote sensing regression models with dynamic vegetation models, the same predictor variables must be available in each, constraining variable selection.

1.6 Research Overview

This work is based on linking together a series of models to predict changes to understory global solar irradiation under the continuation of historical climate and fire trajectories. These models are complex and require a copious number of parameters, which are often process-specific, derived from data or the literature. Estimating reliable parameters is a central limitation of modeling studies, particularly for longer simulation durations whereby model behavior may overcome landscape initialization. A tradeoff was observed between the resolution and scale of parameters available for Canada. While there is ample field data for certain species, times, and places, gridded nationwide data are seldom available. This is particularly true for tree species,

given the specificity of parameters required. While spatiotemporal variation in species attributes linked to genetic or gene expression variation (Aitken *et al.*, 2008) is not included here, organismal plasticity under the assumption of optimality is motivating the development of nextgeneration dynamic global vegetation models (Strigul *et al.*, 2008; Franklin *et al.*, 2012; Scheiter *et al.*, 2013; Falster *et al.*, 2017).

Models of forest dynamics are typically spatial (sites interact) while regeneration models lack spatial interaction, similar to other process-based models (e.g., dynamic global vegetation models). These models are designed for a range of scales and resolutions. Forest landscape models (e.g., LANDIS-II or LANDIS PRO) are designed to operate at a stand resolution (~ 1 ha) and landscape scale (~ 10^6 ha), unlike gap models designed for an organismal resolution and stand scale (Bugmann, 2001). Size- and age-structured models using partial differential equations have also emerged, which operate at an organismal resolution and up to global scale (Moorcroft *et al.*, 2001; Purves *et al.*, 2008; Strigul *et al.*, 2008; Medvigy *et al.*, 2009; Xu *et al.*, 2016). These are the first gap model derivatives that can be applied for terrestrial biosphere modeling. Meanwhile, regeneration models operate at resolutions ranging from individual trees to landscapes and are effectively scale-free, limited by the resolution- and model-dependent accuracy of climate, soils, and species parameters.

While the majority of regeneration models infer establishment suitability from photosynthetic limitations (e.g., LINKAGES, PnET, and 3-PG-based models), the TACA family of models builds on this approach by explicitly modeling a number of regeneration processes. The latest TACA version, presented herein, incorporates germination processes and extreme events, in

addition to phenology. Given the substantial number of tree species parameters required for the TACA and LANDIS-II models, values used in previous studies and the literature were relied upon. Additional parameters were calculated from available geospatial soils, climate, fire, site index, elevation, and tree species distribution, and landcover data. While each of these data represent different spatiotemporal resolutions and scales, sources used were selected for their compatibility with the study design. Model spin-up was used to generate the initial age distribution, as this information was not available and LANDIS-II may be insensitive to spatial parameters when stochastic model components are used (Davis, 2013).

Unknown errors likely exist in the parameterization data, contributing noise to the simulation results. The contribution of such noise to the results requires additional research on specific model components, as well as overall model outputs; statistical models may be used to link the two, as is performed herein for the TACA model. Bayesian methods (e.g., Gaussian process regression) offer a promising approach of quantifying uncertainties in stochastic simulations (Green *et al.*, 2000; van Oijen & Thomson, 2010). The LANDIS family of models was designed to facilitate such inquiries into interchangeable model components (He *et al.*, 2002), allowing it to be used as a tool for ecological inquiry (Davis, 2013). While model parameter sensitivity and validation studies have been conducted for specific components and regions for TACA (Nitschke & Innes, 2008; Mok *et al.*, 2012) and LANDIS-II (Sturtevant *et al.*, 2009; Xu *et al.*, 2009; Davis, 2013; Simons-Legaard *et al.*, 2015), global model validation, parameter optimization, and parameter sensitivity analyses should be conducted.

Finally, the designs of the two models undoubtedly contribute errors, as such models represent coarse simplifications of natural systems. The model simplifications used are detailed in the following chapter. While it is often assumed that compute poses the main limitation, contemporary model design is limited by data first, ingenuity second, and compute third. Nevertheless, detailed simulations for broad scales and/or long durations using physical models (e.g., classical gap models) remain compute-limited. This has motivated the development of hybrid models such as LANDIS-II (Scheller *et al.*, 2007) and SORTIE-PPA (Purves *et al.*, 2008; Strigul *et al.*, 2008).

Chapter 2: Model Data and Descriptions

2.1 Introduction

A considerable portion of this research involved locating and pre-processing datasets for model parameterization. A major goal of this work was to develop a model parameterization methodology utilizing tree species, fire history, soil, and climate data available Canada-wide, in order to facilitate future simulations at the national scale as computational resources improve. It is important to document these datasets separate from the research chapters in order to facilitate both reproducibility and extensibility. In this chapter, datasets used for model parametrization are described. First, fire history data are presented. Next, TACA-GEM model data are discussed, followed by LANDIS-II model data. For each model, distinct classes of parameters are grouped. For LANDIS-II, separate sections are provided for the succession and disturbance submodels. Tree species attributes are presented separately for each model, as they often differ in source and type. Finally, ALS data used to develop regression models of canopy light transmission are described.

2.2 Fire History Data

To estimate parameters for historical fire regimes, the latest Canadian Forest Service National Fire Database (NFDB) spatial wildfire polygon and point data were used (Canadian Forest Service, 2015). The NFDB was formerly known as the Large Fire Database, or LFDB. While the LFDB was previously limited to fires greater than or equal to 200 ha in size, the NFDB contains fires of all size classes. The NFDB data used contains fires from 1919 through 2014, covering 97% of the area burned in Canada (Stocks *et al.*, 2002; Bond-Lamberty *et al.*, 2007). The dataset was assembled from a variety of sources and underwent extensive validation. The NFDB represents the best long-term fire data available for Canada, combining a variety of data and methods commonly used to map disturbances (Stocks *et al.*, 2002; Goetz *et al.*, 2006; Parisien *et al.*, 2006; Gralewicz *et al.*, 2012; Canadian Forest Service, 2015).

The NFDB contains geolocated fire perimeters mapped by the thirteen fire management agencies (provinces, territories, and Parks Canada) using aerial photography and passive optical spaceborne remote sensing (i.e., Landsat and MODIS). The mapping methods vary by source and year (Parisien *et al.*, 2006; Canadian Forest Service, 2015). The data show expected patterns of improved monitoring coverage over time, particularly with the addition of Landsat and MODIS in recent decades. Spaceborne remote sensing provides greatly improved temporal resolution and coverage of fire disturbances compared to airborne remote sensing, at the cost of spatial resolution. The impact of this change in data sources on recorded fire regimes is briefly assessed in Chapter 3. The NFDB also contains ancillary information reported by the fire management agencies, such as the date and severity of disturbances.

2.3 Tree Regeneration Model

Two versions of the Tree and Climate Assessment (TACA) tree regeneration model were applied, TACA-EM and TACA-GEM. Recent advances to the TACA-GEM model are presented in Chapter 4. This section describes data used to parameterize each version of the TACA model.

2.3.1 Model Description

The TACA model is designed to assess climate change impacts on the regeneration niche of trees, the niche most sensitive to climatic change (Nitschke & Innes, 2008). In the TACA model, each year is simulated at a daily resolution to capture phenologically-driven regeneration events. Phenology poses fundamental limitations on species distributions (Chuine & Beaubien, 2001) and plant fitness (Chuine, 2010), thus its inclusion may improve model performance. Regeneration carries particular importance in global change studies, as it regulates forest change at a low level (Fisichelli *et al.*, 2014), providing an important climatic feedback.

The TACA regeneration model simulates tree species regeneration as a function of climatic and edaphic conditions relative to species biophysical constraints (Nitschke & Innes, 2008; Erickson *et al.*, 2015). TACA was originally based on regeneration and phenology functions within the forest gap model, ZELIG++ (Burton & Cumming, 1995; Cumming & Burton, 1996). The TACA model relies upon empirically derived biophysical relationships for regeneration in a process-based approach. Modeled species must navigate seasonal biologically relevant physical thresholds in order to regenerate each year. The regeneration probability output for a species is the sum of each annual probability divided by the number of scenarios in each simulation, producing an average probability for a given decade. Unlike statistical approaches, TACA explicitly models biological processes, enabling more robust extrapolation to novel conditions.

The TACA Germination and Establishment Model (TACA-GEM) builds on the TACA Establishment Model, TACA-EM (Nitschke & Innes, 2008), by including a germination submodel. The latest TACA-GEM version presented herein builds on previous versions

(Nitschke *et al.*, 2012) with four improvements. The growing-degree-day (GDD) response functions from Zelig++ (Burton & Cumming, 1995), JABOWA (Botkin *et al.*, 1972) and FORÊT (Shugart & West, 1977) are used to determine annual establishment suitability as a probabilistic function of temperature, rather than binary responses to GDD and drought conditions for a given year. Second, drought is now calculated based on the proportion of the year where soil water potential is equal or below the turgor loss point (permanent wilting) for a given species, instead of the portion of the year where water deficit occurs per the actual-topotential-evapotranspiration (AET:PET) ratio. This provides a more physiological basis for drought.

Third, soil water potentials are calculated from soil water availability and soil texture classes, using a reformulation of the van Genuchten soil water model (van Genuchten, 1980). Species regeneration suitability is equal to one in years with no water deficit and declines to zero if the proportion of the year under water deficit exceeds a species-specific threshold. Ponding depth is not explicitly modeled. The fourth improvement to the model is the development of an extreme events module. The extreme events module modifies species regeneration by eliminating seedlings that regenerate in favorable years but are subjected to prolonged and/or extreme drought or frost events, which result in mortality over decadal periods. A diagram of TACA-GEM is provided (Figure 2.1). Additional factors such as seed source and canopy conditions are modeled within LANDIS-II, into which TACA-GEM establishment probabilities are integrated.



Figure 2.1 TACA-GEM model diagram (Erickson et al., 2015); germination niche dormancy refers to embryo dormancy

2.3.2 Data Requirements

In addition to species biophysical parameters, the TACA model requires daily weather, soil, and solar radiation parameters for each site modeled. These parameters are decadal-scale daily resolution temperature minima and maxima, precipitation, soil moisture regime, soil texture, rooting zone depth, coarse fragment percent, percolation rate, an optional nitrogen modifier for productivity, and latitude, used in solar modeling. As the following TACA model configuration was designed for integration within LANDIS-II simulations, shared regions were used consisting of the Natural Subregions of Alberta (Natural Regions Committee, 2006). While this reduces site-scale variability in climate and soils, it was necessary for the purposes of this research.

2.3.3 Daily Weather

Most bioclimatic studies use monthly means of weather variables averaged over a climate normal period, typically 30 years. The major factor influencing the selection of this temporal resolution is the widespread availability of monthly resolution general circulation model projections (Intergovernmental Panel on Climate Change, 2014). The use of daily resolution data improves the results of phenological models applied for ecological forecasting (Cook *et al.*, 2010; Richardson *et al.*, 2013). The TACA model was designed to use daily resolution weather data to model soil moisture conditions and species regeneration responses. Acquiring daily resolution climate projections typically involves the use of stochastic weather generators or other statistical disaggregation approaches. Meanwhile, daily resolution historical weather station measurements provide the most robust model data for phenology. Data from the National Oceanic and Atmospheric Administration (NOAA) Global Historical Climate Network Daily (GHCN-D) version 3.11 were used to parameterize daily minimum and maximum temperature, and total daily precipitation, in the TACA model. The GHCN-D dataset is a global weather station database subjected to uniform quality assurance (Menne et al., 2012). Using R (R Core Team, 2015), daily weather values were computed for the median decade of interest within 30-year periods, averaged across each Natural Subregion within the study area for each day, in order to provide results comparable to other vegetation modeling studies. Missing values were imputed using a multivariate expectation-maximization (EM) algorithm with bootstrapping, commonly applied to climate variable imputation, using the R FastImputation package (Honaker et al., 2011; Lounici, 2012). Stations missing 50% or more observations were discarded; this low threshold was used for the regional averaging methods employed, as multiple stations exist per Natural Subregion. Imputed values, which followed the central tendency of time-series, were considered preferable to unduly weighting values for distant stations. Simplified versions of the GHCN-D processing functions and an interface to the NOAA API are available in the *rnoaa* package for R (Chamberlain et al., 2016).

2.3.4 Soil Textural Classes

Biogeoclimatic Natural Regions and Subregions of Alberta (Natural Regions Committee, 2006) were overlaid onto the Soil Landscapes of Canada (SLC) v3.2 database (Soil Landscapes of Canada Working Group, 2010) to generate soil textural class parameters for each modeled region in TACA (Figures 2.2 and A.3; Table A.1). Soils were characterized for each subregion based on the dominant soil type. Soil texture, rooting zone depth, percentage of coarse fragment material, available water holding capacity (AWHC), and derived percolation rate (Derr *et al.*, 1969) were calculated based on corresponding values from the SLC lookup table.



Figure 2.2 Alberta study area overlaid on NASA SRTM version 2 (National Geospatial Intelligence Agency corrected) elevation in NAD83 UTM 11N (meters) coordinates; (a) Natural Subregions of Alberta; (b) Natural Regions of Alberta; (c) soil available water holding capacity; points denote locations of NOAA GHCN-Daily weather stations; refer to Figure 1.1 for geolocation information

Soil moisture levels and mean elevation parameters were obtained from the subregional summaries (Natural Regions Committee, 2006). The soil textural classification for SLC values was based on Agriculture and Agri-Food Canada particle size classes (Soil Classification Working Group, 1998), which follows the USDA Textural Soil Classification pyramid. Soils were classified into textural groups based on SLC values for percent sand, silt, and clay, filtered by parent material texture. Organic soils were designated as the dominant soil type for one subregion, based on the biogeoclimatic region summary (Natural Regions Committee, 2006).

Table 2.1 Soil texture and latitudinal parameters used with TACA-GEM version 4.4;

```
AWSC = Available Water Storage Capacity; L = Loam; CL = Clay loam; SiCL = Silty clay
```

loam; Latitude = centroid Natural Subregion latitude rounded to nearest 5° in WGS84 projection

Natural Subregion	Soil Texture	Rooting Zone Depth (m)	Coarse Fragment %	AWSC (mm/m)	Field Capacity (mm/m)	Percolation (mm/day)	Latitude
Alpine	-	-	-	-	-	-	-
Central Mixedwood	SiCL	1.0	5%	452	560	93.1	55°
Central Parkland	CL	1.0	5%	341	470	122.6	50°
Dry Mixedwood	CL	1.0	5%	341	470	122.6	55°
Foothills Fescue	CL	1.0	5%	341	470	122.6	50°
Foothills Parkland	CL	1.0	20%	341	470	103.2	50°
Lower Boreal Highlands	CL	1.0	20%	341	470	103.2	55°
Lower Foothills	CL	1.0	5%	341	470	122.6	55°
Mixedgrass	CL	1.0	5%	341	470	122.6	50°
Montane	L	1.0	20%	377	460	66.4	50°
Peace River Parkland	CL	1.0	5%	341	470	122.6	55°
Subalpine	L	1.0	20%	377	460	66.4	50°
Upper Boreal Highlands	CL	1.0	20%	341	470	103.2	55°
Upper Foothills	CL	1.0	5%	341	470	122.6	55°

2.3.5 Species Biophysical Attributes

Tree species biophysical parameters were derived from the literature and regional databases, following previously applied methods (Nitschke & Innes, 2008; Nitschke *et al.*, 2012). Existing species compendiums may benefit from updates including genomics information. Sources for species biophysical parameters used in the TACA-GEM model are as follows:

Table 2.2 Source of tree species parameters used in the TACA model; Burns & Honkala (1990) and Thompson *et al.* (1999) cover North America, Klinka *et al.* (2000) covers British Columbia, other sources vary; several parameters adopted by Nitschke & Innes (2008) from the original Zelig++ work (Burton & Cumming, 1995; Cumming & Burton, 1996) were derived from range data; LANDIS-II simulations used only dominant species, listed in Table 2.3

Species	Data Source
Abies balsamea (Balsam fir)	(Burns & Honkala, 1990; Thompson et al., 1999; Greenwood et al., 2008)
Abies grandis (Grand fir)	(Burns & Honkala, 1990; Li et al., 1994; Thompson et al., 1999; Klinka et al., 2000; Nitschke & Innes, 2008)
Abies lasiocarpa (Subalpine fir)	(Edwards, 1982; Leadem, 1989; Burns & Honkala, 1990; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Nitschke <i>et al.</i> , 2012)
Betula papyrifera (White birch)	(Bevington & Hoyle, 1981; Bevington, 1986; Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Grenier & Sirois, 2009)
Larix laricina (Tamarack)	(Pitel & Cheliak, 1986; Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000)
Larix lyallii (Subalpine larch)	(Shearer, 1961; Burns & Honkala, 1990; Carlson, 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000)
Larix occidentalis (Western larch)	(Burns & Honkala, 1990; Sorenson, 1990; Carlson, 1994; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008)
<i>Picea engelmannii</i> (Engelmann spruce)	(Woodard, 1983; Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008)
<i>Picea engelmannii</i> x <i>glauca</i> (Hybrid white spruce)	(Burns & Honkala, 1990; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Renault <i>et al.</i> , 2000; Nitschke & Innes, 2008; Nitschke <i>et al.</i> , 2012)
Picea glauca (White spruce)	(Burns & Honkala, 1990; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Renault <i>et al.</i> , 2000; Nitschke & Innes, 2008; Nitschke <i>et al.</i> , 2012)
Picea mariana (Black spruce)	(Farmer <i>et al.</i> , 1984; Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Sirois, 2000; Meunier <i>et al.</i> , 2007; Nitschke & Innes, 2008)
Pinus albicaulis (Whitebark pine)	(Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Tomback <i>et al.</i> , 2001; Nitschke & Innes, 2008; Bower <i>et al.</i> , 2011)
Pinus banksiana (Jack pine)	(Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Renault <i>et al.</i> , 2000; Greenwood <i>et al.</i> , 2002)
Pinus contorta (Lodgepole pine)	(Barton, 1930; Woodard, 1983; Burns & Honkala, 1990; Li et al., 1994; Thompson et al., 1999; Klinka et al., 2000; Nitschke & Innes, 2008; Nitschke et al., 2012)
Pinus flexilis (Limber pine)	(Barton, 1930; Burns & Honkala, 1990; Thompson et al., 1999; Klinka et al., 2000)
<i>Pinus monticola</i> (Western white pine)	(Barton, 1930; Leadem, 1985; Burns & Honkala, 1990; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Feurtado <i>et al.</i> , 2004; Nitschke & Innes, 2008)
<i>Populus balsamifera</i> (Balsam poplar)	(Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Wolken <i>et al.</i> , 2010; Nitschke <i>et al.</i> , 2012)
<i>Populus tremuloides</i> (Trembling aspen)	(Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Wolken <i>et al.</i> , 2010; Nitschke <i>et al.</i> , 2012)
Populus trichocarpa (Black cottonwood)	(Burns & Honkala, 1990; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Wolken <i>et al.</i> , 2010; Nitschke <i>et al.</i> , 2012)
<i>Pseudotsuga menziesii</i> (Douglas fir)	(Burns & Honkala, 1990; Li <i>et al.</i> , 1994; Thompson <i>et al.</i> , 1999; Klinka <i>et al.</i> , 2000; Nitschke & Innes, 2008; Boberg <i>et al.</i> , 2010)

TACA parameters for a subset of species used for model integration in the LANDIS-II simulations are located in Table 2.3. These simulations utilized the original version of the TACA model (TACA-EM) that does not include a germination sub-model. Species parameters for TACA-EM and TACA-GEM were generously provided by Dr. Craig Nitschke.

Species	Model Code	Physiological Base Temperature (°C)	Heat Sum for Bud Burst (GDD)	Chilling Requirement (Days)	Minimum Temperature (°C)	Drought Tolerance	GDD (5°C) Minimum	GDD (5°C) Maximum	Frost Tolerance	Frost Season	Wet Soils	Heat Moisture Index
Abies balsamea	Sp01	2.8	121	49	-62	0.20	560.0	2,386	0.9	305	0.55	41.4
Abies lasiocarpa	Sp02	2.6	119	70	-67	0.25	197.6	5,444	0.9	320	0.75	28.7
Betula payrifera	Sp03	3.7	231	77	-80	0.30	236.8	4,122	0.9	285	0.30	40.0
Larix laricina	Sp04	2.9	111	42	-76	0.20	150.8	3,331	0.9	300	0.75	33.8
Picea engelmannii	Sp05	3.1	145	49	-64	0.25	74.4	2,150	0.9	335	0.50	28.7
Picea glauca	Sp06	2.7	147	42	-69	0.34	129.6	3,459	0.9	305	0.50	43.2
Picea mariana	Sp07	3.0	123	56	-69	0.30	144.0	3,060	0.9	305	1.00	42.7
Pinus banksiana	Sp08	2.8	108	56	-85	0.50	830.0	2,216	0.9	320	0.30	37.9
Pinus contorta	Sp09	2.9	116	63	-85	0.42	185.6	3,374	0.9	320	0.50	37.9
Populus balsamifera	Sp10	2.1	93	49	-80	0.13	126.0	7,852	0.9	290	0.55	59.0
Populus tremuloides	Sp11	3.5	189	70	-80	0.40	226.8	4,414	0.9	284	0.30	40.0

Table 2.3 TACA-EM parameters used in the LANDIS-II simulations

Parameters used in the updated TACA-GEM model, including a germination submodel, are in Table 2.4. These parameters were used to model regeneration responses to climatic change in the standalone application of TACA presented in Chapter 4. Parameters for drought tolerance, wet soils, frost tolerance, heat-moisture index, germination moisture threshold, and nitrogen availability are unitless coefficients described in previous works (Fuchigami *et al.*, 1982; Urban, 1990; Burton & Cumming, 1995; Nitschke & Innes, 2008; Mok *et al.*, 2012). While *Abies grandis*, *Larix occidentalis*, *Pinus monticola*, and *Pinus ponderosa* are not commonly found in Alberta, they were included in TACA-GEM as future migrants to assess potential for compositional change. Abbreviations used in Table 2.4: GDD = growing-degree days; P50 = leaf water potential causing a 50% decline in hydraulic conductivity; TLP = turgor loss point; threshold = model bounds; b0-b2 parameters for the impact of chilling on breaking physiological seed dormancy; b0-b3 = parameters for germination amount and timing based on GDD accumulation.

Species	Abies balsamea	Abies grandis	Abies lasiocarpa	Betula papyrifera	Larix Iaricina	Larix lyallii	Larix occidentalis	Picea engelmannii	Picea glauca	Picea glauca x engelmannii	Picea mariana
Physiological Base Temperature (°C)	5	4.3	2.6	3.7	2	2.7	3.4	3.1	2.7	2.9	3
Heat Sum for Bud Burst (5°C GDD)	98	307	119	231	111	146	180	145	147	146	123
Chilling Requirement (days)	60	91	60	77	42	56	70	49	42	45	56
Minimum Temperature (°C)	-42	-35	-67	-80	-76	-60	-42	-50	-70	-58	-69
Drought Tolerance	0.25	0.4	0.25	0.3	0.2	0.2	0.4	0.25	0.34	0.3	0.3
Wet Soils	0.9	0.3	0.9	0.9	0.9	0.9	0.7	0.9	0.9	0.9	0.9
5°C GDD Minimum (days)	164	206.4	197.6	236.8	150.8	160	163.2	74.4	129.6	139.2	144
5°C GDD Maximum (days)	3364	3877	5444	4122	3331	2650	3057	2150	3459	3331	3060
Frost Tolerance	0.75	0.55	0.75	0.3	0.75	0.75	0.05	0.4	0.5	0.45	1
Frost Season	285	305	320	285	300	320	305	335	305	320	305
Heat-Moisture Index	43.6	41.4	28.7	40	33.8	18.4	38.7	28.7	43.2	43.2	42.7
Heat Sum (GDD 5°C)	64	127	160	75	106	135	133	82	175	175	114
Stratification (days)	7	0	28	0	0	28	7	0	0	0	0
Chilling x Heat Sum Factor (linear model)	0	-0.0173	-0.0066	-0.0449	-0.0075	-0.0111	-0.0085	0	-0.0016	-0.0016	0
C x H Factor Threshold (days)	40	28	28	7	30	30	80	30	60	60	60
Germination Moisture Threshold	-0.5	-0.5	-0.5	-0.1	-0.5	-0.5	-1	-0.5	-0.5	-0.5	-0.5
Min Temperature for Germination	5	5	5	5	5	5	5	5	5	5	5
Max Temperature for Germination	35	35	35	35	35	35	35	35	35	35	35
b0	0.1922	0.9571	0.257743	1	1	0	0.0753	1	1	1	1
<u>b1</u>	0.0127	0.0008	0.005005	0	0	0.0147	0.023	0	0	0	0
<u>b2</u>	0	0	-0.000011	0	0	0	0	0	0	0	0
Threshold	40	28	364	30	30	80	40	30	60	60	60
					-						
b0	-0.158618	-0.532881	-0.358261	-0.50382288	-1.157836759	- 0.031503408	-1.732323493	-2.648495123	- 1.777235311	-1.777235311	-4.182342657
b1	0.003008	0.005202	0.003631	0.010126041	0.013978789	0.000245723	0.018922241	0.054610675	0.01501801	0.01501801	0.051122351
b2	-8.52E-6	-7.74E-06	-0.00000552	-5.10789E-05	-2.84902E-05	-8.54172E-08	-4.43156E-05	-0.000316429	-2.7636E-05	-2.7636E-05	-0.000125243
b3	6.28E-9	0.00000000	0	7.57734E-08	0	0	0	5.54355E-07	0	0	0
Minimum Threshold	64	127	160	75	106	135	133	82	175	175	114
Maximum Threshold	500	545	529	267	385	2742	294	209	369	369	294
	259	250	200	250	250	250	250	250	250	250	245
Seedfall Julian Date	258	258	288	258	258	258	258	258	258	258	245
Seed Viability (days)	360	360	360	180	300	300	300	300	300	300	300
Photoperiod (days)	275	275	275	275	275	275	275	290	290	290	290
Vogatative Deproduction	Nono	Nono	Nono	Sprouting	Nona	Nono	Nona	Nona	Nono	Nono	Lovoring
	INOILE	None	INOILE	Sprouting	INOILE	INOILE	INOILE	INOILE	None	None	Layening
Low Nitrogen Availability	0.55	0.05	0.55	0.25	0.3	0.25	0.3	0.55	0.3	0.425	1
Medium Nitrogen Availability	1	0.5	1	1	1	1	1	1	1	1	0.5
High Nitrogen Availability	0.75	1	0.75	0.75	0.75	0.3	0.75	0.5	0.75	0.625	0.05
P50 / TLP Minimum	-2.86		-3.27	-2.33	-3.35	-3.35		-4.18	-3	-3.59	-3.3
P50 / TLP Maximum	-2.86		-3.27	-2.33	-3.35	-3.35		-4.18	-3	-3.59	-3.3

Table 2.4 Tree species biophysical parameters used in TACA-GEM; continued on the next page

Species	Pinus albicaulis	Pinus banksiana	Pinus contorta	Pinus monticola	Pinus ponderosa	Pinus flexilis	Populus balsamifera	Populus tremuloides	Populus trichocarpa	Pseudotsuga menziesii
Physiological Base Temperature (°C)	3	5	2.9	4 4	3.9	5	2.1	3 5	4.6	3.4
Heat Sum for Bud Burst (5°C GDD)	120	196	116	468	250	70	93	189	175	255
Chilling Requirement (days)	70	60	63	98	77	70	49	70	70	56
Minimum Temperature (°C)	-55	-65	-85	-40	-41	-40	-80	-80	-60	-47
Drought Tolerance	0.4	0.42	0.42	0.25	0.6	0.5	0.13	0.4	0.13	0.5
Wet Soils	0.9	0	0.9	0.75	0.7	0.05	0.9	0.9	0.5	0.75
5°C GDD Minimum (days)	216	327	185.6	211.2	280.8	109	126	226.8	257.6	176.8
5°C GDD Maximum (days)	3352	3237	3374	3554	5656	4291	7852	4414	5263	3261
Frost Tolerance	0.05	0.9	0.5	0.5	0	0.9	0.55	0.3	0.55	0.25
Frost Season	320	315	320	305	275	320	290	284	295	300
Heat Moisture Index	34.2	36.8	37.9	25.8	65.9	93.3	59	40	62.3	61.9
Heat Sum (5°C GDD)	194	96	141	116	21	151	5	5	5	58
Stratification (days)	60	0	0	21	7	28	0	0	0	7
Chilling x Heat Sum Factor (linear model)	0	-0.0122	-0.0126	-0.0065	-0.0116	-0.0042	0	0	0	-0.0215
C x H Factor Threshold (days)	60	14	21	21	21	84	30	30	30	21
Germination Moisture Threshold	-1	-1	-1	-1	-1.1	-1	-0.2	-0.4	-0.2	-1
Min Temperature for Germination	4	5	5	5	5	5	5	5	5	5
Max Temperature for Germination	35	35	35	35	35	35	35	35	35	40
b0	-0.2	1	0.9684	0.153446077	0.8441	0.516	1	1	1	0.8626
b1	0.0067	0	0.0015	0.014395893	0.0073	0.0202	0	0	0	0.003
<u>b2</u>	0	0	0	-0.00014212	0	-0.0002	0	0	0	0
Threshold	120	14	21	90	21	84	30	30	30	21
	0.147452524	1 209055	2 2(2902(1(0 410 410024	0.249701724	0.147007	0	0.0105507(7	0	0.20(11
DU	-0.14/452534	-1.298055	-3.362802616	-0.418418034	-0.248/91/34	-0.14/996	0.01401	-0.010558/6/	0.01401	-0.28611
b1	6 20702E 07	0.019392	0.04024/109	0.004004438	0.014040249 8 5880E 05	1.40E.6	0.001401	0.0131/440/	0.001401	0.003081
b2	-0.20/03E-0/	-0.00007	-0.000133097	-9.0232E-00	-8.3889E-03	-1.49E-0	-0.000132	-0.000139007	-0.000132	-0.000012
Minimum Threshold	1.13923E-10	96	1.380781-07	116	21	151	1	1	1	58
Maximum Threshold	2299	378	355	401	143	658	106	108	106	400
	/	570	500	101	115	020	100	100	100	
Seedfall Julian Date	244	230	230	274	295	244	152	152	152	244
Seed Viability (days)	360	300	300	300	300	360	180	180	180	300
Photoperiod (days)	290	290	290	290	290	290	275	275	275	290
Vegetative Reproduction	None	None	None	None	None	None	Sprouting	None	Sprouting/ Fallen Branches	None
		0	0	0.55	0.55	0.55	0.55	0.5	0.7.7	0.5
Low Nitrogen Availability	0.3	0.75	0.75	0.05	0.25	0.25	0.05	0.3	0.05	0.3
Medium Nitrogen Availability	1	0.5	1	0.5	1	1	0.5	1	0.5	l
High Nitrogen Availability	0.25	0	0.3	1	1	0.3	1	0.75	1	0.75
D50 / TI D Minimum	2.62	2.0	2.0	2.0	4.05	5.1	1.0	2.74	1.0	4.50
P50 / TLP Minimum	-3.03	-3.9	-3.9	-3.9	-4.05	-5.1	-1.9	-2./4	-1.9	-4.59
P50 / TLP Maximum	-3.05	-3.9	-3.9	-3.9	-4.05	-5.1	-1.9	-2./4	-1.9	-4.59

2.4 LANDIS-II Forest Landscape Model

This section describes the design of the LANDIS-II model and data used for parameterization.

2.4.1 Model Description

Following the original LANDIS model, LANDIS-II is based on the JABOWA-FORET genre of gap models and LANDSIM (Mladenoff & He, 1999). Rather than using the mechanistic formulation of gap models, LANDIS-II closely follows the vital attributes/fuzzy systems approach of LANDSIM. This efficient approximation enables LANDIS-II to model salient spatial and non-spatial forest dynamics at a stand resolution and landscape scale. The LANDIS-II model core is the central hub of a modular system that allows users to specify submodels at a user-defined time-step. In LANDIS-II, each grid cell in the landscape matrix is either active or inactive. Inactive cells are static and active cells are dynamic. Active grid cells can be forested or non-forested. Grasslands are typically the only active non-forested cells, where trees may establish provided seed and favorable conditions for regeneration. Each active forested grid cell represents a stand of trees comprised of horizontally homogeneous species-age cohort classes (Scheller *et al.*, 2007). To better represent regional variation in climate, soils, and fire patterns, I divided the simulation landscape into biogeoclimatic regions. In the simulations, I utilize three submodel configurations: Age-Only Succession, Succession with Base Fire, and Succession with the Dynamic Fuels and Fire System.

The Age-Only Succession submodel was used to model light, reproduction, ontogeny, senescence, seed dispersal, and interspecific competition, accepting external parameters for tree species regeneration. In LANDIS-II, light is internally modeled as a logical function of the

maximum shade tolerance for sexually mature species present at a site. The presence of shade tolerant species is used as an indicator of low-light conditions. A tradeoff was observed here between shade and fire tolerance ($R^2 = 0.58$; p < 0.001). Accordingly, when fires initiate within a cell, younger and more shade tolerant species-age cohorts have higher mortality rates, increasing modeled light values post-disturbance.

Reproduction is limited by propagule presence and light availability provided regeneration probabilities output from a separate model, such as TACA-EM or PnET-II. Fire directly interacts with regeneration through mortality, resprouting, and serotiny. Age-related mortality is a function of species maximum age, with an increasing probability of mortality once species reach 80% of their maximum age. Seed dispersal is represented by a two-part negative exponential probability distribution with a leptokurtic dispersal kernel (Ward *et al.*, 2004), based on observed migration rates (Clark *et al.*, 1998). Interspecific competition occurs through the intersection of species life history attributes (e.g., reproductive timing, vegetative reproduction, serotiny, and tolerances to fire and shade), establishment probabilities, and local disturbance patterns.

We apply two conceptually different LANDIS-II extensions for modeling wildfire: Base Fire and the Dynamic Fuels and Fire System (Dynamic Fire). Base Fire is an empirically-driven stochastic fire-growth model that reproduces parameterized statistical distributions, with variability a result of its stochastic core. In contrast, Dynamic Fire is a semi-mechanistic stochastic fire-growth model that uses topography, fuel conditions, fire weather, and empirical fire distributions to shape fire patterns. The Dynamic Fire model is conceptually analogous to Prometheus in Canada (Tymstra *et al.*, 2010) and FARSITE in the US (Finney, 2004), which are

based on the Fire Behavior Prediction (FBP) System (Forestry Canada Fire Danger Group, 1992) and BEHAVE (Andrews & Chase, 1989), respectively. In both LANDIS-II fire models, fires begin through separate ignition and initiation events (Yang *et al.*, 2004). Mean fire return intervals (Pickett & Thompson, 1978) are used to represent fire frequency.

In the Base Fire model, the frequency of ignitions follows a Poisson distribution. Fire initiation is based on Bernoulli trials, with ignition probability a function of time-since-last-fire. Fire sizes are drawn from a log-normal distribution (Yang *et al.*, 2004), producing episodic large fires. The fire shape is a product of a stochastic percolation algorithm representing wind vectors. Inactive cells may act as fire breaks, stopping fire spread before reaching its target size. Fire severity is determined by fuel and wind curves representing fuel buildup and decay; a site's position on these curves is determined by time-since-last-fire. Fire is modeled as a bottom-up disturbance, whereby younger cohorts have a higher probability of mortality (He & Mladenoff, 1999). This dynamic is well-established and is correlated with tree height, depth-at-breast-height, and bark thickness (Regelbrugge & Conard, 1993; Whittier & Gray, 2016). While some fire models use a uniform fire frequency distribution and exponential fire size distribution (Yang *et al.*, 2004), the Base and Dynamic Fire models use Poisson and log-normal distributions, respectively. A log-normal size distribution has been empirically shown to hold for many regions of the world (Hantson *et al.*, 2016), including for Canada (Appendix A).

The Dynamic Fire model is a process-based fire model that uses a semi-mechanistic representation of fire growth (Sturtevant *et al.*, 2009). Similar to Base Fire, the ignition frequency follows a Poisson distribution, with cells in each fire region selected stochastically.

Unlike Base Fire, fire initiation is modeled probabilistically based on site fuel conditions, calculated using cohort information and daily weather data within FBP and Fire Weather Index (FWI) Systems equations (Van Wagner, 1987; Forestry Canada Fire Danger Group, 1992). Fire sizes are drawn from a lognormal distribution; users can alternatively specify duration-based sizes. Fire shape is modeled using fuel-specific rate-of-spread equations (Hirsch, 1993) and a modified minimal-travel-time cost-path method. The minimum-travel-time method is based on Huygens' Principle of wave propagation, also used in Prometheus and FARSITE. LANDIS-II utilizes the most efficient algorithm implementation of the three fire simulators (Finney, 2002).

In the Dynamic Fire model, the fire spread algorithm contains two core components: wind bias and fuel conditions. Wind bias has an ellipsoidal shape with the length and width based on the magnitude of a wind velocity vector (Finney, 2002). Fuel-based spread is a function of fuel class, wind speed, and topography, using FBP System fuel classes. A cost surface is created using the inverse rate-of-spread to calculate a minimum-travel-time path. The cumulative minimum-traveltime and fire size selected determine the shape of each fire, producing improved disturbance pattern realism.

The probabilities of fire sizes being selected from the lognormal size distribution are classified into five equally spaced fire weather bins, based on the logic that larger fires occur during more severe fire weather conditions. The fire weather bins are typically parameterized by classifying fire weather index (FWI) values. The seasonal distribution of fire frequency is represented probabilistically, incorporating leaf status. Detailed model information and equations are provided in the literature (Forestry Canada Fire Danger Group, 1992; Finney, 2002; Sturtevant *et al.*, 2009).

2.4.2 Data Requirements

The LANDIS-II model core requires a list from the literature containing life history attributes for tree species, including longevity, sexual maturity age, shade tolerance, fire tolerance, seed dispersal, vegetative reproduction, and serotiny (Scheller *et al.*, 2007). The model core also requires a matrix and lookup table specifying tree species-age cohort classes present in each cell. Cohort classes are dynamically updated at each time-step. A biogeoclimatic regions matrix and corresponding lookup tables are optional. A succession model table requires species regeneration probabilities; these values can be unique for each bioregion to represent local climatic patterns.

The Base Fire model requires statistical fire distributions for fire regions, typically set to the biogeoclimatic region matrix. Base Fire requires parameters for the mean, minimum, and maximum event size, ignition probability (λ), and the mean fire rotation period for each of the fire regions. These parameters require adjustment to reproduce empirical fire distributions, typically achieved by manual approximation of the ignition probability and fire rotation period parameters (Syphard *et al.*, 2007). Fit is difficult to achieve if the empirical fire size distribution differs substantially from a lognormal distribution.

The Dynamic Fire model similarly requires fire regions, also typically using the biogeoclimatic region matrix, and a corresponding lookup table. The model requires the expected mean (μ), standard deviation (σ), and maximum fire size for a lognormal distribution. The model requires

low and high averages of seasonal foliar moisture content (FMC), proportion of fires during high FMC conditions, open fuels class designation, and the annual frequency of fire initiation for each region. A fire seasonality table containing leaf status, proportion of fires, percent curing, and fire-day-length-proportion parameters for each season is also needed. Additional parameters include a fuel-type table based on FBP System classes, which consist of parameters for base type, surface type, initiation probability, three fuel type-specific rate-of-spread constants, buildup index (*BUIs* in the FBP System), maximum buildup effect (*q* in the FBP System), and crown base height, which are used to modify the initial spread index. The equations implementing these parameters have previously been described (Forestry Canada Fire Danger Group, 1992; Finney, 2002; Sturtevant *et al.*, 2009).

The Dynamic Fire model's damage table requires parameters for the upper bound of the cohort age range and the minimum difference between fire severity and tolerance for mortality to occur. An initial weather database incorporating daily fire weather data, including fine-fuel moisture code, buildup index, wind speed velocity, fire weather index, fire weather index bin, season, and bioregion, is used to modify fuel conditions. To model the effects of topography on fire shape, users may input percent-slope and upslope-azimuth matrices, which are included here using 90-meter NASA SRTM elevation data (Farr & Kobrick, 2000).

The Dynamic Fire model requires a fuel coefficient for each species and a maximum-sitehardwood-percentage, a classification threshold for the coniferous fuel group. The optional Dynamic Fuels submodel, which is applied herein, requires a fuel type classification table in order to reclassify site fuel conditions following succession and/or disturbance. The table contains parameters for base fuel type, age range, and species presence/absence. A disturbance conversion table can optionally be used to allow other disturbance types to modify the site fuel classification (Sturtevant *et al.*, 2009).

To produce the desired fire regimes at high accuracy, a new fire model parameter optimization method based on stochastic gradient descent (Widrow & Hoff, 1960) was developed and applied to both fire models. Using this method, the error between model results and empirical values is used as an objective function for iterative minimization. The fire simulations are repeated using this error coefficient to update the fire distribution parameters until the error reaches a minimum. Specifically, the ignition probability is adjusted for each region until the simulated fire frequency is within 1% of the target range before the same optimization process is applied to *k* values, equivalent to the fire rotation period. Pareto optimality is approximated by adjusting each parameter separately in this order. The stochastic nature of the model prevents local minima trapping, as is commonly done for model training in deep learning (LeCun *et al.*, 2015).

Firest, coarse-resolution (500 m cell) simulations are run for the maximum duration (~1,000 years) to quickly estimate the fire regime signal for a given parameter space. Next, final parameter optimization is computed by running simulations at full resolution for the target duration. The new method reliably produces fire frequencies within $\pm 1\%$ of empirical values and an area burned R^2 of 0.96, compared to standard values of $\pm 20\%$ and 0.82, respectively. If fire regimes deviate significantly from a lognormal size distribution, Base Fire will be limited in its ability to reproduce them, due to the shape of distribution used for the model (Scheller *et al.*, 2007; Sturtevant *et al.*, 2009).

2.4.3 Model Core

To parameterize the LANDIS-II model core, local species parameters were derived from the literature and species compendiums (Burns & Honkala, 1990; Farrar, 1995a; Klinka *et al.*, 2000). Ward's leptokurtic double-exponential seed dispersal algorithm was applied in the succession model (Ward *et al.*, 2004), as previously noted. To parameterize the initial landscape, a rule-based classification of modeled species abundance for western North American tree species was applied (Gray & Hamann, 2012).

Modeled species abundance values were used to classify the landcover using FBP System classes (Forestry Canada Fire Danger Group, 1992). Forested sites were binned into the following classes (FBP System code): Aspen (D-1); Boreal Spruce (C-2); Lodgepole or Jack Pine (C-3/C-4); Douglas-fir (C-7); Boreal Mixedwood (M-1/M-2). Each site was set to even age classes of 0, 30, 60, and 90 years, relying on model spin-up (running the model for a period) to produce desired forest structure patterns, given an absence of reliable forest age maps. In the absence of validation data, I relied on model behavior to produce realistic age patterns. For biogeoclimatic regions, a provincial classification scheme was used (Natural Regions Committee, 2006).

Landcover for Agricultural Regions of Canada (Agriculture and Agri-Food Canada, 2012) and Earth Observation for Sustainable Development of Forests (Wulder *et al.*, 2007) data were combined and reclassified, each set to year 2000 conditions. Three base cell states were used for the model: active-treed, active-untreed, and inactive. The initial landscape was classified as active-treed cells where tree species cohorts were present. Herb, grassland, and shrubland landcover classes were set to active-untreed, while setting agriculture, annual cropland, perennial

crops and pasture, wetland, water, exposed land, snow/ice, rock/rubble, and built-up cells to inactive. Hence, forests and fires could expand into open natural areas given suitable conditions, but not into developed or resource-limited sites.

As TACA and LANDIS-II require qualitatively different tree species parameters, additional data sources were located for LANDIS-II. Tree species life history attributes for LANDIS-II were derived from the following sources (Table 2.5):

Species	Data Source
Abies balsamea (Balsam fir)	(Xu et al., 2010)
Abies lasiocarpa (Subalpine fir)	(Burns & Honkala, 1990; Farrar, 1995a)
Betula papyrifera (Paper birch)	(Peterson et al., 1997; Government of Alberta, 2009)
Larix laricina (Larch)	(Burns & Honkala, 1990; Farrar, 1995a)
Picea engelmannii (Engelmann spruce)	(McCune & Allen, 1985; Burns & Honkala, 1990; Government of Alberta, 2009)
Picea glauca (White spruce)	(Dobbs, 1976; Groot et al., 2003; Government of Alberta, 2009)
Picea mariana (Black spruce)	(Stanek, 1961; Burns & Honkala, 1990; Government of Alberta, 2009)
Pinus banksiana (Jack pine)	(Flannigan & Wotton, 1994; Farrar, 1995a; Government of Alberta, 2009)
Pinus contorta (Lodgepole pine)	(Lotan & Perry, 1983; Parminter, 1984; Burns & Honkala, 1990; Farrar, 1995a)
Populus balsamifera (Balsam poplar)	(Burns & Honkala, 1990; Farrar, 1995a)
Populus tremuloides (Trembling aspen)	(DeByle & Winokur, 1985; Burns & Honkala, 1990; Huang et al., 1992; Jelinski
	et al., 1992: United States Forest Service, 2013)

Table 2.5 Sources of life history attribute species parameters used in LANDIS-II

The tree species life history attributes derived from these sources for use in LANDIS-II are as

follows (Table 2.6):

Species	Longevity	Sexual Maturity Age	Shade Tolerance	Fire Tolerance	Effective Seed Dispersal Distance	Maximum Seed Dispersal Distance	Vegetative Reproduction Probability	Sprouting Minimum Age	Sprouting Maximum Age	Post-Fire Regeneration
Abies balsamea	150	25	5	1	30	160	-1	-1	-1	None
Abies lasiocarpa	200	20	4	2	30	80	0.05	20	200	None
Betula papyrifera	150	15	2	1	100	200	0.5	1	200	Resprout
Larix laricina	150	10	1	3	38	60	0.05	10	150	None
Picea engelmannii	720	15	3	2	46	183	0.05	15	720	None
Picea glauca	350	25	3	2	100	300	0.05	25	350	None
Picea mariana	150	30	4	1	260	260	0.05	30	200	Serotiny
Pinus banksiana	200	10	2	4	37	60	-1	-1	-1	Serotiny
Pinus contorta	200	5	2	4	27	200	-1	-1	-1	Serotiny
Populus balsamifera	200	9	2	3	50	3000	0.5	1	200	Resprout
Populus tremuloides	200	2	1	4	uni	5000	0.95	1	200	Resprout

Table 2.6 Tree species life history attributes used in LANDIS-II simulations

2.4.4 Base Fire

For Base Fire, historical fire data were used from the Canadian National Fire Database (Canadian Forest Service, 2015) for 1923 to 2014. For the fire regions, the Natural Subregions of Alberta were used. The default fuel curve table values were used to represent five fire severity classes, as it was created for Canadian forests. I wrote functions in R (R Core Team, 2015) to calculate the mean, minimum, and maximum fire size, ignition probability, and fire rotation period for each fire region.

2.4.5 Dynamic Fuels and Fire System

For Dynamic Fire, the expected mean, standard deviation, maximum fire size, and annual fire frequency were calculated using R for each region and period. Functions derived from the FBP System were used to calculate seasonal foliar moisture content (FMC) values. To do so, the regional minimum FMC date was calculated, based on the mean latitude, longitude and elevation, before calculating the mid-season FMC using ordinal dates for the vernal equinox, summer solstice, autumnal equinox, and winter solstice. These values were used to calculate the proportion of fires occurring during the high FMC period. Low and high FMC thresholds were set to 25% and 75% of the maximum, respectively, which is the default model configuration (Sturtevant *et al.*, 2009).

Subregions were used as the fire regions matrix. For percent ground slope and uphill azimuth, NASA SRTM version 2 data were processed using standard techniques (Reuter *et al.*, 2007). For the fire seasons table, the leaf status for spring, summer, and fall were set to leaf-off, leaf-on, and leaf-off, respectively, to represent phenological periods of full dormancy, growing season (full

leaf emergence), and leaf abscission (early dormancy) for deciduous species. The proportion of fires during each season were calculated by using a subset of the fire database, with dates converted to ordinal dates and seasons. The percent curing values for open/grassland fuel types (Wotton *et al.*, 2009) were calculated as a function of FMC values, using a grassland curing index equation (Dilley *et al.*, 2004), with the mean index value used to represent each season. Fire day-length proportion was set to the standard value of one.

An initial fire weather database was calculated using Alberta Agriculture and Rural Development's historical fire weather station data. Fire weather stations were selected with the shortest Euclidean distance to the centroid of each region. Daily resolution fire weather data were used for the April 2012 through March 2013 fire weather season to represent recent climatic influences on fuels; historical fire weather data was otherwise unavailable for the region. The weather metrics used include precipitation, mean temperature, mean humidity, wind speed at 10 m above ground, and wind direction at 10 m above ground. The R *mtsdi* package (Junger & de Leon, 2012) was used to impute missing values for the period, using the default expectationmaximization algorithm and splines method. The R *fwi.fbp* package (Wang *et al.*, 2014c) was used to calculate daily fine fuel moisture content, build-up index, and fire weather index using standard equations (Van Wagner, 1987). Fire weather index values were segmented into five bins based on quantile groups using the R *Hmisc* package (Harrell & Dupont, 2015).

To parameterize the fuel type table, FBP System fuel classes and parameters developed for Canada were used (Forestry Canada Fire Danger Group, 1992). These parameters include base type, surface type, initiation probability, *a*, *b*, and *c* rate-of-spread parameters, a *q* depth dryness parameter, build-up index, maximum build-up effect, and crown base height. Fuel types not currently present in the landscape were set to inactive. A standard fire damage table was used, with probability of mortality inversely related to cohort age. The table includes species-specific fire tolerances, with standard transitions at 20%, 50%, 85% and 100% age percent of longevity. The optional Dynamic Fuels submodel was used, reclassifying site fuel conditions at the end of each simulation year based on species-age cohorts. This enables fire behavior to more realistically respond to succession and disturbance. To parameterize the fuels model, species were assigned an even fuel reclassification weighting coefficient of 1.0. Deciduous stands were given a standard maximum conifer composition threshold of 10%, which is the standard threshold used in the model. The fuel type reclassification table was based on the FBP System, utilizing its definitions for species composition and age classes (Forestry Canada Fire Danger Group, 1992).

2.5 Airborne Laser Scanning Data

Airborne laser scanning (ALS) data was provided by Foothills Research Institute on behalf of Hinton Wood Products, a subsidiary of West Fraser. The sorties were conducted by a Canadian remote sensing company, Airborne Imaging, in the mid-2000s near Hinton, Alberta in the foothills of the Canadian Rocky Mountains. Airborne Imaging used an Optech Airborne Laser Terrain Mapper (ALTM) 3100 mounted aboard a twin-engine fixed-wing Piper Navajo aircraft with an Applanix precision global positioning system-inertial navigation system (GPS-INS) position-orientation system utilizing sensor fusion. Flights were conducted with 50% sidelap between flight lines at an estimated mean velocity of ~ 160 knots (296 km h⁻¹) and altitude of ~ 1,400 m above-ground-level (AGL), yielding an estimated mean point spacing of 0.75 m and

theoretical minimum vertical accuracy between 10 and 15 centimeters (± 1 sigma). The Optech ALTM 3100 emitted near-infrared (1,064 nm) photons at a pulse rate of 70 kHz, using a maximum scan angle from nadir of ~ 14 degrees (0.24 radians), scan rate of 33 Hz, and a sawtooth scanning pattern. While the Optech ALTM 3100 is one of the first commercial ALS systems capable of full-waveform digitization, the system used in this study is a discrete-return system, recording up to four returns for every laser pulse, each with 12-bit dynamic range intensity information (Hilker *et al.*, 2013).

Ground and non-ground returns were classified using Terrasolid TerraScan version 0.6 consumer-off-the-shelf (COTS) software, which applies previously demonstrated methods (Kraus & Pfeifer, 1998). The pre-processed LiDAR data were delivered in standard American Society of Photogrammetry and Remote Sensing (ASPRS) laser (LAS) file specification. The estimated final horizontal and vertical positional accuracy was 0.45 m and 0.3 m, respectively, based on a large sortie conducted on November 19, 2007 (Hilker *et al.*, 2013). A total of 18.6 billion points were collected at a mean point density of 1.64 points m⁻² for the 1,100 km² Hinton area, based on calculations with LAStools software (Isenburg, 2015).

Chapter 3: Past-century Fire Regimes of Western Alberta, Canada

3.1 Introduction

The evolutionary history and paleorecord of North America's boreal forests reflect millennia of cold, dry, and fiery conditions (Hu *et al.*, 2006; Gavin *et al.*, 2007; Tinner *et al.*, 2008; He *et al.*, 2012; Kelly *et al.*, 2013). Global change in the Anthropocene (Crutzen & Stoermer, 2000) has shifted each of these three conditions. Over the past half-century, boreal forests warmed at twice the rate of the global mean (Intergovernmental Panel on Climate Change, 2014). In southwestern Canada, recent climatic change produced warmer and wetter conditions, significantly reduced snowfall, and related reductions in cryomass (Intergovernmental Panel on Climate Change, 2014), or total mass of surface and ground water in a frozen state. Warming is projected to accelerate in the near-term (Smith *et al.*, 2015), with the highest rates of warming expected to occur in mountainous regions (Miller, 2013) and higher latitudes. The northernmost regions are experiencing the most severe temperature extremes of the past 600 years through polar amplification (Miller, 2013; Tingley & Huybers, 2013).

The North American boreal is projected to migrate northward under warming, inducing a net terrestrial loss of carbon storage (Scheffer *et al.*, 2012; Koven, 2013). At lower elevations and latitudes, extant tree species are expected to regenerate less frequently following disturbance under warming, due to an increased frequency and magnitude of physiological drought (Nitschke *et al.*, 2010; Barichivich *et al.*, 2014; Intergovernmental Panel on Climate Change, 2014). Together, changes to regeneration and fire regimes may explain diminished recruitment rates observed for Canada in recent years (de Lafontaine & Payette, 2011; Boisvert-Marsh *et al.*,
2014; Zhang *et al.*, 2015). A reduction in area burned, without a compositional shift toward deciduous trees, may further accelerate warming through reduced albedo (Amiro *et al.*, 2006).

Large stand-replacing fires have characterized circumpolar boreal forests for millennia, reflected in the fire-resisting, -avoiding, and -embracing evolutionary strategies of the resident tree species (Kelly *et al.*, 2013; Rogers *et al.*, 2015). Changes to fire regimes carry particular importance in the North American boreal, where fire has been shown to regulate carbon flux (Bond-Lamberty *et al.*, 2007), energy partitioning (Amiro *et al.*, 2006), compositional change, and tree migration (de Lafontaine & Payette, 2011; Gavin *et al.*, 2013). Warming has increased the severity of fuel conditions in the boreal by increasing evaporative demand (Barichivich *et al.*, 2014; Intergovernmental Panel on Climate Change, 2014) and permafrost thaw (Camill, 2005; Baltzer *et al.*, 2014), accelerating carbon loss through an increased depth of ground-layer burning, particularly for peatlands (Turetsky *et al.*, 2011, 2015).

Recent burn rates for the North American boreal have been reported in excess of Holocene (~11.7 kybp) fire regime limits (Kasischke & Turetsky, 2006; Kelly *et al.*, 2013; Marlon *et al.*, 2013). The global area burned rapidly accelerated with the Industrial Revolution before declining over the past century (Marlon *et al.*, 2008, 2013). Unprecedented high burn rates (short fire rotation periods) are evident for the Alaskan boreal in recent years (Turetsky *et al.*, 2011; Kelly *et al.*, 2013). Yet, Alaska shows little agreement with other regions of the North American boreal. The eastern Canadian boreal shows a fire frequency and biomass burning maximum ~ 4.5 kybp and a steady decline thereafter, currently at a 7,000-year low, due to decreased insolation, shorter fire seasons, and increased precipitation (Marlon *et al.*, 2008, 2013). More recently, early

season warming has produced an increase in spring fire size, with variation in fire patterns attributable to climate-related water table changes and post-glacial topography (Ali *et al.*, 2009, 2012). Regions of the western Canadian boreal similarly show declines in area burned linked to increased precipitation over the past century (Meyn *et al.*, 2013). These studies indicate that co-varying patterns of solar radiation, temperature, precipitation, physiological drought, and human activity explain global variability in the area burned, with human activity playing an increasingly important role post-industrialization (Marlon *et al.*, 2008). The critical role of human activity is shown by a recent analysis of global burned area (Andela *et al.*, 2017). While short-term efficacy of fire suppression was shown for Alberta (Cumming, 2005), long-term efficacy remains poorly understood.

In Scandinavia, boreal fire regimes shifted to their present state in the 17th century, due to increased human activity (Niklasson & Granström, 2000). In Niklasson & Granström (2002), the fires-per-unit-area-time metric was used to indicate physical energetic constraints in the configuration of fire regimes, based on fire frequency, size, and area burned per unit time, following research on phase transitions in the classical Forest Fire Model (Drossel & Schwabl, 1992; Malamud *et al.*, 1998). A recent analysis of global fire regimes supports the presence of both physical energetic constraints and human-dominated fire regimes (Archibald *et al.*, 2013). Archibald *et al.* (2013) estimated energetic constraints from an expanded feature set that includes fire frequency, size, intensity, season length, return interval, and area burned per unit time.

Similar to Niklasson & Granström (2000), Archibald *et al.* (2013) demonstrate that fire frequency and size are inversely proportional for a given area burned per unit time. Fire

frequency strongly regulates fire intensity, while areas with shorter fire return intervals have higher area burned per unit time. Longer fire seasons are related to higher human activity levels, although difficult to uncouple from anthropogenic warming. Maximum fire size is characterized by exponential decay and has a logarithmic relationship with area burned per unit time that quickly approaches an asymptote (Archibald *et al.*, 2013).

These findings reflect fundamental relationships between fire, climate, vegetation, and human activity, supporting the theory of dual energetic controls (fuels and weather) on area burned per unit time along productivity gradients (Meyn *et al.*, 2007, 2010; Archibald *et al.*, 2013). These studies also indicate that human activity poses a third fundamental energetic constraint on fire regimes in the Anthropocene, alongside fuels and weather. Human activity may explain recent changes to fire regimes in actively managed forests of southwestern Canada by providing greater energetic inputs (ignitions), producing many small fires near human hotspots, while reducing energy stores and spread potential (harvest, fuels management, and fire suppression). These past-century changes to management are hypothesized to be evident in the historical fire record.

Following pan-boreal (Bradshaw *et al.*, 2009; Laurance *et al.*, 2014) and regional trends (Linke & McDermid, 2012; Braid & Nielsen, 2015), previous work has shown that increased economic development in the Alberta study area expanded the road network into formerly remote areas, facilitating increased access and use for economic and recreational purposes. Expanded human activity is further evident in an increase in other linear features, such as oil and gas pipelines, seismic lines, and power lines, as well as point features including one-hectare well-sites (Linke & McDermid, 2012). While a number of studies have assessed disturbance patterns here (Forest

et al., 2008; Nielsen *et al.*, 2008; Laberee *et al.*, 2014), existing studies do not explain the drivers of long-term disturbance variability critical to predicting future patterns in simulation studies. Existing datasets may contain valuable information for discerning relationships in space and time between human activity and fire, necessary for simulating disturbance-related changes to understory solar irradiation. In the following sections, the effects of past-century warming and increased human activity on fire regimes are assessed.

3.2 Methods

Here, changes in the statistical patterns of historical wildfire data within the Alberta study area and across Canada are analyzed. The analysis focuses on climatic and anthropogenic changes to fire, including variation in elevation, latitude, cause, size, frequency, and area burned along multiple temporal resolutions, including annual, seasonal, monthly, and daily intervals. Fire seasons were calculated as meteorological quarterly seasons. The analysis is structured to focus on proxies of climatic change and human activity, based on known historical changes and the findings of previous studies in the region. Although there exists significant variation in fire regimes across Canada, national fire patterns provide a baseline for separating regional variation from overall trends.

For the regional analysis, three data sources were used: the latest Canadian National Fire Database (NFDB) fire perimeter data, NASA Shuttle RADAR Topography Mission (SRTM) version 2 data processed using standard correction techniques (Reuter *et al.*, 2007), and Natural Regions and Subregions of Alberta for the biogeoclimatic zones (Natural Regions Committee, 2006). The data were subset to the Alberta study area and zonal statistics calculated for the

minimum, mean, and maximum elevation, as well as slope and aspect for each fire. The latitude and longitude for each fire centroid was also calculated. The NFDB contains many relevant fire attributes including the year, month, day, cause, source, and size. Using the year, month, and day values, the ordinal date and season of fires were calculated. Using values for the elevation, latitude, and ordinal date of each fire, foliar moisture content (FMC) was calculated for each fire. To calculate FMC values, standard equations were applied from the Canadian Fire Behavior Prediction (FBP) System (Hirsch, 1993).

Fire rotation period (FRP), or fire cycle, is a commonly applied metric to indicate the rate of burning, with lower values indicating greater severity (Wagner, 1978). FRP is the average time required for the sum of fire sizes within an area to equal the area in size, calculated over a given time interval. FRP is often presented alongside the mean fire return interval (MFRI), the average time interval between fires for a given area or site, as well as time-since-last-fire.

FRP = time interval / (sum of fire sizes burned in area / area size) MFRI = time interval / number of fires in site or area

Hence, FRP is the area-normalized MFRI. Applied to individual sites, FRP is equal to MFRI. By normalizing for area, FRP provides more information about fire regimes at scales greater than the individual site. MFRI values calculated for areas of different sizes are not directly comparable, unless normalized for area, which yields FRP. FRP is applied in the historical fire regime analysis. While other changes in the distribution of fires provide additional information, FRP provides a single robust metric for fire regimes. Fire size distributions were analyzed to detail variation in regional (Alberta study area) and national patterns, as well as changes to fire regimes between periods. This work follows a study on lightning-caused fires in the boreal mixedwood region of Alberta, using the former LFDB (Cumming, 2001) that showed that fire models should use a truncated exponential distribution to prevent over-predicting large fires. Here, a Weibull distribution was fit to log-transformed fire sizes. A right-tail Anderson-Darling maximum-goodness-of-fit estimation was used to adjust for power-law behavior at the tail of the distribution. Hartigan's dip test was used to test for bimodality. The expectation-maximization (EM) algorithm and Bayesian Monto Carlo Markov Chain (MCMC) simulations were used to fit a mixed normal distribution. Changes to fire size distributions were confirmed by Kullback-Leibler divergence and the Earth Mover's Distance (EMD), or Wasserstein metric, commonly used for comparing empirical probability mass functions (Gottschlich & Schuhmacher, 2014).

Fire regimes were temporally segmented using the binary segmentation algorithm (Scott & Knott, 1974). While other change-point detection algorithms were tested, including pruned exact linear time (Killick *et al.*, 2011), e-divisive (Matteson & James, 2013), and e-divisive with medians (James *et al.*, 2014), binary segmentation showed optimal sensitivity to small variations in the given task. Thus, binary segmentation was applied to classify fire regime periods. First, fire regime periods were classified with *a priori* knowledge on changes to management and climate. Periods of 30 years are used for compatibility with studies using 30-year climate normal data. The four *a priori* fire regime periods are as follows: Pre-Suppression (1923-1952); Early Suppression (1953-1982); Global Change (1983-2012); and, overlapping the Global Change period, the Most Recent Decade (2003-2012). The Global Change period corresponds to an

acceleration of global change conditions (Steffen *et al.*, 2007). The most recent decade is included to represent recent trends independent of the three 30-year periods.

Software used to conduct this work includes ArcGIS 10.2 for spatial analysis, ENVI-IDL 5.2 for processing synthetic aperture RADAR data, R 3.1 for statistical analysis, and Python 2.7 for automation. The *seas* package for R was used for date-time conversion (Toews *et al.*, 2007), while the *fwi.fbp* package for R was used to calculate FMC values (Wang *et al.*, 2014c). The *changepoint* (Killick & Eckley, 2014), *ecp* (James & Matteson, 2015), and *BreakoutDetection* (James *et al.*, 2014) packages for R were used to test change-point algorithms for classifying fire regime periods.

3.3 Results

Across the full 90-year period in the Alberta study area, mean, maximum, and minimum fire sizes declined. Fire frequency initially declined at an inflection point near 1950 before increasing rapidly since approximately 1990. On average, over the 90-year period, fires declined in size by 142.6 ha per year, annual area burned declined by 3,450 ha per year, and fire frequency increased by 5.44 fires per year (Figure 3.1).



Figure 3.1 Mean annual trends for fires in the Alberta study area, 1919 to 2012: (a) log of area burned; (b) fire frequency; (c) log of fire size; (d) latitude in WGS84 (decimal degrees) coordinates; loess smoothing with 95% confidence interval shown

In the Alberta study area, comprised predominantly of boreal forests, an inflection point in fire regimes is apparent near 1970, with patterns in area burned, mean fire size, and mean fire latitude changing thereafter; a rapid rise in fire frequency began a decade later (Figure 3.1). The abruptness of the \sim 1970 and 1990 inflection points suggest a change in management, the former potentially linked to an increase in oil and gas development in the boreal known to occur at the time. An observed linear decrease in area burned and increase in fire frequency was independent of elevation (high-elevation mean = -4607 ha/year, +3.3 fires/year; low-elevation mean = -29643 ha/year, +2.2 fires/year) and latitude (high-latitude mean = - 31211 ha/year, +3.0 fires/year; low-

latitude mean = - 3039 ha/year, +2.4 fires/year), based on median fire elevation and latitude. FRP increased by 298% between the Pre-Suppression (1923-1952) and Global Change (1983-2012) periods, indicating a three-fold reduction in fire regime severity during a period of warming (Intergovernmental Panel on Climate Change, 2014).

FRP increased by 166% between the Pre-Suppression and Early Suppression (1953-1982) periods, before increasing by another 50% between the Early Suppression and Global Change periods. FRP in the Most Recent Decade (2003-2012) reflects patterns of the Global Change period it overlaps, shorter by 0.1% at 923.9 years (Table 4.2). However, Most Recent Decade fires were approximately twice as frequent and half the size of Global Change period fires (*MFRI* Δ = -45%; annual *frequency* Δ = +82%; *MFS* Δ = -43.3%). The stability of FRP values between the Global Change and Most Recent Decade periods is indicative of the temporal depth of past-decade trends (Table 3.1).

Table 3.1 Fire regime statistics by period for the western Alberta study area; mean fire return interval (MFRI) is shown in years for the full region rather than the mean site value, where Burned = 1 / MFRI * MFS * Years; FRP = Area / Burned * Years

Period	Burned (ha)	Area (ha)	Fire Rotation Period (FRP, years)	Mean Fire Return Interval (MFRI, years)	Mean Fire Size (MFS, ha)
1923-1952	3,224,691	24,972,634	232.3	0.011	1,148.4
1953-1982	1,211,806	24,972,634	618.2	0.020	811.1
1983-2012	809,967	24,972,634	925.0	0.020	545.1
2003-2012	270,287	24,972,634	923.9	0.011	308.9

Differences in the mean and variance of fire size between Early Suppression and Global Change periods were not statistically significant at a *p*-value threshold of 0.05 (t = 1.69, *p*-value = 0.09; F = 1.19, *p*-value = 0.06). Area burned declined substantially between these periods (*Burned*_{ES} = 1,211,806 ha, *Burned*_{GC} = 809,967 ha, $\Delta = -33.1\%$), even though remote monitoring improved. While MFRI remained stable across the Early Suppression and Global Change periods (*MFRI*_{ES} = 0.0201, *MFRI*_{GC} = 0.0202, $\Delta = +0.5\%$), mean fire size (MFS) declined at a rate equivalent to that of area burned (*MFS*_{ES} = 811 ha, *MFS*_{GC} = 545 ha, $\Delta = -33\%$). Thus, a decline in mean fire size best explains the reduction in area burned under warming in the Alberta study area. This is particularly evident in the Most Recent Decade, where FRP (area burned) was similar to the Global Change period it overlaps ($\Delta = -0.2\%$) as MFRI (fire frequency) increased by 81.8%.

In the Alberta study area, the ratio of human- to lightning-caused fires increased from 0.93:1 to 1.39:1 (+33%) between the 1970s and 2000s. A spatial analysis of historical ignitions in the study area using NFDB point data demonstrates the proximity of small fires to areas of human activity, typically major roads and river valleys (fire distance from roads: mean = 2.2 km, standard deviation = 4.8 km; fire distance from roads or surface water: mean = 297 m, standard deviation = 363 m), supporting a human origin (Figure 3.2).



Figure 3.2 Fire adjacency to roads by cause overlaid on SRTM 90 m elevation data in the vicinity of Hinton, Alberta in NAD83 UTM 11N coordinates with WGS84 graticules: light blue = human-caused; magenta = lightning-caused; green = roads; top = north

Between the 1980s and 2000s, as Alberta's population doubled, the mean distance of fires from roads declined by 40%, from 2.3 to 1.4 km. The mean distance of fires from roads or surface water (rivers and lakes; proxies of human activity) declined by 32% across the same 30-year period, from 318 to 216 meters. Concurrently, annual fire frequency increased by 33%, from 6,035 to 9,054 fires, in the point data. The increasing influence of human activity in Alberta's

fire regimes is apparent in the percentage of the total area burned attributable to sources over the past three decades (Figure 3.3).



Figure 3.3 Decadal area burned by fire source for the Alberta study area; (a) absolute area burned (ha); (b) percent of total area burned (ha); most fires were unknown in origin (not shown); H = human-caused; H-PB = prescribed burn; L = lightning

A decline in the relative influence of lightning on the total area burned in Alberta was offset by an increase in the percentage of area burned explained be human-caused fires. Between the 1970s and 2000s, the area burned increased by 34% in summer, fire frequency increased in spring and summer, and mean fire size increased by 83% in fall and decreased by 60% in spring for the Alberta study area (Tables 3.2 and 3.3).

Season	Area	Number	Mean Size
Spring	-6.8%	+13.5%	-60%
Summer	+7.6%	+1%	+16.6%
Fall	-2.2%	-18.2%	+82.9%

Table 3.2 Fire regime change by season

Table 3.3 Fire seasonality

Season	Area	Number	Mean Size
Spring	63.2%	51.2%	123%
Summer	33.8%	39.2%	86%
Fall	2.4%	6.8%	35%

An analysis of fire seasonality related to the 'spring dip' in foliar moisture content (FMC) using standard formulations from the Canadian Fire Behavior Prediction System (Forestry Canada Fire Danger Group, 1992; Wotton *et al.*, 2009), shows that the standard FMC equations are not suitable for the Alberta study area. Here, the modeled spring dip in FMC occurs approximately two months after the peak in fire frequency and size (Figures 3.4a and 3.4c) that likely corresponds to the true spring dip (Tymstra *et al.*, 2007; Alexander & Cruz, 2013). The log of fire size shows the strongest density at 138 DOY (late April), followed by a second peak ~ 1 week later at a substantially larger fire size (Figure 3.4a). Meanwhile, modeled spring dip occurs at 200 DOY (Figure 3.4c). Across the full time period, fires declined in size following a structural change around 1990 (Figure 3.4b). In recent years, fires were most frequent and concentrated earlier in the season, with longer fire seasons (Figure 3.4d).



Figure 3.4 Two-dimensional kernel density estimation for fire frequency by ordinal date and year for the Alberta study area, 1919 to 2012: (a) log of mean fire size by ordinal date; (b); log of mean fire size by year (c) modeled foliar moisture content (FMC) by ordinal date; (d) fire ordinal date by year

Across Canada, an increasing rate of area burned declined at a similar inflection point around 1990, when mean fire size and latitude declined as fire frequency rapidly increased (Figure 3.5). Between the 1990s and 2000s, fires nationwide declined in mean latitude at a rate of 14 km/year while fires in the Alberta study area declined at a rate of 24.4 km/year. Nationwide and in Alberta, lightning-caused fires decreased and human-caused fires increased in mean latitude during the period (nationwide = -6/+1.6 km/year; Alberta = -5.9/+1.5 km/year). Characteristic of

the boreal, large lightning-caused fires >= 200 ha increased in mean latitude by 5.4 km/year nationwide and decreased by 10.1 km/year in Alberta. Since 1920, fires >= 200 ha shifted northward at a mean rate of 5.2 km/year ($R^2 = 0.13$; p < 0.001) nationally.



Figure 3.5 Mean annual trends for fires Canada-wide, 1919 to 2012: (a) log of area burned; (b) fire frequency; (c) log of fire size; (d) latitude in WGS84 (decimal degrees) coordinates; loess smoothing with 95% confidence interval shown; NFDB data prior to 1960 are known to be incomplete

For the *a priori* classification in the Alberta study area, the Pre-suppression period (1923-1952) is characterized by frequent fires and the largest annual area burned, while the Early Suppression period (1953-1982) shows a sharp decrease in fire frequency and annual area burned, with the

lowest overall rates of each. The Global Change period (1983-2012) exhibits a rapid increase in fire frequency but a relatively flat annual area burned. The Most Recent Decade (2003-2012), shows the most rapid increase in fire frequency and the most rapid decline in mean fire size, accompanied by a decline in area burned.

For the Alberta study area and Canada, fire regime period classification using the binary segmentation change-point detection algorithm produced fire regime periods distinct from the *a priori* classification. In Alberta, based on time-series of annual area burned and fire frequency (Figures 3.6a and 3.6b), the algorithm shows an initial fire regime segmentation from the late 1930s to the early 1960s, followed by another regime from the 1960s to the 1990s, and final regime characterized by an increase in fire frequency from the 1990s to 2012. For Canada-wide fires, the algorithm shows little consistency between fire regimes for the univariate annual area burned and fire frequency time-series (Figures 3.6c and 3.6d). Nevertheless, the annual area burned and fire frequency time-series (Figures 3.6c and 3.6d). Nevertheless, the annual area burned time-series shows approximate agreement with the *a priori* classification, with regime periods falling from the early 1920s to ~ 1950, ~ 1950 to late 1960s, 1960s to late 1970s, and late 1970s to 2012.



Figure 3.6 Fire regime change-point segmentation using the binary segmentation algorithm: (a) Alberta fire frequency by year; (b) Alberta total area burned by year; (c) Canada-wide fire frequency by year; (d) Canada-wide total area burned by year

Fire regime periods differed for the two scales. Canada-wide, the 1940s through 1970s were characterized by infrequent fires and a steadily increasing area burned, while the inverse was true for Alberta. Nationwide, the first broad shift in fire regimes occurred during the 1970s with a spike in fire frequency and area burned. Yet, area burned was flat from ~ 1980. In the Alberta

study area, similar to nationwide patterns, fire frequency increased rapidly beginning \sim 1990. Yet, Alberta showed little change in area burned from 1960 to 2012, despite strong variability within the period (Figure 3.6).

Over the 90-year period, in the Alberta study area, fire seasons lengthened by ~ 60 days, or two months (mean = +1.2 days/year), due to more frequent human-caused fires (mean = +9.2 fires/year) earlier and later in the season (Figure 3.7a). The fire season experienced a lower rate of lengthening nationwide (Figure 3.7b). At both scales, lightning-caused fires were concentrated in summer, while human-caused fires were concentrated in the spring and fall (Figure 3.7).



Figure 3.7 Fire regime patterns nationwide and Alberta study area changes in seasonality with linear models and 95% confidence intervals: (a) Alberta study area fire ordinal date by year and season; (b) Canada-wide ordinal date by year, season, and cause; salmon = human; aqua = lightning; linear regression with 95% confidence interval shown

Within the Alberta study area, the largest fire sizes and area burned occurred in the boreal, followed by the foothills and Rocky Mountain regions. Within the boreal region, the lowland mixedwood subregions experienced a greater area burned than the highland subregions. Yet, mean fire size and annual area burned declined in the boreal across the study period. Canada-wide, the log-transformed fire size distribution for fires > 2 ha showed reasonable fit with a Weibull distribution (*K*-*S* = 0.02; $\overline{\omega} = 1.60$; $A^2 = 27.34$; *AIC* = 174679.6; *BIC* = 174696.8), with fit improving with the right-tail second-order Anderson-Darling (AD2R) statistic due to power-law behavior at the tail (Appendix A). While the distribution of fire sizes nationwide showed unimodality per Hartigan's dip test (*D* = 0.003, *p*-value = 0.11) despite visual evidence of bimodality, fire sizes in the Alberta study area showed significant bimodality (*D* = 0.02, *p*-value = 0.002). Using a mixed Gaussian model for Alberta study area fire size, the two modes centered on μ of 1.2 and 6.2 log ha, with Expectation-Maximization (EM) and Bayesian Markov Chain Monte Carlo (MCMC) algorithms each converging to these values (Appendix A). This implies that there are two dominant fire regime phases in Alberta.

A further analysis reveals distinct changes in the fire size distribution over time. While previous periods showed approximately Gaussian fire size distributions without skew, fires in the Global Change period were strongly skewed toward smaller values (Appendix A). Bimodality of fire sizes for all years in the Alberta study area is comprised of two distinct components: (1) frequent large fires in 1923-1952; (2) frequent small fires in 1983-2012. The Most Recent Decade showed the second greatest K-L divergence ($D_{KL} = 0.84$, after the Pre-Suppression period ($D_{KL} = 1.05$), and greatest distance from, the fire size distribution for all years, based on the Earth Mover's

Distance (EMD) or Wasserstein metric (EMD = 5.15). Fire regimes in Alberta thus reached a novel state in recent years.

For Canada, monthly aggregations show mean fire size and total area burned were typically largest in June, followed by July and May. Fire frequency peaked in July, followed by June and May (Figures 3.8a - c). These findings are supported by daily resolution data. Given increased temporal resolution, Gaussian and splines models indicate a typical fire frequency peak between 184-185 DOY, mean fire size peak between 172-178 DOY, and area burned peak between 171-178 DOY (Figures 3.8d - f). The splines models shows early season spikes in fire frequency and areas burned corresponding with the 'spring dip' in foliar moisture content indicated in Figure 3.4c - a sharp early season increase in the frequency and size of fires (Van Wagner, 1967) – as well as a skewed fire frequency distribution. The log of mean daily fire size centers at ~ 5.5 ha, while the log of mean daily area burned centers at ~ 6.5 ha. The log of daily fire frequency shows a negative exponential distribution with a large λ value (Figures 3.8g - i). This matches the typical model for the probability distribution of time-since-event for Poisson processes, such as the probability of fire events, as in LANDIS-II (Yang *et al.*, 2004; Sturtevant *et al.*, 2009).



Figure 3.8 Monthly and daily patterns of fire frequency, mean fire size, and total area burned Canada-wide: (a) total area burned by month; (b) mean fire size by month; (c) fire frequency by month; (d) total area burned by ordinal date; (e) mean fire size by ordinal date; (f) fire frequency by ordinal date; (g) log of daily area burned; (h) log of daily mean fire size; (i) log of daily fire frequency; recorded fire detection dates are used to calculate DOY values; blue and red lines in (d-f) are cubic splines and a Gaussian distribution fit, respectively, while the red line in (i) is an exponential distribution fit

3.4 Discussion

The distribution of fire sizes follows well-documented power-law behavior common to selforganized systems (Malamud *et al.*, 1998; Reed & McKelvey, 2002), showing a heavy-tailed distribution. Previous theoretical work suggested that fire size distributions should fit a truncated Pareto distribution (Strauss *et al.*, 1989). However, an empirical study of the boreal mixedwood region of Alberta, using the former Large Fire Database for 1980-1998, showed optimal model fit with a truncated exponential distribution (Cumming, 2001). The above results suggest that the use of the AD2R goodness-of-fit statistic yields reasonable model fit with a Weibull distribution for the logarithm of fire sizes.

The results illustrate that the Alberta study area experienced a sharp rise in human-caused fires and area burned since 1990. This rise in human-caused fires likely combined with warming to facilitate lengthening fire seasons in both early spring and late fall (spring mean = +0.26 days/year; fall mean = +0.67 days/year; $R^2 = 0.83$; p < 0.001), in agreement with previous observations (Stocks *et al.*, 2002; Kasischke & Turetsky, 2006). The combined lengthening of fire seasons by 0.93 days/year is approximately five times faster than the Canada-wide average of 0.2 days/year (spring mean = +0.07 days/year; fall mean = +0.13 days/year; $R^2 = 0.57$; p < 0.001). This difference in fire season lengthening rates is likely attributable to rapidly increasing human activity in the study area. From the 1970s to the 2000s, human-caused fires accounted for a growing proportion of both annual fires (+9.8%) and area burned (+38.9%) for fires of known cause.

While the majority of area burned continues to be produced by lightning-caused fires nationally, this work observed a southern boreal shift to human-driven regimes characterized by more frequent, smaller fires near human activity earlier and later in the year. Climatic warming and a growing human presence are combining to create longer fire seasons, known to have challenged managers in recent years (Tymstra *et al.*, 2007). Fire frequency, area burned, and mean fire size were greatest in spring for all regions, representing 51% of fires and 63% of area burned, except the Rocky Mountain region, where fire frequency and size are greatest in summer due to temperature constraints. The largest fires occurred in May, consistent with a 'spring dip' in foliar moisture content. Although this episodic decline in foliar moisture content remains under investigation (Jolly *et al.*, 2014), it is an important physiological phenomenon in these forests (Little, 1970; Alexander, 2010; Finney *et al.*, 2013; Jolly *et al.*, 2014). Spring dip typically corresponds to intense crown fire activity, producing the largest and most severe fires of the fire season, which these data support.

Boreal fire regimes appear to be tracking a northward shift of boreal climatic conditions (Koven, 2013), reducing the size and severity of fires in the study area, as southern boreal ecosystems transition to Anthropocene fire regimes. Data from southeastern Canada indicate that the inmigration of temperate species into the southeastern reaches of the American boreal is already underway (Fisichelli *et al.*, 2014). Fisichelli *et al.* (2014) proposes that the reduced size of boreal fires, despite warming, is attributable to four key factors: (1) reduced surface fuel loads from frequent small human-caused fires; (2) increased fire suppression; (3) reduced crown fuels and/or forest fragmentation due to extractive industry activities; (4) a northward shift of boreal climatic

conditions, evidenced by changing wildfire patterns and climate-analogue vectors (Koven, 2013).

A recent study shows demographic ageing for the region (Zhang *et al.*, 2015), which may further reduce surface fuels prior to gap formation and understory reinitiation. Previous studies argue little effect of fire suppression on fire regimes in boreal and subalpine systems, as fuel moisture shows greater importance than fuel load in models, while neither fire frequency nor crown-fire potential were correlated with stand age (Johnson *et al.*, 2001). Nevertheless, a shift toward more frequent and smaller fires is evident for fire suppression regions (Kasischke & Stocks, 2000). Subsequent analyses of Ontario and Alberta provide contrasting views on the effectiveness of fire suppression in Canada (Bridge *et al.*, 2005; Cumming, 2005).

The increasing extent and magnitude of industrial activity, recreational usage, and road network expansion in formerly remote areas are combining with record temperature anomalies (Kamae *et al.*, 2014) to produce frequent ignitions and small fires around areas of human activity. Harvest operations are widespread in these forests, reducing canopy fuels while providing new ignition sources. A temporal lag of large fires following periodic pulses in pest populations (Kurz *et al.*, 2008) may amplify fuel conditions, fire regimes, and forest transition rates. Increasingly warm and wet conditions may favor deciduous species in the southern boreal (Terrier *et al.*, 2012), producing a negative climatic feedback through increased summer albedo (Amiro *et al.*, 2006) while reducing the rate of fire spread (Dash *et al.*, 2016).

An increase in fire suppression corresponds to an increasing human presence in previously remote forested regions, related to a 619% increase in Alberta's population during the 1921-2011 period (Statistics Canada, 2011) and economic growth from extractive industry activity (Cross & Bowlby, 2006). The advent of fire suppression is indicated in the historical record by reduced fire activity in the mid-20th century, following the 1950 Chinchaga wildfire in northwestern BC and western Alberta, the largest recorded wildfire in North American history. The disturbance legacy of this large fire is evident in the fire data, with few fires in its recovery zone since, while surrounding boreal areas have burned frequently. This may partially explain the observed decline in mean fire size, but does not explain accelerated decay in recent decades. The mean area burned by fires followed a similar trend, only rising in 1998 at the beginning of an exponentiallike increase in fire frequency, as described for other regions of the boreal (Kasischke & Turetsky, 2006; Kelly et al., 2013). Research for Alberta, conducted parallel to this work, selected a similar fire exclusion period start date of 1948, chosen for its correspondence with the establishment of the Eastern Rockies Forest Conservation Board. This work also shows a general lengthening of fire rotation periods compared to historical burn rates (Rogeau, 2016).

While one may infer that increased fire detection by satellites in recent decades (e.g., Landsat and MODIS) explains the observed rapid increase in fire frequency, decrease in fire size, and increase in latitude of large lightning-caused fires during this period, an analysis of the reported detection source rejects this hypothesis. Recent studies elsewhere in the boreal have shown the effect of human activity on fire frequency (Gaglioti *et al.*, 2016). While disturbance detection source or instrument (spaceborne remote sensing versus traditional air and ground methods)

shows a statistically significant relationship for fire size (p < 0.001) and latitude (p < 0.001), it is not enough to explain recent fire regime changes.

Mean decadal fire frequency and area burned show little change due to inclusion of spaceborne remote sensing over the past three decades (Figures 3.9a and 3.9b). Only mean fire latitude and size were significantly impacted by detection source (Figures 3.9d and 3.9c), with the effect greater for median values; an ANOVA indicates that latitude was more strongly affected than fire size (p = 7.39e-05; p < 2e-16). Since the 1970s, spaceborne detection methods appear to have substituted for traditional methods in northern regions. The mean decadal latitude of lightning-caused fires > 200 ha peaked in the 1970s, prior to broad use of spaceborne monitoring. Large lightning-caused fires were 2 degrees further north on average than fires \leq 200 ha, with a maximum of 5.3 degrees higher in the 1970s (WGS84 coordinates).



Figure 3.9 Fire statistics by reported detection source Canada-wide: (a) fire frequency by decade; (b) area burned by decade; (c) mean fire size by decade; (d) mean fire latitude by decade in WGS84 (decimal degrees) coordinates; blue = traditional detection source; red = modern remote sensing instruments

Thus, the contribution of spaceborne instruments to observed fire patterns remains small relative to traditional methods. In the 2000s, spaceborne monitoring was used to detect less than 9% of recorded fires in Canada, despite reliable Landsat and MODIS coverage for the period (Fensholt

& Proud, 2012; Wulder *et al.*, 2016). Even though spaceborne detection methods often produced a mean fire size twice that of traditional sources during the past decade, likely due to the a combination of the coarse resolution of the MODIS hotspot product (Hantson *et al.*, 2013) and increased coverage in the north, combined mean fire size sharply declined from 1990 onward. Furthermore, a rapid increase in the frequency of small human-caused fires in recent decades may drive the mean fire latitude southward toward population centers. While this is evident for fires of all sizes, large lightning-caused fires > 200 ha representative of classical boreal fire regimes generally increased in latitude over the past 90 years, indicative of high-latitude warming and an increased human presence in the north; disentangling these two factors, as well as the inherent sampling bias of non-satellite detection methods, presents an opportunity for future research. Nonetheless, a poleward shift of boreal fire regimes may correspond to a northward migration of boreal forests under warming (Koven, 2013; D'Orangeville *et al.*, 2016). Further research leveraging the Landsat or AVHRR record is required to confirm this dynamic.

While the inclusion of satellite disturbance detection data in recent decades should increase the apparent area burned, the opposite is observed across regional and national scales. At its peak prior to the current decade, in the 2000-2009 decade, spaceborne observations represented 8% of fire observations and 19.4% of the total area burned; omitting these observations leaves observed patterns generally intact. At its latitudinal peak in the 1990-1999 decade, spaceborne observations were 14% further northward on average compared to traditional detection methods. However, the true northward bias of spaceborne observations is likely greater than 14%, due to the range and thus inherently low variation of latitudinal values, which begin at the 49th parallel

and end near the 66th. Future studies of fire regime migration should rescale latitude values into local Cartesian coordinates using pan-boreal biome bounds.

For the study area in western Alberta, where recent changes to fire regimes are greater than national patterns, the detection source of fire observations shows no effect. According to the National Fire Database, none of the fires in the study area were sourced from modern remote sensing instruments. Hence, the analysis and related conclusions at the national and regional scales remain valid. At the national scale, while the subtraction of remote sensing detected fires would further increase FRP (reduce the rate of burning) during the Most Recent Decade, such large fires were often drawn on a map by hand in previous decades. Absent additional information, I estimate the historical fire size detection threshold at > 40 ha for the study area, based on strong correspondence to a gamma fire size distribution at this threshold (*K*-*S* = 0.028 $\overline{\omega} = 0.231$; $A^2 = 1.621$). Individual fire sizes between periods did not significantly differ in the mean, but did significantly differ in variance (*t* = 0.750, *p*-value = 0.454; *F* = 301.180, *p*-value < 2.2e-16).

Despite declines in fire size, latitude, and area burned for lightning-caused fires Canada-wide between the 1990s and 2000s reported here (mean = -422 ha/year; mean = -15.6 km/year; mean = -744,674 ha/year), a recent analysis of long-term warming suggests that these changes are not climatic (Karl *et al.*, 2015). Results for the study area show a regime shift toward humandominated fires in recent decades. By the 2000s, human-caused fires accounted for 58.1% of fires and 70.8% of area burned in the study area, surpassing the millennia-old dominance of large

lightning-caused fires. These findings contrast with Canada-wide changes during the same period, where human-caused fires declined in contribution to the area burned from 9% to 6%. While human activity has long played a role in fire regimes in the boreal (Bowman *et al.*, 2011), Anthropocene conditions have recently combined to produce fire regimes without historical analogue along the southern boreal. By analyzing fires > 200 ha before the 2000s, due to limitations in the former national fire database, previous studies (Stocks *et al.*, 2002; Kasischke & Turetsky, 2006) were unable to detect this regime shift. Fires < 200 ha in size represent 46.6% of fires in the study area (0.6% of area burned) and 59.3% of fires Canada-wide (0.9% of area burned). Thus, while large fires continue to explain the area burned, they fail to explain variation in fire frequency. As was shown, recent dramatic changes to fire frequency are not explained by the inclusion of spaceborne detection methods.

The Alberta study area results contrast to previous studies suggesting that lightning maintains a dominant role in annual area burned throughout the North American boreal (Stocks *et al.*, 2002; Kasischke & Turetsky, 2006). Here, more effective fire suppression (Cumming, 2005) appears overwhelmed by a combination of warming and increased human activity, beginning at an inflection point ~1970. At higher latitudes and elevation in Canada, warming has been shown to increase biomass production (Hantson *et al.*, 2015; D'Orangeville *et al.*, 2016), partially explaining an increased area burned here under the assumption of fuel limitations.

An increased annual rate of fire frequency since 1980 corresponds with population growth and increased economic activity in Alberta (Statistics Canada, 2011) combined with rapid warming (Karl *et al.*, 2015). Regional and national warming is evidenced by IPCC findings

(Intergovernmental Panel on Climate Change, 2014), previous fire regime analyses (Wotton & Flannigan, 1993; Tymstra *et al.*, 2007), and indirectly by aforementioned observed changes to fire regimes Canada-wide. Human activity may explain most of the increase in the frequency of small fires near roads and surface water, while warming also increases the frequency of lightning strikes and severity of fire weather conditions (Krawchuk *et al.*, 2009).

Although mean annual fire size and area burned declined in the study area over the past decade, the effects of warming on burning appear to have been amplified, rather than attenuated, by human activity. The data do not appear to support a previously reported non-linear U-shaped relationship between human activity and the frequency of fire ignitions (Syphard *et al.*, 2007; Parisien *et al.*, 2012). Due to the relative remoteness of Alberta's burnable land and small urban areas (compared to populous regions, such as California), there appears to be an approximately linear, rather than a U-shaped, distribution between fire frequency, area burned, and human activity. The study area results appear similar to findings for the Alaska boreal (Gaglioti *et al.*, 2016). Successful fire suppression efforts (Cumming, 2005) may partially account for the decline in mean fire size nationally and in Alberta, as well as a declining national annual area burned, despite warmer conditions with more frequent human-caused ignitions. High-frequency small fires and extractive activities have likely also reduced forest fuels, which may together explain an observed demographic shift in these forests (Zhang *et al.*, 2015).

These patterns differ from other recent studies in the North American boreal including Alaska (Stocks *et al.*, 2002; Kasischke & Turetsky, 2006), which show a rapid rise in mean fire size and annual area burned, based on analyses of previous historical fire database versions. The results

presented herein contradict both of these notions across regional and national scales, showing greater agreement with paleoreconstructions from Alaska (Kelly *et al.*, 2013), studies on the relationship between human activity and fire frequency in the Alaskan boreal (Gaglioti *et al.*, 2016), and recent analyses indicating the presence of negative wildfire feedback mechanisms in the North American boreal (Héon *et al.*, 2014; Rogers *et al.*, 2015).

Future studies should assess whether these trends are prominent across North America and northern forests globally. A coupled climatic-human activity dynamic appears to explain the observed changes in fire distribution. This is supported by a recent study showing a global human-driven reduction in burned area (Andela *et al.*, 2017). Studies should seek to better delineate the causes of these patterns in terms of the precise roles of climatic, human, and forest fuels mechanisms responsible. Of primary interest is the unexplained inflection point observed around 1990, for both the Alberta study area and across Canada, related to a rapid increase in fire frequency, reduced mean fire size, and reduced area burned, despite warming. This poorly understood change-point appears to explain many observed dynamics. While historical landcover and demographic change undoubtedly also play a critical role in explaining variations in fire patterns, a dearth of detailed historical maps makes it difficult to assess, with remote sensing records absent earlier than a few decades into the past. Future studies should investigate the coupling of climatic change and human activity to better understand present and future conditions, until more precise maps of landcover history are available.

Results indicate that the application of historical climate-fire correlations to general circulation model projections, absent anthropogenic trajectories, carries diminished predictive power in the

Anthropocene. Short-term boreal ecological forecasts should include spatially explicit dynamics of human-caused ignitions, fire suppression, and structural-demographic changes to forest fuels related to increasing human activity. Long-term forecasts should further include compositional change impacts on fuel conditions (Terrier *et al.*, 2012), as well as coupled climate feedbacks (Amiro *et al.*, 2006).

These requirements may motivate the development of new terrestrial biosphere models incorporating disturbance, succession, and energy partitioning processes, similar to recent hybrid models (Bond-Lamberty *et al.*, 2005; Scheller *et al.*, 2007). The anthropogenically focused Community Earth System Model (CESM1) revisions (Li *et al.*, 2013a) and Human-Earth System Fire (HESFire) model (Le Page *et al.*, 2015) represent such an approach, as do physically based three-dimensional regional models such as WRF-Fire (Coen *et al.*, 2012) and HIGRAD/FIRETEC (Colman & Linn, 2007). New hybrid models may rely on partial differential equation representations of individual tree dynamics (Moorcroft *et al.*, 2001; Purves *et al.*, 2008; Strigul *et al.*, 2008; Medvigy *et al.*, 2009), as well as the use of machine learning to represent pattern-based processes, as first presented herein. In the following chapter, I assess the effects of warming on tree species regeneration to account for potential long-term changes in canopy light transmission.

3.5 Limitations

This research relies on the best available fire history data for Canada (Stocks *et al.*, 2002; Parisien *et al.*, 2006; Burton *et al.*, 2008). Yet, the data contain known sampling biases toward lower latitudes, larger fires of longer duration, and years subsequent to ~ 1960, particularly for data on fire seasonality and cause. Accordingly, 95% confidence intervals are used for regression models to display the relative uncertainty in model estimates over time. For improved estimates of parameter uncertainty or model error, future studies may rely on Bayesian methods (e.g., Gaussian process regression or Hamiltonian Monte Carlo). These methods are also useful for parameter estimation and uncertainty analysis with ecosystem models (Kennedy & O'Hagan, 2001; Larocque *et al.*, 2008; Nagel, 2017). While modern spaceborne imaging systems such as Planet Doves (Hand, 2015) and recent computer vision techniques (LeCun *et al.*, 2015) are poised to alleviate sampling biases in historical fire maps over time by improving the spatiotemporal resolution of detection accuracy, the temporal depth of this remote sensing record remains limited.

Chapter 4: Tree Species Regeneration Modeling¹

4.1 Introduction

Tree development and phenology are related to climate through evolutionary controls, influencing the early niche space of trees, with plasticity potentially providing a buffer to maintain fitness (Aitken *et al.*, 2008; Vitasse *et al.*, 2013). Important tree development and phenology events include germination, establishment, bud burst, growth, bud set, leaf senescence, seed fall, and dormancy, among others (Walck *et al.*, 2011; Richardson *et al.*, 2013). Climatic change can uncouple the phasing of fine-scale seasonal weather variations with developmental processes and phenology beyond the range of plasticity, reducing regeneration rates (Fridley, 2012; Richardson *et al.*, 2013). This phase uncoupling can alter the duration of important phenological processes and timing of phenological events.

The widespread adaptation of trees to local climatic conditions (Alberto *et al.*, 2013) indicates that tree phenology is intricately tuned to optimize fitness for local environmental conditions through gene expression, posttranslational modification, and, genetic and epigenetic inheritance (Liu *et al.*, 2010; Cooke *et al.*, 2012; Matzke & Mosher, 2014). Environmental effects are estimated to exert greater influence on plasticity than genetics in northern forests (Vitasse *et al.*, 2013), while phenotypic variation reflecting phylogeographic origins (Alberto *et al.*, 2013) is not necessarily adaptive (Duputié *et al.*, 2015). Extreme weather events, such as frost or drought,

¹ This chapter is published in *Ecological Modelling*: (Erickson *et al.*, 2015)

occurring at critical times during tree development can have strong demographic effects on forests. Given the importance of fine-scale climatic and phylogenetic variability, high temporal resolution climate data (Cook *et al.*, 2010) along with a range of aggregate species tolerances can aid in the modeling of these dynamics at the landscape scale, where individual- or population-level data is seldom attainable.

Here, it is hypothesized that warmer conditions combined with changes in soil water balance (Dobrowski *et al.*, 2013; Piedallu *et al.*, 2013) and more rapid and severe extreme weather events (Allen *et al.*, 2010; Kamae *et al.*, 2014; Trenberth *et al.*, 2014) are altering regeneration patterns in northern forests. Recent empirical evidence suggests that this shift is already occurring (Lenoir *et al.*, 2009; Urbieta *et al.*, 2011; Boisvert-Marsh *et al.*, 2014; Zhang *et al.*, 2015). However, direct measurement remains confounded by forest turnover, which can increase the amount of space available for recruitment (Zhu *et al.*, 2012, 2014; Park Williams *et al.*, 2013; Woodall *et al.*, 2013). Additional confounding factors include patterns of fine-scale climate (Dobrowski *et al.*, 2013) and ontogenetic niche variation, whereby the niches of species can change throughout development (Cavender-Bares & Bazzaz, 2000; Eriksson, 2002; Donohue *et al.*, 2010; Niinemets, 2010b; Bertrand *et al.*, 2011a; Urbieta *et al.*, 2011).

Here, it is suggested that changes to tree regeneration throughout northern forests in recent decades have been driven by interactions between climatic change and local soil patterns. To test this hypothesis, a species-specific ecophysiological model that explicitly represents major tree regeneration processes is used, based on forest gap models. The model is parameterized for tree species and soil textural classes across a 25.2 million ha study area in Alberta, Canada,
encapsulating an important elevational and latitudinal gradient. Daily resolution historical weather station data is used for three decadal periods over the last century, and for the most recent decade, to model the effects of climatic change on forest regeneration throughout the past 90 years. A previous version of the TACA model used in this study is combined with LANDIS-II to model forest dynamics in Chapter 5. Subsequent chapters develop and apply models for the dynamic simulation of understory irradiation.

4.2 Methods

The methods and Alberta study area are described in previous chapters. A model parameterization diagram is provided below (Figure 4.1), showing alternate climate data sources for the use of monthly or daily temporal resolutions (Erickson *et al.*, 2015). Here, daily weather station data was used to provide the most representative conditions, important for phenological models. In summary, historical daily weather station data was acquired from the NOAA Global Historical Climatology Network Daily (GHCN-D) data set. The data was processed using custom scripts available in reduced form in the *rnoaa* package for R (Chamberlain *et al.*, 2016).



Figure 4.1 TACA-GEM parameterization scheme for Canada

Weather stations were spatially filtered and aggregated within each Natural Subregion of Alberta (Natural Regions Committee, 2006), before calculating median daily weather station values for each of these biogeoclimatic regions. Soil textural class information for each biogeoclimatic region was calculated from the CanSIS Soil Landscapes of Canada (SLC) v3.2 data set. Additional values used from SLC data include soil rooting zone depth, coarse fragment percent, available water storage capacity, and derived percolation rate. Latitude values are used for solar modeling in the Hargreaves-Samani soil moisture submodel.

A regression analysis was conducted to determine the relative importance of different mechanisms in explaining regeneration values, filtering covariates at a threshold of $|\mathbf{r}| > 0.7$ (Dormann *et al.*, 2013), before filtering variables at a significance threshold of $p \le 0.05$. I utilized R² partitioned by averaging over orderings of regressors (LMG) and proportional marginal variance decomposition (PMVD) with the R *relaimpo* package (Grömping, 2006) to determine predictor variable relative importance in linear regression.

4.3 Results

The results show that tree regeneration suitability, modeled as the probability of reaching an age of ten years, declined across the 1923-2012 period for most species in the Alberta study area (Figure 4.2). The establishment of new cohorts for most species was increasingly unlikely. Adding extreme climatic events (i.e., drought and frost) further reduced regeneration conditions, which were poorest in recent decades. It is estimated that the regeneration niches of extant and adjacent tree species are largely out of equilibrium with climatic conditions and have been for decades, with regeneration conditions likely to worsen in the coming years. The frequency and magnitude of drought following germination was the most limiting factor affecting regeneration conditions, due to reduced soil moisture.



Figure 4.2 Modeled mean change in species regeneration across regions for the full period; probabilities were output from TACA-GEM simulations for a 10-year period

The most recent period modeled, 2003 to 2012, shows a slight deceleration in the rate of regeneration suitability change, likely attributable to a slowdown in warming (Kosaka & Xie, 2013). A significant mean decline in regeneration suitability was predicted across the full study period. Compared to simulations without extreme events, including extreme events in the simulations marginally decreased the probability of establishment (mean = 0.085, σ = 0.220; mean = 0.059, σ = 0.216) and the change in establishment across the full study period (mean = -0.138, σ = 0.228; mean = -0.142, σ = 0.248). More frequent drought, diminished germination success, and lengthened bud dormancy resulted in an overall decline in regeneration suitability. Species regenerational responses varied across space and time, often responding similarly in direction to climatic and edaphic conditions within regions and time periods (Figure 4.3). These

trends are indicative of directional climate change, evident in a similar direction of species responses across regions.



Figure 4.3 Mean change in species regeneration probability, 1923-1952 to 1983-2012 period, including extreme events for the five regions; species that consistently failed to regenerate appear unchanged; a value of 1.0 represents a 100% change in regeneration probability; probabilities were output from TACA-GEM simulations for a ten year period; solid red = -1.0; none = 0; solid green = 1.0

The boreal forest and foothills regions showed a transition in the regeneration niche of species toward deciduous poplar species, with improved suitability for Engelmann spruce (*Picea engelmannii*), a high altitude montane species. Other regions indicated regenerational improvements for pine species that are more resilient to drought. The grassland region, which has the lowest regeneration suitability overall due to high hydraulic conductivity, showed a transition toward grand fir (*Abies grandis*), trembling aspen (*Populus tremuloides*), and whitebark pine (*Pinus albicaulis*). The parkland region showed the strongest net improvement in regeneration conditions overall, transitioning toward grand fir, ponderosa pine (*Pinus ponderosa*), and limber pine (*Pinus flexilis*). The Rocky Mountain region showed the most widespread regenerational decline, symptomatic of relatively severe soil moisture limitations. Overall, the highest elevations experienced the greatest regenerational decline, due to a shift in soil water availability toward lower elevations.

The impact of directional warming on species-specific physiological drought frequency varied considerably across regions, due to interactions with regional soil properties, precipitation patterns, and snowmelt timing. Results indicate that in the boreal forest, grassland, and Rocky Mountain regions, the 1983 to 2003 period crossed species drought tolerance thresholds with the greatest frequency, while showing an increased incidence of frost after bud flush, indicative of increased temperature variability. Modeled regeneration suitability for the 2003 to 2012 period reflects a temporary slowdown in warming combined with increased high-precipitation events, in agreement with Clausius-Clapeyron scaling based predictions under warming and observations for the region (Trenberth *et al.*, 2003; Wentz *et al.*, 2007; Allan & Soden, 2008; Trenberth, 2011).

90

The biophysical niche space of species (e.g., species tolerances) accounted for a significant amount of variation in regeneration responses ($p \le 0.001$). However, species often responded with similar directionality to climatic and edaphic changes, particularly for drought and turgor loss. While inter-specific variability was clearly present (mean $\sigma = 0.179$), changes to regeneration suitability were better explained by spatiotemporal variation ($p \le 0.001$; mean $\sigma =$ 0.198). In terms of regeneration, gymnosperms fared similarly to angiosperms across all periods and regions (gymnosperm mean = 0.18, $\sigma = 0.225$; angiosperm mean = 0.14, $\sigma = 0.198$), while the difference diminished with the inclusion of extreme effects (gymnosperm, mean = 0.14, $\sigma =$ 0.221; angiosperm, mean = 0.12, $\sigma = 0.197$). Species, regions, and time periods showed greater distributional heterogeneity than differences between conifers and angiosperms.

A fixed-effects analysis of variance (ANOVA) showed a significant relationship between variance in regeneration probabilities and species, period, region, subregion, growing degree days, killing frosts, drought frequency, germination frequency, germination events, and stratification ($p \le 0.001$), and a less significant relationship with spermatophyte taxon, ordinal date of bud break ($p \le 0.01$), and physiological dormancy ($p \le 0.05$). Chilling requirements met, frost frequency, frost days, frost events, and turgor loss point frequency did not show a significant relationship with species regeneration probabilities (p > 0.05). The frequency of germination success for species varied across the study period, while generally declining. ponderosa pine (*Pinus ponderosa*), an arid fire-adapted specialist, experienced the greatest reduction. With extreme events for all species and periods, both metrics indicated that germination frequency (LMG = 0.28; PMVD = 0.31), drought frequency (LMG = 0.08; PMVD = 0.16), number of growing degree days (LMG = 0.06; PMVD = 0.07), and turgor loss point frequency (LMG = 0.05; PMVD = 0.001) were the most important mechanisms determining regeneration responses, providing details that were absent in the previously described ANOVA. From these metrics, a multi-decadal climatic warming signal is evident, with heterogeneous regional implications.

The modeled frequency of reaching species' turgor loss point and exceeding physiological drought tolerances increased for most species in most regions over the full study period. Turgor-loss-point frequency was relatively homogeneous across species, exhibiting a generalized model response of turgor loss point and leaf water potential at 50% loss of hydraulic conductivity, measures of leaf vulnerability to cavitation that are functions of xylem structure (Bartlett *et al.*, 2012). Species physiological drought frequency was heterogeneous across regions and homogeneous within regions. Specific regeneration probabilities fluctuated primarily in response to climatic change relative to soil moisture conditions. Black cottonwood (*Populus trichocarpa*) and balsam poplar (*Populus balsamifera*) exhibited the greatest sensitivity to drought, as shown in empirical studies (Nitschke *et al.*, 2012). Douglar-fir (*Pseudotsuga menziesii*) and ponderosa pine were the most tolerant of increasingly frequent and severe drought conditions. Species regeneration values varied by species, region, and time period (Figure 4.4).



Figure 4.4 Regeneration probability boxplots: (a) by period; (b) by region; (c) by species; boxplots include native species and potential migrants; boxplots display the median, hinges as the first and third quartiles, whiskers as the product of 1.5 and the interquartile range, and outlier points

At higher elevations and latitudes, modeled frost events following both bud flush and germination events declined in the most recent decades. However, frost events more frequently

exceeded specific frost tolerance threshold parameters, indicative of warming and greater temperature variability. More frequent and severe modeled physiological drought conditions were the main factor limiting modeled establishment values in the boreal, grassland, and parkland regions, with modeled soil moisture particularly meager in the latter two regions due to the high hydraulic conductivity of glacial and aeolian deposits. The inclusion of extreme weather events particularly reduced modeled establishment conditions for fir and spruce species with lower drought tolerance – but similar frost tolerance – than pines. The modeled number of growing degree days and probability of germination success also declined. In essence, a phase decoupling of climatic patterns and species phenology in time and space seems likely from our model results for multiple regenerational processes.

4.4 Discussion

Warmer and more variable climatic conditions are diminishing the conditions for extant tree species regeneration in Alberta, Canada. As multi-decadal warming continues unabated, modeled tree species are likely to fail to regenerate. An increasing magnitude of climatic disequilibrium is likely to reduce forest regeneration, which may be initiated through climate-driven changes to disturbance regimes (Magnani *et al.*, 2007). Some studies indicate that forest regeneration conditions should be improving at higher elevations and latitudes (Brubaker, 1986; Lenoir *et al.*, 2009) and declining in lower elevation forests (Loarie *et al.*, 2009; Bertrand *et al.*, 2011b), while others provide mixed results potentially related to changes in human activity (Boisvert-Marsh *et al.*, 2014). Here, the findings support a relative improvement in regeneration conditions in low-elevation northern forests (Crimmins *et al.*, 2011; Zhu *et al.*, 2012, 2014; Dobrowski *et al.*, 2013). It was found that changes to soil moisture conditions drove species regeneration niches

94

toward the foothills and parkland regions, indicating that changes to soil water balance may drive future species migrations under warming (Crimmins *et al.*, 2011; Piedallu *et al.*, 2013). The inclusion of soil water balance is particularly important in mountain watersheds (Hwang *et al.*, 2014) and in the Canadian boreal forest (Barnett *et al.*, 2005), as it is the key limiting factor driven by climate. The model results provide a potential explanation of complex tree regeneration patterns observed in previous studies (Urbieta *et al.*, 2011; Zhu *et al.*, 2012, 2014; Woodall *et al.*, 2013; Boisvert-Marsh *et al.*, 2014; Zhang *et al.*, 2015), providing direction for future empirical work.

A recent study (Zhang *et al.*, 2015) provides empirical support for the modeling results. Using permanent sample plot data for western Canada, their study shows that competition plays a stronger role in local forest dynamics than climate, long demonstrated in gap and hybrid model studies based on theoretical and empirical formulations (Shugart, 1984; Deutschman *et al.*, 1997; Schumacher *et al.*, 2004). The Zhang *et al.* (2015) study also modeled trends in recruitment rates for western Canadian provinces, based on empirical data. The study shows an overall decline in recruitment across regions, with a linear decline exhibited in Alberta. In agreement with the results presented here and contrary to findings for the Sierra Nevada range (Dolanc *et al.*, 2013), the most dramatic reduction in recruitment and growth rates occurred in the high-elevation montane Cordillera region (Zhang *et al.*, 2015). The present study indicates that this reduction in recruitment is likely due to changes in soil water balance, driven by the interaction of warming and soil textural properties.

In the coming years, increases in the frequency of anthropogenic disturbances (Kurz *et al.*, 2008; Park Williams *et al.*, 2013) may accelerate the currently delayed regenerational response of forests by increasing the number of sites available for recruitment. Concurrently, warmer and wetter conditions projected for northern forests (Trenberth, 2011) may accelerate recruitment by increasing the rate of forest turnover (Zhu *et al.*, 2014). Due to the long-lived nature and relatively rapid dispersal ability of trees (Clark *et al.*, 1998), future compositional changes will likely occur in pulses as climatic change intensifies. Directional changes to the region's forests may occur through rare long-distance migration events (Clark *et al.*, 1998) by species better adapted to low soil moisture, producing no-analogue communities.

Future empirical studies should investigate evidence of regenerational change in northern forests with ground plot data in connection with directly measured local climate data. Future modeling studies should incorporate important forest dynamics, such as competition, dispersal, and disturbance by fusing theoretical and empirical formulations with detailed remote sensing structural measurements. An improved understanding of forest regeneration may help forest managers to meet multiple-use goals, while providing a more complete picture of biospheric climate feedbacks. In the next chapter, we fuse the TACA model with LANDIS-II to simulate a full suite of forest dynamics in the western Alberta study area.

4.5 Limitations

The TACA-GEM model application presented herein relies on species-specific parameters that include observations and species for adjacent regions, including southeastern British Columbia. Some of these species may be adapted to different conditions than those of Alberta, due to

variation in genes or their expression. Other species parameters for TACA-GEM were roughly estimated from species ranges for previous studies (Burton & Cumming, 1995; Cumming & Burton, 1996). Meanwhile, a number of parameters were derived from species compendiums that provide single values for the continent or country (Burns & Honkala, 1990; Farrar, 1995a; Klinka *et al.*, 2000), which is biologically unrealistic regardless of the metric. The effect of these species parameter simplifications is unknown, but may potentially reduce the number of realized niches due to convergence in the parameter space.

Soil and daily weather data used to calculate parameters for TACA also contain limitations. Soil data (Soil Landscapes of Canada Working Group, 2010) was compiled from existing soil survey maps (gridded plot data) at a representative fraction of 1:1000000. Meanwhile, statistically filtered GHCN-Daily weather data (Menne *et al.*, 2012; Hausfather *et al.*, 2016) still contains stations with sporadic temporal coverage in the region; these stations were filtered out if more than half of the observations were missing, while smaller gaps were imputed. Both data may also contain unknown sources of noise or bias (e.g., the proximity of weather stations to roads or non-anthropogenic low albedo surfaces, or topographic effects on solar radiation). As such, a considerable degree of uncertainty is expected for TACA model parameters. Again, Bayesian methods should be used in future studies to jointly estimate parameters and their uncertainties.

Validation of TACA-GEM results was limited to an analysis of general trends provided in Appendix F, which may be expanded in future work. The validation exercise was complicated by changes in forest canopy conditions over the period, lending additional uncertainty to the results. Meanwhile, validating each component of TACA-GEM for each species and bioregion is currently infeasible. Other likely sources of TACA-GEM model error stem from the simplification of complex physical processes into logical or linear model components, as well as knowledge gaps for specific processes; such errors may propagate within the model, requiring further analysis. To account for variation internally, the TACA model is probabilistic rather than deterministic. As such regeneration models grow in complexity, parameter and model uncertainties warrant greater consideration.

Chapter 5: Forest Landscape Modeling

5.1 Introduction

Seasonal fire and climate cycles played a central role in the evolution of boreal forests. Here, large stand-replacing fires have been the dominant disturbance type for millennia (Rowe & Scotter, 1973; Davis & Shaw, 2001; Rogers *et al.*, 2015), while temperature conditions can be severe. In North America, boreal tree species evolved a diversity of adaptations to fire, including vegetative resprouting, cone serotiny, aerial seed banks, fire-enhanced regeneration, and increased flammability (Schwilk & Ackerly, 2001; Keeley *et al.*, 2014; Pounden *et al.*, 2014; Rogers *et al.*, 2015). These adaptations are believed to impart trees with a competitive advantage in the successional phases of disturbance and regeneration.

Trees in the Canadian boreal have high intraspecific genetic variation, exhibiting a high degree of local adaptation (Davis & Shaw, 2001). Trees respond to periodic climatic cycles *in situ* via phenotype plasticity (e.g., gene expression) and to long-term climatic change through migration (Aitken *et al.*, 2008; Matzke & Mosher, 2014). Extreme events beyond physiological tolerances produce mortality. While the distribution of tree species correlates well with historical climate at coarse spatiotemporal scales, disturbance responses dominate fine-scale dynamics (Prentice, 1986). Trees often lag behind climate-space optima (Bertrand *et al.*, 2011b), requiring mortality and recruitment to transition forest composition toward optimality.

When temperature shifts outpace the availability of open niches for plant regeneration given seed dispersal rates (Clark *et al.*, 1998), climatic change may occur too rapidly for migration to track

warming. Given migration failure, *in situ* regeneration conditions can become increasingly suboptimal (Nitschke & Innes, 2008). When multiple species fail to track warming, absent new migrants, short-term forest decline can result, which may explain recent empirical observations (Hogg *et al.*, 2008; van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Mascaro *et al.*, 2011; Michaelian *et al.*, 2011; Martínez-Vilalta *et al.*, 2012; Vilà-Cabrera *et al.*, 2013; Worrall *et al.*, 2013; Cohen *et al.*, 2016). Over longer time-scales, short-term forest decline may give way to compositional or landcover change. A reduction in mortality rates (e.g., due to fire suppression) may temporarily inhibit these changes, obfuscating the latent processes in empirical data.

Given previous results (Chapters 3 and 4), these observations, and, recent climate and fire trends, a decline in regeneration potential is hypothesized to intensify the reduction in total forested area produced by severe burning. Due to an unavailability of empirical plot data and the challenge of controlling variables in these data, this hypothesis was tested with a numerical simulation model. The limitations of this work stem from the uncertainties of this experiment design related to model simplification, parameterization, and optimization.

Due to an accelerated pace of high-latitude warming, boreal climatic conditions are shifting northward at a rate of 430 m yr⁻¹ (Loarie *et al.*, 2009; Hamann *et al.*, 2015). The high rate of recent warming surpasses paleo-rates of species range shifts inferred from the pollen record, while landscape fragmentation may pose a constraint on migration (Lazarus & McGill, 2014). While direct measurements of species migrations and other forest dynamics remain limited by the long timescales of the biological processes involved, simulation models provide an attractive tool for inference. A combination of simulations and adaptive management (Holling, 1978) may eventually facilitate ecological optimization to achieve management goals, such as maximizing carbon storage.

Here, forest compositional and structural changes arising from past-century climate and fire trends are simulated for the Alberta study area. A hybrid forest landscape model is initialized at year 2000 conditions using modeled tree species distributions (Gray & Hamann, 2012) classified into Canadian landcover classes. Four historical climate, fire, and human activity periods were used to simulate past-century forest successional trajectories. Differences in stand conditions are assessed after fifty years of simulation, allowing for ten years of model spin-up. By simulating the historical scenarios, the resilience of extant forests to the persistence of past-century climate and fire conditions is determined.

5.2 Methods

The Alberta study area is detailed in previous chapters. Using the Natural Regions and Subregions of Alberta (Natural Regions Committee, 2006), the majority of the study area is located in the Boreal region (46.2% of the study area), followed by the Foothills (25.5%) and Rocky Mountain (19.5%) regions. The Parkland and Grassland regions together comprise less than 10% of the study area, making over 90% of the study area boreal and montane, characterized by a strong elevational gradient.

The Tree and Climate Assessment (TACA) establishment model (Nitschke & Innes, 2008; Mok *et al.*, 2012) was combined with the Landscape Disturbance and Succession (LANDIS-II) model (Scheller *et al.*, 2007) to simulate forest dynamics across the 25.2 million hectare study area at

one-hectare resolution. Model parameterization is detailed in Chapter 2. While the study area comprises 25.2 million one-hectare cells, 18 million of these cells are active (containing natural vegetation), after masking out developed land, waterbodies, and bare rock.

TACA and LANDIS-II previously underwent validation and sensitivity analysis in North America (Mladenoff *et al.*, 1993; Scheller & Mladenoff, 2004; Scheller *et al.*, 2007; Nitschke & Innes, 2008; Nitschke *et al.*, 2008, 2012; Simons-Legaard *et al.*, 2015). Thus, given a paucity of validation data for Alberta, many model subsystems were not locally validated. Within LANDIS-II, two types of wildfire models are applied: (1) a statistical fire-spread model; (2) a semimechanistic cost-path fire-spread model incorporating fire weather inputs and landcover change to dynamically update site fuel conditions. The semi-mechanistic fire model was developed from forest fire data for Canada (Wagner, 1977; Van Wagner, 1987, 1989; Forestry Canada Fire Danger Group, 1992). For each fire model, a new optimization algorithm based on stochastic gradient descent (Widrow & Hoff, 1960) is applied for parameter tuning, overcoming a longstanding practical limitation of implementing large simulations (He & Mladenoff, 1999). The parameterization and simulation framework is shown below (Figure 5.1).



Figure 5.1 Model parameterization, fusion, and optimization of TACA-EM and LANDIS-II

TACA was run separately for each of the climate scenarios and biogeoclimatic regions (see previous chapter). Resultant tree species establishment probabilities were input into LANDIS-II with other required parameters for each scenario. Simulations were run for a duration of 50 years, with the first 10 years used for model spin-up, in order to produce empirical disturbancerelated age class patterns. This produced more realistic-appearing initial stand conditions, given the absence of age class data for the region and the importance of fire in shaping age class patterns (Boychuk & Perera, 1997). The LANDIS-II model was initially run at 500 m resolution to accelerate convergence of parameter optimization using an algorithm based on stochastic gradient descent (Widrow & Hoff, 1960), shown in yellow in Figure 5.1. The algorithm relies on principles similar to other iterative gradient-based optimization methods. Parameter values are updated in the direction and magnitude of reduced model error (e.g., using only positive first-derivatives), iteratively updated based on previous simulations. The optimization method is widely used alongside the backpropagation algorithm (Dreyfus, 1962; Linnainmaa, 1970) in deep learning for hyperparameter tuning (LeCun *et al.*, 2015). Final model runs were conducted at 100 m resolution to balance computational cost and grain size needed to capture the effects of fine-scale disturbance patterns, approaching the precision limits of model design. The parameter optimization technique dramatically reduced the error of fire simulations ($\overline{R^2} = 0.96$; $\Delta R^2 = +0.14$), returning values nearing Pareto optimality for the two model parameters without the computational expense of exhaustive grid search.

5.2.1 Historical Fire Regimes

Regional fire regime parameters were derived from an analysis of Canadian National Fire Database (NFDB) spatial wildfire data, presented in Chapter 3. These data were produced from an analysis of aerial and satellite imagery together with field plot data.

5.2.2 Model Scenarios

Fourteen 50-year simulations were run at an annual resolution, corresponding to four historical periods, three model configurations, and two extremes scenarios, to determine forest resilience under the persistence of past-century climate and fire trends. A 50-year simulation duration was

selected for its relevance to management timescales and balance between initial conditions and model behavior (e.g., equilibrium at 500-year timescales), as error is known to propagate over time in simulations, increasing uncertainty. Historical climate and fire conditions were classified into the following three 30-year periods: Pre-Suppression Era (1923-1952), Early Suppression Era (1953-1982), and Global Change Era (1983-2012), corresponding to changes in fire suppression, climate, and human activity. A Most Recent Decade (2003-2012) scenario was included to encapsulate current regimes, based on an observed inflection point in fire frequency and size.

With the exception of the Extremes scenarios, each of the four scenarios was run under three different model configurations: (1) Succession only (*ao*); (2) Succession with Base Fire (*ao-bf*); (3) Succession with Dynamic Fire (*ao-dffs*). This was done to control for the effects of climate and fire on forest structural and compositional change. For the two Extremes scenarios, Pre-Suppression Era fire regimes – the most severe burn rate – were applied to Most Recent Decade climatic conditions – the warmest conditions – to determine the relative contributions of climate and fire on forest compositional and structural change in the most extreme cases. The simulation scenarios (configuration and period combinations) are abbreviated as shown below (Table 5.1).

LANDIS-II Configuration	Period	Abbreviation		
Age-only succession	1923-1952	ao-1923-1952		
Age-only succession	1953-1982	ao-1953-1982		
Age-only succession	1983-2012	ao-1983-2012		
Age-only succession	2003-2012	ao-2003-2012		
Age-only succession with base fire	1923-1952	ao-bf-1923-1952		
Age-only succession with base fire	1953-1982	ao-bf-1953-1982		
Age-only succession with base fire	1983-2012	ao-bf-1983-2012		
Age-only succession with base fire	2003-2012	ao-bf-2003-2012		
Age-only succession with dynamic fire	1923-1952	ao-dffs-1923-1952		
Age-only succession with dynamic fire	1953-1982	ao-dffs-1953-1982		
Age-only succession with dynamic fire	1983-2012	ao-dffs-1983-2012		
Age-only succession with dynamic fire	2003-2012	ao-dffs-2003-2012		
Age-only succession with base fire	Extremes	ao-bf-extremes		
Age-only succession with dynamic fire	Extremes ao-dffs-extremes			

Table 5.1 Simulation scenario codes based on model configuration and period

For each scenario, spatiotemporal metrics indicative of directional change at the landscape scale are tracked, including latitudinal and elevational variation in species regeneration and relative abundance, as well as changes to forest structure (inferred from site age classes) and area. A focus on climate and fire is intended to represent changes related to these two fundamental drivers of boreal forest ecosystems.

5.3 Results

Adjusted for area, across all periods, the Boreal region had the shortest fire rotation period (FRP), followed by the Foothills and Rocky Mountain regions. The lower-elevation Parkland region had the longest FRP, followed by the Grassland region (Figure 5.2f). The Boreal shows the greatest area burned and, by a lower margin, greatest proportion of the study area (Figures 5.2d and 5.2c). FRP increased across the three periods, indicative of diminished burning (Figure 5.2e). Between the Pre-suppression and Global Change Eras, FRP lengthened the most in the Boreal and Foothills regions while declining the most in the Parkland and Rocky Mountain regions (Figure 5.2b). An analysis at the finer scale shows an acute increase in the FRP for the Peace River Parkland and Dry Mixedwood subregions, while the Upper Foothills subregion declined. All higher elevation subregions showed intensifying burning indicative of warming (Figure 5.2a).



Figure 5.2 Historical fire statistics by region and time period; change metrics are computed between the periods 1923-1952 and 1983-2012: (a) Fire rotation period (FRP) change by subregion; (b) FRP change by region; (c) proportion of study area by region; (d) area burned by region; (e) FRP by period; (f) FRP by region; Montane region = Rocky Mountain; red = decline; green = increase

The stochastic gradient descent-based optimization algorithm greatly improved fire model calibration ($\overline{R^2} = 0.96$; $\overline{\Delta R^2} = +0.14$), yielding simulation results closely matching observations from the Canadian National Fire Database. Based on a visual analysis of simulation results for maximum cohort age classes resulting from fire region parameterizations, the boreal region exhibited the greatest fire-related structural (i.e., mean and standard deviation of site age class) change across scenarios. Frequent large fires during the Pre-Suppression Era produced a homogeneous structural patchwork of forests, while frequent small fires in the two most recent scenarios produced a diffuse forest landscape age pattern and decline in area burned, corresponding to observed empirical changes.

While base fire better fit aggregate 30-year statistics for observed fire regimes, time-series comparisons between simulated and observed regimes showed that dynamic fire better captured the mean and variability for both annual fire frequency and area burned. Wavelet spectra for annual 1-D time-series showed higher and lower wavelet dissimilarity (Rouyer *et al.*, 2008) for dynamic fire area burned and fire frequency, respectively, compared to base fire (Table 5.2). Wavelet spectra decompose the variance of 1-D time-series over a 2-D time-frequency plane and can be used to analyze the covariance of non-stationary signals with noise (Rouyer *et al.*, 2008).

Period	Simulation	Mean _{area}	SD _{area}	<i>r</i> _{area}	WD _{area}	Mean _{freq.}	SD _{freq.}	r _{freq.}	WD _{freq.}
1923-1952	Base Fire	+70,282	+375,027	-0.10	49.594	+696.8	+82.9	0.42	46.976
1923-1952	Dynamic Fire	-18,385	-168,825	-0.14	48.496	+54.3	-8.8	0.05	39.841
1953-1982	Base Fire	-27,265	-66,458	0.25	46.235	+357.6	+17.5	-0.29	42.179
1953-1982	Dynamic Fire	-3,338	-59,027	0.07	48.456	+39.9	-2.7	0.11	40.394
1983-2012	Base Fire	-20,689	-51,047	0.21	47.059	+202.3	-5.7	0.68	38.613
1983-2012	Dynamic Fire	-1,529	-46,255	-0.02	47.939	+55.4	-14.9	0.17	36.923
2003-2012	Base Fire	-18,363	-40,783	-0.06	15.150	+352.4	-4.6	0.07	14.528
2003-2012	Dynamic Fire	-5,121	-31,994	-0.58	15.377	+152.6	+42.8	0.13	14.360

Table 5.2 Simulated and observed fire time-series statistics; WD = wavelet dissimilarity

In the dynamic fire model results, iteratively updated landscape fuel conditions, based on 2012-2013 fire weather, reduced fire frequency and area burned in each scenario compared to base fire. For the most severe fires, in the Pre-Suppression Era, base fire model results showed large fires during the initial simulation year and relatively flat activity until simulation year \sim 45. The temporal distribution of fire frequency was more stable and realistic in the dynamic fire scenarios due to the fuel-limited semi-mechanistic model design, while base fire exhibited brute-force application of initial model parameters (Figure 5.3c).



Figure 5.3 Simulated annual fire regimes by period (above) and scenario (below): (a) annual simulated area burned by period; (b) annual simulated fire frequency by period; (c) annual simulated area burned by scenario; (d) annual simulated fire frequency by scenario; refer to Table 5.1 for scenario codes

TACA model results indicate that conditions for tree regeneration were increasingly suboptimal, declining across the 1923-2012 study period (Chapter 4). Optimal regeneration conditions occurred most frequently in the Rocky Mountain, Parkland, and Foothills regions. The Boreal region remained the most stable, while Montane regions maintained higher overall regeneration potential. An increased frequency and depth of modeled drought, due to changes to soil water balance, most limited regeneration conditions in the Grassland region, where fluvial and aeolian

soils are abundant. These results were critical to changes observed in LANDIS-II simulations, due to interactions between fire and regeneration.

LANDIS-II model results showed a decline in forested area for the most severe fires and an increase in forested area for mild disturbance scenarios. Forest decline indicates a failure to regenerate post-disturbance and/or an annual rate of burning outpacing the rate of regeneration. Resprouting and serotinous species regenerate post-fire each simulation year, the latter requiring that seed availability and establishment conditions be met. An initial rapid increase in forested area for most scenarios is attributable to recruitment into sites classified as open (i.e., untreed active cells) in the initial landscape. The maximum total forested area was 38% greater than the minimum area, resulting from differences in both fire regime severity and regeneration suitability. For the Pre-Suppression Era and Extremes scenarios, base fire produced the largest disturbances and thus the greatest change in forested area. While greater fire disturbances removed more species-age cohorts, warming climatic conditions reduced post-fire regeneration, further diminishing the forested area (Figure 5.4).



Figure 5.4 Simulated annual total forested area (sum of 1 ha pixels) by year and scenario; includes forests of all age classes; refer to Table 5.1 for scenario codes

While warming reduced the likelihood of regeneration over the simulation period, variation in fire regimes produced more rapid changes, with the interaction of the two processes explaining changes in forested area. Results showed minor declines in the abundance of *Picea*, *Larix*, and *Betula* genera, and minor increases in *Pinus*, across the simulation period. Species richness declined for all scenarios, declining the most under more severe disturbances (Figure 5.5a). The mean number of age classes present at one-hectare sites followed similar patterns, but recovered over time for succession-only scenarios (Figure 5.5b). The central tendency (i.e., median) of the spatial distribution of forests mildly increased in latitude and elevation under the most severe disturbances. While the mean forest latitude increased for all scenarios modeled, mean forest elevation was generally flat or declined (Figures 5.5c and 5.5d).



Figure 5.5 Individual and ensemble (i.e., simulation mean) model results by scenario and species: (a) species richness by scenario; (b) age class count by scenario; (c) mean forest latitude by scenario in WGS84 decimal degrees; (d) mean forest elevation by scenario; (e) incremental mean forest latitude change by species in WGS84 decimal degrees; (f) incremental mean forest elevation change by species; refer to Table 5.1 for scenario codes

A downhill mean forest distribution shift was shown for the Global Change and Most Recent Decade periods (Figure 5.5d). This is explained by an increase in high-elevation burning and reduction in regeneration suitability here, due to modeled water holding capacity limitations of rocky soils for the Montane region. Available water storage capacity was the most important model predictor of regeneration, as described in Chapter 4. In the Pre-Suppression and Extreme scenarios, the spatial distribution of forests shifted uphill on average due to high fire mortality rates at low elevations that surpassed the rate of regeneration. The difference in mean forest elevation between the two scenarios indicates that warming climatic conditions slowed rather than accelerated an uphill mean distribution shift (Figure 5.5d).

Latitudinal and elevational changes were produced by the spatiotemporal distribution of fire mortality more than climate over the 50-year simulation period. This is evidenced by large incremental changes in species elevation and latitude in the initial simulation years (Figure 5.5e and 5.5f), when disturbances were greatest in magnitude. While this spin-up period is often omitted from simulation studies, it is shown here to make model behavior transparent. The weaker effect of warming is also evident in a comparison of Extremes scenarios with Presuppresion Era fire scenarios, which differed only in climate. Species responses varied in mean latitudinal and elevational distribution shifts resulting from fire. Rather than attributable to life history strategy or functional type, differences in species response appear primarily attributable to the initial location of species. This is evidenced by the observation that the greatest mean species distribution shifts were shown by species endemic to the boreal region, in the northeastern portion of the study area, where the rate of burning was greatest. These changes were particularly evident for the large fires of the base fire scenarios (Figures 5.5e and 5.5f).

115

A reduction in the annual area burned slowed changes to the central tendency of the spatial distribution of forests. In the full ensemble results (the mean of all scenarios), the mean latitude of forests shifted mildly poleward while the mean elevation was static (mean latitude = +111 m yr⁻¹; mean elevation = -0.02 m yr⁻¹). All periods showed agreement in a mean latitudinal increase in forests, which may partially be explained by recruitment during the model spin-up period. Forest composition remained stable under the two most recent scenarios (Global Change and Most Recent Decade), but less stable during previous scenarios (Pre-Suppression and Early Suppression) due to greater disturbances. Extreme scenarios combining the most area burned with the warmest climatic conditions showed the most rapid changes in forest demographics (Figure 5.5b) and composition (Figure 5.6).



Figure 5.6 Simulated annual incremental change in species abundance by scenario; refer to Table 5.1 for scenario codes

Ensemble model results showed agreement in forested area decline (Figure 5.7a). An analysis of simulated annual mean incremental changes in area burned, fire frequency, and, forest latitude and elevation (Figure 5.7b) using Spearman's rank correlation coefficient (ρ) to probe for monotonocity showed that latitudinal and elevational changes were strongly correlated (ρ = 0.71), positively correlated with area burned (ρ = 0.49; ρ = 0.34), and negatively correlated with fire frequency (ρ = -0.34; ρ = -0.50). Total forested area was negatively correlated with fire frequency more than area burned (ρ = -0.54; ρ = -0.11) (Figure 5.7c).



Figure 5.7 Mean annual simulated forest change: (a) total forested area for all scenarios with a 95% confidence interval; (b) re-scaled forested area, latitude, elevation, area burned, and fire frequency for all scenarios; (c) Spearman's ρ for re-scaled metrics; (d) Spearman's ρ for autocorrelations of re-scaled metrics; Abun = forest area; Lat = forest latitude; Elev = forest elevation; Area = area burned; Freq = fire frequency

The periodicity (i.e., autocorrelation) of elevational changes was strongly correlated with changes to fire frequency ($\rho = 0.90$). The periodicity of changes in total forested area was negatively correlated with changes to area burned, fire frequency, and, latitude and elevation ($\rho =$

-0.32; $\rho = -0.31$; $\rho = -0.06$; $\rho = -0.24$). The periodicity of changes in mean forest latitude and elevation were positively correlated with changes in area burned and fire frequency, with forest elevation and fire frequency showing the highest correlation (Figure 5.7d).

During the model spin-up decade, where age class distributions were initially homogeneous, shifts in distribution occurred at their most rapid rate. This result was produced by a combination of high severity boreal fires given an even availability of fuels and frequent initial recruitment events. Given an even initial age class distribution, the sexual maturity of trees had equally even coverage, facilitating seed dispersal. These spin-up patterns are critical to note for their role in influencing the interpretation of simulation results. Following the 10-year model spin-up period, all scenarios with fire showed a mild decline in forested area (Figure 5.4).

5.4 Discussion

The combination of reduced regeneration potential and more severe fires produced a significant reduction to the total forested area in simulations. This suggests that declining modeled regeneration potential together with reduced area burned in the Global Change Era may potentially diminish the ability of tree species to track the velocity of warming. The simulated mean northward shift in forest distribution was 319 m yr⁻¹ slower than the velocity of climate change (Loarie *et al.*, 2009; Hamann *et al.*, 2015), with agreement shown across simulations. Even under the highest burning and thus migration rates, northward forest migration lagged 291 m yr⁻¹ behind warming. As exhibited by the Extremes scenarios, migration rates were highest in periods where disturbance rates were the most severe, despite cooler temperatures. This is indicative of reduced competitive limitations to migration.

119

In the simulations, the central tendency of the spatial distribution of forests varied in response to changes in climate and fire, as did species and age-classes. Changes in the distribution of tree species and forests were primarily attributable to fire. Forests tended to shift toward higher latitudes and lower elevations across simulation scenarios, while higher fire mortality reduced species and age-class diversity. The mean of the spatial distribution of forests increased in elevation and latitude when disturbance severity was highest, facilitating more rapid migrations with the removal of stands. Although shifts in mean spatial distribution were mild, they are notable given the simulation period of fifty years, short relative to the duration of succession processes. Despite being confined within a fixed study area at a regional scale, changes in the mean spatial distribution of forests are potentially more robust than range minima or maxima as indicators of migrational change, given the larger sample sizes involved and reduced sensitivity to episodic events produced by leptokurtic (heavy-tailed) seed dispersal kernels.

In addition to fire suppression (Cumming, 2005), forest demographics may partially explain the empirically observed increase in fire rotation period in Alberta (Zhang *et al.*, 2015), due to the bottom-up nature of fire mortality (i.e., younger cohorts are more susceptible to mortality for a given fire intensity, limiting fire crowning through ladder fuels in the absence of young trees). Fire suppression, forest aging, reduced recruitment rates, and related fire energetic constraints may together explain the modest increase in area burned under warming (Kelly *et al.*, 2013; Héon *et al.*, 2014; Zhang *et al.*, 2015). This dynamic was reproduced in simulations with the elimination of young trees during the model spin-up period, yielding older and less species diverse stands and a subsequently reduced rate of burning. Simulation results also suggest that,

120
while secondary to fire, declining regeneration potential may play a role in the decline in forested area observed for the Global Change Era in the adjacent montane Western United States (Cohen *et al.*, 2016).

Some studies have indicated increased forest carbon sequestration under global change conditions (Chen *et al.*, 2006; Fang *et al.*, 2014), while a recent tree-ring analysis indicates no effect of warming on biomass increment in the Canadian boreal (Girardin *et al.*, 2016). Current projections do not take into account expected changes to fire regimes and tree regeneration under warming. Empirical evidence shows diminished recruitment rates for the region (Zhang *et al.*, 2015), in agreement with TACA-GEM model results, while burning is widely projected to increase under warming in the short-term (Flannigan *et al.*, 2001; Groot *et al.*, 2003), before being limited by energetic constraints (Héon *et al.*, 2014). The presented simulation results indicate that the interaction of higher burn rates and diminishing regeneration potential may offset any potential gains to carbon storage over centennial time-scales by reducing the forested area. This dynamic may also offset increases to forest biomass attributable to stand ageing (Huang *et al.*, 2013; Uyeda *et al.*, 2017).

Diminished resilience, or capacity of forests in their current state to respond elastically to perturbation, is evidenced by changes to regeneration, which regulates forest change at a base ecological level. Although variability in interspecific regeneration potential was evident for the region, the dominant regeneration signal across the study period was a long-term decrease in forested area, in agreement with recent ground plot- and remote sensing-based findings on recruitment and forest cover (Bond-Lamberty *et al.*, 2014; Zhang *et al.*, 2015; Cohen *et al.*,

2016). While Zhang *et al.* (2015) attributed reduced growth and recruitment rates in western Canada primarily to competition and secondly to climate, their analysis focused on undisturbed sites, making growth and recruitment rates primarily a function of stand development.

Meanwhile, fire is the dominant driver of mortality in boreal forests (Rowe, 1961; Rowe & Scotter, 1973; Bond-Lamberty *et al.*, 2007), typically providing sites for recruitment (Clark, 1991; Lavoie & Sirois, 1998; Johnstone *et al.*, 2010; Bond-Lamberty *et al.*, 2014), while competition and climate cannot be disentangled. Competitive or mutualistic interactions are a function of climate space, evident in phenotype plasticity (i.e., gene expression) and evolutionary legacies (Aitken *et al.*, 2008). TACA-GEM model results presented herein suggest an alternative interpretation of the results of Zhang *et al.* (2015), as model results indicate that diminished recruitment rates for recent decades in the western Canadian boreal are due to a climatically-induced decline in regeneration potential.

Combined with available empirical evidence for Canada (Leithead *et al.*, 2012; Fisichelli *et al.*, 2014; Zhang *et al.*, 2015; Cohen *et al.*, 2016), simulation results suggest that a mild decline in forested area observed for some parts of intermountain western North America in recent decades may be attributable to a combination of increased fire regime severity and diminished regeneration potential. Future studies should explore the role of disturbance, regeneration, and demographics in changes to forested area observed for western North America. Empirical studies should focus on biome interfaces experiencing the highest rate of forest change. Simulation studies should expland beyond species ranges to incorporate shifts at the edge of range limits. Improved spaceborne monitoring, data assimilation, and landscape genetics analyses will be

important to understanding these dynamics, granting ecological forecasting greater predictive power.

5.5 Limitations

Similar to TACA-GEM, the LANDIS-II simulations presented herein rely on parameters from continental- or national-scale species compendiums (Burns & Honkala, 1990; Farrar, 1995a; Klinka *et al.*, 2000). The previously described fire data was utilized for fire model parameterization. Simulations used landcover maps developed from both remote sensing (Wulder *et al.*, 2007; Agriculture and Agri-Food Canada, 2012) and species distribution models (Gray & Hamann, 2012). Model spin-up was used to produce an initial stand age distribution map, as this information was unavailable for Alberta. Simulations were conducted at annual and 1 ha resolution, whereby species-age cohorts were horizontally homogeneous within stands. Direct validation of LANDIS-II simulations was limited to the two classes of fire model.

The LANDIS-II model contains a number of simplified representations of forest dynamics. The effect of competition on regeneration in LANDIS-II is a critical area for future validation studies. The model core is limited to simple assumptions regarding competition and establishment, whereby light required for regeneration is inversely proportional to the shade tolerance of existing trees. This does little to explain vertical stratification of phototrophic or optical types in forests (Gamon, 2014), which may be corrected by new model formulations. Nevertheless, previous studies using gap models have shown that such simplistic representations of light have little effect on succession (Deutschman *et al.*, 1999). Many other model functions are logic-based

or game-theoretic in relation to vital attributes (Noble & Slatyer, 1980), with variation represented through stochasticity, facilitating efficient computation at the cost of model realism.

The base fire model contains similar simplifications, as fire regimes can only have a log-normal fire size distribution and interactions with weather and fuels are not represented. While the dynamic fire model improves upon these shortcomings by adding fire weather and dynamic changes to fuels, reliable fuels parameters may be unavailable for some regions. The main factor limiting the development and application of LANDIS-II and other forest landscape models is the availability of empirical data needed to calibrate and validate each of the model components in different regions of the world. Advances in the accuracy of remote sensing classification and regression models will therefore be central to future model development, as such broad spatiotemporal information is otherwise difficult to attain.

Chapter 6: Airborne Laser Scanning Models of Canopy Light Transmission

6.1 Introduction

The light environment is a critical factor for the structure and function of vegetation communities (Monsi & Saeki, 1953, 2005; Dengel & Grace, 2010; Gamon & Bond, 2013; Gamon, 2014). In northern forests, tree crown geometries are well suited to a low solar elevation, occluding less light from neighboring trees (Aakala et al., 2016). Understory light is an important factor in the successional trajectory of forests through vegetation establishment and growth, making it a critical parameter required to forecast forest ecosystems (Canham et al., 1999). Although understory light is a function of quantifiable variation in local stand geometry, topographic position, atmospheric conditions, and solar position, it remains difficult and costly to measure. While the importance of understory light has long been understood (Monsi & Saeki, 1953), it is notoriously difficult to measure with remote sensing methods. The advent of angular remote sensing technologies such as airborne laser scanning LiDAR (ALS) and photogrammetric computer vision have made it possible to map canopy light transmission as a proxy for understory light by assuming beam canopy penetration equivalent to a Poisson process. Monsi & Saeki (1953) were the first to represent contact frequency as a Poisson process, equivalent to the Beer-Lambert law (Hancock, 2010).

Due to limitations in spaceborne sensor resolution and coverage, given the large footprint and fixed path of single quantum LiDAR sensors such as IceSat GLAS, understory light is difficult to retrieve for broad scales. NASA's new Global Ecosystem Dynamics Investigation (GEDI) beam-splitting quantum LiDAR instrument for the International Space Station, while improved in

coverage, will not likely resolve this fundamental limitation due to its 25 m footprint and limited sampling area (Dubayah *et al.*, 2014; Coyle *et al.*, 2015). Despite recent advances in deriving forest canopy geometry from commercial passive optical spaceborne sensors (Shean *et al.*, 2016), active optical airborne LiDAR systems remain optimal instruments for estimating understory light conditions at the landscape scale, as the aggregate of fine-scale variation. This is due to their precision, coverage, and ability to collected waveform returns, allowing direct measurement of canopy light transmission with multi-angular pulses of near-infrared photons. While atmospheric conditions are known to effect the quantity and quality of understory light (Dengel *et al.*, 2015), I focus on canopy light transmission (*T*) metrics best captured by LiDAR.

Airborne laser scanning (ALS) is used throughout boreal forests and contains detailed information on forest geometry at scales ranging from stands to landscapes. Recent studies have demonstrated a number of ALS metrics of forest structure over large areas, from area-based to individual tree-based approaches (Lefsky *et al.*, 2002; Popescu *et al.*, 2002, 2004; Zimble *et al.*, 2003; Coops *et al.*, 2007; Hilker *et al.*, 2012; Kaartinen *et al.*, 2012). Studies have also leveraged the increased availability of ALS to estimate understory light regimes in northern forests. Using point-based quantum sensors of photosynthetic photon flux density (PPFD) (Barnes *et al.*, 1993), convex spherical densiometers (Lemon, 1956), or hemispherical photography for ground-level validation, these studies have retrieved a number of relevant metrics from ALS, including canopy transmittance, canopy gap fraction (P_o), vertical canopy cover (VCC), angular canopy closure (ACC), effective leaf area index (L_e), apparent clumping index (Ω_{app}), stem density, and basal area (Parker *et al.*, 2001; Popescu *et al.*, 2002; Morsdorf *et al.*, 2006; Richardson *et al.*, 2009; Kaartinen *et al.*, 2012; Alexander *et al.*, 2013; Musselman *et al.*, 2013; Korhonen & Morsdorf, 2014; Parent & Volin, 2014; Eysn *et al.*, 2015; Moeser *et al.*, 2015). Such individual metrics are desirable for their simplicity and physical basis, which aid interpretation efforts.

Many of these ALS metrics may be used to estimate canopy light transmission, individually or in combination. Some of the earliest, simplest, and most effective metrics of ACC and P_o are based on the ratio of ground-to-canopy returns (Riaño *et al.*, 2004; Morsdorf *et al.*, 2006; Solberg *et al.*, 2009; Korhonen *et al.*, 2011). The metric of Solberg *et al.* (2009) differs in that it corrects for pulses that have returns from both the canopy and ground, assigning a partial cover value to these. A pulse intensity-based approach was designed to correct for two-way transmission loss (Hopkinson & Chasmer, 2007), also novel for utilizing target reflectance information. More recent approaches provide hemispherically projected LiDAR metrics comparable to ground measurements (Varhola *et al.*, 2012; Parent & Volin, 2014), while others further utilize geometric operations to improve the estimation of cover (Alexander *et al.*, 2013). An opportunity exists to improve both simple transmission metrics and advanced representations of forest geometry to estimate cover. While future studies should apply supervised 3-D convolutional neural networks for this task, whereby kernels function similar to voxelization, I focus on simple geometric operations here.

Although these studies show strong agreement with ground measurements for a number of ALS metrics of forest structure, many challenges remain. Models of canopy light transmission are often based on ray tracing (Disney *et al.*, 2000), which can be understood as a form of synthetic LiDAR, or derived from simple canopy metrics, such as Lorey's canopy height or leaf-area index (Niinemets & Anten, 2009). These metrics lack connection to ecosystem processes, are

computationally expensive, or do not fully utilize three-dimensional data for sun-view geometry. Radiative transfer models based on ray-tracing may improve the precision of understory light regime estimates at the landscape scale (Reich *et al.*, 2012; Moeser *et al.*, 2014; Gastellu-Etchegorry *et al.*, 2015). Yet, ray-tracing methods typically require high-point-density data from cutting-edge ALS or terrestrial laser scanning (TLS) LiDAR systems, delivered with rich ancillary data beyond standard (x, y, z, *intensity*) information. Such methods are also computationally demanding, making them time-consuming to apply.

Simple return-ratio approaches of quantifying canopy radiation attenuation may offer improved functioning with low-point-density data, better facilitate wall-to-wall mapping, and be more comparable to historical ground-based methods. These ALS approaches are comparable to methods used in the synthetic aperture RADAR community to estimate forest aboveground volume, such as the semi-empirical Water Cloud Model (Attema & Ulaby, 1978; Graham & Harris, 2003). Hence, ALS canopy radiation attenuation approaches may be extensible to spaceborne RADAR sensors for global forest change studies, despite substantial sensor differences.

Calculations of forest structural parameters from ALS are often distinct from those of traditional ground methods, due to differences in sampling bias, lending to variation in terminology and methodology. Canopy light attenuation calculations based on ALS often assume canopy light transmission (*T*) equal to canopy gap fraction (P_o), each inverses of vertical canopy cover (VCC) and angular canopy closure (ACC), as provided in the following equation (Morsdorf *et al.*, 2006; Hopkinson & Chasmer, 2009; Gonsamo *et al.*, 2013):

$$T = P_o = 1$$
-ACC = 1-VCC

Traditionally, VCC quantifies the 2-D areal canopy coverage, while *T* is a function of incident photosynthetically active radiation (PAR), fraction of absorbed PAR (fPAR) by leaf absorptance, leaf transmissivity, and scattering, incorporating leaf geometry, position, and orientation effects on the bidirectional reflectance distribution function, or BRDF (Gastellu-Etchegorry *et al.*, 1996). While the equivalence of *T* and P_o holds in the absence of detailed information, the two metrics remain distinct, providing different – though complementary – information (Gonsamo *et al.*, 2013).

Although ALS LASER pulses are typically emitted at narrow zenith angles less than 20 degrees from nadir, they provide an empirical test of angular light penetration through the canopy, making ALS suitable for estimating P_o . Meanwhile, VCC is often calculated from ALS for each cell using narrow incoming zenith angles between 0 and 10, opposite to scan and beam divergence source angle (Weiss *et al.*, 2004; Morsdorf *et al.*, 2006). Hence, the measurement of VCC with ALS is often a field-of-view, or scope, function (Lee *et al.*, 2008), rather than a true measure of 2-D areal coverage (although simple grid-based methods exist), making it sensitive to neighborhood effects. Here, as with leaf area index (*L*), gridded ALS-derived metrics (e.g., the ratio of canopy first-returns to ground first-returns) are more compatible with the classical definition of VCC. Similar challenges of sampling bias have been reported for gap fraction (P_o) estimates derived from terrestrial laser scanning (TLS) LiDAR (Vaccari *et al.*, 2013). Variation in ALS metric methodology relative to ground methods is primarily due to four attributes of these systems: ALS is (1) active, (2) narrow-angled, (3) exhibits top-of-canopy bias, and (4) historically had point densities as low as ~ 1 point/m². These differences are also attributable to the desire to harmonize LiDAR forest structural metrics with historical ground-truthing field methods. Modern ALS and TLS systems provide more precise, accurate, and detailed information about forest geometry than ground-based methods used for calibration and validation. While ground methods such as quantum sensor measurements of PPFD provide greater precision, their generalizability is poor given the complexity of dynamics that drive variation in values (e.g., dynamic changes to solar activity, atmospheric conditions, leaf optical properties, and leaf orientation). As it is not a direct measurement technique, photon flux measurements may be strongly affected by noise unrelated to forest geometry.

The objective of this study was to develop new ALS metrics and regression models of *T* that can be extended to forest landscape models to simulate understory irradiation. Four new ALS metrics for retrieving *T* are presented, including the hemispherical Voronoi gap fraction (P_{hv}), pointdensity normalized gap fraction (P_{pdn}), and their inverses, hemispherical Voronoi angular canopy closure (ACC_{hv}) and point-density normalized angular canopy closure (ACC_{pdn}). While P_{hv} and ACC_{hv} are intended to improve estimates of canopy light interception from LiDAR with varying sensor properties, P_{pdn} and ACC_{pdn} are intended to reduce sensor effects by normalizing hemispherical sectors by their surface area and the overall point density. These are the key innovations provided herein.

The four new hemispherical canopy metrics (P_{hv} , P_{pdn} , ACC_{hv} , and ACC_{pdn}), nine vertical canopy cover (VCC) metrics, twelve stem and crown metrics, and five other metrics, for a total of 30 metrics (Table 6.1), were validated against traditional coarse-resolution convex spherical densiometer ground measurements of angular canopy closure (ACC), representing the inverse of *T*. The P_{hv} metric was applied using four different hemispherical lens geometries at canopy height thresholds varying from one meter to five meters in 0.25 m steps, for a total of 68 different P_{hv} configurations for each plot.

New Metrics	Vertical Canopy Cover Metrics	Tree and Crown Metrics	Other Metrics				
Hemispherical Voronoi gap fraction (P _{hv})	Above-height cover index (VCC _{aci})	Moving window <i>n</i> trees (<i>ITC_{mw}</i>)	Beer-Lambert Law gap fraction (P_{bl})				
Point-density normalized gap	Beer's Law-modified-intensity-	Moving window crown area (G_{mw})	Beer-Lambert Law effective leaf area				
fraction (P_{pdn})	return ratio (VCC_{bl})		index (<i>Le</i> _{bl})				
Hemispherical Voronoi angular	Cartesian Voronoi fractional cover	Hierarchical moving window <i>n</i> trees	Ground-to-total-return ratio effective				
canopy closure (ACC_{hv})	(VCC_{cv})	(ITC_{hmw})	leaf area index (Le_r)				
Point-density normalized angular	First ashe cover index (VCC_{-})	Hierarchical moving window crown area	Contact frequency effective leaf area				
canopy closure (ACC_{pdn})	First-echo cover index ($V \in C_{fci}$)	(G_{hmw})	index (Le_n)				
	Canopy-to-total-first-return ratio	Watershed <i>n</i> trees (ITC_{wat})	Apparent clumping index				
	(VCC_{fr})		(Ω app or <i>ACI</i>)				
	Intensity-return ratio (VCC _{ir})	Watershed crown area (G _{wat})					
	Canopy-to-total-pixel ratio (VCC_p)	Hierarchical watershed n trees (ITC_{hwat})					
	Canopy-to-total-return ratio (VCC_r)	Hierarchical watershed crown area (G_{hwat})					
	Salhara'a aguar inday (VCC)	Distance and direction to canopy					
	Solderg's cover index (VCC _{sci})	(C_{dist}, C_{dir})					
		Distance and direction to tree crown					
		(Cr _{dist} , Cr _{dir})					

Table 6.1	Understory	light metrics	betelulated	in this study	evolained i	in detail in th	he following section
	Onderstory	ingin metrics	calculated	in uns study,	capitanicu i	in uctan in u	ic following section

6.2 Methods

Vegetation ground plot measurements were collected in the Hinton Forest Management Area in the early 2000s during summer (leaf-on) conditions (Nielsen *et al.*, 2004, 2006; Nielsen, 2005). Angular canopy closure (ACC), and thus canopy gap fraction ($P_o = 1$ -ACC), was measured from breast-height using a convex spherical densiometer. Densiometer measurements were recorded for each of the four cardinal directions and averaged for each plot (Lemon, 1956; Nielsen, 2005). ALS sorties were conducted in the mid-2000s using an Optech ALTM 3100, detailed in section 2.5. For model development, 100 field plots containing both densiometer measurements and complete ALS coverage were randomly sampled. Each plot contained one value for ACC, measured at the plot center, each representing different levels of forest cover. The wide distribution of ACC values represented is evident in Figure 6.5. Following model development, the top metric was validated for all 950 field plots.

6.2.1 Pre-processing

Using LAStools (Isenburg, 2015), the ALS tiles were height-normalized before extracting circular field plots with a 50 m radius, based on previous research exhibiting a saturation of edge effects below this threshold (Zhao & Popescu, 2009; Alexander *et al.*, 2013). Normalization consisted of extracting the ground plane from the point data and subtracting the Delaunay triangle-position elevation from each return's *z* value. LAStools implements an optimized variant of the best available ground plane extraction algorithm (Axelsson, 1999; Maguya *et al.*, 2014), modified to include Delaunay streaming or triangulated irregular network (TIN) streaming (Isenburg *et al.*, 2006a,b,c) for improved computational efficiency on large datasets. Maximum point height was filtered at 40 m, based on local tree species ground measurements. The ALS

plots were processed with a series of point cloud metrics implemented in custom R scripts (R Core Team, 2015), described below. Finally, the top performing ALS metric (VCC_{fci}) was applied to an expanded set of ALS plots to analyze variation related to species composition and age class.

6.2.2 Spike-free Canopy Height Model Algorithm

One step of pre-processing required the generation of continuous canopy height models (CHMs) without smoothing- or sampling-related artifacts. This was due to pitting in the simple gridded maxima CHMs given a mean point density below 2 points m⁻², known to affect the accuracy of tree detection. In order to improve CHM inputs for individual tree crown (ITC) detection, a layered 2-D adaptation of the spike-free CHM algorithm (Khosravipour *et al.*, 2014, 2016) was implemented. The approach uses vertically stratified 2-D Delaunay triangulation with barycentric interpolation along *z*-values for triangulated irregular network (TIN) generation. The maximum of resulting vertical surface model layers or slices is then computed, yielding a CHM with reduced spiking.

Equivalent in output, the new algorithm vertically stratifies all returns into user-defined windows or slices to constrain Delaunay triangulations, which can be absolute distances or height percentiles. A 2 m height threshold was used with steps at 5, 10, and 15 m, as in the pit-free CHM work (Khosravipour *et al.*, 2014). Delaunay triangles with edge lengths exceeding a user-defined threshold are filtered to limit smoothing, set to the default value. The final CHM consists of continuous height maxima along raster grid points. This adaptation takes advantage of vertical stratification to generate non-overlapping points necessary for 2-D Delaunay triangulation. The

theoretical advantage over the 3-D Constrained Delaunay approach (Khosravipour *et al.*, 2016) is chiefly computational.

At the heart of barycentric interpolation is the local weighted average (Shepard, 1968; Warren *et al.*, 2006). The predicted *z*-value of a point within a Delaunay triangle is the weighted average of each of three known *z*-values, with weights determined by the distance to nodes. Given the three barycentric coordinates (x_1 , x_2 , x_3) of a triangle and the interpolated point x within its interior, barycentric interpolation performs the following to compute the *z*-value of x:

$$f(\boldsymbol{x}) \approx \sum_{i=1}^{3} \alpha_{i} f(\boldsymbol{x}_{i})$$

Here, $\alpha_i > 0$ and $\sum \alpha_i = 1$, where α_i is the barycentric coordinate of triangle point *i*, used as weights in interpolation. Given a linear function $f(x) = w^t x + r$, the interpolation is exact and able to compute in either a piecewise or highly parallel framework, requiring little memory overhead. 2-D barycentric interpolation benefits from its simplicity compared to streaming 3-D Delaunay triangulation methods. Yet, a caveat exists in that vertically stratified point subsets fed into 2-D barycentric interpolation for hierarchical CHM generation should have no interior overlap. Unlike many other 2-D interpolation functions, barycentric interpolation functions with irregularly spaced sets are common in LiDAR remote sensing. For regularly spaced sets (e.g., raster grids), simpler interpolation methods exist. While this adaptation is chiefly computational in innovation, it is nonetheless an important contribution in this work. These and other functions are provided in the *gapfraction* package for R (https://adam-erickson.github.io/gapfraction/).

6.2.3 Hemispherical Voronoi Gap Fraction

The hemispherical Voronoi gap fraction (P_{hv}) metric represents P_o as the areal coverage of Voronoi tessellation cells above a given canopy height threshold from the perspective of standing at the plot center and looking toward the zenith, identical to a traditional hemispherical photograph. The plot center at 3-D local Cartesian coordinate (x=0, y=0, z=0) is set equal to the hemispherical camera model principal point, or intersection of the optical axis and image plane. The ground plane is set equal to the image plane, with the optical axis pointing skyward at the zenith. Once the LiDAR data is pre-processed into normalized heights and local Cartesian coordinates, the first step is to re-project the LiDAR points into image coordinates based on a model of a fisheye (hemispherical) lens.

The projection of a 3-D point $X_w = (X_w, Y_w, Z_w)^T$ into a 2-D image sensor coordinate $x'_j = (x'_j, y'_j)$ requires a mathematical model of a fisheye lens, consisting of a series of transformations with extrinsic and intrinsic camera parameters (Ray, 2002; Abraham & Förstner, 2005). The extrinsic parameters map the real-world coordinates into camera coordinates, while the intrinsic parameters map the camera coordinates onto the image plane. Typically, a distortion model is used to explicitly include optical system discrepancies; this is necessary for improving performance in computer vision applications based on epipolar geometry, such as stereo vision and structure-from-motion (Wallach & O'Connell, 1953; Ullman, 1979; Bolles *et al.*, 1987; Cornelis *et al.*, 2002), but is unnecessary here. This work focuses on the ideal map of the 3-D image sphere projected onto the 2-D image plane, given a virtual fisheye lens without distortion. The image coordinate calculations take the following form (Abraham & Förstner, 2005):

$$x' = c_x \cos(\varphi) r^*(\theta) + x'_H$$
$$y' = c_y \sin(\varphi) r^*(\theta) + y'_H$$

Here, c_x and c_y are the principal distances (this allows for non-square pixels), φ and θ are the azimuthal and polar angles, respectively, $r^*(\theta)$ is the radial projection function, or mapping function, and, x'_H and y'_H are the coordinates of the principal point, or the intersection of the optical axis and the image plane. The distortion model parameters used for real-world lenses, $\Delta x'$ and $\Delta y'$, typically added to the end of their corresponding equations, are omitted. To change to a different hemispherical camera model, the radial projection function can be simply modified.

The classical pinhole camera is described by the *perspective* projection function of the form $r' = c \tan(\theta)$, where r' is the radial distance from the principal point on the image plane and c is the principal distance, a function of the focal length and focal distance (Fourcade, 1928). Fisheye lenses generally use one of four common radial projection functions: *stereographic, equidistant, orthogonal,* and *equisolid angle*. Most consumer fisheye lenses use the *equisolid angle* projection and have a full-frame design (the picture angle is 180° only when measured diagonally and is smaller elsewhere), while scientific lenses utilized for hemispherical photography typically use the *equidistant* projection, where the radial distance is equal to the polar angle, and have a circular design (the full 180° hemisphere is recorded within the image plane). Here, all four projections are implemented with a circular design in the *gapfraction* package for R. The radial projection function, or mapping function, for each projection is as follows (Ray, 2002; Abraham & Förstner, 2005):

$r' = c \tan(\theta/2)$	Stereographic projection
$r' = c \theta$	Equidistant projection
$r' = c \sin(\theta)$	Orthogonal projection
$r' = c \sin(\theta/2)$	Equisolid angle projection

To transform the real-world coordinates to camera coordinates, the normalized point clouds were projected into 3-D local Cartesian coordinates with an (x, y, z) tuple centroid of (0, 0, 0). A function was developed that allows this calculation without plot center geolocation information to ease LiDAR plot processing. The function sets the midpoint of the vector of *X* and *Y* values to half of the range, as shown below:

$$x' = x - x_{min} - \left(\frac{x_{max} - x_{min}}{2}\right)$$
$$y' = y - y_{min} - \left(\frac{y_{max} - y_{min}}{2}\right)$$

To transform the camera coordinates into image plane coordinates, the 3-D local Cartesian coordinates are projected into 2-D polar coordinates (azimuth angle and radial distance, or φ and r) before projecting the 2-D polar coordinates into 2-D Cartesian space with standard trigonometric equations, where $x' = r \cos(\varphi)$ and $y' = r \sin(\varphi)$. The calculations were implemented in their normalized image plane form (Abraham & Förstner, 2005), as the 3-D local Cartesian coordinates were normalized to their true distance values in meters, rather than the typical unit sphere. This was done to preserve 3-D Cartesian distances for calculations that do not require hemispherical or image plane projections.

Once the LiDAR data were projected onto the 2-D hemispherical image plane, the 2-D Delaunay triangulation and Voronoi tessellation were computed for the planar point sets using the *deldir* package for R (Turner, 2015), filtering points below a user-defined canopy threshold. The summed area of filtered cells, or gaps, was calculated as a percentage of the overall plot area, providing the hemispherical Voronoi gap fraction (P_{hv}). This assumes 100% light occlusion by non-filtered cells. The implication of this simplification is that light attenuation is overestimated, which can be adjusted by a simple transmissivity coefficient derived from the slope of linear regression. Since this work focuses on correlations and regression model development, calculating such a coefficient was not necessary. To calculate ACC_{hv} , P_o values were subtracted from 1. Last, a height-threshold sensitivity analysis was conducted by applying the function with each of the four fisheye lens models and each of 17 minimum canopy height thresholds ranging from 1 to 5 m, at a step of 0.25 m, producing 68 unique combinations for each of the 100 plots, for a total of 6,800 iterations.

6.2.4 Point-density Normalized Gap Fraction

The point-density normalized gap fraction (P_{pdn}) is based on partitioning hemispherically projected first-return points into polar and azimuthal sectors, or annuli, then calculating the number of points per sector as a proxy for canopy light occlusion. Removing non-first-returns facilitates the calculation of point-density normalized metrics by evening the point spacing along the Cartesian ground plane, with ground returns representing canopy gaps. Otherwise, the spatial bias of sampling is too high for the normalization procedure. The return values were normalized by the ground point density and the surface area of each hemisphere sector to reduce sensor effects, producing similar P_{pdn} values for vastly different point densities. This follows the logic

that a greater number of points are expected for sections of greater surface area, given evenly spaced sampling and thus a relatively constant point density along the (*X*, *Y*) plane. The procedure begins by filtering for first-returns and projecting the 3-D Cartesian coordinates (*X*, *Y*, *Z*) into spherical coordinates (*r*, φ , θ) using standard equations:

$$r = \sqrt{x^{2} + y^{2} + z^{2}}$$
$$\varphi = \cos^{-1}\left(\frac{z}{r}\right)$$
$$\theta = \tan^{-1}\left(\frac{y}{x}\right)$$

The φ values were rescaled from (- π , π) to the interval (0, 2π) by adding 2π to φ values where φ is less than zero. Based on previous research (Zhao & Popescu, 2009), the spherical coordinates were sectioned at polar and azimuthal increments of 5° and 45°, respectively, producing 18 x 8 sky sectors for a total of 144 sectors. A polar resolution of 15° is also commonly used in LiDAR studies (Korhonen & Morsdorf, 2014), but is likely coarser than necessary for modern sensors. The number of first returns per hemispherical sector was calculated using the following equation:

$$\theta_{returns_{i}} = \{P \mid \theta_{i} < \theta_{P} < \theta_{i+1}\}$$
$$\varphi_{returns_{j}} = \{P \mid \varphi_{j} < \varphi_{P} < \varphi_{j+1}\}$$
$$C(returns_{i,j}) = P \mid P \in \{\theta_{returns_{i}} \cap \varphi_{returns_{j}}\}$$

Here, $C(returns_{i,j})$ is the number of elements contained in a set defined by the intersection of polar and azimuthal angle subsets, $\theta_{returns_i}$ and $\varphi_{returns_j}$, at hemisphere sector intervals defined by steps *i* and *j*, respectively. A matrix is produced containing the frequency of returns within each sector of the hemisphere. In order to account for varying sector sizes, the values are adjusted by the hemispherical surface area of each sector. To do so, the surface area of each hemispherical sector is first calculated, as follows:

$$A_{i,j} = R^2 (\sin \theta_{i+1} - \sin \theta_i) (\varphi_{j+1} - \varphi_j)$$

This produces a second matrix of equal dimensions, i x j. Here, $A_{i,j}$ is the area of a sector for polar angle Θ_i and azimuth angle φ_j at intervals defined by steps i and j, while R is the radius of the sphere. Next, matrix division is performed on the return frequency and surface area matrices, normalized by point density for the full hemisphere along the (X, Y) Cartesian plane. This mitigates issues related to sensor effects (e.g., point density). The filtering of non-first-returns is necessary to also reduce sensor effects along the *z*-axis, as vertical resolution can vary due to a number of factors. Point-density normalized canopy gap fraction (P_{pdn}) was calculated with the following equation:

$$P_{pdn} = \sum_{i=1}^{n} \sum_{j=1}^{n} \left(\frac{\frac{n_{FirstReturns_{i,j}}}{D_{FirstReturns}}}{A_{Sector_{i,j}}} \times \frac{A_{Sector_{i,j}}}{A_{Hemisphere}} \right)$$

Where $n_{FirstReturns_{i,j}}$ is the count of first returns in matrix **C** for hemisphere sector **C**[*i*-*j*], $A_{Sector_{i,j}}$ is the surface area in matrix **A** of sector **A**[*i*, *j*], $D_{FirstReturns}$ is the point density for the full dataset along the Cartesian (*X*, *Y*) ground plane, and $A_{Hemisphere}$ is the surface area of the full hemisphere. The right-hand side of the summation scales the output by the proportion of the hemisphere occupied by each sector, similar to the scaling of L_e by polar angle (Korhonen & Morsdorf, 2014), rather than calculating the mean value without accounting for sector size. In essence, the P_{pdn} function normalizes the number of returns per sector by the overall point density and the sector surface area, with the output values scaled by hemisphere proportion. Double summation is approximate to a double integral. ACC_{pdn} is merely one minus P_{pdn} , as its inverse.

6.2.5 Comparison with Other ALS LiDAR Metrics

A set of standard metrics were also implemented to assess their performance against new methods and ground measurements. The method comparison framework includes estimates of canopy gap fraction, angular canopy closure, vertical canopy cover, individual tree detection, crown area, distance to crown and canopy, leaf area index, and clumping. First, these methods are described in the following paragraphs.

Based on previous research on the estimation of leaf area index (Miller, 1967; Lang & Yueqin, 1986; Zhao & Popescu, 2009; Ryu *et al.*, 2010), the effective leaf area index (L_e) was calculated using the following equation (Korhonen & Morsdorf, 2014):

$$L_e = 2\sum_{i=1}^{n} -\ln\overline{P(\theta_i)}\cos\theta\frac{\sin\theta_i}{\sum_{j=1}^{n}\sin\theta_j}$$

The apparent clumping index (Ω_{app}) was calculated based on a ratio of two L_e estimation methods (Ryu *et al.*, 2010). The previous approach was modified by approximating the integral as a summation, with each L_e method weighted by the *sine* of the given polar angle, θ (Korhonen & Morsdorf, 2014):

$$\Omega_{\text{app}} = \frac{2\sum_{i=1}^{n} -\ln\overline{P(\theta_{i})}\cos\theta\frac{\sin\theta_{i}}{\sum_{j=1}^{n}\sin\theta_{j}}}{2\sum_{i=1}^{n} -\overline{\ln P(\theta_{i})}\cos\theta\frac{\sin\theta_{i}}{\sum_{j=1}^{n}\sin\theta_{j}}}$$

Next, the L_e vector is used for *n* polar angles θ to calculate the canopy gap fraction per the Beer-Lambert Law (Monsi & Saeki, 1953, 2005):

$$P_{o_i} = exp\left(\frac{-L_e G(\theta_i)}{\cos \theta_i}\right)$$

Other metrics include the following vertical canopy cover (VCC) metrics: canopy-to-total-return ratio (VCC_r) (Morsdorf *et al.*, 2006), canopy-to-total-first-return ratio (VCC_{fr}) (Morsdorf *et al.*, 2006), intensity-return ratio (VCC_{ir}) (Hopkinson & Chasmer, 2009), Beer's Law-modifiedintensity-return ratio (VCC_{bl}) (Hopkinson & Chasmer, 2009) or intensity cover index (ICI) (Korhonen & Morsdorf, 2014), above-height cover index (VCC_{aci}) (Richardson *et al.*, 2009), first-echo cover index (VCC_{fci}) (Korhonen *et al.*, 2011; Korhonen & Morsdorf, 2014), Solberg's cover index (VCC_{sci}) (Solberg *et al.*, 2009), canopy-to-total-pixel ratio (VCC_p) (Parent & Volin, 2014), and Cartesian Voronoi fractional cover (VCC_{cv}) (Alexander *et al.*, 2013). These metrics were applied with a canopy threshold of 1.25 m, per two seminal studies demonstrating algorithms that are the primary basis of this work (Morsdorf *et al.*, 2006; Alexander *et al.*, 2013).

Metric	Equation
Canopy-to-total-return ratio	$VCC_r = \frac{\sum N_{All > 1.25 m}}{\sum N_{Last} + N_{Single}}$
Canopy-to-total-first-return ratio	$VCC_{fr} = \frac{\sum N_{All > 1.25 m}}{\sum N_{First}}$
Intensity-return ratio	$VCC_{ir} = \frac{\sum I_{Ground}}{\sum I_{All}}$
Beer's Law-modified-intensity-return ratio	$VCC_{bl} = \frac{\left(\frac{\sum I_{Ground \ Single}}{\sum I_{All}}\right) + \sqrt{\frac{\sum I_{Ground \ Last}}{\sum I_{All}}}}{\left(\frac{\sum I_{First} + \sum I_{Single}}{\sum I_{All}}\right) + \sqrt{\frac{\sum I_{Intermediate} + \sum I_{Last}}{\sum I_{All}}}$
Above-height cover index	$VCC_{aci} = \frac{\sum N_{Single} + N_{All > 1.25 m} + N_{Intermediate} + N_{Last}}{\sum N_{All}}$
First-echo cover index	$VCC_{fci} = \frac{\sum N_{Single > 1.25 m} + \sum N_{First > 1.25 m}}{\sum N_{Single} + \sum N_{First}}$
Solberg's cover index	$VCC_{sci} = \frac{\sum N_{Single > 1.25 m} + 0.5(\sum N_{First > 1.25 m} + \sum N_{Last > 1.25 m})}{\sum N_{Single} + 0.5(\sum N_{First} + \sum N_{Last})}$
Canopy-to-total-pixel ratio	$VCC_p = \frac{\sum N_{CHM > 1.25 m}}{\sum N_{CHM}}$
Cartesian Voronoi fractional cover	$VCC_{cv} = V(P_{First \ Return}) > 1.25 \ m$

Table 6.2 Additional VCC metrics

A suite of proxy metrics relevant to the calculation of P_o was also tested. These include individual tree crown (ITC) counts using maximum and hierarchical variable-moving-window (ITC_{mw}) (Koch *et al.*; Popescu *et al.*, 2002) and watershed (*ITC_{wat}*) algorithms (Hyyppa *et al.*, 2001; Zhao & Popescu, 2007), crown area (G) using detected tree heights with an empirical height-to-crown-radius function, distances and directions to nearest crown (C_{dist} , C_{dir}) and canopy pixels (Cr_{dist} , Cr_{dir}) from the plot center (Moeser *et al.*, 2015), effective leaf area index (L_e) based on the Beer-Lambert Law (Monsi & Saeki, 1953; Korhonen & Morsdorf, 2014), L_e based on the ground-to-total-return ratio (Richardson *et al.*, 2009), and L_e based on contact frequency (Morsdorf *et al.*, 2006), apparent clumping index (Ω_{app}) (Ryu *et al.*, 2010), and Beer-Lambert Law canopy gap fraction (P_{bl}) (Monsi & Saeki, 1953, 2005; Ryu *et al.*, 2010).

While these methods have not been locally validated, they were previously validated for boreal and montane forests. A caveat exists in that the low point densities of the ALS data used are likely a source of tree detection error. Yet, meaning is still inferred from these results, regardless of ITC accuracy (it is likely not optimal), as the focus is on a given metric's ability to faithfully represent *T*. Furthermore, these algorithms may extract valuable information from ALS data not captured by other approaches. Correlations with convex spherical densiometer measurements were calculated before testing univariate and multivariate linear models with stepwise-AIC and -BIC model selection. While it is possible to build multivariate linear models with fewer degrees of freedom using dimensionality reduction techniques, this was not performed in order to simplify model interpretation.

The effect of filtering sites likely disturbed between spherical densiometer and ALS sampling campaigns was tested, in order to correct for a half-decade mismatch in data collection. This filtering process was also used to correct for discontinuity between ground and remote sensing

observations due to seasonal changes in leaf area index, as ground observations were generally collected during summer leaf-on conditions while ALS sorties were conducted in fall leaf-off conditions. The error contribution of leaf state is likely minimal, as the Hinton Forest Management Area is 4.5% deciduous, 8% mixed, and 40% evergreen forest (Nielsen, 2005). Observations with ground-based angular canopy closure (ACC) values below 0.30 were filtered, where disturbances or leaf condition discontinuities were apparent in ground-to-ALS ACC plots.

6.3 Results

Estimation of ACC and P_o as a proxy for T using ALS showed good performance. Regression models using multiple metrics substantially outperformed any single ALS metric, yet individual metrics have utility for their simplicity and physical basis, facilitating interpretation. Of the individual metrics, VCC_{fci} , showed the best performance.

6.3.1 ALS Estimates of ACC and Po

To test for correlations, given the perfectly inverse relationship between gap fraction (P_o) and angular canopy closure (ACC), absolute values were used to calculate Pearson's correlation coefficient (r) against convex spherical densiometer measurements of ACC. The top five results in terms of r were all vertical canopy cover metrics, with the strongest correlation shown for VCC_{fci} (r = 0.61), followed by VCC_{sci} (r = 0.61), VCC_{fr} (r = 0.60), VCC_r (r = 0.58), and VCC_{ir} (r= 0.57). The two variable-window individual tree crown (ITC) detection algorithms followed, at r = 0.57 for each, demonstrating their utility as a proxy for T, while point-density normalized P_o (P_{pdn}) was the highest performing new metric at r = 0.56. Each virtual fisheye lens model in P_{hv} improved in accuracy as the minimum canopy height increased, with the equisolid angle model showing the poorest results (Figure A2.1). An optimal canopy height threshold was indicated of 5 m for all hemispherical lens models tested, indicative of an under-prediction of ACC. Of all the gap fraction metrics, P_{pdn} showed the strongest negative correlation and thus closest agreement with ground ACC measurements. VCC_{fci} , which showed the strongest correlation with ground ACC data, was strongly correlated with the following LiDAR metrics: FC_{fr} (r = 0.99); FC_{sci} (r = 0.99); FC_r (r = 0.98); FC_{ir} (r = 0.97); FC_p (r = 0.97). Correlations between all metrics and ground measurements are provided (Figure A2.2).

ITC count methods show a strong negative correlation with the Beer-Lambert Law gap fraction (P_{bl}) , while the point-density normalized gap fraction (P_{pdn}) shows a strong negative relationship with VCC metrics. Meanwhile, P_o and VCC metrics show strong similarity within metrics. The hierarchical clustering of the hemispherical Voronoi gap fraction (P_{hv}) results indicates that correlations are more strongly linked to minimum canopy height than to the fisheye lens model used. A canopy height threshold of 5 m was indicated for all P_{hv} metrics.

ITC counts similarly have a strong negative correlation with P_{hv} metrics with a higher minimum canopy height, but not with lower height thresholds. Meanwhile, metrics such as Ω_{app} and direction to canopy or crown have very low correlations with other variables, as expected. The strong negative correlation of P_{pdn} with VCC metrics, and weak correlation with P_{hv} metrics, suggests that the two gap fraction metrics capture fundamentally different properties of forest geometry. Meanwhile, the Beer-Lambert Law gap fraction (P_{bl}) shows strong correlations with empirical ITC crown area estimates.

Removing post-disturbance sites (sites with ground ACC values of zero and ALS ACC values greater than zero) before sampling the ground plots, the top seven metrics, in terms of univariate linear model fit with ground measurements, were all vertical canopy cover (VCC) metrics (Figure 6.1). Of these, the first-echo cover index (VCC_{fci}) (Korhonen *et al.*, 2011; Korhonen & Morsdorf, 2014) again achieved the highest score. The seven top metrics include VCC_{fci} ($R^2 = 0.53$), VCC_{fr} ($R^2 = 0.51$), VCC_{ir} ($R^2 = 0.51$), VCC_{ir} ($R^2 = 0.51$), VCC_{rc} ($R^2 = 0.49$), VCC_{cv} ($R^2 = 0.48$), and VCC_p ($R^2 = 0.47$). While P_{pdn} performed well before filtering out sites, at ninth best ($R^2 = 0.32$), it subsequently dropped to eleventh ($R^2 = 0.38$) after filtering sites. Meanwhile, the ITC count metrics and hierarchical watershed-based crown area performed surprisingly well; these metrics produced R^2 values for ACC approximately double those of the P_{hv} metrics.



Canopy Light Transmission Metric

Figure 6.1 Univariate linear model angular canopy closure (ACC) model R^2 by metric for all sites and without disturbed or temporally non-synchronous sites in terms of LAI seasonality; black = all sites; red = without flagged sites

An equiangular hemispherical lens projection appeared particularly sensitive to the inclusion of sites that were disturbed or temporally inconsistent with ALS sorties, as filtering out these sites substantially improved model performance (Figure 6.2).



 P_{hv} Metric by Hemispherical Lens Model and Canopy Height Threshold (m)

Figure 6.2 Change to univariate linear model of angular canopy closure (ACC) model R² by metric due to filtering likely disturbances; red points

represent the filtered values; x-axis labels use the following convention: [lens model] [canopy height threshold]; Stereo = stereographic projection; Ortho

= orthographic projection; Equidist = equidistant projection; Equiangle = equisolid angle projection

The mean R^2 improvement attributable to filtering out disturbances was $\Delta R^2 = +0.05$. The largest gains were shown by VCC_{cv} ($\Delta R^2 = +0.20$), VCC_{ir} ($\Delta R^2 = +0.18$), VCC_{fr} ($\Delta R^2 = +0.16$), VCC_p ($\Delta R^2 = +0.15$), and VCC_r ($\Delta R^2 = +0.15$), while the largest loss was shown by the stereographic and equidistant fisheye lens model P_{hv} metrics at a minimum canopy height of five meters ($\Delta R^2 = -0.01$). Overall, VCC metrics, ITC metrics, and the equisolid angle P_{hv} metrics showed the greatest model improvement, indicating sensitivity to disturbance- or leaf area-related noise. Figure 6.3 shows the full P_{hv} calculation process conducted for each site tested.



Figure 6.3 Example LiDAR plot process colored by point height (blue < green < red) with the orientation onnadir and the circle units in radians with an equiangular projection: (a) nadir view of 50 m radius plot in NAD83 UTM 11N (meters) coordinates; (b) hemispherical view from the plot center toward the zenith projected in local coordinates; (c) Delaunay triangulation of hemispherically projected points; (d) Voronoi tessellation of hemispherically projected points

For the hemispherical view, multiple projections were tested, showing a significant impact on the estimation of ACC and P_o in the above results. The differences in projection are clearly visible for stereographic and orthographic projections, while subtle between equidistant and equiangular projections (Figure 6.4).



Figure 6.4 Example LiDAR plot demonstrating each of the four hemispherical (fisheye) lens geometries tested; colors represent point heights (blue < green < red); axis values are in radians

Applying the *VCC_{fci}* calculation to the full dataset of 950 ALS and ground plots, model fit improvement is again exhibited by filtering out disturbances (Figure A2.4). Both second-order

polynomial ($R^2 = 0.39$) and exponential ($R^2 = 0.35$) models show reasonable model fit before filtering disturbed sites, followed by a simple linear model ($R^2 = 0.32$). After filtering out disturbed sites, model fit improved for the second-order polynomial model ($R^2 = 0.43$), exponential model ($R^2 = 0.42$), and linear model ($R^2 = 0.40$). Thus, linear and exponential models showed the greatest improvement in model fit, which is logical given their relatively inflexible behavior compared to polynomials.

Meanwhile, P_{pdn} showed strong linearity with ACC and thus P_o (Figure A2.5). Errors were higher at lower values of ACC, with the presence of a few strong outliers. The application of exponential and polynomial linear models were tested in terms of their impact on model performance (Table 6.3).

Table 6.3 Comparison of top three univariate ALS models (VCC_{fci} ; VCC_{fr} ; VCC_{ir}) with P_{pdn} ; ACC = ground plot ACC; Exp(ACC) = exponential model ground ACC; Poly(ACC) 1 = first-order polynomial ground ACC; Poly(ACC) 2 = second-order polynomial ACC; Left model values = without filtering sites; Right model values = with filtering sites; standard error shown in parentheses

	Dependent variable																							
	VCC _{fci}						VCCfr					VCC _{ir}					P_{pdn}							
Model	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
ACC	0.382***			0.757***			0.424***			0.770****			0.265***			0.530***			-			-		
	(0.010)			(0.025)			(0.010)			(0.02()			(0.014)			(0.022)			0.140			0.243		
	(0.018)			(0.035)			(0.019)			(0.036)			(0.014)			(0.032)			(0.008)			(0.014)		
Exp		0 /35***			0.435***			0.205***			0.440***			0.310***			0.310***			-				0.130***
(ACC)		0.455			0.455			0.275			0.440			0.510			0.510			0.097***			0.139***	-0.157
		(0.020)			(0.020)			(0.013)			(0.020)			(0.018)			(0.018)			(0.005)			(0.008)	(0.008)
Poly			-			0.000			-			0.070			-			0 (10***			0.041**			
(AČC)1			0.351***			-0.303			0.230***			-0.078			0.308^{***}			-0.640			0.061			
			(0.070)			(0.186)			(0.076)			(0.189)			(0.056)			(0.165)			(0.030)			
Dele																								
(ACC)2			0.989***			0.950***			0.884***			0.759***			0.775***			1.049***			0 272***			
()_			(0.092)			(0.163)			(0.099)			(0.167)			(0.073)			(0.146)			(0.040)			
b	0.280***	-	0.315***	0.031	-	0.301***	0.334***	0.041*	0.364***	0.104***	-	0.320***	0.178^{***}	-	0.204***	0.002	-	0.300***	0.720***	0.816***	0.710***	0.788***	0.899***	0.899***
	(0.010)	(0.317)	(0.010)	(0.022)	(0.317)	(0.052)	(0.011)	(0.022)	(0.011)	(0.022)	0.245	(0.052)	(0.008)	(0.252)	(0.009)	(0.021)	(0.252)	(0, 0.46)	(0.004)	(0,000)	(0.004)	(0,000)	(0.015)	(0.015)
	(0.010)	(0.058)	(0.010)	(0.023)	(0.058)	(0.052)	(0.011)	(0.022)	(0.011)	(0.023)	(0.038)	(0.055)	(0.008)	(0.054)	(0.008)	(0.021)	(0.054)	(0.040)	(0.004)	(0.009)	(0.004)	(0.009)	(0.015)	(0.015)
Ν	945	679	945	679	679	679	950	950	950	679	679	679	950	679	950	679	679	679	950	950	950	679	679	679
R^2	0.315	0.421	0.390	0.404	0.421	0.432	0.336	0.358	0.387	0.406	0.419	0.424	0.263	0.312	0.342	0.289	0.312	0.340	0.263	0.279	0.297	0.303	0.314	0.314
Adj.R ²	0.315	0.420	0.389	0.403	0.420	0.430	0.335	0.358	0.386	0.406	0.418	0.422	0.262	0.311	0.341	0.288	0.311	0.338	0.262	0.278	0.296	0.302	0.313	0.313
	0.174	0.135	0.165	0.137	0.135	0.134 (df =	0.185	0.182	0.178	0.138	0.137	0.137 (df =	0.138	0.122	0.130	0.124	0.122	0.119 (df =	0.073	0.072	0.071	0.055	0.054	0.054 (df =
RSE	(df =	(df =	(df =	(df =	(df =	676)	(df =	(df =	(df =	(df =	(df =	676)	(df =	(df =	(df =	(df =	(df =	676)	(df =	(df =	(df =	(df =	(df =	677)
	943)	677)	942)	677)	677)	256 000***	948)	948)	947)	677)	677)	2 40 000***	948)	677)	947)	677)	677)	174.040***	948)	948)	947)	677)	677)	0,,,
Estat	434.237	492.101	501.499	457.978	492.101	256.980	478.719	529.045	298.685	465.6/0	488.157	248.980	558.476	50/.218	246.053	2/5.828	50/.218	1/4.242	557.608	366.773	200.322	294.661	509.682	309.682 ^{***} (d
r-stat	$(d1 = 1 \cdot 943)$	(ar = 1.677)	$(d1 = 2 \cdot 942)$	(ar = 1.677)	(dI = 1.677)	(u1 = 2; 676)	$(d1 = 1 \cdot 948)$	(a) = (1 - a) + (1 - a)	(dI = 2.947)	(ar = 1.677)	(ar = 1.677)	(u1 = 2; 676)	$(d1 = 1 \cdot 948)$	(dI = 1.677)	$(d1 = 2 \cdot 947)$	(dI = 1.677)	(dI = 1.677)	(u1 = 2; 676)	$(ai = 1 \cdot 948)$	$(d1 = 1 \cdot 948)$	(dI = 2.947)	(ar = 1.677)	(dI = 1.677)	f = 1; 677)
	1, 745)	1,077)	2, 942)	1, 077)	1,077)	070)	1, 940)	1, 740)	2, 147)	1,077)	1, 077)	070)	1, 740)	1,077)	2, 147)	1,077)	1,077)	070)	1, 140)	1, 940)	2, 147)	1,077)	1,077)	0.5 *** .0.01

*p<0.1; **p<0.05; ***p<0.01

6.3.2 Point-density Normalized Canopy Gap Fraction

The P_{pdn} algorithm produced reasonable results, showing agreement with other P_o estimates and ground-level measurements. A visualization of point-density-normalized gap fraction (P_{pdn}), Beer-Lambert Law gap fraction (P_{bl}), and Beer-Lambert Law effective leaf area index (Le_{bl}), and apparent clumping index (Ω_{app}) are provided for an example ALS field plot (Figure 6.5).



Figure 6.5 Comparison with traditional metrics: (a) point-density normalized gap fraction by zenith angle; (b) Beer-Lambert Law gap fraction by zenith angle; (c) Beer-Lambert Law effective leaf area index by zenith angle, scaled by $\sin \theta$; (d) apparent clumping index by azimuth angle; y-axes represent respective values while x-axes represent zenith angle for (a), (b), and (c), and azimuth angle for (d)
Of the P_o metrics tested, the new P_{pdn} metric showed the best absolute correlation with ground measurements of ACC, topping other P_o metrics by a Pearson's r of nearly 0.2. A similar difference was shown for univariate linear model R^2 values, making P_{pdn} the top performing P_o metric tested. Nonetheless, the performance of P_o metrics may benefit from large improvements in accuracy by using more advanced models, such as 3-D convolutional neural networks.

6.3.3 Spike-free Canopy Height Model

The spike-free CHM algorithm (CHM_{sf}) produced expected results, following previous methods upon which it was based (Khosravipour *et al.*, 2014, 2016). While gridded canopy maxima produced results with many pits, the CHM_{sf} algorithm produced a continuous canopy surface model without pits, spikes, or excessive smoothing (Figure 6.6).



Figure 6.6 ALS canopy height models for an example site, 1 m resolution: (a) standard canopy height model with maxima for each grid cell; (b) spike-free canopy height model; color = height (m); axes = coordinates in NAD83 UTM 11N (meters)

While other smoothing algorithms exist, such as the median filter commonly applied in image processing, the benefits of spike-free CHM algorithms over traditional approaches for individual tree detection have been demonstrated (Khosravipour *et al.*, 2014, 2016). The advance provided herein is primarily computational, reducing a 3-D problem to a layered 2-D solution based on voxels (volumetric pixels).

6.3.4 Tree and Crown Metrics

In order to perform individual tree crown (ITC) detection and crown area estimation, empirical data from recent research in the study area (Cortini *et al.*, 2011) was applied to model the height-to-crown-area relationship for deciduous and conifer species, as well as all species as one group. The ground data consist of aggregated minima, means, and maxima for major regional tree species height-to-crown-area, with standard deviations provided. Models for height-to-crown-area were developed for aggregated native species in the study area from these statistical moments. Resultant R^2 values for both univariate linear and second-order polynomial models ranged from 0.87 to 0.97 while RSE ranged from 0.73 to 0.25 (Table 6.4). All models have *p*-values < 0.01.

Table 6.4 Comparison of height-to-crown-area model results: all species (1:2); deciduous species (3:4); evergreen coniferous species (5:6); each observation is the average of many observations $(N_{total} = 17,929)$; models are built from minima, means, and maxima, with standard deviations reported (Cortini *et al.*, 2011); standard error shown in parentheses

	Dependent variable					
	Crown Area (m ²)					
Model	All-Linear	All-Polynomial	Deciduous-Linear	Deciduous-Polynomial	Conifer-Linear	Conifer-Polynomial
#	1	2	3	4	5	6
Height (m)	0.133***		0.168***		0.116***	
	(0.011)		(0.020)		(0.007)	
Poly(Height)1		0.070		0.118		0.036
		(0.042)		(0.082)		(0.021)

Poly(Height)2		0.002		0.001		0.002
		(0.001)		(0.002)		(0.001)
h	-0.225	0.056	-0.270	-0.046	-0.217	0.146
0	(0.108)	(0.264)	(0.268)	(0,522)	(0.125)	(0.131)
	(0.198)	(0.204)	(0.508)	(0.322)	(0.155)	(0.151)
N	24	24	8	8	16	16
R^2	0.876	0.889	0.921	0 927	0 949	0 977
Adjusted R^2	0.870	0.878	0.908	0.898	0.945	0.974
RSE	0.650 (df = 22)	0.630 (df = 21)	0.694 (df = 6)	0.731 (df = 5)	0.363 (df = 14)	0.252 (df = 13)
F-Statistic	155.538^{***} (df = 1; 22)	83.877^{***} (df = 2; 21)	70.251^{***} (df = 1; 6)	31.879^{***} (df = 2; 5)	260.329^{***} (df = 1; 14) 277.576^{***} (df = 2; 13)
					*p<	<0.1; **p<0.05; ***p<0.01

First- and second-order polynomial models were chosen based on a visual analysis of plot data (Figure 6.7). Conifer species showed the best model fit, with a linear and polynomial R^2 of 0.94 and 0.98, respectively, compared to deciduous model R^2 values equal to 0.92 and 0.93. Both linear and second-order polynomial models for all species showed adequate performance ($R^2 = 0.88$; $R^2 = 0.89$). Hence, even though variation attributable to species is evident (Figure 6.7), a single polynomial linear model showing good model performance is used ($R^2 = 0.89$).



Figure 6.7 Empirical height-to-crown-area linear models for (a) deciduous species; (b) conifer species; (c) regression models for major tree species located in the study area based on minima, means, and maxima $(N_{total} = 17,929)$

Variants of the ITC detection algorithms implemented here underwent validation in a number of previous studies (Popescu *et al.*, 2002; Kaartinen *et al.*, 2012). The algorithms were applied to generate predictor variables to test for variable importance in estimating canopy gap fraction (P_o) , and its inverse, angular canopy closure (ACC). Here, ITC results are treated as features for estimating *T*, rather than tree crown counts, as the purpose was to extract additional information from ALS data. Hence, the accuracy of their results is not a consideration in this work. From a

visual analysis of ITC estimates, reasonable algorithm performance is assumed. The ITC algorithms implemented include standard and hierarchical watershed segmentation, as well as standard and hierarchical variable-size moving window methods (Figure 6.8).



Figure 6.8 Individual tree crown (ITC) detection for an example ALS plot with the standard watershed segmentation ITC detection method; center points indicate the likely stem locations; circle radii are scaled to the estimated crown area; brightness = height (m); coordinates are in NAD83 UTM 11N (meters)

Standard and hierarchical variable-size moving window ITC detection counts of tree crowns performed the best in predicting ACC of the ITC methods, each with an R^2 above 0.4, despite not undergoing calibration. While ITC methods were not inferred to be able to predict ACC on their own, as ITC counts and ACC are considered dependent variables (Falkowski *et al.*, 2008; Kaartinen *et al.*, 2012; Wang *et al.*, 2016), they are complimentary to other metrics as an additional feature of forest geometry, as is the apparent clumping index (Ω_{app}).

6.4 Discussion

Following half a century of hemispherical (fisheye) lens photography for estimating light transmission in forests (Evans & Coombe, 1959), based on the seminal work of Monsi and Saeki (1953), this is likely the first work demonstrating the effects of lens geometry on LiDAR calculations of ACC and P_o . While not the focus of this study, these results show that hemispherical projections are an important consideration in the implementation of hemispherical view approaches of calculating *T* from LiDAR or photographic data, as the projections are fundamentally the same. Traditionally, equiangular lenses have been used under an assumption of improved performance (Schwalbe *et al.*, 2009). With mathematical models of lens geometry, ignoring real-world lens distortion due to optical imperfections, this assumption is tested and results presented.

None of the P_{hv} methods tested show strong performance, requiring further development against hemispherical photography measurements closer to the time of ALS acquisition. While step-wise AIC and BIC linear regression models included unacceptably high numbers of coefficients without substantial performance gains, univariate linear models are considered adequate to the task. The overall top three metrics of ACC, VCC_{fci} , VCC_{fr} , VCC_{ir} , all show good univariate linear model fit with ground measurements (adjusted $R^2 = 0.52$; 0.51; 0.50) (Figure A2.3). Despite the general good performance of a number of metrics, the temporal mismatch of field campaigns is plainly visible in the data, as many sites were likely disturbed between the ground measurements and ALS acquisition. Strong agreement between multiple LiDAR-derived predictors of ACC showing only moderate agreement with convex spherical densiometer measurements suggests that the LiDAR metrics should be tested against hemispherical photographs collected closer to the time of ALS acquisitions. It is inferred that this temporal mismatch poses a fundamental limitation on algorithm performance here, as top-performing metrics saturate near the same accuracy level (Figure 6.1).

The modified spike-free CHM algorithm exhibited reliable results, providing continuous canopy values and preserving detail with low computation times. This facilitated the application of ITC detection algorithms. Here, ITC results are treated as an additional feature of the data, rather than measures of tree counts. Although ITC results are likely of low accuracy, variable-window ITC approaches in particular show a strong ability for use in the prediction of ACC.

The most promising finding of the study was the strong performance of the new P_{pdn} metric, which stands as the most accurate of all tested metrics of gap fraction, or P_o . The new metric was designed to harmonize ALS and TLS calculations of P_o with ground-based methods. Further studies should test this metric against hemispherical photography estimates, for which it was designed. Thus, the P_{pdn} metric may be considered a step toward the harmonization of groundbased and airborne estimates of P_o , which remains an outstanding challenge due to the different nature of ground and LiDAR measurement techniques.

While the P_{hv} metric showed disappointing results given the theoretical strength of assumptions of algorithm design, it nonetheless provides important information. Furthermore, its performance may be limited by the low point densities of the ALS data used here. First, the P_{hv} algorithm's inclusion of different hemispherical lens geometries shows the importance of lens models. Second, this new metric remains robust in concept, with many opportunities to improve performance.

From these results, it is concluded that these ALS-based models of T require further development with higher point densities closer to the time of ground data collection. As such, in the following chapter, we develop models of T directly from the ground measurements and environmental covariates. Those with high point density LiDAR datasets may nonetheless benefit from the methods presented above, necessary for pursuing similar studies in regions where there is limited ground sampling coverage, as is often the case in boreal forests.

6.5 Limitations

The main limitation of this work was the half-decade difference in timing between ground and ALS data collection, which produced strong disagreement between ground ACC and ALS metrics for some sites. It was apparent from scatterplots and ALS plot data visualization that disagreement arose from either disturbance or forest regrowth on previously disturbed sites. This temporal mismatch diminished the utility of ground ACC data for use in cross-validation. Meanwhile, even though the ALS data had a low mean point density of 1.64 points m⁻², these data may be of greater precision than coarse spherical densiometer measurements of ACC while providing more complete and even sampling coverage. Thus, I question the use of coarse ground

measurements of ACC (e.g., spherical densiometers), instead favoring of measurement with modern LiDAR systems, structure-from-motion models, 360-degree spherical imagers, or digital hemispherical imagers. The use of full-waveform data may add state-of-the-art vertical canopy sampling and canopy penetration essential for modeling canopy light transmission. It is perhaps ironic that ground-truth data were the largest source of uncertainty in this work, as it appears to have fundamentally limited the development of models.

Chapter 7: Simulation of Understory Global Solar Irradiation

7.1 Introduction

Light is a primary source of life for plants, as its physical energy drives the process of photosynthesis, making light a focus of plant resource competition (Hikosaka & Hirose, 1997; Katahata *et al.*, 2005; Ruban, 2009). While plants have developed adaptations that enable them to tolerate fluctuations in the light environment, long-term or directional changes to light conditions can affect lasting change through successional processes. Unlike open sites, forest canopies place strong limitations on the quantity and quality of light, as can local topographic conditions. Understory light, or understory solar irradiation (I_u), plays a critical role in forest succession and community ecology.

Roles in an array of processes from tree regeneration (Greene *et al.*, 1999) and nutrient cycling to fire frequency have been attributed to boreal understory plants, with some suggesting that the understory drives forest succession (Nilsson & Wardle, 2005). Previous studies have shown the importance of I_u in controlling understory plant diversity and production in boreal forests (Aubin *et al.*, 2000; Grandin, 2004; Bartemucci *et al.*, 2006; Beaudet *et al.*, 2011; Reich *et al.*, 2012). Hence, the prediction and management of boreal understory light are important tasks for scientists and managers (Lieffers *et al.*, 1999). Canopy conditions and topography play a central role in controlling understory light in the boreal, due to lower solar elevations at higher latitudes, despite narrow tree crowns here. While changes in forest structure exert a more pronounced control on canopy light transmission, or *T* (Lieffers *et al.*, 1999; Beaudet & Messier, 2002; Bartemucci *et al.*, 2006), variation is also due to overstory tree species (Canham *et al.*, 1994) or landcover conditions.

While the direct effects of increased solar radiation and warmer air temperatures may be beneficial for understory plant productivity, particularly when met by increases to precipitation (Trenberth, 2011), atmospheric CO₂, nitrogen, and phosphorus, long-term increases in evaporative demand may diminish soil water conditions (Bonan, 2008), limiting regeneration and growth. Although currently understudied, recent work for the Swedish boreal attributed an observed reduction in soil water levels to increased I_u levels (Grandin, 2004). Yet, the quality of light may be more important than the quantity to long-term growth processes (Dengel & Grace, 2010). The ability to predict changes to I_u may better nevertheless facilitate the estimation of understory evaporative demand and thus soil water conditions in forests. This line of work is critical to research on global change and is of key importance to biodiversity research.

My previous chapters show the importance of fire in regulating boreal canopy structure and composition, as boreal systems are predominantly driven by climate and fire conditions. Warming is shown to produce complex changes to stand regeneration and fire regimes, resulting in a weak long-term forest decline signal in some regions. The combined effects of these changes on understory light conditions are the subject of this chapter. Here, I hypothesize that a long-term decline in forested area, modeled in Chapter 5, may increase understory light levels in the forested region of western Alberta, Canada. The effect of these changes on understory species may depend on additional local conditions, such as topographic position, soil conditions, and precipitation patterns. This work focuses on modeling combined canopy, topography, and earth-

sun position controls on understory light, as the key drivers of I_u variation, using hybrid forest landscape model simulations in connection with regression models of gap fraction (P_o).

Landscape changes to I_u are simulated in a model fusion approach. First, linear and machine learning regression models are developed for P_o , designed to be compatible with LANDIS-II model outputs. A global solar irradiation model is used to estimate topographic and latitudinal effects on insolation. By combining P_o with bare-earth insolation, I_u is calculated. Continuing the previously described simulation work, four model scenario periods are tested for changes to I_u levels: Pre-suppression Era (1923-1952); Early Suppression Era (1953-1982), Global Change Era (1983-2012); and, Most Recent Decade (2003-2012). The effects of different climate and fire scenarios, as well as different fire models, on landscape-scale understory light conditions are also tested. Models were run for 50 years of duration, with the first 10 years used for model spin-up.

7.2 Methods

Multiple linear and Random Forest regression models of ACC were developed using ground plot data. 10-fold cross-validation was repeated three times for each of the models to measure performance using robust methods. RMSE, R^2 , and the standard deviations of each were used to select final regression models. Landcover classification was performed on LANDIS-II model outputs using the ABMI Landcover 2010 scheme. Methodological details are provided below.

7.2.1 Data

Plot data used for the development of regression models include area-based canopy and terrain LiDAR metrics calculated with USDA Fusion (McGaughey, 2014), 30-year normal climate

variables output from ClimateWNA (Wang *et al.*, 2011a), Alberta Wet Areas maps derived from LiDAR (Arp *et al.*, 2009), Alberta Biodiversity Monitoring Institute (ABMI) Landcover 2010, Canada Land Inventory (CLI) forest site index, bare-earth insolation calculated with ArcGIS, a NASA SRTM digital elevation model (DEM), and ground-level GPS coordinates and vegetation survey data (Nielsen, 2005). The plot data included the following 58 variables:

Easting, northing, elevation, graminoid abundance, ALS return count, ALS height maximum, ALS height mean, ALS height 5th percentile, ALS height 10th percentile, ALS height 25th percentile, ALS height 50th percentile, ALS height 75th percentile, ALS height 90th percentile, ALS height 95th percentile, ALS ratio of returns above 2m, ALS ratio of returns above mean return height, ALS height relative ratio, ALS height skewness, ALS height standard deviation, ALS terrain aspect, ALS terrain slope, ALS terrain elevation, ALS terrain, ALS terrain plan curvature, ALS terrain profile curvature, ALS terrain solar index, wet areas, convex spherical densiometer ACC, percent conifer, regeneration, degree-days below 0, frost days, frost-free period, growing season precipitation, mean annual precipitation, monthly maximum temperature, monthly minimum temperature, July mean temperature, March precipitation, product of May × September precipitation, June precipitation, December precipitation, summer heat moisture index, January minimum temperature, July minimum temperature, herbaceous plant abundance, ABMI landcover, CLI forest site index, shrub abundance, diffuse radiation, global radiation, product of June × August global solar radiation, product of June × September global solar radiation, ALS compound topographic index (CTI), CTI 150m, CTI 90m, topographic position index, ALS canopy equation

Example maps of variables used in the regression analysis described in Section 7.2.2 are provided, including ClimateWNA 1961-1990 mean July precipitation and minimum January temperature, and modeled bare-earth global solar irradiation (Figure 7.1). The physically based model used to calculate bare-earth solar irradiation is described in Section 7.2.4.



Figure 7.1 Predictor variable maps for the study area: (a) 1961-1990 mean July precipitation in mm; (b) 1961-1990 minimum January temperature in degrees C; (c) mean annual bare-earth global solar irradiation in Wh m⁻² year⁻¹; axis values represent pixel coordinates in NAD83 UTM 11N (meters) coordinates, used for its high positional accuracy at regional scales

7.2.2 Linear and Machine Learning Regression Models of Po

Multivariate linear regression follows the classical form:

$$y_i = \beta_1 x_{i1} + \dots + \beta_p x_{ip} + \varepsilon_i = X_i^T \beta + \varepsilon_i$$
 for $i = 1 \dots n$

Where *T* denotes the transpose, such that $X_i^T \beta$ is the inner product between x_i and weight or β vectors. The ordinary least squares function is used to solve for weights and the intercept term that minimize error. The Random Forest algorithm applied also follows this classical form (Breiman, 2001). The Random Forest algorithm is based on the construction of decision trees, regression trees in this case, falling under the classification and regression tree (CART) umbrella term (Breiman *et al.*, 1984). The Random Forest algorithm is detailed in Appendix A.

Multivariate linear and Random Forest machine learning regression models of P_o were developed. The effects of different predictor variables on model performance were tested. For linear regression, this is done with step-wise AIC and BIC model selection, as well as manual variable selection based on an analysis of variance combined with inference regarding dynamics likely driving variation in P_o . For Random Forest models, variable selection is based mostly on variable importance metrics, while inference-based manual variable selection is also used. To assess the performance of each model, 10-fold cross-validation was implemented three times, randomly selecting 75% of the data for model training and 25% for model testing.

7.2.3 Landcover Classification of LANDIS-II Species-age Cohorts

To model P_o using LANDIS-II outputs, annual simulated species-age cohort maps were classified into landcover classes using the ABMI Wall-to-wall Landcover Map 2010 Version 1.0 scheme (Alberta Biodiversity Monitoring Institute, 2012). Two caveats exist in this data set in that shrubland is often recently disturbed forest and road width is overestimated, lending to an enlarged developed area. This landcover classification scheme and the algorithm used is detailed in Appendix D.

First, species-age cohort maps are classified based on the taxonomic group into either evergreen or broadleaved (i.e., angiosperms). The sum of binary presence values at each site for each group is then calculated in order to calculate the site percent evergreen and percent broadleaved, based on the overall number of species present at a site. Immature trees less than ten years of age were filtered out to remove transient dynamics. ABMI Landcover 2010 class values were applied to inactive sites before classifying LANDIS-II species-age cohort outputs into landcover classes. Sites with greater than 75% evergreen trees were classified as Evergreen Forest. Sites with greater than 75% broadleaved trees were classified as Broadleaf Forest. Sites where both evergreen and broadleaved trees represented 25% or more of the site were classified as Mixed Forest. Active sites without any tree species present were classified as Grasslands to capture sites where regeneration failed.

7.2.4 Bare-earth Global Solar Irradiation Model

The sum of direct, diffuse, and reflected solar radiation components is known as global solar irradiation, with direct and diffuse radiation comprising the majority of the insolation budget. While direct radiation theoretically reaches the surface unimpeded, diffuse radiation is scattered by molecules in the atmosphere, and reflected radiation is returned by surface features. Although only a fraction of incident radiation can be used by plants in photosynthesis, known as the fraction of photosynthetically active radiation (fPAR), changes to full-spectrum radiation are important for monitoring changes in energy balance (Rich, 1990) that may control evaporative demand and soil water levels. To compute landscape bare-earth global solar irradiation for the study area, ArcGIS Spatial Analyst solar radiation tools (Fu & Rich, 1999) was used with an SRTM RADAR digital elevation model (DEM). The algorithm is detailed in Appendix C.

7.3 Results

Supporting the hypothesis provided, model fusion suggests that I_u levels increased with a simulated long-term decline in forested area. Multivariate linear and machine learning regression models of ACC with the Random Forest algorithm showed comparable performance. Both model classes performed well with only two predictor variables, Alberta Biodiversity Monitoring Institute (ABMI) Landcover 2010 and Canada Land Inventory (CLI) Forest Site Index. Multiple linear regression with step-wise AIC produced good model fit (multiple and adjusted $R^2 = 0.949$; *RMSE* = 0.067), but overfit by selecting 25 predictor variables. Step-wise BIC produced comparable results (multiple and adjusted $R^2 = 0.946$; *RMSE* = 0.069) while selecting only nine predictor variables. An analysis of variance for all predictors allowed the manual selection of two predictors logically complementary in their ability to predict P₀: ABMI Landcover 2010 and CLI Forest Site Index. Critically, both variables contain latent information on disturbance legacies, as well as information on regional climate and soil patterns.

CLI site index is treated as a numeric integer, rather than categorical, variable due to its linear scaling. Using only the above two predictor variables, multiple linear regression showed model performance comparable with substantially more complex models (Table 7.2). Multiple linear regression model robustness was tested for the two predictor variables by performing 10-fold cross-validation repeated three times ($R^2 = 0.938$; RMSE = 0.079), yielding only marginally diminished model performance compared to step-wise AIC or BIC model selection models with many variables.

Table 7.1 Multiple linear regression model; LC = landcover; coefficients shown for variables; standard error shown in parentheses; ACC $(1 - P_o)$ is the dependent variable

Independent variables	Dependent variable		
CLI Forest Site Index	ACC $(1 - P_o)$		
ABMI LC Class 2	-0.126*** (0.002) 0.003 (0.011)		
ABMI LC Class 3			
ABMI LC Class 4	0.020 (0.016)		
ABMI LC Class 5	-0.185 ^{***} (0.007)		
ABMI LC Class 6	-0.571 ^{***} (0.014)		
ABMI LC Class 7	-0.157 ^{***} (0.017)		
ABMI LC Class 8	-0.378 ^{***} (0.034)		
ABMI LC Class 9	-0.252^{***} (0.010)		
ABMI LC Class 10	-0.504 ^{***} (0.012)		
ABMI LC Class 11	-0.126 ^{***} (0.032)		
Constant	0.882 ^{***} (0.007)		
N R^{2} Adjusted R^{2} Residual Std. Error <i>F</i> -Statistic	900 0.938 0.938 0.075 ($df = 888$) 1,350.077*** ($df = 10$; 889)		
Note:	*p<0.1; **p<0.05; ***p<0.01		

A Random Forest regression model using all 59 predictor variables, with 10-fold cross-validation repeated three times, only marginally improved upon multiple linear regression with two variables ($R^2 = 0.944$; RMSE = 0.070), despite the substantial increase in model complexity. Three predictors showed particularly high Random Forest variable importance (Figure 7.2): percent conifer, CLI forest site index, and ABMI Landcover 2010.



Figure 7.2 Random Forest variable importance (decrease in node impurities) used for initial feature selection

While percent conifer shows the highest variable importance, better Random Forest model fit was achieved with the two predictors used in multiple linear regression: CLI forest site index (productivity) and ABMI Landover 2010 class. Ten-fold cross-validation was repeated three times to assess Random Forest model performance. Random Forest models including all three variables of the highest importance explained 93.2% of variance, while models including only the CLI and ABMI landcover variables explained 93.6% of variance. For the final two-parameter Random Forest model ($R^2 = 0.936$; RMSE = 0.076), the scale-free variable importance of the

two predictors was 18 for CLI forest site index and 68 for ABMI Landcover 2010. Thus, landcover class is inferred to be the most important predictor tested for P_o , even though Random Forest is shown to be biased toward both continuous and many-predictor categorical variables (Strobl *et al.*, 2007), which may be corrected with one-hot encoding (a binary class membership schema). As such, this work proceeds with models using only CLI site index and ABMI landcover class as predictors. The final two-parameter Random Forest model showed stability in low error using an *ntree* parameter of 500, or a forest of 500 regression trees for averaging (Figure 7.3).



Figure 7.3 Random Forest model out-of-bag MSE (Error) by the number of trees parameter

Despite the strong performance of the final two-parameter Random Forest model ($R^2 = 0.939$; RMSE = 0.074), multivariate linear regression produced only slightly diminished model fit ($R^2 = 0.938$; RMSE = 0.079), although a simpler and smaller model. The multivariate linear regression model did not suffer from the bias of the Random Forest model, which underpredicted P_o maxima. Hence, the two-parameter multivariate linear regression model was selected as the final model for modeling P_o at the landscape scale by applying the ABMI landcover classification scheme to annual LANDIS-II species-age cohort outputs. Using the linear regression model with LANDIS-II species-age cohort landcover classes and a map of CLI forest site index, annual maps of P_o were produced to calculate landscape maps of understory global solar irradiation as the multiple of canopy light transmission and bare-earth global solar irradiation ($P_o * I_{global}$).

Both the lowest and highest global solar irradiation levels are shown for the Rocky Mountain and foothills region, due to local topographic variation. The foothills region showed the highest forest productivity in the region, while the Rocky Mountain region contains moderate levels of productivity. These patterns are important for the following sections on modeling understory solar irradiation. Here, ALS data were not used as a predictor due to the temporal mismatch between ALS sorties and ground validation data collection. Due to this mismatch, disturbances and recovery broke down the correlation structure between datasets. ALS remains an important predictor of P_o due to its broad sampling capabilities, which may provide a more representative picture of forests. Where high point-density or waveform ALS data is available, it is considered preferable to coarse traditional ground measurements.

7.3.1 Simulation of P_o and I_u with Model Fusion

Using the final two-parameter linear regression model with CLI forest site index and the ABMI Landcover 2010 classification scheme applied to LANDIS-II simulated species-age cohort maps, P_o is simulated at a landscape scale (25.2 million ha) and stand resolution (100 m cells) at an

annual time-step for a 50-year duration. Annual understory solar irradiation (Wh m⁻² year⁻¹), or I_u , is computed by multiplying each annual map of mean simulated P_o against the bare-earth mean global solar irradiation map, following a recent approach (Bode *et al.*, 2014). To track landscape-wide changes in I_u over time for each scenario, mean annual understory solar irradiation ($\overline{I_u}$) is computed for each modeled I_u map (Figure 7.4). The results for each scenario show that simulated changes to $\overline{I_u}$ reflect complex changes to disturbance regimes and climate over the past 90 years.



Figure 7.4 Simulation and modeling of mean landscape full-spectrum understory solar irradiation $(\overline{I_u})$ for forested cells in the study area for each of the fourteen model scenarios; the legend text format is as follows: [succession model]-[fire model]-[start year]-[end year]; ao = age-only succession; bf = base fire; dffs = dynamic fuels and fire system; extremes = 1923-1952 period climate with 1983-2012 period fire; see Table 5.1

Simulation scenarios with a Pre-suppression Era (1923-1952) high burn rate show an initial rapid increase in $\overline{I_u}$ during the model spin-up decade. Meanwhile, all other simulation scenarios show a decline in $\overline{I_u}$ due to demographic changes, as stand development outweighed mortality given diminished disturbances. In the absence of disturbance, changes in regeneration are masked. Simulated reductions to burning, due to fire suppression in recent decades, reduced the mean quantity of understory light in forests at the landscape scale by a maximum of 8%, attributable to this demographic shift. Meanwhile, higher burn rates generally produced higher landscape levels of $\overline{I_u}$ *in* forests.

Base Fire (*bf*) model simulations are notable for showing the highest landscape levels of $\overline{I_u}$ in forests. Meanwhile, Dynamic Fuels and Fire System (*dffs*) model configurations produced substantially lower levels of $\overline{I_u}$ even when parameterized with the same empirical fire regimes. This is due to the semi-mechanistic nature of the *dffs* fire model, as initial large fires were followed by fuel limitations. The *dffs* model configuration scenarios surprisingly yielded lower average levels of $\overline{I_u}$ than age-only succession (*ao*) scenarios, producing the lowest simulated levels of $\overline{I_u}$ in the *dffs extremes* scenario (Figure 7.5).



Figure 7.5 Mean understory solar irradiation ($\overline{I_u}$) across all simulation years by scenario; scenario naming conventions follow those of Table 5.1 and Figure 7.4

Low landscape $\overline{I_u}$ produced in the *dffs extremes* scenario may be explained by rapid forest expansion following initial large disturbances, as space for recruitment expanded before fuel limitations reduced disturbance. This pattern of fuel-limited disturbance regimes is apparent for the *dffs* scenarios (Figure 7.6). The *bf* scenarios, which forced the application of empirically derived historical disturbance regimes without fuel or weather limitations, showed an increase in $\overline{I_u}$ for all model scenarios, except for the Early Suppression (1953-1982) and Global Change (1983-2012) Eras. During these two eras, stand development outweighed empirical fire regimes, diminishing the level of $\overline{I_u}$. In the Most Recent Decade (2003-2012) bf scenario, $\overline{I_u}$ increased with the rise in fire frequency, despite diminished fire size.



Figure 7.6 Change in understory solar irradiation ($\overline{I_u}$) between simulation years 0 and 50 by scenario; the scenario naming conventions again follow Table 5.1 and Figure 7.4

7.4 Discussion

Forest stand age, modeled implicitly in the LANDIS-II simulations, plays a central role in landscape levels of $\overline{I_u}$. Higher historical burn rates produced higher levels of $\overline{I_u}$ in simulations, as mean forest age declined with higher rates of burning. The inclusion of fuels and weather limitations in fire models notably limited the continuation of high rates of burning over multiple decades. Whether fuels and weather conditions here currently impose a fundamental energetic limit on the burn rate requires further research. Previous studies indicate that the rate of burning was likely more severe in previous centuries under cooler and drier climatic conditions, as discussed in Chapter 3, which may be attributable to a difference in fuels. The two fire-climate extreme scenarios yielded divergent responses in landscape $\overline{I_u}$ levels depending on the fire model used, due to the inclusion of fuel limitations in the *dffs* fire model. It is evident that a decline in forest cover may drive a long-term increase in landscape $\overline{I_u}$, if stands fail to regenerate under warmer conditions. A long-term decline in regeneration rates in the area may overshadow a demographic shift related to near-term stand development in the absence of fire-related mortality. As the simulations do not include harvest, its contribution to mortality may balance the decline in area burned. The interaction of harvest, fire, and biological disturbance requires further research. In the simulations, sites converted from forestland to grasslands or shrublands due to reduced regeneration rates, caused by modeled soil water limitations under warming. Given the importance of regeneration to the modeling study results, this component requires more extensive regional validation in future studies. While empirical evidence similarly shows a decline in regeneration across the study period, competition appears to be the main driver, with climate inferred to play a weaker role (Appendix F).

The simulated conversion from forest to grassland or shrubland in LANDIS-II explains changes in landscape $\overline{I_u}$. Annual bare-earth global solar radiation and CLI forest site index were fixed for each site, making $\overline{I_u}$ variation purely a function of the effects of simulated landcover change on modeled P_o . Forest demography is not explicitly modeled in the calculation of P_o . Immature trees less than ten years of age are omitted, due to a negligible effect on overstory P_o conditions and no effect of competition on regeneration. Hence, the effect of new forest growth is not apparent until ten years after disturbance. This produces a lag in $\overline{I_u}$ values and does not explain the observed simulation patterns. Landcover was the only non-static variable for sites in the $\overline{I_u}$ model.

Based on simulated rates of forest change described in previous chapters, modeled landscape $\overline{I_u}$ showed divergent responses to changing fire and climate conditions. Modeled $\overline{I_u}$ indicated that understory light levels were highest under greater burn rates and warmer climatic conditions. Yet, this result is dependent on the type of fire model applied. It is suggested to apply empirical fire models for historical analyses of simulated fire regimes, particularly if there is an absence of empirical support for the application of complex semi-mechanistic fire models. Meanwhile, studies concerned with forecasting into novel conditions may benefit from the mechanistic aspects of complex fire models that allow theoretically robust extrapolations.

Here, the primary concern was replicating the continuation of recent historical fire patterns for modeling changes to canopy light transmission (*T*), a task for which both fire models provide useful information. Future studies should extend forest ecosystem simulations over longer (e.g., century) timescales to test for forest decline or compositional change, as model behavior may overcome initial landscape parameterization at century timescales, resulting in eventual equilibrium. Yet, model uncertainty also increases with longer simulation timescales, as errors propagate, motivating the use of half-century simulations. Regardless of temporal scale, most critical are the simulation time-points where regime shifts are likely to occur, which signify transitions in the state-space of forests. Dedicated state-space models designed for linear systems with random disturbances, such as the Extended Kalman filter (Kalman & Bucy, 1961), may be used to model these changes over time.

Based on landscape $\overline{I_u}$ simulations and previously described simulations (Chapter 5), a forest ecosystem state change-point appears to occur near year ten for the study area (Figure 7.5). Yet,

this may be attributable to model spin-up. Evidence is provided that a diminished rate of burning likely decreased $\overline{I_u}$ in recent years, attributable to a demographic shift occurring through stand development processes in the absence of fire-related mortality. This is supported by a precursory analysis of Alberta Permanent Sample Plot data for the region, which shows a reduction in regeneration and mean tree height – inferred to correspond to a reduction in mean tree age – across the Global Change Era, likely reducing understory light levels (Appendix F). Yet, future studies must incorporate the effects of harvest and biological disturbance agents with more sophisticated succession models to estimate the effects of each on understory light.

7.5 Limitations

In this chapter, a physical solar radiation model was combined with a regression model of P_o using forest site index and simulated landcover as predictors. The layering of these models may produce error propagation, common to complex models lacking global parameter optimization (Pacala *et al.*, 1996; Arras, 1998; Larocque *et al.*, 2008). These uncertainties were not explicitly represented given the complexity of models and scope of this research. Additionally, the solar radiation model used in this chapter assumes constant solar output, which is known to be false, but is a reasonable assumption given that work is not concerned with temporal variation in solar activity. Other limitations of the solar radiation model include its reliance on simple geometric relationships and lack of radiative transfer functions related to turbidity or cloud cover.

Of these shortcomings, the absence of cloud cover information is expected to have the largest effect on modeled radiation, as clouds may be the largest source of radiation attenuation in the atmosphere (Hammer *et al.*, 2003). Cloud cover indices derived from geostationary weather

satellite data can be used to generate atmospheric clearness indices. Such indices facilitate a simple but effective method of integrating spatiotemporally resolved atmospheric conditions with models of clear-sky solar radiation and LiDAR canopy light transmission (Tooke *et al.*, 2012). Finally, while changes to landcover were dynamically simulated, forest site index was static (Agriculture and Agri-Food Canada, 2016). Future studies should test the application of NDVI, NIR_v, or SIF for incorporating dynamic changes to site productivity.

Chapter 8: Conclusion

The purpose of this thesis was to investigate past-century changes to regeneration and fire in western Alberta in order to parameterize models for the simulation of understory solar irradiation (I_u) trajectories. To achieve the simulation of I_u , process-based, hybrid, physical, and regression models were combined through model fusion. This work is intended to provide a currently absent variable (I_u) necessary for forecasting changes in the distribution and abundance of understory plants, critical to brown bears (*Ursus arctos* Linnaeus) and other regionally important species. This thesis poses six fundamental questions regarding past-century changes in forests of western Alberta linked to global change:

- 1. Have climatic and anthropogenic changes altered fire regimes in western Alberta and do regional historical fire patterns match those of the national scale?
- 2. Has climate change altered tree species regeneration rates in western Alberta?
- 3. What are the net effects of recent climate and fire trends on forests in western Alberta?
- 4. Can new airborne laser scanning (ALS) models provide an improved ability to estimate understory global solar irradiation in western Alberta?
- 5. Can a forest landscape model be fused with linear or machine learning regression models to simulate dynamics not explicitly represented in the model?
- 6. Have past-century climate and fire trends changed landscape-level I_u in western Alberta?

In Chapter 3, anthropogenic change is shown to combine with warming to produce complex changes to fire regimes. These changes include more frequent, smaller, human-caused fires near

areas of human activity. Only a mild increase in annual area burned was shown under warming for the study area while decreasing nationwide, indicating the expansion of suppression efforts in the absence of broad demographic changes. The shift toward novel fire regimes in recent years is better explained by human activity than by warming, both at regional and national scales. Fire seasons lengthened substantially in the region, while changing little nationwide, likely partially attributable to differences in sampling coverage. In western Alberta, mean fire size declined at a constant rate before accelerating at an inflection point in ~ 1990. A strange pattern occurred at this time-point whereby fires nationwide declined thereafter in mean size, latitude, and total area burned, while increasing in frequency. This same pattern is shown for western Alberta, with the exception of annual area burned. The cause of this pattern remains unknown, but appears attributable to human activity rather than to climate or observational methods.

Nationwide, burning showed spikes of high activity in early spring, likely attributable to winter dead fuel load accumulation (Santana & Marrs, 2016) and phenology-mediated early spring photosynthetic production (Richardson *et al.*, 2013) followed by drying events. A 'spring dip' in conifer live foliar moisture content has also been shown to stem from foliar physio-chemical changes linked to phenology (Jolly *et al.*, 2016). Cold and damp regions have been shown to have the highest rates of fuels accumulation, as decomposition rates are lowest here (Dodge, 1972), given the temperature and microbia-taxa dependence of decomposition rates (Dioumaeva *et al.*, 2002; Oliverio *et al.*, 2017). Spring fire activity is poised to intensify with increased winter liquid-phase precipitation (Trenberth, 2011; Intergovernmental Panel on Climate Change, 2014; Rocca *et al.*, 2014), earlier snowmelt (Westerling *et al.*, 2006), increased primary production (gross and net) under warming (McMahon *et al.*, 2010; Wang *et al.*, 2011b; Pausas & Ribeiro,

2013; Keenan *et al.*, 2014; Liu & Wimberly, 2014), and increased human activity (Balch *et al.*, 2017), which may result in increased burning (Ali *et al.*, 2012).

Nationwide, the largest fires and area burned occurred in June, while fires were most frequent in July. For fires larger than 200 ha, characteristic of typical boreal fire regimes, mean fire latitude increased across the period. This pattern was partially explained by the increased use of satellite disturbance detection since the 1980s. It is inferred from this result and previous work (Scheffer *et al.*, 2012; Koven, 2013) that boreal fire regimes are nevertheless shifting northward due to a combination of warming in the north and more effective short-term fire suppression (Cumming, 2005) in the south. Yet, this hypothesis requires further testing with less spatiotemporally biased remote sensing records.

In Chapter 4, warming is shown to have a negative influence on modeled tree regeneration potential in western Alberta. While soil conditions are shown to play an important role in the regional response of trees to climatic change, the net effect of warming on regeneration was negative across species and regions. Changes in modeled regeneration were primarily attributable to changes in soil moisture, as available water holding capacity (AWHC) is the most sensitive model parameter in TACA-GEM. Despite predictions of improved regeneration conditions in higher elevations under warming, the results show the greatest reduction in regeneration there, due to differences in soil properties. Soil water levels and thus regeneration rates appeared more stable at low elevations, attributable to post-glacial soil textural properties in the boreal and foothills regions.

Germination frequency, physiological drought frequency, growing degree days, and turgor loss point frequency were the most important predictors of regeneration success. Results showed that even species in warmer neighboring regions may experience reduced regeneration potential under warming in the region. Meanwhile, a preliminary analysis of plot data for Alberta suggests that competition explains more of the observed decline tree regeneration rates than climate (Appendix F). The contribution of climate to diminished regeneration rates observed for western Alberta also requires further research. Future studies may incorporate gridded climate data, vegetation indices (e.g., Landsat NDVI and fractional cover, or SAR vegetation optical depth), soil grids, and ground plot data to model regional changes to forest regeneration since ~ 1990. Meanwhile, new ALS methods show strong potential for landscape-scale monitoring of forest regeneration at an individual-tree resolution (Yao *et al.*, 2014; Amiri *et al.*, 2015). Time-series methods using low-cost commercial UAS may facilitate an improved spatiotemporal evenness of sampling coverage.

In Chapter 5, a combination of diminished burning and tree regeneration potential in western Alberta is shown to produce a mean decline in forested area across the 50-year simulation period. Here, the TACA-EM tree regeneration model was fused with the Landscape Disturbance and Succession (LANDIS-II) model to simulate forest dynamics for four periods during the past 90 years. The number of forested sites or cells declined for all simulation configurations, except for the succession-only simulations. In succession-only scenarios, forested sites increased in the absence of fires through recruitment into sites classified as open in the initial landscape. The central tendency of the spatial distribution of forests increased in latitude for all simulations and in elevation for simulations with high burn rates, declining slightly in elevation in the absence of large disturbance levels. It is apparent from the pace of change in the spatial configuration of forests that diminished burn rates are inhibiting forests from migrating toward more optimal regeneration conditions. The simulated rate of forest migration lagged the velocity of warming here. The question remains whether the region's forests may adapt to novel conditions or whether new genotypes may migrate into the region. A reduction in burn rates implies slowed adaptation rates by lengthening the time interval between generations. Future studies should include phenotype plasticity and adaptive capacity in dynamic forest ecosystem simulations.

The choice of fire model is shown to exert substantial influence on simulation results. The statistical fire model brute-forced the parameterized fire regime, while the semi-mechanistic fire model showed strong fuel limitations following large initial fires. An algorithm based on stochastic gradient descent was developed to optimize fire model parameters. The new method was able to quickly converge by optimizing on reduced resolution simulations before refining these parameters on full-resolution simulations. The method overcomes a long-standing challenge in the application of forest fire models across landscapes with millions of interacting cells.

In Chapter 6, new plot-based regression models and ALS metrics were developed for the estimation of canopy gap fraction (P_o). The first new ALS metric was the hemispherical Voronoi gap fraction (P_{hv}) and the second was the point-density normalized gap fraction (P_{pdn}). For the

 P_{hv} metric, the effects of four different lens geometries were tested. In the process, a 2-D variant of the spike-free canopy height model (Khosravipour *et al.*, 2016) was developed for the application of standard individual tree crown (ITC) detection algorithms. Standard ALS metrics were calculated for comparison of their performance in estimating ACC (1 - P_o) and P_o . While the new P_{pdn} metric performed decently ($R^2 = 0.32$), top performing metrics for estimating ACC used existing methods, VCC_{fci} ($R^2 = 0.53$), VCC_{fr} ($R^2 = 0.51$), VCC_{ir} ($R^2 = 0.51$), VCC_{sci} ($R^2 = 0.51$).

In Chapter 7, simulation results from Chapters 4 and 5 were combined with the regression model of P_o from Chapter 6 and a topographic solar radiation model to simulate changes in mean annual global understory solar irradiation (I_u) for each of the model scenarios. Linear and machine learning regression models of P_o were developed from plot and ancillary data, including ALS metrics, for model fusion. Both classes of model showed optimal performance using two predictors: CLI forest site index and ABMI Landcover 2010. While Random Forest produced comparable model fit compared to multivariate linear regression ($R^2 = 0.939$; RMSE = 0.074), the latter produced less bias while benefitting from simplicity ($R^2 = 0.938$; RMSE = 0.079). Thus, a two-parameter linear regression model was used for final model fusion in LANDIS-II simulations. Nevertheless, I demonstrate the first, to my knowledge, fusion of machine learning and forest ecosystem models.

A classification scheme based on ABMI Landcover 2010 was developed for LANDIS-II speciesage cohort outputs to model landcover change for each simulation year. Next, the regression model of P_o was applied for each timestep using landcover maps as a predictor. A solar radiation model was applied to a NASA SRTM digital elevation model (DEM) to calculate bare-earth global solar irradiation (I_{global}) as the sum of direct and diffuse components. The resulting map of I_{global} importantly showed the 'feast-or-famine' light conditions of mountainous regions in the study area, due to topographic position. Finally, each annual map of P_o was multiplied against I_{global} to simulate changes to understory global solar irradiation (I_u).

Hybrid model simulations showed that modeled I_u levels increased under Pre-suppression Era and Most Recent Decade conditions using the statistical fire model. Yet, I_u levels declined in each of the other scenarios. The choice of fire model was a key differentiator in model results. Using the extremes scenarios as an example, where the warmest climate conditions were applied with the most severe rates of burning, I_u levels substantially increased with the statistical fire model and decreased with the semi-mechanistic fire model over the 50-year simulation period. In all other scenarios, the recruitment of new cohorts and stand development outweighed disturbance-related mortality, producing demographic ageing and a mean decline in I_u levels.

Explaining these results requires reference to Figure 6.3d, which shows that the statistical fire model consistently produced the parameterized fire regime, while the semi-mechanistic fire model was strongly constrained by fuel limitations. The choice of fire model architecture is a function of the research question. This research applied both types in an effort to better understand forest ecosystem trajectories using ensembles. Using the statistical model with empirical parameters, it was clear that weakened disturbances reduced modeled I_u across the landscape. However, the past decade showed an increase in the rate of burning and thus in I_u ,
attributable to exponentially increased fire frequency. These patterns may be indicative of future national fire regimes as population levels and temperatures continue to rise in Canada's forests.

While one may infer that increased satellite coverage in recent decades explains the apparent increase in fire frequency and decrease in mean fire size observed in the Canadian National Fire Database, this assumption did not hold. Mean fire size was larger rather than smaller for satellite observations, likely attributable to the coarse sensor resolution of MODIS and improved coverage in the north, while the contribution of satellite observations to fire frequency was minimal. Satellite observations partially explained the northward migration of boreal fires, while none of the Alberta fires were sourced from satellite imagery. Increases to area burned were not evident for western Alberta or nationally. The implications of novel anthropogenic fire regimes are unknown, requiring forest ecosystem simulations together with remote sensing for the investigation of likely systematic changes to forests.

8.1 Limitations

The limitations of the results of this research stem from two fundamental sources: (1) uncertainty in model parameters; (2) uncertainty in modeled processes. Uncertainty in empirical measurements is implicitly included in parameter uncertainty. While some uncertainties are 'known unknowns,' or uncertainties that are known to exist, others are 'unknown unknowns,' or uncertainties that are not known to exist (US Department of Defense, 2002). Known unknowns include imputed values, omitted processes known to exist (e.g., models of lighting ground-strike frequency or solar activity), scale effects on model and data accuracy, spatiotemporal variation in model parameters, and the measurement accuracy of empirical data. Unknown unknowns

involve the omission of unknown factors and thus include processes not known to exist, parameter values not known to exist, or practical issues related to hardware or software not known to exist. Last, there are 'known knowns,' or phenomena that are robustly quantified and treated as certain. While there are many known unknowns and few known knowns, it would be paradoxical to quantify the number of unknown unknowns without statistical inference (i.e., inverse modeling). Therefore, the discussion of research limitations presented in each chapter focuses on known unknowns.

Increased geospatial data would have enhanced model development and parameterization. While fire history data for Canada (Stocks *et al.*, 2002; Parisien *et al.*, 2006; Burton *et al.*, 2008) is more robustly described than for many other regions, it remains limited by spatiotemporal biases and substantial variation in detection methods. These issues with sampling appear readily addressed by modern satellite formations (Hand, 2015) together with recent breakthroughs in computer vision (LeCun *et al.*, 2015), which may demand copious computational resources to fully utilize. While mapping fire, biogeoclimatic regions (Natural Regions Committee, 2006), landcover classes (Wulder *et al.*, 2007; Agriculture and Agri-Food Canada, 2012), and climate data (Menne *et al.*, 2012) have received much attention in recent years, medium-resolution (~ 1 ha) maps of tree species distributions, stand demographics (age classes), soil textural properties, and plant traits essential to parameter estimation where species information is lacking remain absent.

A second data gap stems from the multitude of species parameters used in the models. Some parameters are coarsely estimated, necessitating refinement, while others may only be available for well-studied regions. Meanwhile, single trait values are typically used to describe variation within the entire species ranges (Burns & Honkala, 1990; Farrar, 1995a; Klinka *et al.*, 2000), rather than providing probability distributions. Even though a wide degree of variation in genotypes and gene expression exists in nature (Aitken *et al.*, 2008), this variation is seldom represented in existing species compendiums or models. While next-generation dynamic global vegetation models (Scheiter *et al.*, 2013) take such an ecological-evolutionary approach based on an assumption of optimality, most current-generation forest ecosystem models were not designed to model evolutionary processes, given a typical simulation maximum of 1 kyr.

Even though it is possible to reconfigure existing models to incorporate genetic variation using simple modifications, validation data for genotypic and phenotypic variation may be difficult to attain. Nonetheless, rapid growth is foreseen in the collection of genomics data, given advances in next-generation sequencing techniques (Goodwin *et al.*, 2016) and interest surrounding CRISPR-Cas9 (Doudna & Charpentier, 2014; Sander & Joung, 2014) for targeted applications. New tree species compendiums, consisting of bioinformatics databases rather than books, should be established for use in modeling studies. In order to extrapolate genetic information across the landscape, remote sensing studies should predict genetic variation from canopy spectra using recent advances in machine learning (LeCun *et al.*, 2015). Studies utilizing hyperspectral imagery have demonstrated the feasibility of this task (Asner *et al.*, 2014, 2015; Asner & Martin, 2016; Cavender-Bares *et al.*, 2016). Such maps may resolve some of the most difficult aspects of model parameterization and validation.

8.2 Research Contributions

In Chapter 3, this work showed that fire regimes in western Alberta transitioned from large stand-replacing lightning-caused fires to small frequent human-caused fires in recent decades. This work demonstrated that mean fire size and latitude across Canada steadily declined since the 1990s, irrespective of increased satellite monitoring. Novel anthropogenic fire regimes were characterized for western Alberta and Canada-wide, including changes in size, frequency, seasonality, latitude, elevation, and cause. Fires occurred closer to roads and waterbodies over the past three decades, treated as proxies of human activity. Human-caused fires linearly occurred closer to roads over time, while lightning-caused fires remained at a constant mean distance. This suggests that increased proximity of fires to roads is not due to road expansion, but to an increased number of users on existing road, which is an important distinction for management.

Importantly, this work showed a northward migration of boreal fire regimes, peaking in the 1970s before dipping southward and rising again, only partially explained by spaceborne monitoring. The temporal classification of fire regimes using the binary segmentation algorithm was also demonstrated. A significant bimodality of the fire size distribution was shown for Alberta, explained by the recent emergence of anthropogenic regimes. An anthropogenic theory of energetic constraints to biomass burning was proposed, which includes human activity alongside vegetation and climate as fundamental energetic controls on fire.

A key conclusion of this work is that future wildfire models should define the probability of ignition with raster surfaces, rather than regional coefficients. These raster inputs may be

allowed to vary with the simulation time-step, producing realistic ignition patterns over time to facilitate model validation with new satellite data. The input rasters would serve two other key purposes: (1) to model fire adjacency to human activity, as anthropogenic regimes may eventually dominate northwestern North America (Amoroso *et al.*, 2011; Whitman *et al.*, 2015); (2) to realistically model the spatial distribution of lightning strikes, using data from the GOES-R/GOES-16 Geostationary Lightning Mapper (Goodman *et al.*, 2013) or other sensors.

To better capture spatial wildfire patterns, forest fire models may eventually use separate input maps for the probability of ignition based on the cause, as the size and frequency distribution of lightning-caused and human-caused fires differ markedly. As the input of remote sensing products into forest ecosystem models becomes standardized, similar to data assimilation in weather forecasting models, additional processes may be defined and constrained by raster representations, including landcover, photosynthesis, leaf area index, canopy height, and, carbon, water, and nitrogen flux. Model designers may prepare for these changes by increasing reliance on satellite data for model parameterization. Stacked rasters at defined height intervals may allow volumetric representation of height maps (voxels), as optical stereo photogrammetric imagery may provide global 3-D multi-spectral forest dynamics monitoring in the coming decades (Shean et al., 2016). Meanwhile, modelers may rely on synthetic data for development. In Chapter 4, this work contributed to the development of a new process-based tree regeneration model, TACA-GEM. A national parameterization method was developed for TACA-GEM, based on soil textural classes and NOAA GHCN-D climate data scripts available in the rnoaa package for R (Chamberlain et al., 2016). The TACA-GEM modeling results suggested the potential of a decline in tree regeneration in western Alberta under recent climate change, due to

changes in germination frequency, drought frequency, and growing season length. The modeling work highlights the importance of the sensitivity of tree regeneration to climate change in forest succession, elucidating an important area of future research.

In Chapter 5, new methods were developed for parameterizing LANDIS-II in Alberta, Canada. The most detailed forest ecosystem simulations were conducted for the region, at one-hectare resolution with 25.2 million interacting stands. An algorithm was developed for fire model parameter optimization, resolving a long-standing challenge in the application of fire models across large areas. This work generally showed a modeled decline in forested area for western Alberta across the study period. This result was mostly a product of the integrated regeneration model, highlighting the importance of regeneration in stand succession. This work also showed differences in results related to the application of different classes of wildfire models. Importantly, model results indicated that decreased disturbance rates may slow changes to the central tendency of the spatial distribution of tree species, increasing *in situ* climatic disequilibrium. Increased tree longevity also implies reduced *in situ* adaptation rates, highlighting an important direction for future research.

In Chapter 6, a modified spike-free canopy height model algorithm was developed based on 2-D barycentric interpolation. Two new canopy gap fraction LiDAR metrics were also developed: hemispherical Voronoi gap fraction and point-density normalized gap fraction. An exhaustive comparison of LiDAR metrics of canopy openness (gap fraction and angular canopy closure) was conducted. Empirical tree-height-to-crown relationships were developed for the application of individual tree crown detection methods. An experimental method of individual tree

segmentation based on α -shapes was also tested, which showed promising early results (Figure B.6). Importantly, this research demonstrated the effects of hemispherical lens projections on measures of canopy openness from ALS. This work resulted in a second open-source software package, in the *gapfraction* package in R.

In Chapter 7, using two parameters, linear regression and Random Forest models of angular canopy closure were developed with R^2 values of 0.94 each and RMSE of 0.08 and 0.07, respectively. A new landcover classification scheme was developed for LANDIS-II species-age cohort outputs, based on ABMI Landcover 2010. This work developed new methods of simulating landscape change to angular canopy closure and gap fraction with LANDIS-II. This is also the first study to develop external methods of simulating landscape changes to understory solar irradiation in LANDIS-II. Model results suggest that a decline in forested area and ageing may have counteracting effects on understory solar irradiation levels.

8.3 Areas of Future Research

This work is the first, to my knowledge, to demonstrate the fusion of a machine learning model with a forest ecosystem model to simulate processes not explicitly represented, in a hybrid modeling approach. This work paves the way for a promising new area of research on the fusion of machine learning and process-based models. Following model training with plot data, machine learning models may run inference on remote sensing or model data. Near real-time applications exists whereby remote sensing inputs may be used to iteratively update online simulations.

In deep learning, generative adversarial networks (GANs), convolutional neural networks (CNNs), or recurrent neural networks (RNNs) may be used to facilitate the representation of complex spatiotemporal dynamics (Goodfellow *et al.*, 2014b; LeCun *et al.*, 2015). In recent years, spatiotemporal 3-D CNN and RNN-CNN architectures have been successfully applied to related tasks, such action recognition in video sequences (Ji *et al.*, 2013; Zhao *et al.*, 2017). Meanwhile, 2-D spatial and 1-D temporal sequence generation tasks have been dominated by GANs and CNNs (Ledig *et al.*, 2016; van den Oord *et al.*, 2016a,b; Chen & Tong, 2017). A clear opportunity exists to fuse deep learning and process-based models to implement the first realistic pattern-based models. While I relied on linear regression for the final model in this work given comparable performance to Random Forest, the promise of deep learning for such problem classes is well established (LeCun *et al.*, 2015).

A new class of hybrid model may blend the grid-based spatial interaction of forest landscape models with the within-stand heterogeneity of gap models to produce more realistic forest demographics, energy partitioning, and biogeochemical cycling. These models may benefit from representing individual tree competition with a mathematically tractable model, as with the first-order hyperbolic partial differential equations and integral equation of the perfect-plasticity approximation (Adams *et al.*, 2007; Purves *et al.*, 2007, 2008; Strigul *et al.*, 2008; Weng *et al.*, 2015) or size-and-age-structured equations (Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009). In these works, the temporal dynamics of individual trees are treated as bounded hyperbolic *n*-dimensional system with probabilistic events, retaining information on the size structure and density of trees within stands. As the name of the former implies, tree crown shapes are plastic, representing neighborhood competition for light.

Efficient model reductions may allow better representation of light resources available for regeneration and other physical processes, such as photosynthesis and evapotranspiration, without greatly increasing computational complexity. An alternative approach to systems of partial differential equations may rely on machine learning for model emulation, reducing model dimensionality and complexity while capturing salient dynamics, a common objective in hybrid modeling. Increased use of machine learning may also enable efficient integration of remote sensing products with process-based models.

A new class of hybrid model should be optimized for highly parallel architectures. Yet, a practical challenge exists in overcoming the sequential design of existing process-based models. Heterogeneous architectures, such as CPU-GPU systems, may facilitate efficient computation of sequential and pattern-based processes. These architectures are widely used in modern supercomputers, including ORNL Titan in the United States, Sunway TaihuLight and Tianhe-2 in China, Piz Daint in Switzerland, and forthcoming CSIRO Bracewell in Australia. As of June 2017, the prior four are the world's fastest supercomputers (Strohmaier *et al.*, 2017), not including Google's second-generation tensor processing unit (TPU) datacenters.

The use of dedicated GPGPU (e.g., CUDA, ROCm, OpenCL) and multi-core (e.g., Intel MKL, OpenMP) libraries or natively distributed languages (e.g., Go) may allow for more efficient run times. Highly parallel processor architectures are also ideally suited to training and applying deep learning models. Deep learning models may be included within process-based models by adding deep neural network layers with pre-trained weights, similar to popular ImageNet models (Krizhevsky *et al.*, 2012). Users could optionally apply transfer learning to local datasets for

model calibration. Sequential architectures such as long short-term memory (LSTM) may be used to represent pattern-based processes with ecological memory, beyond what is feasible with partial differential equations.

A new class of hybrid models may also benefit from the inclusion of genomics, including genotypes, gene expression (e.g., phenotype plasticity), mutation rates, and gene flow through evolutionary algorithms. While historically constrained by data availability, next-generation sequencing techniques may facilitate the widespread collection of genetic information with reduced cost and time limitations. Although data on landscape genomics remains sparse, an increased availability of genetic information is foreseeable for the coming years. In the meantime, models may include these processes based on predefined sub-models of gene expression, mutation, flow, and thus, adaptation. These sub-models may initially use coarse abstractions, such as pre-defined ranges or probability density functions of species trait variations, admixture rates for particular genotypes co-occurring at sites, or simple mutation rate coefficients. These additions may allow for an improved theoretical understanding of changes to forest landscape genetics produced by evolutionary processes.

The incorporation of genomics into models may also facilitate preliminary inquiry into the potential and limitations of genetic modifications to populations for directed evolution. This is a promising new area of research parallel to synthetic ecology, or the design of ecological interactions through genetic modification (Dunham, 2007). While genetically modified trees are increasingly common in plantations globally and may find targeted use in the wild for conservation and/or carbon sequestration applications (Jacobs *et al.*, 2009; Newhouse *et al.*,

2014), current models lack direct representation of genetic information. By modeling the potential effects of genetic admixture, mutation, and precise gene editing based on tools such as CRISPR-Cas9 (Cong *et al.*, 2013; Mali *et al.*, 2013; Doudna & Charpentier, 2014), better safeguards can be formulated.

Targeted inheritance tools such as CRISPR-based gene drives (Oye *et al.*, 2014; Hammond *et al.*, 2016) may be probed numerically for potential effects of genetic isolation (Drury *et al.*, 2016) and evolutionary resistance to inheritance (Unckless *et al.*, 2017). Biogeochemical optimization applications also exist, including maximizing the rate of carbon sequestration (Jacobs *et al.*, 2009) or minimizing methane production (Su *et al.*, 2015) in plantations. These efforts may benefit from numerical experiments to, for example, achieve optimality between terrestrial carbon storage and residence times (Bloom *et al.*, 2016) in relation to the timing of climatic oscillations to maximize a cooling effect. This would necessitate optimal partitioning of carbon at a stand, rather than tree, scale, lending to combinatorial optimization methods, as optimal partitioning among organ types depends on ecological context.

Full-waveform LiDAR systems (Amiri *et al.*, 2015) may overcome the challenge of monitoring tree regeneration remotely (Amiri *et al.*, 2015; Polewski *et al.*, 2016). Small unmanned aircraft systems (UAS) operating below tree canopies can also be used to map the understory in unprecedented 3-D spectral detail using structure-from-motion (Polewski *et al.*, 2016). This opens a window into mapping the distribution, regeneration, and succession of understory plants. Hyperspectral imaging and/or terrestrial laser scanning systems may be installed *in situ* across

FluxNet towers (Baldocchi *et al.*, 2001) to automate the capture of overstory and understory plant succession in order to link this information to biogeochemical cycles.

Using time-series of hyperspectral imagery with deep learning or standard computer vision techniques, spatiotemporal changes in productivity may be monitored in three-dimensional detail. Provided dense temporal point cloud data for plants, specific succession events can be monitored and recorded in high precision (Li *et al.*, 2013b), providing an automated stand monitoring system. Together, these technologies may provide critically absent information on the dynamics of understory disturbance, regeneration, and succession. Meanwhile, an extensive analysis of plot data across Canada may provide new insights into the effects of climate and competition on tree regeneration. Empirical regeneration studies should incorporate gridded climate, fire, and productivity data (e.g., NDVI or fPAR) to disentangle the effects of climate and competition.

Dense point-cloud time-series from ALS, UAS, and spaceborne stereo photogrammetry provide a unique opportunity to monitor forest dynamics, particularly when fused with deep learning. Meanwhile, new CubeSat satellite formations may facilitate near-real-time observation (Hand, 2015). These data may be applied to monitor forest dynamics in high temporal resolution in order to advance the development of sophisticated new dynamic vegetation models. This data may allow the fitting of models to observation data in more informative ways by focusing on temporally dense 2-D and 3-D patterns, rather than aggregated 1-D trajectories. Again, generative adversarial, recurrent, and convolutional neural networks (Goodfellow *et al.*, 2014a;

LeCun *et al.*, 2015) show promise for the transfer of spatiotemporal patterns into model behavior.

Data assimilation through machine learning may be critical for the fusion of satellite observations with dynamic global vegetation models (DVGMs), or terrestrial biosphere models. Remote sensing data and DVGMs are likely to merge through deep learning into a new class of hybrid model. This contrasts to the current use of remote sensing merely to parameterize or constrain physical models. While inherently physical processes may remain simple in form, pattern-based dynamics such as fire spread, species distributions, browsing effects, and biotic disturbances may increasingly rely on deep artificial neural networks. This will require large amounts of labeled data to train new supervised learning models. Long-term monitoring ground plot networks, such as Canada's National Forest Inventory network (Gillis *et al.*, 2005), which match satellite observations in time, position, and scale should be constructed to facilitate the collection of training data for deep learning in remote sensing.

The full Landsat record should also be utilized to characterize fire history in Canada. This will improve the spatiotemporal coverage of wildfire maps, granting unprecedented insight into historical fire patterns not visible in the current Canadian National Wildfire Database. This information may be used in models to produce more realistic initial conditions. Meanwhile, fire maps may be linked to Landsat vegetation indices, climate grids, and topography to decipher to drivers of fire patterns in Canada. Landsat studies should use spatiotemporal deep learning models to improve the detection and attribution of disturbances. While simple spectral indices may be efficient, they discard rich information contained in the latent space of raw spectra. Deep

learning may similarly be applied to develop a new class of radiative transfer model with sequence-to-sequence learning, trained on time-series ground validation data, to correct raw spectra before applying supervised classification models.

Finally, the Canadian federal government, provinces, and universities may benefit by collaborating on the development of open cloud computing infrastructure for geospatial data. This would include harmonized remote sensing and gridded climate products for use in ecological forecasting studies, with standard pre-processing applied to provide ready-to-use products. Pre-processing may include pixel quality metrics and interpolation necessary to match a target spatial and temporal resolution. The finest temporal resolutions may correspond to those of FluxNet (Baldocchi *et al.*, 2001) and weather station data. Such a national data cube with processing facilities would support modeling by easing data access while improving study transparency and reproducibility, critically lacking in large ecosystem modeling and remote sensing studies. Important layers for inclusion may be high-resolution soil texture, coarse fragment content, and soil depth maps, valuable for ecological modeling studies in Canada. These data may improve our ability to represent spatiotemporal changes to soil moisture under the effects of warming. Certainly, exciting times are ahead in remote sensing, machine learning, and hybrid modeling.

References

- Aakala, T., Shimatani, K., Abe, T., Kubota, Y. & Kuuluvainen, T. (2016) Crown asymmetry in high latitude forests: disentangling the directional effects of tree competition and solar radiation. *Oikos*, **125**, 1035–1043.
- Abatzoglou, J.T. & Williams, A.P. (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, **113**, 11770– 11775.
- Aber, J.D. & Federer, C.A. (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*, **92**, 463–474.
- Aber, J.D., Ollinger, S. V. & Driscoll, C.T. (1997) Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling*, 101, 61–78.
- Aber, J.D., Ollinger, S. V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W.,
 Melillo, J.M. & Lathrop, R.G. (1995) Predicting the effects of climate change on water
 yield and forest production in the northeastern United States. *Climate Research*, 5, 207–222.
- Abraham, S. & Förstner, W. (2005) Fish-eye-stereo calibration and epipolar rectification. *ISPRS Journal of Photogrammetry and Remote Sensing*, **59**, 278–288.
- Adams, T., Purves, D. & Pacala, S. (2007) Understanding height-structured competition in forests: is there an R* for light? *Proceedings of the Royal Society B: Biological Sciences*, 274, 3039 LP-3048.

Agriculture and Agri-Food Canada (2016) Canada Land Inventory (CLI). Agriculture and Agri-207 Food Canada.

- Agriculture and Agri-Food Canada (2012) *ISO 19131 Land cover for agricultural regions of Canada, circa 2000 – data product specification*, Agriculture and Agri-Food Canada, Ottowa, ON, Canada.
- Aitken, S.N., Yeaman, S., Holliday, J. a., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.
- Alberta Biodiversity Monitoring Institute (2012) *ABMI Wall-to-wall Land Cover Map circa* 2000, Version 2.1: Metadata, Alberta Biodiversity Monitoring Institute, Edmonton, AB, Canada.
- Alberta Sustainable Resource Development (2005a) *Permanent sample plot field procedures manual*, Edmonton, Alberta, Canada.
- Alberta Sustainable Resource Development (2005b) *Stand dynamics system field remeasurement manual*, Edmonton, AB, Canada.
- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O. (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.
- Alexander, C., Moeslund, J.E., Bøcher, P.K., Arge, L. & Svenning, J.-C. (2013) Airborne laser scanner (LiDAR) proxies for understory light conditions. *Remote Sensing of Environment*, 134, 152–161.
- Alexander, M.E. (2010) Foliar moisture content input in the Canadian Forest Fire Behavior Prediction System for areas outside of Canada. Proceedings of the 6th International

Conference on Forest Fire Research, pp. 1–13. Coimbra, Portugal.

- Alexander, M.E. & Cruz, M.G. (2013) Assessing the effect of foliar moisture on the spread rate of crown fires. *International Journal of Wildland Fire*, **22**, 415–427.
- Ali, A.A., Blarquez, O., Girardin, M.P., Hély, C., Tinquaut, F., El Guellab, A., Valsecchi, V., Terrier, A., Bremond, L., Genries, A., Gauthier, S. & Bergeron, Y. (2012) Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. *Proceedings of the National Academy of Sciences*, 109, 20966–20970.
- Ali, A.A., Carcaillet, C. & Bergeron, Y. (2009) Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology*, **15**, 1230–1241.
- Allan, R.P. & Soden, B.J. (2008) Atmospheric warming and the amplification of precipitation extremes. *Science*, **321**, 1481–1484.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., Mcdowell, N., Vennetier, M.,
 Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted) T., Gonzalez, P., Fensham,
 R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S.W., Semerci, A. &
 Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals
 emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684.
- Amiri, N., Yao, W., Heurich, M. & Krzystek, P. (2015) Regeneration detection by 3D segmentation in a temperate forest using airborne full waveform Lidar data. SilviLaser 2015, La Grande Motte, France.
- Amiro, B.D., Orchansky, A.L., Barr, A.G., Black, T.A., Chambers, S.D., Chapin III, F.S.,Goulden, M.L., Litvak, M., Liu, H.P., McCaughey, J.H., McMillan, A. & Randerson, J.T.(2006) The effect of post-fire stand age on the boreal forest energy balance. *Agricultural*

and Forest Meteorology, 140, 41–50.

- Amoroso, M.M., Daniels, L.D., Bataineh, M. & Andison, D.W. (2011) Evidence of mixedseverity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. *Forest Ecology and Management*, **262**, 2240–2249.
- Andela, N., Morton, D.C., Giglio, L., Chen, Y., van der Werf, G.R., Kasibhatla, P.S., DeFries,
 R.S., Collatz, G.J., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F.,
 Mangeon, S., Melton, J.R., Yue, C. & Randerson, J.T. (2017) A human-driven decline in
 global burned area. *Science*, 356, 1356 LP-1362.
- Anderegg, W.R.L., Kane, J.M. & Anderegg, L.D.L. (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Clim. Change*, **3**, 30–36.
- Andrews, P.L. & Chase, C.H. (1989) *BEHAVE: Fire Behavior Prediction and Fuel Modeling System - BURN Subsystem, Part 1*, US Department of Agriculture, Forest Service, Washington D.C.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, 93, 1527–1539.
- Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L. & Bradstock, R.A. (2013) Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences*, 110, 6442–6447.
- Arno, S.F. (1980) Forest fire history in the Northern Rockies. *Journal of Forestry*, **78**, 460–465.
- Arp, P., Castonguay, M., Campbell, D. & Hiltz, D. (2009) Overview of wet-areas mapping and industry applications, University of New Brunswick, Fredericton, NB, USA.
- Arras, K.O. (1998) *An introduction to error propagation: derivation, meaning and examples of equation CY = FX CX FXT*, Lausanne, Switzerland.

- Asner, G.P., Anderson, C.B., Martin, R.E., Tupayachi, R., Knapp, D.E. & Sinca, F. (2015) Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon forest canopy. *Nature Geoscience*, advance on.
- Asner, G.P. & Martin, R.E. (2016) Spectranomics: Emerging science and conservation opportunities at the interface of biodiversity and remote sensing. *Global Ecology and Conservation*, 8, 212–219.
- Asner, G.P., Martin, R.E., Carranza-Jiménez, L., Sinca, F., Tupayachi, R., Anderson, C.B. & Martinez, P. (2014) Functional and biological diversity of foliar spectra in tree canopies throughout the Andes to Amazon region. *New Phytologist*, **204**, 127–139.
- Attema, E.P.W. & Ulaby, F.T. (1978) Vegetation modeled as a water cloud. *Radio Science*, **13**, 357–364.
- Aubin, I., Beaudet, M. & Messier, C. (2000) Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. *Canadian Journal of Forest Research*, **30**, 168–177.
- Axelsson, P. (1999) Processing of laser scanner data—algorithms and applications. *ISPRS Journal of Photogrammetry and Remote Sensing*, **54**, 138–147.
- Badgley, G., Field, C.B. & Berry, J.A. (2017) Canopy near-infrared reflectance and terrestrial photosynthesis. *Science Advances*, 3.
- Bak, P., Chen, K. & Creutz, M. (1989) Self-organized criticality in the 'Game of Life". *Nature*, 342, 780–782.
- Baker, W.L. (2012) Effects of settlement and fire suppression on landscape structure. *America*, 73, 1879–1887.
- Balch, J.K., Bradley, B.A., Abatzoglou, J.T., Nagy, R.C., Fusco, E.J. & Mahood, A.L. (2017)

Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences*, **114**, 2946–2951.

- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K. & Wofsy, S. (2001) FLUXNET: A new tool to study the temporal and spatial variability of ecosystem–scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, 82, 2415–2434.
- Baltsavias, E.P. (1999) Airborne laser scanning: Basic relations and formulas. *ISPRS Journal of Photogrammetry and Remote Sensing*, **54**, 199–214.
- Baltzer, J.L., Quinton, W.L. & Sonnentag, O. (2014) Boreal forests in permafrost landscapes:Changing structure and function in response to climate warming. *AGU Fall Meeting Abstracts*, F3.
- Barichivich, J., Briffa, K.R., Myneni, R., Schrier, G. van der, Dorigo, W., Tucker, C.J., Osborn, T.J. & Melvin, T.M. (2014) Temperature and snow-mediated moisture controls of summer photosynthetic activity in northern terrestrial ecosystems between 1982 and 2011. *Remote Sensing*, 6, 1390.
- Barnes, C., Tibbitts, T., Sager, J., Deitzer, G., Bubenheim, D., Koerner, G. & Bugbee, B. (1993)
 Accuracy of quantum sensors measuring yield photon flux and photosynthetic photon flux.
 HortScience, 28, 1197–1200.
- Barnett, T.P., Adam, J.C. & Lettenmaier, D.P. (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, **438**, 303–309.

Bartemucci, P., Messier, C. & Canham, C.D. (2006) Overstory influences on light attenuation

patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research*, **36**, 2065–2079.

- Bartlett, M.K., Scoffoni, C. & Sack, L. (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, 15, 393–405.
- Barton, L. V. (1930) Hastening the germination of some coniferous seeds. American Journal of Botany, 17, 88–115.
- Beaudet, M., Harvey, B.D., Messier, C., Coates, K.D., Poulin, J., Kneeshaw, D.D., Brais, S. & Bergeron, Y. (2011) Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *Forest Ecology and Management*, 261, 84–94.
- Beaudet, M. & Messier, C. (2002) Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agricultural and Forest Meteorology*, **110**, 217–228.
- Bertrand, R., Gégout, J.-C. & Bontemps, J.-D. (2011a) Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos*, **120**, 1479–1488.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C. & Gégout, J.-C. (2011b) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–20.
- Bevington, J. (1986) Geographic differences in the seed germination of paper birch (Betula papyrifera). *American Journal of Botany*, **73**, 564–573.
- Bevington, J.M. & Hoyle, M.C. (1981) Phytochrome action during prechilling induced germination of Betula papyrifera Marsh. *Plant Physiology*, **67**, 705–710.

- Bloom, A.A., Exbrayat, J.-F., van der Velde, I.R., Feng, L. & Williams, M. (2016) The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times. *Proceedings of the National Academy of Sciences*, **113**, 1285–1290.
- Boberg, P., Raffaele, E., Chaia, E.E., Eneström, J., Pettersson, L.B. & D'Hertefeldt, T. (2010)
 The effect of high temperatures on seed germination of one native and two introduced conifers in Patagonia. *Nordic Journal of Botany*, 28, 231–239.
- Bode, C.A., Limm, M.P., Power, M.E. & Finlay, J.C. (2014) Subcanopy solar radiation model:
 Predicting solar radiation across a heavily vegetated landscape using LiDAR and GIS solar radiation models. *Remote Sensing of Environment*, **154**, 387–397.
- Boisvert-Marsh, L., Périé, C. & de Blois, S. (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, **5**, art83.
- Bolles, R.C., Baker, H.H. & Marimont, D.H. (1987) Epipolar-plane image analysis: An approach to determining structure from motion. *International Journal of Computer Vision*, **1**, 7–55.
- Bonan, G.B. (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.
- Bond-Lamberty, B., Gower, S.T., Ahl, D.E. & Thornton, P.E. (2005) Reimplementation of the Biome-BGC model to simulate successional change. *Tree Physiology*, **25**, 413–424.
- Bond-Lamberty, B., Peckham, S.D., Ahl, D.E. & Gower, S.T. (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature*, **450**, 89–92.
- Bond-Lamberty, B., Rocha, A. V, Calvin, K., Holmes, B., Wang, C. & Goulden, M.L. (2014) Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Global Change Biology*, **20**, 216–227.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a

world without fire. *The New phytologist*, **165**, 525–37.

- Botkin, D.B., Janak, J.F. & Wallis, J.R. (1972) Some ecological consequences of a computer model of forest growth. *Journal of Ecology*, **60**, 849–872.
- Bourbonnais, M.L., Nelson, T.A., Cattet, M.R.L., Darimont, C.T. & Stenhouse, G.B. (2013) Spatial analysis of factors influencing long-term stress in the grizzly bear(Ursus arctos) population of Alberta. *PLoS ONE*, **8**, e83768.
- Bower, A.D., Kolotelo, D. & Aitken, S.N. (2011) Effects of length of storage, and stratification on germination of whitebark pine seeds. *Western Journal of Applied Forestry*, **26**, 24–29.
- Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M.,
 DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Mack, M., Moritz,
 M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S. & Swetnam, T.W. (2011) The human
 dimension of fire regimes on Earth. *Journal of Biogeography*, 38, 2223–2236.
- Boychuk, D. & Perera, A.H. (1997) Modeling temporal variability of boreal landscape ageclasses under different fire disturbance regimes and spatial scales. *Canadian Journal of Forest Research*, **27**, 1083–1094.
- Bradshaw, C.J.A., Warkentin, I.G. & Sodhi, N.S. (2009) Urgent preservation of boreal carbon stocks and biodiversity. *Trends in Ecology & Evolution*, **24**, 541–548.
- Braid, A.C.R. & Nielsen, S.E. (2015) Prioritizing sites for protection and restoration for grizzly bears (Ursus arctos) in southwestern Alberta, Canada. *PLoS ONE*, **10**, e0132501.
- Breiman, L., Friedman, J.H., Olshen, R.A. & Stone, C.J. (1984) Classification and Regression Trees, Chapman and Hall, New York.
- Breiman, L.E.O. (2001) Random Forests. *Machine Learning*, 45, 5–32.
- Bridge, S.R.J., Miyanishi, K. & Johnson, E.A. (2005) A critical evaluation of fire suppression

effects in the boreal forest of Ontario. Forest Science, 51.

Brubaker, L.B. (1986) Responses of tree populations to climatic change. Vegetatio, 67, 119–130.

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

- Burns, R.M. & Honkala, B.H. (1990) Silvics of North America, United States Forest Service, Washington.
- Burton, P.J. & Cumming, S.G. (1995) Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. *Water, Air, and Soil Pollution*, **82**, 401–414.
- Burton, P.J., Parisien, M.-A., Hicke, J. a., Hall, R.J. & Freeburn, J.T. (2008) Large fires as agents of ecological diversity in the North American boreal forest. *International Journal of Wildland Fire*, **17**, 754–767.
- Camill, P. (2005) Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change*, **68**, 135–152.
- Canadian Forest Service (2013a) 6.1 Silviculture Statistics by Province/Territory, 1975-2011. National Forestry Database, 1.

Canadian Forest Service (2015) Canadian Wildland Fire Information System (CWFIS) Datamart.

Canadian Forest Service (2013b) Inventory and land-use change. *Climate change: carbon accounting*.

- Canham, C.D., Coates, K.D., Bartemucci, P. & Quaglia, S. (1999) Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research*, 29, 1775–1783.
- Canham, C.D., Finzi, A.C., Pacala, S.W. & Burbank, D.H. (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy

trees. Canadian Journal of Forest Research, 24, 337-349.

- Cao, M. & Woodward, F.I. (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Carlson, C.E. (1994) Germination and early growth of western larch (Larix occidentalis), alpine larch (Larix lyallii), and their reciprocal hybrids. *Canadian Journal of Forest Research*, 24, 911–916.
- Caron, F., Duflos, E., Pomorski, D. & Vanheeghe, P. (2006) GPS/IMU data fusion using multisensor Kalman filtering: Introduction of contextual aspects. *Information Fusion*, 7, 221–230.
- Casella, E. (2008) Computing light transmission under the forest canopy: Application of the tree model LIGNUM. Scientific Report., Helsinki, Finland.
- Cavender-Bares, J. & Bazzaz, F.A. (2000) Changes in drought response strategies with ontogeny in Quercus rubra: implications for scaling from seedlings to mature trees. *Oecologia*, **124**, 8–18.
- Cavender-Bares, J., Meireles, J.E., Couture, J.J., Kaproth, M.A., Kingdon, C.C., Singh, A., Serbin, S.P., Center, A., Zuniga, E., Pilz, G. & Townsend, P.A. (2016) Associations of leaf spectra with genetic and phylogenetic variation in oaks: prospects for remote detection of biodiversity. *Remote Sensing*, 8.
- Chamberlain, S., Erickson, A., Potter, N., Stachelek, J., Ram, K. & Hart, E. (2016) rnoaa: "NOAA" Weather Data from R. R package version 0.5.2.
- Chazdon, R.L. (2008) Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science (New York, N.Y.)*, **320**, 1458–60.
- Chen, J.M., Chen, B., Higuchi, K., Liu, J., Chan, D., Worthy, D., Tans, P. & Black, A. (2006)

Boreal ecosystems sequestered more carbon in warmer years. *Geophysical Research Letters*, **33**.

Chen, J.M., Ju, W., Cihlar, J., Price, D., Liu, J., Chen, W., Pan, J., Black, A. & Barr, A. (2003) Spatial distribution of carbon sources and sinks in Canada's forests. *Tellus B*, **55**, 622–641.

Chen, Z. & Tong, Y. (2017) Face super-resolution through Wasserstein GANs. ArXiv e-prints.

- Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3149–3160.
- Chuine, I. & Beaubien, E.G. (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500–510.
- Cieszewski, C.J. & Bella, I.E. (1989) Polymorphic height and site index curves for lodgepole pine in Alberta. *Canadian Journal of Forest Research*, **19**, 1151–1160.
- Clark, J.S. (1991) Disturbance and tree life history on the shifting mosaic landscape. *Ecology*, **72**, 1102–1118.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T.I. & Wyckoff, P. (1998) Reid's paradox of rapid plant migration. *BioScience*, 48, 13–24.
- Coen, J.L., Cameron, M., Michalakes, J., Patton, E.G., Riggan, P.J. & Yedinak, K.M. (2012)
 WRF-Fire: Coupled weather–wildland fire modeling with the weather research and forecasting model. *Journal of Applied Meteorology and Climatology*, **52**, 16–38.
- Cohen, W.B., Yang, Z., Stehman, S. V, Schroeder, T.A., Bell, D.M., Masek, J.G., Huang, C. & Meigs, G.W. (2016) Forest disturbance across the conterminous United States from 1985–2012: The emerging dominance of forest decline. *Forest Ecology and Management*, 360, 242–252.

- Colman, J.J. & Linn, R.R. (2007) Separating combustion from pyrolysis in HIGRAD/FIRETEC. *International Journal of Wildland Fire*, **16**, 493–502.
- Cong, L., Ran, F.A., Cox, D., Lin, S., Barretto, R., Habib, N., Hsu, P.D., Wu, X., Jiang, W., Marraffini, L.A. & Zhang, F. (2013) Multiplex genome engineering using CRISPR/Cas systems. *Science*, **339**, 819 LP-823.
- Cook, B.I., Terando, A. & Steiner, A. (2010) Ecological forecasting under climatic data uncertainty: a case study in phenological modeling. *Environmental Research Letters*, 5, 44014.
- Cooke, J.E.K., Eriksson, M.E. & Junttila, O. (2012) The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant, Cell & Environment*, 35, 1707–1728.
- Coops, N., Hilker, T., Wulder, M., St-Onge, B., Newnham, G., Siggins, A. & Trofymow, J.A.
 (Tony) (2007) Estimating canopy structure of Douglas-fir forest stands from discrete-return
 LiDAR. *Trees*, 21, 295–310.
- Cornelis, K., Pollefeys, M. & Gool, L. (2002) Lens distortion recovery for accurate sequential structure and motion recovery. European Conference on Computer Vision, Proceedings, Part II, pp. 186–200. Springer Berlin Heidelberg, Copenhagen, Denmark.
- Cortini, F., Filipescu, C.N., Groot, A., MacIsaac, D.A. & Nunifu, T. (2011) Regional models of diameter as a function of individual tree attributes, climate and site characteristics for six major tree species in Alberta, Canada. *Forests*, 2, 814.
- Costanza, R., Arge, R. d, Groot, R. de, Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem,
 S., O'Neill, R. V, Paruelo, J., Raskin, R.G., Sutton, P. & Belt, M. van den (1997) The value of the world's ecosystem services and natural capital. *Nature*, 387, 253.

- Costanza, R., Wilson, M., Troy, A., Voinov, A., Liu, S. & D'Agostino, J. (2006) *The value of New Jersey's ecosystem services and natural capital*, State of New Jersey, Trenton, NJ, USA.
- Coyle, D.B., Stysley, P.R., Poulios, D., Clarke, G.B. & Kay, R.B. (2015) Laser transmitter development for NASA's Global Ecosystem Dynamics Investigation (GEDI) lidar. Proc. SPIE 9612, Lidar Remote Sensing for Environmental Monitoring XV, 961208 (September 1, 2015), pp. 961207–961208. SPIE, San Diego, CA, USA.
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J. a, Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science (New York, N.Y.)*, **331**, 324–7.
- Critchfield, W.B. (1985) The late Quaternary history of lodgepole and jack pines. *Canadian Journal of Forest Research*, **15**, 749–772.
- Cross, P. & Bowlby, G. (2006) The Alberta economic juggernaut: The boom on the rose. *Canadian Economic Observer*, 3.1-3.12.
- Crutzen, P.J. & Stoermer, E.F. (2000) The Anthropocene. *IGBP Global Change Newsletter*, **41**, 17–18.
- Cumming, S.G. (2001) A parametric model of the fire-size distribution. *Canadian Journal of Forest Research*, **31**, 1297–1303.
- Cumming, S.G. (2005) Effective fire suppression in boreal forests. *Canadian Journal of Forest Research*, **35**, 772–786.
- Cumming, S.G. & Burton, P.J. (1996) Phenology-mediated effects of climatic change on some simulated British Columbia forests. *Climatic Change*, **34**, 213–222.

D'Orangeville, L., Duchesne, L., Houle, D., Kneeshaw, D., Côté, B. & Pederson, N. (2016)

Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science*, **352**, 1452 LP-1455.

- Dash, C.B., Fraterrigo, J.M. & Hu, F.S. (2016) Land cover influences boreal-forest fire responses to climate change: geospatial analysis of historical records from Alaska. *Landscape Ecology*, **31**, 1781–1793.
- Davis, A. V. (2013) Testing LANDIS-II to stochastically model spatially abstract vegetation trends in the contiguous United States.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.
- DeByle, N. V. & Winokur, R.P. (1985) *Aspen: Ecology and management in the western United States*, US Department of Agriculture, Forest Service, Fort Collins, CO, USA.
- Delignette-Muller, M.L. & Dutang, C. (2015) fitdistrplus: An R package for fitting distributions. Journal of Statistical Software; Vol 1, Issue 4 (2015).
- Dengel, S. & Grace, J. (2010) Carbon dioxide exchange and canopy conductance of two coniferous forests under various sky conditions. *Oecologia*, **164**, 797–808.
- Dengel, S., Grace, J. & MacArthur, A. (2015) Transmissivity of solar radiation within a Picea sitchensis stand under various sky conditions. *Biogeosciences*, **12**, 4195–4207.
- Derr, B.D., Matelski, R.P. & Peterson, G.W. (1969) Soil factors influencing percolation test performance. *Soil Science Society of America Proceedings*, **33**, 942–946.
- Deutschman, D.H., Levin, S.A., Devine, C. & Buttel, L.A. (1997) Scaling from trees to forests: Analysis of a complex simulation model. *Science*, **277**, 1684.
- Deutschman, D.H., Levin, S.A. & Pacala, S.W. (1999) Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. *Ecology*, **80**, 1927–1943.

- Dilley, a. C., Millie, S., O'Brien, D.M., Edwards, M., Brien, D.M.O., Edwards, M., O'Brien,
 D.M. & Edwards, M. (2004) The relation between Normalized Difference Vegetation Index and vegetation moisture content at three grassland locations in Victoria, Australia. *International Journal of Remote Sensing*, 25, 3913–3930.
- Dioumaeva, I., Trumbore, S., Schuur, E.A.G., Goulden, M.L., Litvak, M. & Hirsch, A.I. (2002)
 Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research: Atmospheres*, **107**, WFX 3-1--WFX 3-12.
- Disney, M.I., Lewis, P. & North, P.R.J. (2000) Monte Carlo ray tracing in optical canopy reflectance modelling. *Remote Sensing Reviews*, **18**, 163–196.
- Dobbs, R.C. (1976) White spruce seed dispersal in central British Columbia. *The Forestry Chronicle*, **52**, 30–33.
- Dobrowski, S.Z., Abatzoglou, J., Swanson, A.K., Greenberg, J.A., Mynsberge, A.R., Holden,
 Z.A. & Schwartz, M.K. (2013) The climate velocity of the contiguous United States during the 20th century. *Global Change Biology*, **19**, 241–251.
- Dodge, M. (1972) Forest fuel accumulation a growing problem. Science, 177, 139-142.
- Dolanc, C.R., Thorne, J.H. & Safford, H.D. (2013) Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Global Ecology and Biogeography*, 22, 264–276.
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K. & Willis, C.G. (2010) Germination, post-germination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 293–319.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G.,

Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,
Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013)
Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

- Doudna, J.A. & Charpentier, E. (2014) The new frontier of genome engineering with CRISPR-Cas9. *Science*, **346**.
- Dreyfus, S. (1962) The numerical solution of variational problems. *Journal of Mathematical Analysis and Applications*, **5**, 30–45.
- Drossel, B. & Schwabl, F. (1992) Self-organized critical forest-fire model. *Physical Review Letters*, **69**, 1629–1632.
- Drury, D.W., Siniard, D.J., Zentner, G.E. & Wade, M.J. (2016) CRISPR/Cas9 gene drives in genetically variable and non-randomly mating wild populations. *bioRxiv*.
- Dubayah, R., Goetz, S.J., Blair, J.B., Fatoyinbo, T.E., Hansen, M., Healey, S.P., Hofton, M.A., Hurtt, G.C., Kellner, J., Luthcke, S.B. & Swatantran, A. (2014) *The Global Ecosystem Dynamics Investigation*. AGU Fall Meeting 2014,.
- Dunham, M.J. (2007) Synthetic ecology: A model system for cooperation. *Proceedings of the National Academy of Sciences*, **104**, 1741–1742.
- Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015) Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, **21**, 3062–3073.
- Edwards, D.G.W. (1982) Improving seed germination in Abies. International Plant Propagators' Society Combined Proceedings for 1981, p. 69–78 (Volume 31). Canadian Forest Service, Richmond, B.C.

Erickson, A.M., Nitschke, C.R., Coops, N.C., Cumming, S.G. & Stenhouse, G.B. (2015) Past-

century decline in forest regeneration potential across a latitudinal and elevational gradient in Canada. *Ecological Modelling*, **313**, 94–102.

- Eriksson, O. (2002) Ontogenetic niche shifts and their implications for recruitment in three clonal Vaccinium shrubs: Vaccinium myrtillus, Vaccinium vitis-idaea, and Vaccinium oxycoccos. *Canadian Journal of Botany*, **80**, 635–641.
- Evans, G.C. & Coombe, D.E. (1959) Hemisperical and woodland canopy photography and the light climate. *Journal of Ecology*, **47**, 103–113.
- Eysn, L., Hollaus, M., Lindberg, E., Berger, F., Monnet, J.-M., Dalponte, M., Kobal, M.,
 Pellegrini, M., Lingua, E., Mongus, D. & Pfeifer, N. (2015) A benchmark of Lidar-based single tree detection methods using heterogeneous forest data from the alpine space. *Forests*, 6, 1721.
- Fahey, T.J. & Knight, D.H. (1986) Lodgepole pine ecosystems. BioScience, 36, 610-617.
- Falkowski, M.J., Smith, A.M.S., Gessler, P.E., Hudak, A.T., Vierling, L.A. & Evans, J.S. (2008)
 The influence of conifer forest canopy cover on the accuracy of two individual tree
 measurement algorithms using lidar data. *Canadian Journal of Remote Sensing*, 34, S338–S350.
- Falster, D.S., Brännström, Å., Westoby, M. & Dieckmann, U. (2017) Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, **114**, E2719–E2728.
- Fang, J., Kato, T., Guo, Z., Yang, Y., Hu, H., Shen, H., Zhao, X., Kishimoto-Mo, A.W., Tang, Y.
 & Houghton, R.A. (2014) Evidence for environmentally enhanced forest growth. *Proceedings of the National Academy of Sciences*, 111, 9527–9532.

Farmer, R.E., Charrette, P., Searle, I.E. & Tarjan, D.P. (1984) Interaction of light, temperature,

and chilling in the germination of black spruce. *Canadian Journal of Forest Research*, **14**, 131–133.

Farr, T.G. & Kobrick, M. (2000) Shuttle radar topography mission produces a wealth of data. *Eos, Transactions American Geophysical Union*, **81**, 583–585.

Farrar, J.L. (1995a) Trees in Canada, 3rd edn. Fitzhenry & Whiteside Ltd., Ottawa, ON, Canada.

- Farrar, J.L. (1995b) Trees of the Northern United States and Canada, Iowa State University Press, Ames, IA, USA.
- Fensholt, R. & Proud, S.R. (2012) Evaluation of earth observation based global long term vegetation trends — comparing GIMMS and MODIS global NDVI time series. *Remote Sensing of Environment*, **119**, 131–147.
- Feurtado, J.A., Ambrose, S., Cutler, A., Ross, A.S., Abrams, S. & Kermode, A. (2004)
 Dormancy termination of western white pine (Pinus monticola Dougl. Ex D. Don) seeds is associated with changes in abscisic acid metabolism. *Planta*, 218, 630–639.
- Finney, M.A. (2004) FARSITE: Fire Area Simulator model development and evaluation, Ogden, UT, USA.
- Finney, M.A. (2002) Fire growth using minimum travel time methods. Canadian Journal of Forest Research, 32, 1420–1424.
- Finney, M.A., Cohen, J.D., McAllister, S.S. & Jolly, W.M. (2013) On the need for a theory of wildland fire spread. *International Journal of Wildland Fire*, **22**, 25–36.
- Fisichelli, N.A., Frelich, L.E. & Reich, P.B. (2014) Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography*, **37**, 152–161.
- Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P. & Bergeron, Y. (2001)Future fire in Canada's boreal forest: paleoecology results and general circulation model -

regional climate model simulations. Canadian Journal of Forest Research, 31, 854-864.

- Flannigan, M.D. & Wotton, B.M. (1994) Fire regime and the abundance of jack pine.
 Proceedings of the 2nd International Conference on Forest Fire Research, p. 625–639
 (Vol. II, C.09). University of Coimbra, Coimbra, Portugal.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J. a, Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science (New York, N.Y.)*, 309, 570–4.
- Food and Agrigulture Organization of the United Nations (2010) *Global Forest Resources* Assessment 2010, Food and Agrigulture Organization of the United Nations, Rome, Italy.
- Forest, F.M., Berland, A., Nelson, T., Stenhouse, G., Graham, K., Cranston, J., Forest, F.M., Berland, A., Nelson, T., Stenhouse, G., Graham, K. & Cranston, J. (2008) The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *Forest Ecology and Management*, **256**, 1875–1883.
- Forestry Canada Fire Danger Group (1992) *Development and structure of the Canadian Forest Fire Behavior Prediction System*, Ottowa, ON, Canada.
- Fortin, J.K., Rode, K.D., Hilderbrand, G. V, Wilder, J., Farley, S., Jorgensen, C. & Marcot, B.G.
 (2016) Impacts of human recreation on brown bears (Ursus arctos): A review and new management tool. *PLoS ONE*, 11, 26.
- Fourcade, H.G. (1928) The principal point and principal distance in photogrammetry. *Transactions of the Royal Society of South Africa*, **16**, 13–22.
- Franklin, J.F., Cromack, K.J., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981) *Ecological characteristics of old-growth Douglas-fir forests*, US

Department of Agriculture, Forest Service, Portland, OR, USA.

- Franklin, O., Johansson, J., Dewar, R.C., Dieckmann, U., McMurtrie, R.E., Brännström, Å. & Dybzinski, R. (2012) Modeling carbon allocation in trees: a search for principles. *Tree Physiology*, **32**, 648–666.
- Fridley, J.D. (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, **485**, 359–362.
- Fu, P. & Rich, P. (1999) Design and implementation of the Solar Analyst: An ArcView extension for modeling solar radiation at landscape scales. Proceedings of the 19th Annual ESRI User Conference, p. 33. ESRI, San Diego, CA, USA.
- Fu, P. & Rich, P.M. (2002) A geometric solar radiation model with applications in agriculture and forestry. *Computers and Electronics in Agriculture*, **37**, 25–35.
- Fuchigami, L.H., Weiser, C.J., Kobayashi, K., Timmis, R. & Gusta, L. V. (1982) A degree growth stage model and cold acclimation in temperate woody plants. Plant Cold Hardiness and Freezing Stress, Volume 2: Mechanisms and Crop Implications, pp. 93–116. Academic Press, New York, NY, USA.
- Gaglioti, B. V., Mann, D.H., Jones, B.M., Wooller, M.J. & Finney, B.P. (2016) High-resolution records detect human-caused changes to the boreal forest wildfire regime in interior Alaska. *The Holocene*, **26**, 11.
- Gamon, J.A. (2014) *Can vegetation optical types help address plant-climate interactions? AGU Fall Meeting*, American Geophysical Union, San Francisco, CA.
- Gamon, J.A. & Bond, B. (2013) Effects of irradiance and photosynthetic downregulation on the photochemical reflectance index in Douglas-fir and ponderosa pine. *Remote Sensing of Environment*, **135**, 141–149.

- Gastellu-Etchegorry, J.-P., Yin, T., Lauret, N., Cajgfinger, T., Gregoire, T., Grau, E., Feret, J.-B., Lopes, M., Guilleux, J., Dedieu, G., Malenovský, Z., Cook, B.D., Morton, D., Rubio, J., Durrieu, S., Cazanave, G., Martin, E. & Ristorcelli, T. (2015) Discrete anisotropic radiative transfer (DART 5) for modeling airborne and satellite spectroradiometer and LIDAR acquisitions of natural and urban landscapes. *Remote Sensing*, 7, 1667.
- Gastellu-Etchegorry, J.P., Demarez, V., Pinel, V. & Zagolski, F. (1996) Modeling radiative transfer in heterogeneous 3-D vegetation canopies. *Remote Sensing of Environment*, 58, 131–156.
- Gavin, D.G., Brubaker, L.B. & Greenwald, D.N. (2013) Postglacial climate and fire-mediated vegetation change on the western Olympic Peninsula, Washington (USA). *Ecological Monographs*, 83, 471–489.
- Gavin, D.G., Hallett, D.J., Hu, F.S., Lertzman, K.P., Prichard, S.J., Brown, K.J., Lynch, J.A.,
 Bartlein, P. & Peterson, D.L. (2007) Forest fire and climate change in western North
 America: insights from sediment charcoal records. *Frontiers in Ecology and the Environment*, 5, 499–506.
- van Genuchten, M.T. (1980) A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal*, **44**, 892–898.
- Gillis, M.D., Omule, A.Y. & Brierley, T. (2005) Monitoring Canada's forests: The National Forest Inventory. *The Forestry Chronicle*, **81**, 214–221.
- Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J. & Bhatti, J. (2016) No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. *Proceedings of the National Academy of Sciences*, **113**, E8406–E8414.
- Goetz, S.J., Fiske, G.J. & Bunn, A.G. (2006) Using satellite time-series data sets to analyze fire disturbance and forest recovery across Canada. *Remote Sensing of Environment*, **101**, 352– 365.
- Gonsamo, A., D'odorico, P. & Pellikka, P. (2013) Measuring fractional forest canopy element cover and openness definitions and methodologies revisited. *Oikos*, **122**, 1283–1291.
- Goodfellow, I., Pouget-Abadie, J., Mirza, M., Xu, B., Warde-Farley, D., Ozair, S., Courville, A.
 & Bengio, Y. (2014a) *Generative adversarial nets. Advances in Neural Information Processing Systems 27* (ed. by Z. Ghahramani), M. Welling), C. Cortes), N.D. Lawrence), and K.Q. Weinberger), pp. 2672–2680. Curran Associates, Inc.
- Goodfellow, I.J., Pouget-Abadie, J., Mirza, M., Xu, B., Warde-Farley, D., Ozair, S., Courville,A. & Bengio, Y. (2014b) Generative Adversarial Networks. *ArXiv e-prints*.
- Goodman, S.J., Blakeslee, R.J., Koshak, W.J., Mach, D., Bailey, J., Buechler, D., Carey, L., Schultz, C., Bateman, M., McCaul Jr., E. & Stano, G. (2013) The GOES-R Geostationary Lightning Mapper (GLM). *Atmospheric Research*, **125–126**, 34–49.
- Goodwin, S., McPherson, J.D. & McCombie, W.R. (2016) Coming of age: ten years of nextgeneration sequencing technologies. *Nature Reviews Genetics*, **17**, 333–351.
- Gottschlich, C. & Schuhmacher, D. (2014) The shortlist method for fast computation of the Earth Mover's Distance and finding pptimal solutions to transportation problems. *PLoS ONE*, **9**, e110214.

Government of Alberta (2009) Gene Conservation Plan for Native Trees of Alberta,.

Gracia, M., Montané, F., Piqué, J. & Retana, J. (2007) Overstory structure and topographic gradients determining diversity and abundance of understory shrub species in temperate forests in central Pyrenees (NE Spain). *Forest Ecology and Management*, **242**, 391–397.

- Graham, A.J. & Harris, R. (2003) Extracting biophysical parameters from remotely sensed radar data: a review of the water cloud model. *Progress in Physical Geography*, **27**, 217–229.
- Gralewicz, N.J., Nelson, T.A. & Wulder, M.A. (2012) Factors influencing national scale wildfire susceptibility in Canada. *Forest Ecology and Management*, **265**, 20–29.
- Grandin, U. (2004) Dynamics of understory vegetation in boreal forests: experiences from Swedish integrated monitoring sites. *Forest Ecology and Management*, **195**, 45–55.
- Gray, L.K. & Hamann, A. (2012) Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change*, **117**, 289–303.
- Green, E.J., MacFarlane, D.W. & Valentine, H.T. (2000) Bayesian synthesis for quantifying uncertainty in predictions from process models. *Tree Physiology*, **20**, 415–419.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.-J.
 (1999) A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, 29, 824–839.
- Greenwood, M.S., Livingston, W.H., Day, M.E., Kenaley, S.C., White, A.S. & Brissette, J.C. (2002) Contrasting modes of survival by jack and pitch pine at a common range limit. *Canadian Journal of Forest Research*, **32**, 1662–1674.
- Greenwood, M.S., O'Brien, C.L., Schatz, J.D., Diggins, C.A., Day, M.E., Jacobson, G.L., White,
 A.S. & Wagner, R.G. (2008) Is early life cycle success a determinant of the abundance of
 red spruce and balsam fir? *Canadian Journal of Forest Research*, 38, 2295–2305.
- Grenier, M. & Sirois, L. (2009) Reproductive development and seed ripening in Betula papyrifera along an altitudinal thermal gradient in eastern Appalachia (Canada). *Botany*, **87**, 492–500.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H.,

Weiner, J., Wiegand, T. & DeAngelis, D.L. (2005) Pattern-oriented modeling of agentbased complex systems: Lessons from ecology. *Science (New York, N.Y.)*, **310**, 987–91.

- Grömping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**, 1–27.
- Groot, W.J., Bothwell, P.M., Carlsson, D.H. & Logan, K. a. (2003) Simulating the effects of future fire regimes on western Canadian boreal forests. *Journal of Vegetation Science*, 14, 355–364.
- de Groot, W.J., Flannigan, M.D. & Cantin, A.S. (2013) Climate change impacts on future boreal fire regimes. *Forest Ecology and Management*, **294**, 35–44.
- Gustafson, E.J., De Bruijn, A.M.G., Pangle, R.E., Limousin, J.-M., McDowell, N.G., Pockman, W.T., Sturtevant, B.R., Muss, J.D. & Kubiske, M.E. (2014) Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology*, 21, 843–856.
- Hamann, A., Roberts, D.R., Barber, Q.E., Carroll, C. & Nielsen, S.E. (2015) Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, 21, 997–1004.
- Hammer, A., Heinemann, D., Hoyer, C., Kuhlemann, R., Lorenz, E., Müller, R. & Beyer, H.G.
 (2003) Solar energy assessment using remote sensing technologies. *Remote Sensing of Environment*, 86, 423–432.
- Hammond, A., Galizi, R., Kyrou, K., Simoni, A., Siniscalchi, C., Katsanos, D., Gribble, M., Baker, D., Marois, E., Russell, S., Burt, A., Windbichler, N., Crisanti, A. & Nolan, T. (2016) A CRISPR-Cas9 gene drive system targeting female reproduction in the malaria mosquito vector Anopheles gambiae. *Nat Biotech*, 34, 78–83.

Hancock, S. (2010) Understanding the measurement of forests with waveform lidar.

Hand, E. (2015) Startup liftoff. Science, 348, 172 LP-177.

- Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. (1991) Conserving biodiversity in managed forests: lessons from natural forests. *BioScience*, 41, 382–392.
- Hantson, S., Padilla, M., Corti, D. & Chuvieco, E. (2013) Strengths and weaknesses of MODIS hotspots to characterize global fire occurrence. *Remote Sensing of Environment*, **131**, 152– 159.
- Hantson, S., Pueyo, S. & Chuvieco, E. (2016) Global fire size distribution: from power law to log-normal. *International Journal of Wildland Fire*, **25**, 403–412.
- Hantson, S., Pueyo, S. & Chuvieco, E. (2015) Global fire size distribution is driven by human impact and climate. *Global Ecology and Biogeography*, **24**, 77–86.
- Harrell, F.E.J. & Dupont, C. (2015) Hmisc: Harrell miscellaneous.
- Hart, S. a. & Chen, H.Y.H. (2006) Understory vegetation dynamics of North American boreal forests. *Critical Reviews in Plant Sciences*, 25, 381–397.
- Hastie, T., Tibshirani, R. & Friedman, J. (2009) *Elements of Statistical Learning: Data Mining, Inference, and Prediction*, 2nd edn. Springer-Verlag, New York, NY, USA.
- Hausfather, Z., Cowtan, K., Menne, M.J. & Williams, C.N. (2016) Evaluating the impact of U.S.
 Historical Climatology Network homogenization using the U.S. Climate Reference
 Network. *Geophysical Research Letters*, 43, 1695–1701.
- He, H.S., Larsen, D.R. & Mladenoff, D.J. (2002) Exploring component-based approaches in forest landscape modeling. *Environmental Modelling & Software*, **17**, 519–529.
- He, H.S. & Mladenoff, D.J. (1999) Spatially explicit and stochastic simulation of forestlandscape fire disturbance and succession. *Ecology*, **80**, 81–99.

- He, H.S., Mladenoff, D.J. & Boeder, J. (1999) An object-oriented forest landscape model and its representation of tree species. *Ecological Modelling*, **119**, 1–19.
- He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W. & Lamont, B.B. (2012) Fire-adapted traits of Pinus arose in the fiery Cretaceous. *New Phytologist*, **194**, 751–759.
- Héon, J., Arseneault, D. & Parisien, M.-A. (2014) Resistance of the boreal forest to high burn rates. *Proceedings of the National Academy of Sciences*, **111**, 13888–13893.
- Hikosaka, K. & Hirose, T. (1997) Leaf angle as a strategy for light competition: Optimal and evolutionarily stable light-extinction coefficient within a leaf canopy. *Ecoscience*, 4, 501– 507.
- Hilker, T., Coops, N.C., Newnham, G.J., van Leeuwen, M., Wulder, M.A., Stewart, J. & Culvenor, D.S. (2012) Comparison of terrestrial and airborne LiDAR in describing stand structure of a thinned lodgepole pine forest. *Journal of Forestry*, **110**, 97–104(8).
- Hilker, T., Frazer, G.W., Coops, N.C., Wulder, M.A., Newnham, G.J., Stewart, J.D., van Leeuwen, M. & Culvenor, D.S. (2013) Prediction of wood fiber attributes from LiDARderived forest canopy indicators. *Forest Science*, **59**, 231–242.
- Hirsch, K.G. (1993) A brief overview of the Canadian Forest Fire Behavior Prediction (FBP) System. *The International Association of Wildland Fire: HotSheet*, **2**, 3.
- Hogg, E.H. (Ted), Brandt, J.P. & Michaelian, M. (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*, **38**, 1373–1384.
- Holling, C.S. (1978) Adaptive Environmental Assessment and Management, John Wiley & Sons, Chichester, UK.

Honaker, J., King, G. & Blackwell, M. (2011) Amelia II: A program for missing data. Journal of

Statistical Software, 45, 47.

- Hopkinson, C. & Chasmer, L. (2007) *Modelling canopy gap fraction from lidar intensity. ISPRS Laser Scanning 2007 and SilviLaser 2007*, pp. 190–194. Espoo, Finland.
- Hopkinson, C. & Chasmer, L. (2009) Testing LiDAR models of fractional cover across multiple forest ecozones. *Remote Sensing of Environment*, **113**, 275–288.
- Houghton, R.A., House, J.I., Pongratz, J., van der Werf, G.R., DeFries, R.S., Hansen, M.C., Le Quéré, C. & Ramankutty, N. (2012) Carbon emissions from land use and land-cover change. *Biogeosciences*, 9, 5125–5142.
- Hu, F., Brubaker, L., Gavin, D., Higuera, P., Lynch, J., Rupp, T.S. & Tinner, W. (2006) How climate and vegetation influence the fire regime of the Alaskan boreal biome: The Holocene perspective. *Mitigation and Adaptation Strategies for Global Change*, **11**, 829–846.
- Huang, S., Liu, H., Dahal, D., Jin, S., Welp, L.R., Liu, J. & Liu, S. (2013) Modeling spatially explicit fire impact on gross primary production in interior Alaska using satellite images coupled with eddy covariance. *Remote Sensing of Environment*, **135**, 178–188.
- Huang, S., Titus, S.J. & Wiens, D.P. (1992) Comparison of nonlinear height–diameter functions for major Alberta tree species. *Canadian Journal of Forest Research*, **22**, 1297–1304.
- Hwang, T., Band, L.E., Miniat, C.F., Song, C., Bolstad, P. V, Vose, J.M. & Love, J.P. (2014)
 Divergent phenological response to hydroclimate variability in forested mountain
 watersheds. *Global Change Biology*, 20, 2580–2595.
- Hyyppa, J., Kelle, O., Lehikoinen, M. & Inkinen, M. (2001) A segmentation-based method to retrieve stem volume estimates from 3-D tree height models produced by laser scanners.
 IEEE Transactions on Geoscience and Remote Sensing, 39, 969–975.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F.,

Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen,
J.M., Van Veen, F.J.F., Warren, P.H. & Woodward, G. (2009) Review: Ecological networks
– beyond food webs. *Journal of Animal Ecology*, 78, 253–269.

- Intergovernmental Panel on Climate Change (2014) *Climate Change 2013: The Physical Science Basis*, Cambridge University Press, New York, NY, USA.
- Intergovernmental Panel on Climate Change (2003) *Good Practice Guidance for Land-use and Land-use Change in Forestry*, Intergovernmental Panel on Climate Change, Vienna, Austria.
- Iqbal, M. (1983) *An Introduction To Solar Radiation*, 1st edn. Elsevier Science, Amsterdam, Netherlands.
- Isenburg, M. (2015) LAStools: Efficient LiDAR processing software.
- Isenburg, M., Liu, Y., Shewchuk, J. & Snoeyink, J. (2006a) *Streaming computation of Delaunay triangulations. Proceedings of SIGGRAPH*, pp. 1049–1056. Boston, USA.
- Isenburg, M., Liu, Y., Shewchuk, J., Snoeyink, J. & Thirion, T. (2006b) *Generating raster DEM from mass points via TIN streaming. Geographic Information Science, 4th International Conference, GIScience 2006* Lecture Notes in Computer Science. (ed. by M. Raubal), H.J. Miller), A.U. Frank), and M.F. Goodchild), pp. 186–198. Springer, Münster, Germany.
- Isenburg, M., Liu, Y. & Snoeyink, J. (2006c) *Streaming extraction of elevation contours from LIDAR points*, Chapel Hill, NC, USA.
- Ishii, H., Hamada, Y. & Utsugi, H. (2012) Variation in light-intercepting area and photosynthetic rate of sun and shade shoots of two Picea species in relation to the angle of incoming light. *Tree Physiology*, **32**, 1227–1236.

Jacobs, D.F., Selig, M.F. & Severeid, L.R. (2009) Aboveground carbon biomass of plantation-

grown American chestnut (Castanea dentata) in absence of blight. *Forest Ecology and Management*, **258**, 288–294.

- James, N.A., Kejariwal, A. & Matteson, D.S. (2014) Leveraging cloud data to mitigate user experience from Breaking Bad'. *ArXiv e-prints*.
- James, N. & Matteson, D. (2015) ecp: An R Package for nonparametric multiple change point analysis of multivariate data. *Journal of Statistical Software*, **62**, 1–25.
- Jelinski, D.E., Cheliak, W.M., Society, B., Journal, A., Jelinski, D.E., Cheliak, W.M., Society, B., Journal, A., Jelinski, D.E. & Cheliak, W.M. (1992) Genetic diversity and spatial subdivision of Populus tremuloides (Salicaceae) in a heterogeneous landscape. *American Journal of Botany*, **79**, 728–736.
- Ji, S., Xu, W., Yang, M. & Yu, K. (2013) 3D convolutional neural networks for human action recognition. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, **35**, 221– 231.
- Johnson, E.A., Miyanishi, K. & Bridge, S.R.J. (2001) Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. *Conservation Biology*, **15**, 1554–1557.
- Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S. & Mack, M.C. (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, 16, 1281–1295.
- Jolly, W.M., Hintz, J., Kropp, R.C. & Conrad, E.T. (2014) Physiological drivers of the live foliar moisture content "spring dip" in Pinus resinosa and Pinus banksiana and their relationship to foliar flammability, (ed. by D.X. Viegas) Imprensa da Universidade de Coimbra, Coimbra.

Jolly, W.M., Hintz, J., Linn, R.L., Kropp, R.C., Conrad, E.T., Parsons, R.A. & Winterkamp, J.

(2016) Seasonal variations in red pine (Pinus resinosa) and jack pine (Pinus banksiana) foliar physio-chemistry and their potential influence on stand-scale wildland fire behavior. *Forest Ecology and Management*, **373**, 167–178.

Jones, R.H. & Sharitz, R.R. (1998) Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. *Journal of Ecology*, **86**, 574–587.

Junger, W. & de Leon, A.P. (2012) mtsdi: Multivariate time series data imputation.

- Kaartinen, H., Hyyppä, J., Yu, X., Vastaranta, M., Hyyppä, H., Kukko, A., Holopainen, M.,
 Heipke, C., Hirschmugl, M., Morsdorf, F., Næsset, E., Pitkänen, J., Popescu, S., Solberg, S.,
 Wolf, B.M. & Wu, J.-C. (2012) An international comparison of individual tree detection
 and extraction using airborne laser scanning. *Remote Sensing*, 4, 950.
- Kalman, R.E. & Bucy, R.S. (1961) New results in linear filtering and prediction theory. *Journal of Basic Engineering*, **83**, 95–108.
- Kamae, Y., Shiogama, H., Watanabe, M. & Kimoto, M. (2014) Attributing the increase in Northern Hemisphere hot summers since the late 20th century. *Geophysical Research Letters*, 41, 5192–5199.
- Karhu, K., Auffret, M.D., Dungait, J.A.J., Hopkins, D.W., Prosser, J.I., Singh, B.K., Subke, J.-A., Wookey, P.A., Agren, G.I., Sebastia, M.-T., Gouriveau, F., Bergkvist, G., Meir, P., Nottingham, A.T., Salinas, N. & Hartley, I.P. (2014) Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature*, **513**, 81–84.
- Karl, T.R., Arguez, A., Huang, B., Lawrimore, J.H., McMahon, J.R., Menne, M.J., Peterson,
 T.C., Vose, R.S. & Zhang, H.-M. (2015) Possible artifacts of data biases in the recent global surface warming hiatus. *Science*, 348, 1469–1472.

Kasischke, E.S. & Stocks, B.J. (2000) Fire, Climate Change, and Carbon Cycling in the Boreal

Forest, Springer-Verlag, New York, NY, USA.

- Kasischke, E.S. & Turetsky, M.R. (2006) Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters*, **33**.
- Katahata, S., Naramoto, M., Kakubari, Y. & Mukai, Y. (2005) Photosynthetic acclimation to dynamic changes in environmental conditions associated with deciduous overstory phenology in Daphniphyllum humile, an evergreen understory shrub. *Tree Physiology*, 25, 437–445.
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2014) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406–411.
- Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O/'Keefe, J., Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.
- Kelly, R., Chipman, M.L., Higuera, P.E., Stefanova, I., Brubaker, L.B. & Hu, F.S. (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proceedings of the National Academy of Sciences*, **110**, 13055–13060.
- Kennedy, M.C. & O'Hagan, A. (2001) Bayesian calibration of computer models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **63**, 425–464.
- Khosravipour, A., Skidmore, A.K. & Isenburg, M. (2016) Generating spike-free digital surface models using LiDAR raw point clouds: A new approach for forestry applications.
 International Journal of Applied Earth Observation and Geoinformation, **52**, 104–114.

Khosravipour, A., Skidmore, A.K., Isenburg, M., Wang, T. & Hussin, Y.A. (2014) Generating

pit-free canopy height models from airborne Lidar. *Photogrammetric Engineering & Remote Sensing*, **80**, 863–872.

- Killick, R. & Eckley, I.A. (2014) changepoint: An R Package for changepoint analysis. *Journal* of Statistical Software; Vol 1, Issue 3 (2014).
- Killick, R., Fearnhead, P. & Eckley, I. ~A. (2011) Optimal detection of changepoints with a linear computational cost. *ArXiv e-prints*.
- Kimmins, H., Blanco, J.A., Seely, B., Welham, C. & Scoullar, K. (2010) Forecasting Forest Futures: A Hybrid Modelling Approach to the Assessment of Sustainability of Forest Ecosystems and Their Values, Taylor & Francis Group.
- Klinka, K., Worrall, J., Skoda, L. & Varga, P. (2000) The Distribution and Synopsis of Ecological and Silvical Characteristics of Tree Species of British Columbia's Forests, Canadian Cartographics Ltd., Coquitlam, BC, Canada.
- Knight, H. (1967) Information Report A-X-9: Progress of the Canada Land Inventory in Alberta, Calgary, Alberta, Canada.
- Knowles, N. (2002) Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. *Geophysical Research Letters*, **29**, 1891.
- Koch, B., Heyder, U. & Weinacker, H. Detection of individual tree crowns in airborne Lidar data. *Photogrammetric Engineering & Remote Sensing*, **72**, 357–363.
- Korhonen, L., Korpela, I., Heiskanen, J. & Maltamo, M. (2011) Airborne discrete-return LIDAR data in the estimation of vertical canopy cover, angular canopy closure and leaf area index.
 Remote Sensing of Environment, **115**, 1065–1080.
- Korhonen, L. & Morsdorf, F. (2014) *Estimation of canopy cover, gap fraction and leaf area index with airborne laser scanning. Forestry Applications of Airborne Laser Scanning:*

Concepts and Case Studies (ed. by M. Maltamo), E. Næsset), and J. Vauhkonen), pp. 397–417. Springer Netherlands, Dordrecht.

- Kosaka, Y. & Xie, S.-P. (2013) Recent global-warming hiatus tied to equatorial Pacific surface cooling. *Nature*, **501**, 403–407.
- Koven, C.D. (2013) Boreal carbon loss due to poleward shift in low-carbon ecosystems. *Nature Geoscience*, **6**, 452–456.
- Kraus, K. & Pfeifer, N. (1998) Determination of terrain models in wooded areas with airborne laser scanner data. *ISPRS Journal of Photogrammetry and Remote Sensing*, **53**, 193–203.
- Krawchuk, M., Cumming, S. & Flannigan, M. (2009) Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. *Climatic Change*, **92**, 83–97.
- Krizhevsky, A., Sutskever, I. & Hinton, G.E. (2012) *ImageNet Classification with Deep Convolutional Neural Networks*. *Advances in Neural Information Processing Systems 25* (ed. by F. Pereira), C.J.C. Burges), L. Bottou), and K.Q. Weinberger), pp. 1097–1105. Curran Associates, Inc.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J.J., Neilson, E.T., Carroll, A.L., Ebata, T.
 & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452, 987–990.
- Laberee, K., Nelson, T.A., Stewart, B.P., McKay, T. & Stenhouse, G.B. (2014) Oil and gas infrastructure and the spatial pattern of grizzly bear habitat selection in Alberta, Canada. *The Canadian Geographer / Le Géographe canadien*, **58**, 79–94.
- de Lafontaine, G. & Payette, S. (2011) Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene. *Quaternary*

Science Reviews, **30**, 867–875.

- Lang, A.R.G. & Yueqin, X. (1986) Estimation of leaf area index from transmission of direct sunlight in discontinuous canopies. *Agricultural and Forest Meteorology*, **37**, 229–243.
- Larocque, G.R., Bhatti, J.S., Boutin, R. & Chertov, O. (2008) Uncertainty analysis in carbon cycle models of forest ecosystems: Research needs and development of a theoretical framework to estimate error propagation. *Ecological Modelling*, **219**, 400–412.
- Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter,
 O., Edwards, D.P., Phalan, B., Balmford, A., Van Der Ree, R. & Arrea, I.B. (2014) A
 global strategy for road building. *Nature*, **513**, 229–232.
- Lavoie, L. & Sirois, L. (1998) Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. *Journal of Vegetation Science*, **9**, 483–492.
- Lazarus, E.D. & McGill, B.J. (2014) Pushing the pace of tree species migration. *PLoS ONE*, **9**, e105380.
- Leadem, C.L. (1985) Seed dormancy in three Pinus species of the inland mountain west. Conifer Tree Seed in the Inland Mountain West Symposium (ed. by R.C. Shearer), pp. 117–123. US Department of Agriculture, Forest Service, Ogden, UT, USA.
- Leadem, C.L. (1989) *Stratification and quality assessment of Abies lasiocarpa seeds*, Canada-BC Economic & Regional Development Agreement, Victoria, BC, Canada.

LeCun, Y., Bengio, Y. & Hinton, G. (2015) Deep learning. *Nature*, **521**, 436–444.

- Ledig, C., Theis, L., Huszar, F., Caballero, J., Cunningham, A., Acosta, A., Aitken, A., Tejani,
 A., Totz, J., Wang, Z. & Shi, W. (2016) Photo-realistic single image super-resolution using a generative adversarial network. *ArXiv e-prints*.
- Lee, H., Slatton, K.C., Roth, B.E. & Cropper, W.P. (2008) Prediction of forest canopy light

interception using three-dimensional airborne LiDAR data. *International Journal of Remote Sensing*, **30**, 189–207.

- Lee, X., Goulden, M.L., Hollinger, D.Y., Barr, A., Black, T.A., Bohrer, G., Bracho, R., Drake,
 B., Goldstein, A., Gu, L., Katul, G., Kolb, T., Law, B.E., Margolis, H., Meyers, T., Monson,
 R., Munger, W., Oren, R., Paw U, K.T., Richardson, A.D., Schmid, H.P., Staebler, R.,
 Wofsy, S. & Zhao, L. (2011) Observed increase in local cooling effect of deforestation at
 higher latitudes. *Nature*, 479, 384–7.
- Lefsky, M.A., Cohen, W.B., Parker, G.G. & Harding, D.J. (2002) Lidar remote sensing for ecosystem studies. *BioScience*, **52**, 19–30.
- Leithead, M., Silva, L.R. & Anand, M. (2012) Recruitment patterns and northward tree migration through gap dynamics in an old-growth white pine forest in northern Ontario. *Plant Ecology*, **213**, 1699–1714.
- Lemon, P.E. (1956) A spherical densiometer for estimating forest overstory density. *Forest Science*, **2**, 314–320.
- Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D. & Dhôte, J.-F. (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography*, **32**, 765–777.
- Levin, S.A. (1998) Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, **1**, 431–436.
- Levin, S.A. (2005) Self-organization and the emergence of complexity in ecological systems. *BioScience*, **55**, 1075–1079.
- Li, F., Levis, S. & Ward, D.S. (2013a) Quantifying the role of fire in the Earth system; Part 1: Improved global fire modeling in the Community Earth System Model (CESM1).

Biogeosciences, **10**, 2293–2314.

- Li, X.J., Burton, P.J. & Leadem, C.L. (1994) Interactive effects of light and stratification on the germination of some British Columbia conifers. *Canadian Journal of Botany*, **72**, 1635– 1646.
- Li, Y., Fan, X., Mitra, N.J., Chamovitz, D., Cohen-Or, D. & Chen, B. (2013b) Analyzing Growing Plants from 4D Point Cloud Data. ACM Transactions on Graphics, 32, 157:1-157:10.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F. & Comeau, P.G. (1999) Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research*, 29, 796–811.
- Ligot, G., Balandier, P., Courbaud, B. & Claessens, H. (2014) Forest radiative transfer models: Which approach for which application? *Canadian Journal of Forest Research*, **44**, 391–403.
- Lindenmayer, D.B., Banks, S.C., Laurance, W.F., Franklin, J.F. & Likens, G.E. (2014) Broad decline of populations of large old trees. *Conservation Letters*, **7**, 72–73.
- Lindquist, E.J., D'Annunzio, R., Gerrand, A., MacDicken, K., Achard, F., Beuchle, R., Brink,
 A., Eva, H.D., Mayaux, P., San-Miguel Ayanz, J. & Stibig, H.-J. (2012) *Global forest land-use change 1990-2005*, Food and Agrigulture Organization of the United Nations, Rome,
 Italy.
- Linke, J. & McDermid, G.J. (2012) Monitoring landscape change in multi-use west-central Alberta, Canada using the disturbance-inventory framework. *Remote Sensing of Environment*, **125**, 112–124.
- Linnainmaa, S. (1970) The representation of the cumulative rounding error of an algorithm as a Taylor expansion of the local rounding errors.

- Lintunen, A., Kaitaniemi, P., Perttunen, J. & Sievänen, R. (2013) Analysing species-specific light transmission and related crown characteristics of Pinus sylvestris and Betula pendula using a shoot-level 3D model. *Canadian Journal of Forest Research*, **43**, 929–938.
- Little, C.H.A. (1970) Seasonal changes in carbohydrate and moisture content in needles of Balsam fir (Abies balsamea). *Canadian Journal of Botany*, **48**, 2021–2028.
- Liu, C., Lu, F., Cui, X. & Cao, X. (2010) Histone methylation in higher plants. *Annual Review of Plant Biology*, **61**, 395–420.
- Liu, Z. & Wimberly, M. ~C. (2014) The relationship between fire regime and productivity/aridity in the western United States. *AGU Fall Meeting Abstracts*.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–5.
- Lotan, J.E. & Perry, D.A. (1983) Ecology and Regeneration of Lodgepole Pine,.
- Lounici, K. (2012) High-dimensional covariance matrix estimation with missing observations. *eprint arXiv:1201.2577.*
- Luceño, A. (2006) Fitting the generalized Pareto distribution to data using maximum goodnessof-fit estimators. *Computational Statistics & Data Analysis*, **51**, 904–917.
- Luo, Y. & Chen, H.Y.H. (2013) Observations from old forests underestimate climate change effects on tree mortality. *Nat Commun*, **4**, 1655.
- Luyssaert, S., Schulze, E.-D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P. & Grace, J. (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–215.
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A.,
 Hari, P., Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A.,
 Loustau, D., Manca, G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R. & Grace,

J. (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–50.

- Maguya, A.S., Junttila, V. & Kauranne, T. (2014) Algorithm for extracting digital terrain models under forest canopy from airborne LiDAR data. *Remote Sensing*, **6**, 6524–6548.
- Malamud, B.D., Morein, G. & Turcotte, D.L. (1998) Forest fires: An example of self-organized critical behavior. *Science*, **281**, 1840–1842.
- Mali, P., Yang, L., Esvelt, K.M., Aach, J., Guell, M., DiCarlo, J.E., Norville, J.E. & Church,G.M. (2013) RNA-guided human genome engineering via Cas9. *Science*, 339, 823 LP-826.
- Mandel, J., Beezley, J.D., Coen, J.L. & Kim, M. (2009) Data assimilation for wildland fires. *IEEE Control Systems*, **29**, 47–65.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z.,
 Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread
 increase of tree mortality rates in the western United States. *Science (New York, N.Y.)*, 323, 521–4.
- Marlon, J.R., Bartlein, P.J., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., Joos, F.,
 Power, M.J. & Prentice, I.C. (2008) Climate and human influences on global biomass
 burning over the past two millennia. *Nature Geoscience*, 1, 697–702.
- Marlon, J.R., Bartlein, P.J., Daniau, A.-L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner,
 W. & Vanniére, B. (2013) Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. *Quaternary Science Reviews*, 65, 5–25.
- Martínez-Vilalta, J., Lloret, F. & Breshears, D.D. (2012) Drought-induced forest decline: Causes, scope and implications. *Biology Letters*, **8**, 689–691.

Mascaro, J., Hughes, R.F. & Schnitzer, S.A. (2011) Novel forests maintain ecosystem processes

after the decline of native tree species. *Ecological Monographs*, **82**, 221–228.

- Mason Earles, J., Yeh, S. & Skog, K.E. (2012) Timing of carbon emissions from global forest clearance. *Nature Clim. Change*, 2, 682–685.
- Matteson, D.S. & James, N.A. (2013) A nonparametric approach for multiple change point analysis of multivariate data. *ArXiv e-prints*.
- Matzke, M.A. & Mosher, R.A. (2014) RNA-directed DNA methylation: An epigenetic pathway of increasing complexity. *Nat Rev Genet*, **15**, 394–408.
- McCune, B. & Allen, T.F.H. (1985) Forest dynamics in the Bitterroot Callyons, Montana. *Canadian Journal of Botany*, **63**, 377–383.
- McGaughey, R.J. (2014) FUSION/LDV: Software for LiDAR data analysis and visualization. 168.
- McMahon, S.M., Parker, G.G. & Miller, D.R. (2010) Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences*, **107**, 3611–3615.
- Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y. & Moorcroft, P.R. (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research: Biogeosciences*, **114**.
- Menne, M.J., Durre, I., Vose, R.S., Gleason, B.E. & Houston, T.G. (2012) An overview of the Global Historical Climatology Network-Daily database. *Journal of Atmospheric and Oceanic Technology*, **29**, 897–910.
- Meunier, C., Sirois, L. & Bégin, Y. (2007) Climate and Picea mariana seed maturation relationships: A multi-scale perspective. *Canadian Journal of Forest Research*, **77**, 361– 376.
- Meyn, A., Schmidtlein, S., Taylor, S., Girardin, M., Thonicke, K. & Cramer, W. (2013)

Precipitation-driven decrease in wildfires in British Columbia. *Regional Environmental Change*, **13**, 165–177.

- Meyn, A., Taylor, S.W., Flannigan, M.D., Thonicke, K. & Cramer, W. (2010) Relationship between fire, climate oscillations, and drought in British Columbia, Canada, 1920–2000. *Global Change Biology*, 16, 977–989.
- Meyn, A., White, P.S., Buhk, C. & Jentsch, A. (2007) Environmental drivers of large, infrequent wildfires: the emerging conceptual model. *Progress in Physical Geography*, **31**, 287–312.
- Michaelian, M., Hogg, E.H., Hall, R.J. & Arsenault, E. (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, **17**, 2084–2094.
- Miller, I.R. and E.S. and J.R. (2013) Amplified warming projections for high altitude regions of the northern hemisphere mid-latitudes from CMIP5 models. *Environmental Research Letters*, 8, 24040.
- Miller, J.B. (1967) A formula for average foliage density. *Australian Journal of Botany*, **15**, 141–144.
- Mladenoff, D.J. & He, H.S. (1999) Design, behavior and application of LANDIS, an objectoriented model of forest landscape disturbance and succession. Spatial Modeling of Forest Landscape Change: Approaches and Applications, pp. 125–162. Cambridge University Press, Cambridge, UK.
- Mladenoff, D.J., Host, G.E., Boeder, J. & Crow, T.R. (1993) LANDIS: a spatial model of forest landscape disturbance, succession, and management. Second International Conference on Integrating Modelling and GIS,.

Moeser, D., Morsdorf, F. & Jonas, T. (2015) Novel forest structure metrics from airborne

LiDAR data for improved snow interception estimation. *Agricultural and Forest Meteorology*, **208**, 40–49.

- Moeser, D., Roubinek, J., Schleppi, P., Morsdorf, F. & Jonas, T. (2014) Canopy closure, LAI and radiation transfer from airborne LiDAR synthetic images. *Agricultural and Forest Meteorology*, **197**, 158–168.
- Mok, H.-F., Arndt, S.K. & Nitschke, C.R. (2012) Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. *Global Change Biology*, **18**, 1053–1072.
- Monsi, M. & Saeki, T. (2005) On the factor light in plant communities and its importance for matter production. *Annals of Botany*, **95**, 549–567.
- Monsi, M. & Saeki, T. (1953) Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Japanese Journal of Botany*, **14**, 22–52.
- Moorcroft, P.R., Hurtt, G.C. & Pacala, S.W. (2001) A method for scaling vegetation dynamics: The ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–586.
- Mora, T. & Bialek, W. (2011) Are biological systems poised at criticality? *Journal of Statistical Physics*, **144**, 268–302.
- Morsdorf, F., Kötz, B., Meier, E., Itten, K.I. & Allgöwer, B. (2006) Estimation of LAI and fractional cover from small footprint airborne laser scanning data based on gap fraction. *Remote Sensing of Environment*, **104**, 50–61.
- Musselman, K.N., Margulis, S.A. & Molotch, N.P. (2013) Estimation of solar direct beam transmittance of conifer canopies from airborne LiDAR. *Remote Sensing of Environment*, 136, 402–415.

Nagel, J.B. (2017) Bayesian techniques for inverse uncertainty quantification.

- Natural Regions Committee (2006) Natural Regions and Subregions of Alberta, Government of Alberta, Edmonton, AB, Canada.
- Natural Resources Canada (2016) *The State of Canada's Forests: Annual Report 2016*, Natural Resources Canada, Ottowa, ON, Canada.
- Navratil, S., Branter, K. & Zasada, J. (1991) Regeneration in the mixedwoods. Proceedings of 1989 Mixedwood Symposium, September 12-14, 1989, Fort St. John, British Columbia., pp. 32–48. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada.
- Nepstad, D.C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M. & Brooks, V. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **1405**, 1997–2000.
- Newhouse, A.E., Polin-McGuigan, L.D., Baier, K.A., Valletta, K.E.R., Rottmann, W.H., Tschaplinski, T.J., Maynard, C.A. & Powell, W.A. (2014) Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Science*, **228**, 88–97.
- Nielsen, S.E. (2005) Habitat ecology, conservation, and projected population viability of grizzly bears (Ursus Arctos L.) in west-central Alberta, Canada.
- Nielsen, S.E., Cranston, J., Stenhouse, G.B. & Street, M. (2009) Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *Journal of Conservation Planning*, 5, 38–60.
- Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B. & Boyce, M.S. (2004) Grizzly bears and forestry. *Forest Ecology and Management*, **199**, 67–82.
- Nielsen, S.E., Stenhouse, G.B., Beyer, H.L., Huettmann, F. & Boyce, M.S. (2008) Can natural disturbance-based forestry rescue a declining population of grizzly bears? *Biological*

Conservation, 141, 2193–2207.

- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217–229.
- Niinemets, Ü. (2010a) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, **25**, 693–714.
- Niinemets, Ü. (2010b) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, **260**, 1623–1639.
- Niinemets, Ü. & Anten, N.P.R. (2009) Packing the photosynthetic machinery: From leaf to canopy. Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems (ed. by A. Laisk), L. Nedbal), and Govindjee), pp. 363–399. Springer Netherlands, Dordrecht.
- Niinemets, Ü., Keenan, T.F. & Hallik, L. (2015) A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist*, **205**, 973–993.
- Niklasson, M. & Granström, A. (2000) Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, **81**, 1484–1499.
- Nilsson, M.-C. & Wardle, D.A. (2005) Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, **3**, 421–428.
- Nitschke, C., Mathey, A. & Amoroso, M. (2010) An integrated assessment of species and ecosystem vulnerability to climate change from the tree- to stand- to landscape-level in the

sub-boreal forests of northwest British Columbia, Canada, Government of British Columbia, Smithers, BC, Canada.

- Nitschke, C.R., Amoroso, M., Coates, K.D. & Astrup, R. (2012) The influence of climate change, site type, and disturbance on stand dynamics in northwest British Columbia, Canada. *Ecosphere*, **3**, 11.
- Nitschke, C.R. & Innes, J.L. (2008) A tree and climate assessment tool for modelling ecosystem response to climate change. *Ecological Modelling*, **210**, 263–277.
- Nitschke, C.R., Innes, J.L. & Biology, G.C. (2008) Climatic change and fire potential in southcentral British Columbia, Canada. *Global Change Biology*, **14**, 841–855.
- Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5–21.
- van Oijen, M. & Thomson, A. (2010) Toward Bayesian uncertainty quantification for forestry models used in the United Kingdom Greenhouse Gas Inventory for land use, land use change, and forestry. *Climatic Change*, **103**, 55–67.
- Oliverio, A.M., Bradford, M.A. & Fierer, N. (2017) Identifying the microbial taxa that consistently respond to soil warming across time and space. *Global Change Biology*, **23**, 2117–2129.
- van den Oord, A., Dieleman, S., Zen, H., Simonyan, K., Vinyals, O., Graves, A., Kalchbrenner, N., Senior, A. & Kavukcuoglu, K. (2016a) WaveNet: a generative model for raw audio.
 ArXiv e-prints.
- van den Oord, A., Kalchbrenner, N. & Kavukcuoglu, K. (2016b) Pixel recurrent neural networks. *ArXiv e-prints*.
- Oye, K.A., Esvelt, K., Appleton, E., Catteruccia, F., Church, G., Kuiken, T., Lightfoot, S.B.-Y.,

McNamara, J., Smidler, A. & Collins, J.P. (2014) Regulating gene drives. *Science*, **345**, 626–628.

- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996)
 Forest models defined by field measurements: estimation, error analysis and dynamics.
 Ecological Monographs, 66, 1–43.
- Le Page, Y., Morton, D., Bond-Lamberty, B., Pereira, J.M.C. & Hurtt, G. (2015) HESFIRE: A global fire model to explore the role of anthropogenic and weather drivers. *Biogeosciences*, 12, 887–903.
- Parent, J.R. & Volin, J.C. (2014) Assessing the potential for leaf-off LiDAR data to model canopy closure in temperate deciduous forests. *ISPRS Journal of Photogrammetry and Remote Sensing*, **95**, 134–145.
- Parisien, M.-A., Snetsinger, S., Greenberg, J.A., Nelson, C.R., Schoennagel, T., Dobrowski, S.Z.
 & Moritz, M.A. (2012) Spatial variability in wildfire probability across the western United States. *International Journal of Wildland Fire*, 21, 313–327.
- Parisien, M., Peters, V.S., Wang, Y., Little, J.M., Bosch, E.M. & Stocks, B.J. (2006) Spatial patterns of forest fires in Canada, 1980–1999. *International Journal of Wildland Fire*, 15, 361–374.
- Park Williams, A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M.,
 Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R.,
 Gangodagamage, C., Cai, M. & McDowell, N.G. (2013) Temperature as a potent driver of
 regional forest drought stress and tree mortality. *Nature Clim. Change*, 3, 292–297.
- Parker, G.G., Lefsky, M.A. & Harding, D.J. (2001) Light transmittance in forest canopies determined using airborne laser altimetry and in-canopy quantum measurements. *Remote*

Sensing of Environment, 76, 298–309.

- Parminter, J. (1984) *Fire-ecological relationships for the biogeoclimatic zones of the northern portion of the Mackenzie Timber Supply Area: summary report*, British Columbia Ministry of Forests, Victoria, BC, Canada.
- Pausas, J.G. & Ribeiro, E. (2013) The global fire–productivity relationship. *Global Ecology and Biogeography*, **22**, 728–736.
- Peralta, G. (2016) Merging evolutionary history into species interaction networks. *Functional Ecology*, **30**, 1917–1925.
- Perovich, D.K., Light, B., Eicken, H., Jones, K.F., Runciman, K. & Nghiem, S. V. (2007) Increasing solar heating of the Arctic Ocean and adjacent seas, 1979–2005: attribution and role in the ice-albedo feedback. *Geophysical Research Letters*, 34.
- Peterson, E.B., Peterson, N.M., Simard, S.W. & Wang, J.R. (1997) *Paper Birch Managers Handbook for British Columbia*, Natural Resources Canada, Victoria, BC, Canada.
- Pickett, S.T.A. & Thompson, J.N. (1978) Patch dynamics and the design of nature reserves. *Biological Conservation*, **13**, 27–37.
- Piedallu, C., Gégout, J.-C., Perez, V. & Lebourgeois, F. (2013) Soil water balance performs better than climatic water variables in tree species distribution modelling. *Global Ecology* and Biogeography, 22, 470–482.
- Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017) The multilayer nature of ecological networks. *Natural Ecology & Evolution*, 1, 101.
- Pitel, J.A. & Cheliak, W.M. (1986) Enzyme activities during imbibition and germination of seeds of tamarack (Larix laricina). *Physiologia Plantarum*, **67**, 562–569.

Polewski, P., Erickson, A., Yao, W., Coop, N., Krzystek, P. & Stilla, U. (2016) Object-based co-

registration of terrestrial photogrammetric and ALS point clouds in forested areas. ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences, pp. 347– 354. International Society of Photogrammetry and Remote Sensing, Prague, Czech Republic.

- Popescu, S.C., Wynne, R.H. & Nelson, R.F. (2002) Estimating plot-level tree heights with lidar: local filtering with a canopy-height based variable window size. *Computers and Electronics in Agriculture*, **37**, 71–95.
- Popescu, S.C., Wynne, R.H. & Scrivani, J.A. (2004) Fusion of small-footprint lidar and multispectral data to estimate plot-level volume and biomass in deciduous and pine forests in Virginia, USA. *Forest Science*, **50**, 551–565.
- Potter, C.S. (1999) Terrestrial biomass and the effects of deforestation on the global carbon cycle: Results from a model of primary production using satellite observations. *BioScience*, 49, 769–778.
- Pounden, E., Greene, D.F. & Michaletz, S.T. (2014) Non-serotinous woody plants behave as aerial seed bank species when a late-summer wildfire coincides with a mast year. *Ecology and Evolution*, **4**, 3830–3840.
- Power, K. & Gillis, M.D. (2006) Canada's Forest Inventory 2001, Victoria, British Columbia.
- Prentice, I.C. (1986) Vegetation responses to past climatic variation. Vegetatio, 67, 131-141.
- Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005) Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, **20**, 345–353.
- Purves, D.W., Lichstein, J.W. & Pacala, S.W. (2007) Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species. *PLoS ONE*, 2, e870.

- Purves, D.W., Lichstein, J.W., Strigul, N. & Pacala, S.W. (2008) Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences*, 105, 17018–17022.
- Quaife, T., Lewis, P., De Kauwe, M., Williams, M., Law, B.E., Disney, M. & Bowyer, P. (2008) Assimilating canopy reflectance data into an ecosystem model with an Ensemble Kalman Filter. *Remote Sensing of Environment*, **112**, 1347–1364.

R Core Team (2015) R: A Language and Environment for Statistical Computing.

Ramankutty, N. & Foley, J.A. (1999) Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles*, **13**, 997–1027.

Ray, S.F. (2002) Applied Photographic Optics, 3rd edn. Focal Press.

- Reed, W.J. & McKelvey, K.S. (2002) Power-law behaviour and parametric models for the sizedistribution of forest fires. *Ecological Modelling*, **150**, 239–254.
- Regelbrugge, J.C. & Conard, S.G. (1993) Modeling tree mortality following wildfire in Pinus ponderosa forests in the central Sierra Nevada of California. *International Journal of Wildland Fire*, **3**, 139–148.
- Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P. & Adair, E.C. (2012) Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. *Journal of Ecology*, **100**, 539–545.
- Renault, S., Zwiazek, J.J., Fung, M. & Tuttle, S. (2000) Germination, growth and gas exchange of selected boreal forest seedlings in soil containing oil sands tailings. *Environmental Pollution*, **107**, 357–365.
- Reuter, H.I., Nelson, A. & Jarvis, A. (2007) An evaluation of void-filling interpolation methods for SRTM data. *International Journal of Geographical Information Science*, **21**, 983–1008.

- Riaño, D., Valladares, F., Condés, S. & Chuvieco, E. (2004) Estimation of leaf area index and covered ground from airborne laser scanner (Lidar) in two contrasting forests. *Agricultural and Forest Meteorology*, **124**, 269–275.
- Rich, P.M. (1990) Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews*, **5**, 13–29.
- Rich, P.M., Dubayah, R., Hetrick, W.A. & Saving, S.C. (1994) Using viewshed models to calculate intercepted solar radiation: Applications in ecology. *American Society for Photogrammetry and Remote Sensing Technical Papers*, 524–529.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, **169**, 156–173.
- Richardson, J.J., Moskal, L.M. & Kim, S.-H. (2009) Modeling approaches to estimate effective leaf area index from aerial discrete-return LIDAR. *Agricultural and Forest Meteorology*, 149, 1152–1160.
- Rocca, M.E., Brown, P.M., MacDonald, L.H. & Carrico, C.M. (2014) Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. *Forest Ecology and Management*, **327**, 290–305.
- Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E.F., Lenton, T.M.,
 Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der
 Leeuw, S., Rodhe, H., Sorlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M.,
 Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson,
 K., Crutzen, P., Foley, J.A. & Revolution, I. (2009) A safe operating space for humanity. *Nature*, 461, 472–475.

Rogeau, M.-P. (2016) Fire regimes of southern Alberta, Canada.

- Rogers, B.M., Soja, A.J., Goulden, M.L. & Randerson, J.T. (2015) Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience*, 8, 228– 234.
- Rouyer, T., Fromentin, J.-M., Stenseth, N. & Cazelles, B. (2008) Analysing multiple time series and extending significance testing in wavelet analysis. *Marine Ecology Progress Series*, 359, 11–23.
- Rowe, J.S. (1961) Critique of some vegetational concepts as applied to forests of northwestern Alberta. *Canadian Journal of Botany*, **39**.
- Rowe, J.S. & Scotter, G.W. (1973) Fire in the boreal forest. Quaternary Research, 3, 444-464.

Ruban, A. V (2009) Plants in light. Communicative & Integrative Biology, 2, 50-55.

- Ruddiman, W.F. (2003) The anthropogenic greenhouse era began thousands of years ago. *Climate Change*, **61**, 261–293.
- Rudel, T.K., Coomes, O.T., Moran, E., Achard, F., Angelsen, A., Xu, J. & Lambin, E. (2005)
 Forest transitions: Towards a global understanding of land use change. *Global Environmental Change*, 15, 23–31.
- Ryu, Y., Nilson, T., Kobayashi, H., Sonnentag, O., Law, B.E. & Baldocchi, D.D. (2010) On the correct estimation of effective leaf area index: Does it reveal information on clumping effects? *Agricultural and Forest Meteorology*, **150**, 463–472.
- Sander, J.D. & Joung, J.K. (2014) CRISPR-Cas systems for editing, regulating and targeting genomes. *Nature Biotechnology*, **32**, 347–355.
- Santana, V.M. & Marrs, R.H. (2016) Models for predicting fire ignition probability in graminoids from boreo-temperate moorland ecosystems. *International Journal of Wildland*

Fire, **25**, 679–684.

- Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H. & Chapin, F.S. (2012) Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences*, **109**, 21384– 21389.
- Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist*, **198**, 957–969.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J. & Mladenoff, D.J. (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, 201, 409–419.
- Scheller, R.M. & Mladenoff, D.J. (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling*, **180**, 211–229.
- Schumacher, S., Bugmann, H. & Mladenoff, D.J. (2004) Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecological Modelling*, 180, 175–194.
- Schwalbe, E., Maas, H.-G., Kenter, M. & Wagner, S. (2009) Hemispheric image modeling and analysis techniques for solar radiation determination in forest ecosystems. *Photogrammetric Engineering & Remote Sensing*, **75**, 375–384.
- Schwilk, D.W. & Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos*, **94**, 326–336.
- Scott, A.J. & Knott, M. (1974) A cluster analysis method for grouping means in the analysis of variance. *Biometrics*, **30**, 507–512.

- Shean, D.E., Alexandrov, O., Moratto, Z.M., Smith, B.E., Joughin, I.R., Porter, C. & Morin, P. (2016) An automated, open-source pipeline for mass production of digital elevation models (DEMs) from very-high-resolution commercial stereo satellite imagery. *ISPRS Journal of Photogrammetry and Remote Sensing*, **116**, 101–117.
- Shearer, R.C. (1961) A method of overcoming seed dormancy in subalpine larch. *Journal of Forestry*, **59**, 513–514.
- Shepard, D. (1968) A two-dimensional interpolation function for irregularly-spaced data.
 Proceedings of the 1968 23rd ACM National Conference ACM 1968., pp. 517–524.
 Association for Computing Machinery, New York, NY, USA.
- Shugart, H.H. (1984) A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models, Springer-Verlag, New York.
- Shugart, H.H. & West, D.C. (1977) Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the Chestnut Blight. *Journal of Environmental Management*, 5, 161–179.
- Simons-Legaard, E., Legaard, K. & Weiskittel, A. (2015) Predicting aboveground biomass with LANDIS-II: a global and temporal analysis of parameter sensitivity. *Ecological Modelling*, 313, 325–332.
- Sirois, L. (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest - tree line transect. *Canadian Journal of Forest Research*, **30**, 900–909.
- Smith, E. (2011) *Ecological relationships between overstory and understory vegetation in Ponderosa pine forests of the southwest: report prepared for the Kaibab National Forest,*.
- Smith, S.J., Edmonds, J., Hartin, C.A., Mundra, A. & Calvin, K. (2015) Near-term acceleration in the rate of temperature change. *Nature Climate Change*, **5**, 333–336.

- Soil Classification Working Group (1998) *The Canadian System of Soil Classification*, 3rd edn. Canadian Science Publishing, Ottowa, ON, Canada.
- Soil Landscapes of Canada Working Group (2010) Soil landscapes of Canada version 3.2. *Canadian Soil Information System*.
- Solberg, S., Brunner, A., Hanssen, K.H., Lange, H., Næsset, E., Rautiainen, M. & Stenberg, P. (2009) Mapping LAI in a Norway spruce forest using airborne laser scanning. *Remote Sensing of Environment*, 113, 2317–2327.
- Sorenson, F.C. (1990) Stratification requirements for germination of western larch (Larix occidentalis Nutt.) seed, US Department of Agriculture, Forest Service, Portland, OR, USA.
- Stadt, K.J., Huston, C., Coates, D.K., Feng, Z., Dale, M.R.T. & Lieffers, V.J. (2007) Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Annals of Forest Science*, 64, 477–490.
- Stanek, W. (1961) Natural layering of black spruce in Northern Ontario. *The Forestry Chronical*, 37, 245–258.
- Statistics Canada (2011) Population, urban and rural, by province and territory (Alberta). 2011 Census.
- Steffen, W., Crutzen, P.J. & McNeill, J.R. (2007) The Anthropocene: Are humans now overwhelming the great forces of nature. *Ambio*, **36**, 614–621.
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Ruger, N., Alvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, A., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D.,

van Mantgem, P.J., Wang, X., Wiser, S.K. & Zavala, M.A. (2014) Rate of tree carbon accumulation increases continuously with tree size. *Nature*, **507**, 90–93.

- Stewart, J.D., Landhäusser, S.M., Stadt, K.J. & Lieffers, V.J. (2001) Predicting natural regeneration of white spruce in boreal mixedwood understories. *The Forestry Chronicle*, 77, 1006–1013.
- Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan,
 M.D., Hirsch, K.G., Logan, K.A., Martell, D.L. & Skinner, W.R. (2002) Large forest fires
 in Canada, 1959–1997. *Journal of Geophysical Research: Atmospheres*, **107**, 8149.
- Strauss, D., Bednar, L. & Mees, R. (1989) Do one percent of forest fires cause ninety-nine percent of the damage? *Forest Science*, **35**, 319–328.
- Strigul, N., Pristinski, D., Purves, D., Dushoff, J. & Pacala, S. (2008) Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecological Monographs*, 78, 523–545.
- Strobl, C., Boulesteix, A.-L., Zeileis, A. & Hothorn, T. (2007) Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinformatics*, **8**, 1–21.
- Strohmaier, E., Simon, H., Dongarra, J. & Martin Meuer (2017) TOP500 list refreshed, US edged out of third place. *TOP500*.
- Sturtevant, B.R., Gustafson, E.J., Li, W. & He, H.S. (2004) Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. **180**, 153–174.
- Sturtevant, B.R., Scheller, R.M., Miranda, B.R., Shinneman, D. & Syphard, A. (2009) Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. *Ecological Modelling*, **220**, 3380–3393.

Su, J., Hu, C., Yan, X., Jin, Y., Chen, Z., Guan, Q., Wang, Y., Zhong, D., Jansson, C., Wang, F.,

Schnurer, A. & Sun, C. (2015) Expression of barley SUSIBA2 transcription factor yields high-starch low-methane rice. *Nature*, **523**, 602–606.

- Šúri, M. & Hofierka, J. (2004) A new GIS-based solar radiation model and its application to photovoltaic assessments. *Transactions in GIS*, **8**, 175–190.
- Syphard, A.D., Yang, J., Franklin, J., He, H.S. & Keeley, J.E. (2007) Calibrating a forest landscape model to simulate frequent fire in Mediterranean-type shrublands. *Environmental Modelling & Software*, 22, 1641–1653.
- Tande, D. & Tande, G.F. (1979) Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany*, 57, 1912–1931.
- Terrier, A., Girardin, M.P., Périé, C., Legendre, P. & Bergeron, Y. (2012) Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. *Ecological Applications*, 23, 21–35.
- Thompson, P.L. & Gonzalez, A. (2017) Dispersal governs the reorganization of ecological networks under environmental change. **1**, 162.
- Thompson, R.S., Anderson, K.H. & Bartlein, P.J. (1999) Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America, US Geological Survey, Washington, DC, USA.
- Thorpe, H.C. & Daniels, L.D. (2012) Long-term trends in tree mortality rates in the Alberta foothills are driven by stand development. *Canadian Journal of Forest Research*, **1696**, 1687–1696.
- Tingley, M.P. & Huybers, P. (2013) Recent temperature extremes at high northern latitudes unprecedented in the past 600 years. *Nature*, **496**, 201–205.

Tinner, W., Bigler, C., Gedye, S., Gregory-Eaves, I., Jones, R.T., Kaltenrieder, P., Krähenbühl,

U. & Hu, F.S. (2008) A 700-year paleoecological record of boreal ecosystem responses to climatic variation from Alaska. *Ecology*, **89**, 729–743.

- Toews, M.W., Whitfield, P.H. & Allen, D.M. (2007) Seasonal statistics: the "seas" package for R. *Computers & Geosciences*, **33**, 1895.
- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L. & Mellmann-Brown, S. (2001)
 Delayed seed germination in whitebark pine and regeneration patterns following the
 Yellowstone fires. *Ecology*, 82, 2587–2600.
- Tooke, T.R., Coops, N.C., Christen, A., Gurtuna, O. & Prévot, A. (2012) Integrated irradiance modelling in the urban environment based on remotely sensed data. *Solar Energy*, 86, 2923–2934.
- Trenberth, K.E. (2011) Changes in precipitation with climate change. *Climate Research*, **47**, 123–138.
- Trenberth, K.E., Dai, A., Rasmussen, R.M. & Parsons, D.B. (2003) The changing character of precipitation. *Bulletin of the American Meteorological Society*, **84**, 1205–1217.
- Trenberth, K.E., Dai, A., van der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J. (2014) Global warming and changes in drought. *Nature Clim. Change*, 4, 17– 22.
- Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R. & Watts, A. (2015) Global vulnerability of peatlands to fire and carbon loss. *Nature Geosci*, 8, 11–14.
- Turetsky, M.R., Kane, E.S., Harden, J.W., Ottmar, R.D., Manies, K.L., Hoy, E. & Kasischke,
 E.S. (2011) Recent acceleration of biomass burning and carbon losses in Alaskan forests
 and peatlands. *Nature Geoscience*, 4, 27–31.
- Turner, R. (2015) deldir: Delaunay triangulation and Dirichlet (Voronoi) tessellation.

- Tymstra, C., Bryce, R.W., Wotton, B.M., Taylor, S.W., Armitage, O.B. & Service, C.F. (2010) Development and structure of Prometheus: the Canadian wildland fire growth simulation model, Edmonton, AB, Canada.
- Tymstra, C., Flannigan, M.D., Armitage, O.B. & Logan, K. (2007) Impact of climate change on area burned in Alberta's boreal forest. *International Journal of Wildland Fire*, **16**, 153–160.
- Ullman, S. (1979) The interpretation of structure from motion. *Proceedings of the Royal Society of London B: Biological Sciences*, **203**, 405–426.
- Unckless, R.L., Clark, A.G. & Messer, P.W. (2017) Evolution of resistance against CRISPR/Cas9 gene drive. *Genetics*, **205**, 827 LP-841.
- United States Forest Service (2013) Species: Populus tremuloides. *Fire Effects Information System*.
- Urban, D.L. (1990) A versatile model to simulate forest pattern: a user's guide to ZELIG version1.0, Department of Environmental Sciences, University of Virginia, Charlottesville, VA,USA.
- Urban, M.C., Tewksbury, J.J., Sheldon, K.S. & Soc, P.R. (2011) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B*, **2367**.
- Urbieta, I.R., García, L. V, Zavala, M.A. & Marañón, T. (2011) Mediterranean pine and oak distribution in southern Spain: is there a mismatch between regeneration and adult distribution? *Journal of Vegetation Science*, **22**, 18–31.
- US Department of Defense (2002) Department of Defense press briefing by Secretary of Defense Donald Rumsfeld and General Richard Myers.

Uyeda, K.A., Stow, D.A., Roberts, D.A. & Riggan, P.J. (2017) Combining ground-based
measurements and MODIS-based spectral vegetation indices to track biomass accumulation in post-fire chaparral. *International Journal of Remote Sensing*, **38**, 728–741.

- Vaccari, S., van Leeuwen, M., Calders, K., Coops, N.C. & Herold, M. (2013) Bias in lidar-based canopy gap fraction estimates. *Remote Sensing Letters*, 4, 391–399.
- Varhola, A., Frazer, G.W., Teti, P. & Coops, N.C. (2012) Estimation of forest structure metrics relevant to hydrologic modelling using coordinate transformation of airborne laser scanning data. *Hydrology and Earth Systems Science*, 16, 3749–3766.
- Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L. & Retana, J. (2013) Patterns of forest decline and tegeneration across Scots pine populations. *Ecosystems*, 16, 323–335.
- Viña, A., McConnell, W.J., Yang, H., Xu, Z. & Liu, J. (2016) Effects of conservation policy on China's forest recovery. *Science Advances*, 2, e1500965.
- Vitasse, Y., Hoch, G., Randin, C., Lenz, A., Kollas, C., Scheepens, J.F. & Körner, C. (2013) Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia*, **171**, 663–678.
- Wagner, C.E. Van (1978) Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research*, **8**, 220–227.
- Wagner, C.E. Van (1977) Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research*, **7**, 23–34.
- Van Wagner, C.E. (1987) Development and structure of the Canadian Forest Fire Weather Index System, Natural Resources Canada, Ottowa, Ontario.
- Van Wagner, C.E. (1989) Prediction of crown fire in conifer stands. Proceedings of the 10th Conference on Fire and Forest Meteorology (ed. by D.C. MacIver), H. Auld), and R.
 Whitewood), pp. 207–212. Forestry Canada, Ottowa, ON, Canada.

- Van Wagner, C.E. (1967) Seasonal variation in moisture content of eastern Canadian tree foliage and the possible effect on crown fires, Government of Canada, Department of Forestry and Rural Development, Chalk River, Ontario, Canada.
- Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K. & Poschlod, P. (2011) Climate change and plant regeneration from seed. *Global Change Biology*, **17**, 2145–2161.
- Wallach, H. & O'Connell, D.N. (1953) The kinetic depth effect. *Journal of Experimental Psychology*, 45, 205–217.
- Wang, S., Huang, J., He, Y. & Guan, Y. (2014a) Combined effects of the Pacific Decadal Oscillation and El Niño-Southern Oscillation on global land dry–wet changes. *Scientific Reports*, 4, 6651.
- Wang, T., Hamann, A., Spittlehouse, D.L. & Murdock, T.Q. (2011a) ClimateWNA: Highresolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology*, **51**, 16–29.
- Wang, W.J., He, H.S., Fraser, J.S., Thompson, F.R., Shifley, S.R. & Spetich, M.A. (2014b) LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. *Ecography*, **37**, 225–229.
- Wang, W.J., He, H.S., Spetich, M.A., Shifley, S.R., Thompson, F.R., Larsen, D.R., Fraser, J.S. & Yang, J. (2013) A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. *Ecosphere*, 4, 1–22.
- Wang, X., Cantin, A., Parisien, M.-A., Wotton, M., Anderson, K. & Flannigan, M. (2014c)fwi.fbp: Fire Weather Index System and Fire Behaviour Prediction System calculations.
- Wang, X., Piao, S., Ciais, P., Li, J., Friedlingstein, P., Koven, C. & Chen, A. (2011b) Spring temperature change and its implication in the change of vegetation growth in North

America from 1982 to 2006. *Proceedings of the National Academy of Sciences*, **108**, 1240–1245.

- Wang, Y., Hyyppä, J., Liang, X., Kaartinen, H., Yu, X., Lindberg, E., Holmgren, J., Qin, Y., Mallet, C., Ferraz, A., Torabzadeh, H., Morsdorf, F., Zhu, L., Liu, J. & Alho, P. (2016)
 International benchmarking of the individual tree detection methods for modeling 3-D canopy structure for silviculture and forest ecology using airborne laser scanning. *IEEE Transactions on Geoscience and Remote Sensing*, 54, 5011–5027.
- Ward, B.C., Scheller, R.M. & Mladenoff, D.J. (2004) Technical Report: LANDIS-II Double Exponential Seed Dispersal Algorithm, Dept. Forest Ecology and Management, University of Wisconsin-Madison, Madison, WI, USA.
- Warren, J., Schaefer, S., Hirani, A.N. & Desbrun, M. (2006) Barycentric coordinates for convex sets. Advances in Computational Mathematics, 27, 319–338.
- Wehr, A. & Lohr, U. (1999) Airborne laser scanning: an introduction and overview. *ISPRS Journal of Photogrammetry and Remote Sensing*, 54, 68–82.
- Weiss, M., Baret, F., Smith, G.J., Jonckheere, I. & Coppin, P. (2004) Review of methods for in situ leaf area index (LAI) determination: Part II. Estimation of LAI, errors and sampling. *Agricultural and Forest Meteorology*, **121**, 37–53.
- Weng, E.S., Malyshev, S., Lichstein, J.W., Farrior, C.E., Dybzinski, R., Zhang, T., Shevliakova,
 E. & Pacala, S.W. (2015) Scaling from individual trees to forests in an Earth system
 modeling framework using a mathematically tractable model of height-structured
 competition. *Biogeosciences*, 12, 2655–2694.
- Wentz, F.J., Ricciardulli, L., Hilburn, K. & Mears, C. (2007) How much more rain will global warming bring? *Science*, **317**, 233–235.

- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, **313**, 940 LP-943.
- Whitman, E., Batllori, E., Parisien, M.-A., Miller, C., Coop, J.D., Krawchuk, M.A., Chong, G.W.
 & Haire, S.L. (2015) The climate space of fire regimes in north-western North America. *Journal of Biogeography*, 42, 1736–1749.
- Whittier, T.R. & Gray, A.N. (2016) Tree mortality based fire severity classification for forest inventories: a Pacific Northwest national forests example. *Forest Ecology and Management*, 359, 199–209.
- Widrow, B. & Hoff, M. (1960) Adaptive switching circuits, Stanford University, Stanford Electronics Laboratory, Stanford, California.
- Wing, B.M., Ritchie, M.W., Boston, K., Cohen, W.B., Gitelman, A. & Olsen, M.J. (2012)
 Prediction of understory vegetation cover with airborne lidar in an interior ponderosa pine forest. *Remote Sensing of Environment*, **124**, 730–741.
- Wolken, J.M., Landhäusser, S.M., Lieffers, V.J. & Dyck, M.F. (2010) Differences in initial root development and soil conditions affect establishment of trembling aspen and balsam poplar seedlings. *Botany*, 88, 275–285.
- Woodall, C.W., Zhu, K., Westfall, J.A., Oswalt, C.M., D'Amato, A.W., Walters, B.F. & Lintz,
 H.E. (2013) Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *Forest Ecology and Management*, **291**, 172–180.
- Woodard, P.M. (1983) Germination success of Pinus contorta Dougl. and Picea Engelmannii Parry on burned seedbeds. *Forest Ecology and Management*, **5**, 301–306.
- Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J. a & Langor, D. (2004) Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the

Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, **34**, 417–430.

World Resources Institute (2014) Global Forest Watch. Forest Change Statistics.

- Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M. & Gray,
 L.K. (2013) Recent declines of Populus tremuloides in North America linked to climate. *Forest Ecology and Management*, 299, 35–51.
- Wotton, B.M., Alexander, M.E. & Taylor, S.W. (2009) Updates and Revisions to the 1992
 Canadian Forest Fire Behavior Prediction System, Natural Resources Canada, Sault Ste.
 Marie, ON, Canada.
- Wotton, B.M. & Flannigan, M.D. (1993) Length of the fire season in a changing climate. *The Forestry Chronicle*, **69**, 187–192.
- Wright, H.A. & Bailey, A.W. (1982) Fire Ecology: United States and Southern Canada, 1st edn. Wiley, New York.
- Wulder, M.A., Cranny, M., Hall, R.J., Luther, J., Beaudoin, A., White, J.C., Goodenough, D.G.
 & Dechka, J. (2007) Satellite land cover mapping of Canada's forests: the EOSD Land
 Cover Project. North American Land Cover Summit, pp. 21–30. Natural Resources Canada,
 Washington DC, USA.
- Wulder, M.A., White, J.C., Loveland, T.R., Woodcock, C.E., Belward, A.S., Cohen, W.B., Fosnight, E.A., Shaw, J., Masek, J.G. & Roy, D.P. (2016) The global Landsat archive: status, consolidation, and direction. *Remote Sensing of Environment*, **185**, 271–283.
- Xie, S.-P., Noguchi, H. & Matsumura, S. (1999) A hemispheric-scale quasi-decadal oscillation and its signature in northern Japan. *Journal of the Meteorological Society of Japan. Ser. II*, 77, 573–582.

- Xu, C., Gertner, G.Z. & Scheller, R.M. (2009) Uncertainties in the response of a forest landscape to global climatic change. *Global Change Biology*, **15**, 116–131.
- Xu, C., Güneralp, B., Gertner, G. & Scheller, R. (2010) Elasticity and loop analyses: tools for understanding forest landscape response to climatic change in spatial dynamic models. *Landscape Ecology*, 25, 855–871.
- Xu, X., Medvigy, D., Powers, J.S., Becknell, J.M. & Guan, K. (2016) Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist*, n/a--n/a.
- Yang, J., He, H.S. & Gustafson, E.J. (2004) A hierarchical fire frequency model to simulate temporal patterns of fire regimes in LANDIS. *Ecological Modelling*, **180**, 119–133.
- Yang, Y., Titus, S.J. & Huang, S. (2003) Modeling individual tree mortality for white spruce in Alberta. *Ecological Modelling*, 163, 209–222.
- Yao, W., Krull, J., Krzystek, P. & Heurich, M. (2014) Sensitivity analysis of 3D individual tree detection from LiDAR point clouds of temperate forests. *Forests*, 5, 1122–1142.
- Zhang, J., Huang, S. & He, F. (2015) Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, **112**, 4009–4014.
- Zhao, K. & Popescu, S. (2007) *Hierarchical watershed segmentation of canopy height model for multi-scale forest inventory. ISPRS Workshop on Laser Scanning 2007 and SilviLaser 2007*, pp. 436–442. International Society of Photogrammetry and Remote Sensing, Espoo, Finland.
- Zhao, K. & Popescu, S. (2009) Lidar-based mapping of leaf area index and its use for validating GLOBCARBON satellite LAI product in a temperate forest of the southern USA. *Remote*

Sensing of Environment, 113, 1628–1645.

- Zhao, R., Ali, H. & van der Smagt, P. (2017) Two-stream RNN/CNN for action recognition in 3D videos. *ArXiv e-prints*.
- Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.
- Zhu, K., Woodall, C.W., Ghosh, S., Gelfand, A.E. & Clark, J.S. (2014) Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology*, 20, 251–264.
- Zimble, D.A., Evans, D.L., Carlson, G.C., Parker, R.C., Grado, S.C. & Gerard, P.D. (2003) Characterizing vertical forest structure using small-footprint airborne LiDAR. *Remote Sensing of Environment*, 87, 171–182.

Appendix A: Statistical Analysis of Historical Fire Regimes

Applying the Shapiro-Wilks test, log-transformed fire sizes showed strong normality both nationwide (W = 0.99 p-value > 2.2e-16) and in the Alberta study area (W = 0.97, p-value > 2.2e-16), enabling the application of *t*-test and *F*-test statistics. Based on an analysis of individual fire size mean and variance in the study area, using a significance cutoff of p < 0.05, the full 90-year period showed a significant change in variance only (t = 1.918, p-value = 0.056; F = 24.529, p-value > 2.2e-16). While individual fire sizes between the Pre-Suppression and Early Suppression periods showed a significant difference in variance (F = 20.549, p-value < 2.2e-16), differences in the means between these two periods were not statistically significant (t = 1.336, p-value = 0.182). The distribution of log-transformed fire sizes nationwide showed good fit with Weibull and Gaussian distributions (Figure A.1).



Figure A.1 Model fit for log-transformed fire sizes Canada-wide: (a) histogram and theoretical PDFs; (b) empirical and theoretical CDFs; (c) Q-Q plot; (d) P-P plot

The robustness of Weibull model fit for log-transformed fire sizes nationwide is confirmed by the application of five Anderson-Darling maximum goodness-of-fit parameter estimation methods using the *fitdistrplus* package for R (Delignette-Muller & Dutang, 2015). The right-tail second-order Anderson-Darling (AD2R) statistic (Luceño, 2006) shows the best parameter estimations, as it better mitigates truncation at larger fire sizes (Figure A.2).



Figure A.2 Anderson-Darling goodness-of-fit Weibull model parameter estimation for log-transformed fire sizes Canada-wide: (a) histogram and theoretical PDFs; (b) empirical and theoretical CDFs; (c) Q-Q plot; (d) P-P plot; ADR = right-tail Anderson-Darling; ADL = left-tail Anderson-Darling; AD2R = right-tail Anderson-Darling second order; AD2L = left-tail Anderson-Darling second order; AD2 = Anderson-Darling second order

The distribution of fire sizes in Alberta showed significant bimodality. Using a mixed Gaussian model for Alberta study area fire size, the two modes centered on μ of 1.2 and 6.2 log ha, with Expectation-Maximization (EM) and Bayesian Markov Chain Monte Carlo (MCMC) algorithms each converging to these values (Figure A.3).



Figure A.3 Mixed Gaussian model probability density function showing strong bimodality of the logtransformed fire size distribution for the Alberta study area

The fire size distribution for Alberta showed significant bimodality. A further analysis reveals distinct changes in the fire size distribution over time (Figure A.4).



Figure A.4 Fire size distribution (log of ha): (a) 1923-2012; (b) 1923-1952; (c) 1953-1982; (d) 1983-2012

Appendix B: ALS Models of ACC and VCC

The P_{hv} lens geometries tested showed comparable performance, with the exception of the equiangular projection, which performed poorly in predicting P_o . Higher canopy height thresholds showed superior performance for all lens geometries (Figure B.1).



 P_{hv} Metric by Hemispherical Lens Model and Canopy Height Threshold (m)

Figure B.1 Pearson's correlation coefficient (r) for convex spherical densiometer measurements and the ALS hemispherical Voronoi gap fraction (P_{hv}) metric for different canopy height thresholds; Stereo = stereographic projection; Ortho = orthographic projection; Equidist = equidistant projection; Equiangle = equiangular projection; numerical values = height thresholds used to calculate minimum canopy height

Pearson correlations with ground ACC measurements showed good performance for a number of methods. Of the P_o metrics tested, P_{pdn} showed the best overall performance (Figure B.2).



Figure B.2 Pearson's correlation coefficient (r) for convex spherical densiometer ground measurements and ALS metrics; ACC values are omitted, as they are the inverse of P_o

Meanwhile, univariate linear regression models that changed the slope and intercept relationships showed markedly better performance of predicting ACC for the VCC metrics, VCC_{fci} , VCC_{fr} , and VCC_{ir} (Figure B.3). In these tests, the performance of P_{pdn} fell behind.



Figure B.3 Linear regression model fit for the top three univariate models after filtering out observations with likely disturbances: (a) VCC_{fci} ; (b) VCC_{fr} ; (c) VCC_{ir} ; the blue line represents the slope and intercept of the univariate regression model, with VCC_{fr} approaching the 1:1 line

Linear, first-order, and second-order polynomial models were fit between ground ACC and VCC_{fci} for plots with and without observations flagged for quality issues (Figure B.4).



Figure B.4 *VCC_{fci}* model fit for all 950 ground ACC measurement plots; blue = linear; red = second-order polynomial; green = exponential; left = with disturbed sites; right = without disturbed sites

Using on the filtered observations, the same three models were applied to P_{pdn} for the estimation of ACC. As the scatter plot shows, the relationship between ACC and P_{pdn} was more linear than the VCC metrics, while the bias was also greater. The variance was greater for higher P_{pdn} values, corresponding to lower ACC values (Figure B.5).



Figure B.5 Models of P_{pdn} and ground ACC measurements; blue = linear; red = second-order polynomial; green = exponential

An experimental method for individual tree segmentation with ALS data based on threedimensional α -shapes was also tested, based on a simple parametric variant of the convex hull. A visualization of one LiDAR test plot is provided (Figure B.6). While the first results appear promising, the method requires further research with validation data, which were unavailable for this study.



Figure B.6 Individual tree segmentation with low-point-density ALS data using three-dimensional α -shapes; object class membership is signified by color; the ground plane is visible in chartreuse

Appendix C: Random Forest Algorithm

Random Forest builds on the bagging procedure, or bootstrap aggregation, the averaging of many noisy unbiased models to reduce variance, by building a large collection or forest of decorrelated regression trees before performing averaging. Trees are ideal for bagging procedures, as they can capture complex interactions, have low bias, and high noise (Hastie *et al.*, 2009). The bias of bagged trees is identical to that of individual trees, making variance the focus of improvement. Random Forest was designed to improve upon the variance reduction of bagging by minimizing the correlation between trees without substantially increasing the variance. This is achieved by randomly selecting input variables during the tree-growing process. The Random Forest algorithm process functions as described below, adopted from Hastie *et al.* (2009): Algorithm: Random Forest Algorithm for Regression or Classification

- 1. For b = 1 to B:
 - a. Draw a bootstrap sample Z^* of size N from the training data
 - b. Grow a random-forest tree T_b to the bootstrapped data, by recursively repeating the following steps for each terminal node of the tree, until the minimum node size n_{min} is reached
 - i. Select *m* variables at random from the *p* variables
 - ii. Pick the best variable/split-point among the m
 - iii. Split the node into two daughter nodes
- 2. Output the ensemble of trees $\{T_b\}_1^B$

Following model training, to make a prediction at a new point *x*:

<u>Regression</u>: $\hat{f}_{rf}^B(x) = \frac{1}{B} \sum_{b=1}^{B} T_b(x)$

<u>Classification</u>: Let $\hat{C}_b(x)$ be the class prediction of the *b*th Random Forest tree. Then,

$$\hat{C}_{rf}^{B}(x) = majority \ vote \left\{ \hat{C}_{b}(x) \right\}_{1}^{B}$$

Here, I focused on the regression case. In short, the Random Forest algorithm creates *ntrees* decision trees from randomly selected variables with *mtry* splits at each node. Each of these trees is a weak predictor, combined through averaging to produce predictions.

Appendix D: ABMI Landcover 2010 Classification Scheme and Algorithm

The following section describes the lookup table and algorithm used for classifying simulation outputs into landcover classes (Table D.1) at an annual simulation time-step.

Value	Landcover Class				
0	None				
20	Water				
31	Snow/Ice				
32	Rock/Rubble				
33	Exposed Land				
34	Developed				
50	Shrubland				
110	Grassland				
120	Agriculture				
210	Evergreen (Coniferous) Forest				
220	Broadleaf Forest				
230	Mixed Forest				

-1 at 10 17 1 7 13 10 11 1 at 1000 100 20 10 0 1000 100 100 100 100 100	Table D 1	ABMII	andcover	2010	classifi	cation	scheme
---------------------------------------------------------------------------------------------------------------	-----------	-------	----------	------	----------	--------	--------

The pixel classification algorithm used to classify LANDIS-II species-age map outputs is described in detail below:

Algorithm: Classification of LANDIS-II species-age cohorts into ABMI landcover classes

- 1. For each LANDIS-II simulation scenario:
 - a. For each simulation year:
 - i. For each species-age map:
 - 1. Assign pixels to either evergreen or broadleaf classes
 - ii. Count the number of species present for each class
 - iii. Calculate richness as the sum of species present per class
 - iv. Calculate percent evergreen/broadleaf by dividing by species richness
 - v. Classify pixels inactive in LANDIS-II simulations to remove pixels masked in the simulations:
 - 1. Use ABMI Landcover 2010 map to assign values for classes 0-120
 - vi. Classify pixels active in LANDIS-II simulations, overwriting previous classification values for sites that fail to regenerate post-disturbance:
 - 1. Assign pixels to Evergreen Forest (210) where greater than 75%
 - 2. Assign pixels to Broadleaf Forest (220) where greater than 75%
 - Assign pixels to Mixed Forest (230) where both percent evergreen and broadleaf are greater than or equal to 25%
 - 4. Assign pixels to Grassland (110) where both percent evergreen and broadleaf are equal to zero
 - b. Save the raster time-series of landcover change for use in regression models of P_o

Appendix E: Bare-earth Global Solar Irradiation Algorithm

Based on previous work (Rich, 1990; Rich *et al.*, 1994; Fu & Rich, 2002), parallel to GRASS *r.sun* algorithm development (Šúri & Hofierka, 2004), global solar radiation was calculated in the following steps:

- 1. Calculate the 3-D hemispherical viewshed for a DEM cell to 2-D polar chart
- 2. Calculate half-hourly sun position polar chart based on solar zenith (θ) and azimuth (ϑ)
- 3. Calculate half-hourly direct solar radiation for sectors in a 2-D polar chart
- 4. Calculate half-hourly diffuse solar radiation for sectors in a 2-D polar chart
- 5. Calculate total direct solar radiation by masking sky sectors of (3) with pixels of (1)
- 6. Calculate total diffuse solar radiation by masking sky sectors of (4) with pixels of (1)
- 7. Calculate global solar radiation for the cell as the sum of (5) and (6)

Each 2-D polar chart shares the same projection, facilitating simple matrix computations. The computation of the hemispherical viewshed from the perspective of the ground looking toward the zenith is similar to hemispherical photography, convex spherical densiometers, and hemispherical LiDAR approaches of estimating light occlusion, making the solar model compatible with the proposed modeling framework.

The hemisphere calculations used were originally developed for hemispherical photography vegetation studies (Rich, 1990; Fu & Rich, 1999). In the viewshed calculation, twelve equal azimuth angles are searched from the pixel center for computation of the maximum horizon

angle (unobstructed zenith). The horizon angles are then converted into a hemispherical coordinate system as zenith (θ) and azimuth (ϑ) angle sectors of a polar plot. Each cell within the hemisphere sectors takes one of two binary values, visible or occluded.

The half-hourly sun position is calculated using standard equations (Iqbal, 1983), used for calculating direct and diffuse radiation components. The calculation of direct, diffuse, and global radiation for a given sun position follows previous work (Rich, 1990; Rich *et al.*, 1994; Fu & Rich, 2002). Global solar irradiation (I_{global}) is the sum of direct I_{direct} and diffuse $I_{diffuse}$ components, ignoring reflected irradiation:

$$I_{global} = I_{direct} + I_{diffuse}$$

Direct solar irradiation I_{direct} is computed as the sum of irradiation for each sector defined by zenith (θ) and azimuth (ϑ) angles for each hour and month:

$$I_{direct} = \sum I_{direct_{\theta,\vartheta}}$$

The direct solar irradiation for a given zenith and azimuth angle sector is calculated as the solar constant for the mean earth-sun distance (S_{const}), equal to 1367 W m⁻², multiplied by the atmospheric transmissivity for the shortest path raised to the relative optical path length ($\beta^{m_{\theta}}$), the sky sector sun duration ($t_{\theta,\theta}$), equal to monthly and half-hourly intervals or spherical

geometry, the gap fraction for the sun map sector $(P_{\theta,\vartheta})$, and the cosine of the angle of incidence between the sky sector centroid and the surface normal $(\gamma_{\theta,\vartheta})$:

$$I_{direct_{\theta,\vartheta}} = S_{const} * \beta^{m_{\theta}} * t_{\theta,\vartheta} * P_{\theta,\vartheta} * \cos \gamma_{\theta,\vartheta}$$

Relative optical path (m_{θ}) is calculated based on the cell elevation in meters (z) and solar zenith angle (θ) :

$$m_{\theta} = \exp(-0.000118 * z - 1.638 * 10^{-9} * z^{2}) / \cos\theta$$

The angle of incidence $(\gamma_{\theta\vartheta})$ is calculated based on the solar zenith angle (θ) , surface zenith angle (G_z) , and surface azimuth angle (G_a) :

$$\gamma_{\theta\vartheta} = \cos^{-1}\theta * \cos G_z + \sin \theta * \sin G_z * \cos(\vartheta - G_a)$$

Diffuse solar irradiation $I_{diffuse}$ is computed as the sum of irradiation for each sector defined by 8 zenith (θ) and 16 azimuth (ϑ) angle divisions:

$$I_{diffuse} = \sum I_{diffuse_{\theta,\vartheta}}$$

Unlike direct irradiation, $I_{diffuse_{\theta,\vartheta}}$ sectors are calculated as the rolling sum of half-hourly values for a given time interval, due to the multi-directional nature of diffuse radiation, with each

sector predefined rather than based on modeled solar position. The diffuse solar irradiation for a given zenith and azimuth angle sector is calculated as the global normal radiation (R_{glb}) multiplied by the proportion of diffused global radiation flux ($p_{diffuse}$), time interval (t), sky sector gap fraction ($P_{\theta,\vartheta}$), weighted proportion of diffuse radiation originating from a sector ($w_{\theta,\vartheta}$), and cosine of the angle of incidence ($\gamma_{\theta,\vartheta}$):

$$I_{diffuse_{\theta,\vartheta}} = R_{glb} * p_{diffuse} * t * P_{\theta,\vartheta} * w_{\theta,\vartheta} * \cos \gamma_{\theta,\vartheta}$$

Global normal radiation (R_{glb}) is calculated as the solar constant (S_{const}) multiplied by the sum of the atmospheric transmissivity for the shortest path raised to the relative optical path length $(\beta^{m_{\theta}})$, divided by one minus the proportion of diffused global radiation flux $(p_{diffuse})$ to correct for direct radiation:

$$R_{glb} = \left(S_{const} \sum \beta^{m_{\theta}}\right) / \left(1 - p_{diffuse}\right)$$

The weighted proportion of diffuse radiation originating from a sector $(w_{\theta,\vartheta})$ is calculated as the zenith angle range for a sky sector $(\cos \theta_2 - \cos \theta_1)$ divided by the number of azimuth divisions in the sky map (N_{ϑ}) :

$$w_{\theta,\vartheta} = (\cos\theta_2 - \cos\theta_1) / N_{\vartheta}$$

Each of these calculations was performed automatically for each cell in the DEM using ArcGIS solar analyst tools (Fu & Rich, 1999).

Appendix F: Validation of TACA-GEM with Permanent Sample Plot Data

To validate TACA-GEM regeneration model results, I conducted an analysis of Alberta Permanent Sample Plot (PSP) data. This analysis focuses on stand regeneration dynamics and indicators of competitive resource constraints to regeneration (Alberta Sustainable Resource Development, 2005a). Previous versions of these data were used in studies related to stand growth, mortality, and regeneration in the region (Navratil *et al.*, 1991; Stewart *et al.*, 2001; Yang *et al.*, 2003; Stadt *et al.*, 2007). These studies indicate that competition, measured through proxies of stand development and tree growth (e.g., basal area and tree height), plays a key role in inhibiting regeneration success through diminished resource availability. While the TACA-GEM modeling work in Chapter 4 focused on abiotic resource constraints to regeneration (i.e., climate), model fusion with LANDIS-II in Chapter 5 provided competition through logical rules (e.g., an inverse equivalence of understory light levels and the shade tolerance of tree species present in sites). The purpose of this section is to relate TACA-GEM modeling results to empirical observations for the Alberta study area. I infer regeneration changes attributable to abiotic conditions inversely by modeling the effects of competition.

In this analysis, I rely on Permanent Sample Plot (PSP) and Stand Dynamics System (SDS) data from Alberta Sustainable Resource Department (Alberta Sustainable Resource Development, 2005a,b). While the former is intended to provide information on stand growth and yield, and also contains data on mortality and regeneration over time, the latter is designed to monitor postharvest regeneration dynamics for stands up to age 20 (Alberta Sustainable Resource Development, 2005b). The SDS observations begin in 1984, immediately following stand-

290

replacing harvest. While PSP observations date back to 1960, the regeneration component changed to the present format in 1983. The PSP and SDS datasets are complementary in their focus on overstory and understory dynamics, respectively. Both datasets contain measures of regeneration abundance by height class and proxies for competition, including tree height and diameter-at-breast-height (DBH). Both datasets are limited in temporal scale relative to stand development, making long-term analyses difficult, while lacking information on climate, soils, and solar radiation.

With these limitations in mind, I conduct a two-part analysis of tree regeneration in the Alberta study area. I focus on the Global Change Era (1983-2012) for its overlap with PSP and SDS regeneration data for this period, high sampling coverage ($n_{PSP} = 659,607$; $n_{SDS} = 406,117$), and relevance to TACA-GEM model results. While a naïve view of empirical regeneration data shows diminished regeneration rates over time for both datasets, statistical models, previous research (Navratil *et al.*, 1991; Stewart *et al.*, 2001; Yang *et al.*, 2003; Stadt *et al.*, 2007), and forest dynamics theory (Shugart, 1984) suggest that a significant amount of this variation is explained by stand development.

The SDS data show reduced regeneration rates over the period unexplained by sampling frequency bias (Figures F.1a and F.1b). From 1984 to 2013, the rate of regeneration in SDS data declined by 99.9%. A large magnitude effect is expected given the negative relationship between stand development and post-harvest regeneration produced by resource limitations related to competition (Shugart, 1984). Dividing the regeneration rate by the number of observations for

291

each year, a pattern of asymptotic exponential decay is shown for germination frequency under post-harvest stand development (Figure F.1c).



Figure F.1 Changes in regeneration and observation frequency over time in the SDS plot data: (a) germination frequency by year; (b) observation frequency by year; (c) germination frequency divided by observation frequency by year

The reduction in regeneration rates for SDS plots corresponds to changes in stand ageing and height growth (Figures F.2a and F.2b). Linear models show that overstory and understory competition explain 22% and 23% of regeneration variation, respectively, for the SDS data. This suggests that up to \sim 50% of the decline in regeneration may be attributable to abiotic conditions (i.e., climate, soils, and solar radiation). Future studies should directly test this assumption with climate and soils data, which is beyond the scope of this exercise.



Figure F.2 Box plots of (a) mean tree age and (b) tree height for all age classes as proxies of competition for SDS plots; observations begin following stand-replacing harvest

In the PSP data, saplings are binned into five regeneration height classes, ranging from 0.10 m to 1.29 m in height (Alberta Sustainable Resource Development, 2005a). I focus on changes to the smallest height class as indicative of annual germination and regeneration success, using only plots without any treatment applied. The data show a 39% decline in regeneration frequency from 1960 to 2009 and a 6% decline from 1983 to 2009 (Figure F.3a). Temporal autocorrelation suggests periodicity in regeneration change at approximately years four and nine (Figure F.3b),

which may correspond to a combination of the Pacific quasi-decadal oscillation, Pacific Decadal Oscillation, and El Niño-Southern Oscillation (Xie *et al.*, 1999; Wang *et al.*, 2014a). The PSP data indicate that understory competition most reduced regeneration rates; changes to regeneration for the smallest height class (the youngest saplings) were inversely proportional to combined changes for all other classes. The phase of regeneration frequency for both groups showed good agreement (Figure F.3c) after removing sampling bias, which suggests a climatic and/or overstory canopy origin of the phasing.



Figure F.3 Regeneration changes in the PSP data by year: (a) changes to height class 1; (b) autocorrelation of regeneration changes to height class 1; (c) relation of changes to height class 1 to other classes; red = height class 1; blue = sum of all other height classes

The effects of competition were also apparent in the PSP data. Based on few available samples (n = 46), understory angular canopy closure (ACC) showed an exponential increase over time, while overstory ACC appeared affected by a single large disturbance in ~ 1968 (Figures F.4a and

F.4b). Changes in average age for all 915 PSP plots and all age groups (n = 6,584) shows clear stand ageing over the period (Figure F.4c). This finding is in agreement with a recent study of the region showing an ageing signal (Zhang *et al.*, 2015).

However, mean tree height (n = 283,878) is shown to have declined across the period (Figure F.4d). As tree age and height are known to scale well in Alberta (Cieszewski & Bella, 1989), this discrepancy may be due to differences in sampling coverage. As tree height contains over 43 times as many observations as tree age, tree height is considered a more robust indicator of stand development for the region. Mean tree height significantly declined between 1960 and 2009 (p < 0.001), and, between 1983 and 2009 (p < 0.001). This suggests a similar pattern for mean tree age, challenging the recent study of Zhang *et al.* (2015) for the region. An alternative explanation is that this change in mean tree height is a statistical property whereby stand development results in few tall trees and many small trees, reducing the central tendency of tree height.



Figure F.4 Plots for (a) understory and (b) overstory angular canopy closure (ACC) class, (c) mean site tree age, and (d) mean tree height by year for PSP data; few observations of ACC were available

Counterintuitively, competition indicators explained more regeneration variation in PSP than SDS data. Linear models for the PSP data indicate that 75% and 39% of variance in regeneration for the lowest height class is explained by overstory and understory competition, respectively. For the sum of all regeneration height classes in the PSP data, overstory competition (tree height and DBH) explained only 7% of the variance in regeneration rates. Leave-one-out and univariate linear regression models show that changes to total regeneration were strongly correlated with changes to height classes 2 and 3 (Table F.1). The contribution of height class 1 to total regeneration was low, yet critical in that it represents regeneration at a basal level. This low contribution is likely due to low survival rates, as sapling mortality rates have been shown to decline with age (Jones & Sharitz, 1998).

Height Class	Leave-one-out R ²	Univariate R ²
Class 1	0.0005	0.012
Class 2	0.0038	0.989
Class 3	0.0014	0.988
Class 4	0.0001	0.981
Class 5	0.0003	0.621

Table F.1 Linear models of total understory regeneration change by individual height classes

Correlations with total regeneration were stronger for taller height classes (Figure F.5). Only height class 1 was negatively correlated with the year, indicative of diminished long-term regeneration rates. Changes to the lowest regeneration height class were positively correlated with changes to the tallest regeneration height class (r = 0.41), suggesting vertical partitioning of the understory canopy or the development of small gaps.

year	-0.35	0.65	0.71	0.71	0.56	0.67	0.8
	ht1	0.12	0.02	0.02	0.41	0.11	-0.6
		ht2	0.98	0.98	0.76	0.99	-0.4
			ht3	1	0.75	0.99	- 0
				ht4	0.77	0.99	-0.2
					ht5	0.79	-0.4
						net	-0.8

Figure F.5 Correlations between height classes (ht), total regeneration (net), and year, using Pearson's r

This analysis can be broken down further into temporal changes for each of the height classes. Locally weighted polynomial regression (LOESS) was applied with a moving window filter to detect minima and maxima change-points in the regeneration time-series for each PSP tree height class and the total regeneration change (Figure F.6). Moving window and LOESS smoother window sizes of 1.0 and 0.1 were used, respectively. While regeneration declined for the lowest height class, it increased for all other height classes, indicating signs of understory ageing modulated by episodic mortality and growth events.



Figure F.6 Changes to regeneration by height class in the PSP data; minima and maxima change-points were detected by comparing minima and maxima of a loess smoother to those of a moving window filter

Agreement is shown for change-points at years 1975, 1984, 1985, 1987, 1991, 1994, 1995, 1996, 2002, 2004, 2007, and 2008, at a periodicity demonstrated in the autocorrelation analysis. While regeneration in classes taller than height class 1 show little to no relationship with overstory tree age or height, height class 1 shows a relation to both (Figure F.7). Linear regression models indicate that overstory stump age and tree height explain 23% and 78% of the variation in regeneration for height class 1, respectively. Rather than diminishing with greater stand age and tree height, regeneration in height class 1 was positively correlated with stand development. This is likely due to reduced understory competition and the opening of canopy gaps following stand-thinning.


Figure F.7 Frequency of height class 1 regeneration by tree height and age

In sum, regeneration for height class 1 significantly declined across the period (p < 0.01), limited by increased overstory and understory competition. Stands declined in mean height and age over the period, which increased rather than diminished competition pressure on regeneration for the lowest height class. While total regeneration increased, this was likely due to understory succession into older classes. Whether the periodicity of changes in regeneration are attributable to direct climatic effects on biophysical regeneration processes or indirect effects through stand conditions (e.g., fire, wind, or drought mortality) requires further analysis. Some evidence is provided in the SDS and PSP data for abiotic constraints to regeneration in the region. Abiotic constraints appear most outweighed by competition in the understory, whereby increased regeneration following disturbance may be quickly suppressed by understory competition in subsequent years. Future analyses should directly incorporate climate, soils, and competition to better untangle stand regeneration dynamics and abiotic factors under global change.