

ABUNDANCE OF FORAGE LICHENS FOR BOREAL CARIBOU IN THE
BOREAL SHIELD ECOZONE OF SASKATCHEWAN

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By

RUTH J. GREUEL

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ABSTRACT

Several species of terricolous fruticose lichens are important as winter forage for a threatened species, boreal caribou (*Rangifer tarandus caribou* (Gmelin)), in the northern boreal forest of Saskatchewan, Canada. This area is part of the Boreal Shield Ecozone, and experiences very high rates of natural forest fire. Lichens grow very slowly and take decades to develop substantial cover and depth. To understand the development of caribou habitat after fire and the availability of forage lichens across the range, we gathered forest inventory data at 312 sites in a stratified random design across northern Saskatchewan during 3 years of surveys. We took the following measurements at each site: tree ring samples for stand age, measurements of basal area density, moisture regime and species composition of vascular plants, bryophytes and lichens. Destructive samples of lichen biomass were taken at 72 sites. From these destructive lichen samples I tested various types of allometric equations for both measures of cover and volume relative to biomass. Linear allometric equations provided estimates of stand-level biomass (kg/ha) for each of the common stand types using plot-based measurements of lichen cover and volume. I used boosted regression trees (BRTs) to construct decision tree ensembles to assess the relative influence on lichen abundance of several environmental variables. This provides an understanding of the controls on lichen abundance and further insight into the differences between accrual of percent cover (dispersal of lichens) and depth (development of the lichen thalli). The different drivers controlling each of these types of lichen growth have rarely been examined, and while other studies on lichen abundance select one measure, they are typically not both considered within one study. Time since fire was the most important variable controlling both lichen percent cover and volume. UTM northing and basal area density were also important, but to different degrees for each measure. These results are supported by basic tenets of lichen biology, such as their slow growth and light availability requirements, but also indicate that percent cover alone is an insufficient indicator of the lichen availability component of habitat quality for woodland caribou. Increasing our understanding of the factors influencing lichen distribution in Saskatchewan's boreal forest will improve habitat planning for boreal caribou, and will be especially important in the future as fire frequency and severity may be affected by climate change.

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TABLE OF CONTENTS

PERMISSION TO USE	i
ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS.....	iv
TABLE OF TABLES	vi
TABLE OF FIGURES	vii
LIST OF APPENDICES	ix
LIST OF ABBREVIATIONS/ACRONYMS.....	x
1 INTRODUCTION	1
1.1 Background.....	1
1.2 Objectives.....	5
1.3 Hypotheses and Predictions.....	6
2 METHODS	9
2.1 Study area.....	9
2.2 Field sampling	11
2.3 Allometric methods.....	15
2.3.1 Lab methods	15
2.3.2 Analysis	16
2.4 Relationships with environmental characteristics.....	17
2.4.1 Boosted regression trees.....	17
2.4.2 Variables	18
2.4.3 Selection of model parameters	22
2.4.4 Interpreting model output	24
3 RESULTS	27
3.1 Allometry.....	27
3.2 Effects of environmental characteristics on lichen abundance	34
4 DISCUSSION	47
4.1 Allometry.....	47
4.2 Scaling estimates to stand type.....	49
4.3 Relationships of environmental covariates to lichen abundance	53
4.4 Lichen and caribou habitat in Saskatchewan	58
4.5 Conclusions.....	60
REFERENCES	62
APPENDIX A: ALTERNATE ALLOMETRIC RELATIONSHIPS	69
.....	69

APPENDIX B: GRAPHS FOR MODERATE AND LOW ABUNDANCE STAND TYPES73
APPENDIX C: DESTRUCTIVE LICHEN BIOMASS DATA75
**APPENDIX D: PLOT-LEVEL SUMMARIES OF LICHEN AND ENVIRONMENTAL DATA USED IN
BOOSTED REGRESSION TREES80**

TABLE OF TABLES

TABLE 1: COVER CLASSES FOR VEGETATION AND GROUND COVER ESTIMATION, CLASS 0 IS ONLY APPLICABLE TO VEGETATION ESTIMATES, NOT TO GROUND COVER.. ADAPTED FROM FEC FIELD HANDBOOK (JIRICKA ET AL., 2002).	13
TABLE 2: LICHEN SPECIES GROUPINGS USED IN THE FIELD.	14
TABLE 3: LIST OF PREDICTOR VARIABLES USED INITIALLY IN THE BOOSTED REGRESSION TREES. BOLDDED NAMES INDICATE VARIABLES THAT WERE INCLUDED IN AT LEAST ONE FINAL BRT.	20
TABLE 4: CLASSIFICATION OF FOREST STAND TYPES USED IN BRTs. THIS IS A RULE-BASED CLASSIFICATION BASED ON FOREST PLOTS SURVEYED BETWEEN 2014–2016 ($N = 312$)	22
TABLE 5: MAXIMUM VALUES AND MEANS (± 1 SE) OF PROJECTED BIOMASS ESTIMATES (KG/HA) CALCULATED FROM ALLOMETRIC EQUATIONS APPLIED TO ESTIMATES OF LICHEN AREA AND VOLUME ACROSS ALL 2015-2016 PLOTS ($N = 221$). THE MINIMUM VALUE OF LICHEN BIOMASS IS 0 IN ALL CASES. TABLE IS ORDERED ACCORDING TO HIGHEST MAXIMUM LICHEN BIOMASS AS PREDICTED BY AREA- BASED ALLOMETRY.	33
TABLE 6: TWO-WAY AND THREE-WAY INTERACTIONS PRESENT IN THE BEST BRT FOR LICHEN PERCENT COVER IN ALL STANDS. INTERACTIONS ARE SORTED BY FRIEDMAN’S H VALUE*. BOLDDED INTERACTIONS ARE THOSE ABOVE $H > 0.1$ THRESHOLD.	36
TABLE 7: TWO-WAY INTERACTIONS PRESENT IN THE BEST VOLUME BRT FOR LICHEN VOLUME IN ALL STANDS. INTERACTIONS ARE SORTED BY FRIEDMAN’S H VALUE. BOLDDED INTERACTIONS ARE THOSE ABOVE $H > 0.1$ THRESHOLD.	40
TABLE 8: TWO-WAY INTERACTIONS PRESENT IN THE PERCENT COVER BRT COMPRISING ONLY JACK PINE STANDS. INTERACTIONS ARE SORTED BY FRIEDMAN’S H VALUE. BOLDDED INTERACTIONS ARE THOSE ABOVE $H > 0.1$ THRESHOLD.	43
TABLE 9: THESE ARE THE TWO-WAY INTERACTIONS PRESENT IN THE VOLUME BRT COMPRISING ONLY JACK PINE STANDS. INTERACTIONS SORTED BY FRIEDMAN’S H VALUE. BOLDDED INTERACTIONS ARE THOSE ABOVE $H > 0.1$ THRESHOLD.	46
TABLE 10: MEAN LICHEN ABUNDANCE FOUND IN OTHER REGIONS. VALUES FOR THIS STUDY PRESENTED IN THE TABLE ARE ESTIMATES BASED ON LICHEN VOLUME.	53

TABLE OF FIGURES

FIGURE 1: MAP OF STUDY AREA IN THE BOREAL SHIELD ECOZONE OF NORTHERN SASKATCHEWAN. INSET MAP SHOWS LOCATION OF STUDY AREA IN RELATION TO WESTERN CANADA AND THE BOREAL SHIELD ECOZONE. GREY SHADING IS A DIGITAL ELEVATION MODEL (DEM) REPRESENTING TERRAIN. DEM FROM UNITED STATES GEOLOGICAL SURVEY (USGS) NATIONAL ELEVATION DATABASE, ECOZONES OF CANADA LAYER FROM THE ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE (ESRI). PLACE NAMES IN YELLOW INDICATE APPROXIMATE LOCATIONS OF LARGE LAKES AROUND WHICH SAMPLING OCCURRED. GEOGRAPHIC COORDINATE SYSTEM: GCS_NORTH_AMERICA_1983. DATUM: D_NORTH_AMERICA_1983. PROJECTION: NAD_1983_UTM_ZONE_13N..... 10

FIGURE 2: LINEAR ALLOMETRIC RELATIONSHIPS BETWEEN LICHEN AREA (cm^2/cm^2) AND BIOMASS (g/cm^2). CLOCKWISE FROM TOP LEFT, PLOTS ARE A.) CLADONIA MITIS B.) CLADONIA STELLARIS, C.) CLADONIA RANGIFERINA AND D.) CLADONIA UNCIALIS . ALL LINEAR TRENDLINES FITTED WITH A ZERO-INTERCEPT. UNITS OF THE X AXIS (BIOMASS) ARE g/cm^2 , UNITS OF THE SLOPE ARE g/cm^2 . Y-AXIS RANGE VARIES BETWEEN PANELS..... 28

FIGURE 3: LINEAR ALLOMETRIC RELATIONSHIPS BETWEEN LICHEN VOLUME (cm^3/cm^2) (AVERAGE DEPTH AND TOTAL PERCENT COVER) AND BIOMASS (g/cm^2). CLOCKWISE FROM TOP LEFT, PLOTS ARE A.) CLADONIA MITIS, B.) CLADONIA STELLARIS, C.) CLADONIA RANGIFERINA, AND D.) CLADONIA UNCIALIS. ALL LINEAR TRENDLINES ARE FITTED WITH A ZERO-INTERCEPT. UNITS OF THE X AXIS ARE g/cm^2 , UNITS OF THE SLOPE ARE g/cm^3 . Y-AXIS RANGE VARIES BETWEEN PANELS. 29

FIGURE 4: ALLOMETRIC RELATIONSHIPS BETWEEN LICHEN BIOMASS (g/cm^2) AND EITHER A.) LICHEN COVER (cm^2/cm^2) ($N = 72$) OR B.) VOLUME (cm^3) PER UNIT AREA (cm^2) ($N = 72$). ALLOMETRIC EQUATION FOR ALL 4 SPECIES IS A.) $Y = 0.075067X$ WITH A ZERO-INTERCEPT. $R^2 = 0.80$, $p < 0.001$, $SE = 0.004438$ OR B.) $Y = 0.0133234X$ WITH A ZERO-INTERCEPT. $R^2 = 0.91$, $p < 0.001$, $SE = 0.0004834$. BLUE STARS INDICATE POINTS THAT WERE OPPORTUNISTICALLY SAMPLED (NOT AS PART OF THE RANDOM SAMPLING SCHEME)..... 30

FIGURE 5: PROJECTIONS OF ESTIMATED LICHEN BIOMASS (kg/ha) AS RELATES TO STAND AGE AT 220 SITES CALCULATED FROM A.) COVER MEASUREMENTS (cm^2/cm^2) AND B.) VOLUME MEASUREMENTS (cm^3/cm^2) FOR EACH OF THE 4 STAND TYPES WITH THE OVERALL HIGHEST ABUNDANCE. CURVED LINES ARE LOESS SMOOTHING FUNCTIONS FOR EACH STAND TYPE. "X" SITES INDICATE SITES WHICH WERE SURVEYED OPPORTUNISTICALLY, NOT AS PART OF THE RANDOM SAMPLING. IN HIGH-ABUNDANCE STANDS THERE WERE ONLY 2 SUCH SITES AND THEY WERE BOTH IN PINE STANDS. 32

FIGURE 6: PARTIAL DEPENDENCY PLOTS FOR FINAL BOOSTED REGRESSION TREE MODEL OF PERCENT COVER. PARTIAL DEPENDENCY PLOTS DEMONSTRATE THE MARGINAL EFFECT OF THE VARIABLE IN QUESTION ON THE RESPONSE VARIABLE (LICHEN COVER) WHEN ALL OTHER VARIABLES ARE HELD AT THEIR MEAN. THE Y-AXES ARE CENTERED AT A ZERO-MEAN. A.) TIME SINCE FIRE; B.) BASAL AREA DENSITY; C.) STAND TYPE (STAND TYPE CATEGORIES FROM LEFT TO RIGHT, ARE: CM-CONIFER MIX, DE- DECIDUOUS, HC- HARDWOOD-CONIFER, JP- PINE, PS- POORLY-DRAINED BLACK SPRUCE, PN- POORLY-DRAINED NON-FOREST, WS- WELL-DRAINED BLACK SPRUCE, WN- WELL-DRAINED NON-FOREST); D.) NORTHING; AND E.) EASTING. DECILES (INNER TICK MARKS PLOTTED ALONG THE X-AXES) INDICATE THE DISTRIBUTION OF DATA WITH REGARDS TO THE VARIABLE IN QUESTION. THE PERCENTAGE VALUES INCLUDED WITH THE X-AXES LABELS ARE THE RELATIVE INFLUENCE OF THE VARIABLE IN THE MODEL (SUMS TO 100% FOR ALL VARIABLES AND INTERACTIONS). 35

FIGURE 7: INTERACTION PLOTS FOR THE TOP 6 PAIR-WISE INTERACTIONS ($H > 0.1$) IN THE BRT MODEL PREDICTING LICHEN PERCENT COVER. EACH PANEL SHOWS THE EFFECTS OF TWO INTERACTING VARIABLES ON THE FITTED VALUES OF THE RESPONSE VARIABLE WHILE ALL OTHER COVARIATES ARE HELD AT THEIR MEAN. PANELS ILLUSTRATE (CLOCKWISE FROM TOP LEFT): A.) BASAL AREA AND STAND TYPE, B.) STAND TYPE AND STAND AGE, C.) BASAL AREA AND STAND AGE, D.) STAND AGE AND NORTHING, E.) BASAL AREA AND NORTHING, F.) NORTHING AND STAND TYPE. VERTICAL SCALE INDICATES THE FITTED VALUES OF LICHEN PERCENT COVER..... 37

FIGURE 8: PARTIAL DEPENDENCY PLOTS FOR FINAL BOOSTED REGRESSION TREE MODEL OF VOLUME. PARTIAL DEPENDENCY PLOTS DEMONSTRATE THE MARGINAL EFFECT OF THE VARIABLE IN QUESTION ON THE RESPONSE VARIABLE (LICHEN VOLUME DENSITY) WHEN ALL OTHER VARIABLES ARE HELD AT THEIR MEAN. THE Y-AXES ARE CENTERED AT A ZERO-MEAN. A.) TIME SINCE FIRE, 53.8% OF THE VARIANCE B.) NORTHING, 24.3% OF THE VARIANCE, C.) BASAL AREA, 12.8% OF THE VARIANCE, D.) STAND TYPE, 8% OF THE VARIANCE. STAND TYPE CATEGORIES FROM LEFT TO RIGHT, ARE: CONIFER MIX, DECIDUOUS, HARDWOOD-CONIFER, PINE, POORLY-DRAINED BLACK SPRUCE, POORLY-DRAINED NON-FOREST, WELL-DRAINED BLACK SPRUCE, WELL-DRAINED NON-FOREST. E.) EASTING, 1.1% OF THE VARIANCE. DECILES (INNER TICK MARKS PLOTTED ALONG THE X-AXIS) INDICATE THE DISTRIBUTION OF DATA WITH REGARDS TO THE VARIABLE IN QUESTION. THE PERCENTAGE VALUES INCLUDED WITH THE X-AXIS LABELS ARE THE RELATIVE INFLUENCE OF THE VARIABLE IN THE MODEL (SUMS TO 100% FOR ALL VARIABLES AND INTERACTIONS). 39

FIGURE 9: INTERACTION PLOTS FOR THE TOP 3 PAIR-WISE INTERACTIONS ($H > 0.1$) IN THE BRT MODEL PREDICTING LICHEN VOLUME. EACH PANEL SHOWS THE EFFECTS OF TWO INTERACTING VARIABLES ON THE FITTED VALUES OF THE RESPONSE VARIABLE WHILE ALL OTHER COVARIATES ARE HELD AT THEIR MEAN. PANELS ILLUSTRATE (L-R): A.) STAND AGE AND NORTHING, B.) BASAL AREA DENSITY AND NORTHING, C.) EASTING AND STAND TYPE. VERTICAL SCALE INDICATES THE FITTED VALUES OF LICHEN VOLUME (cm^3/M^2). 41

FIGURE 10: PARTIAL DEPENDENCY PLOTS FOR FINAL BOOSTED REGRESSION TREE MODEL OF PERCENT COVER IN JACK PINE STANDS ONLY. PARTIAL DEPENDENCY PLOTS DEMONSTRATE THE MARGINAL EFFECT OF THE VARIABLE IN QUESTION ON THE RESPONSE VARIABLE (LICHEN COVER) WHEN ALL OTHER VARIABLES ARE HELD AT THEIR MEAN. THE Y-AXES ARE CENTERED AT A ZERO-MEAN. A.) TIME SINCE FIRE, 55% OF THE VARIANCE) B.) BASAL AREA DENSITY, 30.4% OF THE VARIANCE, C.) EASTING, 7.1% OF THE VARIANCE, D.) HEAT LOAD INDEX, 3.7% OF THE VARIANCE, E.) NORTHING, 2.4% OF THE VARIANCE, F.) LAST FIRE TYPE, 0.8% OF THE VARIANCE. LAST FIRE TYPE HAS TWO POSSIBLE CATEGORIES: NOT STAND-REPLACING AND STAND-REPLACING. DECILES (INNER TICK MARKS PLOTTED ALONG THE X-AXIS) INDICATE THE DISTRIBUTION OF DATA WITH REGARDS TO THE VARIABLE IN QUESTION. THE PERCENTAGE VALUES INCLUDED WITH THE X-AXIS LABELS ARE THE RELATIVE INFLUENCE OF THE VARIABLE IN THE MODEL, WHICH SUMS TO 100% FOR ALL VARIABLES. INTERACTION EFFECTS ARE INCLUDED IN THESE VALUES..... 42

FIGURE 11: INTERACTION PLOTS FOR THE TOP TWO INTERACTIONS IN THE BRT FOR PERCENT COVER IN JACK PINE STANDS. THE MOST IMPORTANT A.) IS BASAL AREA DENSITY-TIME SINCE FIRE ($H = 0.3458$) AND THE NEXT MOST IMPORTANT B.) IS TIME SINCE FIRE-EASTING, ($H = 0.084$, BELOW THE 0.1 ARBITRARY H THRESHOLD. 43

FIGURE 12: PARTIAL DEPENDENCY PLOTS FOR FINAL BOOSTED REGRESSION TREE MODEL OF LICHEN VOLUME IN JACK PINE STANDS ONLY. PARTIAL DEPENDENCY PLOTS DEMONSTRATE THE MARGINAL EFFECT OF THE VARIABLE IN QUESTION ON THE RESPONSE VARIABLE (LICHEN COVER) WHEN ALL OTHER VARIABLES ARE HELD AT THEIR MEAN. THE Y-AXES ARE CENTERED AT A ZERO-MEAN. A.) TIME SINCE FIRE, 52.6% OF THE VARIANCE) B.) BASAL AREA DENSITY, 21.2% OF THE VARIANCE, C.) EASTING, 11.9% OF THE VARIANCE, D.) NORTHING, 6.4% OF THE VARIANCE, E.) HEAT LOAD INDEX, 6.1% OF THE VARIANCE, F.) LAST FIRE TYPE, 1.8% OF THE VARIANCE. LAST FIRE TYPE HAS TWO POSSIBLE CATEGORIES: NOT STAND-REPLACING AND STAND-REPLACING. DECILES (INNER TICK MARKS PLOTTED ALONG THE X-AXIS) INDICATE THE DISTRIBUTION OF DATA WITH REGARDS TO THE VARIABLE IN QUESTION. THE PERCENTAGE VALUES INCLUDED WITH THE X-AXIS LABELS ARE THE RELATIVE INFLUENCE OF THE VARIABLE IN THE MODEL, WHICH SUMS TO 100% FOR ALL VARIABLES. INTERACTION EFFECTS ARE INCLUDED IN THESE VALUES. 45

FIGURE 13: INTERACTION PLOTS FOR THE TOP TWO INTERACTIONS IN THE PINES VOLUME MODEL. THE MOST IMPORTANT IS A.) BASAL AREA DENSITY AND TIME SINCE FIRE ($H = 0.2718$) AND THE NEXT MOST IMPORTANT IS B.) HEAT LOAD INDEX-EASTING, ($H = 0.1065$). VERTICAL SCALE INDICATES THE FITTED VALUES OF LICHEN VOLUME (cm^3/M^2). 46

FIGURE 14: ALLOMETRIC EQUATIONS WITH NON-RANDOMLY SAMPLED SITES ($N = 2$) REMOVED FOR AREA ($N = 70$) AND VOLUME VALUES ($N = 70$). BIOMASS FOR BOTH PLOTS IS GIVEN HERE IN G/CM^2 . A.) ALLOMETRIC EQUATION FOR ALL 4 SPECIES/SPECIES GROUPINGS (TOTAL AREA/AREA) IS $Y = 0.073411X$ WITH A ZERO-INTERCEPT. $R^2 = 0.79$, $p < 0.001$. B) ALLOMETRIC EQUATION FOR ALL 4 SPECIES (TOTAL VOLUME/AREA) IS $Y = 0.0130955X$ WITH A ZERO-INTERCEPT. $R^2 = 0.91$. $p < 0.001$ 69

FIGURE 15: ALLOMETRIC EQUATIONS WITH ONE OUTLIER REMOVED FOR AREA ($N = 71$) AND VOLUME VALUES ($N = 71$). BIOMASS FOR BOTH PLOTS IS GIVEN HERE IN G/CM^2 . A.) ALLOMETRIC EQUATION FOR ALL 4 SPECIES/SPECIES GROUPINGS (TOTAL AREA/AREA) IS $Y = 0.070412X$ WITH A ZERO-INTERCEPT. $R^2 = 0.85$, $p < 0.001$. B) ALLOMETRIC EQUATION FOR ALL 4 SPECIES (TOTAL VOLUME/AREA) IS $Y = 0.0127531X$ WITH A ZERO-INTERCEPT. $R^2 = 0.90$. $p < 0.001$ 70

FIGURE 16: ALLOMETRIC EQUATIONS IN EXPONENTIAL FORMAT FOR AREA ($N = 72$) AND VOLUME VALUES ($N = 72$). A.) ALLOMETRIC EQUATION FOR ALL 4 SPECIES/SPECIES GROUPINGS (TOTAL AREA/AREA) IS $Y = 0.0024E^{4.1708x}$, $R^2 = 0.0.7548$ AND EQUATION WITH TOTAL VOLUME/AREA IS $Y = 0.0062E^{0.4534x}$, $R^2 = 0.5962$ 71

FIGURE 17: ALLOMETRIC EQUATIONS IN POWER FORM FOR AREA ($N = 72$) AND VOLUME VALUES ($N = 72$). THESE EQUATIONS CREATED IN MICROSOFT EXCEL USING TREND LINE PLOTTING FUNCTION TO OBTAIN STARTING VALUES. A.) ALLOMETRIC POWER EQUATION FOR ALL 4 SPECIES/SPECIES GROUPINGS (TOTAL AREA/AREA) IS $Y = 0.0706x^{1.3129}$, $R^2 = 0.8516$. B.) ALLOMETRIC POWER EQUATION FOR ALL 4 SPECIES (TOTAL VOLUME/AREA) IS $Y = 0.011x^{1.0732}$, $R^2 = 0.8856$ 72

FIGURE 18: PROJECTIONS OF ESTIMATED BIOMASS (KG/HA) AT ($N = 39$) SITES CALCULATED FROM A.) AREA MEASUREMENTS (CM^2/CM^2) AND B.) VOLUME MEASUREMENTS (CM^3/CM^2) FOR EACH OF THE 3 STAND TYPES WITH THE OVERALL LOWEST ABUNDANCE. CURVED LINES ARE LOESS SMOOTHING FUNCTIONS FOR EACH STAND TYPE. OF THESE, 24 SITES HAD ZERO LICHEN. 73

FIGURE 19: PROJECTIONS OF ESTIMATED BIOMASS (KG/HA) AT SITES ($N = 62$) CALCULATED FROM A.) AREA MEASUREMENTS (CM^2/CM^2) AND B.) VOLUME MEASUREMENTS (CM^3/CM^2) FOR EACH OF THE 3 STAND TYPES WITH THE OVERALL LOWEST ABUNDANCE, AS WELL AS THE STAND TYPE WITH THE MOST INTERMEDIATE LICHEN ABUNDANCE (HARDWOOD-CONIFER). CURVED LINES ARE LOESS SMOOTHING FUNCTIONS FOR EACH STAND TYPE. IN "LOW-ABUNDANCE" STANDS THERE WAS ZERO LICHEN, AS THE SITES WERE SELECTED TO CAPTURE UNUSUAL ECOSITES, TYPICALLY ROCKY SHORES OR FENS. OF THE SITES SHOWN HERE, 35 SITES HAD ZERO LICHEN. 74

LIST OF APPENDICES

APPENDIX A: Alternate allometric relationships

APPENDIX B: Graphs for scaled-up lichen biomass estimates in moderate and low abundance stand types

APPENDIX C: Destructive lichen biomass data

APPENDIX D: Plot-level summaries of lichen and environmental data used in Boosted Regression Trees

LIST OF ABBREVIATIONS/ACRONYMS

AP – Athabasca Plain
CRU – Churchill River Upland
CU – Conservation Unit
CV – Cross-validation
BP – Boreal Plain Ecozone
BRT – Boosted regression tree
BSE – Boreal Shield Ecozone
DBH – Diameter at breast height
ESRI – Environmental Systems Research Institute
FEC – Forest Ecosite Classification
GBM – Gradient boosting machine
GPS – Global Positioning System
SK – Saskatchewan, Canada
USGS – United States Geological Survey
UTM – Universal Transverse Mercator

1 INTRODUCTION

1.1 Background

In much of the northern boreal forest of Canada, the main source of natural disturbance is fire (Payette, 1992). With climate change, natural fire regimes are likely to shift to more frequent and severe fires as forests become warmer and drier (De Groot et al., 2013; Wang et al., 2015). In turn, this will affect forest growth, habitat quality for many species and even the species composition of the boreal forest (Johnstone et al., 2010). Among the species that will be affected by changes to disturbance regimes are boreal caribou, (*Rangifer tarandus caribou* (Gmelin)); a federally listed threatened species in Canada (Environment Canada, 2012). Many populations of boreal caribou across Canada have suffered population declines in recent years, often due to disturbance caused by human activity (McLoughlin et al., 2003). Caribou are the only mammal in Canada that use lichens as a major source of forage across their entire range (Aagnes et al., 1995; Storeheier et al., 2003). Understanding how lichen abundance is affected by natural disturbance is therefore fundamental to our understanding of boreal caribou ecology and conservation.

In Saskatchewan, Canada, boreal caribou inhabit two ecozones: the Boreal Plain in the south (the SK2 management unit), and the Boreal Shield in the north, also known as the SK1 management unit (Acton et al., 1998). The Boreal Shield Ecozone of Saskatchewan is very remote, and experiences little anthropogenic disturbance (3% of the land disturbed per year), with most disturbance being in the form of lightning-caused fire (Parisien et al., 2004). The western boreal shield (including the SK1) is drier than the Boreal Plain and eastern boreal forests of Canada, and therefore is subject to more frequent and severe fires (Peng et al., 2011). Indeed, the fire return interval (how often an area burns) is approximately 100 years, which is very short when compared to the 263 year cycle of the Saskatchewan Boreal Plain (Parisien et al., 2004); more than 55% of the SK1 burned between 1974-2014 (Environment Canada, 2012). The disturbance threshold to maintain a self-sustaining population of boreal caribou set by the federal government is 35% of the habitat disturbed within the past 40 years (Environment Canada, 2011). As 55% of Saskatchewan's boreal shield (the SK1 unit) has burned in the past 40 years, this threshold has already been exceeded. Theoretically, this leaves no room for potential future changes in fire regime (climate-

driven) or anthropogenic disturbance such as resource extraction. Alternatively, this threshold may not apply to Saskatchewan or may be more applicable in other areas of the range of boreal caribou.

Fire regimes vary across regions, depending on climate, landform and stand composition (Rowe and Scotter, 1973), and lichen growth rates also vary depending on geographic location. Hence, estimates of lichen biomass determined in other regions of the boreal forest may not apply to places like the boreal shield of Saskatchewan, which has thus far received relatively little attention with respect to fire ecology and habitat dynamics, including lichen abundance (Environment Canada, 2012). For my thesis, I explored various aspects of lichen abundance in the boreal shield of Saskatchewan, where the fire frequency is high and lichen abundance is unknown, with implications for the management and conservation of boreal caribou.

Lichens are the product of a mutualistic symbiosis between a fungal component and an alga or cyanobacterium. The fungus provides structure, the algae/cyanobacteria live within the hyphal tissue of the fungus and produce food through photosynthesis. The form created by this partnership is unlike either partner's original morphology (Brodo et al., 2001). Lichens are relatively poorly-studied, with new discoveries still being made on their biology and ecology. For example, recent research suggests that some lichen species also have a third symbiont, a basidiomycete yeast, in their structure (Spribille et al., 2016). They are highly diverse, with several morphological types comprising approximately 3600 species in North America (Brodo et al., 2001). Morphological type is the growth form of the lichen, which includes such types as crustose (crust-like), foliose (leaf-like) and fruticose (upright or pendulous 3-dimensional structure). Lichens are a common ground cover type in the boreal forest, in addition to occurring on other substrates such as soil, rock, deadwood and live trees.

Lichens grow extremely slowly, perhaps only increasing their depth by 2–8 mm per year (Andreev, 1954; Holt and Bench, 2008). Following disturbance, most lichens require extensive time to regrow, although some species and functional groups recover more quickly than others (Ahti, 1959; Brodo et al., 2001; Scotter, 1964). The lichen species of highest value to caribou are pendulous arboreal lichens, and terricolous fruticose lichens (ground-dwelling upright lichens with a 3-dimensional structure). Terricolous lichens are usually only present in large quantities in stands that are ~80 years old (Ahti, 1959; Schimmel and Granström, 1996; Scotter, 1964; Skatter et al., 2014). Considering the fire regime (~100 years) in northern Saskatchewan, this suggests that few

stands will contain large quantities of forage lichens. These lichens form mats on the forest floor composed of multiple individual thalli, and grow vertically with some lateral branching. Their growth rate will change slightly throughout their life-cycle, and the base of the podetia die off at some point, so that accumulation of growth will slow, and eventually, the biomass of living lichen will cease to increase (Abdulmanova and Ektova, 2015; Ahti, 1959; Jandt et al., 2008). This point, known as peak biomass, indicates the time when lichen growth is equalled by lichen death at the base of the podetia, and therefore the biomass of living lichen remains constant from year to year (Thomas et al., 1996a). This is an important part of lichen biology to consider when estimating lichen abundance, as it may indicate a plateau in the relationship between stand age and lichen biomass. Determination of peak biomass includes a depth component, because vertical growth is an important part of lichen community development (Hammer, 2001).

Although lichens in mechanically disturbed areas have been shown to recover within ~10 years (Tømmervik et al., 2011), fruticose lichens that are destroyed by fire recover more slowly, perhaps taking up to 30 years to begin regrowth, and reaching peak biomass in ~100 years (Ahti, 1959; Andreev, 1954; Morneau and Payette, 1989). The delay of regrowth after fire may be because lichens recolonize severely burned areas asexually, via fragments carried by the wind (Gaare, 1997), while in mechanically disturbed areas the fragments are already present (Andreev, 1954; Webb, 1998). Regardless of disturbance type, lichens grow slowly and it may take many decades to achieve peak biomass or a point at which the lichen mat is sufficiently large to serve as forage.

It has long been hypothesized that boreal caribou forage primarily on lichens during the winter months (Scotter, 1964; Storeheier et al., 2003), and more recently it has been shown that lichens may compose up to 70% of caribou diet year-round (Thompson et al., 2015). This may be because continued use of lichens is necessary to maintain the gut microflora required to digest them efficiently (Person, 1975; Thomas et al., 1996b). Lichens are high in carbohydrates but very low in protein, to the extent that caribou eating mainly lichens during the winter will lose weight and are typically in poor body condition in the spring (Bergerud, 1972; Rominger et al., 1996). Not all caribou rely equally on ground lichens, in mountainous regions arboreal lichens are more important sources of winter forage for mountain caribou. The mesic environment allows for faster arboreal lichen growth, and snow accumulation in winter allows caribou to reach lichens on higher tree branches than in the summer (Rominger and Oldemeyer, 1989; Thomas et al., 1996b). Saskatchewan does not have arboreal lichens in adequate quantities to serve as forage, and the

lower average snow accumulation makes it more efficient to dig for terricolous lichen forage than to source arboreal lichens, as well as restricting caribou from accessing lichens higher than 2 m from the ground (Brown and Theberge, 1990; Rominger et al., 1996).

In general, lichen abundance differs between regions and in different caribou habitats, and is not always available. As such, it is possible for caribou to exist without relying entirely on lichens. Whether or not this is the case in an area will depend to some extent upon the quantity of available lichen forage (Thomas et al., 1996a; Thompson et al., 2015).

The lichens typically sought by woodland caribou are foliose and fruticose species that grow either on tree branches (arboreal) or on the ground (terricolous). Of particular interest as woodland caribou forage are several species of the *Cladonia* genus in the family Cladoniaceae, that, until recently, made up the terricolous and fruticose genus *Cladina* (Brodo et al., 2001). These are *Cladonia mitis* Sandst., *Cladonia stellaris* (Opiz) Pouzar & Vězda, *Cladonia rangiferina* (L.) F.H. Wigg, *Cladonia arbuscula* (Wallr.) Rabenh., and *Cladonia stygia* (Fr.) Ruoss. Lichens in the *Cladoniaceae* family are typically upright thalli, meaning growth is primarily vertical, with lateral growth occurring at the apical fungal meristem (Hammer, 2001). Lichens of this type propagate across the ground to form mats, not by roots or shoots connecting thalli to one another, but by multiple individual thalli. Density of both cover and volume can help a lichen mat avoid desiccation (Roturier et al., 2007), and are thus beneficial to the development of adequate caribou forage, which may contribute to growth rate consistency in intermediately-aged stands (Skatter et al., 2014). However, the mechanisms involved in growth and spread of the lichen are different (Webb, 1998).

Lichens are poor competitors for sunlight and water in many environments because of their slow growth, but their unique adaptations permit them to compete well in areas where vascular plants and mosses exist at a disadvantage. Their growth depends to a large extent on the environmental (abiotic and biotic) characteristics of the forest stand. Lichens are poikilohydrous autotrophs, meaning that when they are dry, they enter a state of physiological inactivity (Kappen and Valladares, 2007). This makes them very resilient to periods of drought and cold temperatures. Most lichens must be moist to photosynthesize, although extended periods of saturation will have negative impacts on growth (Kappen and Valladares, 2007; Lange et al., 2001). Although these relationships are complex and tend to vary among species, they suggest that environmental

characteristics such as canopy cover, age and moisture are important for lichens (Boudreault et al., 2015). Understanding how these variables influence lichen abundance is central to my thesis.

1.2 Objectives

Gathering forest inventory data is time-consuming and can be challenging. Often, cryptic or non-merchantable components (such as lichens) of the forest are under-studied. For my thesis, I determined allometric relationships for lichen to enable more accurate calculations of forage availability (kg/ha) from raw abundance estimates: between area and biomass, and between volume and biomass of forage lichens. While allometric equations for similar groups of species can be used in different regions, it is better to use ones developed specifically for the region in question (Joly et al., 2010; Moen et al., 2007). Lichens of the same species can have different densities in certain regions; for example, tundra lichens are heavier than their southern counterparts (Andreev, 1954). As lichen communities differ greatly across the boreal region, the use of these equations were limited to the most common species of terricolous forage lichens in northern Saskatchewan's Boreal Shield Ecozone.

Patterns of lichen succession from eastern Canada (Ahti, 1959; Maikawa and Kershaw, 1976) may be poor representations of forest dynamics in northern Saskatchewan, where high fire frequency and therefore shorter time frames for succession must be taken into account. Lichens may occur in younger stands in moderate quantities, but it is unclear at what point lichens become useful to caribou as a food source. The fact that there are caribou in this area suggest that more lichen forage may be available in the Saskatchewan boreal shield than fire frequency would suggest, or that caribou in this area are not relying primarily upon lichen, or some combination of these possibilities. The method of estimating lichen abundance through time using stands of many ages is a chronosequence approach, or space-for-time substitution. A chronosequence is a method of accounting for stand age without following individual stand development through an entire fire cycle, and they allow for large quantities of data to be collected efficiently in a limited time frame (Walker et al., 2010). The limitations of this approach include the assumptions that ecological succession is occurring, and that sites with similar history and composition follow similar trajectories, including the occurrence of stochastic events. However, when the time scale is measured in decades, the use of a chronosequence is often the only way to acquire data in a

reasonable time frame. We currently do not know the amount of forage lichen available to boreal caribou in northern Saskatchewan, which consists of many different ages and types of forest. Thus, a central objective of my work is to sample lichen abundance across a range of stand ages and types to acquire data for the breadth of conditions across the region, to better predict and understand lichen succession and availability for caribou. Furthermore, I link environmental covariates to identify patterns and thresholds of caribou forage availability.

1.3 Hypotheses and Predictions

Lichen biomass, as with most plant matter, is linked to the quantity of matter that is present that can be measured using an estimate of area or volume occupied by the lichen. Knowing this, it should be possible to determine lichen biomass abundance using a measure of quantity. I hypothesized that lichen biomass would be related to lichen area and to lichen volume. I predicted that area measures would exhibit reasonable fit with biomass data for destructive samples of lichen biomass because in most stands, cover has a wider potential range of variation than depth does. However, I predicted that a measure of volume would lead to overall higher biomass estimates and a better degree of specificity because it is a more complete measure of the quantity of lichen available. Rather than just displaying patterns in dispersal of lichens, volume will show differences between the growth patterns in different stand types, both in terms of percent cover (distribution over the ground surface) and accrual of height.

As lichen growth is so closely related to forest stand characteristics because of their unique limitations and adaptations to adverse conditions, I hypothesized that lichen abundance will be closely linked to several variables. I predicted that older stands (90+ years) would support the greatest quantity of ground lichen because of the slow growth rates of lichens. This age was suggested by Skatter et al. as the end of the intermediate age group, although some variation is to be expected (Skatter et al., 2014). However, I also predicted that this would depend to a large degree on stand characteristics, as these are essentially what determines habitat suitability for lichens (Carroll and Bliss, 1982; Scotter, 1964). I predicted that high values of basal area density will have negative consequences for lichen abundance, as this indicates decreased light availability (Hart and Chen, 2006; Mitchell and Popovich, 1997). Lichens are unable to thrive in closed canopy conditions (Kershaw, 1977), and mechanical canopy opening has been shown to stimulate lichen growth (Boudreault et al., 2013). However, this will likely interact with stand age, as young stands

which have low basal area density because of a recent fire will also have low lichen cover because of their young age.

Areas which are farther north may support communities with higher lichen abundance, as these areas may tend to have sparser trees (allowing for more light to penetrate to the understory and may experience more frost events (which lichens can survive if dry). The density of trees may be linked to shorter growing seasons, and high lichen abundance could be associated with longer days during these short growing seasons. Areas with the slowest growth rates, the farthest north, have been found to have the shortest lichen but also relatively heavier lichens (Andreev, 1954), which is an unexpected effect of northing which may be concealed within this variable. Easting is unlikely to be an informative variable as the range of values is not as high as that of northing, but has been included as the areas farthest west occur in a different subregion (Athabasca Plain) from the rest of the study area (Churchill River Uplands). This indicates slightly different topography and precipitation patterns.

Lichens are highly tolerant of desiccation, and therefore areas with lower soil moisture may be able to support high lichen abundance due to lack of competition (Kranter and Grill, 1997). At sites which are nutrient poor or dry and sandy, lichen will be more likely able to outcompete mosses or vascular plants (Bonan and Shugart, 1989). However, while water is a crucial factor in lichen biology and understory composition, one study on environmental gradients in lichen communities failed to find any change along a moisture gradient, perhaps because of the occurrence of lichens in both very dry sites and wet sites underlain by permafrost (Lechowicz and Adams, 1973). Because ecological variables are often correlated, interactions may exist between many of the explanatory variables. Moisture will also affect basal area and time since fire, in that wetter sites are less likely to burn frequently, and growth rates for trees will be lower at very high moisture (Bonan and Shugart, 1989). Time since fire will affect basal area, as very young stands have not had time for trees to grow, moderately aged stands may have very thick cohorts of saplings/young trees, and old stands may have larger but fewer trees (Morneau and Payette, 1989). It will also be affected by stand type to some degree, through succession.

I predict jack pine stands would show high lichen abundance, especially when tree density is low, because of increased light availability, typically mesic or xeric moisture regimes, and relative lack of plant cover found in these stands. Understanding the types of stands that contain high lichen

biomass will be important in the designation of boreal caribou critical habitat and will be useful for future management.

2 METHODS

2.1 Study area

My study area was ~65,800 km² of the Boreal Shield Ecozone in northern Saskatchewan (SK) (Figure 1). The Boreal Shield occupies 187,000 km² of northern SK, and is divided into two main ecoregions. The Churchill River Upland comprises the southeast portion of the ecozone, composed of Precambrian Canadian Shield bedrock, with rocky outcrops and high relief. The Athabasca Plain is the ecoregion in the northwest, which has a more homogeneous topography and is mainly composed of sandstone (Acton et al., 1998). The study area is mostly located in the Churchill River Upland Ecoregion. This area is relatively dry, like much of the western boreal forest, experiencing long and cold winters with relatively little snow (average snow depth across 6 winter months in Key Lake, SK, is 35 cm) and a short growing season with long days (Acton et al., 1998; Environment Canada, 2015). Annual precipitation is low but occurs along a latitudinal gradient with the highest precipitation occurring in the south. Of total annual precipitation, 66% falls as rain (Environment Canada, 2015). The dominant tree species are jack pine (*Pinus banksiana* Lamb.), which tends to occur on more xeric soils; and black spruce (*Picea mariana* (Mill) BSP), which favours mesic soils (McLaughlan et al., 2010). Less common tree species include trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marshall), tamarack (*Larix laricina* (Du Roi) K. Koch), and white spruce (*Picea glauca* (Moench) Voss). These form a mosaic of differently-aged mixed and pure stands across the landscape (Acton et al., 1998).

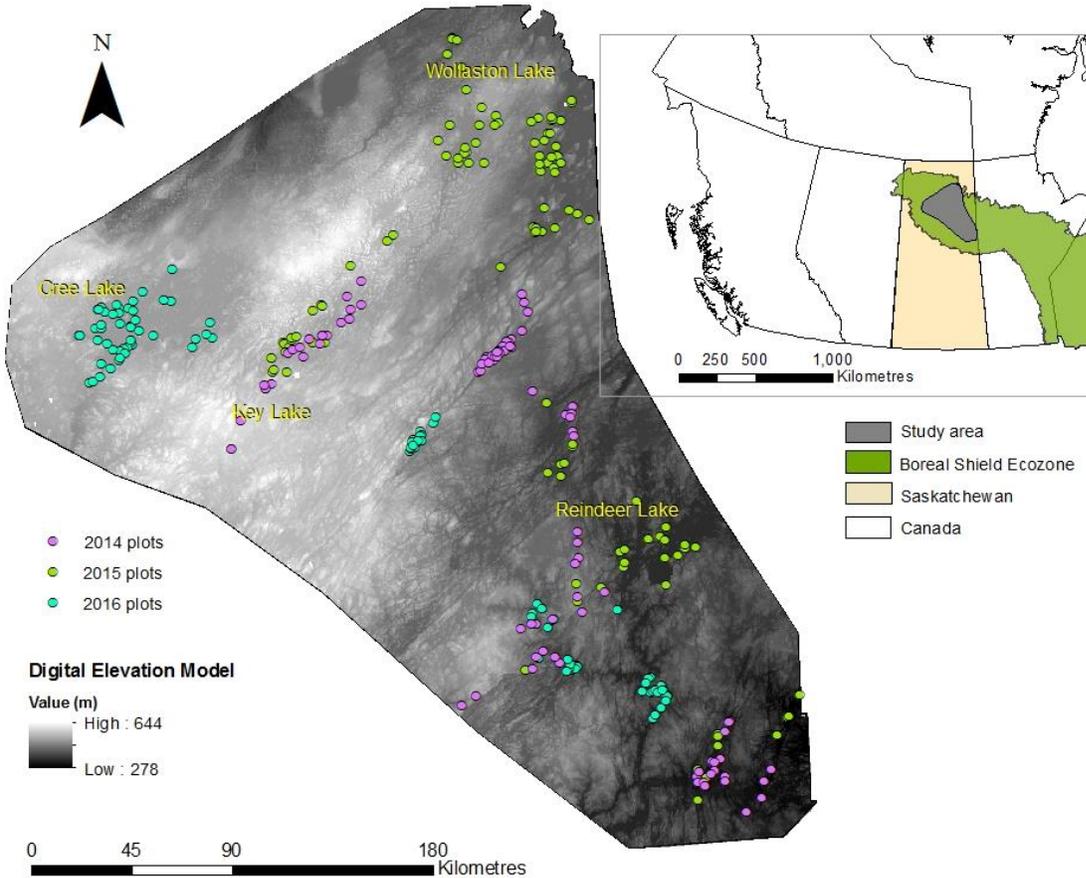


Figure 1: Map of study area in the Boreal Shield ecozone of northern Saskatchewan. Inset map shows location of study area in relation to western Canada and the Boreal Shield Ecozone. Grey shading is a Digital Elevation Model (DEM) representing terrain. DEM from United States Geological Survey (USGS) National Elevation Database, Ecozones of Canada layer from the Environmental Systems Research Institute (ESRI). Place names in yellow indicate approximate locations of large lakes around which sampling occurred. Geographic coordinate system: GCS_North_America_1983. Datum: D_North_America_1983. Projection: NAD_1983_UTM_Zone_13N

Sites within the study area were selected by stratified random sampling using remote sensing before the start of the 2014 field season, to account for the different levels of anthropogenic and natural disturbance present across the study area (Johnstone and McLoughlin, 2013). The strata were: young fire, old fire, and mature. The mature stratum was further divided into jack pine, black spruce, deciduous and wetland. Sites were pre-selected within each stratum, also using remote sensing. The expected type of each site from the stratification was not always correct, we encountered more young stands than expected. Sites were first masked for accessibility based on waterbodies, although some lakes were accessible by vehicle and some by floatplane.

2.2 Field sampling

The study area was sampled by field crews in 2014, 2015 and 2016 ($n = 92, 114, 106$ respectively) for a total of 312 sites (Figure 1). Field sampling was undertaken by a team of 6 in 2014, and a team of 4 individuals in 2015 and 2016. I participated in sampling in 2015 and 2016. Sites selected in the stratified random design were designated with UTM coordinates, which provided the location of the southwest corner of a 10 m \times 10 m plot aligned to compass cardinal directions. All four corners were further delineated into 2 m \times 2 m subplots for density estimates, and the northwest and southeast corners for vegetation composition. We measured forest attributes in each plot such as soil moisture, soil type, tree density and vegetation community composition. Using these characteristics, we determined the ecosite type following the Forest Ecosite Classification of Saskatchewan system (FEC) (Jiricka et al., 2002; McLaughlan et al., 2010).

Every strata (trees, seedlings, saplings of each species) were sampled when there were more than three individuals present within that stratum. Sampling involved measuring diameter at breast height (DBH) and height within subplots until 8 individuals had been measured for each strata, or within the entire plot if there were not enough individuals of the stratum present in the subplots. Values of DBH for all trees were used to determine basal area density of live trees (cm^2/m^2). Individuals were counted as seedlings if <1.3 m tall, and saplings if >1.3 m tall with a DBH <5 cm. Trees were defined as individuals taller than 1.3 m with a DBH of >5 cm.

To establish an estimate of fire history and stand age, four trees of both the dominant and subdominant canopy species (when applicable) were cored (the 2nd closest of each species to each corner) at breast height and at the root collar. In addition to tree cores, we cut disks from saplings and seedlings at the root collar to obtain the ages of these trees. Stand ages were calculated from tree core and disk samples by first mounting cores on boards to prevent breakage, sanding both the disks and mounted cores using a belt sander, with progressively finer-grained sandpaper, then scanning disks and cores on a scanner to load images to the computer. WinDendro™ (WinDendro 6.11, Regent Instruments, Québec) was used to count annual growth rings, and corrections were applied for distance above root collar. Seedling rings were counted using a microscope. Time since fire and time since stand-replacing fire were both determined in this procedure, using burn scars to differentiate. If burn scars were present in the sample, their location marked the time since the most recent fire. The total number of rings of the oldest tree indicated the last stand-replacing fire.

For soil data, our field protocol differed from the FEC protocol (Jiricka et al., 2002) in that we dug two soil pits per plot rather than one. We dug these soil pits to a depth of 1.2 m or as deep as possible (before hitting bedrock or the water table) and soils were assessed for texture, moisture regime and parent material. These pits were located just outside the plot beside the NE and SW corners, to avoid interference with vegetation estimation in the main plot. We classified moisture regime according to the FEC handbook, with 11 classes ranging from Dry to Very Wet (Jiricka et al., 2002). If mottling or gleying was apparent, we recorded this as well.

We determined vegetation community composition in the two 4 m² subplots by estimating cover classes (Table 1) for general ground cover (moss genus, lichen, rock, litter, woody debris, organic soil and mineral soil), and vascular plant species. Additionally, we estimated percent cover of each lichen species group separately within these plots and measured the depth of each lichen species group. Measuring the depth of the lichen entailed pushing the ruler down to the base of the lichen, which was typically the surface of the soil, and repeating this several times for each species and taking the average lichen thallus height (including live and dead material). In some cases where the lichen mat was very deep and the base of the lichen was decomposed, I considered the base of the lichen to be where the structural integrity of the lichen failed and it no longer had a cohesive structure. These detailed estimates of lichen cover and depth were later used for extrapolation to estimates of stand-level lichen abundance. When unknown plant or lichen species were encountered, we collected voucher specimens to be identified later. We estimated canopy cover of trees taller than 1.3 m in the main plot both as cover class of individual species, and as a percent of the total canopy.

Table 1: Cover classes for vegetation and ground cover estimation, class 0 is only applicable to vegetation estimates, not to ground cover.. Adapted from FEC field handbook (Jiricka et al., 2002).

Class	Description
0	< 1 %, only one individual of the species
1	< 1 %, more than one individual of the species
2	≥ 1 and < 5 %
3	≥ 5 and < 15 %
4	≥ 15 and < 25 %
5	≥ 25 and < 50 %
6	≥ 50 and < 75 %
7	≥ 75 %

Of the *Cladonia* spp. in this area that are most commonly used as forage, two species were lumped with others (*C. arbuscula* with *C. mitis*, and *C. stygia* with *C. rangiferina*) as these are difficult to distinguish in the field (Table 2). Another lichen that is important as forage is *Cladonia uncialis* (L.) F.H. Wigg., which was not included in the *Cladina* genus but has a similar growth form as these: fruticose but with a more limited branching structure. *Cladonia uncialis* has been shown to be a much-preferred forage type in some areas and is very common in northern Saskatchewan (Bergerud, 1971; Brodo et al., 2001). Kumpula et al. (2000) also used this grouping of 4 species in a study done in Finland in 2000. Henceforth, in this document “species” can be taken to mean species or lumped species group.

Table 2: Lichen species groupings used in the field.

Lichen species	Includes	Photo
<i>Cladonia mitis</i>	<i>Cladonia mitis</i> & <i>Cladonia arbuscula</i>	
<i>Cladonia stellaris</i>	<i>Cladonia stellaris</i>	
<i>Cladonia rangiferina</i>	<i>Cladonia rangiferina</i> & <i>Cladonia stygia</i>	
<i>Cladonia uncialis</i>	<i>Cladonia uncialis</i> & <i>Cladonia amaurocraea</i>	

In addition to percent composition estimation in subplots, we collected a destructive biomass sample of ground lichens semi-opportunistically at approximately every third plot. This sampling plan was selected to ensure a good representation of lichen cover types across the study area while minimizing sampling bias. Taking samples from every plot visited would have required more field storage capacity than was available, and lab processing is prohibitively time-consuming. Samples were 20 cm × 20 cm areas of ground cover that appeared to visually represent the lichen community in the plot, and typically contained several species. This method does involve some bias, in that the observer selecting the sites must be careful to select sites that have low, moderate and high lichen abundance, to maximise the variability of the total sample collection. However, the fact that sample storage was extremely limited, necessitated this type of selection on the part of the observer. True random sampling would require far more samples to adequately account for the range of variation in lichen abundance. The area for the sample was delineated with a folding ruler to ensure a consistent plot size. We estimated the percent cover and measured the average depth of each lichen species or species group. Depth of the lichen carpet was estimated as above. We took a picture of each sample *in situ* for future reference. We cut the samples out from surrounding vegetation using a serrated knife to ensure precise edges and stored them in labelled paper bags for transport. Upon return to the lab, destructive lichen samples were stored in an air-dry state at ambient room temperature in a well-ventilated space.

2.3 Allometric methods

2.3.1 Lab methods

I sorted the destructive lichen samples collected in the field one at a time to species. Non-lichen components such as leaf and needle litter, moss and soil were discarded. I put these samples into a drying oven (VWR International, LLC) at 30 °C for 24–48 hours, and then weighed them to the nearest 0.001 g.

Only 2015 ($n = 42$) and 2016 ($n = 30$) lichen samples were used as they were the only ones with depth measurements and consistent plot size. In 2014, depth was not measured, and plot area was not standardized so I chose to exclude these samples from allometric equation creation. Based on studies suggesting that the *Cladonia* species are the most valuable to woodland caribou, I chose to focus on the previously mentioned 4 species, as a total.

Both live and dead components of the lichens were included, as caribou likely also ingest the basal necromass while foraging (Storeheier et al., 2002a). It is difficult to distinguish live from dead, and a section of lichen may only live for 9–13 years before it dies, but remains palatable and nutritious thereafter before becoming necromass (Andreev, 1954). Therefore, as mentioned previously, the height measurement in the field included dead biomass, as it was hard to accurately assess the change point between live and dead. Basal necromass that was badly decomposed and had little to no discernible structure was excluded.

2.3.2 Analysis

Allometry is the study of correlations between size-based measures, or how one attribute of an organism changes as its size or shape changes (Enquist and Nicklas, 2001; Gould, 1966). To develop allometric equations I used measures of abundance density: biomass, volume and area were all standardized per unit area (m^2 or cm^2). This followed the units used in other studies (Kumpula et al., 2000; Moen et al., 2007). I produced one allometric equation for lichen area-based density measurements (cm^2/cm^2) and one for lichen volume-based density measurements (cm^3/cm^2), relating both to biomass abundance density (g/cm^2). Some studies of lichen abundance focus only on area-based measurements; however, in this study I produced both types of equations to determine whether volume is a better predictor of biomass. I hypothesized that, given the horizontal and vertical growth habits of ground lichens, volume would yield more accurate biomass estimates, as it involves a measure of lichen height (or depth of the lichen carpet). Nonetheless, there is also value in presenting allometric relationships for cover/area measurements as that has been used in other studies for estimating lichen biomass, and is a quicker measurement to take (Dunford et al., 2006; Sylvester and Wein, 1981; Thomas et al., 1996a). The species groupings were also summed to obtain the highest possible sample size ($n = 72$) after testing each grouping individually (Figure 2 & Figure 3). While each species group showed reasonable fit when plotted alone, a higher R^2 was obtained by using total lichen of the four species groups (Appendix A).

I tested different forms of transformations and equations including linear models with raw or log-transformed biomass and volume, power functions, and models with and without the intercept coerced to zero, several of which are presented in Appendix A. An intercept of zero implies that a value of 0 for lichen volume or area will correspond to a value of 0 grams of biomass. I assessed whether a power function would be appropriate for allometry by plotting the natural

logarithm of y (biomass/area) against x (area/area and volume/area), which is a standard method in allometry (Gould, 1966; Zar, 1968). As this linearized the relationship in neither case, I determined that a power law function resulted in overfitting of the data and therefore an equation of the form $y = mx^b$ was inappropriate. Furthermore, in the case of area-based estimates, as our samples are very small (400 cm²) it is ecologically very easy to reach 90–100% cover in small areas, but this is likely not the case on a larger scale, and so our samples, while useful for development of the allometric relationships, may not be ecologically relevant.

I selected a linear model for each candidate species/group, and decided to avoid transformation to ease the interpretation (Packard, 2013). Because the equations are based on small quantities of lichen, the influence of several high-volume points proved to be strong, (particularly sample 2015-073). Regardless, I chose to keep this site in the analysis, as it was not an error in data collection but rather represented an unusual type of site. In the area-based equation, removal of the outlier improved the R^2 of the relationship (from 0.80 to 0.85) but in the volume-based equation, removal slightly worsened the R^2 of the relationship (0.91 to 0.90). Several sites (called ‘X’ sites) were selected opportunistically to capture high-volume samples, and at two of these a destructive sample was taken. I tested the equations with the removal of these non-randomly sampled sites, and they did not alter the R^2 value or the slope of either equation (Appendix 1). These destructive samples taken at opportunistic sites were also not outliers as expected; the real outliers present were, in fact, part of the stratified random sampling. After equations were developed they were applied to subplot-level estimates of lichen area and volume and extrapolated to kg/ha units to determine stand-level lichen abundance.

2.4 Relationships with environmental characteristics

2.4.1 Boosted regression trees

I used boosted regression trees (BRTs), also known as gradient boosted models (GBM) to parse the relative influence of environmental covariates on 4 separate response variables: percent cover of lichen and volume of lichen, both in all stands and in jack pine stands. This technique has been gaining in popularity recently (Derville et al., 2016; Elith et al., 2008a; Elith and Leathwick, 2007), in part because of how it differs from traditional statistical frameworks such as linear modelling or

generalized linear modelling (GLM) or information theoretic approaches such as AIC (Akaike's Information Criterion) (Burnham et al., 2011; Burnham and Anderson, 2004).

Rather than building strictly from *a priori* hypotheses, BRTs assume the system in question is complex and unknowable to some degree, and seeks to identify patterns within datasets rather than testing various models against each other to determine which best fits the data (Elith and Leathwick, 2007). The construction of these models can be guided, to some extent, by *a priori* knowledge, but the main advantage of this technique is that it can aid in visualizing patterns, thresholds and trends without building from previous findings. It is also useful for assigning relative importance to each covariate, identifying the most important variables. BRTs combine many weak learners (decision stumps) together to create strong learners (regression trees). At each step (adding a new tree), the BRT models the residuals and uses that information in selecting the next step, decreasing predictive error iteratively. This is the "boosting" component (Leathwick et al., 2006). Each new tree is built by selecting an environmental covariate on which to split the tree, as in traditional classification and regression trees. The number of times a covariate is selected will determine its relative importance overall. BRTs handle non-normal (skewed) data, outliers and complex interactions very well, which are all major advantages over the earlier methods described above (De'ath, 2007; Elith and Leathwick, 2007). I used the packages 'gbm' (Ridgeway, 2017) and 'dismo' (Hijmans et al., 2017) in R open-source software (R version 3.2.3, R Core Team, 2015) to create BRTs relating environmental covariates to response variables describing lichen abundance (R Core Team, 2015). I also used package 'corrplot' to determine and visualize collinearity between covariates (Wei and Simko, 2017).

2.4.2 Variables

The environmental covariates used in the construction of the boosted regression trees were time since fire, time since stand-replacing fire, geographical location recorded as Universal Transverse Mercator (UTM) Easting and UTM Northing, moisture regime, basal area density, canopy dominance and stand type (Table 3). Basal area density was used as a proxy for light availability, as canopy cover values were highly subject to observer bias, and it has been shown that basal area density is a reasonable proxy for canopy cover in coniferous species (Cade, 1997; Mitchell and Popovich, 1997; Strong, 2011). Canopy dominance and stand type are collinear, so I selected the one which increased the percentage of explained error the most. These are not

necessarily a problem for BRT, but exclusion of collinear variables can help with interpretation of the final model. Canopy dominance is a derivative of stand type, with stand type being a factor with 10 levels and canopy dominance a factor with 5 levels. FEC type was not used as a variable, as this system of forest classification proved to be a poor representation of forest type for many of the stands we encountered, particularly for young stands (<15 years old). Stand type, created by rule-based classification, was selected via stepwise removal testing as the better variable for “forest type”, as it contains relatively more information (moisture regime is incorporated).

Time since fire and time since stand-replacing fire are strongly collinear, with a Spearman correlation coefficient of 0.79. Time since fire is likely to be a better predictor than time since stand-replacing fire when determining lichen abundance for both percent cover and volume measures, as I believe lichens are susceptible to even mild fires. Therefore, I selected time since fire as the most relevant measure of stand age after testing models with each. The use of a chronosequence approach or space-for-time substitution involves using multiple stands of different ages and relies upon the assumption that stands sharing major characteristics such as topography and moisture regime will be similar. However, sites are not identical, and some variability is to be expected (Walker et al., 2010). Lichens grow very slowly; therefore, older stands will contain more lichen. They are considered a fine fuel type based on their small stature, and have intermediate flammability, thus, even non-severe fires that do not destroy the trees in the stand are likely to wipe out these lichens (Sylvester and Wein, 1981). Because of their growth form, burning in non-severe fires will be limited to the top layer of the lichen mat, which will nonetheless likely destroy the regenerating ability of the lichens. The effect of stand age will be modified by environmental characteristics not directly linked to disturbance, such as humidity, occurrence of frost and drought, and other environmental conditions.

Table 3: List of predictor variables used initially in the boosted regression trees. Bolded names indicate variables that were included in at least one final BRT.

Variable	Type	Derivation	Mean (range)	Units
Time since fire	Numeric	Tree cores	41.5 (1–216)	Years
Time since stand-replacing fire	Numeric	Tree cores	53.1 (1–216)	Years
UTM northing	Numeric	GPS point	6317898 (6145025–6492023)	Metres
UTM easting	Numeric	GPS point	539049.4 (364224.7–687043.3)	Metres
Moisture regime	Numeric	Soil pits	4.3 (1–11)	Ordinal classes (1-11)
Basal area density	Numeric	DBH of trees in plot	9.3 (0–41.66)	cm ² /m ²
Canopy dominance	Factor	Simplified stand type	NA	Categorical (5 levels)
Stand type	Factor	Rule-based classification (Table 3)	NA	Categorical (10 levels)
McCune’s Heat Load Index	Numeric	Calculated	0.5 (0-1.0)	NA
Last fire type	Factor	Calculated	NA	Binary (0,1)

Geographic location is used in the models as two separate covariates, northing and easting. Easting may be a proxy for the effect of different ecoregions, as the sites which were furthest to the west occurred in the Athabasca Plain and the rest of the sites were in the Churchill River Upland.

The effect of moisture will be moderated by other environmental conditions. Therefore, rule-based classification of stand type was based upon canopy species dominance and moisture (Table 4). Effects of this variable on lichen abundance will likely be caused by the factors that are implicit in the stand type, rather than the stand type itself. Therefore, stand type on its own is not necessarily an explanatory variable for lichen abundance, but types such as jack pine (dry, open) will support the most lichen. For analyses, both stand type and the combination of moisture and canopy dominance were tested but only one of these could be used in the final model.

I calculated McCune's heat load index (HLI) for every plot to account for slope and aspect (McCune, 2007; McCune and Keon, 2002). Aspect requires transformation before use in a model, as both 1° and 360° indicate north. Being able to include degree of slope and latitude in the calculation is another benefit. Heat load index is unit-less and ranges from 0.0 – 1.0, with 1.0 having the greatest heat load.

Last fire type was a dummy variable (0,1) coded for whether the most recent fire was stand-replacing or not. A value of 1 indicated that the most recent fire had destroyed the existing trees and initiated stand replacement, and a value of zero indicated that the most recent fire was not severe enough to destroy the existing trees. While I believe time since the most recent fire is the best measure of stand age as even mild fires will destroy the lichen mat, I wanted to account for effects of last fire severity in the model.

I built 4 BRTs, one for percent cover in all stands, one for volume in all stands, and one of each (percent cover and volume) for a subset of the data that included only jack pine stands. The response variable for the first BRT was total percent cover (summed) of the four *Cladonia* lichen species groups that represent the principal sources of caribou forage (*C. mitis/arbuscula*, *C. stellaris*, *C. rangiferina/stygia* and *C. uncialis*). Percent cover was chosen as it is somewhat more intuitive when considering stand-level lichen cover. The second BRT shared the same environmental covariates but the response variable was volume (cm^3/m^2) of the four *Cladonia* lichen species groups. Attempting use of cm^3/cm^2 , as in allometric equation development, made raw deviance values very large and unwieldy, and so I chose to use cm^3/m^2 to simplify. Measures of lichen area and volume were used directly rather than the derived biomass estimates as these analyses were done concurrently. Also, it is more direct to predict abundance of lichen based on actual estimates from the field rather than biomass calculated indirectly, and extrapolation can be performed later if desired. The BRTs for jack pine stands both included a covariate which was not included in the BRTs for all stand types 'last fire type'. Last fire type was a factor coded for whether the most recent fire had replaced the trees in the stand or had simply scarred them and left them living. This covariate was tested in all BRTs but was irrelevant for the two BRTs for all stands (relative influence = 0%).

Table 4: Classification of forest stand types used in BRTs. This is a rule-based classification based on forest plots surveyed between 2014–2016 ($n = 312$)

Cover type	Forested	Drainage	Tree species dominance
Poorly-drained nonforest	nonforest	poorly-drained	NA
Well-drained nonforest	nonforest	well-drained	NA
Deciduous	forest	either poorly- or well-drained	$\geq 75\%$ deciduous
Mixed conifer	forest	either poorly- or well-drained	$< 75\%$ black spruce or jack pine but $\geq 75\%$ black spruce or jack pine combined
Hardwood-conifer	forest	either poorly- or well-drained	$< 75\%$ deciduous or conifer
Jack pine	forest	either poorly- or well-drained	$\geq 75\%$ jack pine
Poorly-drained black spruce	forest	poorly-drained	$\geq 75\%$ black spruce
Well-drained black spruce	forest	well-drained	$\geq 75\%$ black spruce

2.4.3 Selection of model parameters

Selecting the appropriate values for parameters of a boosted model is important. Two parameters in particular must be defined (learning rate and tree complexity), while others can usually be set at their defaults (Leathwick et al., 2006). The learning rate or shrinkage rate (lr), is the contribution of each weak learner (single decision tree) to the BRT as it grows and can range between 0 and 1 (Elith et al., 2008a). Typically, a smaller learning rate will translate to a larger optimum number of trees and more accurate predictions, although making it more computationally expensive (Friedman, 2001). I tested learning rate values of 0.0001, 0.001, 0.005 and 0.01. It appeared that 0.001 was the most appropriate value of learning rate, allowing the optimal number of trees to consistently rise above 1000, which is a suggested rule of thumb (Elith et al., 2008b). Studies often do not control or fix the number of trees if they are between 1000 and 10,000, and if they remain relatively consistent between runs (Chung, 2013; Elith et al., 2008b).

Tree complexity sets the interaction depth (number of nodes) allowed at each node of the BRT. Interactions are handled well in BRT; however, caution must be exercised to avoid overfitting the model. Functions for detecting interactions in BRTs are able to accommodate complex interactions, however, are only able to visualize 2-way interactions, and therefore variables involved in 3-way interactions must be inferred from this (Elith et al., 2008a; Lampa et al., 2014). Friedman's H measures the fraction of variance captured by the interaction between two variables that is not captured by the two variables independently (Friedman and Popescu, 2008). A value of Friedman's H of zero indicates no interaction. Interactions must be between variables explaining a high proportion of the variance. I have chosen to only present in detail the interactions that explained more than 10% of the variance, as this variance is already present in the model, within the individual variables' relative influence (Elith et al., 2008b). Interactions are quantified using a grid of the variables and relationships measured with a linear predictor, separately from individual variables' relative influence (Chung, 2013; Elith et al., 2008a).

In selecting parameters, I aimed first for an optimum number of trees to be greater than 1000 and less than 10,000. Most parameter combinations I selected allowed for that, and those that created small or overly large numbers of trees were eliminated. For tree complexity, a value of 1 led to overly large numbers of trees, and somewhat variable/unstable model results in all cases. I achieved stable results with a tree complexity of $tc = 3$ for percent cover, and $tc = 2$ for volume. The best combination of parameters and explanatory variables for both types of models (either having percent cover or volume of lichen as the response variable) were those in which collinear variables had been removed.

Other parameters may also be modified to ensure they are appropriate for the data and model to be fitted; however, in this case they were mostly left at their defaults. These parameters include but are not limited to: number of initial trees to fit, step size, number of cross-validation folds. The response to each explanatory variable can be constrained to be either positively monotonic or negatively monotonic or left unconstrained. Monotonic (unidirectional increase or decrease) constraints are applied to continuous variables, where appropriate, based on the initial run of the boosted regression tree function and *a priori* knowledge of the system. Northing and easting exhibited an overall pattern of positive monotonicity (increasing, without decrease), as did time since fire and time since stand-replacing fire. I chose not to constrain basal area density monotonically, as lichen biology suggests it should show a unimodal relationship: both low and

high values of basal area density leading to worse conditions for lichens. For example, conditions may not be right for growth in extremely open areas, or in very dense areas because of insufficient light and competition with moss (Maikawa and Kershaw, 1976; Morneau and Payette, 1989). Moisture, an ordinal factor (11 classes) initially showed highly variable relationships with lichen percent cover, and was used in preliminary models as a continuous variable. It was not constrained monotonically, as its relationship with lichen abundance is variable and relatively unpredictable. Lichens overall are more tolerant of extended dry periods than most vascular plants and bryophytes, as they go into a dormant state (not expending energy) when conditions are unsuitable. The moisture variable was removed from the analysis after the first few models, as it is closely tied to vegetation community type and is accounted for in the stand type variable. Some researchers also trim their BRTs to exclude variables explaining less than 10% of the variance (Elith et al., 2008a; Wang et al., 2015); however, this is optional and in analyses with few variables, there is little value in simplifying (De'ath, 2007; Derville et al., 2016), and so I left these variables in.

2.4.4 Interpreting model output

The output of a boosted regression tree includes raw deviance (error) values, so for ease of interpretation I converted them into percentage values (percent error explained, or pseudo- R^2) and used these to assess model performance. Pseudo- R^2 is calculated from the training error, while cross-validation pseudo- R^2 corresponds to test error, or, the error encountered when the model is run on the holdout set at each fold of cross-validation.

Percent error explained (pseudo- R^2) can be used to compare models. The higher the percentage of explained error, the better the model. The formula for calculating percent of error explained by the model (pseudo- R^2) is (Derville et al., 2016; Elith et al., 2008a):

$$\text{Percent error explained} = \frac{\text{Total error} - \text{Residual error}}{\text{Total error}} * 100$$

The formula for calculating percent cross validation (CV) error is the same as above but with CV error replacing residual error in the equation. For each model, one can determine its effectiveness and applicability by comparing percent of CV error explained with percent of residual error explained. Percent CV error explained will always be lower than percent error explained, as percent CV error explained reflects error explained on test sets withheld from training data. Comparing

these two values gives an estimate of how generalizable the model is; consequently, smaller differences between CV error and residual error are preferred (De'ath, 2007). Additionally, each model's CV error must be compared to the CV error of all other models. The goal is to attain as low a value as possible while maintaining stability between several runs.

The best BRT for percent cover did not include a moisture variable, and positive monotonic constraints were imposed upon time since fire, northing and easting (all continuous variables). A similarly good model appeared when time since fire was left unconstrained, with slightly lower values of percent variance explained on test sets (<10% difference). Nonetheless, I selected the model with time since fire constrained as I suspected the relationship was unidirectional, and any apparent decreases followed by increases through time may be by-products of the chronosequence approach.

The design of the best BRT for volume (cm^3/m^2) was like the percent cover model design in many ways; it had a learning rate of 0.001, time since fire was used in place of time since stand-replacing fire, the moisture variable was removed, and the same positive monotonic constraints were applied (to time since fire, northing and easting). The main difference between the constructions of the percent cover model and the volume model was the tree complexity.

The volume BRT only stabilized with a tree complexity of 2, unlike the percent cover model. This was supported when I created an identical BRT but with a complexity of 3, calculated the Friedman's H of each interaction and ranked them. Three-way interactions were extremely low on the list, meaning they were not required by the BRT very often. Allowing three-way interactions also decreased model stability and thus I chose a tree complexity of 2.

The jack pine percent cover BRT was fitted similarly to the previous models, and I performed parameter tuning separately, albeit guided by previous model construction. This tree had no moisture variable, in keeping with the full models. Positive monotonic constraints were imposed upon time since fire, northing and negative monotonic constraints were imposed upon easting and basal area density, based upon initial runs of the model. While jack pine stands typically occur on south-facing slopes, they can occur on flat ground or on slopes of any aspect, so long as they are well-drained. For this reason, I included heat load index and did not test inclusion of moisture as a variable in the model. The best BRT for lichen volume in jack pine stands also had a

tree complexity of 2, and a learning rate of 0.001. The same monotonic constraints were applied as for the jack pine percent cover BRT.

3 RESULTS

3.1 Allometry

Lichen cover and volume both appear to be good predictors of biomass. Linear trendlines for area measurements and their associated biomass density values in *C. mitis* and *C. stellaris* exhibit good fits (Figure 2A & 2B). The linear trendline for *C. uncialis* has the worst fit. The coefficients (slopes) of the *C. mitis* and *C. uncialis* models for area are the most alike, which is a product of their similar morphology (Figure 2A & 2D). Models for *C. stellaris* and *C. rangiferina* (Figure 2B & 2C) have steeper slopes when related to area, but when related to volume (Figure 3B & 3C), *C. stellaris* has a slightly less steep slope while *C. rangiferina*'s slope is highly comparable to *C. mitis* and *C. uncialis*. In the destructive samples, cover for the species ranged from 1 – 100%, while average depth ranged from 0.5 – 12 cm. A depth of 12 cm was only encountered at one plot. *C. mitis* and *C. uncialis* were the most common species, occurring with high cover values, but typically not attaining great depths, especially in young stands. *C. stellaris* and *C. rangiferina* tended to be present in older stands, and were able to attain greater depths than either *C. mitis* or *C. uncialis*. One outlier, sample 2015-073a, was taken at a 171 year old poorly-drained black spruce bog.

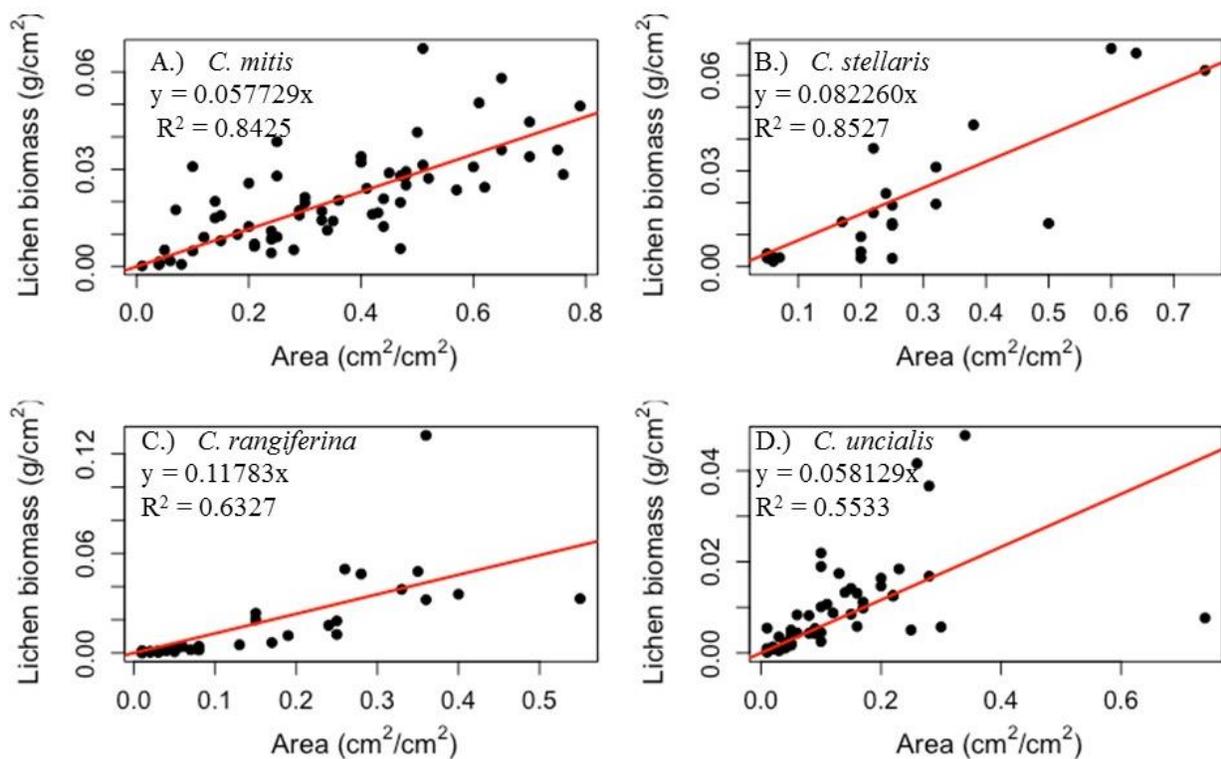


Figure 2: Linear allometric relationships between lichen area (cm²/cm²) and biomass (g/cm²). Clockwise from top left, plots are A.) *Cladonia mitis* B.) *Cladonia stellaris*, C.) *Cladonia rangiferina* and D.) *Cladonia uncialis* . All linear trendlines fitted with a zero-intercept. Units of the x axis (biomass) are g/cm², units of the slope are g/cm². Y-axis range varies between panels.

The slopes of the volume equation trendlines for each species (Figure 3) were less steep than those of the area equation trendlines in all cases. The goodness of fit was similar for both versions of the *C. mitis* and *C. stellaris* equations (Figure 2A, 3A, 2B and 3B). The goodness of fit is much improved for *C. uncialis* in the volume model over the area model (Figure 2D & 3D). *C. rangiferina* has a better fit with the volume model (Figure 2C & 3C), although the slope is much changed by the inclusion of the depth component, being much steeper in the area-based equation. This suggests that depth is a particularly important consideration for this species.

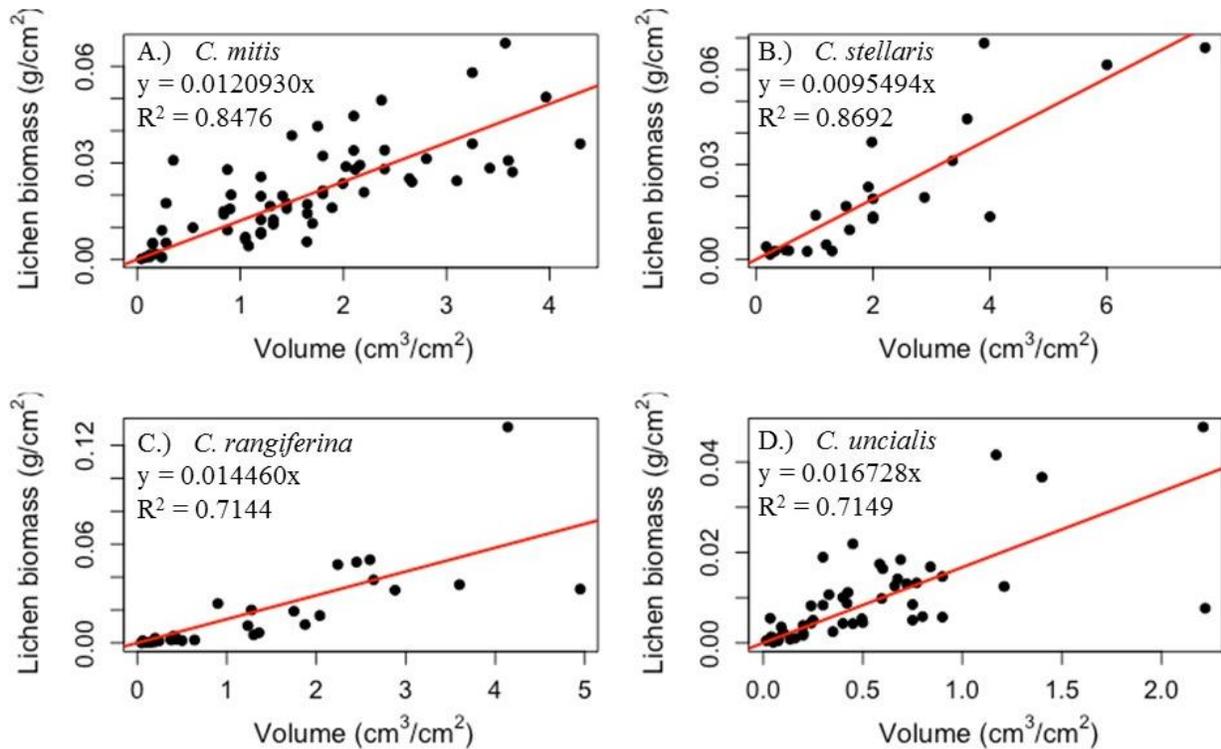


Figure 3: Linear allometric relationships between lichen volume (cm^3/cm^2) (average depth and total percent cover) and biomass (g/cm^2). Clockwise from top left, plots are A.) *Cladonia mitis*, B.) *Cladonia stellaris*, C.) *Cladonia rangiferina*, and D.) *Cladonia uncialis*. All linear trendlines are fitted with a zero-intercept. Units of the x axis are g/cm^2 , Units of the slope are g/cm^3 . Y-axis range varies between panels.

Having built equations for individual species I also built them for the sum of these 4 *Cladonia* species. I selected a linear model both for density-based area and density-based volume measures related to biomass, with a zero-intercept in all cases. The area equation had a slope of 0.075067 with a standard error of 0.004438, and the volume equation has a slope of 0.0133234 with a standard error of 0.0004834. The outlier, sample 2015-073, was included in both equations, because although I tested removal of the outlier I found it to worsen the fit of both lines and therefore the performance of both equations. Without the outlier, the area equation had a slope of 0.070412 (SE = 0.003499). The volume equation without the outlier had a slope of 0.0127532 (SE = 0.0004918). As these coefficients and standard error values were stable whether the outlier (2015-073) was included or not, I chose to include it. The fit of the linear trendlines to points representing destructive samples of lichen was similarly good whether the points' x-values were lichen cover density ($R^2 = 0.80$) or lichen volume density ($R^2 = 0.91$) (Figure 4).

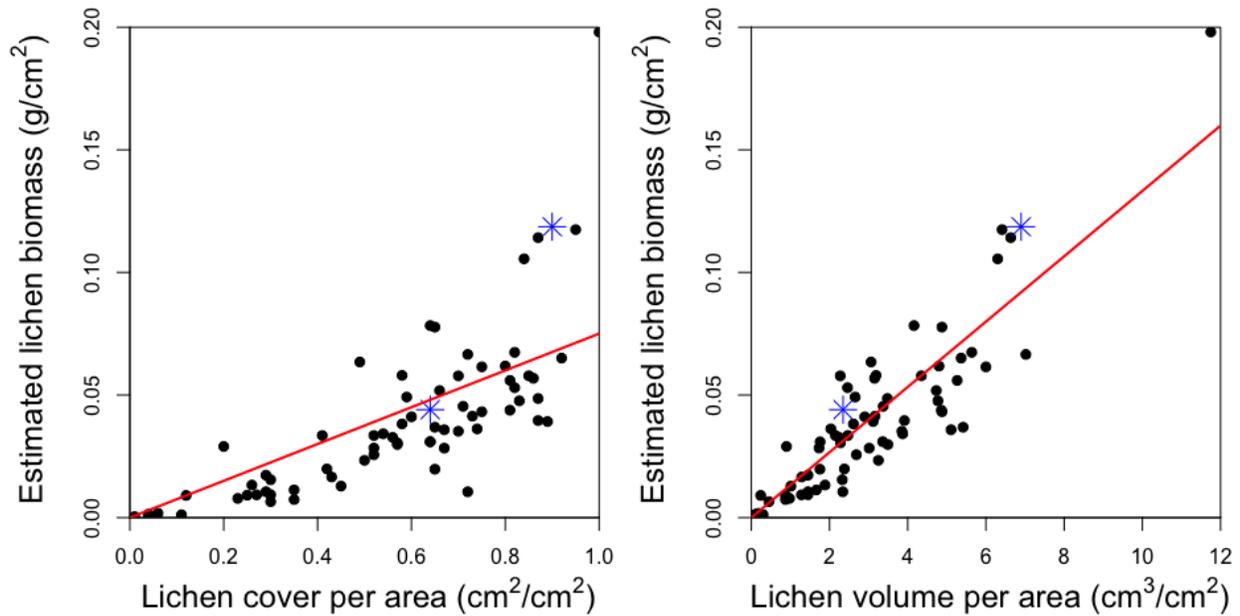


Figure 4: Allometric relationships between lichen biomass (g/cm²) and either A.) lichen cover (cm²/cm²) ($n = 72$) or B.) volume (cm³) per unit area (cm²) ($n = 72$). Allometric equation for all 4 species is A.) $y = 0.075067x$ with a zero-intercept. $R^2 = 0.80$, $p < 0.001$, $SE = 0.004438$ or B.) $y = 0.0133234x$ with a zero-intercept. $R^2 = 0.91$, $p < 0.001$, $SE = 0.0004834$. Blue stars indicate points that were opportunistically sampled (not as part of the random sampling scheme).

Extrapolating from the area and volume estimates made at each plot to biomass abundance produced overall similar trends for each stand type but with some differences (Figure 5 & Table 5). In general, lichen abundance increases as time since fire increases. Jack pine stands accumulated lichen the most rapidly after fire, with high values of lichen present as early as 35 years after fire. Poorly-drained black spruce showed slower lichen accumulation, while mixed conifer and well-drained black spruce stands showed moderate lichen abundance after approximately 40 years after fire. Jack pine and poorly-drained black spruce were the stand types with the highest biomass accumulation for both area and volume calculations (Figure 5). However, lichen biomass in poorly-drained black spruce was notably higher when calculated using the volume equation than when using the area equation (Table 5). The volume equation also greatly magnified the estimated biomass of several points, such that the estimated biomass for the volume point with the largest value was approximately double the value of its estimated biomass when calculated using area (Table 5). Jack pine stands appeared to experience a wider range of variation in lichen abundance at ~35 years of age, which had a more uniform distribution in the estimates calculated using percent cover. While the maximum biomass was approximately the same when calculated with percent

cover and with volume, a t-test on the data in 34–35 year old pine stands showed that the variance of cover-based and volume-based estimates were not the same ($p < 0.001$). Deciduous and poorly-drained non-forest had the least lichen biomass (Table 5). Other stand types (well-drained non-forest, conifer mix, well-drained black spruce, and hardwood conifer) have similar means, with similar ranges of values whether calculated with cover-based or volume-based equations (Table 5).

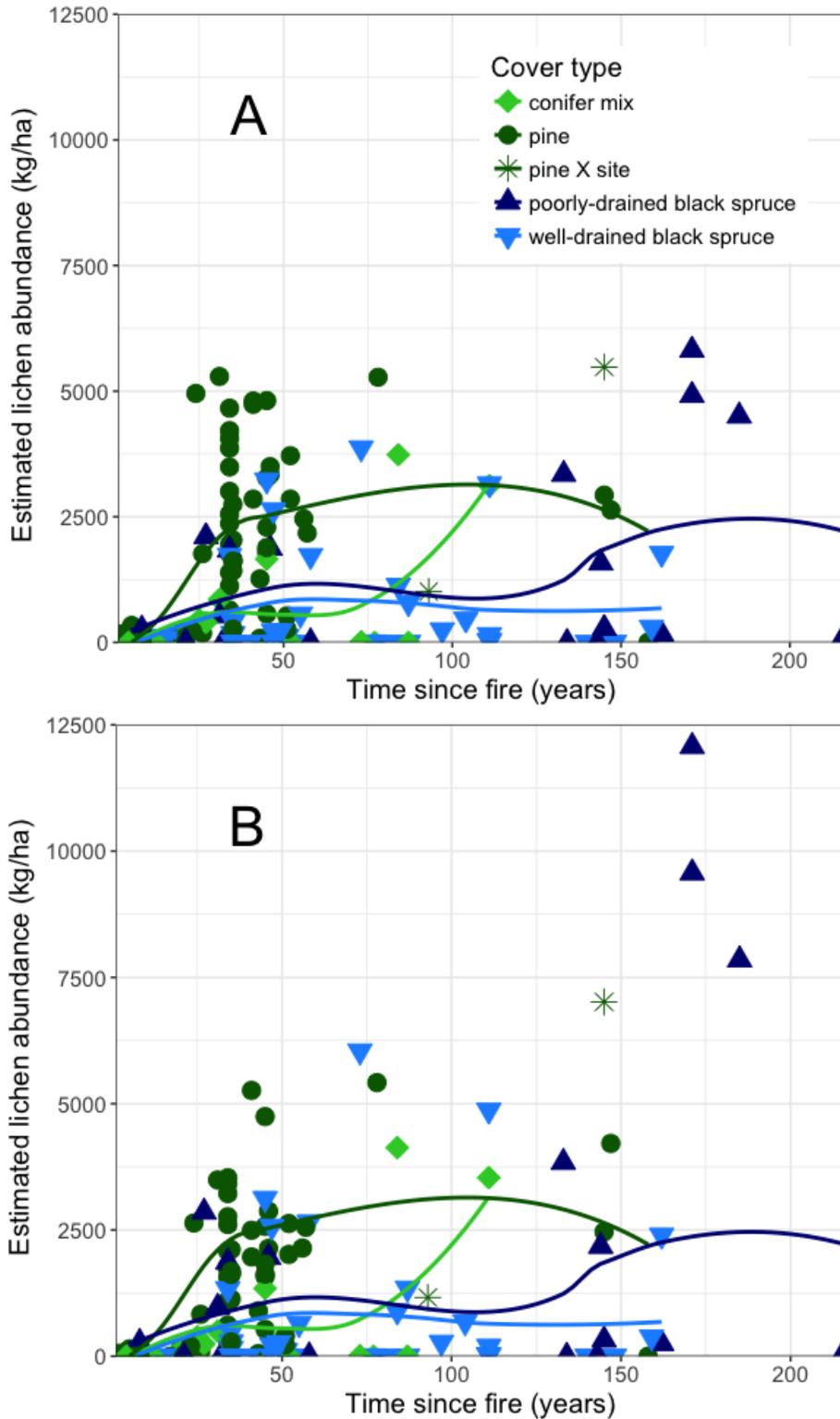


Figure 5: Projections of estimated lichen biomass (kg/ha) as relates to stand age at 220 sites calculated from A.) cover measurements (cm²/cm²) and B.) volume measurements (cm³/cm²) for each of the 4 stand types with the overall highest abundance. Curved lines are loess smoothing functions for each stand type. “X” sites indicate sites which were surveyed opportunistically, not as part of the random sampling. In high-abundance stands there were only 2 such sites and they were both in pine stands.

Ranges for lichen biomass in individual stand types were overall broader when calculated using volume than when calculated using area, except in the two non-forest types (poorly-drained and well-drained) (Figure 5 & Table 5). The main differences between converting to biomass estimates based upon area- or volume- based measures were in overall quantities (volume typically implies larger quantities) and in pine stands, a more even distribution when calculated using area (across a shorter range). In the case of pines, it manifested as a lower mean for volume-based predictions than for area-based predictions. The same pattern was true for the sum of all stand types overall.

Table 5: Maximum values and means (± 1 SE) of projected biomass estimates (kg/ha) calculated from allometric equations applied to estimates of lichen area and volume across all 2015-2016 plots ($n = 221$). The minimum value of lichen biomass is 0 in all cases. Table is ordered according to highest maximum lichen biomass as predicted by area- based allometry.

Stand type	n	Area		Volume	
		Mean (± 1 SE)	Maximum	Mean (± 1 SE)	Maximum
All types	221	908.74 \pm 97.66	5817.69	897.02 \pm 114.08	12071
Poorly-drained black spruce	19	1440.69 \pm 433.81	5817.69	2321.73 \pm 824.60	12071
Pine	78	1576.55 \pm 195.02	5479.89	1292.46 \pm 174.87	7014.77
Well-drained black spruce	44	537.92 \pm 148.71	3869.70	659.37 \pm 200.74	6041.59
Conifer mix	18	586.98 \pm 264.31	3734.58	587.51 \pm 289.85	4130.25
Well-drained non-forest	15	428.63 \pm 254.73	3265.41	260.43 \pm 160.35	2153.73
Hardwood-conifer	23	335.03 \pm 162.65	2574.80	358.28 \pm 190.00	3108.68
Poorly-drained non-forest	15	84.45 \pm 54.56	679.36	47.75 \pm 29.70	341.75
Deciduous	9	2.92 \pm 0.83	7.51	1.96 \pm 0.86	7.99

Poorly-drained non-forest had relatively low lichen biomass, but deciduous stands had the least forage lichen biomass by several orders of magnitude. In my study area, mixed conifer stands had a similar mean whether calculated with area or volume, and had similar values to well-drained black spruce stands (Table 5). Pine stands had higher cover and poorly-drained black spruce stands had amassed greater volume. There is an interesting trend in lichen percent cover in jack pine stands at approximately 35 years since fire (Figure 5). At this age, stands of this type can exhibit nearly

any value of percent cover. This type of temporal patterning is not apparent in any other stand types, and a similar pattern is not observed for volume measures of lichen in these stands. One potential explanation is that we surveyed more jack pine stands ($n = 78$) than any other stand type.

3.2 Effects of environmental characteristics on lichen abundance

The boosted regression trees for percent cover and volume, for all stands and for jack pine stands, share many similarities but their differences indicate important considerations for measuring and estimating lichen abundance. The best BRT for percent cover in all stands explained 45.6% of the total variance on 4600 trees, calculated on the holdout sets (the test data) from each of the cross-validation folds (Figure 6). When calculating the relative influence of each variable, this BRT selected time since fire as the split variable the most often, accounting for 32.3% of total variance explained (Figure 6A), followed by basal area density (21.7%) (Figure 6B). Stand type and northing followed (20.5% and 17.2%, respectively) (Figure 6C & 6D), heat load index (4.8%) and easting showed the lowest contribution to the tree (3.6%) (Figure 6E). A large increase in percent cover occurs at approximately 35 years after fire, with a smaller increase at 150 years (Figure 6A). The effect of basal area density on lichen cover was not constrained monotonically in the model design, and so at both very low ($0\text{--}2\text{ cm}^2/\text{m}^2$) and high values ($20\text{ cm}^2/\text{m}^2$) of basal area density, lichen cover is relatively low, whereas low values ($2\text{--}10\text{ cm}^2/\text{m}^2$), lichen cover is at its highest when all other covariates are held at their mean (Figure 6B). Poorly-drained non-forest exhibits the lowest percent cover of lichens, while jack pine stands have the highest lichen cover relative to other stand types. Northing, even when unconstrained, exhibited a monotonic increase in lichen cover, while areas further east had relatively less lichen than areas in the west. The effect of easting is modified by the shorter east-west range of our study area. Heat load index values were clustered around a value of 0.5, which caused a spike in lichen cover, but overall, higher heat load is related to increased lichen cover.

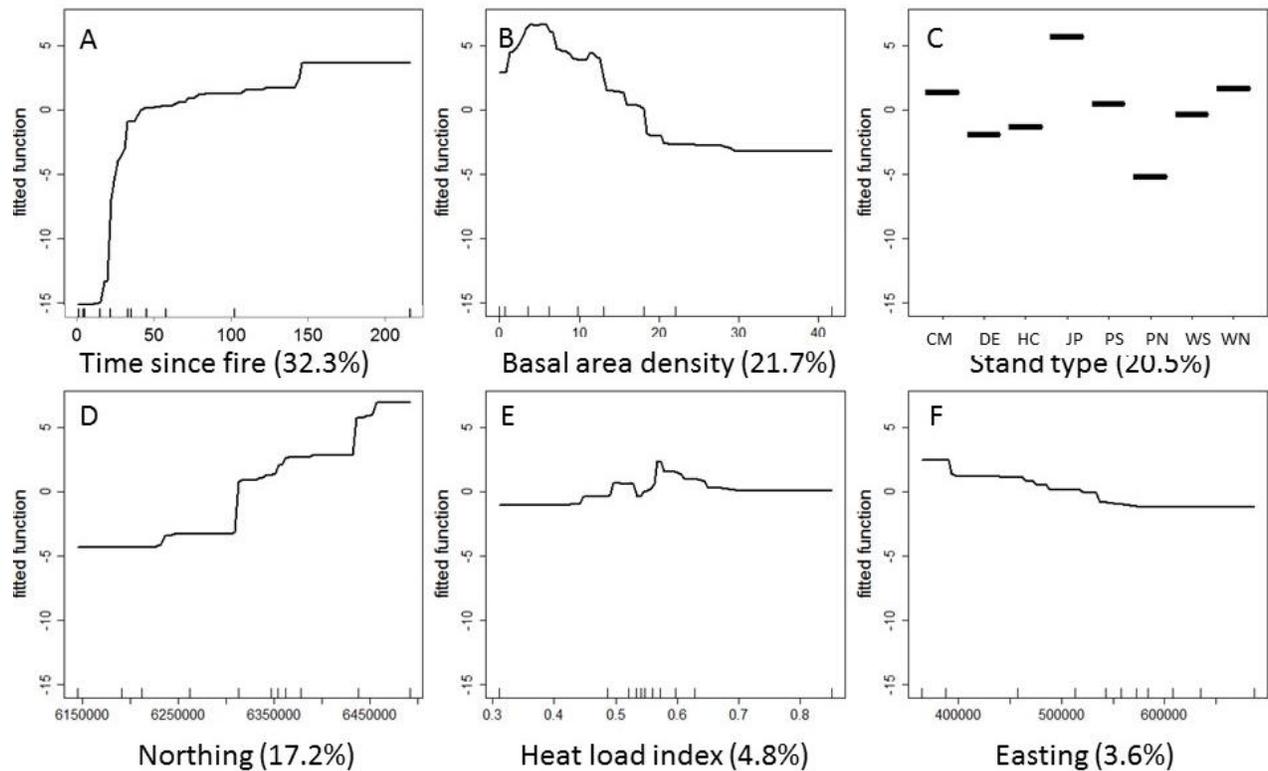


Figure 6: Partial dependency plots for final boosted regression tree model of percent cover. Partial dependency plots demonstrate the marginal effect of the variable in question on the response variable (lichen cover) when all other variables are held at their mean. The y-axes are centered at a zero-mean. A.) Time since fire; B.) basal area density; C.) stand type (Stand type categories from left to right, are: CM-conifer mix, DE- deciduous, HC- hardwood-conifer, JP- pine, PS- poorly-drained black spruce, PN- poorly-drained non-forest, WS- well-drained black spruce, WN- well-drained non-forest); D.) northing; and E.) easting. Deciles (inner tick marks plotted along the x-axes) indicate the distribution of data with regards to the variable in question. The percentage values included with the x-axes labels are the relative influence of the variable in the model (sums to 100% for all variables and interactions).

The most important two-way interactions in the percent cover model (with Friedman’s $H > 0.1$) were heat load index and easting, stand type- basal area density, time since fire-stand type, time since fire-northing, time since fire and basal area density and northing-basal area (Figure 7 & Table 6). Three-way interactions were detected and modelled by the BRT, and while inclusion of three-way interactions was required to achieve stability between repeat runs, the 3-way interaction with the highest importance was only the 7th most important interaction (between time since fire, basal area, and stand type (Table 6). The 2nd and 3rd most important interactions both involved stand type, and it is apparent that these consisted mostly of differences between stand types while patterns relating lichen percent cover to basal area density and time since fire, respectively, follow the same patterns in each stand type of overall decrease and increase (Figure 7). The interaction

between heat load index and easting (Figure 7A) indicates a pattern of the stands farthest to the west with a heat load value greater than 0.5 having the highest lichen percent cover, followed by stands in the west with a value of HLI lower than 0.5 (Figure 7A).

Table 6: Two-way and three-way interactions present in the best BRT for lichen percent cover in all stands. Interactions are sorted by Friedman’s H value*. Bolded interactions are those above H > 0.1 threshold.

Variable 1	Variable 2	Variable 3	Friedman's H
Easting	Heat load index	.	0.3403
Stand type	Basal area density	.	0.2867
Time since fire	Stand type	.	0.2862
Time since fire	Northing	.	0.2253
Time since fire	Basal area density	.	0.2116
Northing	Basal area density	.	0.1412
Time since fire	Basal area density	Stand type	0.1308
Stand type	Easting	.	0.1074
Stand type	Northing	.	0.0885
Easting	Basal area density	.	0.0624
Basal area density	Heat load index	.	0.0506
Time since fire	Northing	Stand type	0.0418
Time since fire	Easting	.	0.0379
Time since fire	Heat load index	.	0.0359
Stand type	Heat load index	.	0.0297
Northing	Heat load index	.	0.0237
Time since fire	Northing	Basal area density	0.0148
Time since fire	Easting	Stand type	0.0144
Easting	Northing	.	0.0115
Heat load index	Stand type	Easting	0.0076
Time since fire	Northing	Heat load index	0.0045
Time since fire	Basal area density	Heat load index	0.0043
Time since fire	Easting	Basal area density	0.0032
Time since fire	Heat load index	Stand type	0.0031
Time since fire	Easting	Heat load index	0.0016
Heat load index	Stand type	Basal area density	0.0014
Heat load index	Stand type	Northing	0.0012
Time since fire	Easting	Northing	0.0008

*Note: Friedman’s H ranges between 0.00–1.00, with higher values meaning greater proportion of total variance of the partial dependence functions of the two variables (Friedman and Popescu, 2008). Calculated using *interact.gbm* in the *gbm* package (Ridgeway, 2017)

Again, all stand types follow the same pattern when they interact with a variable, but pine consistently displays the highest lichen cover, especially at low values of basal area density and in old stands (Figure 7B & 7C). Stands farther north have higher values of lichen, especially in older stands and in stands of low-intermediate tree density (approximately 2–10 cm²/m²) (Figure 7D & 7F). Young stands show low lichen cover regardless of basal area density, with highest lichen cover occurring in older stands with low-intermediate tree density (Figure 7E).

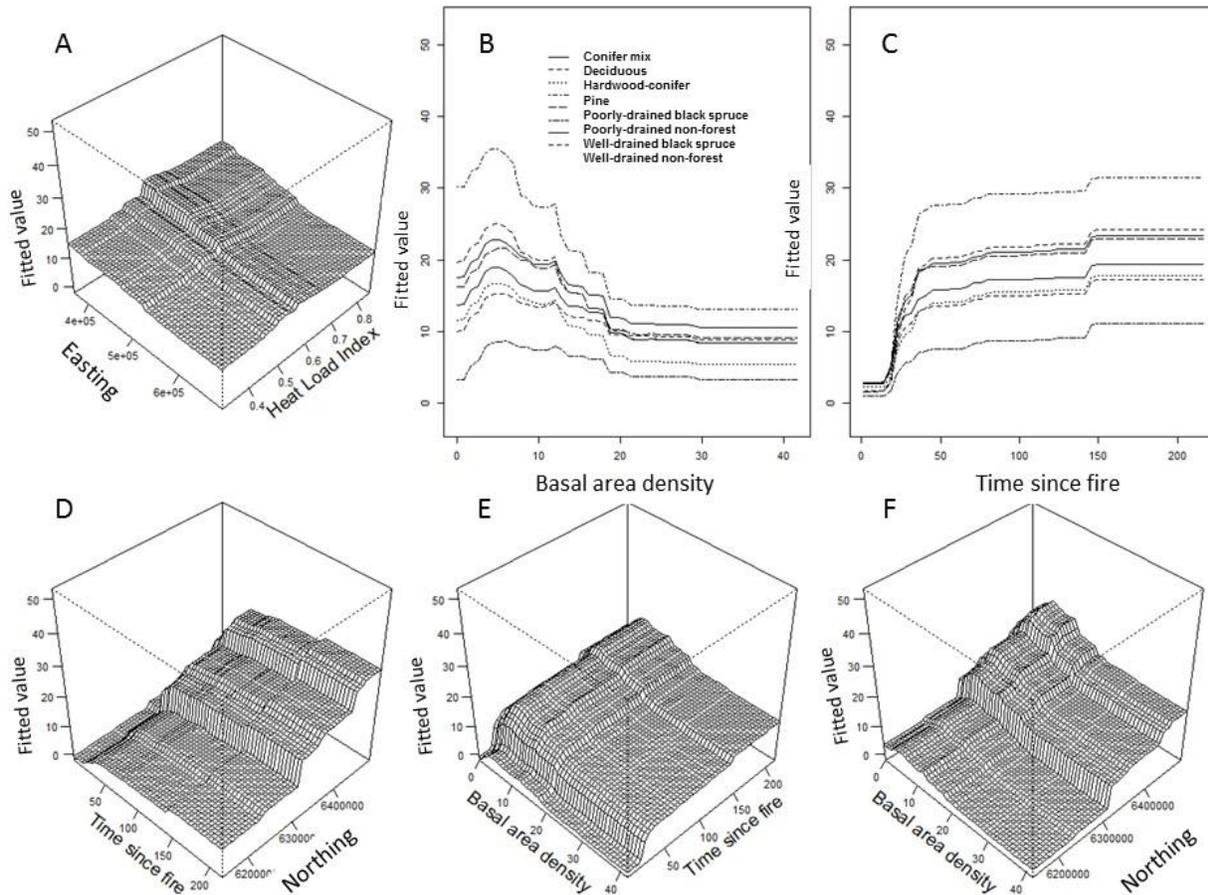


Figure 7: Interaction plots for the top 6 pair-wise interactions ($H > 0.1$) in the BRT model predicting lichen percent cover. Each panel shows the effects of two interacting variables on the fitted values of the response variable while all other covariates are held at their mean. Panels illustrate (clockwise from top left): A.) basal area and stand type, B.) stand type and stand age, C.) basal area and stand age, D.) stand age and northing, E.) basal area and northing, F.) northing and stand type. Vertical scale indicates the fitted values of lichen percent cover.

The volume model grew 5100 trees, and explained 31.3% of the total variance on the holdout sets. While the BRTs for percent cover and volume show similar patterns, the relative importance was different. This model shows, again, time since fire is the most important variable (48.6%) (Figure 8A), but here, northing appears as the second most important variable, accounting for 22.6% of explained variance (Figure 8B). Following this, basal area density explained 13.2% of the variance (Figure 8C), stand type 8.2% (Figure 8D), easting 4% (Figure 8E) and heat load index 3.3% (Figure 8F). In this BRT, time since fire has a major threshold of increase in lichen volume at 150 years after fire, much later than in the percent cover BRT. Notably, here time since fire accounted for nearly half (48.6%; in the percent cover model it was 32.3%) of the explained variance (Figure 8 & 6). Stand type shows different patterns in this BRT than in the previous one. Poorly-drained non-forest still has the least lichen abundance, but jack pine is no longer the clear leader in terms of lichen abundance. Poorly-drained black spruce stands appear to have slightly higher relative volume of lichen than jack pine stands (Figure 8D).

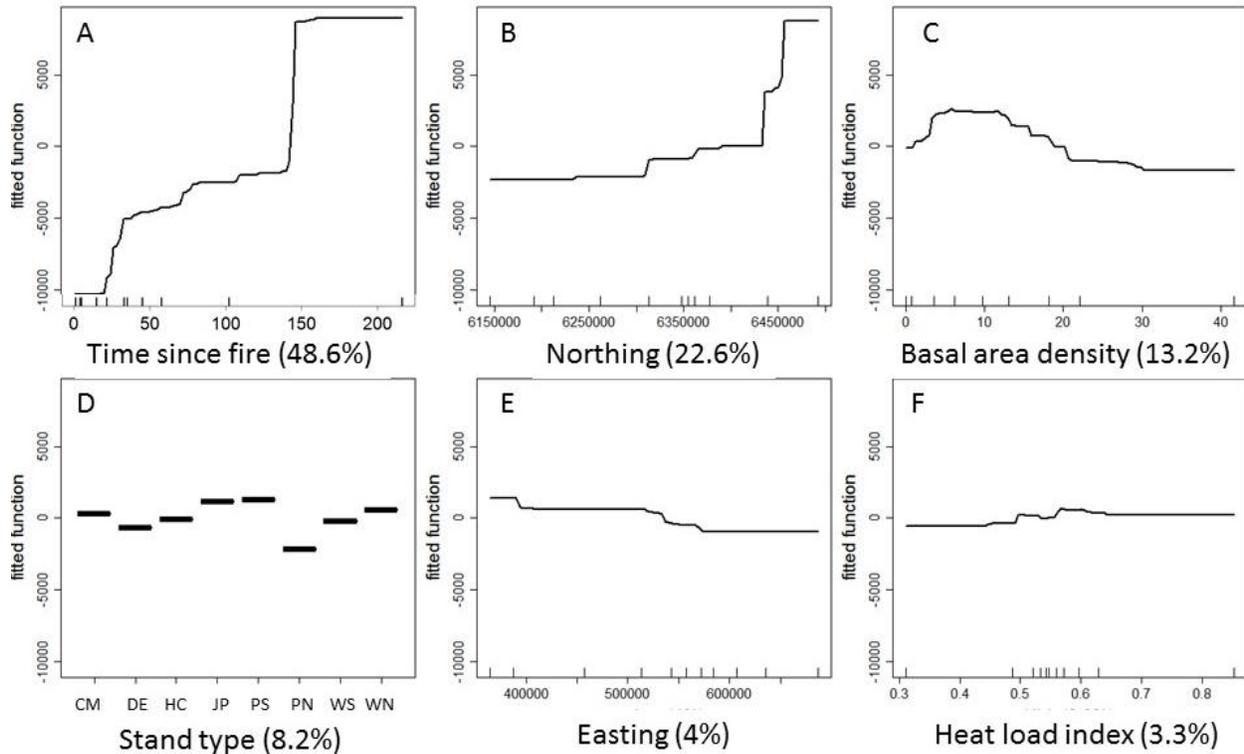


Figure 8: Partial dependency plots for final boosted regression tree model of volume. Partial dependency plots demonstrate the marginal effect of the variable in question on the response variable (lichen volume density) when all other variables are held at their mean. The y-axes are centered at a zero-mean. A.) Time since fire, 53.8% of the variance B.) Northing, 24.3% of the variance, C.) Basal area, 12.8% of the variance, D.) Stand type, 8% of the variance. Stand type categories from left to right, are: conifer mix, deciduous, hardwood-conifer, pine, poorly-drained black spruce, poorly-drained non-forest, well-drained black spruce, well-drained non-forest. E.) Easting, 1.1% of the variance. Deciles (inner tick marks plotted along the x-axis) indicate the distribution of data with regards to the variable in question. The percentage values included with the x-axis labels are the relative influence of the variable in the model (sums to 100% for all variables and interactions).

The volume model did not support the inclusion of three-way interactions. Interactions were generally less important in the volume model, and so I selected a threshold to maintain perspective when comparing interactions between BRTs. I selected an arbitrary threshold of Friedman’s $H > 0.1$, as it appeared from the interaction partial dependency plots that interactions below this were mostly noise. The most important two-way interactions were time since fire-northing, northing and basal area density, and easting-heat load index (Figure 9 & Table 7).

Table 7: Two-way interactions present in the best volume BRT for lichen volume in all stands. Interactions are sorted by Friedman's H value. Bolded interactions are those above $H > 0.1$ threshold.

Variable 1	Variable 2	Friedman's H
Time since fire	Northing	0.1771
Northing	Basal area density	0.1374
Easting	Heat load index	0.1328
Stand type	Easting	0.0858
Stand type	Basal area density	0.0781
Time since fire	Stand type	0.0754
Time since fire	Basal area density	0.0693
Stand type	Northing	0.0599
Easting	Basal area density	0.0307
Basal area density	Heat load index	0.0293
Time since fire	Heat load index	0.0261
Time since fire	Easting	0.0226
Stand type	Heat load index	0.0218
Easting	Northing	0.0068
Northing	Heat load index	0.0058

The threshold visible in the partial dependency plots for time since fire at ~150 years is clearly visible also in the interaction plots, and is further moderated by northing (Figure 8A & 9A). Old stands, far north, contained the most lichen volume, overall, followed by moderately aged northern stands and old stands to the south (Figure 9A). This trend remains true in the second most important interaction, basal area density- northing. Lichen volume is highest in the northernmost stands, especially at low-moderate basal area density (Figure 9B). The interaction between HLI and easting shows a less conspicuous surface when scaled to correspond with others, indicating a small effect size (Figure 9C).

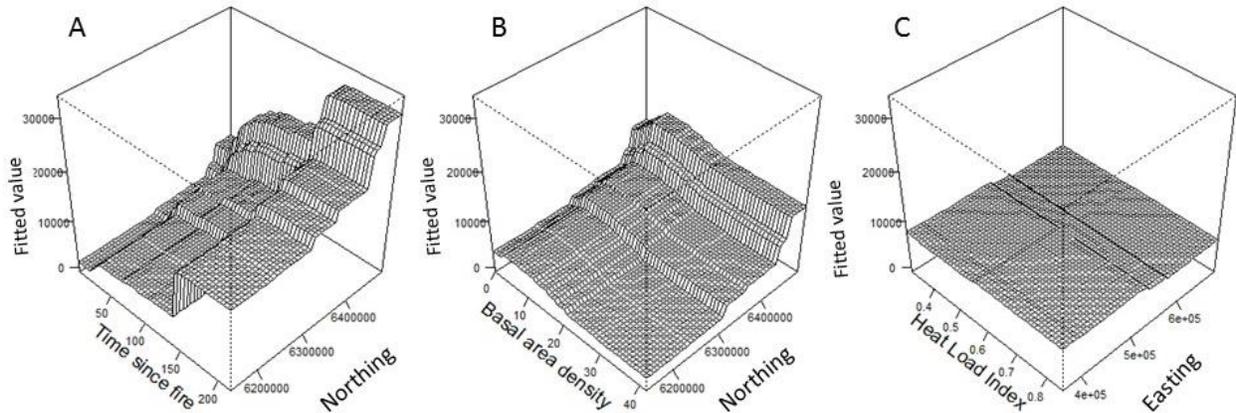


Figure 9: Interaction plots for the top 3 pair-wise interactions ($H > 0.1$) in the BRT model predicting lichen volume. Each panel shows the effects of two interacting variables on the fitted values of the response variable while all other covariates are held at their mean. Panels illustrate (L-R): A.) stand age and northing, B.) basal area density and northing, C.) easting and stand type. Vertical scale indicates the fitted values of lichen volume (cm^3/m^2).

The best model for jack pine percent cover built 4350 trees and explained 56.5% of the error on the holdout sets. Within the model, 55% was explained by time since fire (Figure 10A), 30.4% by basal area density (Figure 10B), 7.1% by easting (Figure 10C), 3.7% by heat load index (Figure 10D), 2.4% by northing (Figure 10E), and 0.8% by a last fire type (Figure 10F).

Having separated the jack pine stand data from the rest of the stand types, the best BRT on this subset indicates, again, that time since fire is the most important characteristic influencing lichen percent cover (%), with a notable threshold in increased cover at around 25 years since fire (Figure 10A). However, basal area density appears to be the next most important variable, and in this case did not appear to have a unimodal relationship but a negative one, with highest lichen appearing in the least densely treed areas. Lichens in jack pine stands exhibited higher cover in the west, and in stands farther north. Interestingly here easting was the third most important variable and showed a higher relative influence (7.1%) than northing (2.4%). The variable ‘last fire type’, which was a factor for whether the most recent fire was stand-replacing or not, accounts for 0.8% of the variance, with non-stand-replacing fires linked to slightly higher lichen cover (Figure 10F).

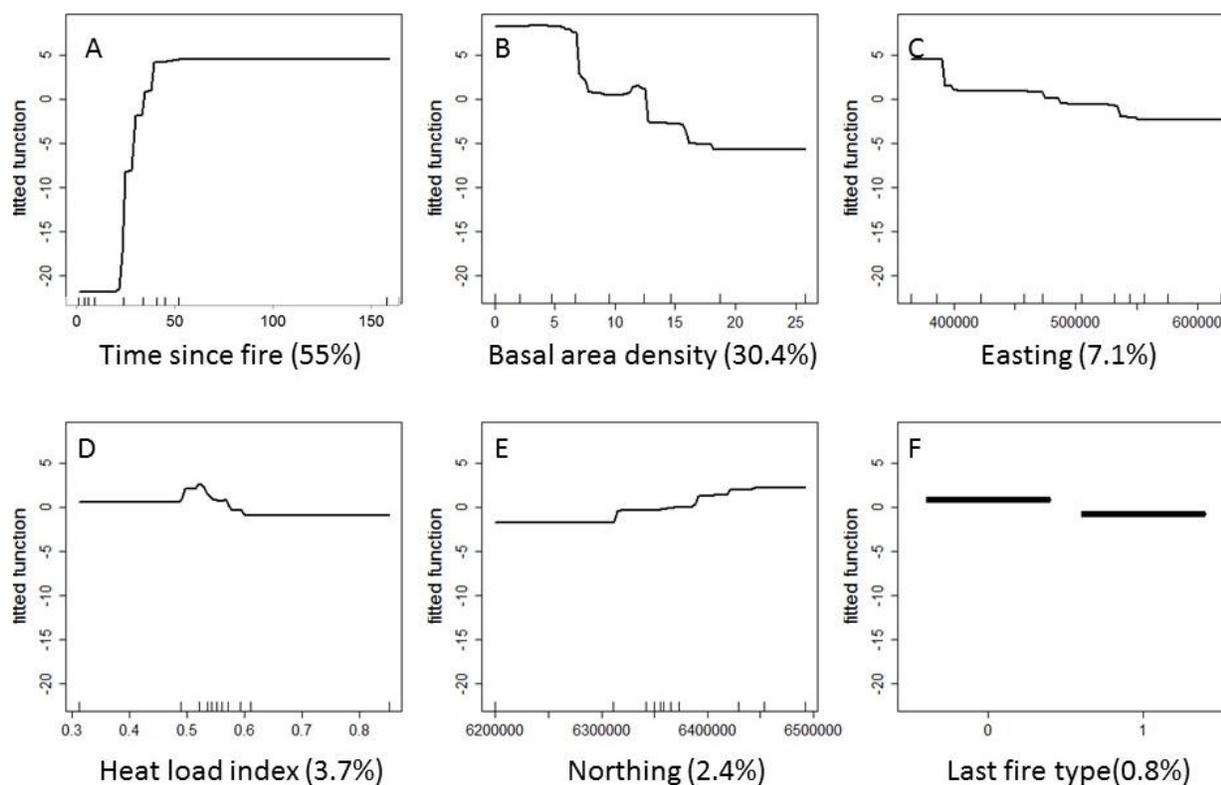


Figure 10: Partial dependency plots for final boosted regression tree model of percent cover in jack pine stands only. Partial dependency plots demonstrate the marginal effect of the variable in question on the response variable (lichen cover) when all other variables are held at their mean. The y-axes are centered at a zero-mean. A.) Time since fire, 55% of the variance) B.) Basal area density, 30.4% of the variance, C.) Easting, 7.1% of the variance, D.) Heat load index, 3.7% of the variance, E.) Northing, 2.4% of the variance, F.) Last fire type, 0.8% of the variance. Last fire type has two possible categories: not stand-replacing and stand-replacing. Deciles (inner tick marks plotted along the x-axis) indicate the distribution of data with regards to the variable in question. The percentage values included with the x-axis labels are the relative influence of the variable in the model, which sums to 100% for all variables. Interaction effects are included in these values.

Interactions in the jack pine percent cover model were overall much less important. The BRT was built with a tree complexity of 2, and only one interaction surpassed the threshold of $H = 0.1$. This interaction was between time since fire and basal area density (Figure 11 & Table 8). This was the fifth most important interaction in the percent cover model for all stand types. The next most important interaction was between time since fire and easting. The next most important interaction, time since fire-easting was even less important in other models (percent cover model, $H = 0.03$; volume model, $H = 0.02$).

Table 8: Two-way interactions present in the percent cover BRT comprising only jack pine stands. Interactions are sorted by Friedman’s H value. Bolded interactions are those above $H > 0.1$ threshold.

Variable 1	Variable 2	Friedman's H
Time since fire	Basal area density	0.3358
Time since fire	Easting	0.0793
Easting	Northing	0.0570
Last fire type	Heat load index	0.0503
Easting	Heat load index	0.0419
Time since fire	Heat load index	0.0344
Northing	Basal area density	0.0214
Easting	Basal area density	0.0197
Last fire type	Easting	0.0189
Last fire type	Basal area density	0.0160
Northing	Heat load index	0.0136
Time since fire	Northing	0.0131
Last fire type	Northing	0.0056
Basal area density	Heat load index	0.0044
Time since fire	Last fire type	0.0035

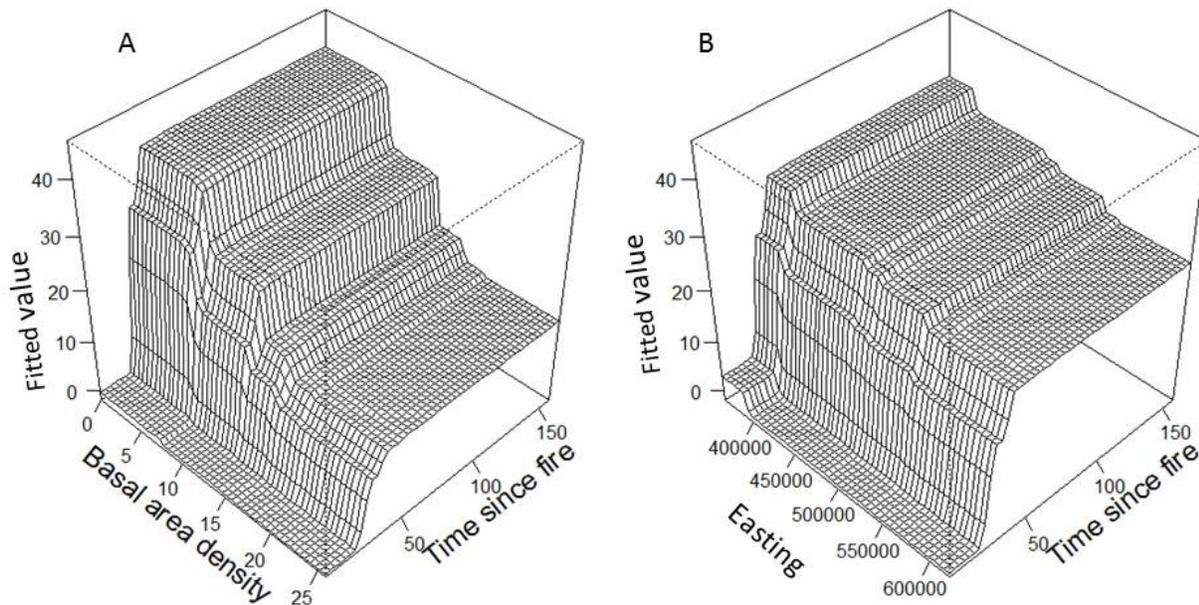


Figure 11: Interaction plots for the top two interactions in the BRT for percent cover in jack pine stands. The most important A.) is basal area density-time since fire ($H = 0.3458$) and the next most important B.) is time since fire-easting, ($H = 0.084$, below the 0.1 arbitrary H threshold).

The BRT for volume of lichens in jack pine stands used 6250 trees and explained 43.7% of the variance. Again, time since fire explained more than half (52.6%) of the CV error (Figure 12A), basal area density followed with 21.2% of the error explained (Figure 12B), then the spatial coordinates (Figure 12C, 12D) easting (11.9%) and northing (6.4%). Heat load index accounted for 6.1% of the error explained (Figure 12E), and last fire type for 1.8% (Figure 12F). In jack pine stands, lichen volume begins to increase rapidly beginning at around 25 years after fire. By 50 years post-fire, its maximum volume has been reached although this is mediated by the low number of jack pine stands older than 50 years (Figure 12A). These stands do not exhibit the same trend of basal area density as all stand types combined, the interaction between stand age and basal area density is less obvious in the partial dependency plots. Here, the most open stands have the highest lichen volume (Figure 12B).

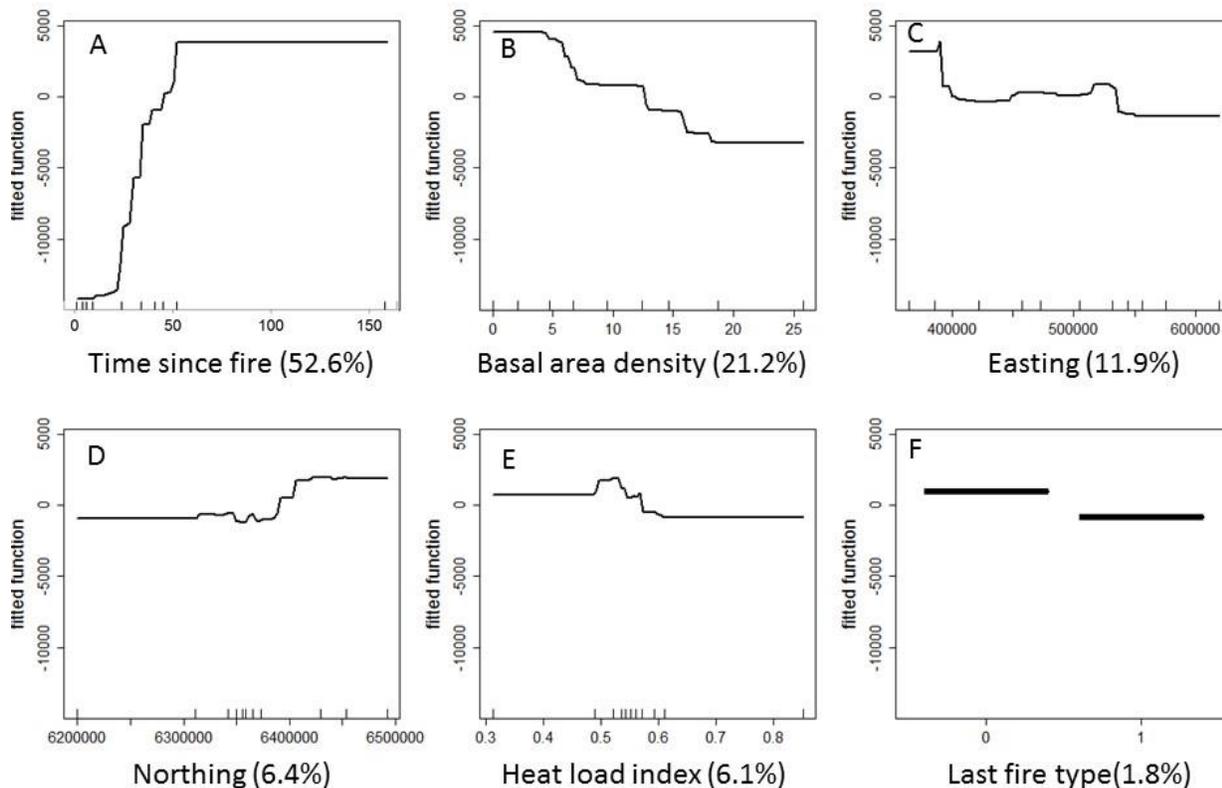


Figure 12: Partial dependency plots for final boosted regression tree model of lichen volume in jack pine stands only. Partial dependency plots demonstrate the marginal effect of the variable in question on the response variable (lichen cover) when all other variables are held at their mean. The y-axes are centered at a zero-mean. A.) Time since fire, 52.6% of the variance B.) Basal area density, 21.2% of the variance, C.) Easting, 11.9% of the variance, D.) Northing, 6.4% of the variance, E.) Heat load index, 6.1% of the variance, F.) Last fire type, 1.8% of the variance. Last fire type has two possible categories: not stand-replacing and stand-replacing. Deciles (inner tick marks plotted along the x-axis) indicate the distribution of data with regards to the variable in question. The percentage values included with the x-axis labels are the relative influence of the variable in the model, which sums to 100% for all variables. Interaction effects are included in these values.

Two interactions stood out in the BRT for volume in jack pine stands (Figure 13 & Table 9). These were time since fire- basal area density, and easting- heat load index. The interaction between time since fire and basal area density follows a similar pattern as in other BRTs, but even when unconstrained, has a strictly negative trend, with highest lichen in the most open stands, regardless of stand age. The interaction between easting and heat load index indicates that areas further west have higher lichen volume in their jack pine stands, especially when heat load index values are equal to 0.5. This is a fairly weak effect as seen on the surface plot (Figure 12B).

Table 9: These are the two-way interactions present in the volume BRT comprising only jack pine stands. Interactions sorted by Friedman's H value. Bolded interactions are those above $H > 0.1$ threshold.

Variable 1	Variable 2	Friedman's H
Time since fire	Basal area density	0.2718
Easting	Heat load index	0.1065
Easting	Northing	0.0876
Time since fire	Easting	0.0660
Last fire type	Heat load index	0.0460
Northing	Heat load index	0.0402
Time since fire	Heat load index	0.0341
Last fire type	Easting	0.0189
Time since fire	Northing	0.0188
Time since fire	Last fire type	0.0182
Last fire type	Basal area density	0.0141
Northing	Basal area density	0.0129
Easting	Basal area density	0.0068
Last fire type	Northing	0.0057
Basal area density	Heat load index	0.0025

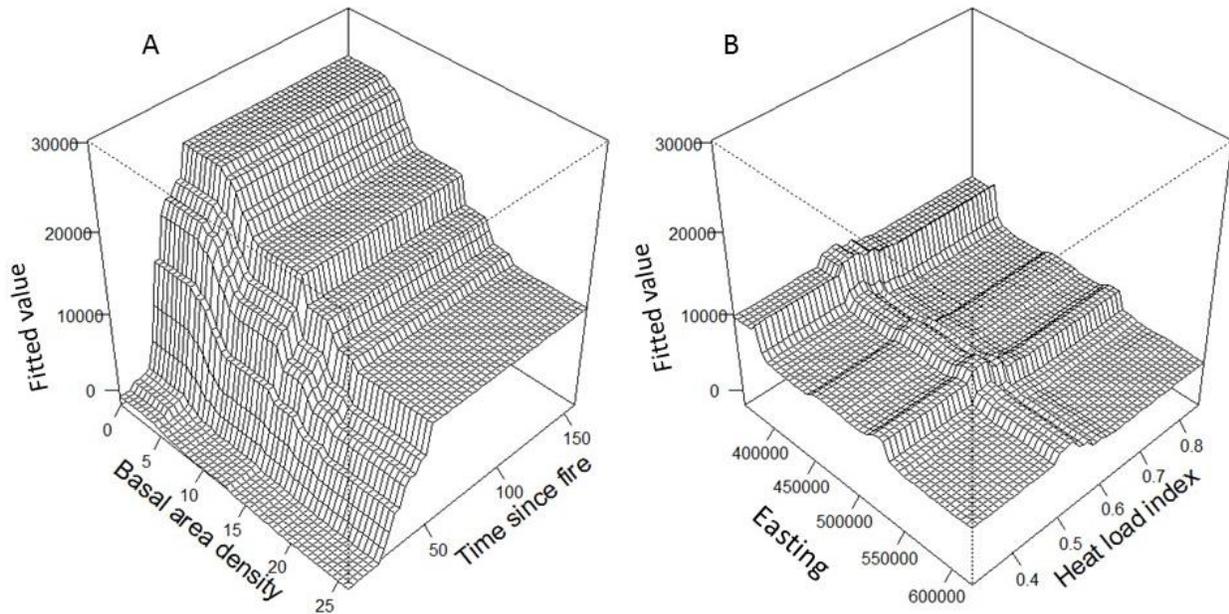


Figure 13: Interaction plots for the top two interactions in the pines volume model. The most important is A.) basal area density and time since fire ($H = 0.2718$) and the next most important is B.) heat load index-easting, ($H = 0.1065$). Vertical scale indicates the fitted values of lichen volume (cm^3/m^2).

4 DISCUSSION

Time since fire was the most important covariate to consider when assessing an area for forage lichen biomass because of the slow growth rates of lichens, although some stand types may recover lichen biomass more rapidly than expected, perhaps as early as 50 years after fire. The type of stand, the basal area density of live trees (proxy for light availability) and latitude modulated the effect of stand age. Lichen abundance relies on many characteristics, and measuring the biomass of lichens in these stands indirectly must involve a measure of cover and a measure of depth. Each measure of lichen growth will be affected differently by environmental covariates.

In my thesis I have shown that estimates of lichen availability for caribou forage should take lichen volume into account rather than simply lichen area. Using lichen area as the measure for prediction in allometric equations may yield more conservative biomass estimates, but could fail to account for stand types with low values of lichen cover but disproportionately high biomass (such as poorly-drained black spruce types). Stand types with the highest potential for lichen biomass are jack pine and poorly-drained black spruce, although these stand types have high variability in their biomass.

4.1 Allometry

Determining the relationships between raw abundance estimates and biomass is an important first step in estimating biomass abundance of vegetation across a large scale. It is even more important when the taxonomic group in question is cryptic and difficult to monitor/survey. While allometric equations for lichen biomass have been developed for lichens in other regions, these equations have sometimes been based solely on area-based measurements (e.g. McMullin et al., 2011; Scotter, 1964; Thomas et al., 1996a). Other authors have used estimates of volume alone (e.g. Arseneault et al., 1997; Moen et al., 2007). There is value in presenting equations based solely on area-based measurements, as they can be useful in cases where not all available data on lichen abundance includes lichen depth, particularly when lichens are not the target of a forest survey campaign.

Allometric equations that use area as the predictor variable can detect patterns of succession in younger stands, but lack the sensitivity to detect changes in older stands or stands which have low cover. Instead, equations incorporating some measure of lichen depth or volume tend to perform better when predicting biomass (Arseneault et al., 1997; Joly et al., 2010; Moen et al., 2007). Using a volumetric allometric equation allows for a more accurate prediction of biomass as it accounts for the cover but also for the depth of the lichen mat, which can be substantial.

While the construction of allometric equations is greatly influenced by sample size (Duncanson et al., 2015), the selection of sample dimensions can also have an effect. Allometric equations for individual organisms, such as for body size-based allometric equations, do not require the researcher to select a particular survey area size or unit since the individual organism is the sampling unit (Gould, 1966). In the case of this project, the sampling unit was not finite, and sampling units of 400 cm² were deemed appropriate. However, the use of small-sized samples and upscaling from the same equations to larger plot sizes makes a power transformation inappropriate in this case. Although extrapolating the equation constructed without the outlier (2015-073, Appendix C) in order to estimate the outlier value yielded a biomass estimate somewhat lower than the outlier's true value, values for other site types were consistent between methods (Appendix A, Figure 15). Inclusion of the outlier in the equation was necessary to capture the range of variation, or indicates that an estimate of percent cover is a poor predictor of sites fitting this description (old, unburned, wet) (Figure 4). Removing non-randomly sampled 'X' sites (opportunistically-sampled rare site types selected to capture the full range of variation did not improve model fit or alter the slope of the equations (Appendix A, Figure 14).

The theoretical maximum area a lichen can occupy is 1.0 cm²/cm², which is easily attainable at small scales, but it is biologically unlikely to exist as a plateau of maximum biomass on a large scale. This also assumes that lichens mainly spread laterally and that they reach a depth of no more than 1.0 cm. For volume/density measures the theoretical maximum also contains an area component but accounts for depth. Theoretical maximum biomass (peak biomass) would thus be linked to the biology of lichens, in that lichens attain a maximum depth at some point. Maximum depth would occur when marginal vertical increase in living tissue slows as the lower parts of the podetia become part of the necromass and then decompose (Crittenden, 1991). It is unlikely that we encountered this often in northern Saskatchewan, because most stands were of relatively young age (only 26% of stands sampled were older than 50 years). Moreover, peak biomass of forage

lichens is reached more slowly in western forests than in eastern forests, with some species in the west attaining peak biomass at 90 years of age and others requiring >150 years (Thomas et al., 1996a).

4.2 Scaling estimates to stand type

When calculating plot-level estimates of lichen abundance using volume-based extrapolation, several outliers became apparent that were not observed while extrapolating from percent cover. These points were all located in poorly-drained black spruce stands. Lichens depend upon alternating states of wet and dry for growth (Harris and Kershaw, 1971; Larson and Kershaw, 1976), and thus cannot outcompete moss in wet stands (Joly et al., 2010). However, when it is established in optimal environments, lichen can achieve higher biomass because areas near the ground have higher humidity and thus conditions for growth are met more frequently (Hojdová et al., 2005). These types of stands (poorly-drained black spruce) are unlikely to attain high cover values, and thus volume will likely be a more important measure in these stands. Hummocks can be very dry on their tops and sides in the summer months, making them an appropriate lichen substrate (Hojdová et al., 2005).

Comparing the plots of jack pine stands using area and volume to upscale to stand-level biomass, the difference in the spread of response at 34 years old suggests that the accumulation of biomass in this stand type is due more to increasing ground cover than to increasing volume. Past work on lichen succession in jack pine stands suggests that lichen cover peaks early (21–30 years after fire), but cover decreases thereafter until a second surge in percent cover occurs after 90 years since fire (Skatter et al., 2014). My results do not show this pattern, but this is likely due to most of our jack pine stands being 50 years old or younger, a symptom of the high fire frequency. Skatter et al. (2010) also used two separate datasets, one of which was composed of mature upland conifer sites used in the designation of FEC forest types, incorporating limited lichen data. Sites were grouped in 10-year age increments, and sites older than 100 years were pooled in that study, reducing precision in exchange for more accurate age estimation. Furthermore, the estimates of lichen recovery presented by Skatter et al. (2010) are based only on percent cover. They speculate that lichen abundance in the second peak (101-110 years) of the bimodal distribution in jack pine stands would be much higher than in the first peak (31-40 years) due to increased depth, but I did not find this pattern. Lichen depth in my study appeared to be approximately equivalent in both 35

year old stands and 100 year old stands. I believe this is due in part to the species composition, as *C. mitis* and *C. uncialis* were by far the most common species in jack pine stands at all ages. These species do not develop mats as deep as those produced by *C. rangiferina* and *C. stellaris*.

Many of the other stand types are very comparable to each other in terms of lichen abundance. Biomass of forage lichens in deciduous stands is extremely low, in all cases less than 8 kg/ha. If the lichen assemblage considered were to include horn and cup lichens, this number would be considerably higher. However, the high litter cover is likely to reduce the amount of available substrate for all species of lichen and these stands will tend to have low light conditions during the growing season. I noticed that in deciduous stands, the horn and cup *Cladonia* spp. occurred almost exclusively upon raised logs and stumps of fallen trees that did not accumulate litter. Most of the other stand types are fairly comparable in terms of their mean lichen biomass estimates as well as their ranges. Hardwood-conifer stands ($n = 23$) had higher lichen abundance than the three stand types with the lowest quantities of lichen, but only when plotted with a log scale. The three stand types with the lowest lichen abundance also tended to be the least common in our area (poorly-drained non-forest, $n = 14$; deciduous, $n = 9$; well-drained non-forest, $n = 15$). Because of this, it is difficult to determine trends along the chronosequence, especially as many of these stand types had a high frequency of zero values for lichen biomass. Mean values of lichen abundance are thus quite low in these stand types (Table 5). The poorly-drained non-forest type encompasses fens and other areas which are decidedly too wet to support most lichen communities, so the low estimates of lichen in these areas are unsurprising.

While total lichen biomass increases until peak biomass is achieved, the caribou forage lichens tend to remain at a relatively constant rate of biomass thereafter rather than undergoing decreases in biomass abundance (Thomas et al. 1996a). Consequently, a decrease at older ages is more likely to be representative of stands that have low lichen biomass for other reasons. For individual species, this trend is mediated by their position in successional trajectories. *C. mitis*, for example, peaks early but biomass declines as later successional species such as *C. stellaris* and *C. rangiferina* take over (Ahti, 1959; Carroll and Bliss, 1982; Kershaw, 1977).

Estimates of lichen forage availability for other areas in North America are comparable to the current study and can help to put Saskatchewan values in context. The mean value of lichen abundance found overall in this study, weighted by stand type to correct for unbalanced sample

size, is 893 kg/ha (volume) or 905 kg/ha (area), however, this fails to account for the range of variation present in different stand types (Table 5). In northeastern Quebec, lichen biomass is estimated to range between 2800–4500 kg/ha (Arseneault et al., 1997), although this includes all ground lichens, not just forage species. Northwestern Ontario is similar, averaging 3120 kg/ha in dry upland stands (McMullin et al., 2011), while lichen biomass in northern Manitoba, on the wintering ground of the Qamanirjuaq herd of barren-ground caribou, can range from 4277–5487 kg/ha (Miller, 1976). However, peatlands in northern Alberta have been found to harbour lichen biomass averaging only 660 kg/ha (Table 10) (Dunford et al., 2006). Methodologies for these studies have varied, and considering the heterogeneity of the boreal forest it is difficult to narrow the range of variability to one number. In Europe, the values for lichen biomass are considerably larger, from 8000 kg/ha in Finland to 11,000 kg/ha in Norway (Gaare and Skogland, 1980) (Table 10). These areas, however, are located near coastal regions and the maritime climate may contribute to these high abundance values (Ahti, 1959; Gaare and Skogland, 1980; Väre et al., 1996). To compare with other estimates, I chose to separate stand types by relative abundance to give an idea of the range of biomass abundance present in the boreal shield. Mean values of lichen biomass for most stand types in my study area (poorly-drained non-forest, well-drained non-forest, deciduous, hardwood-conifer, conifer mix, and well-drained black spruce) were very low when compared to estimates of mean lichen biomass from other areas of Canada (Table 10). I grouped well-drained black spruce, well-drained non-forest, mixed conifer and hardwood-conifer together as “moderate abundance” stand types for the purpose of calculating average lichen abundance, as each of these types had mean values of lichen biomass greater than 100 kg/ha, but not exceeding 1000 kg/ha (Tables 5 & 10). I considered “low abundance” sites to be those with mean biomass below 100 kg/ha, these stand types were deciduous and poorly-drained non-forest (fens were included in this category). Poorly-drained black spruce stands and pine stands had mean values of biomass which are somewhat lower than those found in other areas of Canada but are at least within an order of magnitude of other estimates, and both had mean values exceeding 1000 kg/ha (Table 10). Examining the range of abundance present overall and between stand types, I conclude that providing one value of mean lichen biomass for an area is insufficient to capture the variability across a large heterogeneous area, let alone to make any management decisions for caribou. Stand type and time since fire and location, especially latitude, will play a crucial role in habitat assessment.

It has been suggested that thalli of most *Cladonia* spp. can exhibit a range of heights (up to a ~20% difference) depending on their field moisture at the time of measurement (Andreev, 1954; Gorodkov, 1934; Nekrasova, 1937). This adds a level of uncertainty when scaling up from plot-level measurements, as I could not control the lichen moisture in the field during measurements.

Table 10: Mean lichen abundance found in other regions. Values for this study presented in the table are estimates based on lichen volume.

Authors	Mean lichen abundance (kg/ha)	Region	Stand types
Joly et al. 2010	3007	NW Alaska	Tundra to forest transition
Dunford et al. 2006	660	N Alberta	Peatlands
Miller 1976	4277-5487	Manitoba	Boreal forest
McMullin et al. 2011	3120	NW Ontario	Dry, sandy uplands
Arseneault et al 1987	2800-5400	NE Quebec	Lichen heath, treeline
Gaare & Skogland 1980	11000	Norway	Climax forest stand
Väre et al 1996	8000	Finland	Pine heathlands
This study	1494	N Saskatchewan	High abundance*
This study	517	N Saskatchewan	Moderate abundance†
This study	29	N Saskatchewan	Low abundance‡

*High abundance stand types: jack pine, poorly-drained black spruce.

†Moderate abundance stand types: well-drained black spruce, well-drained non-forest, mixed conifer and hardwood-conifer.

‡Low abundance stand types: Deciduous and poorly-drained black spruce

4.3 Relationships of environmental covariates to lichen abundance

In terms of the effects of environmental characteristics, the percent cover and volume models are similar in their relationships to some variables, but differ in their relationships to others. Overall, percent cover and volume are both most strongly influenced by time since fire, but from there are controlled by different variables. From the partial dependency plots for time since fire of both volume and percent cover models (Figures 6 & 8), the greatest amount of change from 0-50 years is most apparent in the percent cover model and the greatest amount of change after 50 years is seen with the volume model. This pattern corresponds well to what is known regarding lichen succession. For instance, the thresholds seen in the partial dependency plot for time since fire are very different between the volume and percent cover BRTs. While the threshold for percent cover appears at ~20 years after fire, in the volume BRT the escalation is much more gradual until 150 years. This supports the notion that lichens initially spread laterally over the ground, and then gain in depth secondarily (Andreev, 1954; Sveinbjörnsson, 1987). Old sites, which were quite rare in our study area, tended to have the deepest lichen mats (all else held constant). The plateau in lichen abundance after 150 years of age may be due to the low sample size of old stands encountered.

This in turn may be due to the short fire return interval of northern Saskatchewan, as old stands (>100 years) are likely rare on the landscape. The plateau may be due in part to slower growth rates in older lichens (Abdulmanova and Ektova, 2015).

For caribou forage estimates, the volume model is likely to be the most useful, although it should be acknowledged that some estimates should be approached with caution, particularly for points in old and poorly-drained black spruce stands. Forests of this type are unusual, in that many stands of this type do not contain lichen. It is probable that including a measurement of the density of hummocks or height of hummocks would have improved our predictions of lichen abundance in poorly-drained stands (Belland and Vitt, 1995; Hojdová et al., 2005). This is because lichen growth in this type of stand is reliant upon the presence of hummocks to raise lichen thalli above the water table (Harris and Kershaw, 1971; Larson, 1979). Volume estimates of lichen abundance in these stands are very large, with the maximum estimated value being nearly double the estimated maximum value of the percent cover estimates.

Location of the forest stand had a surprisingly strong impact on lichen abundance measures. Northing had a positive effect on lichen abundance with respect both to percent cover and volume, although it had a higher relative influence on volume than it did on percent cover. Higher latitude has been linked to higher lichen abundance and diversity (Holt et al., 2015; Kershaw, 1977). Interactions and variable importance differed between the volume and percent cover models, and the differences between the model interactions may illuminate the differences between the responses of percent cover and volume. Northing switches from being the 4th most important variable for cover to being the 2nd most important variable for volume, with a 6% change in relative influence. This is especially notable when one considers that the ordering of the variables' relative influence does not alter in any other way. Much of the relative influence of northing is likely due to the interaction between time since fire and northing. The general pattern of this interaction for the volume model is increased lichen cover farther north, but with a clear threshold at around 150 years (Figure 8). However, older stands have higher lichen biomass regardless of where they are located. Stands farther north than 6400000 m N show more lichen volume earlier after fire, especially where basal area density is 2–10 cm²/m² (i.e. quite open) (Figure 9). This applied to percent cover of lichens as well, with stands farther north than 6400000 m N having the highest cover regardless of their age or basal area density, although there is a clear spike in lichen cover at 5–10 cm²/m² tree basal area across the entire range of the study area from north to south. Northing

and basal area density do not exhibit collinearity but there is a general pattern of areas farther north having more open stands (Girard et al., 2009; Kershaw, 1977), leading to increased colonization by lichen. However, it does not explain why volume is relatively more affected by northing than percent cover is. In northwestern Alaska in 2010, Joly et al. found that lichen volume was negatively related to latitude, but that percent cover was not significantly affected by latitude. They suggested that because large herds of migratory caribou (*Rangifer tarandus granti*) (Gmelin) had access to these sites both in the spring and fall (during migration) the areas were likely to be overused, and thus show a negative effect of volume with latitude (Joly et al., 2010). All variables in that case were assumed to be moderated by caribou usage, however, this is unlikely to be the case in Saskatchewan as density of boreal caribou in the SK1 range is relatively lower. They imply that lichen growth may also have some link to climate, in that warming temperatures will decrease lichen growth rates. I suggest that northing has a positive impact on volume: areas further north benefit from longer days in the growing season, and thus lichen growth is more consistent.

The fact that easting had so little impact while northing's influence is substantial suggests that the effects of northing are due to characteristics of latitude, rather than to northing manifesting as a purely spatial effect. Notably, easting has a greater effect on lichen in pine-dominated stands than in other forest types. The effect of easting may be due to the underlying topography of eastern areas compared to western areas. As our study area encompassed a relatively small range from east to west, the impacts are likely mainly due to the differences between the Athabasca Plain (AP) and the Churchill River Uplands (CRU). To the east, the AP has more homogeneous topography and sandier soils, while the CRU has rugged terrain, more lakes and wetlands (Acton et al., 1998). On the other hand, this apparent spatial pattern may also be an artefact of sampling, in that our sites to the east were also mainly our southern sites, and our sites farthest to the west were exclusively in the north of our study area (Figure 1). While many studies have focused on the effects of latitude, effects of longitude have been detected in the Pechora North tundra in Russia. Lichen annual growth as well as overall biomass accumulation was higher in the Malozemel'skaya tundra of the east than in the western Bol'shezemel'skaya tundra. This was true both for hummocky grass-sedge bogs as well as for scrub birch tundra (Andreev, 1954). However, the longitude gradient was approximately 1800 km in this study, whereas our study area had only a 323 km gradient of longitude. It is uncertain whether such a short distance gradient would capture large-scale change in lichen growth. In North America, western forests tend to be drier than eastern forests (Peng et

al., 2011). Interactions between heat load index and easting may be due to the short range of easting and that the values of heat load index were clustered together. In jack pine stands, percent cover of lichens is related to similar variables as those observed to be important in other stands except that easting is more important than northing. Heat load index was similarly important here as in the previous BRTs. Jack pine stands are defined by this classification as stands that have $\geq 75\%$ jack pine dominance, and can be poorly- or well-drained, although jack pines are typically found on well-drained soils. The decrease in lichen cover with easting indicates that lichen cover is higher in the west. As our westernmost sites were all in the AP, this may be an effect of different (sandier, flatter, drier) topography (Acton et al., 1998), rather than an effect of climate at this scale.

Lichens require light for photosynthesis, and basal area density can serve as a proxy for light availability in forest stands, as it is a measure of how much of the stand at 1.2 m off the ground is occupied by tree stems. Basal area density had a greater impact on lichen percent cover than on volume, because rates of change in basal area density are highest in young stands (Johnson and Abrams, 2009). In younger stands, I found that lichen cover changes more than volume, which may be caused by the lichens' rate of dispersal across the ground being faster than their vertical growth. Lichens have a greater potential range of percent cover in stands with lower basal area (dependent upon other variables), and tend to have lower percent cover in denser stands. The interaction between time since fire and basal area density for the percent cover model shows low values for percent cover in young stands (0–15 years) regardless of basal area density and the highest lichen cover is found regardless of time since fire at $2\text{--}10\text{ cm}^2/\text{m}^2$.

The mechanisms involved in lichen recovery after fire are varied. One factor which may have a large role to play in lichen re-establishment after fire is the size and severity of the burn. Unlike other lichen species, *Cladonia* spp. do not reproduce primarily by soredia, the granular diaspores used in vegetative reproduction, and depend upon thallus fragmentation to establish new lichen thalli (Heinken, 1999; Roturier et al., 2007). The release of ascospores, the fungal spores produced in the asci is another common method of reproduction, although ascospores do not contain any algal bodies and so this method requires the presence of the algal partner (Honegger and Scherrer, 2008). The light-weight soredia are readily dispersed by wind, while thallus fragments typically do not travel more than 1 m from their origin (Heinken, 1999). If a burn is large and severe enough to have destroyed all the lichens in an area, it may be difficult for fragments of lichen to be dispersed to the center of an area and re-establish, although it can occur over smaller

distances (Schimmel and Granström, 1996). Also, short fire return intervals may not necessarily always lead to lichen declines. In eastern Canada, periods of severe and recurrent fires may cause deforestation and lead to the establishment of open lichen-heath communities by reducing the seedbanks of vascular plants (Lavoie and Sirois, 1998). The heterogeneous nature of many wildfires may also leave patches of intact, live lichen (Schimmel and Granström, 1996), especially in stands with low quantities of ground fuels, such as jack pine stands (De Groot et al., 2009). I found squamules (scale-like precursors to lichen thalli) on the ground in stands as young as 1 year old, however did not count these as lichen cover in my analyses as it is difficult to identify squamules to species. This implies that re-occurrence of lichens is not the limiting process, but again that lichen growth rate is the limiting process. Some studies observed the grazing and trampling of lichen by caribou as disturbances in their own rights, reducing the biomass of lichen abundance significantly at the landscape level. However, these cases are mostly in areas with large herds of barren-ground caribou, unlike in the boreal shield of Saskatchewan, which is home to small groups of boreal caribou (Andreev, 1954; Boudreau and Payette, 2004; Scotter, 1964). In addition to acting as a disturbance, caribou may act to redistribute lichens in several ways. One of these may be by fecal deposition, as during the field work for this project, lichen were often observed growing on old piles of droppings. Another possibility is by wind dispersal during winter, after caribou cratering, when fragments dropped by foraging caribou are blown long distances over the surface of snow (Heinken, 1999).

Aspects of lichen biology such as growth rates may vary depending on region and local conditions. It has been suggested by Skatter et al. (2014) that lichens in Saskatchewan jack pine stands may recover rapidly relative to other areas, perhaps reaching high cover values in jack pine stands within only 21–30 years, rather than just beginning to regrow in 30 years after fire in other regions. Lichen cover in pine stands is low regardless of basal area density or easting for the first ~20 years after a fire (Figure 11). Stands dominated by pine species may begin to experience stand thinning as early as 20 years after fire (Johnstone et al., 2004), which may contribute to increasing lichen abundance in stands older than 20 years. However, I did not find high values of lichen cover between 21–30 years after fire (besides the aforementioned presence of squamules). My results suggest that high cover values of fruiting lichen bodies can be reached as early as 34 years after fire in jack pine stands. Migratory caribou in northern Saskatchewan may avoid jack pine stands until they have reached 35 years since fire (Scotter, 1964). In west-central forests, older jack pine

stands have much higher lichen cover than black spruce stands of a similar age (Dunford et al., 2006; Scotter, 1964; Skatter et al., 2014). This may suggest that jack pine stands are more appropriate as caribou habitat than black spruce stands but my results suggest that this is not always the case. Jack pine stands can serve as good caribou habitat both for boreal caribou and wintering barren-ground caribou (Scotter, 1964; Skatter et al., 2014), and their relatively consistent availability of lichen cover make them particularly dependable as good forage areas. The areas that potentially attain maximum lichen biomass, however, are poorly-drained black spruce wetlands, although poorly-drained black spruce stands do not always have high forage availability (Figure 5). I was unable to parse the variability in poorly-drained black spruce stands as those stands with high biomass appear to be quite rare on the landscape.

Growth and distribution of any organism depends on environmental conditions, such as those included as variables in the BRTs. Little has been done to directly assess the impact of each of these variables on depth or volume as opposed to the impact on area or percent cover. While both volume and percent cover are presumably controlled to some extent by the same variables, the differences in the processes predicting the two measures are made plain by the differences in BRT outcomes. Lichen growth rates can vary across different regions, depending on the abiotic characteristics of the region. Areas with high humidity have fast regrowth capabilities for both arboreal and terricolous lichens (Abdulmanova and Ektova, 2015; Ahti, 1959; Gorodkov, 1934). Growth rates can also vary temporally, with rates slowing down as lichens age (Andreev, 1954; Crittenden, 1991; Sveinbjörnsson, 1987). Lichens occurring at high latitudes also tend to have slower growth rates (Andreev, 1954), although I found that higher quantities of lichen were correlated with areas further north.

4.4 Lichen and caribou habitat in Saskatchewan

Overall, lichen availability in the Saskatchewan Boreal Shield is somewhat lower than in areas to the east, but incorporates a lot of variability depending on stand type and age. This may be because of faster growth rates, or it may be that fires on the landscape are patchier than previously thought. If faster growth rates are the main driver, lichens are better able to recover after fire, and so the high density of fire is less of a cause for concern regarding caribou forage availability. If the available lichen is due to patchier fire and more remnants of unburned area on the landscape, then the main concern is that as fire increases, lichen may be more at risk of decreasing in abundance,

since they may be less adapted to recovering rapidly after fire. Slower growth rates in the west may be due in part to the drier climate. The high availability of lichen biomass in some stands allays the suggestion that boreal caribou in northern Saskatchewan may not be relying as heavily upon ground lichen as caribou in other regions because of lack of availability.

Time since fire still exerts the strongest influence over percent cover in jack pine stands, however the threshold for increase in these stands occurs much earlier in the timeline than in other stands. This suggests that jack pine stands are suitable for lichen colonization early after fire, and may provide good winter habitat (in terms of forage availability) for caribou as early as 30 years after fire. It is interesting here that response to basal area density follows a negative constraint (this pattern occurs when left unconstrained as well), rather than a unimodal pattern as seen in the models containing all stand types.

The relationship between lichen and caribou is well-established in the literature, but as differences exist between caribou populations across Canada, there is some uncertainty about this relationship in northern Saskatchewan, which has not been studied as often as other populations. Preferential grazing of lichens varies across the entire range of boreal caribou, with different lichen species being assigned higher importance in different areas, depending on their availability (Ahti, 1959; Bergerud, 1972; Scotter, 1964). The dietary plasticity of caribou, established in other studies (Aagnes et al., 1995; Person, 1975), suggests there is a possibility that caribou in Saskatchewan may not rely upon lichen to the same degree as other populations. For example, they may not select lichen until it has reached a threshold in volume at which mouthfuls are worthwhile or below which bycatch of mosses, litter, or soil is inevitable (Ahti, 1959; Bergerud, 1972; Thomas et al., 1996a). If this is the case, then cover alone does not provide enough information from a purely mechanical perspective. Gaäre and Skogland have suggested that a minimum of 25 g/m² (250 kg/ha) is required for grazing to sustain a herd of caribou through a winter, while Kumpula et al. have stated that 1000 kg/ha is required (Gaare and Skogland, 1980; Kumpula et al., 2000). These values are not associated with caribou density or length of time for grazing and so are somewhat arbitrary. While it may be true that caribou in this area rely on vascular plants to a greater degree, as has been seen in other areas (Bergerud, 1972; Storeheier et al., 2002b), the answer to that question is well beyond the scope of this study.

As the climate warms and fire frequency and severity increase, fewer stands in the boreal shield of northern Saskatchewan will contain thick mats of lichen (~10 cm). In turn, this will decrease the availability of habitat typically associated with winter survival of boreal caribou. While young stands of jack pine demonstrate the ability to regain lichen cover relatively quickly and may have higher biomass, it is also important to consider areas which show low cover values but overall higher volume (e.g. poorly-drained black spruce stands >100 years old). Caribou can sense lichens through snow, especially when it is not deep or there are holes in the snow from vegetation (Bergerud and Nolan, 1970; Brown and Theberge, 1990; Goward, 1999), but digging to access the lichens requires a large energy expenditure, so they typically dig small craters (Fancy and White, 1985; LaPerriere and Lent, 1977; Rominger and Oldemeyer, 1990). Areas where caribou can get the most lichen with the least amount of digging will be important for them, particularly in less densely treed stands where snow accumulation on the ground is typically higher. As such, old (>100 years) poorly-drained black spruce stands are likely critical as caribou habitat, because their biomass is concentrated in smaller areas with substantial depth rather than spread thinly across a wide area. Future study efforts should prioritize sampling of poorly-drained black spruce stands to better capture the range of variation.

An increase in fire frequency and severity may lead to fewer old stands and reduce the number of stands dominated by black spruce, favouring replacement by jack pine (Lavoie and Sirois, 1998). Jack pine stands can serve as excellent caribou habitat from a reasonably young age, as their lichen cover appears to recover rapidly (Skatter et al., 2014), but the functional volume of lichen available for winter consumption may be limited. In the Northwest Territories, boreal caribou have been shown not to make use of stands younger than 60 years old, even though many stands possessed adequate forage at 40 years after fire (Thomas et al., 1996a). The near-exclusive use of older stands even when lichen is abundant in young stands indicates there are other stand age-related factors at play in caribou habitat selection.

4.5 Conclusions

When assessing caribou habitat in an area it is important to have established relationships between biomass and easily-collected estimates of lichen abundance, such as percent cover and height of the lichen mat (and therefore volume). In my thesis, I have presented such relationships which can be used in the future to extrapolate lichen biomass estimates from future forest inventory data.

Another important step in assessing forage lichen availability is associating lichen abundance with environmental characteristics that are relatively easy to detect. Since lichens are typically not part of forest monitoring and survey protocols, it is important to understand the variables affecting lichen abundance for which data are more readily available. In this way, more extensive estimates of forage availability can be made which is useful for a far-ranging large herbivore such as boreal caribou.

Here I have determined the environmental covariates that are most useful for estimating lichen biomass: time since fire (stand age), basal area density of live trees, UTM northing and easting, and stand type. These findings are supported by much of what is already known about terricolous forage lichens in boreal systems. The concurrent analyses of the same data presented as raw percent cover values and volumetric abundance show the value of including a measure of lichen depth in forage assessment. High cover does not necessarily mean high biomass abundance, and low cover does not necessarily mean low biomass. For this reason, lichen cover alone is not an adequate metric for assessing caribou habitat. Volume of the appropriate species of lichens should be estimated in the field by using cover and depth of the lichen mat. It is important to consider stand type when assessing lichen availability, because of the differing relationships between biomass and volume vs. biomass and area in each stand type. The estimates of lichen biomass I have generated for different types and ages of forests in Saskatchewan's Boreal Shield can be used in habitat assessments to inform generalizations made based on stand type and age.

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APPENDIX A: ALTERNATE ALLOMETRIC RELATIONSHIPS

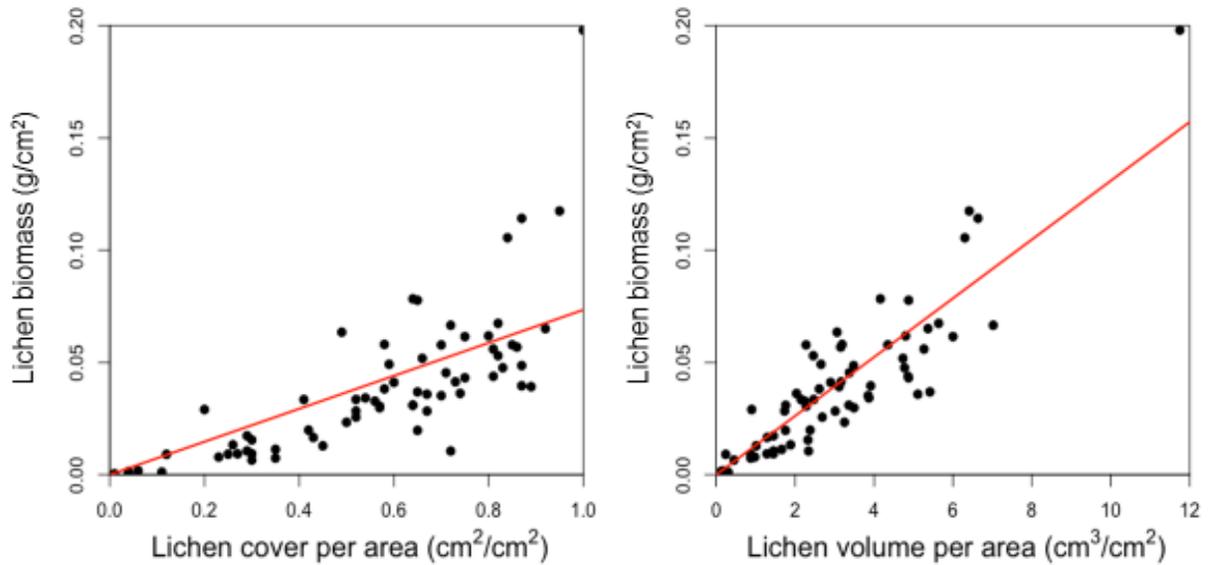


Figure 14: Allometric equations with non-randomly sampled sites ($n = 2$) removed for area ($n = 70$) and volume values ($n = 70$). Biomass for both plots is given here in g/cm^2 . A.) Allometric equation for all 4 species/species groupings (total area/area) is $y = 0.073411x$ with a zero-intercept. $R^2 = 0.79$, $p < 0.001$. B) Allometric equation for all 4 species (total volume/area) is $y = 0.0130955x$ with a zero-intercept. $R^2 = 0.91$. $p < 0.001$.

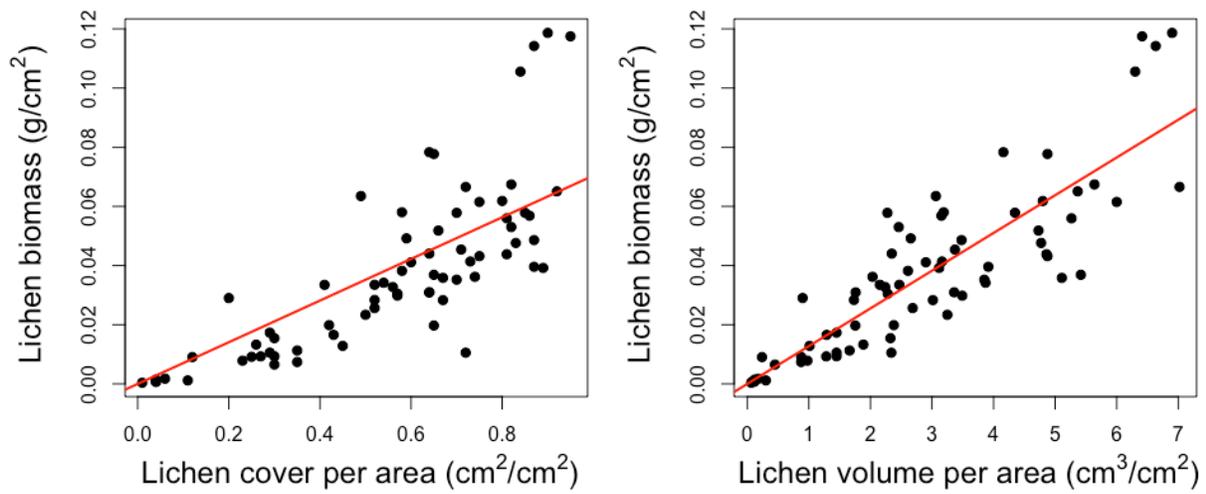


Figure 15: Allometric equations with one outlier removed for area ($n = 71$) and volume values ($n = 71$). Biomass for both plots is given here in g/cm². A.) Allometric equation for all 4 species/species groupings (total area/area) is $y = 0.070412x$ with a zero-intercept. $R^2 = 0.85$, $p < 0.001$. B) Allometric equation for all 4 species (total volume/area) is $y = 0.0127531x$ with a zero-intercept. $R^2 = 0.90$. $p < 0.001$.

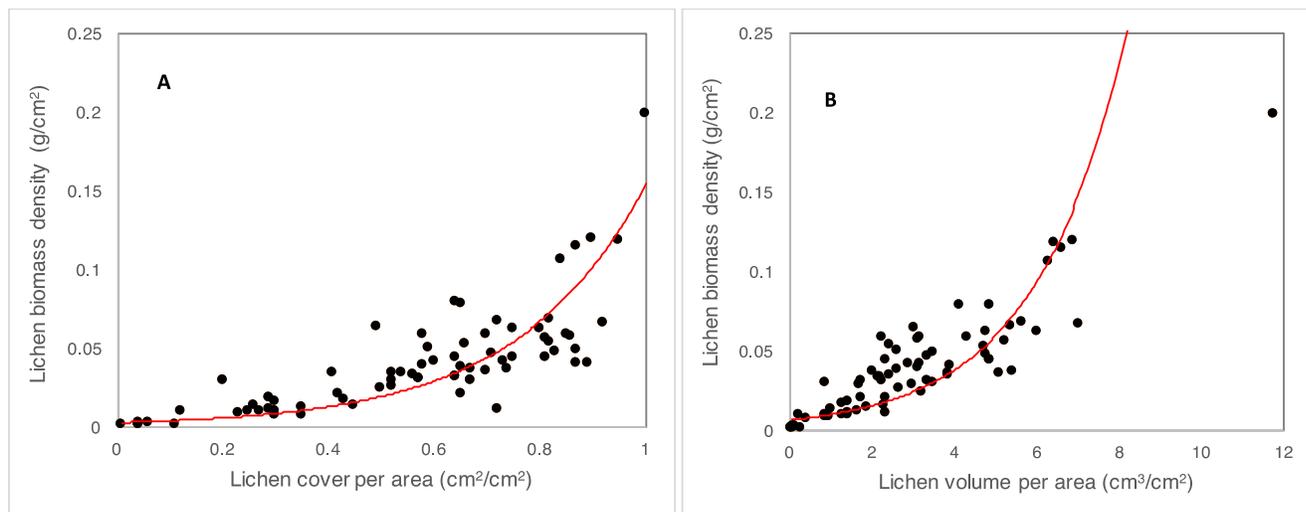


Figure 16: Allometric equations in exponential format for area ($n = 72$) and volume values ($n = 72$). A.) Allometric equation for all 4 species/species groupings (total area/area) is $y = 0.0024e^{4.1708x}$, $R^2 = 0.07548$ and equation with total volume/area is $y = 0.0062e^{0.4534x}$, $R^2 = 0.5962$

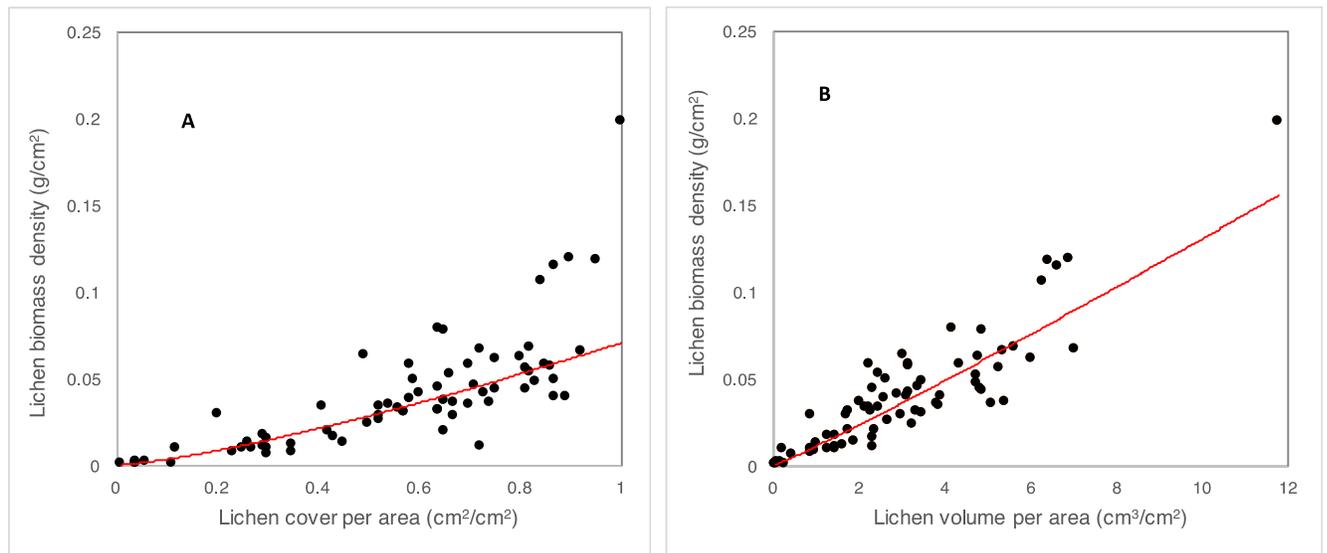


Figure 17: Allometric equations in power form for area ($n = 72$) and volume values ($n = 72$). These equations created in Microsoft Excel using trend line plotting function to obtain starting values. A.) Allometric power equation for all 4 species/species groupings (total area/area) is $y = 0.0706x^{1.3129}$, $R^2 = 0.8516$. B.) Allometric power equation for all 4 species (total volume/area) is $y = 0.011x^{1.0732}$, $R^2 = 0.8856$

APPENDIX B: GRAPHS FOR MODERATE AND LOW ABUNDANCE STAND TYPES

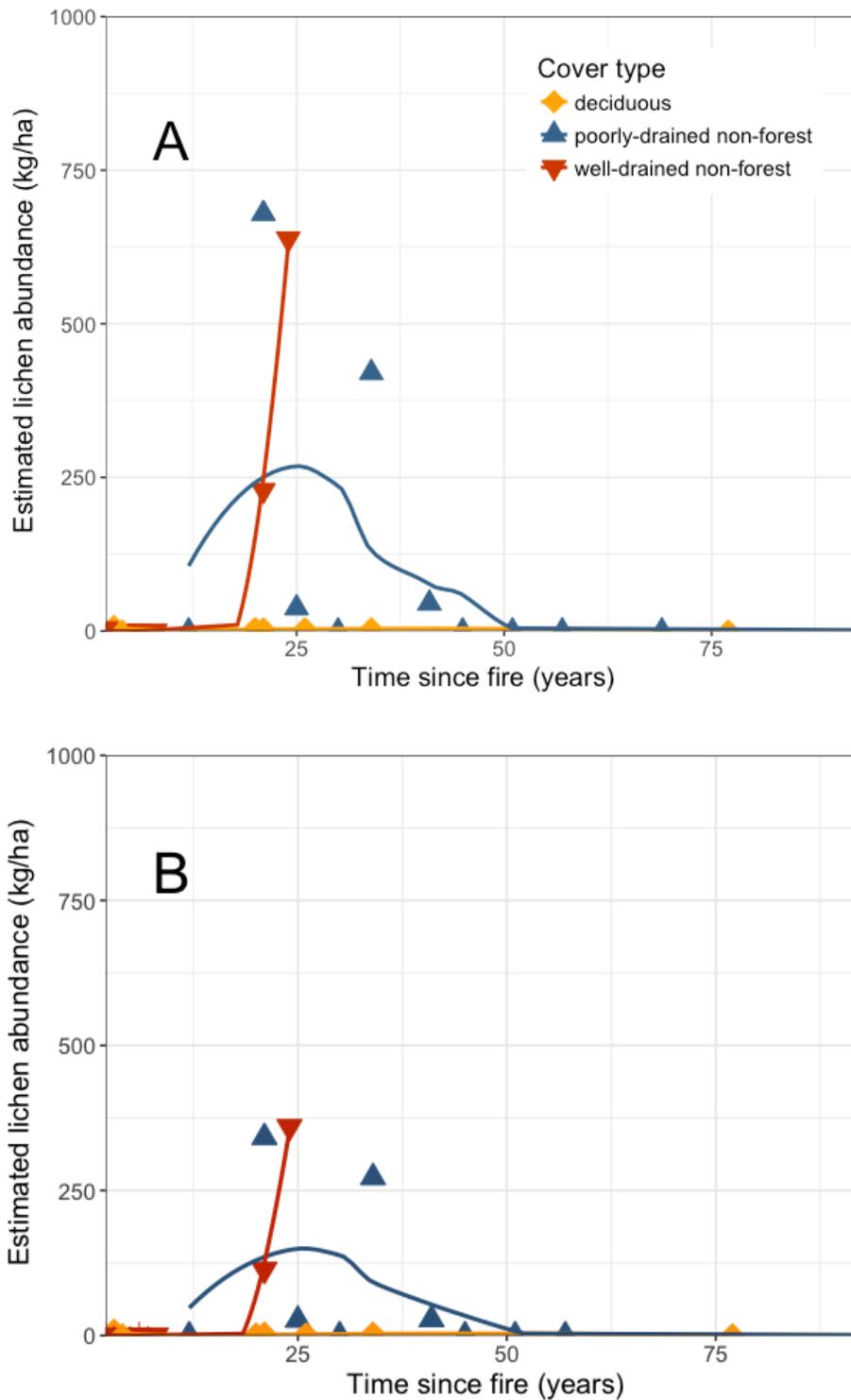


Figure 18: Projections of estimated biomass (kg/ha) at ($n = 39$) sites calculated from A.) area measurements (cm^2/cm^2) and B.) volume measurements (cm^3/cm^2) for each of the 3 stand types with the overall lowest abundance. Curved lines are loess smoothing functions for each stand type. Of these, 24 sites had zero lichen.

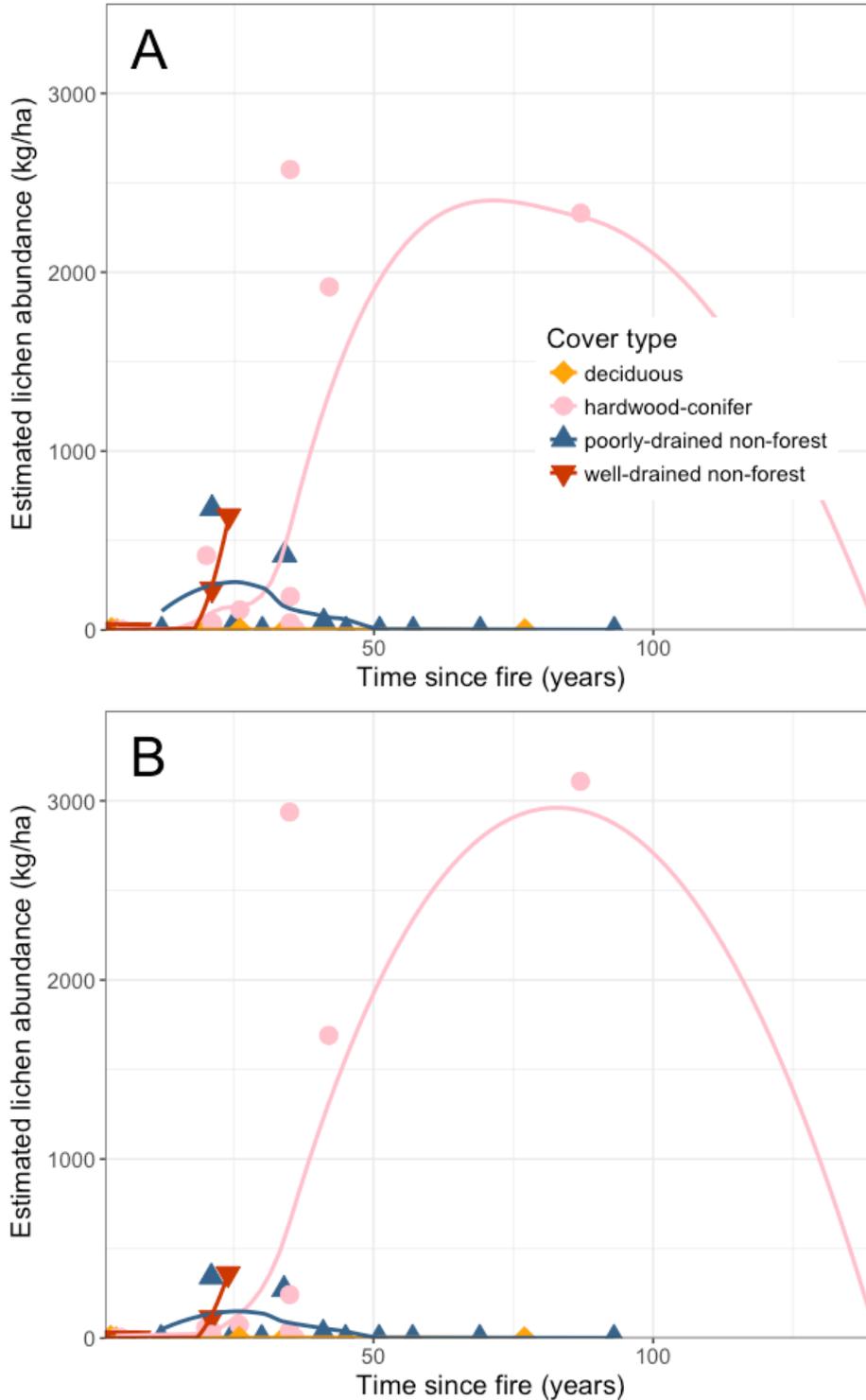


Figure 19: Projections of estimated biomass (kg/ha) at sites ($n = 62$) calculated from A.) area measurements (cm^2/cm^2) and B.) volume measurements (cm^3/cm^2) for each of the 3 stand types with the overall lowest abundance, as well as the stand type with the most intermediate lichen abundance (hardwood-conifer). Curved lines are loess smoothing functions for each stand type. In “low-abundance” stands there was zero lichen, as the sites were selected to capture unusual ecosites, typically rocky shores or fens. Of the sites shown here, 35 sites had zero lichen.

APPENDIX C: DESTRUCTIVE LICHEN BIOMASS DATA

Column	Meaning	Units	Format
plot	Plot location/sample number	YEAR-xxx (a,b,c if multiple samples taken at the same site)	String
species	Species name	Name	String
biomass	Biomass of the lichen, live and dead included	g	Numeric
depth	Average depth of the lichen species in cm, to the nearest 0.5	cm	Numeric
percent.cover	Percent cover of the lichen species	Percent	Numeric

plot	species	biomass	depth	percent.cover
2015-001a	C.mitis	14.388	5	65
2015-001a	C.uncialis	5.054	3	22
2015-004a	C.mitis	5.613	2.4	35
2015-004a	C.uncialis	2.28	3	30
2015-004b	C.mitis	1.926	1.5	10
2015-004b	C.stellaris	1.028	3.5	25
2015-007a	C.mitis	12.335	3.5	10
2015-007a	C.rangiferina	0.28	4	5
2015-007a	C.uncialis	3.065	3	74
2015-007b	C.mitis	11.176	3.5	25
2015-007b	C.stellaris	1.871	6	20
2015-007b	C.uncialis	3.398	5	15
2015-008a	C.mitis	16.564	3.5	50
2015-008a	C.uncialis	6.563	3	20
2015-011a	C.mitis	6.999	4	7
2015-011a	C.rangiferina	4.466	7.5	25
2015-011a	C.stellaris	5.412	8	50
2015-011a	C.uncialis	2.178	3.5	1
2015-011b	C.mitis	11.357	4.5	76
2015-011b	C.rangiferina	1.142	4	5
2015-011b	C.uncialis	3.338	5	6
2015-020a	C.mitis	14.374	5.73	75
2015-020a	C.uncialis	8.766	4.5	10
2015-024a	C.mitis	2.208	3.5	47
2015-024a	C.rangiferina	0.01	0	0
2015-024a	C.uncialis	2.009	3	25
2015-029a	C.mitis	3.661	3.5	25
2015-029a	C.rangiferina	0.333	0	0
2015-029b	C.mitis	2.04	3	5

2015-029b	C.rangiferina	9.569	6	15
2015-031a	C.rangiferina	19.647	7	35
2015-031a	C.stellaris	27.341	6.5	60
2015-031b	C.mitis	12.869	4.5	40
2015-031b	C.rangiferina	0.526	6	1
2015-031c	C.rangiferina	0.16	6.5	1
2015-035a	C.mitis	15.407	6	25
2015-035a	C.rangiferina	7.996	8.5	15
2015-035a	C.stellaris	7.681	8	25
2015-035b	C.mitis	10.285	6	20
2015-035b	C.rangiferina	7.707	7	25
2015-035b	C.stellaris	1.071	6.5	20
2015-035b	C.uncialis	5.666	4.5	15
2015-042a	C.mitis	5.731	5	33
2015-042a	C.uncialis	7.367	3	23
2015-047a	C.mitis	0.313	3	4
2015-047a	C.rangiferina	0.012	0	0
2015-047a	C.uncialis	0.002	0	0
2015-050a	C.mitis	12.295	6	60
2015-050a	C.rangiferina	0.032	0	0
2015-050a	C.uncialis	1.796	5	10
2015-052a	C.mitis	0.273	2	4
2015-052a	C.uncialis	0.009	0	0
2015-053a	C.mitis	9.444	3.5	57
2015-053a	C.rangiferina	0.135	5	3
2015-053a	C.uncialis	6.974	4.5	13
2015-056a	C.mitis	1.687	4.5	24
2015-056a	C.rangiferina	0.044	5	1
2015-056a	C.uncialis	2.005	5	5
2015-058a	C.mitis	4.378	5.5	24
2015-058a	C.rangiferina	1.49	7	6
2015-058a	C.stellaris	1.068	6.5	5
2015-058a	C.uncialis	4.993	5.5	22
2015-058b	C.mitis	8.05	6.5	14
2015-058b	C.rangiferina	6.646	8.5	24
2015-058b	C.uncialis	16.631	4.5	26
2015-061a	C.mitis	3.97	3	18
2015-061a	C.stellaris	0.649	4	6
2015-061a	C.uncialis	6.732	3	28
2015-064a	C.mitis	11.25	5	48
2015-064a	C.uncialis	4.036	4	10

2015-067a	C.mitis	10.061	5.5	48
2015-067a	C.uncialis	2.327	5	16
2015-069a	C.mitis	20.187	6.5	61
2015-069a	C.rangiferina	0.131	11	1
2015-069a	C.uncialis	0.413	4	4
2015-069b	C.mitis	6.347	5	29
2015-069b	C.rangiferina	0.715	8	8
2015-069b	C.uncialis	0.881	4	5
2015-072a	C.mitis	8.36	5	44
2015-072a	C.rangiferina	0.15	6.5	2
2015-072a	C.uncialis	1.747	4	6
2015-073a	C.mitis	4.872	0	0
2015-073a	C.rangiferina	52.471	11.5	36
2015-073a	C.stellaris	26.76	12	64
2015-079a	C.rangiferina	4.185	6.5	19
2015-079a	C.stellaris	1.129	8	7
2015-079b	C.rangiferina	0.779	7.5	5
2015-079b	C.stellaris	5.403	8	25
2015-083a	C.mitis	0.07	0	0
2015-083a	C.rangiferina	14.156	9	40
2015-083a	C.stellaris	12.474	10.5	32
2015-083a	C.uncialis	0.186	0	0
2015-086a	C.mitis	6.857	5	33
2015-086a	C.rangiferina	2.485	8	17
2015-090a	C.mitis	11.199	4.5	47
2015-090a	C.uncialis	1.001	3.5	10
2015-096a	C.mitis	0.279	3	8
2015-096a	C.uncialis	0.191	2.5	3
2015-100a	C.mitis	2.068	1	28
2015-100a	C.uncialis	0.542	2	2
2015-103a	C.mitis	9.786	5	62
2015-103a	C.uncialis	1.546	4	5
2015-106a	C.mitis	6.442	4.5	42
2015-106a	C.rangiferina	0.853	9	5
2015-106a	C.stellaris	6.723	7	22
2015-106a	C.uncialis	3.511	3.5	12
2015-106b	C.mitis	2.498	5	21
2015-106b	C.uncialis	1.727	5	8
2016-001a	C.mitis	6.928	5	29
2016-011a	C.mitis	6.627	3	43
2016-016a	C.mitis	4.938	3	44

2016-016a	C.uncialis	0.201	1.5	1
2016-019a	C.mitis	13.553	3	70
2016-019a	C.uncialis	0.927	2.5	4
2016-021a	C.mitis	19.796	3	79
2016-021a	C.rangiferina	0.004	0	0
2016-021a	C.uncialis	1.406	3	3
2016-022a	C.mitis	17.836	3	70
2016-022a	C.rangiferina	1.611	5	8
2016-022a	C.uncialis	3.286	3	8
2016-024a	C.mitis	3.625	2	12
2016-024a	C.uncialis	0.155	0	0
2016-026a	C.mitis	11.551	4.5	45
2016-026a	C.rangiferina	0.541	6	4
2016-026a	C.uncialis	7.582	3	10
2016-028a	C.mitis	7.867	4	30
2016-028a	C.rangiferina	0.771	5.5	7
2016-028a	C.stellaris	5.594	6	17
2016-028a	C.uncialis	3.929	3.5	17
2016-029a	C.mitis	12.533	5.5	51
2016-029a	C.rangiferina	12.824	8	36
2016-029a	C.stellaris	0.525	0	0
2016-029a	C.uncialis	0.671	4	5
2016-036a	C.mitis	26.892	7	51
2016-036a	C.rangiferina	15.326	8	33
2016-036a	C.uncialis	0.837	0	0
2016-037a	C.mitis	23.227	5	65
2016-037a	C.rangiferina	0.405	8.5	2
2016-037a	C.stellaris	1.192	8.5	6
2016-037a	C.uncialis	2.139	5.5	9
2016-041a	C.mitis	8.166	5	36
2016-041a	C.rangiferina	0.015	0	0
2016-041a	C.uncialis	5.237	4.5	16
2016-046a	C.mitis	7.91	3	47
2016-046a	C.uncialis	4.461	2.5	17
2016-054a	C.mitis	3.382	5	24
2016-054a	C.uncialis	0.339	4.5	3
2016-060a	C.mitis	2.791	5	21
2016-060a	C.uncialis	0.346	3.5	2
2016-072a	C.mitis	0.19	0	0
2016-072a	C.stellaris	24.6	8	75
2016-072a	C.uncialis	0.048	0	0

2016-073a	C.mitis	0.578	3	4
2016-075a	C.mitis	6.295	6	15
2016-075a	C.rangiferina	0.009	0	0
2016-075a	C.uncialis	19.096	6.5	34
2016-082a	C.mitis	0.7	3	6
2016-085a	C.mitis	4.486	5	34
2016-085a	C.rangiferina	0.028	4.5	1
2016-087a	C.mitis	3.187	8	15
2016-087a	C.stellaris	5.182	8	25
2016-087a	C.uncialis	5.309	5.5	14
2016-088a	C.mitis	4.94	6	20
2016-088a	C.rangiferina	1.962	10	13
2016-088a	C.stellaris	7.846	9	32
2016-089a	C.mitis	6.001	6	14
2016-089a	C.rangiferina	20.212	10	26
2016-089a	C.stellaris	17.761	9.5	38
2016-089a	C.uncialis	1.708	5	9
2016-092a	C.mitis	9.644	6.5	41
2016-092a	C.rangiferina	0.557	10	5
2016-092a	C.stellaris	3.744	8	20
2016-092a	C.uncialis	0.388	6	1
2016-095a	C.mitis	8.549	6	30
2016-095a	C.stellaris	0.065	0	0
2016-095a	C.uncialis	14.655	5	28
2016-097a	C.mitis	10.88	7	52
2016-097a	C.rangiferina	0.52	8	3
2016-097a	C.uncialis	5.874	4.5	20
2016-100a	C.mitis	0.079	4	1
2016-100a	C.rangiferina	13.082	9	55
2016-100a	C.stellaris	9.168	8	24
2016-100a	C.uncialis	0.054	5	1
2016-X4a	C.mitis	11.725	4.5	48
2016-X4a	C.stellaris	1.616	3.5	5
2016-X4a	C.uncialis	4.272	3	11
2016-X6a	C.mitis	13.582	6	40
2016-X6a	C.rangiferina	19.048	8	28
2016-X6a	C.stellaris	14.829	9	22
2016-X6a	C.uncialis	0.263	0	0

APPENDIX D: PLOT-LEVEL SUMMARIES OF LICHEN AND ENVIRONMENTAL DATA
USED IN BOOSTED REGRESSION TREES

Column	Meaning	Units	Type
plot	plot name (year followed by number in sequence)	year-XXX	String
basal.area.density	basal area of trees	cm ² /m ²	Numeric
TSSRF	Time since stand-replacing fire	years	Numeric
TSF	Time since fire	years	Numeric
standtype	Rule-based classification of stand type	Factor	String
easting	UTM coordinate for easting in metres	metres	Numeric
northing	UTM coordinate for northing in metres	metres	Numeric
HLI	McCune's heat load index	NA	Numeric
lastfireSR	Factor describing whether the most recent fire was stand-replacing (1) or not (0)	NA	Numeric
percent.cover	Average percent cover of 4 lichen species in plot	%	Numeric
volume.cm3.m2	Average volume density of 4 lichen species at plot	cm ³ /m ²	Numeric

plot	basal.area density	TSSRF	TSF	standtype	easting	northing	HLI	lastfireSR	percent.cover	volume.cm3.m2
2014-001	7.84	48	31	well-drained black spruce	535440	6192733	0.561435	0	0.25	0
2014-002	35.48	78	78	well-drained black spruce	568944.3	6214637	0.559386	1	0	0
2014-003	8.93	19	19	hardwood-conifer	572334.9	6217024	0.558474	1	0	0
2014-004	2.52	31	31	well-drained black spruce	542024.9	6197136	0.550408	1	0	0
2014-005	14.29	78	52	conifer mix	562536.6	6377122	0.539159	0	13.75	6050
2014-006	19.66	52	33	pine	563543.1	6373326	0.539589	0	16	5800
2014-007	20.58	52	52	pine	565345.2	6368830	0.602455	1	4.5	1800
2014-008	22.64	168	168	poorly-drained black spruce	562628.7	6360636	0.487976	1	0	0
2014-009	0.03	33	33	poorly-drained non-forest	567429.9	6333524	0.544098	1	0.625	0
2014-010	0	4	4	spruce	582271.8	6323004	0.636375	1	0	0
2014-011	0	4	4	conifer mix	585543.4	6315420	0.41242	1	0	0
2014-012	0	4	4	well-drained black spruce	586159.7	6313595	0.560202	1	0	0
2014-013	0.02	5	5	well-drained non-forest	587539.3	6270421	0.565304	1	0	0
2014-014	3.59	27	8	pine	587745.4	6265827	0.643761	0	3	675
2014-015	0.01	4	4	poorly-drained non-forest	588033.8	6258928	0.55263	1	0	0
2014-016	0	4	4	well-drained black spruce	586639.1	6256223	0.668114	1	0	0
2014-017	28.15	51	51	conifer mix	587635.8	6241739	0.575183	1	11	4050
2014-018	0.92	19	19	well-drained black spruce	568933.7	6229329	0.455411	1	0	0
2014-019	5.31	19	19	deciduous	562033.9	6227025	0.61407	1	0.375	0
2014-020	25.91	49	49	conifer mix	576548.8	6231236	0.5445	1	0.25	0
2014-021	17.24	45	45	well-drained black spruce	579741.8	6211927	0.509822	1	13.5	4350
2014-022	20.16	68	68	deciduous	577330.5	6214834	0.535516	1	0	0
2014-023	15.8	31	31	pine	585375.4	6326631	0.693595	1	14.75	2925
2014-024	0	4	4	conifer mix	584738.2	6323622	0.572543	1	0	0
2014-025	0	4	4	well-drained black spruce	584333.7	6321926	0.56197	1	0	0
2014-026	8.27	83	83	well-drained black spruce	599634	6243927	0.485412	1	30.25	10800
2014-027	27.68	51	51	deciduous	589434.4	6234835	0.493602	1	0.25	0
2014-028	1.42	19	19	well-drained black spruce	566748.3	6229525	0.570112	1	18.5	2700
2014-029	22.13	83	83	poorly-drained black spruce	567534.3	6209118	0.600812	1	0	0

2014-030	8.1	83	10	pine	490745.3	6382628	0.527299	0	0.05	0
2014-031	10.54	83	83	conifer mix	484228.7	6376025	0.31109	1	21	8050
2014-032	7.13	163	163	poorly-drained black spruce	490538.4	6372227	0.539659	1	20.125	15300
2014-033	13.79	163	75	pine	486040.2	6369831	0.490654	0	15	5900
2014-034	0	6	6	pine	485339	6365930	0.547226	1	0	0
2014-035	0	6	6	pine	481846.2	6364117	0.602975	1	0	0
2014-036	0	6	6	pine	475239.2	6358424	0.559061	1	0	0
2014-037	0	6	6	pine	473401.1	6358247	0.554859	1	0	0
2014-038	6.73	41	41	pine	472247.7	6354919	0.523862	1	77	19500
2014-039	0	5	5	poorly-drained non-forest	467242.5	6356824	0.541412	1	0	0
2014-040	0.97	102	102	poorly-drained non-forest	457724.7	6350530	0.542134	1	0.25	0
2014-041	0.24	102	102	poorly-drained non-forest	459941.7	6352024	0.541963	1	2.125	800
2014-042	0	10	10	pine	463335.5	6353336	0.604801	1	0	0
2014-043	6.24	41	41	pine	464842.5	6348929	0.650267	1	30.75	10450
2014-044	0.02	11	11	pine	450532.3	6337022	0.543673	1	0	0
2014-045	2.83	193	193	poorly-drained black spruce	448031.1	6334827	0.543925	1	20.5	10400
2014-046	5.03	41	41	pine	447338.9	6336027	0.613781	1	30	7500
2014-047	12.2	66	24	pine	432352.7	6307730	0.547026	0	12	2200
2014-048	7.36	24	24	pine	436542.8	6320622	0.577261	1	25	2500
2014-049	0	4	4	pine	543277	6342034	0.543097	1	0	0
2014-050	0.75	33	4	conifer mix	543921.2	6342471	0.561055	0	0	0
2014-051	0	4	4	pine	546838.9	6348675	0.536855	1	0	0
2014-052	0	3	3	well-drained black spruce	546104.2	6347693	0.54246	1	0	0
2014-053	0	11	11	pine	544869.5	6345590	0.519807	1	0	0
2014-054	2.14	33	4	pine	549753.5	6347437	0.542494	0	0	0
2014-055	9.84	118	33	conifer mix	552573.3	6352367	0.736804	0	1.5	750
2014-056	0	4	4	pine	547906.5	6346319	0.614068	1	0	0
2014-057	4.58	33	4	pine	549510.8	6349223	0.395036	0	1.125	100
2014-058	3.53	105	22	well-drained black spruce	550622.1	6348997	0.542318	0	35.5	12100
2014-059	1.67	192	4	conifer mix	551001.6	6350420	0.542158	0	0.125	0
2014-060	13.08	52	18	conifer mix	557934.5	6356771	0.511741	0	35.125	13000

2014-061	12.97	52	52	pine	556727.6	6355164	0.851401	1	4.25	1200
2014-062	1.18	33	4	conifer mix	555641.9	6354709	0.534253	0	4	1200
2014-063	3.22	205	33	poorly-drained black spruce	555510.2	6355656	0.541572	0	14.875	5200
2014-064	1.34	205	33	poorly-drained black spruce	554273.7	6353718	0.541789	0	48.5	19650
2014-065	13.38	116	33	conifer mix	554480.1	6351511	0.542039	0	37.5	11000
2014-066	7.18	33	33	pine	552829.5	6350359	0.613677	1	18.75	5900
2014-067	18.78	33	33	pine	551488.2	6348915	0.513816	1	8.25	1600
2014-068	0.13	4	4	well-drained black spruce	551823	6351578	0.533254	1	0	0
2014-069	25.79	33	33	pine	551749.4	6350900	0.485558	1	0.25	0
2014-070	20.35	49	49	pine	557996.6	6352970	0.546143	1	18	5400
2014-071	11.04	49	49	pine	557570.7	6353494	0.513611	1	13.25	5200
2014-072	35.19	53	33	deciduous	674245.5	6164124	0.63749	0	0	0
2014-073	9.22	53	53	deciduous	671332.3	6159127	0.691559	1	0.625	150
2014-074	0	2	2	hardwood-conifer	651440.9	6168531	0.792045	1	0	0
2014-075	0	2	2	deciduous	651538.8	6169322	0.385301	1	0	0
2014-076	22.77	97	97	spruce	649042.1	6163526	0.590331	1	0	0
2014-077	18.28	19	19	hardwood-conifer	647651.6	6168028	0.628878	1	0.125	0
2014-078	5.99	19	19	conifer mix	648743.8	6167420	0.582437	1	0.25	0
2014-079	21.85	25	25	deciduous	640848.2	6161224	0.502338	1	0.125	0
2014-080	3	26	26	deciduous	641805.7	6163425	0.52665	1	0	0
2014-081	10.07	26	26	deciduous	641441.9	6158326	0.843808	1	0	0
2014-082	5.13	19	19	hardwood-conifer	655836.9	6185830	0.582161	1	0.125	0
2014-083	8.1	19	19	conifer mix	655039.6	6185229	0.475623	1	5	1000
2014-084	4.52	19	19	deciduous	653743.7	6181041	0.536915	1	0	0
2014-085	10.18	25	25	deciduous	644348.9	6158727	0.726914	1	0	0
2014-086	19.04	25	25	deciduous	644838.2	6157020	0.683712	1	2	800
2014-087	25.63	97	97	well-drained black spruce	647538.9	6162027	0.808401	1	0.375	0
2014-088	41.66	97	97	conifer mix	653731.2	6160918	0.529263	1	0	0
2014-089	3.72	18	18	deciduous	653837.3	6159023	0.594892	1	0	0
2014-090	28.67	83	83	hardwood-conifer	670040	6151420	0.468258	1	0	0
2014-091	10.99	19	19	conifer mix	663140	6145025	0.578846	1	0.375	0

2015-001	3.92	41	41	pine	450639.3	6348425	0.542381	1	55.1	18720
2015-002	0	8	8	pine	455632.3	6355228	0.602165	1	0	0
2015-003	0.1	41	8	well-drained non-forest	456241.3	6354722	0.541662	0	0	0
2015-004	11.52	41	41	pine	458241	6353215	0.542308	1	31	14750
2015-005	0	8	8	pine	459242	6356418	0.554404	1	0	0
2015-006	6.06	73	8	pine	459545	6357219	0.550685	0	0	0
2015-007	5.16	34	34	pine	461443.3	6358123	0.582889	1	35.6	19572.5
2015-008	7.18	34	34	pine	469041.7	6369521	0.571413	1	41	15600
2015-009	14.02	34	34	pine	472942	6372126	0.539852	1	17	13350
2015-010	9.42	34	34	pine	473346.3	6371922	0.457632	1	17.5	11775
2015-011	15.68	67	34	pine	485843.7	6389521	0.554706	0	40	24175
2015-012	2.8	34	34	pine	504839	6403531	0.600594	1	23.05	12970
2015-013	8.93	34	34	pine	502241.3	6400633	0.554154	1	22	8050
2015-014	0.06	127	41	poorly-drained non-forest	456944.7	6350916	0.542091	0	0.6	207.5
2015-015	0	7	7	pine	474141.7	6355320	0.490741	1	1	312.5
2015-016	0	30	30	poorly-drained non-forest	473342.7	6358318	0.541238	1	0	0
2015-017	0.05	11	11	pine	469241.3	6355518	0.52534	1	0.05	2.5
2015-018	5.51	160	34	pine	457543.3	6342220	0.607046	0	37.55	20730
2015-019	4.02	46	46	pine	450841.3	6342024	0.531894	1	42.1	21560
2015-020	6.38	46	46	pine	451443.7	6342920	0.448504	1	36	16025
2015-021	17.19	82	46	poorly-drained black spruce	447936.3	6334835	0.543924	0	23.5	14700
2015-022	15.8	67	25	conifer mix	432436	6307935	0.383094	0	5.05	2870
2015-023	0	1	1	pine	614136.7	6284418	0.560025	1	0	0
2015-024	2.04	20	20	pine	619438	6267423	0.496373	1	2	1025
2015-025	29.85	49	49	conifer mix	640230.7	6263534	0.609907	1	2.55	2277.5
2015-026	0	3	3	well-drained non-forest	635447	6263124	0.708742	1	0	0
2015-027	0.3	3	3	well-drained non-forest	635452	6264635	0.67291	1	0	0
2015-028	0.23	25	25	poorly-drained non-forest	627034.7	6246929	0.554114	1	0.5	200
2015-029	0.17	107	3	well-drained black spruce	626645.7	6259217	0.316279	0	0	0
2015-030	0	3	3	conifer mix	632525.3	6260130	0.399847	1	0	0
2015-031	11.74	112	32	poorly-drained black spruce	606357.3	6261724	0.574815	0	0.05	10

2015-032	21.63	87	87	well-drained black spruce	608649	6262634	0.582195	1	0	0
2015-033	3.43	20	20	hardwood-conifer	627045.7	6272927	0.673015	1	2.55	437.5
2015-034	30.22	148	148	well-drained black spruce	624440.3	6268420	0.622718	1	0	0
2015-035	10.04	87	87	hardwood-conifer	626728.3	6267018	0.602257	1	29.05	23332.5
2015-036	18.08	51	51	pine	607943.3	6254722	0.574259	1	6.05	2995
2015-037	21.33	51	51	well-drained black spruce	608844	6256924	0.590521	1	1.5	835
2015-038	20.97	51	51	well-drained black spruce	597838.7	6245622	0.571079	1	0	0
2015-039	3.53	20	20	deciduous	564026	6208541	0.558352	1	0.05	7.5
2015-040	3.48	21	21	hardwood-conifer	687043.3	6197824	0.466479	1	0.5	150
2015-041	9.65	21	21	deciduous	681445.7	6187432	0.577164	1	0	0
2015-042	9.9	21	21	hardwood-conifer	682238.3	6188323	0.541182	1	0.5	325
2015-043	24.65	54	21	deciduous	676720	6179419	0.590238	0	0.05	22.5
2015-044	7.1	20	20	deciduous	650546	6180129	0.50114	1	0.05	5
2015-045	16.08	46	20	conifer mix	650540	6179235	0.575428	0	1.6	980
2015-046	14.04	140	140	hardwood-conifer	650634.3	6174839	0.756491	1	0	0
2015-047	6.17	26	26	hardwood-conifer	641433.3	6150329	0.617527	1	1.5	550
2015-048	18.98	26	26	deciduous	641352	6164130	0.510195	1	0.05	15
2015-049	20.02	53	53	well-drained black spruce	645245.3	6160720	0.56482	1	0	0
2015-050	21.27	35	35	pine	537551.7	6468227	0.567152	1	19.05	8505
2015-051	14.58	43	43	pine	535538.7	6478428	0.442558	1	1.05	392.5
2015-052	5.3	21	21	pine	529439.7	6484225	0.547419	1	1.5	175
2015-053	12.4	41	41	pine	531634.7	6492023	0.49523	1	61	39500
2015-054	1.18	17	17	pine	531643.3	6491425	0.573911	1	1.25	0
2015-055	22.07	81	58	well-drained black spruce	533744.7	6490522	0.526626	0	22.5	19950
2015-056	12.37	35	35	pine	544442.3	6460321	0.536111	1	24.15	12367.5
2015-057	3.12	216	216	poorly-drained black spruce	550838.7	6456737	0.5302	1	1.5	725
2015-058	12.87	167	45	pine	551836	6453632	0.675825	0	18.55	11845
2015-059	11.99	45	45	pine	525338.7	6445823	0.529615	1	33.1	19295
2015-060	14.67	45	45	conifer mix	530146	6452831	0.333713	1	20.1	10072.5
2015-061	7.57	35	35	pine	543439.3	6452526	0.515513	1	30.1	15852.5
2015-062	20.46	34	34	pine	537834.3	6440226	0.565107	1	8.5	2287.5

2015-063	10.28	34	34	pine	536934.7	6439726	0.571131	1	17.5	8250
2015-064	4.15	34	34	poorly-drained black spruce	537440	6442630	0.531762	1	21.5	13975
2015-065	11.43	138	34	pine	534138.7	6435428	0.569113	0	45.1	26515
2015-066	0	5	5	pine	533937.7	6437624	0.583627	1	3	1100
2015-067	20.08	45	45	pine	528534.3	6438924	0.595508	1	20.15	12217.5
2015-068	10.66	45	45	well-drained black spruce	545946	6435726	0.575384	1	33.55	23432.5
2015-069	18.02	57	57	pine	538839.7	6435928	0.544823	1	23.5	19175
2015-070	0.05	57	57	poorly-drained non-forest	542139.7	6444624	0.531543	1	0	0
2015-071	13.46	45	45	pine	569845	6456025	0.544857	1	7.5	4000
2015-072	2.85	45	45	pine	566938.3	6454323	0.533097	1	56.6	35610
2015-073	8.44	171	171	poorly-drained black spruce	580140	6454624	0.53049	1	77.5	90600
2015-074	5.65	171	171	poorly-drained black spruce	584737	6462918	0.500174	1	65.5	71825
2015-075	0	5	5	pine	575741.3	6454819	0.642223	1	0	0
2015-076	0	5	5	pine	576637.3	6455122	0.492929	1	0	0
2015-077	0	5	5	pine	575842.3	6456226	0.549355	1	0	0
2015-078	5.89	104	3	deciduous	574534	6449043	0.493753	0	0.1	60
2015-079	30.67	104	104	well-drained black spruce	575146.7	6449125	0.58128	1	6.15	5122.5
2015-080	32.58	55	55	well-drained black spruce	572739.3	6445521	0.505288	1	7	4850
2015-081	4.66	5	5	well-drained black spruce	579134	6438238	0.672045	1	0	0
2015-082	0	5	5	pine	578440	6438919	0.591284	1	0	0
2015-083	24.66	111	111	well-drained black spruce	577940.3	6442829	0.441551	1	2.05	1472.5
2015-084	13.48	45	45	pine	550528.7	6452769	0.520389	1	28.05	13715
2015-085	18.16	111	111	conifer mix	568444.7	6444927	0.520116	1	41.5	26537.5
2015-086	11.97	111	111	well-drained black spruce	570344.7	6432722	0.488214	1	0.55	222.5
2015-087	22.72	111	111	well-drained black spruce	571140.3	6432129	0.519809	1	0.3	182.5
2015-088	5.95	185	185	poorly-drained black spruce	574340.7	6435722	0.532593	1	58	58900
2015-089	0	5	5	poorly-drained black spruce	576031.7	6438424	0.526345	1	0.15	95
2015-090	10.74	42	42	hardwood-conifer	570839	6435129	0.576756	1	22.5	12687.5
2015-091	23.17	111	111	well-drained black spruce	570819.3	6438640	0.561125	1	41	36550
2015-092	0	5	5	well-drained black spruce	579942.7	6435626	0.532616	1	0	0
2015-093	0.54	5	5	well-drained black spruce	572435.7	6415331	0.449656	1	0	0

2015-094	0	5	5	well-drained non-forest	576942	6433426	0.551966	1	0	0
2015-095	0	5	5	well-drained black spruce	577640.7	6431715	0.596015	1	0	0
2015-096	10.7	79	21	well-drained black spruce	553236.3	6389026	0.508118	0	0	0
2015-097	0	2	2	well-drained non-forest	592544.3	6410331	0.606522	1	0	0
2015-098	0.25	37	6	well-drained non-forest	587750.7	6412826	0.532751	0	0	0
2015-099	2.66	134	134	poorly-drained black spruce	583841.3	6414629	0.534981	1	0	0
2015-100	0.52	21	21	well-drained non-forest	577442.3	6406423	0.599529	1	2.05	852.5
2015-101	12.46	82	34	well-drained black spruce	568136.7	6407225	0.455279	0	16.05	9990
2015-102	0.26	21	21	poorly-drained non-forest	571839.3	6405225	0.548772	1	9	2565
2015-103	0.95	34	34	poorly-drained non-forest	569149	6406424	0.535872	1	5.05	2045
2015-104	20.48	34	34	pine	568340.3	6404627	0.536451	1	13.5	4625
2015-105	3.21	34	34	pine	569139.7	6405127	0.52133	1	33.65	25645
2015-106	19.28	84	84	well-drained black spruce	573735.3	6328124	0.533099	1	14.05	6710
2015-107	37.88	52	52	conifer mix	587339.3	6239322	0.51354	1	0.05	22.5
2015-108	26.36	133	133	poorly-drained black spruce	587230	6247326	0.573512	1	41.05	28807.5
2015-109	10.66	84	5	well-drained black spruce	585640.7	6308730	0.562665	0	0	0
2015-110	0.4	5	5	pine	585141.7	6309622	0.678589	1	0	0
2015-111	0.01	9	9	well-drained black spruce	580034.3	6300624	0.378573	1	0.05	2.5
2015-112	15.29	34	34	deciduous	574051.3	6297125	0.521993	1	0.05	22.5
2015-113	0	9	9	well-drained black spruce	581441	6301116	0.486831	1	1.05	80
2015-114	0.29	5	5	conifer mix	580343	6295726	0.812706	1	0	0
2015-X1	0	-9999	9999	poorly-drained non-forest	585048	6463747	0.522629	1	0	0
2016-001	18.38	51	51	pine	576841.3	6231325	0.575064	1	3.25	1700
2016-002	0.49	51	51	poorly-drained non-forest	576041.3	6230822	0.555819	1	0	0
2016-003	0	5	5	hardwood-conifer	587243.7	6210630	0.667836	1	0	0
2016-004	0	5	5	well-drained non-forest	585842	6210623	0.558157	1	0	0
2016-005	0.01	5	5	hardwood-conifer	584941.3	6208624	0.604467	1	0	0
2016-006	18.5	93	5	well-drained black spruce	587744.3	6210523	0.62961	0	0	0
2016-007	17.73	75	36	hardwood-conifer	586451	6209230	0.597146	0	0	0
2016-008	0	5	5	hardwood-conifer	583943.3	6209230	0.616727	1	0	0

2016-009	0.04	5	5	conifer mix	583846.7	6209624	0.653547	1	0	0
2016-010	0	5	5	conifer mix	584440.7	6211522	0.529392	1	0	0
2016-011	9.59	26	26	pine	424239.7	6357628	0.541815	1	2.2	732.5
2016-012	18.66	158	158	pine	421441.7	6359024	0.578236	1	0.05	7.5
2016-013	0.48	8	8	pine	423039.7	6364429	0.525488	1	0	0
2016-014	0.33	8	8	pine	416836	6356928	0.564065	1	0	0
2016-015	0.89	8	8	poorly-drained black spruce	415042.3	6353225	0.541904	1	3.55	2047.5
2016-016	11.09	89	31	conifer mix	397441.3	6358522	0.52172	0	10.5	3720
2016-017	0	6	6	well-drained non-forest	402343.7	6374127	0.518968	1	0	0
2016-018	0	2	2	pine	405944.7	6387923	0.431093	1	0	0
2016-019	7.16	43	43	pine	392837.3	6378130	0.562417	1	16.5	6745
2016-020	0.06	6	6	pine	405742.3	6373629	0.551125	1	0	0
2016-021	2.16	31	31	pine	391142.7	6360729	0.437069	1	64	26200
2016-022	7.72	84	84	conifer mix	387640	6362662	0.568029	1	45.75	31000
2016-023	5.96	145	145	poorly-drained black spruce	387555.3	6362240	0.54096	1	3.75	2425
2016-024	5.06	30	2	pine	388416	6373537	0.554457	0	2	457.5
2016-025	1.98	69	69	larch	386686.3	6370663	0.540012	1	0	0
2016-026	8.82	145	145	pine	388598	6369746	0.446138	1	36.55	18480
2016-027	9.6	52	52	pine	388268	6354405	0.592432	1	34.5	15125
2016-028	14.51	162	52	pine	387676	6355114	0.600159	0	36.5	19725
2016-029	4.52	162	162	poorly-drained black spruce	386040.3	6353086	0.541999	1	2.15	1880
2016-030	0	15	15	well-drained black spruce	384307.7	6352593	0.548472	1	0	52.5
2016-031	29.8	97	97	well-drained black spruce	382640.3	6351830	0.485249	1	3.25	2060
2016-032	0	45	45	poorly-drained non-forest	369216.7	6337513	0.543819	1	0	0
2016-033	0	12	12	poorly-drained non-forest	370723	6337915	0.543768	1	0	0
2016-034	0.09	-9999	9999	poorly-drained non-forest	373683.7	6339968	0.543525	1	0	0
2016-035	7.79	144	12	conifer mix	378300.3	6343837	0.562402	0	0	7.5
2016-036	7.92	144	144	poorly-drained black spruce	384758.7	6350360	0.528493	1	19.5	16332.5
2016-037	11.89	78	78	pine	382443.7	6347503	0.596905	1	56.8	40660
2016-038	17.52	162	162	well-drained black spruce	387328.7	6356433	0.503861	1	23.05	17987.5

2016-039	5.02	162	58	poorly-drained black spruce	379388.7	6352132	0.548439	0	0.15	50
2016-040	0.44	8	8	pine	372525.7	6356411	0.552525	1	0	0
2016-041	14.67	56	56	pine	371613.3	6361729	0.559687	1	23.75	16075
2016-042	6.63	26	26	pine	374555.7	6361368	0.548968	1	21.5	6225
2016-043	0	2	2	pine	377182.7	6354626	0.522216	1	0	0
2016-044	0.03	8	8	pine	364224.7	6358557	0.559427	1	0.05	10
2016-045	0.68	93	93	poorly-drained non-forest	364718	6358321	0.541481	1	0	0
2016-046	5.27	93	24	pine	374322.7	6363081	0.566249	0	34.5	19800
2016-047	1.12	31	31	poorly-drained black spruce	374221.7	6371223	0.53999	1	7.05	7260
2016-048	0	-9999	9999	poorly-drained non-forest	382147.3	6370449	0.540051	1	0	0
2016-049	0	2	2	pine	376041	6369219	0.480891	1	0.15	7.5
2016-050	2.35	31	2	pine	381230.7	6371955	0.558743	0	0.1	30
2016-051	0.14	24	24	well-drained non-forest	382148.3	6368685	0.545664	1	8.5	2700
2016-052	0	-9999	9999	poorly-drained non-forest	379878	6367812	0.540356	1	0	0
2016-053	0	2	2	pine	382748.7	6363675	0.577794	1	0	0
2016-054	5.52	27	27	conifer mix	624941.3	6191627	0.534214	1	5	1820
2016-055	16.13	77	77	conifer mix	624939.3	6201620	0.494003	1	0	0
2016-056	0	4	4	hardwood-conifer	626236.7	6199914	0.497963	1	0	0
2016-057	16.06	159	159	well-drained black spruce	620245	6198723	0.644417	1	4	2850
2016-058	0	-9999	9999	well-drained non-forest	621439.7	6199020	0.553517	1	0	0
2016-059	16.99	140	140	hardwood-conifer	622648.7	6199936	0.547981	1	0	0
2016-060	18.61	23	23	pine	616742	6199126	0.513602	1	3	1500
2016-061	18.6	77	77	well-drained black spruce	620238.3	6205529	0.661813	1	0	0
2016-062	32.04	77	77	well-drained black spruce	619437	6205231	0.528746	1	0.1	42.5
2016-063	28.96	77	77	deciduous	618234.3	6202825	0.599823	1	0	0
2016-064	21.77	140	140	well-drained black spruce	623743.7	6198829	0.604017	1	0	0
2016-065	0.4	4	4	deciduous	627835.3	6197516	0.701738	1	0	0
2016-066	0.03	4	4	hardwood-conifer	627439.3	6197027	0.53887	1	0	0
2016-067	0	4	4	hardwood-conifer	627939.3	6196427	0.576595	1	0	0

06

2016-068	0	4	4	conifer mix	627741	6196928	0.568394	1	0	0
2016-069	33.86	143	143	poorly-drained black spruce	625837.7	6199822	0.559706	1	0	0
2016-070	2.96	5	5	hardwood-conifer	627336.3	6195127	0.60233	1	0	0
2016-071	33.05	87	87	conifer mix	621249	6186845	0.615434	1	0	0
2016-072	26.99	87	87	well-drained black spruce	622237	6188729	0.532888	1	10.5	10100
2016-073	7.33	35	35	well-drained black spruce	555783	6355770	0.542035	1	6.25	3675
2016-074	12.21	118	35	well-drained black spruce	552472.3	6352176	0.539498	0	2.05	1175
2016-075	11.65	47	47	well-drained black spruce	605537.7	6235722	0.628644	1	23.1	19287.5
2016-076	8.81	47	47	well-drained black spruce	583245.7	6213726	0.558486	1	3	1650
2016-077	0.13	5	5	hardwood-conifer	582632.3	6208430	0.52757	1	0	0
2016-078	16.65	49	49	well-drained black spruce	569739	6238226	0.545054	1	3	1985
2016-079	13.47	21	21	pine	571843	6236123	0.564728	1	0.3	95
2016-080	4.44	21	21	hardwood-conifer	567241.7	6234115	0.532262	1	0.05	15
2016-081	2.49	49	21	poorly-drained black spruce	574141.3	6227835	0.556157	0	0.05	45
2016-082	3.4	21	21	hardwood-conifer	566944.3	6232323	0.545652	1	0.5	150
2016-083	36.24	81	81	well-drained black spruce	569838.3	6214032	0.570916	1	0	0
2016-084	19.57	94	47	well-drained black spruce	514146.3	6312031	0.559115	0	0.05	5
2016-085	8.07	35	35	well-drained black spruce	513838	6309024	0.763568	1	5.5	2125
2016-086	19.84	35	35	hardwood-conifer	522739.3	6319331	0.567798	1	0.55	325
2016-087	10.33	73	35	hardwood-conifer	524036.3	6321712	0.397015	0	2.5	1825
2016-088	20.02	73	35	pine	517132.7	6315627	0.610291	0	19	12650
2016-089	15.27	147	147	pine	516539.3	6312826	0.311531	1	35.05	31627.5
2016-090	5.16	73	27	poorly-drained black spruce	517943	6314225	0.547713	0	26.55	21415
2016-091	25.03	35	35	hardwood-conifer	512443.7	6306731	0.5699	1	0.05	10
2016-092	20.52	73	73	well-drained black spruce	517246.3	6313725	0.564296	1	46.05	45345
2016-093	16.23	35	35	pine	513447	6311027	0.612167	1	1	350
2016-094	31.23	73	73	conifer mix	516041.3	6310729	0.511225	1	0.15	65
2016-095	15.65	73	35	pine	517442	6311119	0.531802	0	18	12145
2016-096	21.76	35	35	pine	515843.7	6311534	0.541616	1	0.3	135
2016-097	4.78	35	35	hardwood-conifer	514443.7	6308427	0.609112	1	29.55	22042.5
2016-098	10.53	35	35	pine	513140.7	6307627	0.592541	1	3.05	2110

2016-099	10.78	35	35	well-drained black spruce	512739.3	6308116	0.407084	1	0.05	15
2016-100	19.76	142	40	well-drained black spruce	513939	6309425	0.660577	0	0	0
2016-X1	0	6	6	well-drained non-forest	402550.7	6374292	0.516774	1	0	0
2016-X2	0	2	2	well-drained non-forest	374570.7	6345522	0.483297	1	0	2.5
2016-X3	0.24	-9999	9999	well-drained non-forest	382812	6348353	0.547977	1	24.55	16165
2016-X4	7.9	93	93	pine	372534	6370249	0.389239	1	11	8725
2016-X5	0	-9999	9999	well-drained non-forest	373351.3	6370248	0.618183	1	20	9600
2016-X6	4.32	145	145	pine	389614	6365450	0.566203	1	67.5	52650