Assessing vegetation dynamics in a changing Arctic-Boreal Region using field data and modeling approaches

A Doctoral Dissertation

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Abstract

The tundra-taiga ecotone (TTE), the transitional zone between the boreal forest and the Arctic tundra, spans over 3 million km² and is dynamically responding to climate change. The morass of interacting and conflicting environmental drivers can make the TTE dynamics difficult to predict. The TTE is crucial for global carbon budgets, as it contains important forest resources growing above large stores of labile carbon held in the unfrozen soil and permafrost. The goal of my dissertation is to examine the growth drivers within the TTE of various plant functional types (PFTs), which are aggregations of species with similar structure and function. Research on vegetation response to climate change in the TTE typically focuses on single drivers in narrow spatial and temporal ranges, leaving a gap in integrating ecosystem drivers and responses across large, heterogenous landscapes. By taking an interdisciplinary, multivariate approach, and leveraging both field data and model outputs, I can assess shifting vegetation dynamics in the TTE which can aid in predicting their impact on global carbon budgets.

In my first chapter, I assess variability in growth drivers of black and white spruce trees in the TTE, using the NOAA International Tree Ring Database. Challenging the assumption that growth increases with warmer temperatures, I examined the strength of climate variables influence on annual growth, and how site-specific environmental variables interact with climate. I found that the climate in the "shoulder" seasons, particularly May temperature, has increased in importance for predicting tree growth, as summer temperature importance has decreased.

My second chapter analyzes the community composition of vegetation in the Canadian Northwest Territories using Canada's National Forest Inventory dataset applying multivariate analyses. One of the challenges to predicting vegetation dynamics in the TTE is the high heterogeneity (climate, soil, vegetation) of the landscape. By combining the NFI species-level composition dataset and local site measurements, I determined what drives specific plant

functional type (PFT) changes and how they manifest in remote sensing records. Each of the 11 represented PFTs responded to different abiotic and biotic drivers, which could result in novel plant communities in the future.

The third chapter reviews the dynamic vegetation models (DVMs) that are currently being used to predict the future of the TTE. As climate shifts in the Arctic, vegetation is responding across the landscape in novel ways. DVMs are able to not only predict vegetation change across remote areas, but also project vegetation composition into the future. However, many of these models are challenging to understand for non-modelers, and the ecosystem elements they are modeling are difficult to determine. I also surveyed experts on what is needed in dynamic vegetation models to improve model predictions and found a demand for models with permafrost and active layer dynamics. Reviewing the state of the science on modeling and outlining these ecosystem processes increase accessibility and understanding of this class of models for future applications.

My fourth chapter conducts a sensitivity analysis of SIBBORK-TTE, to determine the influence of adding three tall shrub genera to the model. I assessed how different combinations of shrub genera influence black and white spruce growth both with historical climate and a warming climate. I found that the shrubs were not only successfully able to compete with the spruce, but they also alter the importance of certain variables under different growing conditions.

To summarize, my first two chapters assess interacting ecosystem drivers of community composition and growth variation utilizing field data sets and multivariate analysis. Applying these findings, the second half of my dissertation focuses on improving dynamic vegetation models for the TTE. My dissertation will advance the state of the science on growth drivers in the Arctic-Boreal Region and will support the further development of model simulations by highlighting which drivers should be incorporated to create better ecosystem facsimiles. The TTE is a crucial biome transition zone and a highly dynamic carbon sink; by understanding how this area is responding to climate change, we will be able to more accurately predict its fate.

Introduction

The Arctic-Boreal Zone (ABZ) is warming four times faster than the rest of the globe due to the Arctic amplification of climate change (Ballinger et al. 2021, Rantanen et al., 2022). This increase in temperature (2.7°C since 1970 [Box et al., 2019]) has already begun to affect the terrestrial landscape by changing vegetation dynamics, destabilizing permafrost, and altering fire regimes. At the southern edge of the Arctic tundra, the ecotone between the tundra and the boreal forest/taiga is rapidly shifting. The tundra-taiga ecotone (TTE) occurs where the boreal forest has less than 30% tree cover (Montesano et al., 2020) through to the treeline (the latitudinal extent of trees) where there is no tree cover.

The TTE is a highly heterogeneous landscape that is dynamically responding to anthropogenic climate change. The shifts in the ecotone are harbingers of what is expected to occur in the tundra as warming continues to increase in the Arctic. Vegetation growth at northern high latitudes is cold-limited, and thus the logical assumption is that increasing temperature would increase growth and facilitate tree seedling establishment, allowing trees to expand northward; the subsequent result being that the ecotone extends northward and encroaches on the tundra. However, many studies have found that the ecotone is not responding as expected (Harsch et al. 2009, Reese et al. 2019, Timoney et al. 2019). The ecotone is indeed responding with increased growth, and trees are in some cases growing larger and moving northward (Dial et al., 2022); however, the same phenomena that limit the treeline (e.g., wind, extreme temperatures, drought, herbivory) continue to remain important controls on ecotone vegetation growth (Maher et al., 2019, Marquis et al., 2020, Stevens-Rumann et al., 2022).

Understanding how the Arctic-Boreal Zone (ABZ) will respond to climate change is critical to projecting future Arctic-Boreal ecosystems. Shifts in the characteristic abiotic (albedo, permafrost, fire) and biotic (vegetation composition and growth) features of the landscape can have cascading effects on water, carbon, nutrient and energy budgets of the ecosystem. While it is clear that the TTE is rapidly changing, the mechanisms behind the shifts are dynamic and frequently interactive, and different vegetation types may respond in different ways.

1.0.1 Hypotheses on carbon implications of vegetation change

There are two main hypotheses regarding the carbon implications of treeline dynamics: a carbon sink hypothesis and a carbon source hypothesis. The sink hypothesis focuses on the direct effect of temperature on the ability of plants to assimilate carbon and focuses on the effect of cold temperature limitation on cell division and tree growth (McNown and Sullivan 2013). The implication of the carbon sink hypothesis is that any release from this thermal limitation would increase the growth of trees, allowing for northward expansion.

The carbon source hypothesis suggests that treeline is determined by factors that limit net carbon accumulation from indirect effects of air temperature, such as drought stress, low soil temperatures, nutrient limitations, and damage or loss of tissues (McNown and Sullivan 2013). The implication of the carbon source hypothesis is that the treeline is controlled by multiple interacting factors that cannot be universally surmised.

The sink and source hypotheses are better considered to be complementary, as they address both the direct and indirect effects of anthropogenic climate warming. Broadening the scope of the source and sink hypotheses from just treeline trees to all vegetation within the ecotone, we can assume that vegetation in the Arctic-Boreal region is, or was, limited by cold temperatures, but that each species thermal limitation is different, and that all are also limited by other factors. The drivers and effects of altered plant growth in the TTE are complex and intertwined, and while the region is becoming warmer, that is no guarantee that it is any easier to survive.

1.0.2 Abiotic drivers of vegetation in the tundra-taiga ecotone

Increasing temperatures are directly and indirectly impacting vegetation dynamics in the tundra-taiga ecotone. The increase in temperatures has reduced the thermal limitation on photosynthesis, shifting the growth limitation to other variables (McNown and Sullivan 2013, Reich et al. 2018, Hofgaard et al. 2019). Increased temperatures are also reducing sea ice and increasing humidity, as well as reducing albedo through reduction in snow cover (Box et al., 2019), all of which feeds back to increase warming. The expected increase in precipitation projected for the region (+1-2% per decade [Box et al., 2019]) is at odds with the literature citing an increase in drought conditions in the Arctic (Maguire et al., 2010, Boulanger et al., 2017, Buchwal et al., 2020); however, this drought stress is mostly due to decreases in soil moisture, through increases in vapor pressure deficit. Soil moisture is an important driver of growth in the TTE and can be a strong limiting growth variable given the increased evaporative demand, but is also driven by precipitation patterns (Sullivan et al., 2021) and active layer depth (Thunberg et al., 2021). There has been a shift in late fall precipitation from snow to rain (Mekonnen et al. 2021), reducing snowpack depth, and ultimately decreasing soil insulation. The shift from snow to rain has been seen across snow-adapted ecosystems (Campbell et al. 2005) and typically causes colder soil temperatures. Reduced soil temperatures can reduce stomatal conductance in plants, limiting their carbon uptake (McNown and Sullivan 2013).

Summer warming has increased active layer depth and permafrost thaw, leading to short term increases in soil nutrients (Heijmans et al., 2022, Ogden et al., 2023) that can subsequently turn into soil nutrient limitations once all the labile nutrients are absorbed, and the remaining soil organic matter is recalcitrant (Semenchuk et al., 2026). Permafrost thaw can either increase or decrease soil moisture (Heijmans et al., 2022), depending on the local site conditions; but where

soil moisture is increasing, vegetation has been able to take advantage of the additional water to offset increased temperatures (Kirdyanov et al., 2024). The TTE is within the discontinuous permafrost zone, where there is 50-90% of the landscape with underlying permafrost (Obu et al., 2019), but it is very difficult to predict presence and depth of permafrost at precise locations, and the overlying vegetation, such as shrubs, moss, and lichen, can further complicate permafrost predictions by altering soil temperatures (Myers-Smith and Hik 2013, Chen et al., 2019, Mallen-Cooper et al., 2021). The resulting permafrost mosaic can have large effects on aboveground processes and vegetation dynamics (Blume-Werry et al., 2019, Standen and Baltzer 2020). *1.0.3 Biotic drivers of vegetation in the tundra-taiga ecotone*

The above-mentioned interacting abiotic factors are leading to shifts in the vegetation in the tundra-taiga ecotone. There is an increase in shrub abundance (shrubification), especially in the Low Arctic tundra, which has led to a general "greening" of the Arctic (Myers-Smith et al., 2020). However, this shrubification is not universal, and dwarf shrubs and evergreen shrubs have not increased growth consistently with increasing temperatures (Myers-Smith et al.2015, Ackerman et al. 2018). Further south, the boreal forest is extending northward into the ecotone, while losing area along its southern edge (Timoney et al., 2019, Rotbarth et al., 2023). Increasing fire frequency and severity is driving the southern shift toward deciduous trees (Mack et al., 2021, Massey et al., 2023), as the black and white spruce trees require longer fire intervals to regenerate. Within the ecotone, the density and size of trees is increasing (Aune et al., 2011, Kruse et al., 2018), and taller PFTs are able to shade out many lower statured species, such as moss and lichen (Marshall and Baltzer 2015). Moss and lichen have a moderating effect on soil temperature via insulation and evaporation, and can ameliorate some of the effects of climate change (Chen et al. 2019, Mallen-Cooper et al., 2021), and decreases in their abundance may

lead to warmer summer soils. Graminoids are also increasing in the Low Arctic tundra and have been documented to be able to take advantage of thawing permafrost and grow deeper roots to capitalize on newly labile nutrients (Blume-Werry et al., 2019).

However, much of what we know about patterns in Arctic-Boreal PFTs, has been observed using remote sensing techniques which cannot discern species identities. Within every PFT, are multiple species that are uniquely adapted to their specific niche and responding individually to the new conditions across the landscape (Loehle 2018). Thus, it is important to assess ecosystem changes at the species level whenever possible. Because the Arctic-Boreal Zone is expansive and challenging for field work, species level datasets are rare, and we must rely on these coarser resolution analyses. Modeling helps to bridge this gap, especially when parameterized to fine vegetation resolutions.

1.0.4 Dissertation Goals

The complexities of vegetation growth and species community development in the Arctic-Boreal Zone are nuanced and interactive. The carbon balance implications of increasing vegetation growth and destabilizing permafrost make the TTE an important area to understand; however, the morass of interacting and conflicting environmental drivers makes the TTE dynamics difficult to predict. The purpose of this dissertation is to elucidate the growth drivers of various plant functional types in the TTE by analyzing many environmental variables in concert. By examining both field data and model outputs, I assessed the shifting vegetation dynamics in the TTE and highlight new patterns developing on the landscape.

The first two chapters focus on large field data sets that analyze drivers of annual growth and vegetation change across spatial and temporal gradients. Chapter one focuses on the annual growth of black and white spruce over a long time period (>100 years) at 35 sites across Alaska

and Canada. The second chapter leverages greater species data to analyze the community level drivers of ecosystem change but at a shorter time scale (10 years) across the Northwest Territories, Canada. Both chapters highlight the importance of multivariate analyses to analyze how vegetation is responding to variables that are shifting in concert.

The third and fourth chapters focus on modeling applications in the North American Arctic-Boreal Zone. The third chapter surveys 18 dynamic vegetation models and their utility in the region, and the fourth chapter applies one of these models, SIBBORK-TTE, to determine the effect of shrub genera on spruce growth in the model. By first outlining the state of modeling in the Arctic-Boreal Zone, I was able to identify areas of strength and weakness in model applications. Then in the SIBBORK-TTE model, with a permafrost submodule and greater vegetation resolution, I was able to determine the effects of tall shrubs on spruce growth.

My dissertation applies multivariate analyses to examine environmental drivers in concert rather than individually from both field data and model simulations. By analyzing the temporal and spatial differences in environmental drivers and how they vary by plant functional type, I am able to elucidate interactions that are potentially overlooked. From the analysis of the field data and the SIBBORK-TTE output, I am able to assess the utility of the model in simulating the tundra-taiga ecotone. This research supports the further development of model simulations by highlighting which drivers are overlooked and need to be incorporated to create better ecosystem predictions.

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Chapter 1: Changing environmental drivers of growth of black and white spruce in boreal North America due to climate warming

2.0 Abstract

With climate change, the thermal limitation on vegetation growth in the Arctic-Boreal Zone is being reduced; however, that has not corresponded to a universal increase in growth. The recent decoupling of growth with summer temperature for white spruce was first described as the "Divergence Problem" by D'Arrigo et al. (2008), and much has since been written on what is driving growth in the Arctic-Boreal, but studies addressing drivers of growth have been primarily limited to univariate analyses. I used bootstrap linear regression to assess tree growth and the relative importance of three annual climate variables (temperature, vapor pressure deficit, precipitation) across three seasonal groupings (summer, May, previous fall), along with a modeled maximum annual thaw depth, for 35 sites across Alaska and northwestern Canada. Tree ring and climate data were separated into pre-1980 and post-1980 time periods to assess shifts in responses during a pre- and post-climate warming period. I also analyzed how topographic and edaphic characteristics at each site mitigated the response to climate variables. I found that as the summer growing season is expanding into spring and fall, these shoulder seasons are becoming more important for predicting growth. Warmer May and previous fall temperatures consistently showed a negative correlation with tree growth post-1980, while VPD had either a mixed correlation (May) or positive correlation (previous fall) with growth. Increased thaw depth was negatively correlated with tree growth post-1980. Soil texture and drainage had interactive effects with May climate variables, which were most different between the pre- and post-1980 time periods. Overall, I found that while summer temperature was generally decreasing in importance to tree growth, there is not a universal response for all sites in the warming climate. My results indicated that shoulder seasons have increased in their importance to tree growth,

either because the growing season is becoming longer, or because the variability of these seasons has become a greater liability.

2.1 Introduction

In the Arctic-Boreal Zone, it has historically been assumed that annual tree-ring growth was predominantly driven by summer temperature (Hofgaard et al., 2019, Tei & Sugimoto 2017, Labrecque-Foy et al., 2023, Wang et al., 2022), and paleo-climatological studies have employed that assumption in climate reconstructions (e.g., Grudd et al., 2002). However, D'Arrigo et al. (2008) diagnosed the Divergence Problem, which identified a recent, weakened relationship between temperature and annual tree ring growth. The implications of the Divergence Problem are that as global temperatures increase, tree growth is no longer limited by temperature in the boreal forest, but by other factors.

While it is clear that the influence of growing season temperature on annual tree growth is decreasing, there have been myriad reasons put forth to explain the divergence: drought stress (D'Arrigo et al. 2008, Buermann et al., 2013, Buchwhal et al. 2020), global dimming (increased anthropogenic air pollution in the atmosphere decreasing surface irradiance; Kirdyanov et al., 2020), aspect and elevation (Dearborn and Danby 2018), snowpack (Dearborn and Danby 2018), phenology shifts (D'Arrigo et al. 2008), and shifts in precipitation to increasing winter rain events (Opala-Owczarek et al. 2018, Dial et al., 2024). These factors are frequently analyzed independently, but likely work in concert to affect growth; this dynamic has been noted in a variety of studies and shows important regional variation (Bontemps and Bouriaud 2014, Montesano et al., 2023, Camarero et al., 2024, Neigh et al., 2024).

For example, while increasing air temperatures may be favorable for growth in the northern boreal forest, they also may increase drought stress and cause stomatal closure, inhibiting growth (McNown and Sullivan 2013, Reich et al. 2018). The decoupling of summer temperature and growth is variable and nonlinear (Dial et al., 2024, Montesano et al., 2024),

which not only affects our ability to predict future vegetation growth patterns (Mann et al., 2012, Girardin et al., 2016), but cascades into climate feedbacks such as shifting surface albedo (Cook et al., 2008, Massey et al., 2023), hydrologic processes (Barichivich et al., 2014, Thunberg et al., 2021), and carbon storage (Cabon et al., 2022).

Many climate and aboveground factors have been addressed, but the absence of data on soil conditions, particularly active layer depth, suggests the picture is incomplete. Soil conditions influence important growth factors such as drought stress and nutrient availability (Ellison et al. 2020), which interact with climate factors to affect vegetation growth (Sullivan et al., 2016, Opala-Owczarek et al. 2018, Holtmeier and Broll 2019, Dial et al., 2022). Permafrost creates an impermeable layer that limits root growth and access to nutrients, but a warming Arctic-Boreal has increased the active layer depth in many areas (Biskaborn et al., 2019, Nyland et al., 2021) and potentially mobilized previously unavailable nutrients (Finger et al., 2016, Heijmans et al., 2022). Additionally, thawing permafrost shifts hydrologic patterns, which can locally alter soil water content (Miner et al., 2022, Jorgenson et al., 2022) potentially offsetting drought stress in trees (Kirdyanov et al., 2024).

My goal in this analysis was to examine the interactive effects that dynamic annual climate variables and relatively static topographic and edaphic variables have on tree growth and how these patterns might have changed with climate warming to affect the North American Arctic-Boreal region. I asked two main questions:

 a) Has the strength of the effect of summer temperature on tree growth changed over time with climate warming? b) If the effect of summer temperature on tree growth is no longer limiting, what other climate variables are influencing growth? 2. How do local site characteristics (topographic, edaphic) interact with climate variables to control growth?

2.2 Methods

2.2.1 Collecting tree ring and climate data at study sites

Tree ring data were accessed from the NOAA International Tree Ring Database in 2020. I limited site selection to those within the NASA Arctic Boreal Vulnerability Experiment (ABoVE) Domain (Alaska and western Canada), and used white spruce (*Picea glauca*) and black spruce (*Picea mariana*) datasets. From the International Tree Ring Database, each study site provided 20-80 raw tree ring widths stored as ring width index (RWI) files. My study focused on white and black spruce, two dominant evergreen conifers in the ABoVE Domain, and there were at least ten monospecific sites per species, giving power to within-species analysis. I selected sites that had an average tree age of at least 100 years old to maximize the temporal depth of my sample to compare to the climate data; the total analysis had 35 sites (Figure 2.1).



Figure 2.1: A map of the 35 study sites from the NOAA International Tree Ring Database (<u>https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring</u>). Some points have been offset to decrease overlap. Basemap is from USGS topographic map in ArcGIS Pro.

To obtain site climate, I used Climatic Research Unit (CRU; Harris et al., 2020) data from 1901-2015 for annual and monthly means of temperature, precipitation, and vapor pressure (converted to vapor pressure deficit) for each site (Figure 2.2). The CRU data are gridded at a 0.5° resolution and derived from statistical interpolations of point-based station observations; due to the large CRU gridded block, some of my sites have the same input climate data to analyze against tree growth. Annual data were separated into two time periods, pre-1980 and post-1980, so that I could determine the effect of warming on the growth patterns. The year 1980 was chosen to separate the growth trends, as it is the year that climate warming begins to have noticeable impacts in the Arctic (Box et al., 2019).



Figure 2.2: A flow chart of methods and subsequent outputs. Blue boxes/lines represent annual data that was used in the bootstrap linear regression analysis, and green boxes/lines represent inputs to the soil and topographic variable assessments for interaction with climate variables. Orange boxes/lines represent the analysis and outputs. Words outside of the boxes represent analysis steps.

To derive a time series of active layer data per site, I used the SIBBORK-TTE model, a version of the spatially explicit, individual-based forest gap model (Brazhnik and Shugart 2016),

updated to account for key drivers of forest growth that are particular to the taiga-tundra ecotone (TTE), the northern edge of the boreal forest in North America (see Chapter 4 for more detailed model description). This update includes a permafrost module rewritten from Bonan's boreal forest model (Bonan 1989). The climate data from CRU were used to create statistical climate values (temperature and precipitation averages and standard deviations) for each month from 1901-1980 and from 1981-2015.

Tree ring sites were not associated with a specific georeferenced area, thus modeled stem count was derived using two key inputs. The first input was a spaceborne-based (Landsat) 30m resolution percent tree canopy cover map calibrated with LiDAR to improve sensitivity to the boreal forest gradient (Montesano et al., 2016, Montesano et al., 2020, Montesano et al., 2024). The second input came from observations of stem counts from Canada's National Forest Inventory (NFI) plots (National Forest Inventory 2013, National Forest Inventory 2021). Together, they were used to build a linear relationship between percent tree canopy cover and recorded stem count for white spruce (p-value < 0.001, Supplemental Equation 2.1). The relationship for black spruce stem count and tree canopy cover was negative and less reliable (pvalue = 0.4, Supplemental Equation 2.2), likely due to the narrow growth form and the likelihood that the negative relationship between black spruce stems and tree cover is due to the presence of other species of conifers or broadleaf trees. While the relationship for black spruce was not strong, I needed an estimate for stem density to run the model, as surface radiation drives thaw depth in the SIBBORK-TTE model. When stem count was calculated to be negative, I assumed one black spruce tree per 10 m^2 to be present.

I limited the species simulation in SIBBORK-TTE to only black or white spruce, since I did not have any additional species composition information. I ran the model for each site using

temperature and precipitation averages and standard deviations from the CRU data between 1901-1980; each site had a 300-year period of acclimation (spin-up) and began simulations at the year 2015 minus stand age. In 1980, the model turned on warming temperatures that had been calculated from the average CRU temperatures from 1980-2015. The maximum annual thaw depth output (resolved monthly) for each year from 1901-2015 was added to the annual climate driver dataset (Figure 2.2).

2.2.2 Detrending methods for tree ring widths

In order to assess the impact of climate on trees ring width, I applied five detrending methods (basal area index [BAI], regional curve standardization [RCS], mean, mean negative exponential [MNE], and C-method [CMS]; Sullivan et al., 2016), from the dplR package (Bunn 2008) in R (version 4.2.1, R Core Team 2022). Using multiple detrending methods helps to ensure that the detrending method did not bias the results; I also included the raw ring width as an additional check. I tested each detrended tree ring series within a site against the annual climate and active layer data, because my goal was to examine annual environmental drivers, and I wanted to preserve individual patterns and responses to climate and maintain the noise of the dataset that is not smoothed by detrending. While the regional curve standardization is reportedly more robust to climate signals (Cook and Kairiukstis 1990, Sullivan et al., 2016), the large dataset has many factors, thus it was important to test multiple detrending methods. For regression analysis, the BAI detrended values were log transformed to accommodate the strong right skew of the data, and outliers >500 mm² were removed. The detrended data split into preand post-1980 datasets and the annual growth trend was calculated using simple linear regression and year as the independent variable to determine whether annual increment growth was increasing or decreasing over the time period.

2.2.3 Regression analysis for climate variables and thaw depth

Climate variables from the CRU dataset (monthly average temperature, VPD, and precipitation), were averaged (temperature and VPD) and summed (precipitation) for three time periods (previous fall [September, October November], May, and summer [June, July, August], Figure 2). I chose to use only the May values rather than an aggregate for spring, because in preliminary correlation analyses, the May values better represented the variability of the spring shoulder season than the average with April and March, when tree dormancy has not yet ended. The annual maximum active layer depth from SIBBORK-TTE was also included in the regression analysis. Year was included in the model to account for annual variability. The detrended chronology for each tree within each site was used as the response variable.

I used the *BootStepAIC* package (Rizopoulos 2022) to conduct linear regressions of tree growth with the 11 independent variables (summer temperature, May temperature, previous fall temperature, summer VPD, May VPD, previous fall VPD, summer precipitation, May precipitation, previous fall precipitation, thaw depth, and year) for 500 iterations for each site and detrending method (Site*DM, n = 210). For each bootstrapped iteration, the 11 variables were tested to see which ones were significant predictors for the dataset (Figure 2.2); the bootstrap analysis generates a "chosen" frequency, sign frequency, and significance frequency. The chosen and significant frequencies report how often (percent) the variable was selected and/or significant (alpha = 0.05) in the 500 iterations (i.e., if a variable has a chosen frequency of 90%, it was selected in 450 of the iterations); the sign frequency reports how often the variable when chosen had a positive or negative correlation with growth. When chosen and significance frequency are considered together, they indicate how important a variable is to predicting the growth response for a given Site*DM. I used a simple linear regression instead of a mixed-

effects model, because my objective question was focused on the importance (i.e., significant chosen frequency) of the variable to each Site*DM, and how the variables interacted at each site independently, rather than in aggregate. Additionally, by bootstrapping the data, a more robust analysis of the climate drivers can be achieved for each site, increasing the confidence of the results. Regressions for the historical climate period (1901-1980) and the onset of climate warming (1981-2015) were used to assess if the climate drivers changed between pre- and post-1980 in the Arctic-Boreal region (Box et al., 2019, Hofgaard et al., 2019).

The regression output reports how often a variable was selected, the frequency of positive or negative relationships, and the frequency of the variable being significant (Figure 2.2). From these data, I created quartiles of summer temperature importance to analyze how other climate variables influenced growth when summer temperature was chosen 0-25%, 25-50%, 50-75%, and 75-100% of the time. The frequencies of each variable chosen for each Site*DM were then analyzed using a multivariate analysis of variance (MANOVA) and a Linear Discriminant Analysis (LDA) post-hoc ordination (*MASS* package, Venables and Ripley 2002) with summer temperature quartile, detrending method, soil order, growth trend (positive or negative slope), and species as independent grouping factors. I used the MANOVA to compare the suite of chosen climate variables and their relative importance at each Site*DM and to determine if the grouping variables mattered.

To determine what climate variables were most important across all sites, I limited them for each Site*DM to those that had a significance percent (how often the variable was significant) greater than 95%. Aggregating all climate variables that were important to each Site*DM, I analyzed what variables were chosen most often, their associated positive or negative correlation, and their variation within grouping variables.

2.2.4 Assessing the effects of site characteristics on tree growth

To address the second question of how site characteristics interact with climate variables, I analyzed how static site characteristics influenced the importance of each climate driver. I extracted aspect, slope, and elevation data for each site from 10 m digital elevation models (DEMs; Porter et al., 2018). From SoilGrids (250 m resolution, Poggio et al., 2021), I obtained edaphic characteristics (bulk density, soil organic matter, total nitrogen, soil texture, and soil order type [only Cambisol or Cryosol were identified within the sites], Figure 2.2).

Using an analysis of covariance (ANCOVA), I first assessed the significance of time period (pre- vs post-1980) on the interaction between climate variable importance (positive or negative correlation), and each site characteristic extracted from the DEMs and SoilGrids. Using a Bonferroni adjustment (alpha value = 0.00045), I determined which relationships were significantly different between the pre- and post-1980 datasets. I then ran the linear regressions of the resulting relationships (climate variable importance (\pm %) = a*soil variable + b), and limited the analysis to those with an adjusted R² greater than 0.2, and with significant p-values (alpha value = 0.00045) for the intercept and the soil variable predictor. This analysis allowed me to compare data elements (topographic and soil variables) that did not have any documented temporal change, with the annually resolved climate variables by using the climate variable importance at each Site*DM. It highlighted how sites were changing their responses to climate variables, and how static or slowly changing site characteristics might be moderating the response.

2.3 Results

2.3.1 Summary of findings on drivers of tree growth in the TTE

Growth trends were evenly divided in the pre-1980 period (48% positive, 52% negative) and the post-1980 period (51% positive, 49% negative) (Figure 2.3). Summer temperature decreased in importance for tree growth in the years since climate warming has begun affecting the Arctic-Boreal region (Figure 2.3). Summer temperature (positive correlation) and VPD (negative correlation) were the most important variables across all sites and detrending methods to predict growth pre-1980 (Figure 2.4). In contrast, May temperature (negative correlation) and May VPD (both positive and negative correlations) were the most important climate variables for post-1980, suggesting that the expansion of the growing season may be impacting May climate and giving that time period increased importance. The frequency of the most important climate variables being selected in the post-1980 period (May temperature and VPD) was 17% lower than the frequencies that summer temperature and VPD were chosen pre-1980, suggesting that post-1980 period (May temperature and VPD) was 17% lower than the frequencies that summer temperature and VPD were chosen pre-1980, suggesting that post-1980 growth had a less spatially uniform response to climate.



Figure 2.3: Summer temperature importance decreased from pre-1980 to post-1980 with most sites having a strong importance in the pre-1980 period, and a much lower importance (25-50%) in the post-1980 period. The distribution of positive (blue) and negative (red) growth trends is not significantly different between time periods.



Figure 2.4: The importance and correlation (positive correlation = blue, negative correlation = red) of climate variables to tree growth between pre- and post-1980. Summer temperature and VPD dominated importance in the pre-1980 period, while May temperature and VPD were most important in the post-1980 period. Mixed correlation indicates that Site*DM had different correlations among each other and were responding to the climate variables differently

2.3.2 Regression analysis for climate variables and thaw depth

The bootstrap linear regression revealed that pre-1980 the importance of summer temperature remained in the highest quartile (75-100%) for the majority of Site*DM (68%), but the post-1980 data showed a decreased importance of summer temperature, with the majority of Site*DM shifting to the 25-50% quartile (58%). Pre-1980, only 1.4% of the Site*DM were in the lowest quartile (0-25%), but this increased to 10% in the post-1980 period. Year was a significant variable for every analysis, as expected; however, to assess the environmental controls on growth, it was not included in subsequent analysis.

The MANOVA tested the suite of climate variables important to each Site*DM and their correlation (positive or negative), and how the results are grouped within summer temperature quartile, detrending method, soil order, growth trend, and species (Figure 2.5). Time period (pre-vs post-1980), summer quartile, soil order, growth trend, and species were all significant (p < 0.001) across the entire time period, while detrending method was significant for pre-1980 (p = 0.001) but not for post-1980 (p = 0.55). The LDA showed that when comparing across time periods, there was a significant difference and discrimination by time period (x-axis), and growth trend (y-axis) (Figure 2.5a); the cumulative explanatory power of the two axes was 53%. Within time periods, summer temperature quartile (x-axis) and soil order (y-axis) had strong discrimination (Figure 2.5b, 3.5c) with a cumulative explanatory power of 81% (pre-1980) and 82% (post-1980). While species was significant, it was not strongly associated with one of the two primary ordination axes.





Figure 2.5: The linear discriminant analysis post-hoc results of the MANOVA show the strongest grouping variables of the for the combined dataset (pre- [teal] and post-1980[red]) Site*DM climate variable importance (a). Time period (x-axis) and growth trend (y-axis) are the strongest grouping variables, explaining 59% of the variation. Pre-1980 (b) and post-1980 (c) datasets have much greater separation in climate variable importance across (75% explained) and notable separation across the secondary axis with soil order.

2.3.3 Important climate variables for tree growth by significant groups

To determine patterns in the most important variables for each Site*DM, I limited my analysis to the climate variables that were significant at least 95% of the time for each Site*DM, and were important for at least three sites. Each climate variable was represented at least once among all of the significant variables, and the correlations for each variable were consistent within the sites (i.e., if a variable was significant for the site, it was either positive or negative in >95% of the bootstrap regressions). However, there were instances where the variable was selected at multiple sites, but with different correlation signs. The variables were compared within the four groups found to be significant in the MANOVA (summer temperature quartile, growth trend, species, and soil order) (Figure 2.5). I found that warm, wet summers (positive temperature and precipitation correlation, negative VPD correlation) were important for growth irrespective of growth trend, summer temperature quartile, or soil order (Figure 2.6); white spruce had a negative correlation with warmer temperatures in the post-1980 period. Previous fall and May temperatures were generally negatively correlated with growth, indicating cooler shoulder seasons are better for growth.

The summer temperature quartile grouping indicated that the sign of May VPD and May precipitation changes from pre- to post-1980 (VPD changes from negative to positive correlation; precipitation switches from a mostly positive correlation to a strong negative correlation) (Figure 2.6a). The previous fall drivers also had inconsistent climate correlations across the summer temperature quartiles in the pre-1980 time period, being at first weak in the pre-1980 period and then strong correlations in the post-1980 period, showing negative correlations for the previous fall temperature and precipitation, and positive correlations for VPD (Figure 2.6a). Thaw depth was mostly negatively associated with growth in the post-1980 period, but had mixed correlations in the pre-1980 period (Figure 2.6a).

Within positive and negative growth trends, there is consistency in variable correlations between time periods (Figure 2.6b). Summer temperature was only negatively correlated with the positive growth trend post-1980, confirming that the increase in summer temperature is compromising growth in black and white spruce at the sites (Figure 2.6b). When grouped by growth trend, thaw depth had a weak positive correlation in the pre-1980 time period and shifted to a stronger negative correlation in the post-1980 period, similar to the pattern seen with summer temperature (Figure 2.6b).







Figure 2.6: Distribution of important climate variables and their correlation among the significant grouping variables (summer temperature quartile [a], growth trend [b], species [c] soil order [d], and time period [top half vs bottom half]). Mixed correlation indicates that while within each Site*DM had 100% consistency of positive (blue) or negative (red) correlation for significant variables, among Site*DM there were differing responses. White boxes indicate there were fewer than 3 sites that had the climate variable as a significant predictor of growth.

The difference between black and white spruce climate patterns could be attributed to single differences among the two species within the two time periods. For example, black and white spruce were strongly positively correlated with summer temperature in the pre-1980 time period, but only white spruce sites became negatively correlated in the post-1980 period (Figure 2.6c). In the post-1980 period, white spruce was dominant in its preference for cool, dry spring and fall weather; however, black spruce had a strong positive correlation with May precipitation, and a corresponding negative correlation with May VPD (Figure 2.6c). Both species had negative correlations with thaw depth in the post-1980 time period, marking a change for white spruce, which formerly had a positive association with thaw depth (Figure 2.6c).

When comparing the importance of thaw depth within the topsoil types, the pattern between thaw depth and growth changes from pre- to post-1980. Cryosols show a strong
negative correlation between thaw depth and growth pre-1980 and a weak negative correlation post-1980, while Cambisols shift from a weak positive correlation to a strong negative correlation (Figure 2.6d). With respect to soil order, climate variables stay relatively consistent between pre- and post-1980, except Cryosol summer VPD, which switches from a negative correlation in the pre-1980 time period to a strong positive correlation in the post-1980 period. *2.3.4 Effect of site characteristics on tree growth*

The results of the ANCOVA showed 84 relationships that were significantly different by time period (alpha = 0.00045), but only 17 of those relationships had an adjusted R² greater than 0.2, and had significantly different (alpha = 0.00045) slope and intercept estimates (Figure 2.7). The nine site characteristics that interacted with climate variable importance were latitude, slope, sand, silt, clay, elevation, bulk density, soil organic carbon, and soil nitrogen; the importance of only four climate variables on growth were significantly affected by these soil characteristics: summer temperature, May temperature, May VPD, and May precipitation (Figure 2.6). Summer temperature was only significantly different between time periods for latitude. Sand and clay were significant for all of the May climate variables; May precipitation had the greatest number of significant relationships (7). The results of the ANCOVA and site characteristic analysis highlight the increasing importance of May as a climate driver and its interactions with site characteristics.

2.4 Discussion

2.4.1 Climate Variable Importance

The decrease in importance of summer temperature from the pre- to post-1980 datasets confirmed the decoupling between summer temperature and growth (D'Arrigo et al., 2008, Sullivan et al., 2016, Boulanger et al., 2017, Sherriff et al., 2017, Baltzer et al., 2021, Wang et

al., 2022), regardless of detrending method. The shift from high summer temperature and VPD importance in the pre-1980 dataset to May temperature and VPD importance in the post-1980 dataset suggests an increasing importance of shoulder seasons. The associations between climate and growth in the shoulder seasons (May and previous fall) support the idea that while the temperature limitation is decreasing, the non-temperature limitations (such as water availability and frost damage), continue to limit growth.

May temperatures were negatively correlated with growth across all time periods (Walker et al., 2015). A possible cause is that the risk of spring frosts following snowmelt from seasonal weather variability were detrimental to growth (Marquis et al., 2020) and reduced the total annual growth by inhibiting the initial spring flush. Additionally, Buermann et al. (2013) found a similar negative correlation with earlier spring onset, attributing reduced summer productivity to reduced soil moisture throughout the growing season from a longer drying period, and an increased exposure to soil freezing in early spring. Extending the growing season has a counterintuitive decrease in productivity; soil moisture is prematurely depleted and thus limiting during the height of the summer (Girardin et al., 2016). Decreased soil moisture is exacerbated by decreasing snowpack (Barichivich et al. 2014), which can be attributed to climate conditions in both the spring and previous fall. Warmer springs can also run the risk of causing "spring desiccation" where air temperatures are warm enough to initiate transpiration, but the soils are not yet thawed enough for water to be available (Walker et al., 2015). Given the importance of increased precipitation, it was surprising that May precipitation had a consistently negative correlation with tree growth post-1980, but it is possible that because precipitation increased along with increasing temperatures, the negative correlation with precipitation is related to the larger influence of temperature increase.

The switch from inconsistent correlations with previous fall climate to strong climate variable correlations post-1980 suggest that a cool, dry fall has become increasingly important for tree growth. This shift might be due to fall temperature and precipitation increases leading to a shift from snow to rain and decreased snowpack. Rain-on-snow events and increased early season snow melt decrease soil temperatures and delay growth in the spring as the insulation provided by snow is reduced (Barrere et al., 2018). Additionally, rain during colder months can cause ice damage which will negatively impact growth (Bokhorst et al., 2009, Callaghan et al., 2011).

The largely negative correlation of active layer depth with growth was unexpected as increased active layer depth can have a positive effect on growth (Kirdyanov et al., 2024). I hypothesized that the negative correlation could be caused by changes in the underlying hydrology, leading to increased runoff and potential soil drying (Walker et al., 2015, Painter et al., 2022). The CRU data showed only a slight increase in precipitation over time, so it is unlikely that the negative correlation in the post-1980 dataset is due to inundation. The Cryosol sites had the opposite pattern, shifting from a negative growth relationships with active layer depth pre-1980 to a mixed correlation post-1980, suggesting that at sites with permafrost in the top meter, the increased permafrost thaw is facilitating tree growth (Barichivich et al. 2014, Kirdyanov et al., 2024), while for warmer sites it is reducing tree growth (Jorgenson et al., 2022).

May temperature was consistently negatively correlated with growth, except in the highest summer temperature quartile (75-100%) for both pre- and post-1980, and in the Cambisol sites. Given the overlap in site grouping, it is possible that the Cambisol sites that remained highly coupled with summer temperature may be benefiting from the extended

growing season (a warmer May), while the threat of a warmer shoulder season for frost damage would be pushed earlier (April).

The important climate variables for black vs. white spruce follow much of the same patterns as the other grouping variables. Both species showed decreased growth in warm and dry conditions. The largest difference is that black spruce had no significant importance for summer temperature (other than one positive site). White spruce highlights the decoupling, and even reversal of summer temperature importance, having a positive correlation pre-1980, and a slightly negative correlation post-1980. Sheriff et al. (2017) and Wang et al. (2022) both found mixed correlations with white spruce depending on topography and water availability. The observed difference between white and black spruce summer temperature importance may be due to black spruce being generally found in sites with higher soil moisture (Viereck and Little 2000), and thus are able to compensate for increased temperatures without as strong of a negative effect on growth as white spruce.

2.4.2 Site Characteristics

Overall, the interactions between climate variable importance and site characteristics were driven by how different the climate variable importance was between pre- and post-1980. The interaction of summer temperature with latitude is well established, but it was surprising that only the May climate variables were significant, potentially highlighting a new spring climate regime, or expanding growing season (Figure 2.7). May temperature and precipitation were both consistently negatively correlated with growth, while VPD was positively correlated. Likely, the magnitude of the difference between pre- and post-1980 was greatest for the May variables, and thus they were the only relationships with site characteristics that were significant. The dramatic difference in the May variables between pre- and post-1980 might be the result of May no longer





Figure 2.7: The interactions between climate variable chosen percent and their significant site characteristic predictors. Importance decreases as it approaches 0; a large negative value on the y-axis indicates a high importance but negative correlation. Graphs are colored by climate variables (May temperature = yellow, May VPD = purple, May precipitation = teal, summer temperature = orange), while site characteristics are grouped horizontally where possible. A 95% confidence interval surrounds the linear regressions (gray). May temperature was negative for growth in the post-1980 (red), especially in sites with fine textured soils, at low elevations and high latitudes. May VPD had a largely positive effect on growth post-1980, with greater influence at sites with high clay content and high bulk density, and low elevation. May precipitation has a negative effect on growth post-1980, with increased importance at sites with coarse soils, low soil organic carbon, at high elevations. As expected, summer temperature had a decreased importance on growth post-1980

The interaction of summer temperature importance and latitude (Figure 2.70) is consistent with studies showing that plants are being released from thermal limitations further north (Barichivich et al., 2014). The importance of summer temperature increased with latitude pre-1980, while the post-1980 period showed that relationship to be highly diminished, but marginally still present at higher latitudes.

May temperatures had the greatest negative associations with sites at high latitudes, low elevations, and fine textured soils (high clay content; Figure 2.7a, 3.7c, 3.7i respectively). May VPD was more important for sites at lower elevations, with fine soils (high clay content), and lower organic matter (high bulk density; Figure 2.7d, 3.7j, 6m respectively). May precipitation had greater negative importance on sites at high elevations, coarser soils (high sand content), and low soil organic carbon (Figure 2.7e, 3.7h, 3.7p respectively). While these patterns are playing out across the sites, irrespective of species, the patterns with soil texture might be heavily influenced by the northeastern cluster of sites near the Mackenzie River Delta (Figure 2.1).

May temperature did not exhibit a strong relationship with latitude pre-1980, but there was a significant increase in importance with higher latitudes (with a negative correlation) in the post-1980 period (Figure 2.7a). The negative importance of May temperature with increasing latitude is consistent with the suggestion that May temperatures may be negatively correlated with tree growth due to increased risk of frost damage (Moreau et al., 2020). The CRU data (Harris et al., 2020) showed a decrease in frozen days of up to 35% at the higher latitudes, with very minimal decreases in the number of frozen days in May at latitudes lower than 67.5°N. At northern sites with more fluctuation around 0°C, the risk of frost damage is greater. Latitude also interacted with the importance of May precipitation, having a positive relationship in the pre-

1980 period, but no effect in the post-1980 period (Figure 2.7b). This pattern with respect to latitude mirrors the relationship between Cryosols (colder, higher latitude soils, positive correlation) and Cambisols (warmer, lower latitude soil, negative correlation) and May precipitation (Figure 2.6d). Colder climates had a greater positive importance of May precipitation, but with warming, the importance of precipitation at higher latitudes has become similar to the previously observed pattern at lower latitudes.

Elevation interacted with all three May climate variables. In the post-1980 warming period, May temperature (negative correlation) and VPD (positive correlation) importance decreased with elevation (Figure 2.7c, 3.7d), possibly due to elevation mitigating the effects of warming. Given that most of the lower latitude sites were at higher elevations, this effect might be exacerbated (Sherriff et al., 2017). The relationship between May precipitation importance and elevation was consistent (negative slope) from pre- to post-1980 (Figure 2.7e). However, pre-1980, the importance of May precipitation was high and positive at low elevations, and then decreased with elevation. In the post-1980 period, May precipitation had low importance at low elevations but increased with elevation (greater negative correlation, Figure 2.7e). The effect of elevation could again suggest that the climate at higher elevations is becoming more like the climate at lower elevations, and growth is no longer limited by temperature at these relatively low elevations (maximum elevation 1480 m, Okano et al., 2021). A similar pattern occurred between May precipitation and topographic slope (Figure 2.7n), likely due to steeper slopes having greater surface flow, and thus precipitation would not have as strong of an influence on steeper slopes; however, at shallower slopes, where precipitation could infiltrate the soil, the importance of May precipitation was much higher (and positively correlated with growth) in the pre-1980 period.

Soil organic carbon and nitrogen only interacted with May precipitation. Pre-1980, soil organic carbon had moderate but consistent positive influence on the importance of May precipitation, but post-1980, low soil organic carbon led to precipitation having greater negative importance (Figure 2.7p). At high soil organic carbon contents, the pre- and post-1980 importance values are similar, suggesting that soil microbes may be more stressed under the new climate regime (Allison and Treseder 2008), but that enough precipitation can compensate. The relationship with nitrogen was consistent between time periods, but crossed a threshold where the correlation became negative in the post-1980 period (Figure 2.7q). Nutrient limitations on growth were found to be strongest in spring, before water limitation became the dominant limiting factor in black spruce (Yarie and Van Cleve 2010). Soil nitrogen might be tied to May precipitation, as it could represent water sufficiency, causing nutrient availability to be the next growth limitation. The importance of May precipitation decreases with greater available nutrients in the post-1980 period, perhaps because leaching from greater precipitation is less likely to limit growth when nutrients are already abundant. However, these patterns should be accepted cautiously, as I had to assume that soil variables were constant through time.

2.5 Conclusion

Climate change has decreased the importance of summer temperature almost uniformly for black and white spruce growth in Arctic-Boreal North America, but that is the only uniform response that I found. However, it is clear that the new climate regime of a warm, wet May has a negative impact on growth. Sites are responding uniquely to environmental variables (climate, topography, soil), but now that the characteristic cold temperature limitation is alleviated, new limitations are emerging. Importantly, the mitigation of cold temperatures has not uniformly meant an increase in growth, as we have seen that increased summer temperatures can have a negative impact on tree growth (Mann et al., 2012, Girardin et al., 2014, Boulanger et al., 2017, Wang et al., 2022). Growth across the Arctic-Boreal region is no longer easily predicted by growing season climate, and as the growing season is extending into May, it may be paradoxically counterproductive to growth; shoulder seasons are becoming increasingly important for both their temperature variability (e.g., freeze-thaw dynamics), and water storage or use (drought conditions) (Walker et al., 2015, Tei & Sugimoto 2017, Barrere et al., 2018, Brown et al., 2019). As water availability is shifting away from the summer growing season, and variable spring and fall conditions become riskier for frost damage and snowpack, these shoulder seasons should be considered when predicting future tree growth dynamics.

3.6 Acknowledgements

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2.8 Supplemental Materials

Equation 3.1 White spruce stem count stem count = 14.316* forest cover - 2.91, $R^2 = 0.22$, p-value < 0.001

Equation 3.2

stem count = -7.645*forest cover + 25.195, R² = 0.001, p-value = 0.4

Chapter 2: Decadal vegetation responses in the Northwest Territories, Canada, using plant functional type and taxa- level analysis

3.0 Abstract

The Arctic-Boreal Region is experiencing rapid climate change, and the myriad impacts are being integrated within the vegetation (plants and lichen). The forest-tundra ecotone is the frontline of boreal forest expansion and acts as a bellwether for future changes to the tundra. However, the vegetation response can be difficult to parse, as different genera and species are adapted to certain environmental conditions, and are responding independently to shifting environmental gradients. Using highly resolved species distribution and cover data from Canada's National Forest Inventory from ~2008 - ~2018, I have analyzed the shifts at multiple plant scales (plant functional types [PFTs], family, genera, and species), and used taxa-level analysis to track changes in community distribution. To identify PFT and taxa level responses to environmental drivers, I employed an NMDS ordination in conjunction with generalized additive models, to determine how different taxa and PFTs are responding on the landscape. I found that biotic interactions were the most reliable predictors for the plant functional types, but that mean annual temperature and tree biomass were also consistent drivers for most PFTs. My analysis of PFT environmental drivers highlighted the utility of multipronged statistical approaches, and the importance of assessing vegetation responses at multiple scales. When analyzed by taxa, I the reliability of the models increased and gave greater insight into the often contradictory drivers of taxa within the same PFT. Ultimately, I confirmed that taxa level analyses highlight important response variables that may be masked at the PFT level.

3.1 Introduction

The Arctic-Boreal region is home to harsh ecosystems that are undergoing rapid change with climate warming. Due to Arctic amplification, the Arctic is warming faster than the rest of the globe, and that has caused rapid responses of vegetation (Berner et al., 2020, Myers-Smith et al., 2020). Some vegetation types (shrubs and deciduous trees) are increasing their cover in the region (Elmendorf et al., 2012, Myers-Smith et al, 2015, Terskaia et al., 2020, Massey et al, 2023), while others (conifers and lichens) are decreasing in cover (Myers-Smith et al., 2019, Batlzer et al., 2021). The region is exhibiting local responses of both increasing (Myers-Smith et al, 2020) and decreasing productivity (Sulla-Menashe et al., 2018). Shifts in productivity, as well as increasing fire frequency and severity (de Groot et al., 2013), destabilizing near-surface permafrost (Macket al., 2011, De Baets et al., 2016), and alterations to nutrient cycling (Mack et al., 2004, Machmuller et al., 2023, Jilková et al., 2024) are all causing the long-term carbon balance to be in question (Virkkala et al., 2024).

There is a wide ecotone (over 800 km) between the boreal forest and the Arctic tundra (Montesano et al., 2020) that is potentially acting as a bellwether for future changes in the tundra (Danby 2011, Marfo et al., 2018). While an ecotone is defined as a transition zone between two ecosystems, the tundra-taiga ecotone (TTE) is large enough that it may be treated as an ecosystem in its own right. For this paper, I am defining the TTE as the area of tree canopy cover between 0-30% (Montesano et al., 2020). The TTE thus has characteristics of both the tundra and the boreal forest, and this overlap creates a highly variable vegetation distribution due to both abiotic and biotic interactions (Holtmeier and Broll 2005). The sparse tree canopy allows greater solar radiation at the ground surface, compared to the forest (Holtmeier and Broll 2005, Martin et al., 2022); additionally, the distributed trees in the ecotone enables high wind velocities due to

reduced buffeting capacity (Holtmeier and Broll 2005). Soil moisture is highly variable in the ecotone due to heterogeneity in solar radiation and wind, and the importance of microtopography (Holtmeier and Broll 2005, Maguire et al., 2019).

North of the treeline, tundra species dominate, but as latitude decreases, the cover of shrub species increases, followed by trees which increase in canopy height and cover, creating a challenging environment for lower statured plants (Marshall and Baltzer 2015). Additionally, a deepening active layer permits graminoid species to outcompete shallower rooting or nonrooting vegetation, such as mosses and lichens (Blume-Werry et al., 2019, Heijmans et al., 2022). In the boreal forest (defined as greater than 30% tree canopy cover [Montesano et al., 2020]), deciduous tree cover is encroaching with shifting fire regimes, especially at southern latitudes (Timoney et al., 2019, Mack et al., 2021). Near the ecotone, tree density and productivity are generally increasing over time (Aune et al., 2011), but the treeline is staying relatively stable, with slow progress of conifers migrating northward (Aune et al., 2011, Brown et al., 2019, Rees et al., 2019); most evidence suggests that tree density is increasing with some evidence of migration outposts (Dial et al., 2022) and some retraction (Rees et al., 2019). The expansion and contraction of the TTE is thus highly determined by local conditions and the local vegetation response. Montesano et al. (2024) projected increased productivity at the northern and far western edges of the North American TTE, with no net change in the boreal forest, but offsets from various sites between growth increases and decreases into 2100. With changes that are visible now expected to exacerbate in the future, it is critical to look at the local flora to see what is driving community change.

Changes in plant assemblages can signal integrated ecosystem change with individual species responding differently to a variety of drivers. Plants in the boreal forest and ecotone are

responding to shifts due to changes in temperature (Myers-Smith et al., 2019), precipitation (Callaghan et al., 2011, Addis and Bret-Harte 2018), solar radiation (Weston et al., 2007), soil moisture (Shirley et al., 2022), active-layer depth (Limpens et al., 2020, Heijmans et al., 2022), and soil nutrient availability (Salmon et al., 2016, Sullivan et al., 2016), which all contribute to cascading biotic interactions. The presence/abundance of a species can indicate its success in an environment, and dynamics can be assessed over time. However, attaining species-level community data is incredibly time intensive and requires specialized knowledge.

Canada's National Forest Inventory (National Forest Inventory 2013, 2021) provides a comprehensive look at the vegetation and site conditions across Canada. In order to assess the dynamics occurring at the TTE in western Canada, this study focuses on sites within the Northwest Territories (NWT, Figure 1). The data from the NWT were collected during the summer, initially from 2003-2009, and then partially remeasured from 2015-2018, covering approximately a decade of vegetation changes. These data provide a close look at how vegetation has changed in the TTE and northern boreal forest. The goals of this study are:

- To investigate PFT and species level differences between the two time periods for the TTE and boreal forest ecosystems, and,
- To analyze the drivers of different plant functional types (PFTs), and taxa (families, genera, or species) to assess how these aggregate groups are responding to local site conditions under new climate regimes.

3.2 Methods

3.2.1 Canada National Forest Inventory Data

The National Forest Inventory (NFI) data covers 134 plots across the Northwest Territories (NWT) of Canada. I was granted permission to use these data on 23 November 2022

as per the NFI data use agreement with Canada's National Forest Inventory, a collaboration between federal, provincial, and territory governments. Each site has two nested "ecological" plots to assess percent cover of trees and tall shrubs (10 m radius, 314 m²) and low shrubs, herbs, mosses, and lichens (5.64 m radius, 10 m²); each site also had four microplots (1 m²) to survey forest floor biomass, as well as soil bulk density. A soil pit was dug just outside each plot to measure soil characteristics, such as humus form and drainage. Two 30 m, perpendicular transects bisect the plot to measure woody debris biomass. Each site was also assessed for disturbance type and history using remote sensing, field maps and records. Field and lab protocols can be found in Canada's National Forest Inventory Ground Sampling Guidelines (National Forest Inventory 2008). Two field campaigns were conducted in July and August 2003-2009 (initial; National Forest Inventory 2013), and then a subset of the sites (68) was measured again in 2015-2018 (remeasure; National Forest Inventory 2021); the remeasured sites did not include a majority of the northern sites (Figure 3.1).

Vegetation (plants and lichen; lichen is included as a "plant" functional type) was identified to genus and species using four and three letter codes, respectively. Due to changing naming conventions and taxonomy, names were cross-referenced with USDA Plants (https://plants.sc.egov.usda.gov/) to confirm the species using their range maps, as well as to convert any out-of-date names. There were 370 species (including lichen) from 95 genera identified, with 67 additional records identified to genus and 42 that were unable to be identified from their species code (Appendix 1). Each species identified was assigned a plant functional type (PFT) as ascribed to it by USDA Plants; in total 15 PFTs were identified (Table 3.1). **Table 3.1:** Plant functional type breakdown by species richness. The species richness values include all values that were identifiable to species, including rare species. The decreased richness in the remeasured sites is due to the reduction of plots surveyed; lichens and mosses which increase in species diversity with increasing latitude and decreasing canopy (Marshall and Baltzer 2015) appear to have reduced richness, but as the farthest north plots were not resurveyed, this pattern cannot be confirmed.

Diant Functional Type	Genus	Species	richness
Flant Functional Type	count	Initial	Remeasure
		Deciduous P.	<u>FTs</u>
Deciduous tree	3	6	5
Tall shrub	4	13	13
Deciduous low shrub	7	9	9
Dwarf deciduous shrub	8	14	12
Woody vine	1	1	1
Graminoid	5	12	8
Forb	29*	35	31
Horsetail	1	5	4
Clubmoss	1	1	1
		<u>Evergreen P</u>	<u>FTs</u>
Evergreen tree	2	3	3
Evergreen low shrub	2	2	1
Dwarf evergreen shrub	10	15	13
Liverwort	4	4	3
Moss	13	19	16
Lichen	5	16	16
Total	95	385	259

*14 families used in GAM analysis due to data limitations

Whereas 134 plots were surveyed across the Northwest Territories, 120 were used for analysis, as they had a full complement of data for multivariate analyses, particularly the nonmetric multidimensional scaling ordination (NMDS, discussed below). Species and community analysis were based on the 149 species that were found in >5% of the plots so that any observed species movement or response would be less likely due to outlier identifications. While unidentified species were removed, those that were able to be identified to genus (labeled "SPP" or "SP" by field ecologists) were included in genus and PFT analysis, but not in species level analysis.

The Northwest Territories NFI plots follow the gradient from boreal forest through the tundra-taiga ecotone (TTE), stopping at the treeline. I overlayed the TTE classification layer from Montesano et al., (2020) to classify the points into boreal forest and ecotone. With the original and remeasurement dates, I created four categories for plots: boreal initial (59 plots), boreal remeasure (53), ecotone initial (61), ecotone remeasure (15) (Figure 3.1).



Figure 3.1: Map of Northwest Territories NFI sites using rounded GPS points. Forest (blue) and ecotone (purple) classification from Montesano et al. (2020), with sites remeasured sites (solid) contrasting with sites only surveyed initially (hollow). Basemap is from ArcGIS Pro.

3.2.2 Analyzing species and PFT shifts from original to remeasurement

In order to test the utility of the grouping variables of ecosystem and time period (boreal vs ecotone x initial vs remeasure), I conducted a multi-response permutation procedure (MRPP) using the *vegan* package (Oksanen et al., 2022) in R (version 4.2.1, R Core Team 2022); Bray-Curtis distance was used to determine differences among the four groups. MRPP is a non-parametric test to determine whether species composition is different between two or more groups (Mielke and Berry 2001, McCune and Grace 2002, Dearborn and Danby 2017).

Once the groups were established, I did a primary analysis of species (including rare) that were lost from the species list in the 53 remeasured forest plots, to determine what species might be most vulnerable in these ecosystems. I also identified the species that were added to the forest ecosystem upon remeasurement as an acknowledgement of any potential northward migration into the Northwest Territories. Because a majority of the ecotone sites were not remeasured, I could not assess which species are at risk within the ecotone; however, I was able to assess what species were added to the ecotone. I also conducted indicator species analysis with 10,000 permutations using the *indicspecies* package (De Cáceres and Legendre 2009). The indicator species analysis assigns specific group identity to species found in a group or groups that have certain environmental conditions; by looking at species group identity through time I was able to determine which species have high specificity to their ecosystem, and also which species might be moving northward, if they were associated with the ecotone remeasurement data.

Additionally, I conducted a t-test of the plots that were remeasured to determine if there were differences in total cover for each PFT between time periods, within each of the ecosystem types. In order to avoid false positives, a Bonferroni adjustment was applied. Three PFTs (woody

vine, clubmoss, liverwort) could not be analyzed, because they did not have a sufficient number of observations (<5 plots per time period).

3.2.3 Determining underlying environmental drivers of community composition

To determine what environmental drivers contributed to species composition among the four groups, I ran a non-metric multidimensional scaling (NMDS) ordination for each PFT (Table 3.1); three PFTs (woody vines, clubmoss, and liverworts) were not analyzed, as there were not enough individual observations. A NMDS is an effective ordination technique for ecological data, because it is able to handle datasets with many 0s (the result of limited cooccurrence of species) and also overlay environmental gradients (McCune and Grace 2002). I ran the NMDS using the *vegan* package applying Bray-Curtis distance, with a 3-dimensional solution over 100 iterations to find the lowest stress; evergreen tree PFT was analyzed using a 2dimensional solution, as it was more reliable, based on the resulting stress. The evergreen low shrub NMDS had an unreliable stress of 0.01 at 2 dimensions due to limited species diversity (2) with a majority of the observations (97% of 294 observations) being from one species; it was therefore not considered for subsequent analyses. To determine ecosystem drivers, I combined the species matrices across the time periods (initial vs remeasure) and ecosystem (forest vs ecotone), and included these divisions as categorical groupings. I included only environmental variables that had a full complement of data from the NFI field surveys: 13 continuous variables, and 10 categorical variables (Supplemental Table 3.1). Additionally, each PFT total cover was calculated and considered as an environmental variable for each NMDS; the target PFT was removed from consideration for its own analysis. Topographic variables (slope, aspect converted to northness and eastness) were acquired from DEMs (from Amazon Web Services Terrain Tiles), and edaphic variables (clay, silt, sand, nitrogen content) were collected from SoilGrids

(250 m, Poggio et al., 2021), using the *elevatr* (Hollister 2023) and *soilDB* (Beaudette et al., 2024) packages, respectively, in R. These variables were partially recorded in the field for each of the NFI sites, but in order to have a full data complement and standard measurements, I chose to replace the field measurements with these other sources. Additionally, to complement the four climate variables provided by the NFI data, I added snow water equivalent from TerraClimate (Abatzoglou et al., 2017), as snow cover is frequently a driver of community composition and responses of Arctic PFTs (Addis and Bret-Harte 2018, Blume-Werry et al., 2019).

Once the NMDS identified which drivers were significant (alpha = 0.001) to community composition, I applied a generalized additive model (GAM) from the mgcv package (Wood 2011) using those significant variables as predictors. I ran the GAM using a random factor smooth for the continuous variables with individual smooths calculated for each taxa (species/genus/family; Wood 2011, Pederson et al., 2018); each significant grouping variable was tested as a parametric coefficient. I allowed the GAM to penalize each term to eliminate extraneous variables. In order to increase the reliability of the GAM, I tested each model with all variables identified by the NMDS with smoothed variables interacting with each species/genus/family within the PFT, and compared it to a model without interactive taxa. Species, genus, or family was chosen based on data limitations. Species was chosen for PFTs with three or fewer genera, and fewer than ten species (deciduous trees, evergreen trees, and horsetail). The high species (35) and genus (29) count for forbs required a coarser level of taxonomic distinction, and the 14 families that represented the forb species were used instead. All other PFTs (tall shrubs, deciduous low shrubs, dwarf deciduous shrubs, dwarf evergreen shrubs, graminoids, moss, and lichen) were tested in the GAM by genus.

3.3 Results:

3.3.1 PFT trends

Of the PFTs resurveyed in the approximate decade between the initial and remeasured data, the ecotone experienced increases in both evergreen and deciduous trees, as well as dwarf evergreen shrubs and graminoids. Meanwhile the boreal forest saw increases in evergreen shrubs, graminoids, horsetails and liverworts, but has largely decreased in percent cover for the remaining PFTs (Figure 3.2). In the forest there was a significant decrease in moss cover (-10.4% \pm 2.4%, p-value = 0.001, Supplemental Figure 3.1a). While no PFT cover changes were significant in the ecotone, there were substantial losses in moss (9.0% \pm 4.6%, Supplemental Figure 3.1a), particularly from *Ceratadon purpurea* and *Sphagnum capillifolium*. Consistent with existing literature (Jolly et al., 2009, Elmendorf et al., 2012), lichen cover decreased in both the forest (-3.6% \pm 1.6%) and ecotone (-2.5% \pm 1.34%, Figure 3.1b), while evergreen tree cover was reduced in the forest (-5.2% \pm 1.8%, Supplemental Figure 3.1c). While these results are limited to the sites that were remeasured and do not include the northern plots in the ecotone, there remeasurement surveys demonstrate a rapid change in the boreal forest and ecotone, driven by a select few species.



Figure 3.2: Percent difference of growth form percent cover averaged across plots (each plot had total cover of (remeasure – initial)/initial). Analysis is limited to only plots that were resurveyed, and thus does not demonstrate changes in the northern part of the TTE. Error bars represent standard error. The one woody vine species only had 2 observations and was thus not included; clubmoss, and liverwort PFTs could not be analyzed using the t-test due to insufficient observations.

3.3.2 Group and species identity

The MRPP indicated that there was no significant difference between the communities found in the forest and ecotone (A = 0.0011, p-value = 0.104), and a weak but significant difference between the time periods (A = 0.011, p-value = 0.001); however, there was a significant difference among all four groups (A = 0.016, p-value = 0.001). From these results, I tested the difference between the ecotone communities exclusively using the plots that were remeasured and found that there was no difference (A=0.0004, p-value = 0.4). Thus, I was able to use the four groupings for ecosystem and time period to separate community patterns when appropriate; however, greater consideration was given to comparisons between time periods than between ecosystems.

The indicator species analysis identified 28 species within ten group combinations (Table 3.2). There were three species that were associated with just the forest ecosystem (*Cladonia cornuta, Equisetum variegatum, Pedicularis macrodonta*), and seven that were associated with just the ecotone (*Chamaedaphne calyculata, Spinulum annotinum, Salix reticulata, Dicranum fuscescens,* and *Ledum palustre*). *Populus balsamifera* was associated with the forest at both time periods and the remeasured ecotone, suggesting that this deciduous tree species has moved northward during the intervening years. The largest group was 11 species that were identified in the remeasured forest and ecotone (Table 3.2), confirming a similarity between ecosystems in the second time period, potentially due to the limited northward extent of the ecotone plots. While the specificities of the indicator species analysis were generally high for most of the species, indicating they have a high probability of only being found in the noted group(s), the fidelity (probability of being found in every plot) was relatively low.

Table 3.2: Indicator species analysis for forest and ecotone ecosystems within each time period. The specificity indicates the probability that the species will be found exclusively in the plots of the group it was assigned to (e.g., *Equisetum variegatum* was found exclusively in remeasured forest plots, but not necessarily in every one); fidelity indicates the probability of the species only existing in that group (e.g., *Cladonia mitis* has moderate fidelity to the remeasured forest and ecotone remeasure group, and can likely be found in 58% of the plots, and has relatively high specificity). The specificity of the species tends to be higher than fidelity for the identified indicator species. Species listed for multiple groups indicates that there is overlap in the community.

Species	Functional Type	Fidelity	Specificity	p-value
	Remeasured Forest	<u>t</u>		
Cladonia cornuta	lichen	0.83	0.26	0.010**
Equisetum variegatum	horsetail	1.0	0.10	0.011*
Pedicularis macrodonta	forb	0.98	0.10	0.011*
	Initial Ecotone			
Chamaedaphne calyculata	deciduous dwarf shrub	0.86	0.19	0.016*

Species	Functional Type	Fidelity	Specificity	p-value	
Spinulum annotinum	clubmoss	0.78	0.11	0.050*	
	Remeasured Ecoto	ne			
Salix reticulata	dwarf deciduous shrub	0.73	0.19	0.009**	
Dicranum fuscescens	moss	0.85	0.13	0.018*	
	Initial and Remeasured	Ecotone			
Ledum palustre	dwarf evergreen shrub	0.69	0.28	0.049*	
	Initial Forest and Eco	otone			
Mitella nuda	forb	1.0	0.22	0.010**	
	Remeasured Forest and Init	ial Ecotone			
Sanionia uncita	moss	0.98	0.17	0.046*	
	<u>Remeasured Forest and</u>	Ecotone	0.50	0 0001***	
Cladonia mitis		0.81	0.58	0.0001***	
Salix myricoides	tall shrub	0.86	0.47	0.0001***	
Ceratadon purpurea	moss	0.90	0.28	0.004**	
Salix planifolia	tall shrub	0.82	0.28	0.005**	
Aulacomnium palustre	moss	0.81	0.42	0.006**	
Salix bebbiana	tall shrub	0.80	0.23	0.009**	
Carex scirpoide	graminoid	0.92	0.16	0.009**	
Betula nana	low deciduous shrub	1.0	0.12	0.012*	
Betula neoalaskana	deciduous tree	0.97	0.14	0.018*	
Sphagnum fuscum	moss	0.89	0.14	0.033*	
Brachythecium salebrosum	moss	0.71	0.22	0.036*	
Initial ar	nd Remeasured Forest and R	emeasured Ec	otone		
Populus balsamifera	deciduous tree	0.82	0.25	0.038*	
Initia	l Forest and Initial and Rem	easured Ecoto	ne		
Retula numila	tall shrub	0.96	0.23	0.011*	
Pinus hanksia	evergreen tree	0.90	0.23	0.041*	
1 inus bunksiu	evergreen nee	0.72	0.22	0.041	
Remeasu	ared Forest and Initial and R	temeasured Ec	otone		
Vaccinium uliginosum	dwarf deciduous shrub	0.95	0.60	0.0001***	
Betula glandulosa	tall shrub	0.89	0.49	0.0007***	
Salix glauca	tall shrub	0.97	0.28	0.002**	
Empetrum nigrum	dwarf evergreen shrub	0.93	0.42	0.01*	

There were ten species that were found in the forest initial survey and not found in the

forest remeasured survey (Table 3.3a), with only Lupinus arcticus also being found in the

remeasured TTE. Of the species lost in the forest resurvey, Orthillia secunda had the most notable decline; while it had a relatively low average percent cover (0.2%), it was identified in >10% of the plots (15). Six species were found in the remeasured forest (Table 3.3b), and two species were identified in the remeasured ecotone (Table 3.3c) that were not previously identified. The two species identified in the remeasured ecotone, Actaea rubra and Fragaria virginia, were previously found in the initial forest plots, suggesting northward migration.

Table 3.3: List of species lost from (a) and added to (b) the forest ecosystem (a) in the Northwest Territories, as well as those added to the ecotone (c).

a.	Lost	from	forest
----	------	------	--------

Species	Plant functional type	Average percent cover	Number of initial plots with species
Arctous alpina	dwarf deciduous shrub	4.2%	2
Dryas integrifolia	dwarf evergreen shrub	19.8%	1
Eriophorum chamissonis	graminoid	2.2%	3
Homalothecium aeneum	moss	7.0%	1
Lophozia ventricosa	liverwort	7.0%	2
Lupinus arcticus*	forb	3.1%	1
Orthillia secunda	Dwarf evergreen shrub	0.2%	15
Pedicularis macrodonta	forb	1.0%	1
Pyrola chlorantha	forb	0.5%	1
Salix arctica	dwarf deciduous shrub	4.5%	1

* Found in remeasured ecotone

b. Added to forest

Species	Species Plant functional type		Number of remeasured plots with species		
Cladonia sulphurina	lichen	0.6%	5		
Marchantia polymorpha	liverwort	< 0.1%	3		
Mylia anomala	liverwort	< 0.1%	1		
Ribes oxyacanthoides	low deciduous shrub	0.3%	1		
Salix prolixa	tall shrub	3.5%	1		
Symphyotrichum boreale	forb	<0.1%	1		

Species	Plant functional type	Average percent cover	Number of remeasured plots with species
Actaea rubra*	forb	2.0%	4
Fragaria virginia*	forb	<0.1%	1

c. Added to ecotone

* Species was found in Forest initial plots

3.3.3 Plant functional type drivers

An NMDS was run for each PFT to determine the environmental factors that are important to their distributions. Of the 36 continuous variables tested, 26 were found to be significant at the 0.001 level (Table 3.4a). The significant variables fell into four categories: vegetation cover, climate, plot-level characteristics, and topography. Each PFT was significant for at least one other PFT, except horsetails. Dwarf evergreen shrub cover was the most frequently significant vegetation cover variable, being associated with all PFTs except tall shrubs, graminoids, and horsetails. Within the climate group, mean annual temperature was also significant for all PFTs except evergreen trees, horsetails, mosses, and lichen. Isothermality was significant for each of the tested shrub types (tall, deciduous low, dwarf deciduous, and dwarf evergreen), as well as graminoid (Table 3.4a). Within plot characteristics, live tree biomass was most frequently significant, being identified for all PFTs except graminoid and horsetail. Evergreen tree was the only PFT associated with dead tree biomass. Within the topographic variables, latitude and longitude were the most frequent significant variables, with at least one being significant for all PFTs except evergreen trees, deciduous low shrubs, horsetails and lichen. Elevation was the only significant predictor for horsetails. Dwarf evergreen and deciduous shrubs had the most significant predictor variables (16 each), and there were many variables that were only significant for one of these PFTs (tall shrub, graminoid, and soil bulk density for dwarf deciduous shrubs, and summer climate moisture index and soil nitrogen for

dwarf evergreen shrubs). Considered together in the NMDS plots (Supplemental Figure 3.2), a vector cluster of lichen cover, moss cover, and latitude, are consistently correlated, and trend in the opposite direction from annual mean temperature, live tree biomass, and isothermality vectors (when applicable).

The 13 grouping variables were further grouped into four categories: ecosystem type by time period, vegetation structure, pedology, and hydrology (Table 3.4b). Vegetation structure was the most commonly significant grouping factor (Table 3.4b, Figure 3.3). Time period and ecosystem were significant grouping variables for both dwarf evergreen and deciduous shrubs, and time period was also significant for tall shrubs. The vegetation structure group variables were distributed among the PFTs, but had the most significant variables associated with dwarf deciduous shrub, forb, and moss distributions. The hydrology variables (upland/wetland, drainage, moisture, Supplemental Table 3.1) were mostly significant for the woody species.

While all the significant NMDS variables were tested in the GAM, 17 of the 26 continuous variables significant in the NMDS were also found to be significant in the GAM (Table 3.5a, Figure 3.3). Each PFT, except horsetail, had at least one significant continuous predictor variable (Table 3.5a, Figure 3.3). Both live tree biomass and dwarf evergreen shrub cover were significant for all PFTs except deciduous trees, graminoids, and horsetails. When significant, mean annual temperature was negatively associated with forb families (Supplemental Figure 3.9), as well as the genera for low and dwarf evergreen shrub genera (Supplemental Figure 3.6, 3.7); however, it was positive for the two dwarf evergreen shrub genera (Supplemental Figure 3.8). There were no uniformly positive or negative responses of significant genera for any continuous variable, underscoring the importance of analyzing these drivers by taxa. Of the five genera of graminoid, only *Carex* was identified as having significant predictors (moss, latitude,

and longitude, Table 3.6a, Supplemental Figure 3.10). Tall shrubs, deciduous low shrubs and lichen similarly had limited genera as significant with the GAM variables (Supplemental Figures 3.5, 3.6, 3.12).

All the grouping variables except land position, wetland designation, and drainage were considered to be significant (Table 3.5b, Figure 3.3). Taxa was significant for every PFT except deciduous trees, dwarf deciduous shrubs, and horsetails. Lichen did not have any significant grouping factors. Dwarf evergreen shrub was the only PFT to be significant for time period, and was negatively associated with the remeasured time period. Low deciduous shrub was the only PFT significantly associated with moisture (positive for mesic and hygric soils). The four grouping variables for moss support a preference for some but sparse tree density (negative for no tree cover and positive for herbaceous cover; negative for broad leaf and mixed tree cover, but positive for early seral ecosystems).

Each GAM was tested with continuous variables having an individual smooth for each member of the corresponding taxa, and then compared to a model with the continuous variable having a global smooth for the PFT (Table 3.6). On average, including the taxa level smooth with each factor resulted in a deviance explained of 40%, compared to 27.2% without the taxa interaction. The difference between the model predictive power when the taxa interaction was included was greater than 10% for every PFT except horsetail (species, 1.9%) and lichen (2.5%). Dwarf deciduous shrubs (20.0%), dwarf evergreen shrubs (22.3%), and deciduous trees (species, 21.0%) had the greatest improvement when taxa was considered; other PFTs saw improvements between 6-15%.

					Dwarf	Dwarf					
	Deciduous	Evergreen	Tall	Deciduous	deciduous	evergreen		~ · · ·	TT (1)	3.6	
	tree	tree	shrub	low shrub	shrub	shrub	Forb	Graminoid	Horsetail	Moss	Lichen
Deciduous tree		0.168	0.131			0.164					
Evergreen tree										0.147	
Tall shrub					0.132						
Deciduous low shrub	0.175	0.145			0.208	0.204					
Evergreen low shrub	0.161	0.181			0.123	0.171				0.130	
Dwarf deciduous shrub										0.107	
Dwarf evergreen shrub	0.426	0.190		0.133	0.386		0.179			0.213	0.203
Forb		0.109				0.185					
Graminoid					0.101						
Liverwort					0.098	0.135					
Moss	0.238				0.151	0.188	0.113	0.265			
Lichen	0.162	0.140			0.180	0.227	0.178				
Annual mean temp	0.159		0.275	0.214	0.485	0.429	0.138	0.327			
Annual precip					0.203	0.277					
Mean summer CMI*						0.113					
Isothermality			0.201	0.189	0.365	0.374		0.224			
Snow water equivalent				0.154							0.194
Bulk density					0.213						

Table 3.4a: Continuous environmental variables (a) and categorical environmental variables (b) from the NMDS; only significant variables are reported (p-value ≤ 0.001) and R² values are shown.

	Deciduous tree	Evergreen tree	Tall shrub	Deciduous low shrub	Dwarf deciduous shrub	Dwarf evergreen shrub	Forb	Graminoid	Horse	tail	Moss	Lichen
Soil organic		0.103			0.204	0.112						
Soil organic Nitrogen						0.112						
Dead tree biomass		0.149										
Live tree biomass	0.223	0.148	0.269	0.214	0.327	0.294	0.245				0.194	0.177
Elevation						0.142			0.14	43		
Slope			0.157	0.150	0.124							
Longitude	0.176		0.133		0.333	0.272		0.257			0.104	
Latitude	0.176		0.222		0.432	0.400	0.134	0.319				
*CMI is cli	imate moisture	e index										
Table 3.4b	Deciduous	Evergreen		Deciduous	Dwarf deciduous	Dwarf evergreen						
Table 3.4b	Deciduous tree	Evergreen tree	Tall shrub	Deciduous low shrub	Dwarf deciduous shrub	Dwarf evergreen shrub	Forb	Grami	noid I	Moss	I	Lichen
Table 3.4b Time period	Deciduous tree	Evergreen tree	Tall shrub	Deciduous low shrub	Dwarf deciduous shrub 0.081	Dwarf evergreen shrub 0.060	Forb	Grami	noid 1	Moss]	Lichen
Table 3.4b Time period Ecosystem	Deciduous tree	Evergreen tree	Tall shrub 0.055	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.081	Dwarf evergreen shrub 0.060 0.060	Forb	Grami	noid I	Moss	1	L ichen 0.047
Table 3.4b Time period Ecosystem Density	Deciduous tree	Evergreen tree	Tall shrub 0.055 0.060	Deciduous low shrub 0.109	Dwarf deciduous shrub 0.081 0.081 0.102	Dwarf evergreen shrub 0.060 0.060	Forb	Grami	noid 1	Moss]	L ichen 0.047
Table 3.4bTime periodEcosystemDensityLand cover	Deciduous tree	Evergreen tree 0.125	Tall shrub 0.055 0.060	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.102	Dwarf evergreen shrub 0.060 0.060	Forb 0.052	Grami 2	noid I	Moss 0.08	1 9	L ichen 0.047
Table 3.4bTime periodEcosystemDensityLand coverStand Structure	Deciduous tree	Evergreen tree 0.125 0.145	Tall shrub 0.055 0.060	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.081 0.102 0.065	Dwarf evergreen shrub 0.060 0.060	Forb 0.052 0.077	Grami 2 7 0.11	<u>noid</u>	Moss 0.08 0.11	9 5	L ichen 0.047
Table 3.4bTime periodEcosystemDensityLand coverStand StructureSuccessionalstage	Deciduous tree	Evergreen tree 0.125 0.145	Tall shrub 0.055 0.060	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.102 0.065	Dwarf evergreen shrub 0.060 0.060	Forb 0.052 0.077 0.070	Grami 2 7 0.11 0 0.15	noid 1 8 3	Moss 0.08 0.11 0.07	9 5 8	L ichen 0.047
Table 3.4bTime periodEcosystemDensityLand coverStand StructureSuccessionalstageVegetationorigin	Deciduous tree 0.112	Evergreen tree 0.125 0.145	Tall shrub 0.055 0.060	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.102 0.065 0.065	Dwarf evergreen shrub 0.060 0.060	Forb 0.052 0.077 0.070	Grami 2 7 0.11 0 0.15	noid 1 8 3	Moss 0.08 0.11 0.07	9 5 8	Lichen 0.047
Table 3.4bTime periodEcosystemDensityLand coverStand StructureSuccessionalstageVegetationoriginVegetation type	Deciduous tree 0.112 0.227	Evergreen tree 0.125 0.145 0.266	Tall shrub 0.055 0.060 0.060 0.0092	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.081 0.102 0.065 0.065	Dwarf evergreen shrub 0.060 0.060	Forb 0.052 0.077 0.070	Grami 2 7 0.11 0 0.15 7	noid 1 8 3	Moss 0.08 0.11 0.07 0.15	9 5 8 3	0.047 0.097
Table 3.4bTime periodEcosystemDensityLand coverStand StructureSuccessionalstageVegetationoriginVegetation typeDeposition	Deciduous tree 0.112 0.227	Evergreen tree 0.125 0.145 0.266	Tall shrub 0.055 0.060 0.060 0.0092	Deciduous low shrub	Dwarf deciduous shrub 0.081 0.081 0.102 0.065 0.065	Dwarf evergreen shrub 0.060 0.060 0.060	Forb 0.052 0.077 0.070 0.070	Grami 2 7 0.11 0 0.15 7	noid 1 8 3	Moss 0.08 0.11 0.07	9 5 8 3	0.047 0.097
Upland/Wetland	0.059	0.060		0.066	0.069							
----------------	-------	-------	-------	-------	-------							
Drainage	0.148	0.140	0.105		0.130							
Moisture	0.135	0.093	0.093	0.094	0.110							

Table 3.5a: Continuous variables and the individual taxa (species, genus, or family) smooth that are significant in the GAM. Direction (+) indicates general positive relationship, (-) indicates a general negative relationship, (+)-) and (-|+) indicates that the relationship changes direction over the range of the predictor variable, and (+/-) indicates a mostly neutral relationship. Asterisks indicate level of significance (* p-value < 0.05, ** p-value < 0.01, *** p-value < 0.001).

	Deciduous tree	Evergreen tree	Tall shrub	Deciduous low shrub	Dwarf deciduous shrub	Dwarf evergreen shrub	Forb
Deciduous tree		Pinus banksia** (-)					
Evergreen tree							
Deciduous low shrub	B. neoalsakana* (+ -)				Rosa** (+) Vaccinium* (-)	Arctostaphylos** (+)	
Evergreen low shrub	P. tremuloides** (- +)	Pinus banksia** (-)			Betula* (-) Vaccinium* (+)	Empetrum* (+) Vaccinium*** (+)	
Dwarf deciduous shrub							
Dwarf evergreen shrub	L. larcina* (+) P. tremuloides*** (-)			Shepherdia* (-)	Chamaedaphne* (- +)		Caprifoliaceae** (+) Fabaceae* (+) Onagraceae* (- +)
Forb		Pinus banksia* (+ -)					
Moss	L. larcina* (+ -)						Onagraceae*(+)
Lichen						Andromeda* (+/-) Vaccinium*** (+)	
Annual mean temperature	L. larcina*(+)			Viburnum* (+ -)	Vaccinium*** (-)	Andromeda* (+) Arctostaphylos*** (+)	Rosaceae** (-) Pyrolaceae*** (-) Santalaceae** (-) Saxifragaceae* (-)

	Deciduous tree	Evergreen tree	Tall shrub	Deciduous low shrub	Dwarf deciduous shrub	Dwarf evergreen shrub	Forb
Annual precipitation					Rosa*** (+ -)	Arctostaphylos** (-) Vaccinium*** (-)	
Isothermality				Shepherdia** (-)		Dryas* (+) Rhododendron*** (+)	
Snow water equivalent				Viburnum** (-)			
Live tree biomass		Picea glauca** (+) Picea mariana*** (-)	Alnus* (+)	Shepherdia*** (+ -)	Rosa** (+/-) Salix* (- +)	Empetrum** (+/-) Rhododendron** (+) Vaccinium** (+/-)	Caprifolaceae*** (+ -) Rosaceae*** (-) Saxifragaceae*** (+)
Dead tree biomass						Ledum* (-) Vaccinium* (-)	
Longitude					Rubus*(-)	Arctostaphylos*** (-) Dryas* (-) Ledum** (- +) Vaccinium*** (-)	
Latitude	P. balsamifera** (- +)				<i>Cornus**</i> (- +)	<i>Empetrum</i> *** (+ -)	Caprifolaceae* (+) Rosaceae** (-) Pyrolaceae** (-)

Table 3.5a continued

	Graminoid	Moss	Lichen
Deciduous tree			
Evergreen tree		Ceratadon*** (-) Sanionia* (-) Tomentypnum** (+)	
Deciduous low shrub			
Evergreen low shrub		Hylocomium*** (+) Pleurozium* (+) Polytrichum** (+) Sphagnum* (- +) Tomentypnum** (+ -)	
Dwarf deciduous shrub		Aulacomnium*** (+)	
Dwarf evergreen shrub		Pleurozium* (-) Sphagnum** (+)	Cladonia*** (+) Peltigera* (+)
Forb			
Moss	$Carex^{*}(+)$		
Lichen			
Annual mean temperature			
Annual precipitation			
Isothermality			
Snow water equivalent			
Live tree biomass		Hylocomium*** (+) Pleurozium** (+)	Cladonia* (-)
Dead tree biomass			
Longitude	<i>Carex</i> ***(-)		
Latitude	<i>Carex</i> ***(-)		

Table 3.5b: Significant GAM results for grouping variables, estimates are reported for each factor that was significant to indicate positive or negative relationship. Asterisks indicate level of significance (* p-value < 0.05, ** p-value < 0.01, *** p-value < 0.001).

					Dwarf		
		Evergreen	T II I I	Deciduous low	deciduous	Dwarf evergreen	
	Deciduous tree	tree	I all shrub	shrub	shrub	shrub	Forb
Time period						-0.3 remeasurement**	
Ecosystem							
Density							
Successional Stage							
Stand structure					0.2 Complex* 0.3 Multiple layers*		
Land cover		-1.5 No trees*					
Vegetation origin							
Vegetation type		-0.7 Broadleaf tree**	0.8 Shrub*			0.3 Mixed Tree*	
Deposition					-2.1 Colluvial**		
Humus type	0.7 Moder*** -0.8 Mull*				0.9 Mull**	0.3 Moder*	
Drainage							
Moisture				1.0 Hygric*** 1.3 Mesic***			
Species/ Genus/ Family		0.5 Picea mariana***	-1.5 Amelanchier*** -0.5 Salix***	1.5 Myrica*** 0.7 Shepherdia**	-0.9Cornus* -0.9 Rubus*	0.5 Arctostaphylos* 0.6 Ledum* -0.6 Orthillia**	0.3 Caprifoliaceae*** 1.6 Polygonaceae*** 0.3 Ranunculaceae*

0.5 Rosaceae*** -0.2 Rubiaceae***

Table 3.5b continued

	Graminoid	Horsetail	Moss
Time period			
Ecosystem		0.4 Forest*	
Density			
Successional Stage	-0.7 Late seral*		0.4 Early seral*
Stand structure			0.3 Complex
Land cover			-2.3 No trees*
Vegetation origin			
Vegetation type			-0.7 Broadleaf tree**
Deposition			
Humus type			-0.5 Moder**
Drainage			
Moisture			
Species/ Genus/ Family	0.9 <i>Carex</i> **		1.0 Hylocomium*** -0.9 Polytrichum** 0.7 Sphagnum** 0.7 Tomentypnum***



Figure 3.3: The center column is the PFT that were modeled using NMDS and GAM to determine the important drivers to their distribution. On the left are the significant continuous driver variables colored by category (biotic = green, climate = orange, plot variables = yellow, topographic variables = blue). On the right are the significant grouping variables, colored by category (Time period x ecosystem group = purple, vegetation structure = green, pedology = red, hydrology = teal). Dashed lines (a) denote variables that are likely correlational, while solid lines (b) show variables that are likely influencing the target PFT. Taxa was significant for every PFT are not shown.

3.4 Discussion

3.4.1 Plant functional type cover

In the ten years between the initial and remeasured survey, moss cover in the forest significantly decreased in the remeasured plots (Figure 3.2). Among the 17 species identified in remeasured plots, *Hylocomium splendens* decreased by 12.8% (Supplemental Figure 3.1a), and *Ceratadon purpurea* decreased by 10.4%; of note, only two species increased in cover in the forest remeasured plots, *Sphagnum fuscum* (8.5%) and *Pleurozium schreberi* (5.3%). In the ecotone, *Ceratadon purpurea* decreased by an average of 16.3%, and *Sphagnum capillifolium* decreased 14.0%, with increases seen in *Pleurozium schreberi* (1.5%) and *Dicranum flagellare* (4.0%). Considering the dramatic decrease in moss in the forest and ecotone in conjunction with the NMDS and GAM results, which point to the importance of cover structure variables over climate, the results suggest that mosses are likely being outcompeted for light (Marshall and Baltzer 2015). The large losses in mosses are mostly driven by a few species in both the forest and ecotone, which highlights the information that is lost when PFTs are analyzed as a whole. The individual species responses are important to monitor, as species are responding to changes within their specific niches (Saccone et al., 2017).

Lichen decreased in both forest and ecotone plots (-3.6% and -2.5% respectively, Supplemental Figure 3.1b), coinciding with previous observations (Jolly 2009, Elmendorf et al., 2012). However, the general decrease in lichen species was in contrast to a large increase in *Cladonia mitis*, which increased by 7% in the forest and 2.7% in the ecotone. The forest and ecotone diverged on changes in evergreen tree cover with most of the forest decrease being due to *Picea mariana* (-6.8%, Supplemental Figure 3.1c), whereas the ecotone increased in both *Picea mariana* (2.8%) and *Picea glauca* (2.2%), while decreasing in *Pinus banksia* (14.8%), indicating increased boreal tree expansion across the ecotone (García Criado et al., 2025). Deciduous tree cover had limited changes, but showed similar species level divergence between the forest and ecotone. Both ecosystems increased in *Betula papyrifera* (3% forest, 1% ecotone), while the forest decreased in *Larix larcina* (-1.4%). *Popoulus tremuloides* increased by 2.7%, having the greatest increase among the deciduous trees. While moderate, the shifts in tree species, especially the decrease in evergreen trees in the forest (Baltzer et al., 2021 Mack et al., 2021), point to shifting ecosystem structure, which has important effects on smaller statured species (Marshall and Baltzer 2015), and can alter soil nutrient cycling and hydrology (Vankoughnett and Grogan 2016, Terskaia et al., 2020).

The larger changes in percent cover were mostly in the smaller statured, and non-woody PFTs, which might be because ten years is enough time for these species with shorter life-cycles to respond (Smith and Beaulieu 2009). Slower growing, woody species are not able to respond as quickly to climate change as herbaceous species (Smith and Beaulieu 2009). However, my results showing decreasing evergreen tree cover in the forest, and increasing tree cover in the ecotone (Timoney et al., 2019) are consistent with longer term studies (Reid et al., 2022, Rotbarth et al., 2023). The general decrease across all shrub types is surprising given the overall "shrubification" of the Arctic (Myers-Smith et al., 2020, Terskaia et al., 2020). While there were large increases in evergreen shrub cover over the ten years, it was limited to few plots.

3.4.2 Group and species identity

The species level analysis suggested that there has been both a northward migration of species and a shift in conditions in the ecotone to facilitate such migration. Notably, two species (*Actaea rubra* and *Fragaria virginiana*) were identified in the remeasured ecotone plots that were only present in the forest during the first survey (Table 3.3c). Their presence in the ecotone

plots could suggest that the southern edge of the ecotone is beginning to show effects of borealization (García Criado et al., 2025). However, given the limited observations of the species, and that both Actaea rubra and Fragaria virginiana are dispersed by birds (Stiles, 1980, Wilson 1983), their presence in the ecotone might not be persistent. Continued monitoring of these plots will confirm the permanence of these additions. Six species were added to the forest plots (Table 3.3b), but because all of these species are known to the boreal system, they seem likely to be the result of local migration. There were ten species that were lost from the forest over the remeasurement time period (Table 3.3a). Of greatest concern is the disappearance of Orthillia secunda, an ericaceous dwarf evergreen shrub, which was found in 15 initial plots. The other species were found in 1-3 plots and, while worth further monitoring, their loss is more likely due to local plot level extirpation, rather than a notable shift in the ecosystem. With these analyses, I accepted a level of uncertainty when it comes to species identification, especially for the cryptic species, and when species are only identified during one field visit (reducing the utility of indicative phenological traits). I am relying on the high-level skill of the NFI ecology team and collaborating botanists and lichenologists when making these reports.

My indicator species analysis used the four groups confirmed by the MRPP, which enabled me to compare across compositions (ecosystems) and conditions (time period) (Bakker et al., 2008). The difference between time periods was greater than the difference between ecosystems, which is in part due to the small area and southern skew of the remeasured ecotone. The lack of significance between ecosystems is likely due to the southern part of the ecotone being similar to the forest, while the initial ecotone was significantly different, having a greater northern extent. When the northern portion of the ecotone was excluded from the MRPP, there was no difference between the ecotone communities, suggesting that that difference between forest and ecotone ecosystems is mostly driven by the northern ecotone communities. Thus, I would infer that the southern end of the ecotone is experiencing borealization (García Criado et al., 2025); however, I cannot determine if this process was already underway during the initial survey.

Of the 28 species identified as indicators, 11 of them were in the remeasured forest and ecotone group, suggesting a strong overlap of composition in the later time period (Table 3.2). Considering that the remeasured ecotone plots were in the southern portion of the ecotone, it is likely that the overlap in species is due to the borealization of the ecotone. Additionally, one species was identified for the initial forest and remeasured forest and ecotone, *Populus balsamifera*, a deciduous tree and the northernmost hardwood (Zasada and Phipps n.d.), further suggesting a tree encroachment at the southern end of the ecotone.

3.4.3 Plant functional type drivers

Overall, the PFTs are predicted by a wide array of variables. From the NMDS 39 variables (continuous and grouping) are associated with the 9 analyzed PFTs; most of these variables persisted for at least one PFT, with 17 continuous and 11 grouping variables being significant within the GAM (Figure 3.3). The myriad variables that correlate within the NMDS highlight how difficult it is to predict vegetation responses in the region. While the "macro" variables of annual temperature, live tree biomass, latitude, and longitude tended to be strong predictors for the majority of PFTs, many other variable interactions complicate the overall controls on vegetation composition. In the NMDS plots (Supplemental Figure 3.2), while latitude is typically directly opposed to annual mean temperature, the biotic variables do not have consistent distributions across these gradients, with the exception of moss and lichen which trend toward increasing latitudes. The joint plots imply that while there is a strong limitation on distribution due to latitude and temperature, the other variables are interacting differently with each PFTs (Supplemental Figure 3.2). Live tree biomass is associated with annual mean temperature, as expected, as the boreal forest increases in density as going southward in the Northwest Territories. Dwarf evergreen shrubs and snow water equivalent tended to trend with latitude, moss, and lichen; isothermality, and slope tended to be more correlated with mean temperatures. The separation of biotic variables trending with higher latitudes and the abiotic variables trending with mean temperature (implied at lower latitudes) suggests that at higher latitudes, the community is driven more strongly by biotic interactions, and at lower latitudes within the sites, the community is driven by climate variables.

Because a separate smooth was calculated for each continuous variable and each taxa, I was able to determine how different taxa were responding to the different variables. However, some of the variables analyzed in the GAMs are better interpreted as correlative, such as live tree biomass and evergreen trees (*Picea mariana* [-] and *Picea glauca* [+]); likely the positive association of live tree biomass with *P. glauca* is from the robust growth of *P. glauca*, whereas *P. mariana* has a more slender form and limited biomass accumulation could lead to a negative relationship. Live tree biomass may be causal or correlative within the same PFT, such as for the shade tolerant mosses *Hylocomium* (+) and *Pleurozium* (+), where tree presence may directly limit competition from other species; whereas for *Sphagnum* (-) and *Tomentypnum* (-), which prefer bog and fen conditions where trees struggle to grow, tree biomass is likely to be correlative (Table 5a). No continuous variable had a uniformly significant positive or negative effect on taxa within a PFT, suggesting that analysis at the PFT level misses much of the nuance in vegetation response (Anderegg et al., 2022). Even at the genus or family level, we are likely missing responses that could be identified from species level analysis.

The analysis of the grouping variables for the GAM were limited by the data, and priority was given to individual taxa smooths, rather than parametric groups. However, the PFT level analysis of the grouping variables does shed some light on general trends (Table 3.5b). Dwarf evergreen shrub was the only PFT to be negatively associated with the remeasurement data, despite many other PFTs suffering large losses in percent cover. Moss was negatively associated with the "no tree" cover type, which was unexpected, as moss cover generally increases with decreasing tree cover. However, this result might be due to tree cover limiting competition from other low statured vegetation, and allowing shade-tolerant mosses to thrive. The graminoid PFT was negatively associated with late seral forests, suggesting that they are shaded out in the later stages of succession; mosses were positively associated with early seral stages, which follows the characterization of some mosses being important pioneer species. The distinction for deciduous trees having a positive association with moder humus vs a negative association with mull humus may reflect a potential future stress for deciduous trees in the region. Moder humus is characterized by organic debris accumulation below northern hardwoods (though to a lesser degree than below conifer forests), while the mull humus type is characteristic of soils where organic matter decomposition is accelerated (Labaz et al., 2014). Given the increase in organic matter decomposition in the Arctic due to warming, this discernment of the deciduous tree PFT may predict ecosystem shifts in the future and open the system to species that are better able to tolerate this soil type. The only grouping variable that consistently was significant for the GAMs was the taxa (species, genus, family), again highlighting the importance of considering finer vegetation resolution.

Accounting for genus or species in the GAM improved most of the PFT models by at least 10% (Table 6). Of the two PFTs for which explained deviance increased minimally, lichens

were already well predicted by the global smooths model (23.3%), and horsetail (13.8%) may have been limited by low observations. While the deviance explained for most of the models is still below 50%, species distribution models tend to have low explanatory power (le Roux and Luoto 2014), and increasing GAM deviance explained by 10-15% helps to understand how these taxa are responding on the landscape. The coarse distinction of PFT does not account for many adapted preferences, such as moisture or shade tolerance.

	Taxa not considered	Taxa considered	Difference
Deciduous tree	30.5%	51.5%	21.0%
Evergreen tree	33.0%	45.1%	12.1%
Tall shrub	14.1%	20.8%	6.8%
Deciduous low shrub	41.3%	51.6%	10.3%
Dwarf deciduous shrub	30.9%	50.9%	20.0%
Dwarf evergreen shrub	34.5%	56.8%	22.3%
Forb	22.5%	38.4%	15.8%
Graminoid	29.4%	38.0%	8.6%
Horsetail	13.8%	15.7%	1.9%
Moss	26.0%	41.6%	15.6%
Lichen	23.3%	25.8%	2.5%

Table 3.6: Deviance explained by the GAM for each PFT when genus or species was considered. Species was considered for evergreen trees, deciduous trees, and horsetail due to a low species count (Table 3.1); family was considered for forbs.

PFTs in the Arctic are a useful convention, because the relatively low species count aggregates few species within each PFT, and there is also a strong latitudinal gradient frequently described using PFTs: the boreal forest (evergreen and increasingly deciduous trees), to tundra taiga ecotone (trees, shrubs, plus increasing low statured plants), to Low Arctic tundra (shrubs and graminoids), to High Arctic tundra (forbs, mosses, and lichen). With anthropogenic climate change, PFTs are responding at different rates, but within each PFT, taxa are responding to

different drivers, and we can learn more about how climate change is playing out across the landscape by looking at these higher resolution actors.

3.5 Conclusion

From my PFT to taxa analyses, I have documented important shifts in vegetation over a ten-year period. Coverage among PFTs has on average decreased, but these changes are mostly driven by select species. I documented multiple shifts in species distributions, and have found evidence of borealization in the southern extent of the ecotone via the increase in evergreen and deciduous trees. These results are consistent with existing literature, but further define the narrative by highlighting the species most driving the change. The drivers of these taxa are equally nuanced, highlighting the divergent responses within PFTs. As vegetation taxa are responding to different environmental drivers, we are likely to see new communities forming in the Arctic in the future.

3.6 Works Cited

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3.7 Supplemental Tables and Figures

Predictor	Range	Significant in NMDS	Significant in GAM
Deciduous tree	0-12%	X	
Evergreen tree	0-18%	Х	
Tall shrub cover	0-18%	х	
Deciduous shrub cover	0-9%	Х	
Evergreen shrub cover	0-3.5%		
Dwarf deciduous shrub cover	0-12%	Х	х
Dwarf evergreen shrub cover	0-14%	Х	Х
Forb cover	0-10%	Х	
Graminoid cover	0-9%	Х	
Horsetail cover	0-6%		
Clubmoss cover	0-1.5%	х	
Moss cover	0-18%	х	х
Liverwort cover	0-4%		
Lichen cover	0-14%	х	Х
Annual mean temperature	negative 9 to 1 °C	Х	х
Annual precipitation	200-465 mm	Х	
Mean summer Climate Moisture Index	negative 5 to 0	х	
Isothermality	0.15-0.26 °C/°C	Х	х
Snow water equivalent ^a	15-190 mm	Х	
Fire percent mortality	0-100%		
Bulk density	0.03-0.33 g/cm3	х	
Soil organic carbon	195-565 g/kg	Х	

Supplemental Table 3.1: NMDS data used as environmental variables. All data is from the NFI, unless otherwise noted.

Predictor	Range	Significant in NMDS	Significant in GAM
Nitrogen	1- 7 g/kg		
Dead tree biomass	0-70 Mg/ha	х	
Live tree biomass	0-270 Mg/ha	Х	х
Woody debris biomass	0-560 Mg/ha		
Clay ^b	13-35%		
Sand ^b	22-55%		
Silt ^b	27-50%		
Elevation ^c	44-751 m	Х	
Slope ^c	0-16 °	Х	
Northness ^c	-1-1		
Eastness ^c	-1-1		
Longitude	112-134 W	Х	Х
Latitude	60-68.5 N	Х	Х
Time period	Initial/Remeasure	X	Х
Ecosystem	Forest/Ecotone	Х	Х
Density	Open/Sparse/Dense	Х	Х
Land cover	Trees/No Trees	X	Х
Stand Structure	Single Layer/Complex/Multiple Layers/No Trees	Х	Х
Successional stage	Early-/Mid-/Late-/Mature-Seral/Old Growth	Х	
Vegetation origin	Disturbance/Succession/Unknown	Х	х
Vegetation type	Coniferous Tree/Broadleaf Tree/Mixed Tree/Shrub/Mixed Tree/HerbGraminoid	Х	Х
Deposition	Lacustrine/Morainal/Bog/Colluvial/Fluvial/Wind	Х	Х
Humus type	Mor/Peaty Mor/Moder/Anmoor/Mull	X	Х
Upland/Wetland	Upland/Wetland	Х	
Drainage	Xeric/Mesic/Hygric	X	Х
Moisture	Very Rapidly/Rapidly/Well/Moderately Well/Imperfectly/Poorly/Very Poorly	X	

^a Data is from TerraClim; ^b Data is from SoilGrids; ^c Data is from DEMs

















i. Dwarf Evergreen Shrubs



Supplemental Figure 3.1: Percent change per species within the plots that were remeasured, separated by forest (dark green) and ecotone (light green) ecosystems. Error bars represent standard error.

















Supplemental Figure 3.2: NMDS ordination plots with jointplots (left) and species (right). Grouping variables were chosen from those that were found significant in the GAM.





Supplemental Figure 3.3: Partial effects plots from deciduous tree GAM; only species that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).


Supplemental Figure 3.4: Partial effects plots from evergreen tree GAM; only species that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).



Supplemental Figure 3.5: Partial effects plot from tall shrub GAM; only *Alnus* was found to have a significant relationship. Asterix represent level of significance in the GAM model (* p-value <0.05).



Supplemental Figure 3.6: Partial effects plots from deciduous low shrub GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).





Supplemental Figure 3.7: Partial effects plots from dwarf deciduous shrub GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).







Supplemental Figure 3.8: Partial effects plots from dwarf evergreen shrub GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).





Supplemental Figure 3.9: Partial effects plots from the forb GAM; only families that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).



Supplemental Figure 3.10: Partial effects plots from the graminoid GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).





Supplemental Figure 3.11: Partial effects plots from the moss GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).



Supplemental Figure 3.12: Partial effects plots from the lichen GAM; only genera that were significant are shown. Asterix represent level of significance in the GAM model (* p-value <0.05, ** <0.01, *** <0.001).

Chapter 3: Comparing assumptions and applications of dynamic vegetation models used in the Arctic-Boreal Zone of Alaska and Canada.

4.0 Abstract

Modeling Arctic-Boreal vegetation is a challenging but important task, since this highly dynamic ecosystem is undergoing rapid and substantial environmental change. In this work, I synthesized information on 18 dynamic vegetation models (DVMs) that can be used to project vegetation structure, composition, and function in North American Arctic-Boreal ecosystems. I reviewed the ecosystem properties and scaling assumptions these models make, reviewed their applications from the scholarly literature, and conducted a survey of expert opinion to determine which processes are important but lacking in DVMs. I then grouped the models into four categories (specific intention models, forest species models, cohort models, and carbon tracking models) using cluster analysis to highlight similarities among the models. The application review identified 48 papers that addressed vegetation dynamics either directly (22) or indirectly (26). The expert survey results indicated a large desire for increased representation of active layer depth and permafrost in future model development. Ultimately, this paper serves as a summary of DVM development and application in Arctic-Boreal environments and can be used as a guide for potential model users, thereby prioritizing options for model development.

4.1 Introduction

The Arctic-Boreal zone (ABZ) constitutes a range of highly dynamic ecosystems that are rapidly changing due to anthropogenic climate change (Fyfe et al., 2013, Box et al., 2019, Ballinger 2021). Warming is occurring at an accelerated rate as a consequence of Arctic amplification (Goosse et al., 2018, Chylek et al., 2022), in turn causing decreased spring snowpack (Callaghan et al., 2011, Heijmans et al., 2022), decreased albedo (Chapin et al., 2005), permafrost thaw (Campbell et al., 2021, Miner et al., 2022), higher severity and frequency of fires (Timoney et al., 2019, Cahoon et al., 2022), increased available nitrogen (Salmon et al., 2016), and changes to carbon cycling (Schuur et al., 2022, Pedron et al., 2023). These effects of warming influence vegetation dynamics, and in turn are impacted by changing vegetation properties (Figure 4.1). The ABZ spans boreal and tundra biomes, where these climate effects are manifesting in diverse vegetation shifts such as Arctic shrubification (Myers-Smith et al., 2015, Maliniemi et al., 2018, Rees et al., 2020), altered treeline extent and density (Rees et al., 2020, Dial et al., 2024), decreased lichen abundance (Elmendorf et al., 2012), and shifts in deciduous tree cover (Mack et al., 2021, Massey et al., 2023).

Cycles of succession and shifting vegetation are characteristic of the heterogeneous ABZ landscape, especially in the fire-adapted boreal forest (Rogers et al., 2015). Connecting environmental processes to vegetation changes and subsequent interactions in the ABZ (Figure 4.1) is critical to better predict vegetation dynamics in the region. However, because anthropogenic climate change has been altering Earth's ecosystems for decades and is amplified in the Arctic (Previdi et al., 2021, Rantanen et al., 2022), a static representation of vegetation in the ABZ locks assumptions into a model simulation that may not be representative of either a pre-warming Arctic, nor of an 'adapted' Arctic (Loehle 2018). Thus, predictions of the Arctic-Boreal future must include vegetation that can respond to changing environmental properties.

With advances in computing power, ecosystem simulation models are now able to better represent their target systems. Dynamic vegetation models (DVMs) are a class of ecosystem simulation model making great advances due to increased availability of input data, as well as heightened model development and sophistication in simulating ecosystems (Fisher et al., 2018a, 2018b, Bugmann and Seidl 2022). For this study, a DVM was defined as having the capability for terrestrial vegetation (be it plant species, functional type, cohort, community, or ecosystem type) to respond (via yearly growth, changing stem density, vegetation migration, and mortality, among others) to climate and other environmental factors. As a result, an area represented by a DVM must be capable of having its vegetation composition, its structure, and/or function fluctuate over time in response to changing conditions. A DVM can predict how vegetation competition (from intra and interspecific to inter-community type) will respond to environmental inputs and determine ecosystem level changes. This broad suite of models can simulate a range of possibilities and highlight the largest uncertainties (Fisher et al., 2018a, Krause et al., 2019, Gädeke et al., 2020, Argles et al., 2022).

DVMs can require substantial parameterization, as they often have fine vegetation resolution with regard to plant species/type information. Because the ABZ has a relatively small number of vascular plant species, DVMs with coarse vegetation resolution can often be applied across large extents due to the similarity of genera within plant functional types (PFTs) (Sulman et al., 2021). However, while vascular plant species diversity may be low, microsite variation in soil, hydrological, thermal, and permafrost conditions in the Arctic can lead to high heterogeneity in moss, lichen, and vascular plant communities (Le Roux et al., 2013, MallenCooper et al., 2021, Jorgenson et al., 2022), adding challenges to parametrization and calibration. Furthermore, accumulating the data required for ecosystem inputs, and at the appropriate scale, to run a DVM is a large undertaking and makes this class of models less accessible to managers, scientists, and other practitioners, who do not have modeling experience. Even the most experienced modeler must contend with balancing the greater breadth of a global simulation from large-scale models with the detailed and more spatially variable, and more highly resolved simulation of fine scale models.



Figure 4.1: An illustrated representation of model properties and interactions that drive vegetation dynamics in the Arctic-Boreal Zone. Blue arrows represent water fluxes and red arrows represent carbon and nutrient processes.

Among existing DVMs, there is a wide variety of inputs and ecosystem properties (Figure 4.1) that are incorporated, and choosing which properties to represent is critical to model function. The built-in assumptions of each model inform the scope of its findings, but the functions and assumptions of each model are not always apparent from a review of the literature or codebase, and detailed technical model descriptions and user guides are not always available

or accessible. The original intention of a model, or its foundation, frequently carries over as its strongest asset (e.g., a gap dynamics model is very good at simulating stand level tree growth and mortality; Shugart et al., 2020). However, many models that share the same lineage have diverged since initial development to target specific processes or locations (Shugart and West 1977, Urban et al., 1990, Yan and Shugart 2005, Shuman et al., 2014, Brazhnik and Shugart 2016, Foster et al., 2016). These model descendants often adjust the inputs and parameterization to their specific needs and various submodules, such that models that share origins may have divergent goals (Fisher et al., 2018b), making ensemble model assessments more challenging. However, by bringing various model lineages to the ABZ, models must be adapted to the new system and model convergence intensifies the diversity of model and submodules being run in the region.

DVMs are powerful tools, yet challenging to implement. The goal of this paper is to demystify a collection of 18 commonly used DVMs that have been implemented across the North American boreal forest and tundra. My specific objectives are:

- To summarize and clarify ecosystem properties and processes being simulated in different DVMs for users to more easily determine which model(s) would be best suited to answer their research questions.
- To review the literature to determine what types of questions have been asked using DVMs to highlight the breadth of application across the ABZ.
- 3. To survey practitioner opinion to inform future model development and application.

4.2 Methods

4.2.1 Model ecosystem properties

Model selection was based on two criteria: (1) that the model fit the definition of a DVM (i.e., has the ability for vegetation composition and distribution to change over the simulated landscape as a response to environmental forcings), and (2) that the model be applied within the North American ABZ to study vegetation dynamics or impacts thereof published over the past two decades. I found eighteen models that fit these criteria (Figure 4.2). Models were found via literature search and review using Web of Knowledge/Web of Science, Google Scholar, expert knowledge from the NASA Arctic Boreal Vulnerability Experiment (ABoVE) Science Team. Once established that the model fit the criteria, information was collected through Web of Knowledge/Web of Science and Google Scholar (search terms included the model name and/or abbreviation with each of the following: Arctic, Boreal, Alaska, Canada); additionally, model websites, manuals, and technical documentation were reviewed when available. The search was finalized in June 2023. The literature search prioritized sources with model descriptions and papers showing the different applications of DVMs and their input and simulated ecosystem properties. Each DVM was reviewed and categorized based on a suite of 22 ecosystem properties (based on their documented importance from previous observational studies in determining vegetation function, composition, structure, and competition; Figure 4.3), as well as model resolution parameters addressing spatial, temporal, and vegetation resolution. For the purposes of this chapter, an ecosystem property was a state variable or process that could impact vegetation growth, reproduction, competition, or spread on the landscape; the properties were divided into categories as being a characteristic of soil (soil moisture, nitrogen, active layer depth/permafrost, heterotrophic respiration, cryoturbation, phosphorus), plant growth (succession, litterfall, light

competition, seed dispersal, photosynthesis), disturbance (fire, browse herbivory, insect damage, pathogens), or land-atmosphere interactions (evapotranspiration, precipitation form, albedo, methane, CO₂ fertilization). The ecosystem properties were marked as present or absent, along with vegetation, temporal, and spatial resolution (Supplemental Figure 4.1). The resulting matrix was analyzed using hierarchical cluster analysis to identify common traits among models using the *hclust* function (default settings, *stats* package; Bugmann and Seidl 2022) in R (4.2.1 R Core Team 2022). Using Euclidean distance, the cluster analysis measured the dissimilarity among the models in terms of each ecosystem property they represented; I used hierarchical clustering so as to not influence the number of clusters (as would be necessary for k-means clustering). Using the silhouette method, I identified three clusters among the dataset as maximizing the similarity of in-group models. Once the clusters were identified, I qualitatively interpreted the results to identify common traits among the groups and further split the cluster into two groups to highlight certain similarities of resolution and application.

4.2.2 Model application review

A literature review was conducted to assess how DVMs were being applied in the ABZ. For this literature review, the criteria required that the papers: (1) be published from 2017 to 2022; (2) address the North American ABZ (e.g., could be a local analysis in the North American ABZ, or could be a global study that highlighted a finding from the North American ABZ); (3) apply at least one of the models identified by the model properties literature review. Studies were accessed through Web of Knowledge/Web of Science and Google Scholar and were surveyed from January 2023 to April 2023 using the same search parameters as the ecosystem properties search (model name + Arctic, Boreal, Alaska, Canada). I limited the search to the six-year period to focus on the most recent modeling developments; the focus on the North American ABZ allowed me to align the literature review with the scope of the expertise surveyed in the next section. Studies were separated into two categories based on whether the research question explicitly addressed vegetation dynamics (e.g., shifts in evergreen vs deciduous cover), or they indirectly included vegetation dynamics (e.g., permafrost dynamics under climate change scenarios, as mediated by vegetation; Melton et al., 2019).

4.2.3 Model process survey

Importance of each of the ecosystem properties was assessed through an online Qualtrics survey. The anonymous survey was approved by the UVA IRBSBS (Protocol #5607); and was sent to the NASA ABoVE listserv (sent to anyone associated with ABoVE in March 2023) to solicit practitioner opinion. The survey asked respondents to rank their most important seven properties out of the 22 ecosystem properties outlined in the *Model Ecosystem Properties* section. Air temperature was not one of the properties that could be chosen, as it was found in every model. Participants were also asked about their experience with models (e.g., collects data, creates models, reads papers, etc.) and their experience level. Survey questions are available in Supplementary Material 5.2.

Survey results were then compared with the *Model Ecosystem Properties* review to find gaps between the processes that were deemed important by practitioners, and the processes that were being represented in the models. The survey responses were ranked and compared against the corresponding ranked order frequency of the property in the *Model Ecosystem Properties* review; when properties were tied in frequency, their rank values were averaged.

4.3 Results and Discussion

4.3.1 Model ecosystem properties

The Arctic-Boreal ecosystems simulated by models are extremely complex (Figure 4.1), and there will always be a balance between simple and complex representations of the target ecosystem(s). Knowing which aspects of an ecosystem are included across the 18 surveyed DVMs is important to understanding the scope, challenges, and opportunities of each model.

Each model that was reviewed had a unique suite of ecosystem properties (represented in Figure 4.1). Some models used external temperature forcing with either hourly (e.g., Chang et al., 2020), daily (e.g., Murphy 2014) or monthly (e.g., Foster et al., 2019) timesteps, while others used less mechanistic representations or proxies (e.g., Rupp et al., 2000 or Epstein et al., 2007). Some properties were more frequently represented than others in the 18 models: fire disturbance (17 models), succession (17), soil moisture dynamics (15), litterfall (13), and light competition (13). Together, these properties represent a coarse rendering of growth, mortality, and ontogeny. The analysis was limited to looking at the presence of ecosystem properties rather than the ways each model individually represented and ecosystem process; thus, some processes, like mortality, were assessed through proxy variables such as how the system recycles nutrients or responds to a disturbance. Phosphorus (1, ecosys; e.g., Chang et al., 2020), pathogens (2; e.g., Murphy 2014, Boulanger et al., 2018), methane (3; e.g., Arora et al., 2018, Chang et al., 2020, Arndt and Natali 2022) and the presence of herbivory (5; e.g., Murphy 2014, Yu et al., 2017, Longo et al., 2019, Haynes et al., 2020, Hansen et al., 2021) were the least common ecosystem properties addressed (Figure 4.3).

The models represented in this review aggregated into four main groups from the cluster analysis (Figure 4.2): models with a specific intention (ALFRESCO [fire], and ArcVEG

[nitrogen]); the forest-species group (SIBBORK-TTE, UVAFME, Iland, LANDIS-II, SORTIE-ND); the cohort group (ED2, CABLE-POP, FATES); and the carbon cycling group (*ecosys*, SiB4, DVM-DOS-TEM, LPJ-GUESS, ORCHIDEE, CTEM-CLASS, JULES, SEIB-DVM). These models have all been modified from their original version, frequently from different biomes to the ABZ, to generate predictions of the Arctic-Boreal ecosystems (see next section). The underlying mechanics of the original model family and architecture were persistent in their grouping, with some outliers addressed below (Bugmann 2001, Shugart et al., 2018).



Figure 4.2: Cluster analysis dendrogram of ecosystem process presence, temporal, vegetation, and spatial resolution. Hierarchical-means clustering identified four groups: cohort models (red), forest species model (orange), specific intention models (green), and carbon tracking models (gold). Ecosys is surprisingly grouped with the earth system models, likely because it has more specialized soil-climate feedbacks (phosphorus, methane, heterotrophic respiration, cryoturbation) that some of the other models do not address

4.3.1.1 Specific intention models

The specific intention models group consisted of ArcVeg, 'a nutrient based, plant community and ecosystem model' (Epstein et al., 2000) and ALFRESCO, 'a frame-based, spatially explicit fire model' (Rupp et al., 2000, Hewitt et al., 2016, Melvin et al., 2017, www. frames.gov/catalog/7132). These models were mainly unified by their parsimony, rather than the overlapping ecosystem properties they represent. ArcVeg was initially conceived as a way to simulate the impacts of climate change and herbivory (from caribou) across the Arctic tundra with vegetation dynamics driven by the nitrogen cycle (Epstein et al., 2000, Yu et al., 2017). Daanen et al., (2008) added a cryoturbation element to address the localized effects of non-sorted circles (frost boil). ALFRESCO was designed to focus on the impacts of fire disturbance and seed dispersal in Alaska (Rupp et al., 2000). ALFRESCO utilizes an ecosystem-level vegetation resolution, but is able to cycle through the expected stages of fire-adapted vegetation succession. ArcVeg and ALFRESCO simulated the impact of increased temperatures using growth periods (see Epstein et al., 2000) and map inputs (see Rupp et al., 2000), respectively, to streamline the manipulation of temperature in their simulations. By employing simple and robust approaches to shifts in climate, the two models are potentially easier to apply.

4.3.1.2 Forest species models

The forest species model group contained SIBBORKTTE, 'an individual-based, spatially explicit, gap model' (Brazhnik and Shugart 2016; https:// github.com/SIBBORK/SIBBORK), UVAFME, 'an individual-based gap model' (Foster et al., 2019, 2022, https://uvafme.github.io/), iLand, 'a multiscale processed-based model' (Seidl et al., 2012, Hansen et al., 2021, 2023, https://iland-model.org/startpage), LANDIS-II, 'a landscape change model' (Scheller and Domingo 2005, Boulanger et al., 2017, 2018, Boulanger et al., 2022, www.landis-ii.org/), and SORTIE-ND, 'an individual-based forest simulator' (Murphy 2014, Maleki et al., 2019, 2021, www.sortie-nd.org/). Plant growth processes are well represented across all models, but especially within the forest species models. This group is uniquely driven by each model having species-level vegetation resolution for trees; UVAFME and SIBBORK-TTE both have additional PFT representations within their models for non-trees (Foster et al., 2022, 2021). The fine vegetation resolution limits the potential geographic extent of these models, and thus many represent local areas where the species distribution is generally known. Both UVAFME and SIBBORK can be run at larger scales directly or gridded mapping approaches and/or high computing power. The forest-species group also prioritized a light competition growth model over a biochemical photosynthesis (carbon accounting) process. The models bypassed the photosynthesis mechanism and calculated growth potential directly from the light input (Scheller and Domingo 2005, Seidl et al., 2012, Murphy 2014, Brazhnik and Shugart 2015, Foster et al., 2019). Additionally, these models are resolved at monthly (for climate inputs), or annual timesteps (for biomass outputs; Seidl et al., 2012, Brazhnik and Shugart 2016, Boulanger et al., 2017, Foster et al., 2019); whereas SORTIE-ND was resolved at only the annual timestep (Maleki et al., 2019, 2021).

The forest species models have the greatest diversity and inclusion of ecosystem disturbances (Figure 4.3). Within the disturbance processes category, each forest model had a fire module, but LANDIS-II (Boulanger et al., 2018) and SORTIE-ND (Murphy 2014) were the only two models to address forest pathogens. LANDIS-II, SORTIE-ND, and UVAFME are able to run simulations on insect pests, such as the spruce budworm (Maleki et al., 2019) and spruce beetle (Steenberg et al., 2013, Foster et al., 2019). Browse herbivory was addressed by just two of the forest species models (Murphy 2014, Hansen et al., 2021). The high representation of

disturbance by this group was likely tied to their higher spatial and vegetation resolution, and the importance of disturbances in the boreal forests in general. A fire can be assumed to affect all the vegetation within a model pixel; however, a finer scale disturbance, such as the spruce budworm, requires differentiation in tree species and size (Werner et al., 2006) to mimic pest preferences, but also a higher spatial resolution (hectares) to accurately represent the extent of damage. The forest species models, with their finer spatial and vegetation resolution, are thus better suited to simulating fine scale disturbances such as forest insect outbreaks and pathogens.

The models represented in the forest species group specialize in forest growth, with some adding other PFTs to better account for community composition and understory vegetation in the model adaptation to the ABZ (Foster et al., 2019, 2021). They are well suited to the ABZ because of the focused spatial resolution, especially across the Arctic-Boreal ecotone, where there is high landscape heterogeneity and rapid shifts in vegetation cover (Holtmeier and Broll 2019). Increasing the understory representation in the forest species models, particularly with shrub and moss PFTs, will increase their predictive power. With such improvements, these models could be utilized to predict Arctic shrubification, a well-documented result of climate warming (McManus et al., 2012, Myers-Smith et al., 2015, 2020, Ackerman et al., 2018, Reid et al., 2022). Additionally, representing a moss PFT that can influence soil insulation will increase reliability of belowground simulations (Chen et al., 2019).

Within the forest species group, there was some geographic separation in where the models were being applied. LANDIS-II and SORTIE-ND have been primarily applied in the boreal forest of eastern Canada (Bose et al., 2015, Boulanger et al., 2018, 2017, Maleki et al., 2019, 2021, Boulanger and Puigdevall 2021, Molina et al., 2022), while UVAFME and SIBBORK-TTE have been primarily being applied in northwestern Canada and Alaska (Foster et



al., 2019, 2022). This pattern is likely an artifact of specific project focus rather than model capability.

Figure 4.3: A matrix graph representing the ecosystem processes that were identified in each model surveyed. Models are ordered according to their cluster group (Grp 1 [Specific Intention models], Grp 2 [Forest species models], Grp 3 [cohort group], Grp 4 [Carbon cycling models]). Ecosystem processes are grouped by whether they are a soil, plant growth, disturbance or climate process or input; the processes are then organized from most frequent (bottom) to least frequent (top) of their respective section.

4.3.1.3 Cohort models

The cohort group models were ED-2 'the Ecosystem Demography model' (Longo et al., 2019, https:// github.com/EDmodel/ED2), FATES, 'a cohort model of vegetation physiology, growth, and dynamics' and companion model to CLM5.0 (Lambert et al., 2022, https://fates-users-guide.readthedocs.io/en/ latest/index.html), and CABLE-POP, a 'tree demography and landscape structure model' (Haverd et al., 2014). The cohort group was largely unified by the utilization of PFTs further classified by growth stages (cohorts). These models have elements of both the forest species models, such as defined disturbance regimes, while also having more detailed representation of land-atmosphere interactions (Figure 4.3). All three of the cohort models can address precipitation form (Haverd et al., 2014, Fisher et al., 2015, Longo et al., 2019, Kim et al., 2021), which is a critical and changing climate property. The interaction of snow with vegetation on the landscape and shift from snow to rain, especially in the shoulder seasons have large impacts on vegetation during the growing season (Barrere et al., 2018, Addis and Bret-Harte 2019).

Employing a cohort tracking system to their PFTs allows vegetation ontogeny to factor into the simulations (Haverd et al., 2014, Longo et al., 2019, Li et al., 2022). CABLE-POP was frequently used in model comparison studies, which made it unique in many ensemble studies as the only cohort model. By allowing PFTs to have higher resolution by attending to life stage, models can better predict carbon storage, seed production, and growth accumulation, with tailored allometries for each life stage.

Within the cohort group, the ED-2 model has the finest spatial resolution; the model focuses on micro-environment and specifically tries to resolve the problem of high heterogeneity (Longo et al., 2019). FATES and CABLE-POP have been implemented at much larger spatial

scales and resolutions, typically applied in global studies (Table 4.2). The cohort group models did not have any applications for the direct assessment of vegetation dynamics (see next section), suggesting they are well suited to studying ecosystem properties tangential to vegetation dynamics, and that there is an opportunity to ask vegetation dynamics questions of these models. The cohort group would be well suited to answer questions pertaining to the interactions between climate and disturbance, and how the vegetation life stage interacts with climate, especially within the tundra-taiga ecotone where adult recruitment is critical to future predictions (Harsch et al., 2009, Stevens-Rumann et al., 2022).

4.3.1.4 Carbon tracking models

The carbon tracking group has the most diverse of model origins, including SEIB-DVM, an individual based Dynamic Global Vegetation Model' (Sato et al., 2007, http://seibdgvm.com/), and SiB4, also 'a mechanistic, prognostic land surface model' (Haynes et al., 2019, 2020), LPJ-GUESS, 'a process-based global dynamic vegetation model' (Smith et al., 2014, https://web.nateko.lu.se/lpj-guess/faq.html), DVM-DOS-TEM, 'a process based bio-geochemical ecosystem model' (Euskirchen et al., 2022, https:// github.com/uaf-arctic-ecomodeling/dvm-dos-tem), CLASS-CTEM, 'an earth system model with a terrestrial ecosystem model' (Melton and Arora 2016, https://cccma.gitlab.io/classic_pages/info/ ctem/), ORCHIDEE, 'a land surface model' (Druel et al., 2017, Bowring et al., 2019, https://orchidee.ipsl. fr/), JULES, 'a community land surface model' (Best et al., 2009, 2011, Clark et al., 2011, https://jules.jchmr. org/), and *ecosys*, 'a terrestrial ecosystem biochemistry model' (Chang et al., 2020, https://ecosys.ualberta. ca/). Among the carbon tracking models, SiB4 was unique in representing browse herbivory and insect damage but does so at a coarse resolution; the rest of the group simulated fire but not browse herbivory or insects (Figure 4.3). However, the carbon tracking models all represented photosynthesis, heterotrophic respiration, and evapotranspiration.

The carbon tracking models also each included different precipitation forms, and frequently included snowpack dynamics (Burke et al., 2017, Krause et al., 2019, Gädeke et al., 2020, Chadburn et al., 2022, Shirley et al., 2022a). The ability to track liquid vs. solid precipitation is critical for modeling in the ABZ, as the recent shift in precipitation from snow to rain has cascading effects on vegetation response (Callaghan et al., 2011, Addis and Bret-Harte 2019, Rees et al., 2020).

The majority of the carbon tracking models included in this study have fine temporal resolutions, either daily (or finer) or monthly; however, there is a tradeoff for many in spatial scale. These models, with the exception of *ecosys* and SEIB-DVM, have largely been applied at $0.25^{\circ} \times 0.25^{\circ}$ or coarser resolution (Slevin et al., 2017, Gädeke et al., 2020, Zhang et al., 2014, Euskirchen et al., 2022, Shirley et al., 2022a, Yu et al., 2022); DVM-DOS-TEM represents a middle spatial resolution, typically running at 1–4 km² (Euskirchen et al., 2016). This tradeoff is typical of many land atmosphere submodules, and enables a larger extent of application; however, it may be at the expense of spatial resolution. A coarse spatial resolution risks homogenizing the highly heterogeneous landscape of the ABZ and ecotone especially (Holtmeier and Broll 2019). All of these models maintained PFT-level vegetation resolution, but the number of PFTs defined by each model included in this study varies from 5 to 15 (Clark et al., 2011, Haynes et al., 2020).

Ecosys and SEIB-DVM were surprising inclusions in the carbon tracking group, which mostly highlights land-atmosphere interactions (Figure 4.3). Potential, their inclusion of heterotrophic respiration aligned these two models with the carbon tracking models (Shirley et

al., 2022b, Yu et al., 2022); both models simulate active layer depth (Mekonnen et al., 2018a, Sato et al., 2020), and *ecosys* can also track methane fluxes, along with CLASS-CTEM and DVM-DOSTEM (Grant et al., 2017, Arora et al., 2018, Briones et al., 2022). These properties, along with snowpack, are critical to simulating carbon emissions and resolving the status of below-ground hydrology, temperature, nutrient cycling and subsequent vegetation type and success. The belowground processes that the carbon tracking models simulate are critical to accurately predicting how the ABZ will respond aboveground.

4.3.1.5 Evaluation of model properties

The 18 models surveyed were grouped largely by their vegetation resolution (forest species vs cohort groups vs general PFTs in the carbon tracking groups). This breakdown among the forest species, cohort, and carbon tracking groups highlights the importance of vegetation representation in the models.

As the Arctic is a dynamic system in the process of adapting to a new climate, complex models are needed to evaluate and accurately project change. With each model representing a unique suite of ecosystem properties, the importance of each property in their respective models weighs differently on the model processes and outputs. For example, while the models (almost) all include temperature or fire, these properties are weighted differently in each model depending on internal structure. Thus, it is important for future studies to test an ensemble of models to understand the breadth of possibilities for the future ABZ.

In the Arctic, vegetation growth is especially limited by hydrological processes that are highly variable, difficult to model, and even more difficult to ground truth or remotely sense (Campbell et al., 2021, Miner et al., 2022). Permafrost and active layer depth (Miner et al., 2022), snow depth (Barrere et al., 2018), and water logging (Simard et al., 2007) govern plant

distribution and growth rates, but are not universally represented in models. When these properties are included, they are usually resolved at spatial scales too coarse to adequately capture realistic heterogeneity (Figure 4.3; Siewart et al., 2021). Thus, a model that does not factor in the shifts in dynamic belowground hydrology might have a skewed representation of vegetation growth as compared to one that does. Presently, models that addressed belowground processes in the Arctic can simulate permafrost dynamics (Clark et al., 2011, Druel et al., 2017, Arora et al., 2018, Foster et al., 2019, Sato et al., 2020, Euskirchen et al., 2022, Hansen et al., 2023, 2021); however, some of the models with permafrost submodules operate at scales too great for permafrost variability (Krogh and Pomeroy 2021, Siewart et al., 2021).

One limitation of many models is that the ecosystem processes they attempt to simulate occur at finer spatial scales than the inputs that are available (e.g., running a model on a m² resolution, but the input is 250 m², (Fritsch et al., 2020)). This pseudo high resolution may be appropriate for some ecosystem processes, if the appropriate stochasticity is simulated. For example, SoilGrids data are resolved at 250 m² (Poggio et al., 2021), but the soil carbon variation across that area would be misrepresented by a single value. While all the model scales could benefit from increasing resolution, the nuances of noise would be more pressing for the high spatial resolution models in the forest species group. Sub-meter belowground properties, such as active layer depth, could be highly variable within a site and would dictate which species could exist in different areas (Duchesne et al., 2018, Heijmans et al., 2022, Foster et al., 2022, Shirley et al., 2022b).

4.3.2 Model application review

The literature review yielded 48 studies that applied DVMs within the North American ABZ since 2017. Twenty-two studies focused on shifts in vegetation (Table 4.1); they range in

location, scale, and model manipulation (e.g. climate change, harvesting), as well as single model vs. ensemble model approaches. Only two studies addressed direct management questions about harvesting (Maleki et al., 2021) and spruce budworm outbreak (Maleki et al., 2019). Many of the studies were focused on the future species composition. Studies that investigated climate change scenarios found that evergreen trees/PFTs are likely to do poorly in warming climates, and broadleaf trees/PFTs are likely to do well (Boulanger et al., 2017, 2018, Chaste et al., 2019, Foster et al., 2019, Mekonnen et al., 2019, Cadieux et al., 2020, Boulanger and Puigdevall 2021, Foster et al., 2022). Twenty-six studies addressed other research questions, leveraging the abilities of models that simulate dynamic vegetation to parse interactions among ecosystem processes that are indirectly related to vegetation growth (e.g., methane sinks, influence of microtopography, phenology of carbon source/sink, peatland source/sink, carbonyl sulfide, snow phenology, etc.; Table 4.2). With increasing model capabilities, the studies that implicitly assessed vegetation dynamics (Table 4.2) demonstrate the versatility of a DVM to increase understanding of different responses and interactions of ecosystem properties with changing vegetation.

Table 4.1: Studies that used models to investigate shifts in vegetation.	Studies are	briefly
summarized by their manipulation and location and overall result.		

Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation Result	Citation
ALFRESCO	Alaska and NW Canada: Western Alaska	ecosystem	Climate change: A1B	Decrease in late successional forest types and increase in early successional deciduous forests	Euskirchen et al., 2016
ArcVeg	Circumpolar tundra	PFT	Climate change: RCP 8.5	Southern subzones increased in biomass; Combined net effect of herbivory and climate change is still net increase in biomass	Yu et al., 2017
CLASS- CTEM	Circumpolar	PFT	Model comparison	Increase in plant area index across most of Arctic. Larger increase when using CTEM	Teufel et al., 2019

Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation Result	Citation
CLASS- CTEM	North America	PFT	Model comparison	CTEM-CLASS overestimated vegetation; After 1960s, CO2 fertilization and climate warming increased fraction of tree PFTs	Shrestha et al., 2017
ecosys	Alaska boreal forest	PFT	Climate change: RCP 8.5 Fire module	Evergreen PFTs decreased in climate change + fire scenario; Evergreen PFT and deciduous able to keep pace in fire no climate change scenario	Mekonneen et al., 2019
iLand	Alaska	species	Climate change; RCP 8.5; Also tested seed dispersal, fire regimes, browse pressure	Mixed forest and black spruce forests were maintained when fire return intervals were long, deciduous browse pressure was high and seed source was distant	Hansen et al., 2020
JULES, LPJ- LM, LPJGuess, SEIB DGVM, CABLE-POP	global	PFT	Model comparison Climate Change: RCP 8.5	Tree mortality should decrease in boreal, but models had the least agreement in boreal forest	Yu et al., 2022
LANDIS-II	Boreal plains of NE Alberta Canada	ecosystem	Climate change; RCP 2.6, 4.5 & 8.5 Harvesting pressure	Under RCP 4.5 & 8.5: Increase in treeless area, decrease in conifer forest. slight increase in deciduous forest; Climate change had greater effect than harvesting	Cadieux et al., 2020
LANDIS-II	Southern Canada boreal transition zone	ecosystem	Climate change; RCP 2.6, 4.5 & 8.5	Shift towards younger forests dominated by a few species, especially early to mid- successional species; decrease in coniferous species.	Boulanger et al., 2017a
LANDIS-II	Southern Canada boreal transition zone	ecosystem	Climate change; RCP 2.6, 4.5 & 8.5	Decrease in boreal species, increase in temperate species, especially under RCP 8.5	Boulanger et al., 2017b
LANDIS-II	Boreal forest in Quebec, CAN	species	Climate change; RCP 8.5 Disturbance type	Increase in non-fire adapted species in RCP8.5 scenario Hardwoods and mixed forests were favored after forest management disturbance while conifers were favored after fire disturbance.	Molina et al., 2022
LANDIS-II	Quebec, CAN	ecosystem	Climate change; RCP 2.6, 4.5 & 8.5	Decrease in boreal conifers. Hardwoods would increase but not enough to completely offset the loss of biomass. Black spruce would disappear in west boreal by 2150 under RCP 8.5	Boulanger and Puigdevall, 2021

Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation Result	Citation
LPJ-LMFire (LPJ-GUESS + SPITFIRE)	Eastern Canadian Boreal Forest	PFT	Climate Change: RCP 4.5 and 8.5	Increase in Populus in southern ecozones and co-dominance with Picea in northern	Chaste et al., 2019
LPJ-LMFire (LPJ-GUESS + SPITFIRE)	Eastern Canadian Boreal Forest	PFT	Calibrating model	Overestimated Picea and Populus biomass across region; underestimated Pinus and Abies in the north but underestimated in the south	Chaste et al., 2018
ORCHIDEE	Circumpolar (CAVM)	PFT	Climate Change: RCP 4.5 and 8.5	Boreal band, trees coverage increases (42% and 68%) at the expense of shrub cover; in Arctic band; trees increase 120% and 250% in the two scenarios; at the expense of shrubs and grasses.	Druel et al., 2019
SEIB DGVM	global	PFT	Light vs Water gathering biomass	Total vegetation increased 119 Pg (1901-2015), 97% due to light gathering biomass; water gathering biomass increases most in boreal zones	Tong et al., 2022
SEIB DGVM	Circumpolar	FPT	Model Comparison Climate Change: RCP 8.5	Model predicted increase in growth while RWI based model predicted spatial variability in tree growth trends	Tei et al., 2017
SEIB DGVM + ensemble	North America	PFT	Model Comparison Climate Change: RCP 8.5 vs Last Glacial Maximum and modern historic	Increase in C ₄ species but models disagree where	Still et al., 2022
SORTIE-ND	Lake Duparquet Research and Teaching Forest, Quebec, CA.	species	Spruce budworm outbreak	Cedar infills into old stands; spruce budworm significantly affected balsam fir	Maleki et al., 2019
SORTIE-ND	Lake Duparquet Research and Teaching Forest, Quebec, CA.	species	Clear cutting	Clear cut: reset of succession and aspen dominance - Partial Harvest: maintain general composition of original stands	Maleki et al., 2021
TEM	Boreal Alaska and Canada	PFT	Historical carbon balance	After 25 years following fires, difference in vegetation carbon decreased to 773.0–1242.2 g C $/m^2$ from the initially removed carbon 1512 g C/m ²	Zhao et al., 2021
Model	Location(s)	Vegetation resolution	Model manipulation	Vegetation Result	Citation
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UVAFME	Tanana River Basin, AK, USA	species	Climate change; RCP 4.5 & 8.5	Overall decrease in spruce forest and increase in deciduous forest. Greater increase in biomass under RCP 4.5 than under RPC 8.5	Foster et al., 2019
UVAFME	AK and Western Canada	species	Climate change; RCP 4.5 & 8.5	RCP 4.5 Total biomass will slightly increase and the fraction of deciduous areas will slightly increase. RCP 8.5: total biomass will decrease and fraction of deciduous areas will increase greatly	Foster et al., 2022

While difficult to simulate at larger scales, the models were frequently used to study belowground properties, such as permafrost (Burke et al., 2017, Melton et al., 2019, Shirley et al., 2022a), and soil carbon (Larson et al., 2022), methane cycling (Grant et al., 2017), and peat accumulation (Chaudhary et al., 2017, 2020, Chadburn et al., 2022, Chaudhary et al., 2022, Mekonnen et al., 2022, Shirley et al., 2022a). Model comparisons (both model sensitivity and ensemble model comparisons) were a frequent research goal, but were limited to large-scale models, almost all of which were in the carbon tracking group (CABLE-POP, CLASS-CTEM, ED2, JULES, LPJ-GUESS, ORCHIDEE etc.; Burke et al., 2017, Krause et al., 2019, Rogers et al., 2019, Gädeke et al., 2020, Yang et al., 2020). The ecosys model stood out particularly as a model that was able to address many different types of questions about Arctic-Boreal ecosystems, such as how climate change and fire will influence vegetation (Mekonnen et al., 2019), how CO₂ and CH₄ are affected by tundra polygons (Grant et al., 2017), and the effects of microtopography and soil heterogeneity on vegetation (Mekonnen et al., 2018b, 2021, Shirley et al., 2022b). The suite of ecosys papers demonstrates how creative questions can be asked of models to focus on different ecosystem properties and the subsequent effects on vegetation, highlighting the dynamism of Arctic vegetation in a changing climate. It is important for models to predict what the ABZ future vegetation will look like, but knowing how ecosystem property

interactions are likely to shift under stress is equally important.

Table 4.2: Model studies that focused on other topics in the North-American ABZ but utilized
the dynamic vegetation capabilities of each model.

Model	Location	Vegetation Resolution	Paper focus	Citation
ALFRESCO	Alaska boreal forest	ecosystem	Wildfire	Melvin et al., 2017
CABLE-POP, CLASS-CTEM, JULES, LPJ-GUESS, ORCHIDEE, ORCHIDEE-MICT, etc.	global	PFT	Model comparison	Yang et al., 2020
CABLE-POP, LPJ- GUESS, LPJ	global	PFT	Model comparison; carbon flux	Krause et al., 2019
CLASS-CTEM	Circumpolar	PFT	Permafrost	Melton et al., 2019
ecosys	Alaska	PFT	Soil organic carbon and wildfire	Mekonneen et al., 2022
ecosys	Barrow Experimental Observatory, AK, USA	Tundra polygon type	CO ₂ and CH ₄	Grant et al., 2017
ecosys	North American Arctic	PFT	Microtopography	Mekonnen et al., 2018
ecosys	Kougarok Hillslope, AK	PFT	Microtopography	Mekonnen et al., 2021
ecosys	Alaska	PFT	Phenological source/sink	Shirley et al., 2022
ecosys	Seward Penninsula, AK	PFT	Soil and permafrost heterogeneity	Shirley et al., 2022b
ecosys	Alaska	PFT	Machine learning comparison	Shirley et al., 2023
ED2	Imnavait Creek watershed, Alaska	PFT	Soil carbon	Larson et al., 2022
ED2	Alaska	PFT	Snow phenology	Kim et al., 2021

Model	Location	Vegetation Resolution	Paper focus	Citation
ED2, JULES, ensemble	Barrow Environmental Observatory (BEO), AK	PFT	photosynthesis	Rogers et al., 2019
JULES	global	PFT	GPP comparison	Slevin et al., 2017
JULES	Circumpolar	PFT	Peatlands	Chadburn et al., 2022
JULES, ORCHIDEE, LPJ	6 largest Arctic watersheds	PFT	Hydrology - river discharge	Gädeke et al., 2020
LPJ-GUESS	Circumpolar	PFT	Peatlands	Chaudhary et al., 2020
LPJ-GUESS	Circumpolar	PFT	Peatlands	Chaudhary et al., 2022
LPJ-GUESS	Mer Bleue, Ottawa, CAN	PFT	Peatlands	Chaudhary et al., 2017
LPJ-GUESS	Circumpolar	PFT	Sea Ice ~ Vegetation feedback	Zhang et al., 2020
ORCHIDEE and JULES	Circumpolar	PFT	Climate permafrost feedback	Burke et al., 2017
SEIB DGVM	Canada, Austria, Switzerland, Panama	PFT	Nonstructural carbon	Ninomiya et al., 2023
SiB4	Circumpolar	PFT	Carbonyl sulfide	Vesala et al., 2022
SiB4	global	PFT	Carbonyl sulfide	Kooijamans et al., 2021
TEM	Alaska	PFT	Model sensitivity	Euskirchen et al., 2021

One limitation that the model application review highlighted is how individual models tend to be primarily used by single research groups. A research group can produce many studies using one model, but the models might not be readily transferred, or even transferable, making versatility a challenge. Model transference can be limited by code availability, code complexity and language (i.e., how steep is the learning curve), and input data requirements. The ensemble model comparison approach would increase reproducibility and connection among research teams; however, it can be limited by the internal structure of each model and whether the required inputs are available, especially for the individual-based gap model structures. An ensemble of models can yield many different outcomes and enable a more reliable, averaged outcome with uncertainties. However, while both managers and modelers would benefit from a suite of models to predict future scenarios, parameterizing models is both time and computationally intensive.

4.3.3 Model process survey

The survey asked respondents to select their top seven out of 22 ecosystem properties (same properties listed in Figure 4.3; questions in Supplemental Materials 4.2). One hundred fifty-five respondents from the NASA ABoVE listserv completed the survey over a two-week period (13–27 March 2023). The respondent demographic included a mix of advanced (20%, 31 respondents), intermediate (41%, 65 respondents), and novice (34%, 54 respondents) practitioners. Of the respondents, 51% (79 respondents) collected data that could be used in models, 24% (37 respondents) worked to develop models, 31% (48 respondents) ran models, and 63% (98 respondents) read papers about models (multiple responses were accepted for this question). I found no trends between respondent experience and/or application and the ecosystem properties they selected.

The top three ecosystem processes selected as important to DVMs were soil moisture dynamics, fire, and active layer depth/permafrost (Table 4.3). Soil moisture properties, and active layer depth, create a highly heterogeneous belowground matrix which influences vegetative community and individual success (Limpens et al., 2021, Kemppinen et al., 2021, Heijmans et al., 2022); however, soil moisture is already well represented, simulated in 15 of the models. These factors (i.e., soil moisture and active layer depth), while important for larger-scale models, are critical for the finer-scale, local models. Fire, nearly universally represented in the models (17), represents a much larger scale disturbance that influences landscape structural heterogeneity, especially in the boreal forest (Mack et al., 2011, 2021, Reid et al., 2022). Of these three most 'in demand' modeled ecosystem properties as ranked by respondents, active layer depth/permafrost had the largest discrepancy between its practitioner demand and the number of models in which it was incorporated (Table 4.3). This demand suggests that there is an important modeling gap to be filled, which should increase the confidence of model predictions. Including active layer depth and permafrost in more models would be a positive step to more accurately capture ABZ vegetation dynamics; however, these data are spatially and temporally limited and challenging to accurately model.

Table 4.3: Survey responses highlighting the ecosystem properties that practitioners think are most important to arctic vegetation dynamics. The difference column is the demand column (survey respondent rank) minus the supply (model rank). The ecosystem properties are ordered by the highest difference to highlight the ecosystem model properties that are most mismatched between demand and supply. Half ranks are the result of tied rank orders being averaged.

Ecosystem Model Property	Survey Rank	Model Rank	Difference
Active layer depth	3	12	-9
Thermokarst	13	22	-9
Insect outbreak	10	16.5	-6.5
Nitrogen cycling	6	10.5	-4.5
Herbivory (browse) Precipitation and form (snow vs	11.5	15	-3.5
rain)	4	7	-3
Soil moisture dynamics	1	3	-2
Photosynthesis	7	9	-2
Phosphorus cycling	19	21	-2
CO2 fertilization	15.5	16.5	-1
Methane emissions	18.5	18.5	0

Fire	2	1.5	0.5
Albedo	14	13.5	0.5
Seed dispersal	9	8	1
Pathogens	21.5	20	1.5
Variable growth mechanisms	16.5	13.5	3
Cyroturbation	21.5	18.5	3
Succession	5	1.5	3.5
Evapotranspiration	8	4	4
Light competition	11.5	5.5	6
Heterotrophic respiration	17.5	10.5	7
Litterfall	20	5.5	14.5

The survey identified five ecosystem processes that were in high practitioner demand relative to the number of models that had the process incorporated (i.e., supply). Active layer depth/permafrost and thermokarst had the highest difference between practitioner demand and model supply (rank 3 vs. 12, and rank 13 vs. 22, Table 4.3). The other processes that are in practitioner demand (insect outbreaks, nitrogen cycling, and herbivory) had lower disparities between demand and supply (differences in rank of 6.5–3.5). Many of the ecosystem processes were in lower demand than model supply, suggesting that the models are mostly satisfying practitioner use and application for these properties.

Thermokarst is an important element of landscape change and indicates a sudden structural failure of the permafrost due to thaw (Miner et al., 2022). While the demand for thermokarst in DVMs was not large, the lack of representation in the models of thermokarst presents an opportunity for development. Vegetation can both insulate permafrost (Turetsky et al., 2012, Domine et al., 2022), and exacerbate loss (Kropp et al., 2021), making DVMs a good model type to simulate thermokarst processes. Because large thermokarst events can expose

carbon and shift the source/sink status of a site (Pegoraro et al., 2021), the inclusion of this landscape change is important to consider. Active layer cryoturbation was similarly absent from most models; however, the demand was lower, showing a practitioner preference for the larger landscape process than the smaller freeze-thaw soil cycles.

There are some ecosystem properties that are represented to a greater extent than demanded, having a greater than six rank order discrepancy (light competition, heterotrophic respiration, and litterfall). Light competition and litterfall are important processes to vegetation growth and thus would be expected to be commonly found in DVMs. However, I expect this result is also from a bias in question design. The IRB-SBS Study Information Sheet stated that 'the purpose of the study is to highlight the gap between what ecosystem processes are being simulated in vegetation models and what processes are considered important to growth but have not been accounted for in vegetation modeling. This statement could have biased respondents to select ecosystem processes that are less common in models, particularly as I had many respondents with high familiarity with model design and application. Additionally, the question was framed to ask respondents to select ecosystem properties that were important to vegetation dynamics, which may have biased the answer away from carbon tracking answers. Another cause for the over-representation of some of these processes could be an artifact from models that were designed for lower latitudes, or global applications, where certain properties might be more fundamentally important to understanding those ecosystems. However, I do not think that these biases in question design reduce the significance of the above outcomes and what ecosystem properties were desired to improve DVMs in the ABZ.

4.4 Conclusion

The ABZ is a highly dynamic and heterogeneous region, and DVMs are an important tool for predicting its future. The suite of models outlined in this paper cover a breadth of ecosystem properties and temporal, spatial, and vegetation resolutions depending on the scope of the model. This study offers a summary of these models to document the present state and applications of DVMs in the North American ABZ, and to serve as a future reference point in model development. The applications of these models highlight the versatility of the DVMs to simulate and understand ecosystem properties that can be difficult to otherwise approach at large scales. With computing power being alleviated as a primary limitation, DVMs are more limited by the diversity of questions and tests being asked of them and the ecosystem properties they represent. The survey suggests that modeling permafrost-vegetation dynamics is the next frontier in advancement and demand; developing this ecosystem property will greatly reduce uncertainties in predictions of ABZ vegetation composition and structure.

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4.6 Ethical statement

This human study was approved by Institutional Review Board for the Social and Behavioral Sciences (Protocol Number: 5607). All adult participants provided written informed consent to participate in this study.

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4.8 Supplemental Materials

4.8.1 Survey Questions

1. Please select the 7 most important processes for models to explicitly represent that drive vegetation dynamics in the Arctic-Boreal Zone. *Note - temperature was not included because it is represented in all the models surveyed.*

Evapotranspiration CO2 fertilization Litterfall Soil moisture dynamics Nitrogen cycling Active layer depth/Permafrost Pathogens Insect outbreak Methane emissions Seed dispersal Variable growth mechanisms (e.g., single stem, multi-stem, growth form) Heterotrophic respiration Precipitation and form (snow vs rain) Herbivory (browse) Photosynthesis Phosphorus cycling Cyroturbation Albedo Light competition Thermokarst Fire Succession Other

2. What is your level of engagement/comfort level with models?

Novice Intermediate Advanced

3. How do you primarily interact with dynamic vegetation models? (choose all that apply)

Collect data for input Develop model (i.e. write model code) Run model and use output Reads model papers and applies output to other research ideas Other



Supplemental Figure 4.1: A matrix graph representing the different temporal (blue), spatial (gold), and vegetation (green) resolutions that each model uses. Models are ordered according to their cluster group (Grp 1 [Specific Intention models], Grp 2 [Forest species models], Grp 3 [cohort group], Grp 4 [Carbon cycling models]). Models can have multiple scaling resolutions within the same category which could be from having different resolutions for different processes (such as daily temporal resolution for temperature or moisture processes, but a monthly resolution for growth).

Chapter 4: The impact of including tall shrub genera in the SIBBORK-TTE model 5.0 Abstract

As the Arctic-Boreal Zone warms, the vegetation in the Arctic is experiencing a shift towards increasing shrubification, and dynamic vegetation models are working to increase prediction accuracy. However, many models are unable to increase resolution to the genus or species level, which risks homogenizing the responses and inadequately predicting vegetation heterogeneity on Arctic-Boreal landscapes. The spatially explicit, individual-based, gap dynamics model, SIBBORK-TTE has been updated to include a tall shrub PFT, resolved to genus, that can improve the applicability of simulating and future-casting Artic-Boreal landscapes, including shrubification. I conducted model runs for 17 sites, each with eight shrub scenarios (combinations of the three genera: Alnus, Betula, Salix) for Picea glauca and Picea mariana forests, and applied a warming scenario using CMIP6 RCP8.5 model predictions. I statistically compared biomass and stem map outputs between simulations with and without shrubs included, for current climate as well as warming scenarios. Using random forest, I conducted a global sensitivity analysis to determine how including shrubs with warming altered the importance of different variable inputs for Picea biomass. My analysis of the model output for each shrub scenario determined that shrubs cause competition with trees by taking up seeding space. However, under warming climate, encroaching shrubs did not reduce the growth of Picea glauca, which increased in biomass.

5.1 Introduction

The North American Arctic-Boreal Zone is a highly dynamic ecosystem that is experiencing rapid climate change, warming faster than the rest of the globe (Ballinger et al., 2021, Previdi et al., 2021). This warming has shifted vegetation patterns in the Arctic due to increasing temperatures (Berner et al., 2020), altered precipitation regimes (Aune et al., 2011, Addis and Bret-Harte 2018), and thawing permafrost (Frost et al., 2013, Chen et al., 2020). One widespread vegetation shift in the Arctic is known as shrubification (Frost et al., 2020, Kropp et al., 2021, Mekonnen et al., 2021); shrub cover is increasing dramatically across Alaska and western Canada (Timoney et al., 2019), particularly encroaching on the tundra and the tundra taiga-ecotone where tree competition is absent or minimal (Frost and Epstein 2013, Kitagawa et al., 2019, Wallace and Baltzer 2020).

Shrubs are structurally and functionally different from trees in the Arctic-Boreal region. Here I define shrubs as woody, multi-stemmed, low to mid-stature vegetation. Arctic shrubs are classified into five types based on height and leaf lifespan: dwarf evergreen shrubs (<40 cm), dwarf deciduous shrubs (<40 cm), low deciduous shrubs (<1 m), low evergreen shrubs (<1 m), and tall (deciduous) shrubs (>1 m) (Walker et al., 2005, Reynolds et al., 2019). In the rapidly shifting landscape of the Arctic, shrubs are at a competitive advantage over trees due to their relatively shorter life cycles (Smith and Beaulieu 2009), and are also able to spread clonally by ramets (Deslippe and Simard 2011, Addis and Bret-Harte 2018) to further exploit their local environment.

Overall, shrub cover is increasing in the Arctic due to many different abiotic drivers. Shrubs are responding strongly, but unevenly, to summer temperatures in the North American Arctic, with wetter sites showing a greater shrub response to increasing temperatures (MyersSmith et al., 2015). Tall shrubs have increased growth to a greater degree than other shrub PFTs due to warming (Elmendorf et al., 2012, Myers-Smith et al., 2015, Mekonnen et al., 2021). The increase in shrub cover decreases albedo, especially in the winter when tall shrubs extend above snow cover (Belke-Brea et al., 2020); this decrease in albedo has been shown to contribute to greater heat retention and warming (Blok et al., 2011). Buchwal et al. (2020) connected a decrease in sea ice to an increase in shrubs across the Arctic, but cautioned that the decrease in sea ice was causing the duality of warming and drying, which in turn led to decreased shrub growth in areas with dry soils. Chen et al. (2020) found that summer precipitation was responsible for 30.8% of shrub expansion into upland tundra, but also noted that surface water pooling due to thermokarst can lead to decreases in shrubs in lowland tundra. Active layer disturbances, in the form of frost heave, allowed for increased *Alnus* colonization in northwest Siberia (Frost et al., 2013). Finally, the increased frequency and severity of fires across the boreal forest and tundra is expected to facilitate increased shrub growth, as shrubs are reported to have increased growth on old burn scars (Mekonnen et al., 2021).

The structure of shrubs, which typically comprises multiple stems in close proximity, can increase snow retention in and around shrub patches (Sturm et al., 2001, Myers-Smith and Hik 2013), which coupled with thermal stem conductivity influences soil temperatures below shrub canopies. Soils that are below shrubs completely buried by snow, are insulated from winter temperatures and on average are 4-5°C warmer than soils without shrubs (Myers-Smith and Hik 2013); however, underneath shrubs that are taller than snow depth, branches create a thermal bridge and can cool soils in the autumn and winter by up to 3°C (Domine et al., 2022). The thermal bridging can accelerate snow melt in the spring (Wilcox et al., 2019), as well as decrease snowpack during the fall (Barrere et al., 2018), though both are structure dependent (Bueno et

al., 2016, Wilcox et al., 2024). In the summer, shrub canopies reduce soil warming through shading by ~2°C (Myers-Smith and Hik 2013). However, Lafleur and Humphreys (2018) hypothesized that shrubs have greater transpiration rates than other vegetation and will thus increase surface temperature by increasing localized humidity.

While the direct relationships among shrubs, snow, and nutrients have been shown to be weak (Myers-Smith and Hik 2013), shrubs indirectly influence nutrient cycling by altering microbial interactions (Broadbent et al., 2024). Shrubs can affect local substrate through association with mycorrhizal fungi, such that increases in ericaceous shrub cover (e.g., *Vaccinium spp. Rhododendron spp., Andromeda spp.*) and their associated ericoid mycorrhizal fungi leads to greater organic matter, slower decomposition, and increased nutrient limitation (Fanin et al., 2022). Furthermore, the interaction of shrub expansion and generally reduced snow decreased soil microbial biomass but increased denitrifier abundance, leading to greater nitrogen limitation (Broadbent et al., 2024). *Alnus*, a shrub in the *Fabaceae* family, has the potential to greatly increase the rate of shrub expansion in the Arctic, because it is buffered from soil nitrogen limitation by its symbiotic association with *Frankia*, a nitrogen-fixing bacteria, and its litter can increase soil nitrogen in colonized areas (Schore et al., 2023). *Betula nana* has been shown to use mycorrhizal fungi in transferring carbon stores among roots of multiple individuals (Deslippe and Simard 2011), also suggesting a competitive advantage for *Betula*.

While responding strongly to abiotic factors, shrubs are interacting with other vegetation on the landscape in competitive and facilitative ways. Shrubs were found to increase tree seed germination by ameliorating harsher Arctic climate conditions (Limpens et al., 2020); however competitive interactions can ultimately reduce seedling survival (Grau et al., 2012). Shrub establishment can be limited to the presence of bare ground (Frost et al., 2013); shrubs were less

able to establish in moss, forb, or graminoid vegetation, and were also reduced by plant allelopathy from *Cassiope tetragona* (Angers-Blondin et al., 2018). These interactions are complex and continue to be elucidated as shrubification is changing Arctic plant communities.

The speed at which the Arctic is warming is unprecedented, and dynamic vegetation models have been parameterized across the Arctic in an attempt to parse future conditions and vegetation outcomes. However, many models simulate at a vegetation resolution that is too coarse to include more than just trees, and the importance of shrubs in the Arctic has been generally overlooked (Heffernan et al., 2024). Models that include shrubs tend to treat them as a monolithic plant functional type, and while this decision is typically made to accommodate internal model structural limits, genus and species level differences within PFTs are compromised and limit the applicability of results (Saccone et al., 2017, Anderegg et al., 2021). As noted in Chapter 3, model architecture typically dictates what modifications can be made; even in the high species resolution of forest gap models, accounting for non-tree growth forms runs counter to the internal framework designed to simulate specifically how trees grow. Additionally, shrubs are challenging to model within the context of current model frameworks, and require adapting individual-based gap-dynamics models to approximate their distinct growth form.

The SIBBORK-TTE model has been adapted to include tall shrubs resolved at the genus level, to better simulate the North American boreal forest and tundra-taiga ecotone. The main objective of this study is to determine the capability of the SIBBORK-TTE model to simulate competition between tall shrubs and two target tree species, *Picea glauca* (white spruce) and *Picea mariana* (black spruce), two dominant species across Alaska and western Canada, under both existing climate conditions and conditions of a future climate. Therefore, I asked: \

- 1. What are the ecosystem drivers of *Picea glauca* and *Picea mariana*, and how do they shift with the addition of tall shrub genera in the SIBBORK-TTE model; and
- 2. How are the shrubs interacting with trees in the model under climate change scenarios?

5.2 Methods

5.2.1 SIBBORK-TTE framework

Dynamic vegetation models have been shown to provide critically accurate predictions towards understanding the future of the Arctic-Boreal region. Individual-based gap dynamics models (IBGM) are a high-resolution modeling framework within the broader dynamic vegetation model type. The IBGM was initially designed in the FORET model by Shugart and West (1977). A hallmark property of IBGMs is their ability to simulate tree growth on the individual tree level, allowing the responses of each tree (germination, growth, competition, regeneration, mortality) to external forcing variables to be assessed. This feature of IBGMs make them critical for studying how trees will respond to climate change, because they are able to respond differently based on ontology, landscape position, and competitive or facilitative interactions, bringing an element of realism to simulations. SIBBORK-TTE is a spatiallyexplicit, IBGM written in Python 3 that has been adapted from the SIBBORK model (Brazhnik and Shugart 2016). SIBBORK arose from the FORET (Shugart and West 1977) and ZELIG (Urban et al., 1990) lineage of models, and was improved upon by creating a 360° light module that is critical to northern latitudes, as well as creating a simulation with interactive 10 m² cells (Brazhnik and Shugart 2016), focusing on the Siberian boreal forest. The SIBBORK model has been designed to integrate top-down forcing variables (radiation, temperature, precipitation) with bottom-up controls (site quality, soil water content, nutrient availability) into dynamic tree responses (growth, biomass accumulation, competition, mortality).

5.2.2 Model additions and developments

SIBBORK-TTE was adapted to simulate the complex interactions within the tundra-taiga ecotone (TTE) in North America, where climate change is rapidly affecting the ecosystem, and future projections are critical for determining vegetation growth patterns and carbon stocks. SIBBORK-TTE integrates remote sensing data from NASA, such as solar radiation and cloud cover (NASA LARC), topographic information from the ArcticDEM (10 m DEMs, Porter et al., 2018), and soils data (250 m SoilGrids, Poggio et al 2021), to create the growing environment, including a species-specific threshold for permafrost tolerance. An upgrade to the SIBBORK-TTE model is the addition of a tall shrub PFT (resolved at the genus level), presently for *Alnus* (alder), *Betula* (birch), and *Salix* (willow) genera. Each species or genus (tree species, or tall shrub genus) is parameterized for height, leaf area index, biovolume, and biomass (Ker and van Raalte 1980, Bragg 2001, Ter-Mikaelian and Korzukhin 1997, Chojnacky et al 2014). Growth is controlled by growth increments that utilize the solar inputs (total solar radiation moderated by cloud cover and shading) and are scaled to site conditions.

SIBBORK-TTE is highly specialized to site inputs, making it very good at local simulations. The user-supplied site environmental inputs (Supplemental Table 5.1) are layered to generate a simulation with high reproducibility while being faithful to site conditions. Each species also has a suite of site-specific allometric equations (using diameter at breast height [DBH] to calculate height, leaf area, biovolume, and biomass [Supplemental Table 5.2a]), and species-specific silvicultural parameters (Supplemental Table 5.2b). The model is capable of conducting high resolution simulations to the individual tree scale, with an environment resolution of 10 m. The typical extent for a local run is ~9 km²; however, the user is only limited by computing power. For this paper, 100 m² plots were simulated to balance local extent with

computing power and time. The model generates a suite of site characteristics at an annual scale for time series analysis, and vegetation characteristics are output at an annual scale at the resolution of each stem.



Figure 5.1: Distribution of sites with *P. mariana* (black) and *P. glauca* (blue) across Alaska and northwestern Canada.

5.2.3 Model Simulation Setup

Sites are initiated by seeding values which are calibrated from percent cover and stem density values from field data. It takes ~300-500 years of model spin up for species ratios to stabilize, allowing for user adjustments to match field data. The maximum amount of growth per site is determined by the ratio of maximum height to maximum diameter at breast height (DBH); however, the optimal increment follows Bragg (2001). Optimal growth is limited by the amount of solar radiation received, with further considerations from growing degree days (temperature), water availability, site quality, soil fertility, permafrost, shade tolerance and seed occurrence.

Tree mortality occurs by accumulating two stress flags; if the growth threshold for a tree is not met in one year, the tree will accumulate one stress flag, and if in any subsequent year the growth threshold is again not achieved, the tree will die. The stress threshold is user-defined as a percentage of a species annual growth. Additionally, the age maximum will limit the age of trees by implementing a negative exponential of probability of survival, such that as the tree gets closer to the age maximum for the species, it will be more likely to die $(1 - e^{(-4.605/maximum age)})$.

A permafrost module update to SIBBORK (Brazhnik and Shugart 2016) accounts for the species-specific limits of permafrost on their growth. If the active layer is greater than 1.68 m, then there is no permafrost limit on growth; if the active layer depth is less than 0.886 m, then there is no growth due to shallow permafrost. In between these two thresholds, growth limitation is determined by the permafrost tolerance of each species. The permafrost module was derived from model code by Bonan (1989) and Foster et al. (2019), rewritten into Python from Fortran (by Armstrong and Osmanoglu). The module, added into the existing soil and climate framework, uses temperature, light, slope, aspect, and lapse rate to calculate the depth of freezing and thawing, using the Bonan (1989) model. The permafrost layer output is resolved at a monthly time scale, allowing users to determine both the changes in maximum and minimum depth, as well as track the rate of thaw and freeze between years.

Historical climate is simulated through one of two mechanisms: using statistical climate data, or by subsetting the NASA MERRA-2 climate model dataset, typically from 1980-1995 (but is ultimately user defined). For historical data, the average and standard deviation for temperature and precipitation from either source is used to initialize the model runs. The user has the option to switch on actual data values for the site from the MERRA-2 data from 1980-2020, simulating monthly temperature and precipitation from daily values for that time period. After

2020, if climate warming is activated, monthly values for predicted temperature and precipitation average and standard deviations from CMIP6 for the site are used. The transition from historical climate to future climate applies a linear rate of change for each month from the previous averages to the new values. In other SIBBORK versions, future climate can also be ingested directly from ensembled CMIP6 climate model datasets, adjusting the rate of change to a reflect the site-specific trajectory. Depending on what climate the user wants to run, a combination of these inputs can be used to simulate the targeted site.

5.2.4 Simulating Shrubs

In order to test the influence of shrubs, I parameterized 17 sites distributed across central Alaska and northwestern Canada (Figure 5.1). For these selected model run sites, there was little information in the literature and NOAA's International Tree-Ring Database on species composition or biomass values, other than which spruce species was dominant; thus they presented a good opportunity for use as hypothetical sites to test the influence of shrubs across a range of environmental and climatic conditions. Each of the selected sites had a different climate input from gridded CRU (see Chapter 1). In order to test the effect that shrubs had on the growth of *Picea mariana* and *Picea glauca*, I ran eight different combinations of the three shrub genera: no shrubs, *Alnus, Betula, Salix, Alnus + Betula, Alnus + Salix, Betula + Salix, Alnus + Betula + Salix.* Within these shrub run-combinations, I tested levels of simulated inseeding, setting half of the runs to 0.31 (low shrub) or 0.56 (high shrub) values for potential shrub growth. All shrubs were set to the same inseeding level within the site, and each were given a stress tolerance of 0.3. Stress tolerance dictates the proportion of the maximum annual growth that an individual tree/shrub needs to reach in order to not trigger a "stress flag," where two stress flags result in

the death of that stem in the model. The *Picea* species were given high inseeding values (0.56) and low stress (0.1).

I ran the simulations at each site from 1500-2300. In order to test the effect of climate on the shrub-tree interactions, I initially used MERRA2 data as the historical climate and then, an RCP8.5 climate scenario began in the year 2017. The RCP8.5 climate scenarios are the average and standard deviation of thee CMIP6 models (Supplemental Table 5.4) accessed through the Copernicus Climate Change Service, Climate Data Store (2021). Climate change was implemented linearly from 2017-2100, and then the vegetation had 100 years to stabilize to the new climate. Because I was most interested in the importance of environmental drivers acting on *Picea* growth, I chose to let the vegetation stabilize in the future climate for 100 years to determine which factors were important under the new climate regime. Thus, I used the 100 years from 1900-2000 as the historical climate data period, and 2200-2300 as the climate change period. I extracted annual biomass for each species, as well as the annual site-level variables: growing degree days, radiation, and thaw depth.

5.2.5 Data Analysis

In order to test the impact of each of the shrub treatment scenarios, I evaluated total biomass of *Picea*, separated by species and shrub intensity, in the no shrub environment compared to each of the shrub combinations (no shrubs vs. *Alnus, Betula, Salix, Alnus + Betula, Alnus + Salix, Betula + Salix, Alnus + Betula + Salix*). To avoid inflating significance due to multiple testing, I used a Bonferroni adjustment. I ran a t-test under the same conditions for warming to determine the effect of climate change on the target species.

In order to assess the model sensitivity (Harper et al., 2011) of *Picea* biomass to the inclusion of shrub species, I ran a random forest regression using the *randomForest* package

(Breiman 2001, Liaw and Wiener 2002) in R (version 4.2.1, R Core Team 2022) for each of the shrub scenarios, as well as for both of the climate scenarios. Whereas the t-test was used to reveal the cumulative impact of the different shrub treatments and climate conditions, the random forest regression was used to assess which input variables have the greatest influence on *Picea* biomass. Random forest regression does not assume linearity, and because the data are bootstrapped for each tree, it is able to handle temporally autocorrelated datasets (Harper et al., 2011). I included radiation, growing degree days, thaw depth, *Alnus* biomass, *Betula* biomass, and *Salix* biomass as annually resolved variables; my static variables included average precipitation for each month, as well as latitude, longitude, bulk density, depth to bedrock, cation exchange capacity, water holding capacity, silt, sand, and clay content. Precipitation did not have an annually resolved value, and thus I could not include it with the other climate variables; temperature and cloud cover were incorporated in the calculations for growing degree days and radiation, respectively. I tested the random forest regression for Picea mariana and Picea glauca individually, for each of the shrub scenarios, as well as the two climate scenarios (historical and warming climate) individually to determine how the increased stress of warming manifested in the model. I used a 75:25 training: testing framework to validate the models. I compared which variables had the greatest importance and analyzed the variable relationships to *Picea* biomass using the *pdp* package (Greenwell 2017). Variable importance is discussed in terms of percent increase of mean square error; I analyzed the top five important variables.

5.3 Results

5.3.1 Focus on three specific sites

I selected three representative sites on which to focus my results: one high shrub intensity (MDJC1) and one low shrub intensity (FARO) for *P. glauca*, as well as one high shrub intensity

(TVC) for *P. mariana*. Both high shrub intensity sites are from higher latitudes (> 68°N), to facilitate comparisons across species. Assessing the historical climate, present climate, and future climate demonstrates the ability of the model to simulate shrubification, and also a potential threshold limitation on this phenomenon. Using 1970 as a pre-warming (historical) sample, 2015 as a current time period, and 2200 as a future cast, each site exhibits an increase in shrub biomass and stem density from 1970 to 2015, but warming eventually decreases shrub abundance by 2200 (Figure 5.2). The *P. glauca* sites had lower tree stem density than *P. mariana* (Figure 5.2c), despite the *P. mariana* site having the shallowest thaw depth (Supplemental Table 5.4), which is potentially a simulation of the dense "dog-hair" stands that *P. mariana* will sometimes form.




Figure 5.2: Stem maps for three sample sites (MDJC1 [a], FARO [b], and TVC [c]) to compare three time points: 1970 (historical), 2015 (current), and 2200 (future). Shrub scenarios [d] are contrasted for MDJC1 only. Each site has been limited to the top northeast quadrant to maximize readability.

5.3.2 Influence of shrubs

The total effect of each shrub scenario decreased *Picea* biomass and was significant for

all scenarios for Picea glauca, as well as the Alnus + Salix and Alnus + Betula + Salix scenarios

for *Picea mariana* (Table 5.1a, Figure 5.2a). Within the high shrub category, the greatest reduction in *Picea* biomass came from the *Alnus* + *Betula* + *Salix* group, causing a 27.6% decrease in *Picea glauca* biomass and a 14.2% decrease in *Picea mariana* biomass; these biomass decreases corresponded with a 37% and 44% decrease in stem count respectively (Figure 5.3a). The low shrub category for this shrub scenario caused a 17.9% decrease in *Picea glauca* each shrub scenario with multiple shrub genera caused a decrease in biomass of >20%, while independently, *Alnus* decreased biomass by 9.6%, *Betula* by 16.2%, and Salix by 12.4% (Figure 5.2a). Conversely, the reduction in biomass for *P. mariana* was only 1.8% for *Alnus*, 12.0% for *Betula* and 6.1% for *Salix* (Figure 5.2a).

	Shrub	No Shrubs ~				
Species	intensity	[shrub scenario]	t-statistic	adjusted p-value		
		Alnus	-5.41	< 0.001 ***		
		Betula	-10.37	< 0.001 ***		
	TT: - 1.	Salix	8.25	< 0.001 ***		
	shrub	Alnus + Betula	-13.46	<0.001 ***		
	intensity	Alnus + Salix	-12.72	< 0.001 ***		
		Betula + Salix	-16.10	< 0.001 ***		
Diaga		Alnus + Betula + Salix	-18.37	<0.001 ***		
riceu alauca						
giuucu	Low shrub intensity	Alnus	-3.46	0.01*		
		Betula	-4.82	<0.001 ***		
		Salix	5.35	<0.001 ***		
		Alnus + Betula	-8.75	<0.001 ***		
		Alnus + Salix	-5.93	<0.001 ***		
		Betula + Salix	-11.63	<0.001 ***		
		Alnus + Betula + Salix	-11.18	< 0.001 ***		
		Alnus	-0.63	1		
Picea	High shrub	Betula	-2.60	0.19		
mariana	intensity	Salix	1.56	1		

Table 5.1a: Results of t-test effect of each individual shrub scenario on *Picea* biomass, as compared to the no shrub scenario.

Species	Shrub intensity	No Shrubs ~ [shrub scenario]	t-statistic	adjusted p-value
_		Alnus + Betula	-3.37	0.02 *
Picea mariana	High shrub intensity	Alnus + Salix	-2.05	0.84
		Betula + Salix	-3.02	0.063
		Alnus + Betula + Salix	-4.13	<0.001 ***

Table 5.1b: Results of t-test between the two climate scenarios (historical and warming) effect on *Picea* biomass.

	Shrub			
Species	Intensity	Shrub scenario	t-statistic	Adj p-value
		No shrubs	-3.38	0.02*
		Alnus	-4.11	0.001**
		Betula	-1.21	1
	High shrub	Salix	-1.91	1
	intensity	Alnus + Betula	-3.49	0.01*
		Alnus + Salix	-1.55	1
		Betula + Salix	-4.22	<0.001 ***
Picea		Alnus + Betula + Salix	-5.06	<0.001 ***
glauca		No shrubs	7.38	< 0.001 ***
	Low shrub intensity	Alnus	6.87	< 0.001 ***
		Betula	3.71	0.005**
		Salix	5.94	<0.001 ***
		Alnus + Betula	6.24	<0.001 ***
		Alnus + Salix	6.87	< 0.001 ***
		Betula + Salix	4.34	< 0.001 ***
		Alnus + Betula + Salix	5.67	<0.001 ***
		No shrubs	3.44	0.01*
	High shrub intensity	Alnus	3.70	0.006**
Picea mariana		Betula	4.94	< 0.001 ***
		Salix	3.55	0.01*
		Alnus + Betula	4.58	<0.001 ***
		Alnus + Salix	3.15	0.04*
		Betula + Salix	4.24	< 0.001 ***
		Alnus + Betula + Salix	4.23	<0.001 ***

Each shrub model exhibited high predictive accuracy for *Picea* biomass when evaluated using out-of-bag observations (OOB $R^2 > 0.99$). Radiation was the most important variable for *P. glauca* biomass (28.2-38.2% increase in mean square error [incMSE]), with a consistent negative association, for each shrub scenario (Figure 5.4a, Supplemental Figure 5.2a-h), while growing degree days was the most important variables for P. mariana biomass (20.6-24.5% incMSE), with a consistent positive to negative association in each of the significant shrub scenarios (Figure 5.4b, Supplemental Figure 5.2i-k). For P. glauca biomass, thaw depth (12.5-25.6% incMSE) and growing degree days (14.1-22.6% incMSE) were also frequent important variables (Figure 5.4b). Cation exchange capacity (16.0-21.6% incMSE) and sand percent (14.9-23.9% incMSE) were the most frequent soil variables in the top five most important variables to predict P. glauca biomass; both cation exchange capacity and sand percent were generally positively associated with *P. glauca* biomass (Figure 5.4a, Supplemental Figure 5.2a-h). The *P.* mariana random forest analysis highlighted Salix (15.8-16.6% incMSE) and Alnus (18.2-20.1% incMSE) biomass as important for *P. mariana* biomass (Supplemental Figure 5.2j, k), while *P.* glauca had Betula (13.6-20.1% incMSE) as important for two scenarios (Supplemental Figure 5.2c, g).



Figure 5.3: The relative percent change in biomass from the "No shrub" scenario compared to each of the other shrub scenarios (a) and the difference for each scenario between the warming and historical climate.

5.3.3 Influence of warming

The warming climate caused a significant decrease in P. mariana biomass (>15%) for all

shrub scenarios (4-11% reduction in P. mariana stem count). In the high shrub scenario, P.

glauca biomass increased for each scenario, and was significant (10-14% biomass, <1% increase in stem count), in all scenarios except *Betula, Salix,* and *Alnus* + *Salix* (3.4-5.5%, \leq 1% increase in stem count: Figure 5.2b, 6.3b). At the low shrub intensity, *P. glauca* biomass decreased in all shrub scenarios (-8-18%, 1.5-5% increase in stem count) (Figure 5.2b).

Each climate model exhibited high predictive accuracy for *Picea* biomass when evaluated using out-of-bag observations (OOB $\mathbb{R}^2 > 0.97$). Assessing the five most important variables, the random forest models showed some overlap in important predictor variables for each tree species in both climate scenario (Figure 5.5c). Shrub scenario, *Alnus, Betula*, and *Salix* biomass were four of the five most important predictors for each species and climate scenario (Supplemental Figure 5.3a-d). Solar radiation was important for both *P. glauca* and *P. mariana* for the warming time periods (31.4% and 50.5% incMSE, respectively). *P. glauca* had silt content (20.9% incMSE) as the fifth most important variable in historical time period, while *P. mariana* had June precipitation (20.1%).







Figure 5.4: Comparison between percent biomass (a) and percent stem count (b) for each shrub species within the eight shrub scenarios, only the high shrub intensity is shown for *P. glauca*. The greater values for stem count suggest that despite their relatively low biomass, the shrubs are successfully establishing and competing with the spruce in the model runs.

5.3.4 Shrub interactions with warming

Examining the relationships between shrub biomass and tree biomass, there is an initial tandem increase at lower biomass levels, likely where species are mutually limited by temperature or soil moisture (Figure 5.6). Then, both species reach a threshold, and *P. mariana* and *P. glauca* have differing responses to shrub presence (Figure 5.6). For *P. mariana*, competition begins to decrease *Picea* biomass in both climate scenarios, which aligns with the biomass of each shrub genera having negative relationships with *P. mariana* biomass (Figure 5.6b, Supplemental Figure 5.3c, 5.3d). However, while the increase in shrub biomass causes a consistent decrease in *P. mariana* biomass above 150 kg/ha of shrub biomass (and 50 stems/ha), the relationship with shrub stem count becomes positive after 100 stems/ha (Figure 5.6a). This may be due to a the more productive sites having greater biomass and stem counts at the higher

biomass values. The climate scenarios cause a different response in *P. glauca* to shrub biomass and stem counts. After the initial tandem increase, *P. glauca* biomass begins to decrease at ~25 shrub stems/ha (~25kg/ha), with warming yielding slightly greater *P. glauca* biomass (Figure 5.5). There are no notable differences in the patterns of *P. glauca* biomass response to shrub biomass or stem count, suggesting that the tree and shrub PFTs are mutually constrained by other factors and not by their interaction.

5.4 Discussion

5.4.1 Focus of three specific sites

The three sample stem maps of Alnus + Betula + Salix shrub scenarios for MDJC1 (P. glauca - high shrub intensity), FARO (P. glauca - low shrub intensity), and TVC (P. mariana high shrub intensity) demonstrate the ability of the model to simulate shrubification, as noted by the increase in shrubs from the 1970 to 2015 stem maps (Figure 5.2a-c); the stem maps then illustrate that there will be a decrease in shrubs when the climate experiences severe warming. In the 2200 stem maps, there are many more large trees in the *P. mariana* site (TVC, Figure 5.2c) than in the earlier years; considering the latitude >68°N for this site, this increase in tree biomass may be reflecting the impacts of climate change that are projected for the upper boreal forest (Rotbarth et al., 2023). However, the FARO and MDJC1 sites have more small trees and shrubs, and have lower biomass than the 2015 maps, with FARO having one large tree (Figure 5.2a, 5.2b). As latitude was not one of the important drivers for *P. glauca*, the similarity between FARO and MDJC1 is expected, as the greatest difference among their important variables was shrub intensity. Growth of *P. mariana* sites were much more driven by the abundance of each shrub, which suggests that competition for space is a greater driver in the future warming scenario, as there are fewer shrub stems simulated.

While the stem maps act as a snapshot to illustrate how the model is simulating tree and shrub growth, the overall growth drivers are better assessed by examining vegetation that has stabilized in the model, and thus the transition period (between 2000 and 2100) was not analyzed for growth drivers, because the temperature inputs were not static.

5.4.2 Influence of shrubs

The SIBBORK-TTE model update that included three tall shrub genera successfully simulated shrub competition with trees (Figure 5.3a). The negative effect of shrubs was greater on *P. glauca* than *P. mariana*, which is possibly due to site conditions, as *P. mariana* is frequently found in lower quality, boggy sites with shallower active layers (Viereck and Little 2000). However, even in the most intense shrub scenario (high intensity *Alnus* + *Betula* + *Salix*), shrubs only amounted for 10% of the total biomass, but 40% of the stem count. In the *Alnus* + *Betula* + *Salix* scenario, 10% of the total biomass attributed to shrubs corresponded to a 27% reduction in *P. glauca* biomass compared to the no shrub scenario, suggesting that the shrubs are having a greater impact than just replacing biomass and are functionally competing in the model. Likely the greater stem density of shrubs is driving competition with *P. glauca*.

The drivers for the *P. glauca* shrub scenarios unanimously indicated radiation as a key factor for *P. glauca* biomass growth. The other most important drivers included additional variables that are known to influence *P. glauca*, thaw depth (Anderson et al., 2020), sand percent (drainage, Huang et al., 2012, also seen in Chapter 1), and cation exchange capacity. The top five variables for the no shrubs scenario were radiation, thaw depth, growing degree days, silt content and depth to bedrock. Among the shrub scenarios, there were seven additional important variables (*Betula* biomass, shrub intensity, clay content, silt content, bulk density, cation exchange capacity, and July precipitation). This variety of the five most important drivers

suggests that the different shrub scenarios are forcing *P. glauca* to grow differently in the model in the presence of these tall shrubs, and that the genera of the shrub(s) is also important to the response of *P. glauca*.



a. Picea glauca





Figure 5.5: Variable importance plots for top five most important variables for the significant shrub scenarios for *P. glauca* (a) and *P. mariana* (b) biomass in the SIBBORK-TTE model, as well as the variable importance for the climate scenarios (c). Full variable importance plots are in Supplement Figure 5.1a, 5.1b, and 5.1c.

The shrub scenarios had a more limited effect on the growth of *P. mariana*; however, each shrub genera was identified as important, and having a positive to negative relationship (Figure 5.5b, Supplemental Figure 5.2i-k). The most important variables for *P. mariana* without shrubs were growing degree days, thaw depth, water holding capacity, cation exchange capacity, and radiation. The significant shrub scenarios (*Alnus + Salix* and *Alnus + Betula + Salix*) weighed shrub biomass much more heavily, with each applicable shrub genera being in the top five most important variables for these two scenarios. Radiation and silt content were negatively associated with *P. mariana* biomass in the *Alnus + Salix* scenario, while only latitude was positively associated with the *Alnus + Beltua + Salix* scenario (Supplemental Figure 5.2i-k) The importance of shrub biomass on *P. mariana* biomass is suggestive of a more direct competition with *P. mariana* than with *P. glauca*, and might be based more on shading rather than other resource co-limitation.

Growing degree days had a generally positive effect on biomass, but frequently reached a threshold, above which it began to have a negative effect. This pattern is an accurate representation of the divergent growth witnessed across latitudes. In southern boreal regions, increased summer temperatures have been shown as leading to reduced growth rates, while higher latitudes have been seeing increases (Rotbarth et al., 2023). However, growing degree days, being annually resolved, may still be too coarse of a representation of temperature in the model. Monthly temperature is used to determine thaw depth, soil moisture (via potential evapotranspiration), as well as growing degree day. The seasonal changes to temperature and precipitation were shown in Chapter 1 to be important for growth of in *P. mariana* and *P. glauca*, and compiling temperature increases into an annual metric obscures some of this nuance. Thus, while examining how the *Picea* species responded to warming in the model and weighing different inputs, I was unable to test the direct effects of monthly temperature increases. Similarly, I was unable to test how annual effects of precipitation or soil moisture (Girardin et al., 2016) interact with temperature to influence growth.

5.4.3 Influence of warming

Warming reduced *P. mariana* biomass by $\sim 15\%$ in the no shrub scenario, but by 22% in the *Alnus* + *Betula* + *Salix* scenario. Surprisingly, *P. glauca* had divergent responses to shrub intensity, with low shrub intensity leading to decreased biomass while greater shrub intensity led to greater biomass in the warming climate.

Shrub scenario (shrub presence and abundance) was a significant variable for biomass accumulation of both *Picea* species in the two climate regimes. *Alnus, Betula*, and *Salix* biomass were each important for both *P. mariana* and *P. glauca* biomass accumulation in both the historical and warming time periods. Across both species and climate scenario, each shrub genera had a negative effect on *Picea* biomass (Supplemental Figure 5.3a-d); however, the dynamic relationships seen in the shrub scenario analysis may be muted when considered in aggregate. In the historical climate, *P. mariana* had a negative association with June precipitation, but in the warming climate, *P. mariana* instead had radiation as a top five most important variable. *P. glauca* added radiation as an important variable in the warming period, whereas silt content was important in the historical period. Surprisingly, *P. glauca* only had solar radiation as important in the warming climate, despite it being unanimously most significant in the climate scenarios. While for *P. mariana*, growing degree days was not significant in the climate scenarios, despite being significant for all the shrub scenarios.

5.4.4 Modelling shrubs

The diverging response of *P. glauca* to warming and shrub intensity suggests that there might be a facilitation of this tree species by having tall shrub genera present in the model. The low shrub intensity saw greater decreases in shrub stem count in the warming scenario compared to the high shrub intensity. Thus, fewer stems in the low shrub scenario caused a decrease in *P. glauca* biomass compared to the increase in *P. glauca* biomass in the warming scenario with greater shrub competition. This pattern may be suggestive of a shrub facilitation in which more shrub stems may be able to increase tree cover by decreasing stress from solar radiation (Limpens et al., 2020). Determining the effect of shrub presence on soil temperature and moisture through shading could confirm this mechanism, as well as show that the model has a

good representation of natural processes. However, while the low shrub sites were randomly assigned, they did have greater productivity than the high shrub sites, and while the relative percent biomass loss was assessed, overall, this still may be skewing the data.



Figure 5.6: Comparison between influence of total shrub stem count (a) and total shrub biomass (b) on the biomass output of *P. glauca* (left) and *P. mariana* (right). The lines are drawn using the "loess" method, with warming trends shown in red, and the historical pattern shown in blue. The distinct separation of *P. mariana* site productivity may have outsized influence on these patterns.

It is difficult to parameterize shrub characteristics from satellite data at present. *P. mariana* structure and coverage are already challenging to detect through remote sensing, and many tall shrubs can be confused with small trees on the landscape (Timoney and Mamet 2020). Furthermore, currently existing remote sensor coverage does not adequately parse species or

genus information to improve parameterization. As of now, our existing technology relies on field data to ground-truth parameterization, which is challenging to collect and verify.

One limitation of the SIBBORK-TTE model is that shrubs were simulated similar to the growth form and reproduction pattern of small trees, reducing the ability to grow shrubs in clusters and simulate clonal growth that contributes to their competitive success. Potentially, creating a nearest neighbor positive feedback for shrubs and negative feedback for trees could encourage clustered growth for shrubs and dispersed growth for trees. However, we know that trees in the Arctic, and especially in the tundra-taiga ecotone tend to cluster in microrefugia (Holtmeier and Broll 2017, Wurth et al., 2018), and this approach may limit that solution.

Future developments to the model include adding a moss PFT, which will improve the thermal conductivity between air and soil temperatures, and better mimic Arctic-Boreal ecosystems. Additionally, a litter decomposition and nitrogen submodule is in development which will help answer questions on shrub-soil feedbacks. Finally, a fire disturbance submodule is in development which will improve the ability of the model to predict the effect of shifting fire regimes on the landscape. All these developments will enhance what we know about shrub interactions, and the method outlined in this study can be adapted to new questions to determine potential underlying drivers of shrub effects.

5.5 Conclusion

The SIBBORK-TTE model can successfully simulate competition between tall shrub genera and *Picea* tree species, and it affects how *Picea* is growing within the model by shifting variable importance. Additionally, each *Picea* species is responding to the shrubs differently, with *P. glauca* appearing to be competing for indirect model resources, while *P. mariana* seems to be competing directly with shrubs through their biomass and occupied space. This analysis highlights the importance of having vegetation resolution at the genus and species level to better account for nuances in how species interact on the landscape.

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5.8 Supplemental Tables and Figures

Source	Resolution (implemented)
NASA cloud cover layer (LARC)	10 km
NASA DEM	10 m
SoilGrids	250 m
NASA MERRA or statistical	Monthly, 0.5° lat x 0.625° lon
RCP 8.5 predictions	Monthly averages and standard deviations
optional	
User defined	10 m ² plot
User defined	Scale 1 (high) - 5 (poor)
User defined	Annual (includes model spin up)
User defined	annual
	SourceNASA cloud cover layer (LARC)NASA DEMSoilGridsNASA MERRA or statisticalRCP 8.5 predictionsoptionalUser definedUser definedUser definedUser definedUser definedUser defined

Table 5.1: Site specific inputs to the SIBBORK-TTE model.

Variable	Equation
Height	$-b*DBH^2 + a*DBH + 1.37$
Leaf Area	(Foliar biomass * specific leaf area) / 10 Foliar biomass = $b * DBH^a$
Biovolume	$b * \mathrm{DBH}^a$
Biomass	<i>b</i> * DBH ^{<i>a</i>} From Ter-Mikaelian, Chojnacky et al 2014, Ker and van Raalte 1980

Table 5.2a: Species specific allometric inputs for the SIBBORK-TTE model vegetation parameterization.

Table 5.2b: Species specific silvicultural inputs for vegetation paramterization.

	Range	Purpose
Seeding	0-1	Based on occurrence data
Stress threshold	0-1	Percent of annual growth increment that must be met before stress flagged
Maximum DBH	Species specific	Put a size limitation on plants (helpful for small statured plants)
Age maximum	Species specific	Maximum age of a tree before dies
Maximum height	Species specific	Growth maximum (in cm)
Maximum growth increment	Species specific	Amount of annual growth per year to DBH
Permafrost tolerance	0-1	Scalar to determine if permafrost depth will limit growth
Degree Day Factor	Degree Day accumulation that permit growth	Minimum and maximum range
Light factor	1-5 species dependent (discrete)	Shade tolerance measure (1=shade tolerant, $5 =$ shade intolerant)
Nutrient Factor	1-3 species dependent (discrete)	Relative nutrient stress tolerance (1=intolerant of nutrient stress; 3 = tolerant of nutrient stress)

	Range	Purpose
Drought Tolerance Factor	1-5 species dependent (discrete)	Relative drought otlerance (1 = intolerant of drought; 5 = tolerant of drought)
Crown Base Max Percent	Conifer = 0.533, Deciduous = 0.467	Tree geometry based on family

	MDJC1		FARO		TVC	
	historical	warming	historical	warming	historical	warming
Latitude	68.5° N		62.3° N		68.7° N	
Longitude	135.1° W		133.3° W		133.5° W	
Radiation	0.8 kcal/cm ²	0.7 kcal/cm ²				
Growing degree days	525.9	526.9	414.8	415.8	433.8	434.7
Thaw depth	1.3 m	1.3 m	1.3 m	1.3 m	1 m	1 m
Water holding capacity	39.3%		21.2%		32.5%	
Sand content	38.3%		56.2%		25.5%	
Silt content	37.0%		33.3%		43.5%	
Bulk Density	917.7 kg/m ³		1065.9 kg/m ³		1019.5 kg/m ³	
Cation Exchange Capacity	74.3 cmolc/kg		23.7 cmolc/kg		34.7 cmolc/kg	

Supplemental Table 5.4: Site characteristics of three selected sites for the close look comparison.







c. Climate scenario

Supplemental Figure 5.1: Variable importance for all tested variables for shrub scenarios that were significantly different from the no shrub scenario for *P. glauca* (a), and *P. mariana* (b). Variable importance for the climate scenarios (c) is shown for both *Picea* species.

historical

warming

Climate Scenario









Supplemental Figure 5.2: Partial dependence plots for top five most important variables for each shrub scenario for *Picea glauca* (a-h) and *Picea mariana* (i-k).



Supplemental Figure 5.3: Partial dependence plots of the random forest regression for the historical and warming climate change scenario. The "run" denotes the shrub scenario where N is no shrubs, A: *Alnus*, B: *Betula*, S: *Salix*, AB: *Alnus* + *Betula*, AS: *Alnus* + *Salix*, BS: *Betula* + *Salix*, ABS: *Alnus* + *Betula* + *Salix*.

Conclusion

This dissertation assessed the shifting environmental drivers of vegetation in the Arctic-Boreal Zone by first conducting a spatio-temporal analysis of field data sets and then assessing the drivers of growth in the SIBBORK-TTE model.

Overall, the first chapter answered the question of what is driving annual tree growth in the recent past vs. the pre-warming period. This chapter highlighted the decreasing importance of summer temperature for annual growth of black and white spruce in Alaska and western Canada using NOAA's International Tree-Ring Database. I analyzed multiple climate variables across multiple seasons, and combined these annual data with static site characteristics to determine how these variables are interacting to affect tree growth. I found that there has been a general shift towards May and previous fall temperatures being negatively correlated with annual growth in black and white spruce, as well as a positive correlation with previous fall VPD. The climate variables in May interacted the most with soil variables, supporting previous findings that soil moisture availability in the spring can enhance or limit summer growth.

The second chapter analyzed the National Forest Inventory (NFI) species cover dataset to determine how species and PFTs are shifting in the Northwest Territories, Canada. The NFI dataset revealed a significant decrease in mosses in the boreal forest over ten years, as well as notable decreases in lichens in both ecosystems and evergreen trees in the boreal forest. These changes were driven mostly by few species, highlighting the need for high vegetation resolution when monitoring vegetation shifts across the landscape. I also identified a species at risk, *Orthillia secunda*, that was lost from 15 plots in just ten years. Finally, I addressed the environmental drivers for each PFT and documented important relationships at the family, genus, and species level that were often contradictory to other members of the PFT. At the PFT level,

no environmental driver had a universal positive or negative effect, reinforcing that as the climate is shifting, each PFT is responding differently, and within each PFT each taxa is further reacting to landscape change to stay within its niche.

My third chapter investigated the state of dynamic vegetation models that are applied in the Arctic-Boreal Zone by first outlining which ecosystem properties were simulated by each model, then reviewing how they are applied throughout North America, and finally surveying expert opinion on what is missing from the models. I found four main categories of model that were mostly related to their original intention, but included how they were applied throughout the region. Many models asked similar questions about shifts in dynamic vegetation, but few investigated how the vegetation could feedback on environmental drivers. The survey identified active layer and permafrost dynamics as priority model developments for dynamic vegetation models in the future. The study overall acts not only as a guide for novice modelers, who may use it to get a comprehensive assessment of the types of dynamic vegetation models being used in the Arctic, but also as a call to action for experienced modelers to increase collaboration and update models to better simulate this rapidly changing landscape.

The final chapter of my dissertation focused on the SIBBORK-TTE model and conducting a sensitivity analysis of the additions of shrub genera to the model, to determine how the shrubs might be competing with black and white spruce. I found that shrubs were able to compete for space with and reduce biomass accumulation of black and white spruce. The drivers of spruce biomass accumulation were affected by both shrub scenario and climate warming; however, radiation and growing degree days were consistent for white and black spruce, respectively, as primary drivers across the model simulations. The addition of shrub genera

enables the SIBBORK-TTE model to better simulate the tundra-taiga ecotone and the effects of shrubification in the ecosystem.

Across the varied analyses of my dissertation, the main take away is that with the thermal limitation of summer growth being alleviated, the Arctic-Boreal Zone is experiencing divergent responses from vegetation based on underlying site characteristics as well as species- and genus-level acclimations. The alleviation of summer temperature has largely increased growth across the Arctic-Boreal region, but the variables that limit growth (nutrient availability, winter damage, herbivory, etc.) have not yet been alleviated, and the balance between growth and death is shifting. In the SIBBORK-TTE chapter, I found a surprising increase in white spruce growth in the warming and high shrub intensity scenario. The result is likely a remanent of the assumption that temperature increase will subsequently influence growth, but has not yet been adjusted to incorporate other limitations, like that of the Divergence Problem (see Chapter 1). The unfettered tree growth and distribution has not been persistent in the recent past and is being limited by many different factors. However, choosing which factors to prioritize to incorporate is limited by model structure and empirical data.

The expansiveness of the Arctic-Boreal Zone and its importance for global carbon storage has necessitated large scale assessments and predictions of what is currently changing and what might change in the future. However, the next step in research should be to delve deeper into the nuances of species level responses, as we may be able to identify interactive responses to that are thus far overlooked.

One limitation of this dissertation is the lack of annually resolved soils data, other than permafrost thaw. The necessary assumption I made throughout was that soil characteristics are relatively static, which is only reasonable in a static climate. Multiple studies have pointed to soil moisture being critical to explaining changing tree growth patterns, and it is also vital for predicting species distributions. However, there are limited soil moisture data sets, and still fewer for soil characteristics such as nitrogen availability and organic matter. Some models are able to simulate these data annually, but at large spatial resolutions, and because soils have high heterogeneity, the spatial resolution at which they could be made available reduces their utility.

The analysis of environmental drivers I conducted highlights how vegetation is responding in divergent ways and responding to different climate and site variables; however, these drivers are only informative for previous and current conditions. My chapter on SIBBORK-TTE highlighted that under future conditions, these drivers are likely to shift in potentially predictable, but fundamentally unknowable ways. Continued analyses of these changes in environmental drivers, and at the species level, when possible, will improve our understanding of the nuances at play in the dynamic vegetation responses we are witnessing and predicting.
Appendix 1

List of species codes from Canada's National Forest Inventory, and their assigned plant names using United Stated Department of Agriculture <u>https://plants.sc.egov.usda.gov/</u> to determine species name, confirm range, and assign plant functional type

NFI Species Code	USDA plants designation	USDA plant functional type
THUIABI	Abietinella abietina	moss
ACHIMIL	Achillea millefolium	forb
ACONDEL	Aconitum delphiniifolium	forb
ACTARUB	Actaea rubra	forb
ADOXMOS	Adoxa moschatellina	forb
AGROPYR	Agrostis	graminoid
AGROSCA	Agrostis scabra	graminoid
ALISPLA	Alisma triviale	forb
ALLISCH	Allium schoenoprasum	forb
ALNUINC	Alnus incana	tall shrub
ALNUTEN	Alnus incana	tall shrub
ALNURUG	Alnus incana	tall shrub
ALNUSPP	Alnus sp.	shrub
ALNUVIC	Alnus spp	tall shrub
ALNUCRI	Alnus viridis	tall shrub
ALNUSIN	Alnus viridis	tall shrub
ALNUVIR	Alnus viridis	tall shrub
AMBLSER	Amblystegium serpens	moss
AMELALN	Amelanchier alnifolia	tall shrub
ORCHROT	Amerorchis rotundifolia	forb
ANDRPOL	Andromeda polifolia	dwarf evergreen shrub
ANEMMUL	Anemone multiceps	forb
ANEMPAR	Anemone parviflora	forb
ANEMSPP	Anenome spp	forb
AQUIBRE	Aquilegia brevistyla	forb
AQUICAN	Aquilegia canadensis	forb
AQUIFOR	Aquilegia formosa	forb
ARALNUD	Aralia nudicalis	dwarf deciduous shrub
ARCTLAT	Arctagrostis latifolia	graminoid
ARCTRUB	Arctostaphylos rubra	dwarf evergreen shrub
ARTCRUB	Arctostaphylos rubra	dwarf evergreen shrub
VACCUVA	Arctostaphylos uva-ursi	dwarf evergreen shrub
ARCTUVA	Arctostaphylos uvaursi	dwarf evergreen shrub
ARTCUVA	Arctostaphylos uvaursi	dwarf evergreen shrub

NFI Species Code	USDA plants designation	USDA plant functional type
ARCTALP	Arctous alpina	dwarf deciduous shrub
ARNICHA	Arnica chamissonis	forb
ASTERSP.	Aster sp.	forb
ASTRAME	Astragalus americanus	forb
ASTRSPP	Astragalus sp.	forb
ASTREUC	Astragualus eucosmus	forb
AULAPAL	Aulacomnium palustre	moss
BARBFLO	Barbilophozia floerkei	liverwort
BARBLYC	Barbilophozia lycopodioides	liverwort
BARBILO	Barbilophozia spp	liverwort
BETUGLA	Betula glandulosa	tall shrub
BETUNAN	Betula nana	deciduous shrub
BETUN	Betula nana?	deciduous shrub
BETUNEO	Betula neoalaskana	deciduous tree
BETUPAP	Betula papyrifera	deciduous tree
BETUPAL	Betula platyphylla*	deciduous tree
BETUPLA	Betula platyphylla*	deciduous tree
BETUPUM	Betula pumila	tall shrub
BETUPUN	Betula pumila	tall shrub
BETUSPP	Betula spp	
BRACHYL	Brachythecium hylotapetum	moss
BRACRIV	Brachythecium rivulare	moss
BRACSAL	Brachythecium salebrosum	moss
BRACHYT	Brachythecium spp	moss
BRACSPP	Brachythecium spp	moss
BRACVEL	Brachythecium velutinum	moss
BRACHYTHECIUMSP.	Bracythecium sp.	moss
BROMCIL	Bromus ciliatus	graminoid
BRYOSPP	bryophyte spp	moss
BRYUPSE	Bryum pseudotriquetrum	moss
CALACAN	Calamagrostis canadensis	graminoid
CALAPUR	Calamagrostis purpurascens	graminoid
CALARUB	Calamagrostis rubescens	graminoid
CALASPP	Calamagrostis sp.	graminoid
CALASTR	Calamagrostis sp.	graminoid
CALAMAG	Calamagrostis spp	graminoid
CALANEG	Calamagrostis stricta	graminoid
CALAINE	Calamagrostis stricta	graminoid
CALLGIG	Calliergon giganteum	moss

NFI Species Code	USDA plants designation	USDA plant functional type
CALLRIC	Calliergon richardsonii	moss
CALLSPP	Calliergon spp	moss
CALLSTR	Calliergon stramineum	moss
CALLTRI	Calliergon trifarium	moss
CALOCER	Caloplaca cerina	lichen
CAMPROT	Campanula rotundifolia	forb
CAMPSTE	Campylium stellatum	moss
ASTEMOD	Canadanthus modestus	forb
CAREVAR	Carex albicans	graminoid
CAREALB	Carex albonigra	graminoid
CAREAQU	Carex aquatilus	graminoid
CAREATH	Carex atherodes	graminoid
CARECAP	Carex capillaris	graminoid
CARECON	Carex concinna	graminoid
CAREDIS	Carex disperma	graminoid
CAREGYN	Carex gynocrates	graminoid
CARELAS	Carex lasiocarpa	graminoid
CARELEP	Carex leptalea	graminoid
CARELIM	Carex limosa	graminoid
CAREMED	Carex media	graminoid
CAREROS	Carex rossii	graminoid
CARESCI	Carex scirpoide	graminoid
CAREXSP.	Carex sp.	graminoid
CARESPP	Carex spp	graminoid
CARESUP	Carex supina	graminoid
CARETEN	Carex tenuiflora	graminoid
CAREUTR	Carex utriculata	graminoid
CAREVAG	Carex vaginata	graminoid
CASTRAU	Castilleja raupii	forb
CERAPUR	Ceratadon purpurea	moss
CERASPP	Ceratadon sp	moss
CETRARI	Cetraria	lichen
CETRERI	Cetraria ericetorum	lichen
CETRISL	Cetraria islandica	lichen
CETRARIASP.	Cetraria sp.	lichen
CETRSPP	Cetraria spp	lichen
CHALCAL	Chamaedaphne calyculata	deciduous dwarf shrub
CHAMCAL	Chamaedaphne calyculata	deciduous dwarf shrub
CHAMCHA	Chamaedaphne calyculata	deciduous dwarf shrub

NFI Species Code	USDA plants designation	USDA plant functional type
CHHACAL	Chamaedaphne calyculata	deciduous dwarf shrub
EPILANG	Chamerion angustifolium	forb
EPLIANG	Chamerion angustifolium	forb
CINCSTY	Cinclidium stygium	moss
CLADARB	Cladina arbuscula	lichen
CLADRAG	Cladina rangiferina	lichen
CLADINA	Cladina spp	lichen
CLADONI	Cladonia	lichen
CLADSPP	Cladonia	lichen
CALDAMA	Cladonia amaurocraea	lichen
CLADAMA	Cladonia amaurocraea	lichen
CLADBOR	Cladonia borealis	lichen
CLADONIABOREALIS	Cladonia borealis	lichen
CLADCAR	Cladonia cariosa	lichen
CLADCAN	Cladonia carneola	lichen
CLADCEN	Cladonia cenotea	lichen
CLADCER	Cladonia cervicornis	lichen
CLADCHL	Cladonia chlorophaea	lichen
CLADCOR	Cladonia cornuta	lichen
CLADCRI	Cladonia cristatella	lichen
CLADECM	Cladonia ecmocyna	lichen
CLADECO	Cladonia ecmocyna	lichen
CLADFIM	Cladonia fimbriata	lichen
CLADGRA	Cladonia gracilis	lichen
CLADMIT	Cladonia mitis	lichen
CLADMUL	Cladonia multiformis	lichen
CLADPYX	Cladonia pyxidata	lichen
CLADRAN	Cladonia rangiferina	lichen
CLADSCA	Cladonia scabriuscula	lichen
CLADONIASP.	Cladonia sp.	lichen
CLADSTE	Cladonia stellaris	lichen
CLADSUL	Cladonia sulphurina	lichen
POTEPAL	Comarum palustre	forb
COPTASP	Coptis aspleniifolia	forb
COPTTRI	Coptis trifolia	forb
CORNCAN	Cornus cadensis	dwarf deciduous shrub
CORNSTO	Cornus stolonifera	deciduous shrub
CORYAUR	Corydaliss aurea	forb
CORYSEM	Corydaliss sempervirens	forb

NFI Species Code	USDA plants designation	USDA plant functional type
PENTFLO	Dasiphora fruticosa	deciduous shrub
POTEFRU	Dasiphora fruticosa	forb
POTIFRU	Dasiphora fruticosa	forb
DASIFRU	Dasiphora fruticosa	deciduous shrub
DELPGLA	Delphinium glaucum	forb
DESCCAE	Deschampsia cespitosa	graminoid
DESCSOP	Descurainia sophioides	forb
DICRANU	Dicranum	moss
DICRACU	Dicranum acutifolium	moss
DICRFLA	Dicranum flagellare	moss
DICRFUS	Dicranum fuscescens	moss
DICRPLA	Dicranum pallidsetum	moss
DICRPOL	Dicranum polysetum	moss
DICRSCO	Dicranum scoparium	moss
DICRANUMSP.	Dicranum sp.	moss
DICRSPP	Dicranum spp	moss
DICRUND	Dicranum undulatum	moss
DISTCAP	Distichium capillaceum	moss
DISTFLE	Ditrichum flexicaule	moss
DITRFLE	Ditrichum flexicaule	moss
DREPSPP	Dpreanocladus spp	moss
DRACPAR	Dracocephalum parviflorum	forb
DREPANOCLADUSSP.	Drepanocladus sp.	moss
DROSANG	Drosera anglica	moss
DROSROT	Drosera rotundifolia	moss
DRYASPP	Drya sp.	shrub
DRYAING	Dryas integrifolia	moss
DRYAINI	Dryas integrifolia	moss
DRYAINT	Dryas integrifolia	dwarf evergreen shrub
ELYMGLA	Elymus glaucus	graminoid
ELYMSPP	Elymus spp	graminoid
AGROTRA	Elymus trachycaulus	graminoid
EMPENIC	Empetrum nigrum	dwarf evergreen shrub
EMPENIG	Empetrum nigrum	dwarf evergreen shrub
EPILSIL	Epilobium ciliatum	forb
EPILWAT	Epilobium ciliatum	forb
EPILCIL	Epilobium ciliatum	forb
EPILPAL	Epilobium palustre	forb
EQUIARV	Equisetum arvense	horsetail

NFI Species Code	USDA plants designation	USDA plant functional type
EQUIHYE	Equisetum hyemale	horsetail
EQUIPRE	Equisetum hyemale	horsetail
EQUIFLU	Equisetum laevigatum	horsetail
EQUIPAL	Equisetum palustre	horsetail
EQUIPRA	Equisetum pratense	horsetail
EQUISCI	Equisetum scirpoide	horsetail
EQUISPP	Equisetum spp	horsetail
EQUISYL	Equisetum sylvaticum	horsetail
EQUIVAR	Equisetum variegatum	horsetail
ERIGACR	Erigeron acris	forb
ERIOANG	Eriogonum heracleoides	forb
ERIOBRA	Eriophorum brachyantherum	graminoid
ERIOCHA	Eriophorum chamissonis	graminoid
ERIOVAG	Eriophorum vaginatum	graminoid
ASTECON	Eurybia conspicua	forb
FESTALT	Festuca altaica	graminoid
FESCSPP	Festuca spp	graminoid
FESTSPP	Festuca spp	graminoid
FESTUCA	Festuca spp	graminoid
PETASPP	Fetasites spp	forb
CETRCUC	Flavocetraria cucullata	lichen
FLAVCUC	Flavocetraria cucullata	lichen
CETRNIV	Flavocetraria nivalis	lichen
FLAVNIV	Flavocetraria nivalis	lichen
FRAGVES	Fragaria vesca	forb
FRAGVIR	Fragaria virginia	forb
GALIBOR	Galium boreale	forb
GALILAB	Galium labradoricum	forb
GALITRI	Galium trifidum	forb
GALIUMTRIFLORUM	Galium triflorum	forb
GAULHIS	Gaultheria hispidula	dwarf evergreen shrub
GENTAMA	Gentianella amarella	forb
GENTPRO	Gentianella propinqua	forb
GEOCLIV	Geocaulon lividum	forb
GEOVLIV	Geocaulon lividum	forb
GERABIC	Geranium bicknellii	forb
GOODREP	Goodyera repens	forb
GRAMSPP	grass spp	graminoid
GRASSPP	grass spp	graminoid

NFI Species Code	USDA plants designation	USDA plant functional type
HEDYALP	Hedysarum alpinum	forb
HEDYBOR	Hedysarum boreale	forb
HEDYMAC	Hedysarum boreale	forb
HEDYSAR	Hedysarum spp	forb
HELOBLA	Helodium blandowii	moss
HERBSPP	herbaceous spp	forb
HIERODO	Hierochloe hirta	graminoid
HOMAAEN	Homalothecium aeneum	moss
HYLDSPL	Hylocomium splendens	moss
HYLOSPI	Hylocomium splendens	moss
HYLOSPL	Hylocomium splendens	moss
HYPNLIN	Hypnum lindbergii	moss
HYPNLTN	Hypnum lindbergii	moss
HYPNREV	Hypnum revolutum	moss
НҮРОРНҮ	Hypogymnia physodes	lichen
ICMAERI	Icmadophila ericetorum	lichen
JAMEAUT	Jamesoniella autumnalis	moss
JUNCALP	Juncus alpinoarticulatus	graminoid
JUNCSPP	Juncus sp.	graminoid
JUNICOM	Juniperus communis	dwarf evergreen shrub
JUNIHOR	Juniperus horizontalis	dwarf evergreen shrub
JUNISCO	Juniperus scopulorum	evergreen tree
KALMMIC	Kalmia microphylla	evergreen shrub
KALMPOL	Kalmia polifolia	evergreen shrub
LARILAR	Larix laricina	deciduous tree
LARIOCC	Larix occidentalis	deciduous tree
LATHOCH	Lathyrus ochroleucus	forb
LATHVEN	Lathyrus venosus	forb
LATHVER	Lathyrus vernus	forb
LEDUGLA	Ledum glandulosum	dwarf evergreen shrub
LEDOGRO	Ledum groenlandicum	evergreen shrub
LEDUGRO	Ledum groenlandicum	evergreen shrub
RHODGRO	Ledum groenlandicum	evergreen shrub
LEDUDEC	Ledum palustre	dwarf evergreen shrub
LEPISPP	Lepidium spp	forb
LEPIREP	Lepidozia reptans	liverwort
ELYMINN	Leymus innovatus	graminoid
LICHSPP	lichen spp	lichen
LILYSPP	Lily spp	forb

NFI Species Code	USDA plants designation	USDA plant functional type
LINNBOR	Linea borealis	forb
LISTCOR	Listera cordata	forb
LIVESPP	Liverwort spp	liverwort
LONIDIO	Lonicera dioica	vine
LONIINV	Lonicera involucrata	deciduous shrub
LONIOBL	Lonicera oblongifolia	evergreen shrub
LONIVIL	Lonicera villosa	deciduous shrub
LOPHOZI	Lophozia spp	liverwort
LOPHVEN	Lophozia ventricosa	liverwort
LUPIARC	Lupinus arcticus	forb
LUZUPAR	Luzula parviflora	graminoid
LUZUSPP	Luzula spp	graminoid
LYCOPOD	Lycopod sp.	lycopod
LYCOCOM	Lycopodium complanatum	lycopod
ASTECAN	Machaeranthera canescens	forb
MAIACAN	Maianthemum canadense	forb
SMILSTE	Maianthemum stellatum	forb
SMILTRI	Maianthemum trifolium	forb
MARCPOL	Marchantia polymorpha	liverwort
MEESULI	Meesia uliginosa	moss
MEESTRI	Meesia uliginosa	moss
MELALIN	Melampyrum lineare	forb
MENYTRI	Menyanthes trifoliata	forb
MERTPAN	Mertensia paniculata	forb
MITENUD	Mitella nuda	forb
MNIUSPI	Mnium spinosum	moss
MNIUSPP	Mnium sspp	moss
MONEUNI	Moneses uniflora	forb
MOSSSPP	moss spp	moss
MYLIANO	Mylia anomala	liverwort
MYRIGAL	Myrica gale	deciduous shrub
MYRIALT	Myriophyllum alterniflorum	forb
MYURJUL	Myurella julacea	moss
NEPHARC	Nephroma arcticum	lichen
ORTHSEC	Orthilia secunda	dwarf evergreen shrub
PYROSEC	Orthilia secunda	forb
OXYTDEF	Oxytropis deflexa	forb
PARMSUL	Parmelia sulcata	lichen
PARMAMB	Parmeliopsis ambigua	lichen

NFI Species Code	USDA plants designation	USDA plant functional type
PARNKOT	Parnassia kotzebuei	forb
PARNPAL	Parssia palustris	forb
PEDIGRO	Pedicularis groenlandica	forb
PEDILAB	Pedicularis labradorica	forb
PEDILAP	Pedicularis lapponica	forb
PEDIPAR	Pedicularis macrodonta	forb
PEDICUL	Pedicularis spp	forb
PELTEGE	Pelitgera spp	lichen
PELTIGE	Pelitgera spp	lichen
PELTAPH	Peltigera aphthosa	lichen
PELTAPT	Peltigera aphthosa	lichen
PELTCAN	Peltigera canina	lichen
PELTDID	Peltigera didactyla	lichen
PELTLEU	Peltigera leucophlebia	lichen
PELTMAL	Peltigera malacea	lichen
PELTNEO	Peltigera neopolydactyla	lichen
PELTRUF	Peltigera rufescens	lichen
PELTSCA	Peltigera scabrosa	lichen
PELTIGERASP.	Peltigera sp.	lichen
PELTSPP	Peltigera spp	lichen
PFLTEGE	Peltigera spp	forb
PETAFRI	Petasites frigidus	forb
PETAPAL	Petasites frigidus	forb
PETASAG	Petasites frigidus	forb
PHILFON	Philonotis fontana	moss
PICEABI	Picea abies	evergreen tree
PICEGLA	Picea glauca	evergreen tree
PICEMAR	Picea maria	evergreen tree
PICESPP	Picea spp	evergreen tree
PINUBAN	Pinus banksia	evergreen tree
PINUCON	Pinus contorta	evergreen tree
PLAGASP	Plagiochila asplenioides	moss
PLAGCUS	Plagiomnium cuspidatum	moss
PLAGELL	Plagiomnium ellipticum	moss
PLAGSPP	Plagionium spp	moss
НАВЕНҮР	Platanthera aquilonis	forb
HABEDIL	Platanthera dilatata	forb
HABEOBT	Platanthera obtusata	forb
HABEORB	Platanthera orbiculata	forb

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PLATANTHERASP.	Platanthera sp.	forb
HABESPP	Platanthera spp	forb
PLATJUN	Platydictya jungermannioides	moss
PLATSPP	Platydictya spp	moss
PLENSCH	Pleurozium schreberi	moss
PLEUSCH	Pleurozium schreberi	moss
POAAPAL	Poa palustris	graminoid
POAXPAL	Poa palustris	graminoid
POASP.	Poa sp.	graminoid
POASPP	Poa spp	graminoid
POAXSPP	Poa spp	graminoid
POHLNUT	Pohlia nutans	moss
POHLSPP	Pohlia spp	moss
POLEBOR	Polemonium boreale	forb
POLEPUL	Polemonium pulcherrimum	forb
POLYTRI	Polygonum ramosissimum	forb
POLYVIV	Polygonum viviparum	forb
POLYALP	Polytrichastrum alpinum	moss
POLYCOM	Polytrichum commune	moss
POLYJUN	Polytrichum juniperinum	moss
POLYPIL	Polytrichum piliferum	moss
POLYSPP	Polytrichum spp	moss
POLYSTR	Polytrichum strictum	moss
POPUBAL	Populus balsamifera	deciduous tree
POPUTER	Populus tremuloides	deciduous tree
POPUTRE	Populus tremuloides	deciduous tree
PTILCIL	Ptilidium ciliare	liverwort
PTILPUL	Ptilidium pulcherrimum	liverwort
PTILIDIUMSP.	Ptilidium sp.	liverwort
PTILIDI	Ptilidum spp	liverwort
PTILSPP	Ptilium	moss
PTILCRI	Ptilium cristacastrensis	moss
PYROASA	Pyrola asarifolia	forb
PYROASI	Pyrola asarifolia	forb
PYROCHL	Pyrola chlorantha	forb
PYROVIR	Pyrola chlorantha	forb
PYROMIN	Pyrola minor	forb
PYROSPP	Pyrola spp	forb
RANULAP	Ranunculus lapponicus	forb

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RHIZGLA	Rhizomnium glabrescens	moss
RHIZPSE	Rhizomnium pseudopunctatum	moss
RHOOALB	Rhododendron albiflorum	evergreen shrub
RHODLAP	Rhododendron lapponicum	dwarf evergreen shrub
LEDUPAL	Rhododendron tomentosum	dwarf evergreen shrub
RHYTIDIADELPHUSSP.	Rhytidiadelphus sp.	moss
RHYTRUG	Rhytidium rugosum	moss
RIBEAME	Ribes americanum	deciduous shrub
RIBEGLA	Ribes glandulosum	deciduous shrub
RIBEHUD	Ribes hudsonianum	deciduous shrub
RIBELAC	Ribes lacustre	deciduous shrub
RIBEOXY	Ribes oxyacanthoides	deciduous shrub
RIBETRI	Ribes triste	deciduous shrub
ROSAACI	Rosa acicularis	dwarf deciduous shrub
ROSAASI	Rosa acicularis	dwarf deciduous shrub
RUBUACA	Rubus arcticus	dwarf deciduous shrub
RUBUARC	Rubus arcticus	dwarf deciduous shrub
RUBUAUC	Rubus arcticus	dwarf deciduous shrub
RUBACHA	Rubus chamaemorus	dwarf deciduous shrub
RUBUCHA	Rubus chamaemorus	dwarf deciduous shrub
RUBAIDA	Rubus idaeus	dwarf deciduous shrub
RUBUIDA	Rubus idaeus	dwarf deciduous shrub
RUBUPUB	Rubus pubescens	dwarf deciduous shrub
RUMESAL	Rumex salicifolius	forb
RUMESPP	Rumex sp.	forb
SALIMAR	Salicornia maritima	forb
SALIALA	Salix alaxensis	tall shrub
SALIACU	Salix arbusculoides	tall shrub
SALIARB	Salix arbusculoides	tall shrub
SALIARC	Salix arctica	dwarf deciduous shrub
SALIATH	Salix athabascensis	deciduous shrub
SALIALB	Salix barrattiana	deciduous shrub
SALIBEB	Salix bebbiana	tall shrub
SALIBRA	Salix brachycarpa	dwarf deciduous shrub
SALILAN	Salix calcicola	deciduous shrub
SALICAN	Salix candida	deciduous shrub
SALIDIS	Salix discolor	tall shrub
SALIGLA	Salix glauca	tall shrub
SALILAS	Salix lucida	tall shrub

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SALILUC	Salix lucida	tall shrub
SALIMAC	Salix maccallia	tall shrub
SALIMYR	Salix myricoides	tall shrub
SALIPED	Salix pedicellaris	deciduous shrub
SALIPET	Salix petiolaris	tall shrub
SALIPLA	Salix planifolia	tall shrub
SALIPRO	Salix prolixa	tall shrub
SALIPSE	Salix pseudomyrsinites	tall shrub
SALIRET	Salix reticulata	dwarf deciduous shrub
SALISCO	Salix scouleriana	tall shrub
SLAISCO	Salix scouleriana	tall shrub
SALISPP	Salix spp	deciduous shrub
SALISTO	Salix stolonifera	dwarf deciduous shrub
DRAPUNC	Sanionia uncinata	moss
DREPUNC	Sanionia uncita	moss
SAUSANG	Saussurea angustifolia	forb
SCIRPUS	Scirpus spp	graminoid
SCIRSPP	Scirpus spp	graminoid
DREPREV	Scorpidium scorpioides	moss
SCORSCO	Scorpidium scorpioides	moss
SCUTGAL	Scutellaria galericulata	forb
SELASEL	Selaginella selaginoides	clubmoss
SENELUG	Senecio lugens	forb
SENEPAU	Senecio pauciflorus	forb
SENEPUA	Senecio pauciflorus	forb
SHEPCAN	Shepherdia cadensis	deciduous shrub
SHRBSPP	shrub spp	
SIUMSUA	Sium suave	forb
SOLICAN	Solidago canadensis	forb
SOLIMUL	Solidago multiradiata	forb
SOLISPA	Solidago simplex	forb
SOLISPP	Solidago spp	forb
SORBSCO	Sorbus scopulina	tall shrub
species	SpeciesUSDA	form
SPHAANG	Sphagnum angustifolium	moss
SPAGCAP	Sphagnum capillifolium	moss
SPHACAP	Sphagnum capillifolium	moss
SPHAFUS	Sphagnum fuscum	moss
SPHAGIR	Sphagnum girgensohnii	moss

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SPHAMAG	Sphagnum magellanicum	moss
SPHARUB	Sphagnum rubellum	moss
SPHAGNUMSP.	Sphagnum sp	moss
SPHASPP	Sphagnum spp	moss
SPHAWAR	Sphagnum warnstorfii	moss
LYCOANN	Spinulum annotinum	clubmoss
SPIREEA	Spiraea spp	deciduous shrub
SPIRSPP	Spiraea spp	deciduous shrub
SPIRBEA	Spiraea stevenii	deciduous shrub
SPIRROM	Spiranthes romanzoffiana	forb
STELLON	Stellaria longpipes	forb
STELMED	Stellaria media	forb
STELSPP	Stellaria spp	forb
STERPAS	Stereocaulon paschale	lichen
STERTOM	Stereocaulon tomentosum	lichen
SYMPALB	Symphoricarpos albus	dwarf deciduous shrub
ASTESPP	Symphyotrichum	forb
ASTEAME	Symphyotrichum amethystinum	forb
ASTEBOR	Symphyotrichum boreale	forb
ASTECIL	Symphyotrichum ciliolatum	forb
ASTESPA	Symphyotricum spathulatum	forb
SENEATR	Tephroseris atropurpurea	forb
THALOCC	Thalictrum occidentale	forb
THUIREC	Thuidium recognitum	moss
TIMMAUS	Timmia austriaca	moss
TOFIPUS	Tofieldia pusilla	forb
TOMENIT	Tomentypnum nitens	moss
TORTRUR	Tortula ruralis	moss
TOFIGLU	Triantha glutinosa	forb
SCIRHUD	Trichophorum alpinum	graminoid
SCIRCAE	Trichophorum cespitosum	graminoid
TRIGMAR	Triglochin maritima	graminoid
TRIGPAL	Triglochin palustris	graminoid
CALLVER	UNKNOWN	moss
CAREPUR	UNKNOWN	graminoid
CARESPA	UNKNOWN	graminoid
CARRSPP	UNKNOWN	
CASSTET	UNKNOWN	
CETRPUR	UNKNOWN	lichen

NFI Species Code	USDA plants designation	USDA plant functional type
CLADSEN	UNKNOWN	lichen
CLADSTO	UNKNOWN	lichen
CLANCOR	UNKNOWN	lichen
DICRSPE	UNKNOWN	moss
ERIOPHO	UNKNOWN	forb
LARIARB	UNKNOWN	
LUDOGRO	UNKNOWN	
MYCIANO	UNKNOWN	
MYRAGAL	UNKNOWN	
PAINFIM	UNKNOWN	
PELIREP	UNKNOWN	
PELTATH	UNKNOWN	lichen
PELTECM	UNKNOWN	lichen
PELTING	UNKNOWN	lichen
PLATANT	UNKNOWN	moss
RHIZSPP	UNKNOWN	
SALESAL	UNKNOWN	
SPAGGAP	UNKNOWN	
SPHACAI	UNKNOWN	moss
UNKNSPP	UNKNOWN	
VACCULT	UNKNOWN	dwarf evergreen shrub
BRYOPHYTASP.	UNKNOWN	moss
CHAMCAN	UNKNOWN	
DREDSPP	UNKNOWN	
EPANANG	UNKNOWN	
GRAMINOIDSP.	UNKNOWN	graminoid
POLYVUN	UNKNOWN	forb
RUSHSPP	UNKNOWN	graminoid
BRYUSPP	UNKNOWN	
ACTONUA	UNKNOWN	
ALACPAL	UNKNOWN	
ALUAPAL	UNKNOWN	
CARECOC	UNKNOWN	graminoid
CAREMIR	UNKNOWN	graminoid
CARESPB	UNKNOWN	graminoid
CARESPC	UNKNOWN	graminoid
UTRIINT	Utricularia intermedia	forb
VACCANG	Vaccinium angustifolium	dwarf deciduous shrub
VACCCAE	Vaccinium cespitosum	dwarf deciduous shrub

NFI Species Code	USDA plants designation	USDA plant functional type
VACCMYR	Vaccinium myrtilloides	dwarf deciduous shrub
VACCINIUMMYRTILLOIDES	Vaccinium myrtilloides	dwarf shrub
OXCYMIC	Vaccinium oxycoccos	dwarf evergreen shrub
OXYCMIC	Vaccinium oxycoccos	dwarf evergreen shrub
OXYCOXY	Vaccinium oxycoccos	dwarf evergreen shrub
VACCOXY	Vaccinium oxycoccos	dwarf deciduous shrub
VACCUGL	Vaccinium uliginosum	dwarf deciduous shrub
VACCULI	Vaccinium uliginosum	dwarf deciduous shrub
VACCVIS	Vaccinium vitis-idaea	dwarf evergreen shrub
VACCVIT	Vaccinium vitis-idaea	dwarf evergreen shrub
VEBUEDU	Viburnum edule	deciduous shrub
VIBAEDU	Viburnum edule	deciduous shrub
VIBEEDU	Viburnum edule	deciduous shrub
VIBREDU	Viburnum edule	deciduous shrub
VIBUEDU	Viburnum edule	deciduous shrub
VICIAME	Vicia america	forb
VICIAMI	Vicia america	forb
VIOLADU	Viola adunca	forb
VIOLNEP	Viola nephrophylla	forb
VIOLPAL	Viola palustris	forb
VIOLREN	Viola renifolia	forb
VIOLASP.	Viola sp.	forb
VIOLSPP	Viola spp	forb
VULPPIN	Vulpicida pistri	lichen
DREPFLU	Warnstorfia fluitans	moss
XANTFAL	Xanthoria fallax	lichen
ZIGAELE	Zigadenus elegans	forb
ZIGEELE	Zigadenus elegans	forb
ZYGAELE	Zigadenus elegans	forb
ZYGEELE	Zigadenus elegans	forb

* Denotes species name that is uncertain