A niche-constrained productivity model for white spruce in Alberta: predicting suitable forestry regions under climate change

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Abstract

White spruce is an economically and ecologically important tree species in Alberta, but projected climate change implies substantial threats to the species, with extensive northward shifts of suitable habitat according to climatic niche models. Niche models are, however, unsuited for strong inferences on health and survival of established trees, unless the fundamental and realized niche space coincides. Further, growth projections relevant for forestry operations are not available from distribution models. To address this knowledge gap, I develop a nice-constrained growth model that observes the species fundamental niche limitations, where the boreal forest transitions to grasslands. The model predicts site-indexed tree height (from dated plot and test plantations), based on two relevant climate variables: mean annual temperature and Hogg's climate moisture index, which was specifically calibrated to delineate the grassland-boreal forest transition. The model predictions capture white spruce forestry regions of Alberta very well, when based on 1961-1990 climate training data. For this period, high productivity is predicted for all areas of Alberta, where commercial white spruce forestry operations actually take place. Under recent climate change trends (represented by the subsequent 1991-2020 climate normal period), southern forest management areas generally see a 10-20% decline in productivity, while northern management areas may show increased productivity. By the 2050s, substantial productivity declines are projected for all current forest management areas, and areas suitable for white spruce forestry can only be found outside current management areas, northward and at higher elevation. In conclusion, the modeling results imply a substantial climate change threat to health and productivity of white spruce forests in Alberta.

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1. Introduction

White spruce (*Picea glauca*) is a coniferous tree native to northern temperate and boreal forests in North America. It is one of the most commonly planted species in Canada, with over 130 million seedlings planted annually (Carles et al., 2015). The species has adapted to extremely cold temperatures in Northern Canada and Alaska, yet spreads as far south as South Dekota USA; suggesting a range of adaptations to differing climate conditions, and thus described as a "plastic" species (Rweyongeza et al., 2007; Nienstaedt & Zasada, 1990). It is a prominent component of the Alberta boreal forest, most commonly found in either pure or mixed stands, across the province (Nienstaedt & Zasada, 1990), and holds great importance to both the local ecology and forestry industry (Government of Canada, 2019; Nienstaedt & Zasada, 1990).

The forestry industry is the second largest industry in Alberta and relies heavily on white spruce harvest (Alberta government, 2020). Canada has the world's largest forest products trade balance, with the forest sector contributing about \$23.7 billion to Canada's nominal gross domestic product (GDP)(Government of Canada, 2019). In Alberta, the forestry industry is a staple of the economy for rural and Indigenous communities. It directly employs over 17,500 Albertans and an additional 23,900 people in supporting occupations (Alberta government, 2020). The forestry industry revenues exceed \$7.6 billion from harvesting operations a year and an estimated \$6.5 billion has been invested in forest product manufacturing operations (Alberta government, 2020). White spruce is commonly used as lumber for general construction and furniture production, as well as for pulp and paper production, horticulture and Christmas trees (Nienstaedt & Zasada, 1990).

White spruce stands are a corner stone of boreal forest ecology (Rweyongeza et al., 2007). They provide shelter and cover for various herbaceous species such as: elk, hares and moose, a food source for red squirrels, spruce grouse and various song birds, as well as hunting grounds for predators like wolverines, lynx and wolves. In addition, they have a significant role in maintaining soil stability and watershed values (Nienstaedt & Zasada, 1990). When conditions are suitable, trees will typically grow up to 30 meters, and live for 100 to 250 years, with substantial seed production expected of trees 33 years or older. The growing season begins in the spring but varies depending on climate conditions. In Alberta, the harvest rotation length ranges from 90 to 120 years and is based on observed tree productivity and regeneration rates (Controlled Parentage Program Plan for the Region G2 White Spruce, 2007). Tree harvest is most commonly done using the clearcutting method, and the areas that are most in use are the lower foothills of the Rocky Mountains and central mixedwood ecozones (Rweyongeza et al., 2011).

The observed and expected climate variables in Alberta are significantly different than historic records, and are changing at a fast rate in comparison to the rest of the world (Bush et al., 2019). Climate trends appear to stand in line with the North American projections (IPCC, 2021), showing overall increases in temperature and susceptibility to drought and frequency of extreme events (Jiang et al., 2017). Future projections anticipate a continuous temperature increase by up to 6.8°C by 2080 (Jiang et al., 2017). The warming is likely to cause more rainfall, creating a shorter snow season and diminished snowpack, leading to earlier onset and increased spring snowmelt (IPCC, 2021). These conditions, along with the expected increase in evapotranspiration loss, are estimated to severely diminish Alberta's climate moisture index (Jiang et al., 2017; Hogg et al., 2017). Thus, due to the consequences of climate change,

economic losses to the private, agriculture and forestry sectors are expected (Kuo et al., 2015; Gizaw & Gan, 2016; Newton et al., 2021).

Despite the assumed positive outcomes some researchers had in earlier years, the effects of climate change prove to be a great challenge. Some studies have suggested the temperature increase (along with the increase in carbon dioxide) will benefit tree productivity by creating conducive growth conditions and a longer growth season (Xu et al., 2007; Way & Oren, 2010; Wertin et al., 2012). Other publications claim the increase in temperature will have unfavorable implications such as: drought stress, introduction of competing and/or invasive species, increase in disease and insect infestation, and increased fire risk (Peng et al., 2011; Candau & Fleming, 2011; Gray & Hamann, 2013; Boulanger et al., 2017; Searle & Chen, 2017; Sang et al., 2019; Oboite & Comeau, 2020; Liu et al., 2021). Furthermore, rought-induced forest decline has emerged as a critical climate change concern for forests in the western North American boreal zone (Hogg et al., 2017b). Since 2001, climatic conditions have been notably drier than normal across large areas of the western Canadian interior, leading to widespread impacts on the boreal forest (Nenzen et al., 2019). Namely, a reduction in growth rate, susceptibility to disease and tree mortality (Candau & Fleming, 2011; Hogg et al., 2017b). This poses a major concern for the future, given the previously described climate projections.

Given the severity of climate change in Alberta, and its implications for forestry both ecologically and commercially, there's a pressing need to create an action plan (Price et al., 2013; De La Torre et al., 2014; Ste-Marie, 2015). While in the past, the forestry sector relied on historic yield models to estimate future productivity, this approach is no longer pertinent (Williamson, 2009). Instead, researchers push for using ENM modeling and productivity analysis

to offer a more reliant alternative (Williamson, 2009). The different negative effects of climate change on the boreal forest are well documented and accompanied by suggestions for potential mitigation strategies (Peng et al., 2011; Candau & Fleming, 2011; Gray & Hamann, 2013; Boulanger et al., 2017; Searle & Chen, 2017; Sang et al., 2019; Oboite & Comeau, 2020; Liu et al., 2021). Yet, there is a major knowledge gap in understanding the basic climatic niche for white spruce and the potential effect of climate change to its ranges. Asserting this climatic niche can shed light on the future of the boreal forest in Alberta and by proxy on the provinces forestry industry.

1.1 Objectives

For this project I set out to map the climatic niche of white spruce in order to predict its future range in Alberta. Comparing current climate to future climate projections allows to foresee tree productivity in coming decades. This understanding is important because it underlines the need for action within the forestry sector and policy makers. As it stands, the timber industry continues to harvest and plant trees within Alberta's forest management agreements (FMAs) with the expectation to achieve yields that are similar to past growth performances (Controlled Parentage Program Plan for the Region G2 White Spruce, 2007). Similarly, both municipal and provincial governments invest substantial funds in reforestation and tree planting schemes, without considering the selected species' future fitness (Alberta government, 2020; Government of Canada, 2019). Creating a visualization of tree productivity according to climate projections will give practitioners a "bigger picture" understanding of what the future holds and hopefully encourage forward thinking management actions that are appropriate for a realistic tomorrow. In

addition, introducing this model for white spruce can prompt research into climatic niches of other species and shed light on potential future ecosystems in Alberta.

2. Literature review

2.1 Climate

2.1.1 Observed & predicted climate change

The effects of rising temperatures due to climate change around the world, and in North America specifically, cause alarm and warn of severe environmental changes. Observed climate trends show that 2011–2020 was the warmest decade on record, with a surface global temperature of +0.82°C above the 20th century average (NOAA, 2021). This rapid change has affected the atmosphere, water cycle, and socio-economic systems globally. In the context of North America, the IPCC Sixth Assessment Report (AR6), predicts decreases in frost days, and increases in heavy precipitation over much of the continent (IPCC, 2021). Under the 2°C increase projection, global warming is expected to lead to more frequent extreme heat events and daily precipitation extremes, more frequent low-snow years, and shifts toward earlier snowmelt runoff over much of the western USA and Canada (IPCC, 2021). Under the 4°C increase projection, locally novel temperature regimes are expected to produce similar results with higher severity and frequency (IPCC, 2021). Additionally, climate extreme events like intense droughts, and increased precipitation variability, are projected to cause increased stresses on water availability, thus negatively affecting agriculture, economic activities, and urban and rural settlements (IPCC,

2021). At northern latitudes, where the average temperature has increased at nearly twice the rate of the global average temperature (during 1906–2005), many areas have become prone to drought due to decreased precipitation and increasing evaporation loss (Jiang et al. 2017).

2.1.2 Climate projection models

There are many different climate projections models. In this project we focused on Shared Socioeconomic Pathways (SSPs), which are scenarios of projected socioeconomic global changes that go up to year 2100. These projections are used to derive greenhouse gas emissions scenarios with different climate policies and implement the estimation to understand the implication for climate change (Riahi et al., 2017). The scenarios are: (1) SSP1: Sustainability (Taking the Green Road), (2) SSP2: Middle of the Road, (3) SSP3: Regional Rivalry (A Rocky Road), (4) SSP4: Inequality (A Road divided), and (5) SSP5: Fossil-fueled Development (Taking the Highway). The SSPs provide a description of different socio-economic developments. In terms of quantitative features, they provide information on national population, urbanization and GDP (per capita), but can also be used with various Integrated Assessment Models (IAMs), to explore future directions of socioeconomic and climate pathways (Riahi et al., 2017).

2.1.3 Climate change forecasts for Alberta

In the province of Alberta, climate trends appear to stand in line with the North American projections, showing overall increases in temperature and susceptibility to drought and frequency of extreme events (Williamson, 2009). Alberta is one of the three Canadian Prairie provinces, and is characterized by a semi-arid, continental climate, caused in part by the Canadian Rocky rain shadow, which blocks moist, Pacific westerly winds on its windward side (Schneider, 2013).

Due to these conditions, precipitation is highest in the higher altitudes and foothills of the Rocky Mountains, where it increases with elevation. In the rest of province, the highest rates of precipitation are found at mid latitudes and decline north or south wards (Schneider, 2013). In the past 112 years Alberta has exhibited a trend of warmer and dryer conditions (Jiang et al., 2017). Over the period of 1951-2017, the annual average temperatures have increased by 1-2.5°C in Southern Alberta, and by 2- over 3°C in Northern Alberta. Furthermore, winter temperatures are showing stronger warming trends with 4-5°C in the South and 6-7°C in the North (Environment Canada, 2015). Future projections anticipate a continuous temperature increase by up to 6.8°C by 2080 (Jiang et al., 2017). In accordance with the current trend, Alberta's northern latitudes are expected to exhibit the most extreme changes in temperature and precipitation. Southern Alberta is projected to experience a decrease in precipitation, especially in the prairies, while a change for central Alberta and other regions has not been established (Jiang et al., 2017). The warming is likely to cause more rainfall, creating a shorter snow season and diminished snowpack, leading to earlier onset and increased spring snowmelt. These conditions, along with the expected increase in evapotranspiration loss, are estimated to severely diminish Alberta's streamflow (Jiang et al., 2017). Another consequence of climate change for Alberta is an increase in extreme weather events frequency and severity (Brimelow et al., 2017; Gizaw & Gan, 2016; Kuo et al., 2015). Extreme weather events such as snow, hail and ice can cause severe damage to tree stands in the form of: breaks, stem lesions, and leader or terminal bud mortality (Nienstaedt & Zasada, 1990). In addition, heavy rain events are likely to cause flooding, especially during the summer months (Jiang et al., 2017). Thus, due to the consequences of climate change, economic losses to the private, agriculture and forestry sectors are expected (Newton et al., 2021; Gizaw & Gan, 2016; Kuo et al., 2015).

2.2 White spruce back ground

2.2.1 Ecological importance

White spruce is widely distributed from northeastern USA throughout Canada, and to Alaska and is thus described as a "plastic" species that can withstand highly variable conditions, including extreme climates and soils (Rweyongeza et al., 2007; Nienstaedt & Zasada, 1990). It is a prominent component in its habitat and is most commonly found in either pure or mixed stands, due to its intermediate shade tolerance. Large numbers of white spruce may become established immediately following disturbance and form even-aged stands, but because seedling and juvenile growth is slower than its early successional associates, it can remain in the understory for 50 to 70 years. Although white spruce survives this period of suppression, growth rates significantly decline (Nienstaedt & Zasada, 1990). Most commonly white spruce associated species include: black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), quaking aspen (*Populus* tremuloides), red spruce (Picea rubens), and balsam fir (Abies balsamea). In Western Canada specifically, white spruce is found in pure stands in the north, and is associated with subalpine fir (Abies lasiocarpa), balsam fir, Douglas-fir (Pseudotsuga menziesii), jack pine (Pinus banksiana), and lodgepole pine (*P. contorta*) on its southern range. Two other common associations are: white spruce with willow (Salix spp.)/Buffaloberry (Shepherdia spp.)/Northern goldenrod (Solidago multiradiata)/Crowberry (Empetrum spp.), and white spruce with willow/Buffaloberry/Huckleberry (Gaylussacia spp.)/Dewberry (Rubus spp.)/Peavine (Lathyrus spp.), which are typical in northwestern Canada and Alaska (Nienstaedt & Zasada, 1990). White spruce-aspen and white spruce-paper birch are early successional stages, usually leading to pure white spruce stand development, whereas black spruce-white spruce stands can in themselves be

a climax stage (especially in northern altitudes), referred to as the lichen-woodland type. In wetter conditions, at higher elevations, black spruce may replace white spruce as the climax species of this cohort (Nienstaedt & Zasada, 1990).

White spruce is monoecious, and primarily wind-dispersed (Nienstaedt & Zasada, 1990). When conditions are suitable, trees will typically grow to 30 meters, and live for 100 to 250 years, with substantial seed production expected of trees 33 years or older (Nienstaedt & Zasada, 1990). The growing season begins in the spring but varies depending on climate conditions. 6-8 weeks after the start of the growing season, trees will begin the pollination stage, again, depending highly on climate conditions (Nienstaedt & Zasada, 1990). Female receptivity, pollen shedding and dispersal, seed crops quantity and quality, are all highly dependent on temperature and climate events. This is particularly important since germination rates are linked to seed production rate, which relies on the aforementioned qualities (Nienstaedt & Zasada, 1990). Pollination usually occurs during May, June, or July, depending on climate and geographic location but can be delayed for up to 5 weeks if temperatures are cold. In addition, both the initiation and pattern of seed dispersal can be delayed due to precipitation events, until conditions become dry. Seed dispersal usually occurs in September with a small number of seeds dispersed in August. Seeds falling during the peak period are of higher quality than ones dispersed earlier or later in the season (Nienstaedt & Zasada, 1990). Germination occurs from mid-May through early August, and given adequate conditions, seeds germinate as soon as soil surface temperatures are warm enough. Generally, germination is 75 to 100 percent complete by early July (Nienstaedt & Zasada, 1990). Adverse conditions can delay germination until the next growing season, and trigger vegetative reproduction (in the form of layering). Germinants developing after the middle of July have a lower survival probability than those originating in early summer (Nienstaedt & Zasada, 1990).

White spruce stands are a corner stone of boreal forest ecology (Nienstaedt & Zasada, 1990). They provide shelter and cover for various herbaceous species such as: elk, hares and moose, a food source for red squirrels, spruce grouse and various song birds, as well as a hunting grounds for predators like wolverines, lynx and wolves. In addition, they have a significant role in maintaining soil stability and watershed values (Nienstaedt & Zasada, 1990).

2.2.2 Commercial importance

White spruce is one of the most important commercial tree species in Canada, where forestry is an imperial part of the economy. Canada has the world's largest forest product trade balance, with the forest sector contributing about \$23.7 billion to Canada's nominal gross domestic product (GDP) and the value of Canadian forest product exports at about \$33 billion (Government of Canada, 2019). Spruce trees constitute 47.3% of the Canadian forests (Government of Canada, 2019). In Alberta, the industry is a staple of the economy for rural and Indigenous communities. It directly employs over 17,500 Albertans and 23,900 people in supporting occupations (Alberta government, 2020). The forestry industry revenues exceed \$7.6 billion from harvesting operations a year and an estimated \$6.5 billion has been invested in forest product manufacturing operations (Alberta government, 2020). White spruce is commonly used as lumber for general construction and furniture production, pulp and paper production, horticulture and Christmas trees (Nienstaedt & Zasada, 1990).

2.2.3 Engelmann/white spruce hybrids

In the intermediate climate conditions where related species' boundaries overlap, hybridization is often observed, giving rise to new adaptations and possibilities in the face of climate change (De La Torre et al., 2014). White spruce and Engelmann spruce (*Picea engelmannii Parry ex* Engelm.) are closely related, wind-dispersed, long-lived tree species that hybridize extensively in areas where their ranges overlap, namely in British Columbia and the western Alberta Rocky Mountains foothills. Engelmann spruce is adapted to short growing seasons and high snowfall, associated with the southern range of the subalpine forest range and it has relatively low tolerance to high temperatures and drought (De La Torre et al., 2014). Hybridization of these two species occurs on the boundaries of the original parental habitats. Generally, hybrid individuals are considered fitter than the parental species in intermediate environments, but are less fit in parental native habitats (Goulson, 2009; Miglia et al., 2005). In the case of white spruce and Engelmann spruce hybrids, research of managed populations show that selecting individuals that have more white spruce ancestry produces higher productivity, suggesting that most hybrids on the natural species boundary may be poorly adapted to new, warmer climates (De La Torre et al., 2014). While some researchers push for categorizing both tree species as one (Rajora & Dancik, 2000), and despite the common practice of lumping these two species under the "interior spruce" category, the distinction between the two and between their associated preferred conditions is made important by the future climate conditions, especially when considering future forest management and reforestation strategies.

2.3 Observed climate change impacts on forestry & forest ecosystems

Researchers strive to understand the potential consequences of climate change for tree growth.

Some studies suggest that the temperature increase (along with the increase in carbon dioxide)

will benefit tree productivity by creating conducive growth conditions (Xu et al., 2007; Way & Oren, 2010; Wertin et al., 2012), while others claim that the increase in temperature will likely have unfavourable implications such as: drought stress, introduction of competing and/or invasive species, increase in disease and insect infestation, and increased fire risk (Boulanger et al., 2017; Candau & Fleming, 2011; Gray & Hamann, 2013; Liu et al., 2021; Oboite & Comeau, 2020; Peng et al., 2011; Sang et al., 2019; Searle & Chen, 2017).

2.3.1 Drought

Drought-induced forest decline has emerged as a critical climate change concern for forests in the western North American boreal zone (Hogg et al., 2017). Since 2001, climatic conditions have been notably drier than normal across large areas of the western Canadian interior, leading to widespread impacts on the forests of this region (Nenzen et al., 2019). Namely, reduction in growth rate, susceptibility to disease and tree mortality (Candau & Fleming, 2011; Hogg et al., 2017). This poses a major concern for the future, given the previously described climate projections. Furthermore, temperature caused drought has been proclaimed as the main limiting factor for forest productivity in Western Canada, with researchers reporting a strong negative impact of summer temperatures on radial growth (Chen et al., 2017).

2.3.2 Competition

Another significant effect of climate change is the increase in competition, which some researchers suggest may lead to a decline in desired tree species productivity (Chen et al., 2017;

Hogg et al., 2017). There are several indications from recent publications pointing to an increase in intraspecific competition pressure on white spruce, causing reduced growth rates in high latitude forests (Alam et al., 2017; Wright et al., 2018; Jiang et al., 2018). Competition is considered an important driving force for stand dynamics and succession, yet in unstable ecosystems, the added pressure may result in negative implications. Zhang et al., showed that both the decrease in growth rate and mortality rate are closely correlated with long term competition stress (2015). Furthermore, Zhang et al., claim that the competition effect is so severe it outweighs the effect of climate change (2015). Other experts disagree by connecting the competition pressure directly to climate variables, and by extension climate change (Price et al., 2015). Wright et al., while considering both approaches, moderates the controversy by stating that: "climate-driven competition at the stand level is an important factor that will influence the relationship between rising temperatures and radial growth" (2018). In contrast to these findings, other researchers suggest instead an intraspecific mutualism mechanism within coniferous groups, claiming interactions of neighboring trees improve survival (Jiang et al., 2018). Interspecific competition stress (especially between white spruce and trembling aspen in the boreal forest) is more common in habitats with benign site conditions, whereas in harsh environments, trees often promote facilitative interactions by increasing tree cover and shade that reduce the rate of evapotranspiration. This interaction variation is in line with the general principles of the stress gradient hypothesis (Chhin & Wang, 2016).

2.3.3 Pest Infestations

The warmer temperatures and consequential drought have led to unprecedented intensity of pest infestations in the boreal forest of North America (Andrei & Ifrim 2021). This is mainly due to

the physiological stress, fungal diseases or intense competition, that weaken the tree and create prime habitat for bark beetle and other insect species (Andrei & Ifrim 2021). The most common pest damages that influence white spruce mortality and productivity are: (1) cones damage, caused by spruce cone maggot (Hylemya (Lasiomma) anthracina), the fir coneworm (Dioryctria abietivorella), and the spruce seed moth (Laspeyresia youngana), (2) dormant seedlings damage caused by snow blight (*Phacidium infestans*) and various species of Pythium, Rhizoctonia, Phytophthora, and Fusarium, (3) bark damage, caused by the genera Dendroctonus, Ips, Trypodendron, Dryocoetes, Scolytus, Polygraphus and spruce beetles, (4) foliage and bud damage, caused by the spruce budworm (Choristoneura fumiferana) and the western spruce budworm (C. occidentalis), and the yellowheaded spruce sawfly (Pikonema alaskensis), (5) destruction of chlorophyll-bearing cells, caused by spruce spider mites (Oligonychus spp.), (6) spruce needles destruction, caused by needle worms, loopers, tussock moths, the spruce harlequin, and the spruce bud scale, (7) gall-forming insects belonging to the Pineus and Mayetiola genera deform and stunt growth of seedlings and saplings, (8) Engelmann spruce weevil, is an important pest in plantations in Alberta, and finally (9) Warren's collar weevil (Hylobius warreni) cause appreciable damage on young trees (Nienstaedt & Zasada, 1990). The expansion of outbreak ranges has been observed for major insect guilds in boreal and temperate biomes, which has led to reproductive loss, limited treeline expansion and increased tree mortality (Pureswaran et al., 2018). There is evidence that some recent outbreaks of bark beetles and other defoliating insects are positively correlated with climate change, which can be attributed to the waning of freezing winter temperatures which in the past effectively exterminated most pests allowing trees to recover before the next growing season (Candau & Fleming, 2011; Hogg et al., 2017; Pureswaran et al., 2018).

2.3.4 Fire

Many studies across North America have examined the changes in fire regimes in the face of future climate projections. The results suggest a range of likely changes, from the lengthening of the fire season, to increased spread potential, increase in fire occurrences and increased area burned (Balshi et al., 2009; Flannigan et al., 2013; Flannigan et al., 2005; Kirchmeier-Young et al., 2017; Krawchuk et al., 2009; Liu et al., 2013; Wang et al., 2015). These projected increases are expected to affect the forest stand composition by moving away from late successional conifers and towards broad leaf trees and early successional species. More extreme projections anticipate a change of habitat type from boreal forest to grasslands on over half of Alberta's boreal natural range due to changing fire regimes (Searle & Chen, 2017; Sebastian-Azcona et al., 2019; Stralberg et al., 2018). According to these findings, future forest systems will become dependent on areas with a lower fire events frequency that will serve as "refugia" for post fire regeneration, namely in the form of peatlands and wetlands (Stralberg et al., 2018).

Tree productivity in the boreal forest is at an intersection due to the effects of climate change, and while there is still some debate as to the exact results, most publications agree that management actions should be taken. Though some studies suggest that the projected climate change (along with the increase in carbon dioxide) will benefit tree productivity by creating conducive growth conditions such as higher metabolic rates and photosynthetic capacity (Xu et al. 2007; Way & Oren 2010; Wertin et al. 2012), the previously mentioned consequences are likely to cause significant stresses that hinder tree productivity and render local plant populations maladapted to their new habitat (Boulanger et al., 2017; Liepe et al., 2016; Sang et al., 2019). In the near future, application of conservation and adaptation practices will be necessary to buffer

against climate stresses, by increasing system resilience and reducing co-occurring non-climate stresses (IPCC, 2021).

2.4 Niche theory, habitat suitability and ENM modeling

Historically, the definition of niche had various meanings. The first definition of niche was introduced by Grinnell as the place in an environment that a species occupies (1917). Another, likely unrelated definition was Elton's description of it as a species functional role within the food chain and its impact on the environment (1927). In later times the niche concept was further split into: fundamental niche- a pre-interactive, potential range set by the environmental conditions, and realized niche- a post interactive, factual presence of the organism within a set area (Hutchinson, 1957). To bring the definitions together, later work opted to identify the ecological niche as the n-dimensional hypervolume within which the conditions are suitable for the species survival (Vandermeer, 1972). In addition, Hutchinson introduced the idea that the niche boundaries are the geographical limits, outside which the species exhibits zero survival probability (absence) (Sillero et al., 2021). Building on Hutchinson's ideas, a body of research papers grew under the umbrella of "Niche Theory", which established conceptual models that investigated how many and how similar coexisting species could be within a given community (Chase & Leibold, 2003). For a long period of time, the concept of niche was almost exclusively associated with interspecific competition which gradually declined in perceived importance as the main influencer of community structure. This association hurt the standing of niche theory research, until a new take was introduced by Chase and Leibold, framing niche theory as the local environment which meets the ecological requirements of a species and allows it to persist for prolonged periods of time (2003).

Ecological niche models (ENMs) are empirical or mathematical estimates of ecological niches that use statistical methods or theoretically derived surfaces, with the aim of describing the distribution of species. There are different approaches to configuring ENMs that differ based on the goals and the type of data, but overall ENMs aim to describe species distribution within the scope of niche theory (Sillero, 2011; Sillero et al., 2021). In the face of climate change, uncertainty and shifting species ranges, the analysis of habitat suitability trends based on ENMs can help identify the threat levels to species of interest and help inform future interventions (Arenas-Castro et al., 2018; Arenas-Castro & Sillero, 2021).

2.5 Predictions and guide-lines for forest management

Given the severity of climate change in Alberta, and its implications for forestry both ecologically and financially, there's a pressing need to create an action plan (Price et al., 2013; De La Torre et al., 2014; Ste-Marie, 2015). In the past, the forestry sector relied on historic yield models to estimate future productivity, but this approach is no longer pertinent (Williamson, 2009b). Instead, using ENM modeling and productivity analysis in different environmental conditions could offer a more reliant alternative (Williamson, 2009b). The aim of these analyses is to assess the changes in species distribution by predicting habitat reduction and species turnover, under the assumption that niche characteristics cannot evolve fast enough to adapt to environmental changes (Hirzel & Le Lay, 2008). Understanding which areas of the niche are most likely to be affected gives managers a "heads-up" and allows for premeditative actions or for retreat from unproductive regions (Hirzel & Le Lay, 2008). In addition, the predictions ascertain potential new ranges where new climate conditions will allow the expansion of the realized niche, giving way to novel possibilities (Schneider, 2013).

2.5.1 Alberta seed zones

The seed zonation system for Alberta has been developed for natural seed movement, and replaces the old Seed Provenance Rule. Seed zones are geographic subdivisions of Natural Regions and Subregions. They are based on general genetic and ecological standards and regulate seed movement to avoid maladaptation or risk to its genetic integrity. Seed zones were originally created for tree species yet are in use for all vegetation types in current time. Seed collections can be moved freely within the seed zone of origin. There are a total of 90 described seed zones for Alberta, which cover all species and areas of the province. Forestry Seed Zones of Alberta are defined for all areas of the province, and are applicable to all native forest plant species. Seed zone allocation is hierarchical and based on Alberta's six Natural Regions, their Natural Subregions and Ecodistricts. When Natural Regions failed to represent the adaptive genetic variation, elevation contours are used for the division (Alberta Forest Genetic Resource Management and Conservation Standards, 2009).

2.5.2 Alberta Forest Management Agreements (FMAs)

A Forest Management Agreement (FMA) is a 20 year, renewable, area based contract of forest tenure established between a forestry company and the government of Alberta. Through the FMA, a company is given certain rights, including the right to establish, grow, harvest and remove Crown timber, in exchange for various responsibilities such as forest management planning and creation and maintenance of the forest inventory within the boundary of the FMA. Alberta currently has 21 forest management agreements. The size of a forest management agreement varies and agreement holders must adhere to set forest management practices that are designed to provide a yield consistent with sustainable forest management principles and

practices. Through the FMA the industry assumes a large share of the forest management responsibility. In return for this commitment, the Crown grants the company long-term tenure security upon which to base investments in manufacturing timber. This long-term security includes a compensation mechanism if lands are withdrawn from their FMA (Alberta government, 2020).

2.5.3 ABMI abundance model

The Alberta Biodiversity Monitoring Institute (ABMI) monitors Alberta local species and habitat structures at 1656 sites systematically located across the province, and at additional targeted sites. Two of the main goals of the institute are to support natural resources management by providing empirical models of the relationship of species and habitat elements to natural vegetation types, human footprint and climate and geographical gradients. This information is readily available on the ABMI website and aims to provide relevant and objective information to policy-makers, scientists, and the general public (Alberta Biodiversity Monitoring Institute, 2014).

The reference abundance model used for this project was calculated using a multiple regression approach. This method allows to separate the effect of human footprint variables and summarize the total area occupied by the species in the province. An estimated abundance of the species at each site is generated using presence/absence data and age analysis, for different stand types (Alberta Biodiversity Monitoring Institute, 2014).

2.5.4 Provenance trials

Provenance trials are commonly used to study genetic adaptations of tree populations to environmental conditions (Mátyás, 1996). Provenance trials are transfer experiments where seed sources from various locations (provenances) are grown in a common garden trial with a systematic experimental design that quantifies genetic population differences (Sebastian-Azcona et al., 2020). The identified adaptations are expressed as differences in survival or productivity of tree populations at the test site and can be used to guide seed transfer to address climate change concerns (McLachlan et al., 2007). For this project, a long-term provenance trial in Alberta, Canada was used to collect productivity insight (height in meters) from different locations across Alberta (Gray et al., 2016).

2.6 Response function analysis & growth

Response Function analysis is a multivariate method based on Principal Components Analysis that was introduced in the field of dendrochronology (Fritts et al. 1971). This technique was implemented to mediate the issues related to dealing with many predictor variables (mainly climate variables) in correlation analysis. Such issues include: increased probability of type-I errors, interference with the ability to detect climate signals, and reconciling time series data. Fritz addressed these issues by creating a regression analysis of tree ring width based on the principal components of climate data. The advantage of doing this is that principal components are, by definition, not correlated to each other (Fritts et al. 1971).

Response function is the term used to describe the growth of a population as a function of climate at the test site. Other names include: population response function or reaction norm (Rehfeldt et al., 2002). Response functions are commonly used to predict productivity of forests

in current and future climate conditions, and specifically to assess the change in population's growth in changing environmental conditions (O'Neill, Hamann, et al., 2008).

2.7 Options for adaptation in forestry

2.7.1 Assisted migration

The main intervention that has been suggested to increase resilience is human assisted migration; which was developed to be implemented within reforestation and forest management programs (Azcona et al. 2019). Through this process, certain species or populations are chosen as seed donors, based on the qualities of their habitat (i.e. climate and geographic characteristics) and are transported to areas that are projected to match these conditions in the future in the hopes of allowing germination of individuals that are better adapted to the new conditions, thus promoting the conservation of a species or habitat (McLachlan et al. 2007). In widespread tree species, like white spruce, a range of unique genetic adaptations to local environments is frequently observed (Gray & Hamann, 2013). These distinctive genetic differences are key in selecting donor sites to allow for tree establishment in areas experiencing fast climate changes, and replacing the maladapted local population (Gray & Hamann, 2013).

2.7.2 Assisted migration debate

Assisted migration is a concept that was introduced in the context of conservation, aiming to address the problems of: disappearing climates, climate change, shifting habitat conditions and especially extinction rate and biodiversity (Hewitt et al., 2011). The term was first introduced in a paper by Peters and Darling published in 1985, but had only gained momentum after 2007,

with over 60 papers addressing it published by 2011 (Hewitt et al., 2011). The topic became controversial quickly, sparking debate among scientists and practitioners. Supporters of assisted migration pointed to clear benefits like: range shifts mitigation, vulnerable species protection, biodiversity loss mitigation, ecosystem services provision, improvement of genetic fitness, and creation of proactive management tools ("Botanic Gardens Science for Conservation and Global Change," 2009; Davis & Shaw, 2001; Hagerman et al., 2010; Hoegh-Guldberg et al., 2008; Honnay et al., 2002; Savolainen et al., 2004). On the other side of the debate, opponents called attention to the possible risks, warning of: alien species invasion and the impacts they can bring to the surrounding environment, negative genetic impacts, diversion of resources from higher conservation priorities, bias towards specific species, logistical constraints, and weak justification of conservation potential (McLachlan et al., 2007; Park & Talbot, 2012; Parker, 2008). Furthermore, researchers raised alarm to new introduced pathogens, and competition with local species (Park & Talbot, 2012). In a literature review of the topic published in 2011, researchers found that roughly 60% of publications were in favor of assisted migration, 20% expressed concern, and another 20% indicated no clear position (Hewitt et al., 2011). To try and bridge the opposing arguments, several barriers were identified; the main barrier was the broad definition which included both long-distance, economically focused translocations, and intraregion, continental transport. While the former has been shown to have serious ecological consequences, the latter is considered of low risk (Schlaepfer et al., 2009; Vitt et al., 2010). Another barrier is the unjustified underlying assumption of adversaries that assisted migration will be executed without careful planning (Vitt et al., 2009). Most importantly, the researchers point to a need for a focused debate that is centered on particular scenarios, and anchored in scientific data and insight from applied research (Hewitt et al., 2011). Other identified barriers

include: management paradigms (interventions labeled as "unnatural"), opposing conservation perspectives (e.g. species preservation vs. integrity of recipient communities), and lack of public involvement.

In the context of forestry, assisted migration isn't proposed as a mean to address extinction threats, instead the goal is to maintain forest productivity despite the shifting climate conditions and mismatch of genetic adaptations (Pedlar, 2012). Forestry assisted migration does not introduce species to new environments, rather, it moves seed which is potentially fitter to the anticipated environmental conditions within its own species range, or close to it (O'Neill, Ukrainetz, et al., 2008). Although this practice allows for fitter individuals to establish in new locations, it is merely a form of speeding up already occurring natural processes of range expansion (O'Neill, Ukrainetz, et al., 2008). Bearing in mind this distinction, the threat of introducing invasive species and the associated consequences, become inapplicable (Pedlar, 2012). Other concerns about feasibility and funds can also be put to rest, since prices would not significantly differ by integrating assisted migration into traditional forestry practices (Kreyling et al., 2011; Pedlar et al., 2011). Lastly, apprehension of genetic diversity losses are lacking, seeing as gene flow across the range of commercial tree species is high (Levin & Kerster, 1974). Furthermore, the similar concept of selecting high performance genotypes (for traditional forestry) doesn't have a significant effect on genetic diversity, thus making it an unlikely concern (Krakowski & El-Kassaby, 2004; Pedlar et al., 2011).

2.7.3 Other options for adaptation

One approach to combating climate induced changes recognizes the establishment phase as the most vulnerable to climate factors and promotes intensive management as a possible solution

(Millar et al., 2007). While this approach might be of use for commercial forestry on a small scale, it will not be suitable as a wide-spread solution for the boreal forest as a whole. Other proposed interventions focus on the individual expected effects of climate change. For fire prevention, researchers suggest increasing the proportion of broad-leaf tree species in the boreal zone, since broad-leaved stands are about 24 times less likely to burn in stand-replacing fires than pure needle-leaf stands (Astrup et al., 2018). While there is some apprehension to creating competition on already stressed systems, a study looking at aspen-white spruce stands points to possible benefits; the presence of aspen in the overstory serves as a shield from frost and winter injury threats and overwhelms understory vegetation that may compete with white spruce (Kabzems et al., 2016). A second promising benefit to fire prevention by promotion of mixed stands is insect outbreak prevention; tree injuries caused by fire can increase trees susceptibility to bark beetle attacks and lead to increased tree mortality (Marini et al., 2022). Another potential management practice aiming to combat the individual effects of climate change is genetic improvement. Researchers are working to develop genetically modified trees with an inherent resistance to spruce budworm using genomic selection methods (Beaulieu et al., 2020). Similar methods are used in recent efforts to develop resistance to weevil infestations (Whitehill et al., 2021). While most genetic improvement projects seem to focus on wood quality and productivity (Chang et al., 2019; El-Kassaby et al., 2020), drought resistance genetic engineering is also on the rise (Carraro & Di Iorio, 2022; Polle et al., 2019). Though all these efforts separately might make sense to combat individual stresses, in a future where these stresses occur simultaneously, management is likely to fall short, causing disappointment and wasted public funds.

3. Methods

In this project I set out to find and map the climatic niche of white spruce in Alberta. In addition, I used the niche to create a model that predicts white spruce productivity according to habitat climate conditions. In order to reach my objective I followed the following steps: (1) developing a climatic niche model using white spruce distribution data, (2) creating a dataset of tree growth data for an expected age of 50 years from dendrochronological data and test plantation records of known age, and (3) creation of a niche-constrained tree productivity model, where growth outside the species range (here, grassland ecosystems) is constrained to zero.

3.1 Climate data

Climatic characterization of Alberta was sourced by spatially interpolated climate data for the 1961–1990 climate normal period, and climate projections: SSP 245, SSP 370 and SSP 585, for the time periods of 2011-2040 and 2041-2070. The projections were generated using the software package ClimateWNA v4.62 (Hamann et al., 2013) which is freely available at http://tinyurl.com/ClimateWNA. This software uses gridded climate surfaces made with the Parameter Regression of Independent Slopes Model (PRISM) (Gray et al., 2016).

3.2 Growth data expected at 50-years

Tree height data was derived from dendrochronological records sourced by the Alberta Biodiversity Monitoring Institute (ABMI), freely available at https://abmi.ca/home/data-analytics/da-top/da-product-overview/Species-Habitat-Data.html. A second set of data was retrieved from genetic trials performed in the province and are available in the appendices of the publication (Gray et al., 2016).

In order to compare the tree heights in different growing conditions and ages, a site index was constructed. This practice is widespread in forestry research. To do that, the top height at age 50 was calculated using the formulas provided by: "Site index curves and tables for British Columbia- interior species" (Thrower et al., 1994). The asserted top height at age 50, was used to normalize all the data points (SI table can be seen in appendix 1). The asserted top height at age 50, was used to normalize all the points and compare the growth under different climate conditions. Namely climate moisture index (CMI) and mean annual temperature (MAT).

3.3 Niche-constrained growth model

A raster layer of white spruce abundance was sourced by the ABMI. The ABMI abundance model is calculated using a multiple regression approach. Predicted counts are converted into densities (/ha) and then into basal areas of trees or snags (m2 /ha) or volumes of downed wood (m3 /ha), using quadratic mean diameters of the size classes and the known sampling areas or transect lengths. A two-stage procedure is used to estimate species relative abundances in the human footprint and vegetation types. The analysis is looking at SPECIES MODELING & INTACTNESS; VERSION 2014-09-19 9. The residual (incremental) effect of age on the species' abundance in the stand type. These age curves are used to predict the relative abundance of the species in each age class of each stand type (Alberta Biodiversity Monitoring Institute, 2020).

The abundance model was generated by using ABMI Predicted Relative Abundance data and the Alberta seedzones map, by RStudio version R-4.1.1, and libraries: mgcv, npreg, plotly, RSAGA. The 3D model was fitted using the gsm function.

The model was later used to extract the zero values which represented the edges of the climatic niche where white spruce could no longer persist.

The model was created using RStudio version R-4.1.1, and libraries: mgcv, npreg, plotly, RSAGA. The 3D model was fitted using the gsm function. All raster editing and zonal statistics were performed using ArcGIS PRO 9, and QGIS3.

4. Results

4.1 Climatology of Alberta

In order to gage a general understanding of the climate in different seedzones I created a visual representations of the climate conditions. The seedzones are a good representation of areas with different climate conditions, which highlights the connection between genetic variations within a species as a result of habitat conditions. For example the dry mixedgrass sub-region shows the same outline as the dry patch in the South-Eastern corner of the MAP figure (see figure 1.A and 1.C). Temperatures differ significantly throughout the province and are mainly affected by elevation, latitude and the Jetstream that crosses Alberta in a diagonal pattern (see figure 1.B). High precipitation concentrate along the Rocky Mountain foothills, and stretch to central Alberta, while the North and South-Eastern areas are drier (see figure 1.C). When considering the overall habitat moisture a clear divide of wet and dry habitats can be identified; with the foothills and central Alberta exhibiting wet to moderate conditions, and the prairies and parklands together with the Peace river area displaying dry conditions.

4.1 White spruce climactic niche

The climatic niche of white spruce was generated based on abundance data provided by the ABMI (See figure 2.A). The values were averaged by seedzone (see figure 2.B) and fitted into a 3D model that plotted the abundance based on its relashionship with MAT and CMI (see figure 2.C). The analysis resulted in a ring of absence points that represent the edges of the climatic niche.

When habitat conditions rank below -10 on the CMI scale, it is too dry for white spruce growth. Whereas CMI values of over 90, are indicative of a habitat that is too wet. Similarly, I identified the lower limit of the MAT scale at -6 °C, but could not seal the niche ring at the highest temprature recorded of 6 °C, because tree growth persisted in this temprature. The upper limit of MAT is likely around 8 °C, which is the temperature at the species' most southern range edge, at an isolated population in South Dekota, USA.

The peak abundance according to the model can be anticipated in areas where the CMI values are within the range of 23-40, and the MAT values are between -2 °C and 2 °C (see table 1). for current and historic climate conditions the corresponding seedzones that fall within these conditions are the southern foothills and some of the Dry and central mixwood ecoregions.

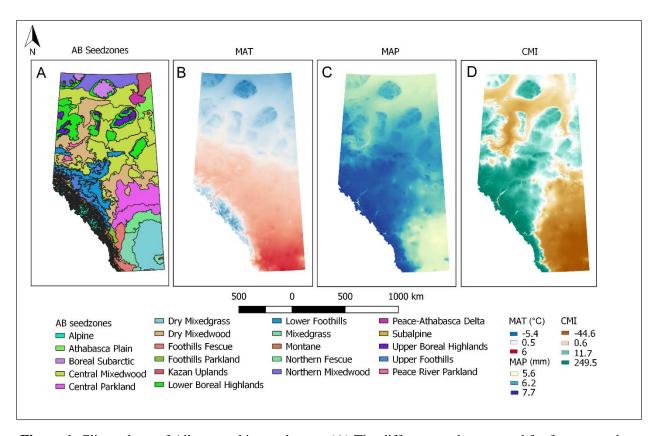


Figure 1. Climatology of Alberta and its seedzones. (A) The different seedzones used for forestry and agriculture, (B) Mean annual temperature based on climate data collected during 1960-1990 in degrees Celsius, (C) Mean annual moisture based on climate data collected during 1960-1990 in millimeters, (D) Climate moisture index based on climate data collected during 1960-1990.

Table 1. Average white spruce abundance by MAP and CMI

Abundance	CMI											
		-25	-8.89	7.22	23.33	39.44	55.56	71.67	87.78	103.89	120	
	-6	0	0	0.06	0.17	0.17	0.01	0	0	0	0	
	-4.67	0	0.02	0.22	0.33	0.33	0.17	0.02	0	0	0	
	-3.33	0	0.21	0.41	0.52	0.51	0.36	0.2	0.08	0	0	
	-2	0.05	0.32	0.52	0.63	0.63	0.47	0.32	0.19	0.04	0	
MAT	-0.67	0.06	0.33	0.53	0.64	0.64	0.48	0.33	0.2	0.05	0	
	0.67	0.12	0.39	0.59	0.7	0.69	0.53	0.38	0.26	0.11	0	
	2	0.05	0.31	0.52	0.63	0.62	0.46	0.31	0.18	0.04	0	
	3.3	0	0.21	0.41	0.52	0.52	0.36	0.21	0.08	0	0	
	4.67	0	0.11	0.31	0.42	0.42	0.26	0.11	0	0	0	
	6	0	0	0.19	0.3	0.3	0.14	0	0	0	0	

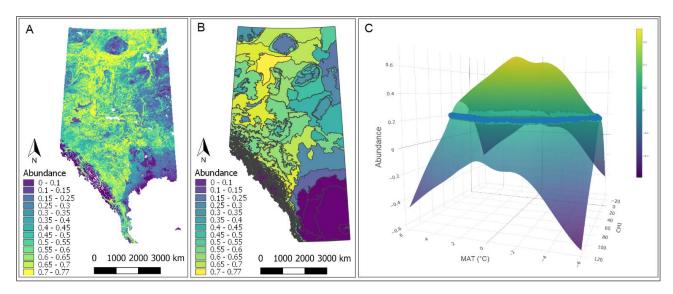


Figure 2. White spruce climactic niche modeling. The figure describes the process of the white spruce climactic niche identification. (A) White spruce abundance map provided by ABMI (Alberta Biodiversity Monitoring Institute, 2020), (B) White spruce abundance average values per seedzone, (C) 3D model of white spruce abundance based on MAT and CMI.

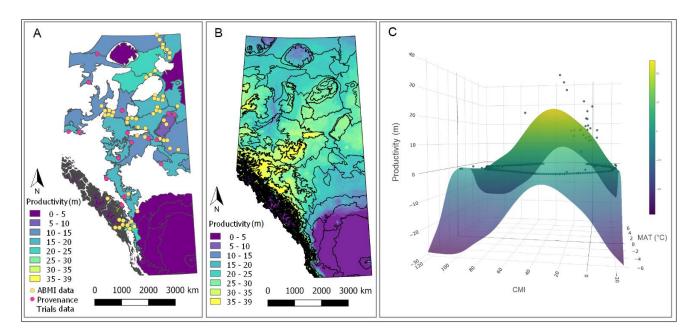


Figure 3. Niche-constrained productivity model. The figure describes the process of the white spruce productivity model creation. (A) Dendrochronological samples mapped on their corresponding seedzones, which are colored according to the average height of trees sampled within that zone, (B) Modelled white spruce productivity by seedzones for 1960-1990 time period, (C) 3D model of white spruce productivity based on MAT and CMI.

The ring of absence points derived from the abundance model, was used in addition to dendrochronological data and field height measurements to create the productivity model (see figure 3). The model is designed to predict productivity of white spruce given the site climate conditions.

White spruce productivity has a parabolic relationship with MAT and CMI (see figure 3.C). When CMI values are above 95, it indicates that the conditions are too wet for white spruce growth (see table 2). Similarly when CMI values equal -25 or below, conditions are too dry leading to white spruce absence (see table 2). The temperature limit for growth is -6 °C for MAT. The upper limit could not be identified due to trees persistence in the highest observed temperatures of 7 °C. This creates a gap in the model and prevents us from closing the climatic niche on white spruce's southernmost, warmest niche edge. The created model does not aim to calculate an exact tree height, rather it presents a general expectation of tree productivity given the particular climate conditions. It also provides information on areas outside the climatic niche, where trees are not likely to survive.

Table 2. Average white spruce productivity by MAP and CMI

Productivity								CMI						
		-25	-15	-5	5	15	25	35	45	55	65	75	85	95
	-7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	-6	0.00	0.00	0.00	0.00	0.00	0.22	0.91	0.00	0.00	0.00	0.00	0.00	0.00
	-5	0.00	0.00	0.00	0.00	1.72	4.82	5.50	2.85	0.00	0.00	0.00	0.00	0.00
	-4	0.00	0.00	0.00	4.87	8.89	11.99	12.67	10.02	4.49	0.00	0.00	0.00	0.00
	-3	0.00	0.00	6.15	11.81	15.84	18.93	19.61	16.96	11.43	5.26	1.05	0.00	0.00
	-2	0.00	2.46	9.56	15.22	19.24	22.34	23.02	20.37	14.84	8.66	4.46	1.34	0.00
	-1	0.00	3.58	10.68	16.34	20.36	23.46	24.14	21.49	15.96	9.78	5.58	2.46	0.00
MAT	0	0.00	3.79	10.88	16.54	20.57	23.66	24.34	21.69	16.16	9.99	5.78	2.66	0.00
	1	0.00	3.28	10.37	16.04	20.06	23.15	23.84	21.19	15.66	9.48	5.27	2.16	0.00
	2	0.00	2.65	9.75	15.41	19.43	22.53	23.21	20.56	15.03	8.85	4.65	1.53	0.00
	3	0.00	0.00	6.64	12.30	16.33	19.42	20.10	17.45	11.92	5.74	1.54	0.00	0.00
	4	0.00	0.00	1.62	7.28	11.30	14.40	15.08	12.43	6.90	0.72	0.00	0.00	0.00
	5	0.00	0.00	0.00	4.11	8.13	11.22	11.91	9.26	3.73	0.00	0.00	0.00	0.00
	6	0.00	0.00	0.00	2.20	6.23	9.32	10.00	7.35	1.82	0.00	0.00	0.00	0.00
	7	0.00	0.00	0.00	0.71	4.73	7.83	8.51	5.86	0.33	0.00	0.00	0.00	0.00

The expected productivity for the climate conditions of 1960-1990 can be seen in figure 4.A and table 3. This time period serves as a baseline, or historic reference point to which one can compare current and future tree productivity. White spruce is most productive on the north western part of the province and along the foothills of the Rocky Mountains (see figure 4.A). In contrast, the prairies on the South Eastern corner (and generally along the Eastern border of the province), either had no trees or displayed lesser productivity (see figure 4.A). When considering the period of 1990-2020 (Figure 4.E), changes in productivity are especially evident in the Rocky Mountains foothills and central Alberta. In these areas the yellow color which represents the tallest trees, is much less frequent, indicating that trees are likely to grow slower than their historic counterparts during this time period. In addition, the prairies climate conditions appear to be advancing northwards with more overall area colored in dark purple. Increased productivity is observed for some of the FMAs at the current conditions- P8, P20, P19, and G1 (See figure 4E and appendix 2). In addition, the Caribou Mountains region that is in part allocated to the FMAs F10 and F20, are shown to become more appropriate for white spruce productivity in all future projections (See figure 4.B-4.H and appendix 2). Despite the few instances of increased projected productivity during current climate conditions (see table 3), the overall trend shows a decline in white spruce productivity and mortality throughout the different FMAs. When comparing historic, and expected 2070s productivity values using the SSP2 climate model (which is considered by some researchers as the more realistic scenario (Hausfather & Peters, 2020), productivity reduction ranges from 40% to 95% (see table 3). Less optimistic projections paint a much darker picture with only a select few FMAs supporting semi-productive trees (see figure 4.G and 4.H). The missing values in future climate projections stem from the southern gap in the climatic niche. MAT values greater than 7.5 °C create blank spaces.

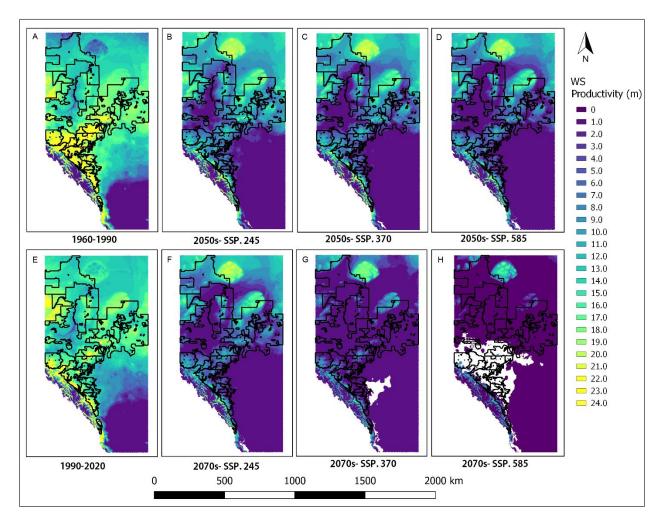


Figure 4. White spruce productivity projections. The figure gives a visual representation of the predicted white spruce productivity, based on different climate projections. (**A**) White spruce modeled productivity based on historic climate conditions (1960-1990), (**B**) White spruce modeled productivity based on ssp. 245 climate projections for the 2050s, (**C**) White spruce modeled productivity based on ssp. 370 climate projections for the 2050s, (**D**) White spruce modeled productivity based on ssp. 585 climate projections for the 2050s, (**E**) White spruce modeled productivity based on current climate conditions (1990-2020), (**F**) White spruce modeled productivity based on ssp. 245 climate projections for the 2070s, (**G**) White spruce modeled productivity based on ssp. 370 climate projections for the 2070s, (**H**) White spruce modeled productivity based on ssp. 585 climate projections for the 2070s. Empty pixels are climate conditions that are missing from historic data and couldn't be interpolated by the model.

Table 3. Productivity predictions for FMAs

FMA name	His	listoric productivity			Current productivity				2050s productivity SSP.245				2070s productivity SSP.245				Productivity	
	MIN	MAX	MEAN	STD	MIN	MAX	MEAN	STD	MIN	MAX	MEAN	STD	MIN	MAX	MEAN	STD	reduction (%)	
Tolko Industries Ltd. and Footner Forest Products Ltd.	0.6	18.0	12.9	1.9	8.8	20.2	14.4	1.9	1.3	20.2	10.6	3.2	0.0	18.9	7.6	4.3	40.6	
Manning Diversified Forest Products Ltd.	12.1	18.7	15.8	1.2	13.0	21.4	17.8	1.3	1.7	16.7	11.3	2.5	0.0	15.5	7.1	3.7	55.1	
Daishowa-Marubeni International Ltd.	2.6	24.3	14.7	2.6	2.2	24.0	15.0	2.7	0.0	20.2	8.1	4.3	0.0	15.9	3.9	4.2	73.6	
Alpac Forest Products Incorporated	12.1	21.2	16.7	1.4	9.1	20.2	15.6	1.8	0.0	18.8	10.0	3.6	0.0	17.6	5.3	4.2	68.1	
Canadian Forest Products Ltd.	7.3	23.7	19.9	2.3	5.5	22.5	15.9	2.2	0.0	13.0	7.0	2.8	0.0	11.2	4.5	3.1	77.3	
Tolko Industries Ltd. (High Prairie)	7.2	19.7	17.0	2.2	4.6	17.2	14.5	2.4	0.0	12.3	7.0	3.9	0.0	7.3	3.1	2.2	81.6	
Gordon Buchanan Enterprises Ltd. and Tolko Industries Ltd.	14.0	23.4	19.0	2.6	12.0	19.6	15.6	1.5	1.4	11.8	7.0	2.0	0.0	9.9	3.6	2.5	80.9	
Tolko Industries Ltd., Vanderwell Contractors (1971) Ltd. and Alberta Plywood Lt	16.9	24.2	19.7	1.6	12.7	22.0	17.2	1.6	3.8	18.0	10.4	2.9	0.2	15.2	6.0	2.7	69.2	
Weyerhaeuser Company Limited (Grande Prairie)	5.5	23.9	20.2	2.4	6.0	23.9	17.1	3.2	0.0	18.1	8.3	3.3	0.0	13.6	5.9	3.4	70.9	
Slave Lake Pulp Corporation	16.7	23.7	21.3	1.8	12.7	23.4	17.9	2.5	3.8	13.6	9.2	2.4	0.2	11.6	6.6	2.8	69.0	
Vanderwell Contractors (1971) Ltd.	15.4	17.8	17.2	0.4	12.0	15.1	13.6	0.6	2.7	7.3	4.3	0.7	0.0	2.4	0.9	0.6	95.1	
Blue Ridge Lumber Inc.	16.4	23.7	20.8	1.5	12.1	23.1	16.0	2.3	2.4	13.6	7.6	2.3	0.0	11.5	5.2	2.5	74.8	
Millar Western Forest Products Limited	13.9	23.7	19.3	1.9	10.3	22.9	14.6	2.2	0.1	13.6	5.9	2.4	0.0	11.2	3.4	2.6	82.6	
ANC Timber Ltd.	18.2	24.1	21.8	1.2	11.9	24.1	16.9	2.2	4.5	19.4	9.1	2.2	1.4	15.6	6.8	2.1	68.7	
Hinton Pulp A division of West Fraser Mills Ltd.	0.0	24.1	21.6	2.1	4.0	24.1	17.9	3.4	0.0	20.3	9.8	3.9	0.0	16.4	7.0	3.6	67.7	
Weyerhaeuser Company Limited (Edson)	15.5	22.4	19.3	1.3	8.3	18.8	13.8	1.6	0.2	9.9	5.3	1.6	0.0	7.7	2.7	1.6	86.2	
Sundance Forest Industries Ltd.	0.0	24.1	20.9	2.2	0.0	23.7	16.5	3.4	0.0	18.5	8.1	3.6	0.0	15.3	5.0	3.3	75.9	
Weyerhaeuser Company Limited (Drayton Valley)	0.0	24.3	18.6	2.2	1.2	23.9	13.8	3.0	0.0	21.2	5.3	3.9	0.0	17.4	2.4	3.6	86.9	
Sundre Forest Products A division of West Fraser Mills Ltd.	8.0	24.5	21.7	1.9	11.9	24.0	18.6	3.2	1.3	21.8	10.3	5.1	0.0	18.1	6.4	4.6	70.3	
Spray Lake Sawmills (1980) Ltd.	0.0	24.4	20.5	3.2	2.0	24.1	19.2	3.5	0.0	21.8	10.2	5.9	0.0	18.2	6.6	5.6	67.9	
Other	7.2	24.1	16.9	1.8	4.6	23.8	15.1	1.9	0.0	19.2	9.2	3.0	0.0	18.0	4.4	2.9	74.2	

5. Discussion

The results of this work show a clear decline in white spruce productivity in future decades. The final model predicted the productivity of white spruce in meters of height at age 50 across Alberta. According to what we know about white spruce ecology and range, the model delivers impressively accurate predictions. This can be seen in both figure 3.B and 4.A, where productivity estimations of the historic time period, lined up clearly with the productive

seedzones and FMAs. The accuracy of the predicted productivity created for the historic period, verifies the likelihood of this model to correctly predict future productivity of white spruce in light of the changing climate. For all climate projections we looked at (SSP2, SSP3, and SSP5) white spruce productivity was in decline for most areas. The severity of the decline corresponded with the severity of CO₂ emissions estimation of the associated climate model. The cause of the decline can simply be expressed as a diversion from white spruce climatic niche. The future climatic conditions of Alberta will not fit into the climatic niche that I have mapped out for white spruce.

In some FMAs, a slight improvement in productivity in current times was observed, but an overall trend of decline is expected in the long term. This improvement in productivity might be attributed to higher growth rates due to a longer growth season and better metabolic rate in higher temperatures; but it does not reflect the future productivity. Thus, practitioners should be warry of false conclusions following improvement observations in the near future.

5.1 Loss of areas suitable for white spruce forestry

According to my results, after the upcoming harvest of Alberta's Dry Mixedwood region, white spruce regeneration will no longer be viable. Furthermore, growth rates in most other ecoregions will significantly decline. The forestry industry relies heavily on the ability of harvested forest stands to regenerate postharvest, and supply wood for the next harvest round. In Alberta, the harvest rotation length ranges from 90 to 120 years (Controlled Parentage Program Plan for the Region G2 White Spruce, 2007), meaning that any harvesting done this decade will rely on tree regeneration in future climate conditions. Harvest rotation lengths are based on observed tree productivity and regeneration rates, to ensure similarly profitable future yields (Nienstaedt &

Zasada, 1990). Unfortunately, my results show that the observations made many decades ago to assert the rotation length are no longer practical. I found that the increasing annual temperatures along with the changing habitat moisture, will reduce the total stand productivity by up to 95% in the 2070s, even when considering a conservative climate projection (SSP2). This means that full regeneration after any forthcoming harvest is unlikely. This notion must be taken into account when considering harvest costs verses benefits. In addition, this work shows that postharvest reforestation by planting of white spruce seedlings is futile and wasteful. Industry funds can be better spent put into finding solutions and planning for future climate and habitats.

The foreseen climate conditions for Alberta will cause widespread mortality of white spruce in most of Alberta's seed zones and FMAs by the 2070s. In this work, white spruce mortality is represented by height 0 at age 50. The results of my work show extensive areas that will not be climatically appropriate for white spruce growth by the 2070s. Both the CMI and MAT values in Alberta are expected to change drastically in the coming decades. These estimations prevail in all future climate projections, with a changing degree of severity depending on future carbon emissions. Even for the most conservative projection (SSP2), climate variables in many regions were outside of the white spruce climate niche or on the far end of the model. While it is true that the maximum temperature niche boundary could not be identified and lead to missing data from the 2070s productivity projections, it is safe to assume white spruce will not grow beyond 8 °C, which is the MAT of its southernmost population. Unfortunately, Alberta is expected to reach mean annual temperatures of 10-12 °C, which is well outside the suitable temperature range for this species. Similarly, CMI values are expected to decline in many areas; changing from a driest values of -44 at historic times, to (-69)-(-92) in future climate projections. For reference, white spruce climate niche closes at the value of -10. These climatic changes are already happening,

and the increased mortality of white spruce is well documented (Hogg et al., 2017). Many publications attribute this effect to fires and disease (Balshi et al., 2009; Girardin et al., 2021), despite them being merely secondary consequences of a bigger problem- Alberta's climate no longer fits within the white spruce climatic niche.

5.2 Widespread projections of productivity decline

For the vast majority of FMAs, growth rates are estimated to decline considerably regardless of which climate projection is used. One of many examples to that effect is the lower Rocky Mountains foothills where trees currently grow to an average of 24 meters at age 50. This ecoregion is considered one of the most productive areas for the forestry industry, and contains some of the most harvested FMAs (Rweyongeza et al., 2011). Yet, when looking at the SSP2 climate projection for this region, tree height at age 50 is expected to average around 18 meters, which is a 6 meter decrease. Moreover, the less conservative models predict tree heights of under 5 meters at age 50, making the currently highly productive FMAs unprofitable. Other areas are estimated to no longer be an appropriate habitats for white spruce. These regions are predicted to experience widespread mortality (productivity equating to 0 meters at age 50). Such ecoregions include: central mixwood and dry mixedwood, according to SSP2. For the two more pessimistic projections, white spruce is expected to die out in most ecoregions by the 2070s. The Caribou Mountains region was the only location that showed increased productivity in future climate conditions. This change most likely stems from warmer temperatures and drier soil conditions, seeing as currently the low temperature and oversaturated soil serve as limiting factors and result in result in sparse, secluded stands (Allen 2006; Nienstaedt & Zasada, 1990). Both the forestry industry and other environmental bodies (like reclamation practitioners, conservationists and

governmental agencies) must take into account the many approaching changes to the environment, and plan for the future, instead of clinging to past visions.

5.3 Implications for forest management

In coming decades, climate conditions will no longer support commercial production of white spruce in Alberta. Judging by the results presented in this project, fewer ecoregions will fit into the climatic niche requirements of white spruce, leading to its decline across most FMAs. Furthermore, persisting trees will demonstrate a much slower growth rate, requiring longer harvest cycles. In addition, future white spruce stands will have to survive disease, fire and drought, which will further stunt growth (Boulanger et al., 2017; Liepe et al., 2016; Sang et al., 2019). Due to the above, commercial use of this species should no longer be considered sustainable. Furthermore, the financial losses should also be accounted for; the investment that goes into seedling planting post-harvest, will not be returned, deeming the practice wasteful and futile. There is room to consider alternatives to white spruce by planting tree species that are more likely to survive new climate conditions and be of commercial interest to timber and paper production; but a careful planning of both the species and planting location is crucial. Despite the fact we can roughly estimate the anticipated conditions, it is noteworthy that a significant body of research points to a non-consistent climate change, with many extremities like late spring frost, cold snaps and floods (IPCC, 2021). Due to this pattern, many potential species will succumb to the harsh conditions in spite of the overall warmer climate (Chuine & Beaubien, 2001).

5.4 Ecological implications

The expected deterioration of white spruce stands across Alberta will likely lead to shifts in ecosystem type and to the decline of the boreal forest ecology. White spruce stands are a corner stone of boreal forest ecology; they provide shelter and food sources, and play a significant role in maintaining soil stability and watershed values (Nienstaedt & Zasada, 1990). Increased tree mortality and lack of regeneration can trigger a cascading effect on all the dependent plant species and wildlife. Historically, the widespread ecozone allowed for species movement, which mitigated harvesting and other disturbances. In upcoming decades this will no longer be the case, as connectivity between remaining forest stands suffers and edges form. With both shelter and food sources declining, many species will be at risk of extinction. While some researchers point to white spruce range shift northwards, the lag caused by trees longer life span, remains a barrier (Gray & Hamann, 2013). A potential mitigation strategy would be assisted migration of white spruce to northern locations and intensive management actions (like fire prevention, genetic improvement, tree planting, etc.) to maintain ecological corridors and connectivity. Yet, white spruce assisted migration is likely to suffer from the unpredictable extreme climate events (Chuine & Beaubien, 2001). Another possible way to maintain some populations of white spruce outside its climatic niche is promoting "climate refugia". This management tactic aims to establish habitat strongholds that help maintain ecosystem functions of neighboring areas (Balantic et al., 2021). A potential option for such stronghold would be the Caribou Mountains, where I have shown climate conditions will become most suitable for white spruce in the long term. Yet unfortunately, the short timeline is an obstacle for this tactic seeing as white spruce stands in the area are sparse (Allen, 2006) and the creation of functional white spruce habitats would take a long time.

5.5 Mitigation options and opportunities

While the results of this work may seem discouraging, it is important to use the acquired insights for planning and mitigation strategies. The new setting can be perceived as an opportunity to integrate novel tree species and promote the development of new ecosystems. Even though the exact future climate conditions are unknown, educated estimations that are based on climate models can provide planning guidelines. Historic habitats that share similar climate conditions to future Alberta climate, can serve as templates for new desired habitats. Many predictions foresee the establishment of broadleaf forest in extensive areas (Price et al., 2013b; Wang et al., 2015). Promoting range expansion of common broadleaf tree species by tree planting and seed spreading, can help accelerate their establishment and prompt the creation of novel ecosystems. This practice could help improve biodiversity and provide opportunities for sustainable forestry practices in the future.

6. Conclusions

Through mapping the climate niche of white spruce, I was able to show the mismatch between future climate conditions and white spruce biologic requirements. This understanding allowed me to foresee the fast decline of the boreal forest in Alberta and the resulting implications to both the economy and ecology of the region. The forestry industry should prepare for a gradual decline in tree productivity and refrain from replanting white spruce for postharvest reforestation. Regeneration of stands after disturbance is unlikely considering the divergence of future climate conditions from white spruce climatic niche. Now is the time to consider innovation in forest management and embrace the changing future. Promoting assisted migration

of boreal species to northern latitudes while supporting the spread of broadleaf forests in Alberta may very well be the way forwards. Future research should expand the white spruce climate niche model to southern locations in order to close the niche at the southernmost edge and provide a more accurate prediction for hotter temperatures. In addition, this method can be applied to other tree species to help select appropriate candidates for assisted migration and reforestation endeavors in Alberta and other fast changing regions. There is no one right answer to this predicament, yet a plan of action is essential if forestry practices are to continue in this province.

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8. Appendices

White spruce site index table (Thrower et al., 1994).

Site Index Table for Interior White Spruce bh age Top height (m) (years) 9 10 11 12 13 14 15 16 17 18 19 20 Site Index (m) 23 27 31 34 16 19 13 15 10 12 13 14 Site Index 12-13 Years to bh

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30	32	33	34	35	36	37	39	40	•	-	-	-	*	-	-	30
27	28	30	31	32	33	34	35	36	37	38	39	40	-	•	-	35
25	26	27	28	29	30	31	32	33	34	35	36	37	38	40	-	40
23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	45
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	50
20	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	55
18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	60
17	18	19	20	21	22	23	24	25	26	26	27	28	29	30	31	65
16	17	18	19	20	21	22	22	23	24	25	26	27	28	29	30	70
15	16	17	18	19	20	21	21	22	23	24	25	26	27	28	29	75
14	15	16	17	18	19	20	21	21	22	23	24	25	26	27	28	80
14	14	15	16	17	18	19	20	21	22	22	23	24	25	26	27	85
13	14	15	15	16	17	18	19	20	21	22	23	24	24	25	26	90
12	13	14	15	16	16	17	18	19	20	21	22	23	24	25	26	95
12	12	13	14	15	16	17	18	18	19	20	21	22	23	24	25	100
11	12	13	13	14	15	16	17	18	19	20	21	21	22	23	24	105
11	11	12	13	14	15	15	16	17	18	19	20	21	22	23	24	110
10	11	12	12	13	14	15	16	17	18	18	19	20	21	22	23	115
10	10	11	12	13	14	14	15	16	17	18	19	20	21	22	23	120
9	10	11	12	12	13	14	15	16	17	17	18	19	20	21	22	125
9	10	10	11	12	13	13	14	15	16	17	18	19	20	21	22	130
9	9	10	11	11	12	13	14	15	16	17	17	18	19	20	21	135
8	9	10	10	11	12	13	13	14	15	16	17	18	19	20	21	140
8	9	9	10	11	11	12	13	14	15	16	17	18	19	20	21	145
8	8	9	10	10	11	12	13	14	14	15	16	17	18	19	20	150
7	8	9	9	10	11	12	12	13	14	15	16	17	18	19	20	155
7	8	8	9	10	10	11	12	13	14	15	16	17	17	19	20	160
7	8	8	9	9	10	11	12	12	13	14	15	16	17	18	19	165
7	7 7	8	8	9	10 10	11	11	12	13	14	15	16	17	18	19	170
			8	9		10	11	12	13	14	15	16	17	18	19	175
6	7	7	8	9	9	10	11	12	12	13	14	15	16	17	18	180
6	7	7	8	8	9	10	10	11	12	13	14	15	16	17	18	185
6	6	7	7	8	.9	9	10	11	12	13	14	15	16	17	18	190
6	6	7	7	8	8	9	10	11	12	12	13	14	15	16	18	195
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Forest management areas used for growth projections (Government of Alberta, 2022).

