

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

ÉVALUATION DE L'IMPACT DU CHANGEMENT CLIMATIQUE SUR LA
DÉFOLIATION DE L'ÉPINETTE NOIRE PAR LA TORDEUSE DES
BOURGEONS DE L'ÉPINETTE

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EVALUATING THE IMPACT OF CLIMATE CHANGE
ON THE BLACK SPRUCE DEFOLIATION BY SPRUCE BUDWORM

THESIS

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FOREWORD

This Master's thesis is sectioned into three parts: the first chapter will give a general introduction to the study, the second chapter includes the scientific article submitted for publication in the *Agricultural and Forest Meteorology* journal, and the third chapter puts forward some concluding remarks and forest management implications. More specifically, Chapter I includes the literature review and the problem statements. Chapter II presents the major elements of the research including the objectives, study area, methodology, results, and discussion. It takes the form of an article entitled "*Warmer climate increases black spruce vulnerability to spruce budworm outbreaks*" with the co-authorship of Marchand, P., Bergeron, Y., Morin, H., & Girona, M. M. Finally, Chapter III elaborates the conclusion and contribution to forest management, according to findings presented in Chapter II. My advisors as well as the research committee guided and assisted during the entire process—from conceptualization to reporting —of this thesis project.

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LIST OF ABBREVIATIONS AND SYMBOLS

AIC	: Akaike's Information Criterion
BAI	: Basal Area Increment
CMI	: Climate Moisture Index
Cum.Def	: Cumulative Defoliation
GAM	: Generalize Additive Model
GREMA	: Groupe de Recherche en Écologie de la MRC Abitibi
LOG	: Logarithm
SBW	: Spruce Budworm
TBE	: Tordeuse des Bourgeons de l'Épinette

RÉSUMÉ

Les modèles écologiques actuels prévoient de profonds effets des changements climatiques sur les régimes de perturbations naturelles des forêts. La tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*) (TBE) est le principal insecte défoliateur dans l'est de l'Amérique du Nord. Les épidémies de TBE ont un impact majeur sur la structure et la fonction de la forêt boréale canadienne puisque la défoliation entraîne une diminution de la croissance des arbres, une augmentation de la mortalité et une baisse de la productivité forestière. Les épidémies de TBE sont devenues plus sévères au cours du dernier siècle à cause des changements climatiques; cependant, nous savons peu de choses sur la manière dont l'effet intégré du climat et du TBE modifie la croissance des espèces hôtes. Nous évaluons ici comment l'interaction entre le climat et la gravité de l'épidémie affecte la croissance de l'épinette noire (*Picea mariana*) pendant l'épidémie de TBE qui a eu lieu entre 1968-1988 et 2006-2017. Nous avons compilé des séries dendrochronologiques (2271 arbres), des données de sévérité de l'épidémie (estimée par la défoliation aérienne observée) et des données climatiques pour 164 sites au Québec, Canada. Nous avons utilisé un modèle linéaire à effets mixtes pour déterminer l'impact des paramètres climatiques, de la défoliation cumulative (des cinq années précédentes) et de leur effet couplé sur la croissance en surface terrière. À la gravité maximale de l'épidémie, la croissance en surface terrière de l'épinette noire a été réduite de 14 à 18 % sur les cinq années en raison de l'effet TBE. Cette croissance a été affectée par le climat : des températures minimales estivales précédentes plus élevées et un indice d'humidité climatique estival plus élevé ont réduit la croissance de 11 % et 4 % respectivement. En revanche, l'effet négatif de la défoliation a été atténué de 9% pour une température minimale plus élevée au printemps précédent et de 7% pour une température maximale plus élevée l'été précédent. Cette étude améliore notre compréhension des effets combinés de la TBE et du climat et aide à prévoir les dommages futurs causés par cet insecte dans les peuplements forestiers afin de soutenir la gestion durable des forêts. Nous recommandons également que les projections des écosystèmes dans la forêt boréale incluent plusieurs classes de défoliation de la TBE et plusieurs scénarios climatiques.

Mots-clés : changements climatiques, défoliation, dendroécologie, épidémie, gestion forestière, perturbation, modélisation écologique

ABSTRACT

Current ecological models predict profound climate change-related effects on the natural disturbance regimes of forests. Spruce budworm (*Choristoneura fumiferana*) (SBW) is the principal insect defoliator in eastern North America, and SBW outbreaks have a major impact on the structure and function of the Canadian boreal forest, as defoliation leads to decreased tree growth, increased mortality, and lower forest productivity. SBW outbreaks have become more severe over the last century with the changing climate; however, little is known about how the integrated effect of climate and SBW alters the growth of host species. Here we evaluate how climate and outbreak severity combined to affect black spruce (*Picea mariana*) growth during the SBW outbreak that occurred between 1968-1988 and 2006-2017. We compiled dendrochronological series (2271 trees), outbreak severity (estimated by observed aerial defoliation), and climate data for 164 sites in Québec, Canada. We used a linear mixed effect model to determine the impacts of climatic parameters, cumulative defoliation (of the previous five years), and their interaction effect on basal area growth. At maximum outbreak severity, basal area growth of black spruce was reduced by 14%–18% over five years due to SBW effect. This outbreak growth response was affected by climate: warmer previous summer minimum temperatures and a higher previous summer climate moisture index (CMI) further decreased growth by 11% and 4%, respectively. In contrast, the negative effect of defoliation was attenuated by 9% for a warmer minimum temperature in the previous spring and 7% for a warmer maximum temperature in the previous summer. This study improves our understanding of combined insect–climate effects on growth and helps in the predictions of future SBW-related damage to forest stands to bolster sustainable forest management. We also recommend that projections of boreal forest ecosystems include several classes of SBW defoliation severity coupled with multiple climatic scenarios.

Keywords: climate change, defoliation, disturbances, dendroecology, ecological modeling, forest management, outbreaks

CHAPTER I

GENERAL INTRODUCTION

1.1 Context

Climate change has major and widespread effects on forest ecosystems worldwide (Bergeron et al., 2010; IPCC, 2019; Seidl et al., 2017). One of these impacts is when climate brings abrupt variations in the timing, intensity, frequency, and extent of disturbances (Allen et al., 2010; Brice et al., 2019; Girona et al., 2023a; Overpeck et al., 1990). Along with the climate-modulated changes in the disturbance regimes of the forest (Burton et al., 2020; Ciesla, 2011; Gauthier et al., 2023), heightened disruption occurs in those ecological processes associated with the forest. The forest and the associated ecosystem in the boreal and temperate biomes are regulated by different cycles of natural disturbances (Ciesla, 2011; Seidl et al., 2020). These disturbances include insect outbreaks, fire, drought, windthrows, hurricanes, ice storms, and pathogens (Bergeron et al., 1998; Chapin et al., 2004; Dale et al., 2001; Gauthier et al., 2015). Not only are boreal forests more vulnerable to climate change, they are the site of more large-scale insect outbreaks than any other biome in the world (Kneeshaw et al., 2015).

Insect outbreaks are the most important disturbance in the boreal biome of Canada in terms of affected area (Bergeron et al., 1998; Blais, 1983; MacLean, 2016). Eastern Canada is more affected by the eastern spruce budworm (SBW) (*Choristoneura fumiferana*) (Clemens), even though it is distributed throughout the country (Natural Resources Canada, 2022). In Quebec, more than 12 million hectares of forest were

affected from moderate to severe defoliation by the SBW in 2021 (MFFP, 2021). The changing climate and rising global warming has exacerbated the consequences of SBW outbreaks in the eastern Canadian forests (Fleming & Volney, 1995; Pureswaran, et al., 2015; Staudt et al., 2013), and this could become worse in the near future. During the last century, the severity and extent of SBW outbreaks is increasing, changing and shifting towards more northern latitudes in eastern Canada (Aakala et al., 2023; Berguet et al., 2021; Blais, 1983). Hence, the evaluation of the dynamic interaction between SBW disturbance and climate with respect to changing global scenarios is a major concern in eastern Canada (Axelson et al., 2015; Bergeron et al., 1995; Langston, 2009; Swetnam & Lynch, 1993; Thom et al., 2017).

1.2 State of knowledge

1.2.1 Spruce budworm outbreaks and climate

SBW, a tortricid moth, is recognized as the principal defoliator in the North American boreal forest (Blais, 1983; Cappuccino et al., 1998; Girona et al., 2018b; Gray & MacKinnon, 2006). It is distributed widely across North America from Alaska to Nova Scotia (Ciesla, 2011) (Figure 1.1). This lepidopteran species, being native to the Canadian boreal forest, feeds on the needles of fir (*Abies* spp.) and spruce (*Picea* spp.) to complete its life cycle, causing severe ecological disturbances in the boreal forest (Blais, 1983). The SBW completes its life cycle within a duration of one year. In July and August, the female adult moth lays eggs on the host tree needles which hatch within two weeks and the first-instar larva builds a silk cocoon to stay safe for the winter (Ciesla, 2011; Natural Resources Canada, 2022). At the following spring season, the larva emerges out and starts feeding causing major damage to the host species (Hughes et al., 2015). Later, the larva undergoes a metamorphosis to develop the moth-form

(Boulanger et al., 2017) in July or August, and lays eggs on the foliage to complete its life cycle.

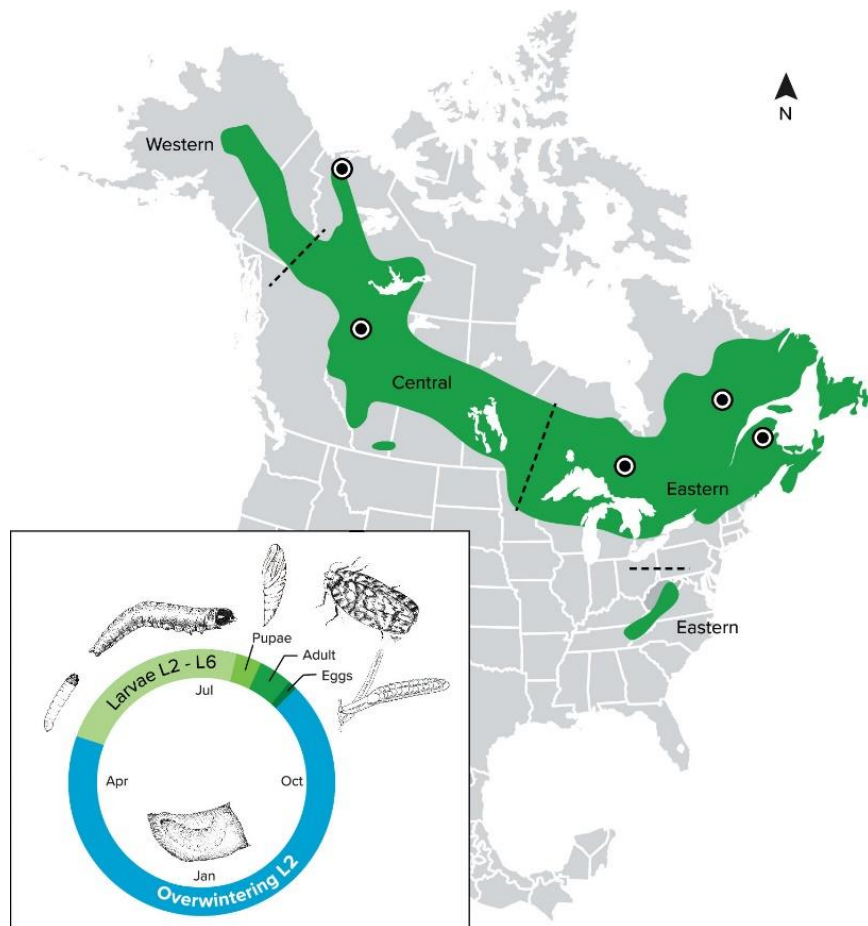


Figure 1.1 The distributional range of SBW in Canada and a graphical representation of its life stages. Adapted from (Marshall & Roe, 2021)

All these life stages of the SBW are sensitive to weather and climatic factors, particularly temperature and precipitation (Gray, 2013; Kneeshaw et al., 2015; Wellington et al., 1950). They regulate the insect population and can have effects ranging from favorable to detrimental (Ciesla, 2011; Liebhold & Bentz, 2011). For the development and the survival of defoliators like SBW, warm and dry summer climatic

conditions are considered to be favorable (Ciesla, 2011). For example, while early frost in the northern stands prevent the eggs from hatching, hot summer temperatures are necessary for its life cycle to be completed (Pureswaran et al., 2015). It has been recorded that hot and dry summers influenced the 1912 and 1949 SBW breakout in New Brunswick (Greenbank, 1956). So, the patterns of outbreak severity over space and time are affected by the climate (MacLean, 2016); specifically, winter temperature, growing-season temperatures and the changes in moisture availability are recognized to be the important climatic metrics contributing the insect outbreaks (Weed et al., 2013).

In eastern Canada, the population density of SBW oscillates in landscape-wide synchrony, with an average periodicity of outbreaks ranging from 30 to 40 years at the regional level (Boulanger & Arseneault, 2004; Royama, 1984), with local outbreak durations of approximately 10 years (MacLean, 1996). Three main outbreak periods occurred in Quebec over the last century: 1905-1930 (moderate), 1935-1965 (long and less severe) and 1968-1988 (short and severe) (Navarro et al., 2018). The first outbreak started from the south and extended, with some delay, towards the north of the 50th parallel, the second outbreak affected four major areas (Abitibi region, southwest of lake Saint-Jean, the upper north shore, and lake Mistassini), and the third outbreak was distributed along the fir domain in the western and the eastern parts of Quebec (Navarro et al., 2018). The more recent outbreak was recorded within the boundary of the commercial forest which shows its extension towards northern latitudes (Berguet et al., 2021). In the 21st century, an outbreak began in 2006 from the north shore of St. Lawrence river (Natural Resources Canada, 2022), and is predicted to last for more than 20 years.

1.2.2 Black spruce and climate interface

Black spruce (*Picea mariana*) is an abundant tree species in eastern North America with a wide geographic distribution between 49-51° N latitude and 70-73° W longitude (OECD, 2010; Viereck & Johnston, 1990). In Canada, it is distributed over an area of 365 million hectares of forested land (Figure 1.2; Beaudoin et al., 2014). Thus, it is the most widespread tree species, however, it is also exploited at a great extent because of its high commercial timber value (Girona et al., 2023b). Because of its wide distribution, it is considered to be an important tree species for research purpose, particularly, for recording past outbreaks (Simard et al., 2011). It has been affected by budworm defoliation (Lavoie et al., 2019; Pureswaran et al., 2016), and identified as a good host for budworm in terms of favorable environment (Blais, 1957), nutritional value (Morin et al., 2021), and high survival rate of late instar larvae in spruce stands (Nealis & Régnière, 2004). Nevertheless, the tree is more likely to survive multiple disturbances, and thus records the signals of outbreaks in its growth rings.

In lichen-spruce woodlands of Eastern Canada, the growth of black spruce was found closely associated with climatic variables, particularly precipitation, spring & summer temperature, and snowmelt/snow cover (Girard et al., 2011). The growth is influenced negatively by extreme climate change (Marchand et al., 2019), for instance, higher temperature (summer heat stress) during the month of June and July limited the basal area growth in black spruce (Chavardès et al., 2021) and the overall productivity of the forest (Girardin et al., 2016). When considering moist and cool habitats, black spruce showed negative growth in response to the temperature and positive response to annual precipitation in the boreal habitat of Alaska (Walker et al., 2017; Walker & Johnstone, 2014). So, even though black spruce is sensitive to temperature (Hoffer & Tardif, 2009), its effect on the growth can also be influenced by the water availability (Pappas, et al., 2022a). The change in precipitation has both positive and negative effects on the

growth depending upon the temperature; for example, growth is gained with 5-15% increase in mean annual precipitation and 2⁰C increase in mean annual temperature, however, warming greater than 2⁰C can display growth declination (D'Orangeville et al., 2018). In black spruce stands, while increased winter (January and February)

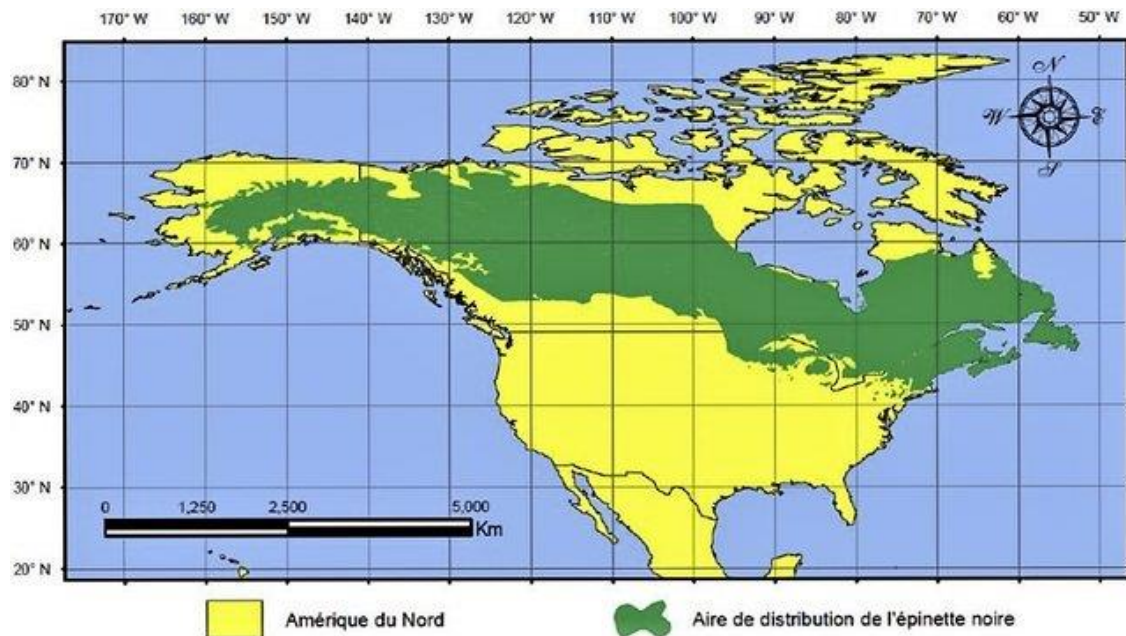


Figure 1.2 Distribution range of black spruce in North America (Girona, 2017)

precipitation has a negative influence on growth, a positive growth relationship was seen with increased precipitation levels in the month of August (Chavardès et al., 2021). Besides, drought stress i.e. warm spring temperature and low climate moisture index (CMI) was identified as another parameter that can reduce the growth in black spruce (Walker et al., 2015). The increase in drought due to climate warming in the near future may alter the entire composition and structure of the forest, thus, drought is also an important climatic metric in the simulation of the forest dynamics (Gustafson & Sturtevant, 2013). Soil temperature in the month of August, which is the important month for the spruce trees, also has an important effect on changing the growth (Dufour & Morin, 2013). Thus, sunlight and summer soil temperature (specifically August) are

additional factors to fluctuate the growth dynamics of black spruce (Dufour & Morin, 2013).

Climate variability also influences the growth of black spruce due to its interaction with the SBW. An increase in the temperature in the late winter or early summer highly alters the phenology of black spruce (Guo et al., 2021). It is predicted that climate warming has made black spruce phenologically suitable for the defoliation by SBW i.e., the summer has become warm enough to make the budworm complete its lifecycle in advance resulting a situation where actively feeding larval-phase matches with the buds bursting period in host species (Pureswaran et al., 2015; 2018a). Even though budburst in black spruce is affected by several climatic and environmental characteristics (De Barba et al., 2016), temperature is the primary climate metric determining the timing of budburst. For each degree rise in temperature, it was found that budburst in black spruce occurs 3 days earlier (Pureswaran et al., 2018a). A tighter synchrony between the host species and the spruce budworm, consequently, increases the severity of outbreaks with the change in defoliation patterns (Bognounou et al., 2017; Candau & Fleming, 2005). Thus, climate change ultimately makes the host trees more prone to the outbreak as it changes the weather variables that can modify the response of host species like black spruce (Candau & Fleming, 2011).

1.2.3 Defoliation damages

Damage occurs when the larvae of the budworm feed repeatedly upon the annual shoots, foliage, needles, leaf tissue, pollen, and sometimes seeds and cones of a seedling or tree (Blais, 1983; Cooke et al., 2007; Lavoie et al., 2021). Such consumption resulting in the loss of the tree foliage is referred as defoliation (Figure 1.3). Continuous defoliation by an insect over years may result in the reduction of seed-



Figure 1.3 Forest damage from spruce budworm defoliation [Photo: J. Lavoie, M.M. Girona & H. Morin]

yields, growth loss, dieback of branches, and tree mortality (Ciesla, 2011; Houndode et al., 2021; Mattson & Haack, 2009). The growth reduction results from the diminished photosynthetic capacity of the tree after successive damage of needles (Kneeshaw et al., 2015). The structure of the tree is also affected by the defoliation; for example, the damage to the terminal buds and parts of the axes by SBW affects the architecture of black spruce (Simard & Payette, 2003). The study by Krause et al. (2012) in black spruce found that, after moderate to severe defoliation, the reduction in growth is evident either from a first or successive years: effects are visible firstly among the directly impacted parts (after 1.5 years), and then spread to the different

sections of a tree (after 3 years). Later, within 5 years, reduction in growth is recorded in the growth rings of a tree.

The severity of defoliation and the extent to which a stand is susceptible to defoliators is influenced by different factors: species, age of the tree, stand composition, presence or absence of non-host species, ecoregion (Houndode et al., 2021; Kneeshaw et al., 2015; MacLean, 2016), and climate (Candau & Fleming, 2005, 2011). The defoliation preference of the SBW differs by species; for example, in a study by Hennigar et al. (2008), if balsam fir (*Abies balsamea*) had 100% defoliation, white spruce (*Picea glauca*), red spruce (*Picea rubens*), and black spruce had 72%, 41% and 28% respectively. This shows balsam fir is highly vulnerable to defoliation in comparison to other tree species (Bose et al., 2023; Houndode et al., 2021; MacLean, 1980), with a higher mortality rate in fir than that in spruce over successive defoliation periods (Pothier et al., 2012). Similarly, fir-dominated stands having a higher proportion of over-matured or matured trees are highly sensitive to defoliation compared with spruce stands (MacLean, 1980). A study on balsam fir by Houndode et al. (2021) showed mature stands experiencing higher mortality rate (more than 5%) in comparison to immature stands after a 5-year defoliation period. Gray (2013) found that locations having the higher volume of black spruce experience a severe, but a shorter outbreak. The mixed stands of black-spruce-balsam fir having taller seedlings were less vulnerable to be affected by the SBW in comparison to pure stands of balsam fir (Girona et al., 2018a; Houndode et al., 2021; Lavoie et al., 2021). In the similar spruce-fir stands, the mortality of fir decreased with an increasing proportion of black spruce (Pothier et al., 2012). In mixed stands having a higher abundance of non-host species, balsam fir suffers a lower level of defoliation (Bergeron et al., 1995; MacLean, 1980). During an intensive SBW outbreak, the defoliation rate in fir regeneration is higher for softwood stands than hardwood stands (Nie et al., 2018). The location also has some influence on the defoliation severity. For instance, the defoliation severity is moderate

in western Canada but is more severe in the eastern part where there are increasing episodes of forest mortality causing the loss of forest productivity (MacLean, 2016). Even though there are other underlying factors, the predicted expansion of some defoliators towards the higher elevation zones in comparison to the past suggests variation in defoliation intensity among those zones. The changes in defoliation severity is also influenced by the climatic parameters. Candau & Fleming (2005) found that temperature (winter and spring), and precipitation (June) are associated with defoliation, i.e. dry Junes (precipitation < 86 mm) and cool springs (mean minimum temperature < -2.7°C) increase the defoliation severity whereas cold winters (mean minimum temperature < -23.3°C ; mean maximum temperature > -11.0°C) in the north limits the extent of defoliation.

1.2.4 Dendroecology

Dendroecological approaches are considered as a suitable approach to better understand disturbances in the forest ecosystem, functions and processes (Bergeron et al., 2002; Boulanger et al., 2012; Girona et al., 2016, 2017; Jardon et al., 2003; Pohl et al., 2006); these have higher temporal resolution (with detailed annual changes), even though the temporal scale is small compared to the paleoecological approach (like the study of fossils). Dendroecology, though an indirect method, provides an effective insight about the impact and activity of the insect (Aakala et al., 2023; Navarro et al., 2018), including timing and sequence of past outbreaks to understand forest disturbance dynamics (Bergeron et al., 2002). As such, the study of tree rings is considered as one of the reliable means to reconstruct the effect of defoliations on the trees (Simard & Payette, 2003). Insect activity can be measured indirectly from the analysis of the tree rings because years of growth reductions during the outbreak periods can be identified in the rings (Boulanger et al., 2012; Boulanger & Arseneault,

2004; Krause, 1997). Retrospective study of the tree rings helps to identify the possible impact of the budworm regime (Anderson et al., 1987; McCune, 1983). Analysis of such long-term history of insect outbreaks with the aid of some external information like defoliation map provides crucial information about the interaction between climate and insect within the disturbance regime. Otherwise, it would be extremely difficult to identify whether the reductions in the growth were specifically due to the climate or the defoliation. Hence, dendrochronological reconstruction has been a baseline tool to assess the long-term spatiotemporal variability in relation to the outbreaks (Boulanger et al., 2012).

In the eastern Canadian boreal forest, different studies have been conducted with major contributions to insect outbreak reconstruction using the dendroecological approach. Morin et al. (1993) developed a chronology for the SBW for a period of 200 years using dendrochronology and identified three outbreaks in the last century (1970-1987, 1930-1950 & 1919-1929). Krause (1997) used materials from churches to construct historical outbreak for the last century and identified the major defoliation periods. Simard & Payette (2003) detected the consequences of budworm effect with high precision and resolution: at the branch level and at the exact year of feeding. Boulanger & Arseneault (2004) used the materials from old buildings and tree-rings to construct the budworm dynamics over 450 years in southeastern Quebec. Girard et al. (2011) found an association of black spruce growth with climate and recorded a significant epidemic in the northern portion of Quebec. Similarly, Boulanger et al. (2012), through the use of dendrochronological materials from old building and old growth stands, reconstructed a more reliable and multi-century (400 years) outbreak history at the northern limit of the temperate forest in southern Quebec, and showed the variations in budworm dynamics. Navarro et al. (2018) documented budworm dynamics at the landscape level in the first reconstruction of spatiotemporal patterns across 1 million km² area, including sites in both the fir and spruce domain. Recently, using

dendrochronological series, Berguet et al. (2021) reconstructed SBW outbreak patterns across its range in southern Quebec. Large scale analysis based on dendrochronological approaches considering major influencing factors can provide a more complete portrait of historical budworm outbreak in a larger spatiotemporal context.

1.2.5 Problem statement

Decades of continuous research by different organizations, agencies, and researchers led us to understand the SBW outbreak cycle (Berguet et al., 2021; Girona et al., 2018b; Lavoie et al., 2019; Ryerson et al., 2003), effects on forestry regime (Bergeron et al., 1995), and the synchronization of outbreaks over a large area (Bouchard et al., 2018; Sturtevant et al., 2015). However, these studies have only in a limited way integrated climate factors and associated outbreak-and-host species growth relation during outbreak periods. The understanding about the role and impacts of insect outbreaks at a larger scale remains incomplete (De Grandpré et al., 2018a; Robert et al., 2017). There are still gaps to identify the spatial and temporal interaction in relation to the climatic parameters that explores the historical host-budworm interface as well as to make predictions at the landscape-level (De Grandpré et al., 2019; Fuentealba et al., 2017). Specifically, the available information do not suffice to deeply understand the relation between climate parameters and black spruce defoliation in the face of climate change (Girona et al., 2018b). Hence, it has been essential to extend studies towards wider boundaries such as the provincial level considering the changing global scenario (Berguet et al., 2021; Girona et al., 2023c). Similarly, there are also some methodological challenges to understand the historical impact of climate on defoliation, the severity of this impact, and outbreak dynamism over long period. Most of the reconstruction studies in the past were carried with a major consideration that the reduction in the growth were evident in the growth rings specifically because of

defoliation. However, the complementing effect of both defoliation and other climatic events could have played a crucial role leading to the growth suppression. This has been confirmed by a few studies that have shown that the most severe outbreaks of the last century were preceded by the stress developed from the climatic events, however, the exact interaction affecting both tree growth and the budworm effects is still lacking (De Grandpré et al., 2019). This might be because of the methodological complexity, for example, only dendrological data are insufficient to describe such complex phenomenon. This project addressed such issues through the extension of study integrating dendrochronological, defoliation proxy and detailed climatic factors on the growth of black spruce during outbreak period (Figure 1.4). This research will contribute to improve our understanding between SBW-climate and growth interactions, which could be essential to establish forest management strategies in the face of climate change.

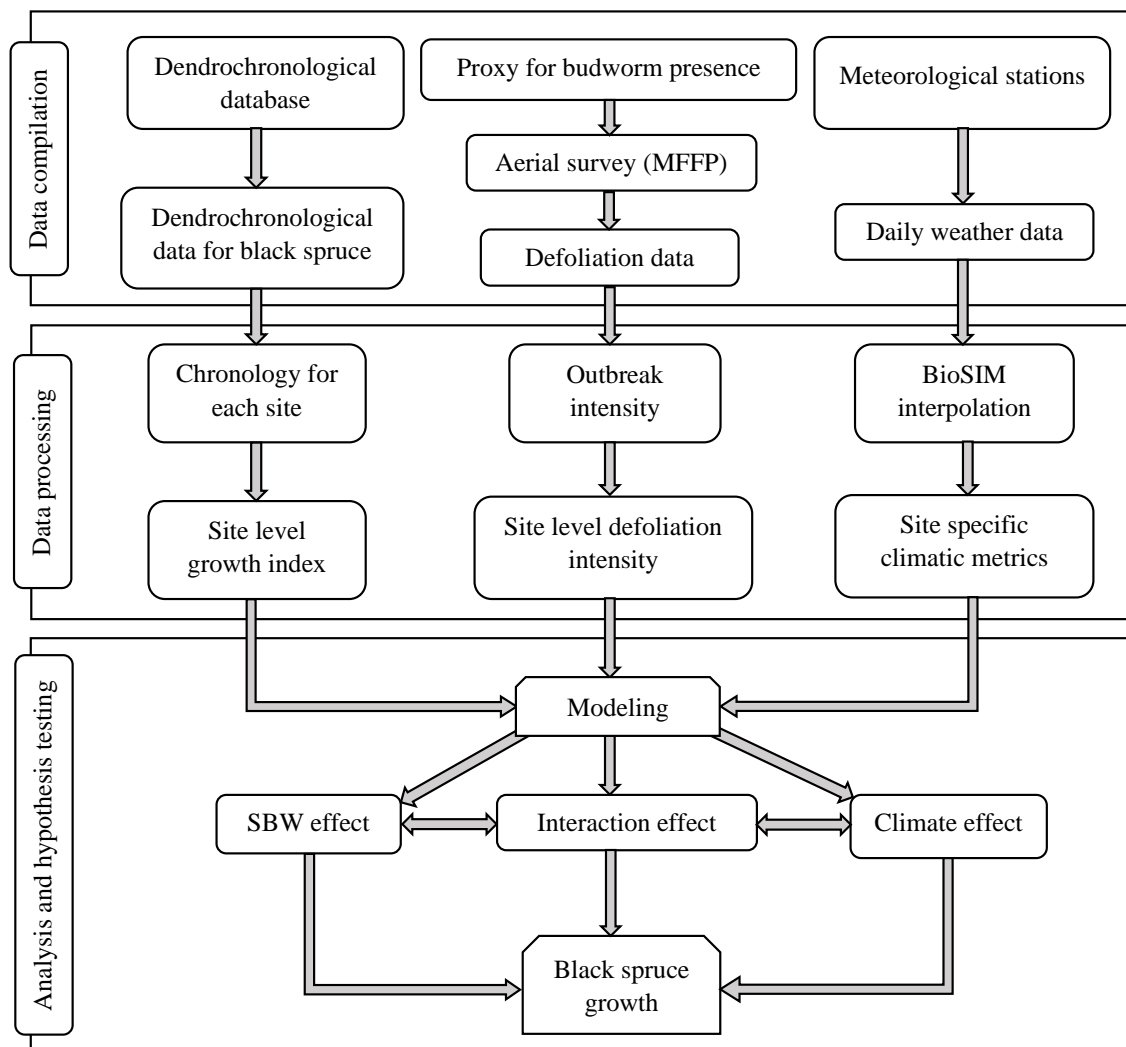


Figure 1.4 Schematic representation of the study

CHAPTER II

MANUSCRIPT

WARMER CLIMATE INCREASES BLACK SPRUCE VULNERABILITY TO SPRUCE BUDWORM OUTBREAKS

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2.1 Highlights

- Historical defoliation records can be a proxy to quantify budworm outbreak severity.
- Climate modulates the Spruce budworm effect on the growth of host trees.
- Increasing summer minimum temperatures of the previous year make black spruce more susceptible to budworms.
- Defoliation severity is lowered with higher maximum summer temperature.
- High June temperature of the current year, during an outbreak period, critically lowers radial growth.

2.2 Introduction

Disturbance shapes the structure and functioning of the boreal forest ecosystem (Feldman et al., 2020; Gauthier et al., 2014, 2023; Girona et al., 2019; Labrecque-Foy et al., 2020). Natural disturbances in the boreal biome, such as fire and insect outbreaks, are likely to become more severe and frequent because of climate change (Aakala et al., 2023; Dale et al., 2001; Seidl et al., 2017; Volney & Fleming, 2000). Including disturbances and their relationship to climate variables within ecological models will help managers attain sustainable management goals and adapt these forests to the context of global change (Bergeron & Leduc, 1998; Ciesla, 2011; Girona et al., 2023a; Kwon et al., 2021; Pickett & White, 1985; Reyes et al., 2010). However, forecasting the impacts of future climate requires understanding about how climate change alters forest ecosystem dynamics (Achim et al., 2022; Girona et al., 2023c; Hof et al., 2021; Molina et al., 2022).

In the boreal forest, insect outbreaks are major disturbances (Bergeron et al., 1998, 2002; MacLean, 2016). The eastern spruce budworm (*Choristoneura fumiferana* Clemens, hereafter SBW), a tortricid moth, is recognized as the most important defoliator in the North American boreal forest because of its wide distribution and the marked impact on forest productivity and forest dynamics (Blais, 1983; Cappuccino et al., 1998; Gray & MacKinnon, 2006). The economic and ecological consequences of SBW disturbances have placed these events among the priority topics of Canadian forestry research. Decades of continuous research by various organizations and agencies have improved our understanding of the epidemic cycle (Boulanger & Arseneault, 2004; Girona et al., 2018b; Navarro et al., 2018; Ryerson et al., 2003), SBW effects on forest succession (Bergeron et al., 1995; Lavoie et al., 2021; MacLean, 1980, 2016; Martin et al., 2020), the synchrony of outbreaks over large areas (Bouchard et al., 2018; Sturtevant et al., 2015), and SBW population dynamics (Pureswaran et al., 2016; Régnière & Nealis, 2007; Régnière et al., 2019a; Royama, 1984).

The population density of this lepidopteran moth increases periodically to reach an outbreak level (Boulanger & Arseneault, 2004; Régnière & Nealis, 2007; Royama, 1984). In eastern Canada, SBW outbreaks follow a synchronized 30–40 year periodicity (Boulanger & Arseneault, 2004; MacLean, 1996). Over the twentieth century, outbreaks were concentrated into three main periods: 1905–1930 (moderate severity), 1935–1965 (long and less severe), and 1968–1988 (short and severe) (Aakala et al., 2023; Berguet et al., 2021; Navarro et al., 2018). Recent outbreaks became more severe (Blais, 1983), synchronized over large forest territories (Jardon et al., 2003), and reached more northern latitudes (Navarro, et al., 2018). The final outbreak of the last century (1968–1988) in eastern Canada affected a maximum area of 6 million ha at a moderate defoliation level and 21 million ha at a severe defoliation level. At its peak in 1975, SBW had killed 3 million ha of forest (Lavoie et al., 2019; MFFP, 2021).

The increasing trend of SBW defoliation was interlinked to complex processes occurring within the forest stands. The extent and intensity of defoliation are influenced by factors such as species, tree age, stand composition, the presence or absence of nonhost species, the ecoregion (Houndode et al., 2021; Kneeshaw et al., 2015; MacLean, 2016), and climate (Candau & Fleming, 2005, 2011; Debaly et al., 2022). The vulnerability of the host (Nealis & Régnière, 2004), phenological synchrony or resistance (Blais, 1957; Pureswaran et al., 2015), nutritional composition of the needles (Bauce et al., 1994; Fuentealba & Bauce, 2012), and food quality provided by the host (Carisey & Bauce, 2002) also play roles in intensifying or limiting the defoliation impacts on growth. During the defoliation period, SBW generally starts affecting the architecture of the host by causing major damage to (Hughes et al., 2015) and/or mortality of the terminal buds and parts of the axes (Krause et al., 2012; Simard & Payette, 2003). Eventually, successive defoliation over multiple years leads to growth suppression and heightens the probability of tree mortality (Houndode et al., 2021; MacLean, 1980; Pothier et al., 2012). Balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg), and red spruce (*Picea rubens* Sargent) are the main host species of SBW (Hennigar et al., 2008). Black spruce has become increasingly vulnerable to defoliation, leading to marked growth losses (Girona et al., 2023b; Hennigar et al., 2008; Hughes et al., 2015; Lavoie et al., 2019; Simard & Payette, 2003). In sum, defoliation has a multidimensional impact linked to multiple ecological factors interacting within the forest ecosystem (species, stand, climate, and ecoregion), including the active feeding phase of the SBW.

The SBW completes its life cycle within 12 months, which extends over two different years. In late summer, the adult moth mates and lays groups of 10 to 150 eggs on the needles of host trees. The hatched larvae (1st instar) build a silk cocoon to start diapause and be protected during the winter (Ciesla, 2011; USDA, 1985). The 2nd instar larvae—

inside the hibernaculum—do not feed and their survival depends on the quality of food reserves in the hatched eggs transferred from parent moth. Once suitable conditions occur, the larvae emerge (Dickison et al., 1986; Marshall & Roe, 2021). At the beginning of spring, the larvae molt into the 3rd instar phase, and successive larval phases (4–6th instars) feed voraciously on the buds, foliage, and new shoots of host species. The defoliation/infestation peak occurs in summer, mainly in June; such voracious feeding on nutritious foliage strengthens a larva's chances of survival and the following generation's offspring overwintering success (Marshall & Roe, 2021). The 6th instar larvae metamorphose into the pupal phase and then develop into a moth form (Boulanger et al., 2017) in July or August. Adult moths lay eggs on the foliage under favorable climate conditions (Régnière & Nealis, 2007).

All the biological events of SBW are linked to climate conditions (Dale et al., 2001; Gray, 2013; Han & Bauce, 1997; Wellington et al., 1950). Temperature and precipitation affect SBW development (Bellemin-Noël et al., 2021; Régnière & Nealis, 2007; Régnière et al., 2012), survivability and mortality (Han & Bauce, 1995, 1997; Régnière et al., 2012), range expansion (Régnière & Nealis, 2007; Régnière et al., 2019b), and SBW behavior in defoliating their hosts (Candau & Fleming, 2011; Gray, 2013). During spring, for example, an increased larval emergence from diapause is observed once the temperature increases above 10 °C (Pureswaran et al., 2018a), and moisture availability in summer alters the SBW diet during its active feeding phase (Carisey & Bauce, 2002). Climate changes in spring and summer (past and current) can affect both the insect and the host species; therefore, climate is a critical element influencing the SBW life cycle activities, e.g., accelerates or delays each stage to affect SBW feeding. This is linked directly to the growth of the host species.

Similarly, tree growth and development are influenced by climate (D'Orangeville et al., 2016; 2018; Girard et al., 2011; Girardin et al., 2016a; 2016b; Pappas, et al., 2022a).

Factors such as temperature, precipitation, and moisture availability influence the phenological cycle and, thus, growth (Guo et al., 2022; Pureswaran et al., 2018a; Rossi et al., 2011). An example is the earlier budburst because of recent warming (Blais, 1983; Pureswaran et al., 2018a). Several studies have documented that the radial growth of black spruce can be influenced in response to changes in climate—specifically climate of the growing season (Chavardès et al., 2021; D’Orangeville et al., 2018; Walker et al., 2015). For example, the onset of growth in black spruce, occurring from late May to mid-June, confirms the importance of favorable temperatures and moisture levels in the summer months (Rossi et al., 2011). Warmer temperatures in the short growing period in cold boreal regions favor black spruce growth (D’Orangeville et al., 2016; Rossi et al., 2011), and increased precipitation also benefits spruce by lowering moisture stress (Fierravanti et al., 2015). As climate also mediates SBW activity, the response of black spruce growth is modified by the SBW–climate links.

Climate fluctuations affect both the insect population and its impact on tree growth (De Grandpré et al., 2018a; Pureswaran et al., 2018b). It is expected that the spring and summer climate of the current and preceding year—closely associated with the active feeding period of SBW larvae and the tree growth—mainly regulate the characteristics of defoliation and the growth of the host species. Moreover, altered temperatures and precipitation during the summer (June–August), the active feeding period of SBW, can alter host–SBW interactions. Recent climate change, for example, has reduced the phenological and climatic mismatch existing between black spruce and SBW (Fuatealba et al., 2017; Pureswaran et al., 2018a). Thus, the recent defoliation trend during SBW outbreaks has raised questions about whether climate change is a major driving factor of the increased defoliation severity and decreased forest productivity observed during more recent outbreaks. This understanding of climate–defoliation interaction on host trees during insect outbreaks remains incomplete, despite their

importance within the context of global change (De Grandpré et al., 2018b; Pureswaran et al., 2018b; Robert et al., 2017). Specifically, no studies have yet to analyze the historical evidence of how climate fluctuations affect SBW defoliation severity, causing growth reductions for vulnerable host species like black spruce.

Here, our main goal is to evaluate climate–outbreak severity links on black spruce growth during outbreaks in the latter part of the twentieth century (1968–1988) and a part of the prior outbreak of twenty-first century (2006–2017). We rely on a dendroecological database for the province of Québec, Canada, to determine the climatic drivers influencing defoliation severity and leading to growth reductions in black spruce stands during outbreaks. We propose that (1) high temperatures and greater precipitation in the previous spring and summer reduce the current year growth of black spruce because of increased defoliation severity during an outbreak period; and (2) higher June temperatures limit growth by favoring a greater abundance and impact of SBW. Although there are ubiquitous factors influencing growth–defoliation interactions, directly and indirectly, spring and summer climate conditions are expected to have a greater influence. During non-outbreak years, black spruce remains vulnerable to severe defoliation, despite warmer temperatures favoring growth, as the warmer and wetter climate also favors SBW activity. Therefore, this project aims to improve our understanding of how temperature and precipitation modulate growth and SBW severity in the context of climate change. Our growth models attempt to produce accurate future predictions and forecasting of forest growth and productivity within various scenarios of future defoliation and climate in the boreal forest.

2.3 Methodology

2.3.1 Study area

The study area covers nearly 900 000 km² of the boreal and northern temperate vegetation zone of Québec (Canada) from 45° to 51°N and 65° to 80°W (Figure 2.1).

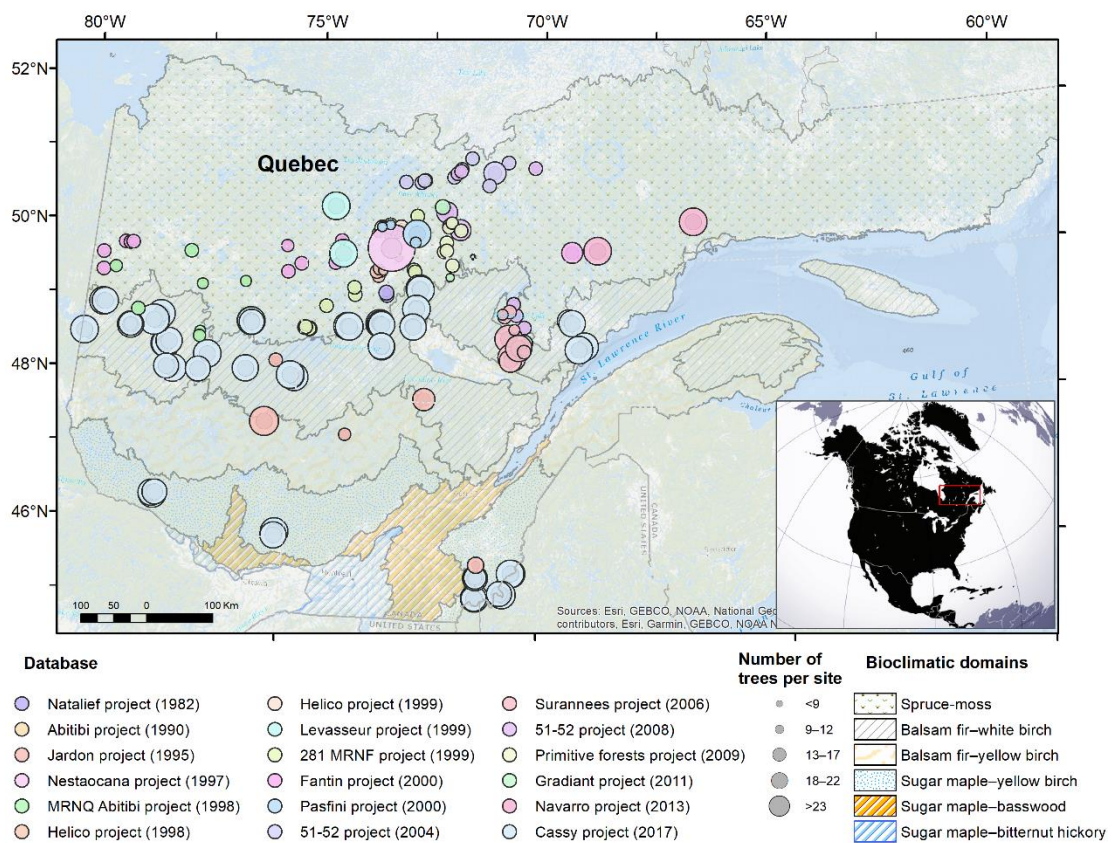


Figure 2.1 Location of study sites across the various bioclimatic domains in Québec, Canada. The colored circles correspond to those projects included within the dendrochronological database; circle size indicates the number of tree series for each site

Regional climate is subpolar–subhumid continental, characterized by long, cold winters and short, cool summers (Ministère des Ressources naturelles et de la Faune, 2008). The northern region is characterized by relatively colder/lower precipitation conditions with an annual average temperature of -7.5°C and annual precipitation of 500 mm, whereas the southern portion is warmer with an annual average temperature of 1°C and an annual precipitation of 1000 mm (Ministère des Ressources naturelles et de la Faune, 2008). In Québec, the closed boreal forest is dominated by pure black spruce stands in the north and the mixed forests of white spruce, fir, and broadleaf trees in the south (Rossi et al., 2009). The black spruce domain has a relatively short growing period of 93 to 142 days, extending between late May to early October (Rossi et al., 2011). In the eastern Canadian boreal forest, SBW outbreaks represent one of the major natural disturbances affecting these forests (Cappuccino et al., 1998; MacLean, 2016; Navarro, et al., 2018). In the twenty-first century, 17 million ha of forest has already experienced severe defoliation by SBW since the onset of an outbreak in 2006 (Annex I; MFFP, 2021). Fire, with a return interval of 270 to >500 years, is another disturbance influencing insect outbreak dynamics in the boreal forest (Bergeron & Leduc, 1998; Cyr et al., 2007).

2.3.2 Data compilation and experimental design

Our study relied on collected cross-dated dendrochronological series, defoliation surveys, and interpolated weather data sets. Because of the limitations of these various data sets in terms of the years covered, we selected to study the period from 1951 to 2017 (a period for which all data sets overlapped), which covers the third SBW outbreak of the twentieth century (1968–1988) and part of the current outbreak (2006–present; our data set covers 2006–2017). We compiled cross-dated dendrochronological series from 18 existing/previous projects conducted in Québec

over the past three decades (1982–2017). The combined database included approximately 4700 trees. From this compilation, we retained only those series corresponding to black spruce, as well as 11 sites of white spruce from the southern portion of study area where no black spruce were recorded, which resulted in a total of 2271 tree-ring series (Table 2.1). These trees were distributed across 164 sites, with an average of 14 trees sampled per site; site size was 400 m². In some cases, trees from the same project and ecoregion were merged, based on the geographic proximity, to form a single site and increase the number of trees for sites having significantly lower numbers of black spruce trees.

2.3.2.1 Dendrochronological data sets

Dendrochronology is a powerful tool for studying tree response to anthropogenic and natural disturbances (Gennaretti et al., 2018; Girona et al., 2016). All selected dendrochronological projects followed standardized protocols for collecting, preparing, measuring, and cross-dating (Krause & Morin, 1995). The ring cores were taken from the field, air-dried, and then sanded after mounting on wooden boards. Ring width was measured either with a WinDendro™ system (Guay et al., 1992; Tremblay et al., 2011) or a manual Henson micrometer having an accuracy of 0.01 mm. The annual growth rings were counted for each sample, and diagnostic rings (light, dark, narrow, or incomplete) were identified to facilitate dating (Girard et al., 2011).

These tree rings were cross-dated visually and cross-checks were made using COFECHA (Holmes, 1983) to identify missing or false rings and verify measurement errors. Accurate cross-dating minimizes errors related to growth anomalies, e.g., missing or false rings (Swetnam et al., 1985). We assigned a calendar year to each ring. The ring records in our database covered 67 years and varied in yearly abundance from

Table 2.1 Dendrochronological projects compiled for this study

ID	Project name	Sampling year	Number of sampled trees	Total number of sites	Trees per site (Min.–Max.)	Max. tree age	Reference
1	281 MRNF	1999	162	16	9–12	218	–
2	51–52 I	2004	116	11	10–16	247	(Tremblay et al., 2011)
3	51–52 II	2008	90	8	10–15	200	
4	Abitibi	1990	7	1	7	212	
5	Cassy	2017	1084	57	14–22	227	(Berguet et al., 2021)
6	Fantin	2000	124	12	9–15	179	(Fantin & Morin, 2002)
7	Gradiant	2011	38	5	3–12	171	–
8	Helico I	1998	65	7	7–11	131	–
9	Helico II	1999	49	5	9–11	229	–
10	Jardon	1995	88	6	9–21	352	(Levasseur, 2000)
11	Levasseur	1999	40	2	20	173	
12	MRNQ Abitibi	1998	62	7	8–10	198	
13	Natalief	1982	31	3	10–11	157	–
14	Navarro	2013	40	2	20	278	(Navarro et al., 2018)
15	Nestaocana	1997	34	1	34	175	–
16	Pasfini	2000	42	4	7–20	191	–
17	Primitive forests	2009	78	8	9–10	276	–
18	Surannees	2006	121	9	8–20	251	–
Total			2271	164			

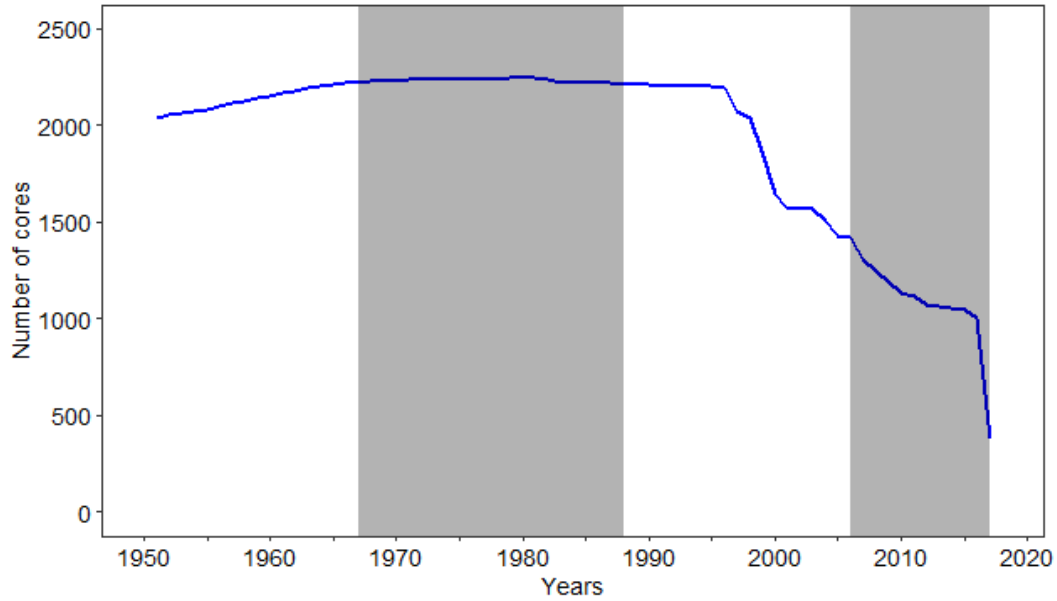


Figure 2.2 The number of tree cores sampled for each year from 1951 to 2017. The shaded area represents the two SBW outbreak periods, 1968–1988 and 2006–2017

381 to 2248 tree cores per year (Figure 2.2). We converted these ring-width series into basal area increments (BAI, basal area growth is named growth hereafter, Eq. 1) using the *bai.out* function of the *dplR* package in R (Bunn et al., 2022).

$$\text{BAI}_t = \pi r_t^2 - \pi r_{t-1}^2, \quad (\text{Eq.1})$$

where r denotes tree radius, and t is the year of ring formation.

2.3.2.2 Defoliation surveys

The defoliation survey data were collected from Québec’s Ministry of Forests, Wildlife and Parks (MFFP). The collected defoliation data were derived from annual defoliation maps produced by the ministry on a yearly basis since 1967 from aerial surveys of SBW-affected areas (Annex A; Gray et al., 2000). Surveys were conducted from late

June in the southwest to early August in the northeastern areas. A topographic map was used to delineate the polygons of insect damage for SBW, and each polygon was assigned a defoliation level for the current year (Gray & MacKinnon, 2006). The defoliation was categorized as light (1%–35%; loss of foliage in the upper third of the crown of some trees), moderate (36%–70%; loss of foliage in the upper half of the crown of most trees), and severe (71%–100%; loss of foliage across the entire length of the crown of most trees) (MFFP, 2021). Because the survey primarily detects defoliation of balsam fir, we created a circular buffer of 20 km around each site and retained only those sites in which balsam fir was present (by relying on the Québec forest inventory data). Therefore, we used the defoliation class as a proxy of SBW outbreak severity in the landscape surrounding our sampled black spruce stands. For each stand in our dendrochronological data set, we computed for each growth year, the cumulative defoliation of the last five years. For this, the defoliation class for each year was converted to a numerical value: 0 for no active defoliation, 1/3 for light, 2/3 for moderate, and 1 for severe defoliation. We used the five years preceding the sample year, as SBW defoliation generally does not affect radial growth of the same year but rather affects growth with a lag up to five years (Bergeron et al., 1995; Krause et al., 2003, 2012; MacLean, 1980); this means that the defoliation index can reach up to 5 at maximum. Thus, we obtained a time series of outbreak severity within our study zone from 1968 to 2017.

2.3.2.3 Climate series

For each site, we modeled elevation using digital elevation model (DEM) data for Québec. We relied on latitude, longitude, and elevation to interpolate weather variables (at a daily resolution) for each site and year between 1951 and 2017 using the BioSIM software (Régnière et al., 2017). For selecting the predictors for our model, we

calculated climatic summary variables related to important stages in the phenology and biology of SBW (Candau & Fleming, 2005, 2011). These variables included temperature (°C, minimum and maximum) and precipitation (mm) at a seasonal scale—spring (March–May) and summer (June–August)—and at a monthly scale for June, July, and August. We also calculated the climate moisture index (CMI) for the spring, summer, and June-August (for each month) following D’Orangeville et al. (2018); monthly potential evapotranspiration (PET) values were estimated with the Standardized Precipitation Evapotranspiration Index (SPEI) package in R and running the Penman–Monteith algorithm with inputs of monthly average daily minimum and maximum temperature, latitude, incoming solar radiation, temperature at dew point, atmospheric pressure, wind speed at 2 m, and elevation, where all the weather variables were interpolated using BioSIM. The spring and summer CMIs were calculated as the difference between precipitation and potential evapotranspiration over a period I (in mm of water; Eq.2).

$$\text{CMI}_i = \text{Prec}_i - \text{PET}_i \quad \text{Eq.2}$$

2.3.3 Statistical analysis

Statistical modeling was performed in two steps. In the first step, we modeled the logarithm of the basal area increment (log BAI) for each ring as a function of the log of the current basal area (cumulative BAI of previous rings) and its cambial age (Eq. 3) using a generalized additive model (GAM) to evaluate tree-specific effects on growth. The effect of logarithm of the basal area (log BA) was expected to be linear, whereas the age effect was modeled as a smoothing spline with $k = 50$ basis functions using the *mgcv* package in R (Wood, 2011).

$$\log(\text{BAI}) = \log(\text{BA}) + s(\text{Age}, k = 50) + \text{Residuals} , \quad \text{Eq.3}$$

The first model, thus, removed the long-term trend specific to each tree (i.e., because of the differences in age, size, and genetics). The residuals therefore contain the effects of interannual climate variation and SBW outbreaks, which we modeled in the second step. This two-step approach was applied in part because of the excessive computational costs associated with including all effects within the same model, given the size of our database.

In the second step, we used linear mixed effect (LME) models to estimate the effects of climate, outbreak severity, and the links between the two using lme4 package (Bates et al., 2015). At this step, the response variable consisted of the residuals of log(BAI) from the GAM model, averaged by site and year. The predictors were different combinations of cumulative defoliation of the last five years with seasonal (spring and summer of the previous year) and monthly (June, July, and August of the current year) climatic variables, along with their relationship to cumulative defoliation. All climatic predictors were standardized (i.e., values are centered around mean with a standard deviation) before including them in the models to simplify comparing the effect size between the predictors. We also included the random effects of site and year on the intercept in the models.

Because precipitation and CMI are correlated—via the definition of CMI—we used Akaike’s information criterion (AIC) to determine which of these two predictors to use in our models. We also used AIC to determine whether to include a random effect of site, year, or both (Mazerolle, 2020). For the base model including all climate variables and their effect on cumulative defoliation (Annex F-ID.7 and Annex H-ID.7), we used diagnostic plots to visually assess whether the model assumptions were met (normality of residuals and random effects, homoscedasticity, absence of residual trend). We also verified that there was no important collinearity between the variables ($VIF < 10$, Graham (2003); Annex B & Annex C). Then, we determined the statistically significant

relationship between predictors and the response on the basis of 95% confidence intervals ($\alpha = 0.05$). Finally, we tested whether we could create a more parsimonious model from our base model by using a backward selection approach to eliminate associations between some of the climate predictors and defoliation; we selected the best model using the model with the lowest AIC. We repeated the same process—analysis of the base model and creation of a parsimonious model—for the monthly climate variables since both seasonal and monthly variables can interchange the interaction effect on the growth of black spruce. All statistical analyses were performed using various packages in R version 4.2.0 (R Core Team, 2022).

2.4 Results

2.4.1 Growth, defoliation, and climate trends over time

All predictors of the GAM model had a significant effect on tree growth, and the model explained approximately 65% of the variation in basal area increment (Table 2.2). The model indicated that the average growth–increment process decreased continuously, following a nonlinear trend with tree age (Annex D).

Table 2.2 Summary of the generalized additive model (GAM) estimates for the effect of tree size and age

	Estimate	Std. error	<i>p</i>-value	Adj. R^2
Intercept	−3.853	0.023	0.001	0.65
log(BA)	1.001	0.002	0.001	
Significance of the				
smoothing predictor	edf	<i>F</i>	<i>p</i> -value	
<i>s</i> (age)	42.11	2504	0.001	

Mean individual tree growth varied year to year across all sites. Black spruce growth peaked around 1960 and again around 2010 (Figure 2.3a). A sharp drop in growth occurred between the early 1960s to around the 1980s, after which there was growth release in the ring widths for approximately five years. The minimum growth was observed between 1990 and 2000. Similarly, the mean cumulative defoliation across all sites reflected peak defoliation between 1970 and 1990; this period overlapped with a period characterized by a steep decline in black spruce growth (Figure 2.3b).

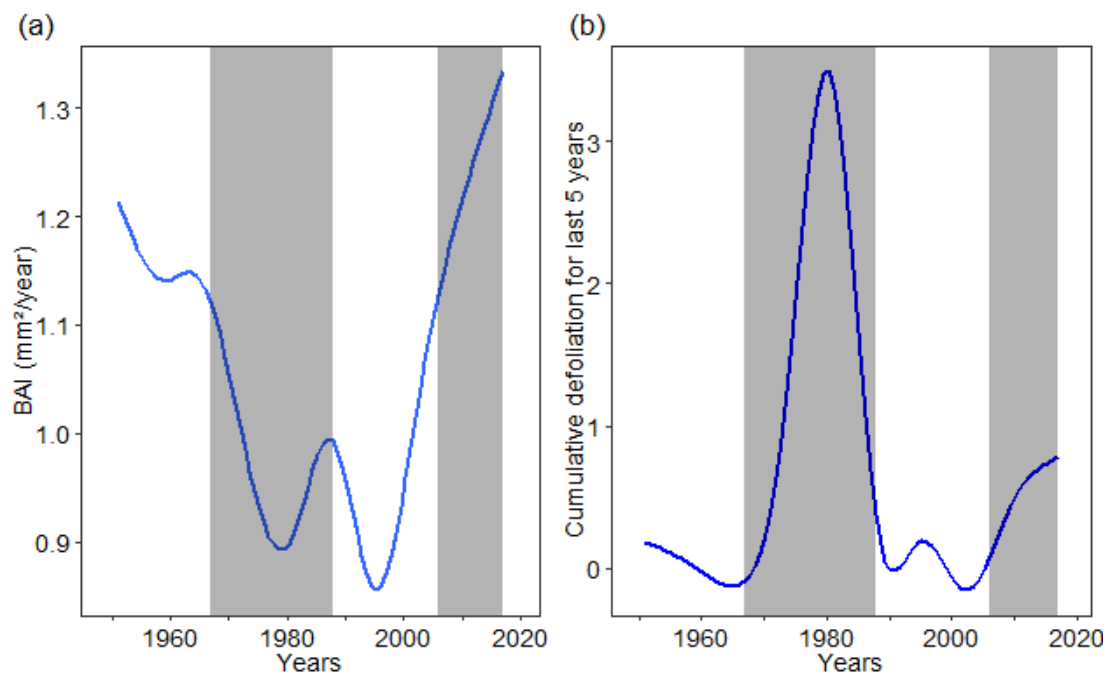


Figure 2.3 (a) Estimated yearly basal area increment of black spruce after the removal of tree-specific effects and (b) the cumulative defoliation by spruce budworm obtained from the defoliation survey. The shaded regions represent SBW outbreak periods

Regional climate, averaged across all sites over the 67 years, showed several patterns. Mean spring and summer temperatures were $-0.5\text{ }^{\circ}\text{C}$ (min. = $-7.0\text{ }^{\circ}\text{C}$, max. = $5.9\text{ }^{\circ}\text{C}$) and $14.8\text{ }^{\circ}\text{C}$ (min. = $8.5\text{ }^{\circ}\text{C}$, max. = $21.1\text{ }^{\circ}\text{C}$), respectively. Similarly, the average spring

and summer CMI were -6.5 mm and -19.1 mm, respectively. Nevertheless, the seasonal climate variables showed a significant ($p < 0.05$) increasing trend for the spring and summer temperatures, whereas the observed decreasing trend for spring and summer CMI was not significant (Figure 2.4).

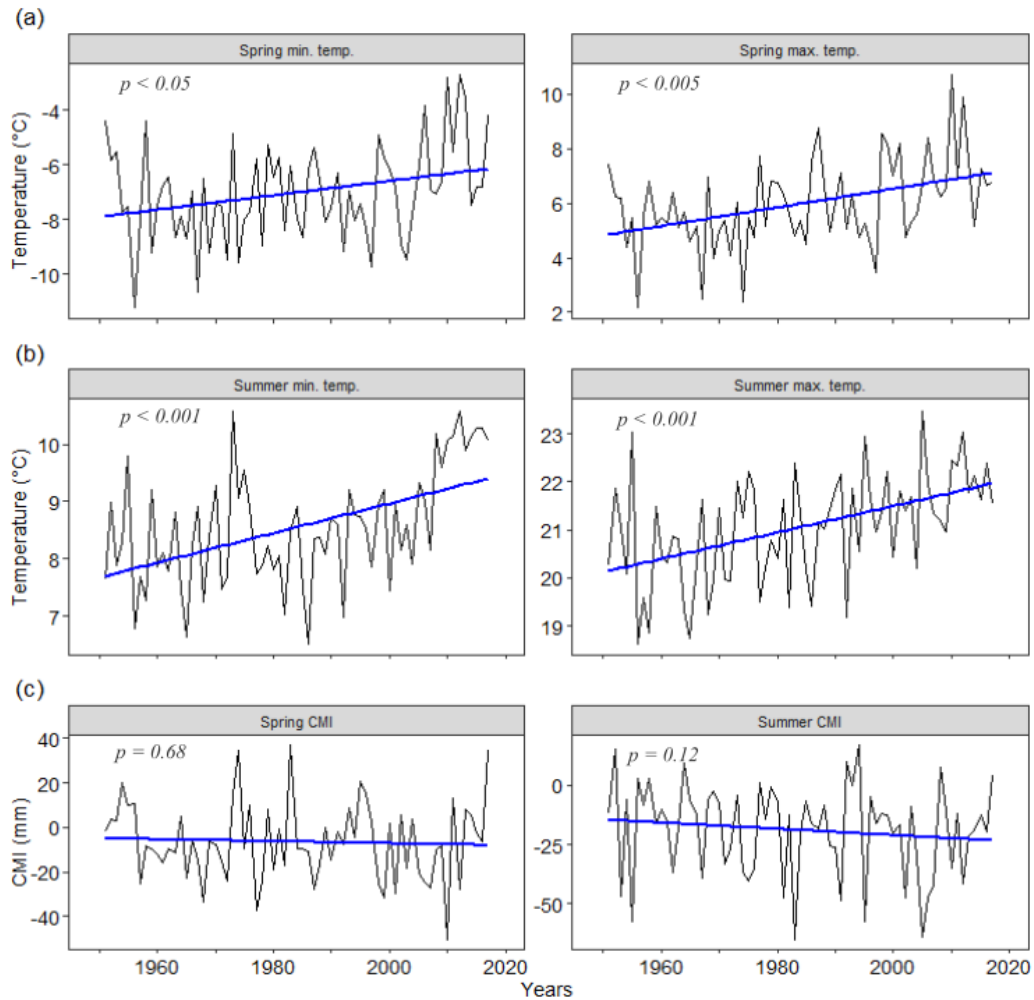


Figure 2.4 Trends of the averaged climatic metrics for all sites during the study period; (a) spring minimum and maximum temperatures, (b) summer minimum and maximum temperatures, and (c) spring and summer CMI

2.4.2 Growth model in response to defoliation and climate

We found that the model including site and year with CMI—rather than precipitation—produced the lowest AIC when choosing between different versions of the random effects and whether to use precipitation or CMI as a predictor. Therefore, for all models we used both site and year as random effects and CMI rather than precipitation.

The mixed effect model revealed that the variance of the intercept described by the random effects of the site and year were 0.09 and 0.01, respectively, with a residual variance of 0.04 (Figure 2.5). These model parameters comprising both random and fixed effects explained approximately 70% of the variation in black spruce growth. The main effect of SBW was that with a severe outbreak level within the previous five years, black spruce growth was reduced by 14% (i.e., $\exp(0.027 \times 5) = 0.14$). This effect on growth varied according to its relationship with the climate variables and, here, it is interpreted as a standardized effect, i.e., based on changes in the standard deviation of the climate predictors. Normally, previous summer minimum temperature is positively related to growth (11% growth increase), but during the outbreak, this climate effect is null (reduced by 11%). Like wisely, one standard deviation increase in the previous summer CMI uplifts the annual growth of black spruce by 8%; however, such positive response was lowered to 4% due to the SBW pressure. Contrarily, growth decrement due to increased summer maximum temperatures was attenuated by 7% due to the defoliation. Also, the growth was significantly increased by 9% with increasing spring minimum temperature during outbreak. Thus, SBW effect on black spruce growth varied with the change in temperature and CMI among the levels of defoliation severity.

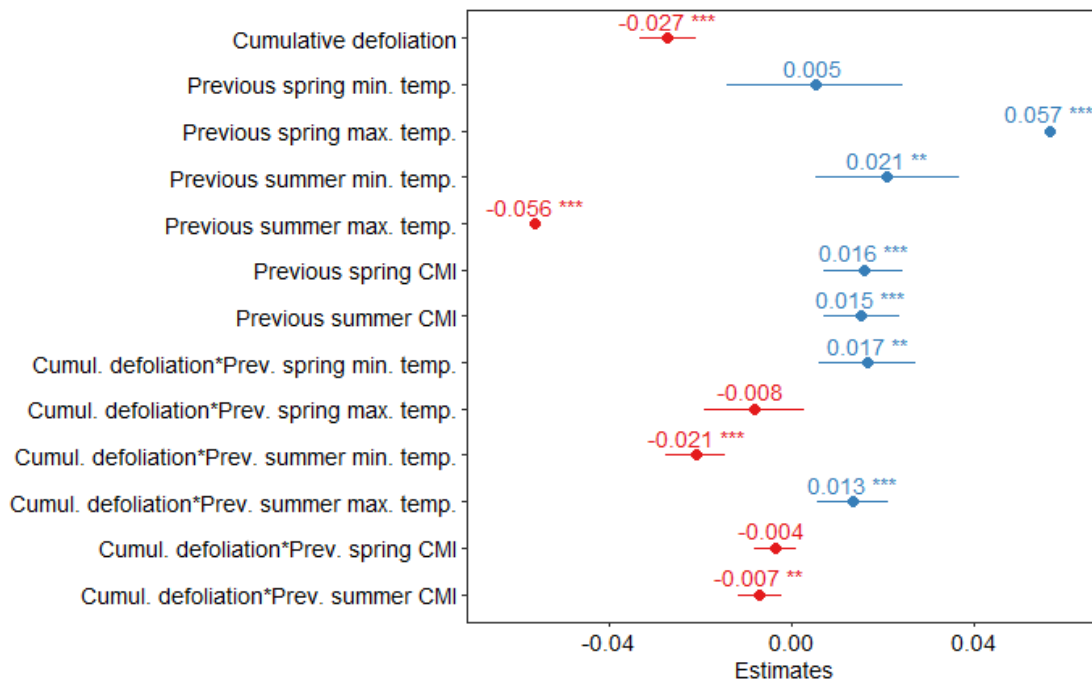


Figure 2.5 Effect of seasonal climate variables and defoliation on the annual growth of black spruce. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity (71-100% defoliation) across a site over the past five years. Significance: *** $P < 0.0001$; ** $P < 0.001$; * $P < 0.01$

Our best model improved its performance, as measured by AIC, when we removed the effects of cumulative defoliation coupled with the previous spring CMI and the previous spring maximum temperature (Annex F & Annex G). The effect on growth was not significantly lower or higher, i.e., this optimal model preserved almost the same effects of the predictors as they had on our base model, and we identified a linear relationship between growth and the seasonal climatic parameters. The prediction graph showed that at the same defoliation level, the slope linking black spruce growth with climate conditions was either negative or positive depending upon the specific climate variable (Figure 2.6a).

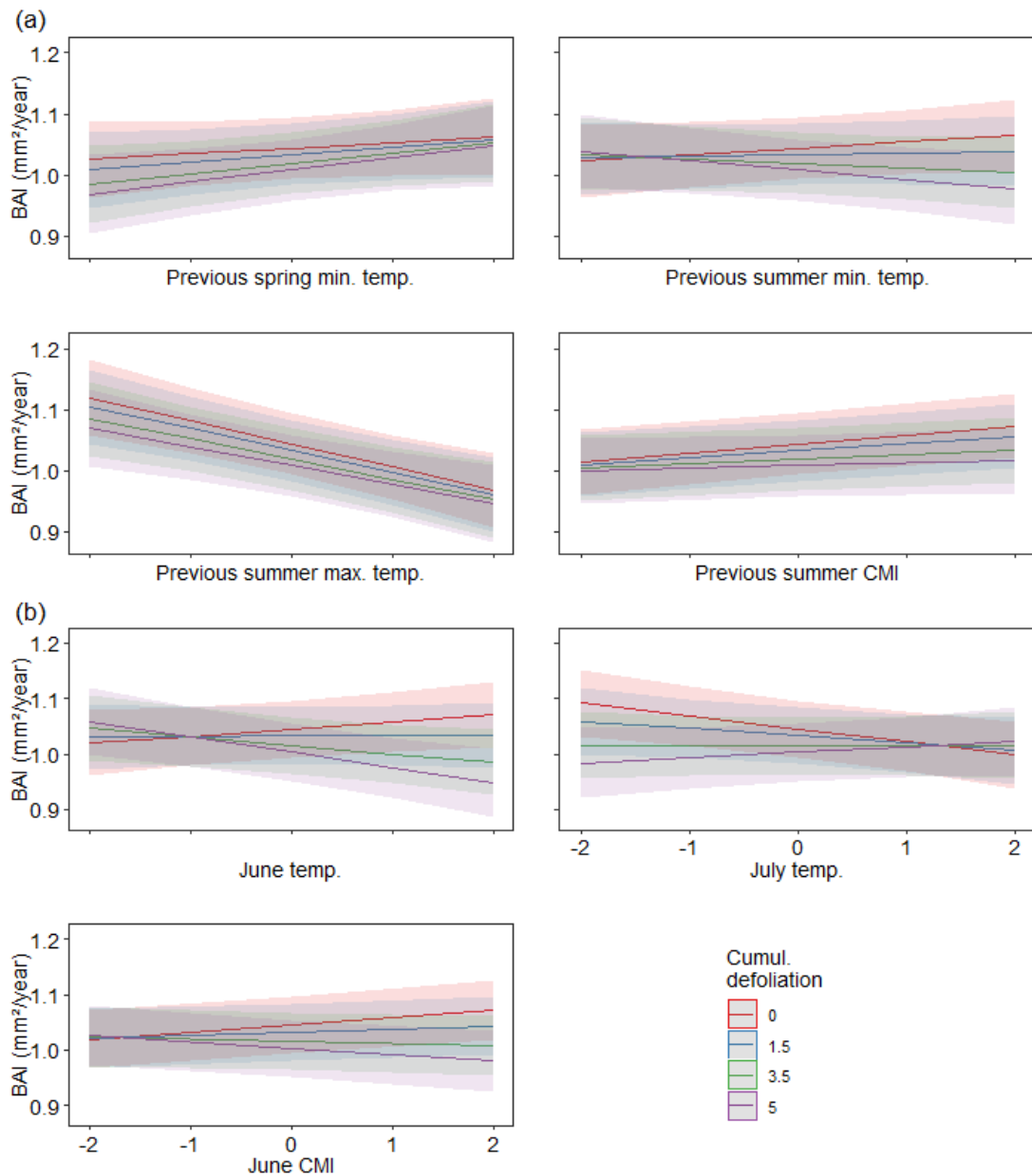


Figure 2.6 The effect of interaction of (a) seasonal climate variables and (b) monthly climate variables with defoliation on basal area growth. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years; the cumulative defoliation represents the sum of maximum outbreak severity (71-100% defoliation) across a site over the past five years

Table 2.3 The detailed parameter estimates for the best model identified after comparing the AIC for monthly predictors. The response represents the residuals of log(BAI) after accounting the effects of tree size and age. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity (71-100% defoliation) across a site over the past five years. Note: The width of the confidence interval may have been underestimated as we obtained the estimates after the model comparison

Response: LogBAI			Marginal R2	Conditional R2
Random effects:			0.028	0.715
	Variance	Std.Dev.		
Site	0.095	0.308		
Year	0.014	0.119		
Residual	0.045	0.212		
Fixed effects:				
Predictors	Coefficients	Std. Error	Confidence interval	
			2.5%	97.5%
Cumul. Defoliation (Cum.Def.)	-0.032	0.003	-0.039	-0.026
June Temp.	0.006	0.007	-0.008	0.021
July Temp.	-0.016	0.008	-0.032	0.000
August Temp.	0.013	0.008	-0.004	0.029
June CMI	0.016	0.004	0.009	0.024
July CMI	0.019	0.003	0.013	0.026
August CMI	0.007	0.003	0.000	0.013
Cum.Def.:June Temp.	-0.032	0.003	-0.038	-0.025
Cum.Def.:July Temp.	0.030	0.004	0.023	0.038
Cum.Def.:Aug Temp.	0.005	0.003	-0.001	0.012
Cum.Def.:June CMI	-0.020	0.002	-0.024	-0.016

The model with monthly climate predictors as well as SBW effect described 72% of the variation in black spruce growth with the inclusion of the random effects of site and year. During the outbreak period, the monthly model indicated that the growth of black spruce was reduced by 18% due to cumulative severe defoliation for last five years (Annex E). Black spruce showed an improved growth with increased June temperature (not significant) and June-August CMI (4-10%), but a significantly negative response with warmer July temperatures (8%). However, all these growth-climate interfaces were reversed due to the SBW effect. With this impact, an increase in June temperature and June CMI led to a further growth reduction of 17% and 11% respectively. The growth reduction slope because of the relationship between June temperature and defoliation was steeper than for June CMI and defoliation (Figure 2.6b). Nevertheless, the SBW effect led to increase the growth by 17% with the increase in the July temperature—even if it has negative growth relation in the absence of defoliation. Our best-selected monthly model showed improved performance when the combined effect of cumulative defoliation and July and August CMI was removed (Table 2.3 & Annex H).

2.5 Discussion

Climate change and disturbance regimes are major drivers in the Canadian boreal forest (Dale et al., 2001; Seidl et al., 2017). We found that 70% of growth variation in black spruce depended on site characteristics and the relationship between insect disturbance and climate. Because climate can alter the life cycle of SBW, which depends on a host tree species for survival, the effects of defoliation on growth are also driven by climate. Multiple previous studies have found an independent relationship between defoliation and/or climate (Candau & Fleming, 2005, 2011; Debaly et al., 2022) and host species' growth (Girard et al., 2011; Marchand et al., 2019; Walker & Johnstone, 2014) in the

boreal forest. In contrast, here we highlight the effect of climate–defoliation on black spruce growth by relying on dendrochronological databases and SBW outbreak records covering the large ecoregion of Québec (Canada).

Our models highlighted a reduced black spruce growth in response to defoliation and climate change. This defoliation-related growth reduction (14%–18% per cumulative five-year defoliation when the other climatic variables are at their mean) is ecologically significant, particularly for a slow-growing species within the boreal zone, which is characterized by a relatively short growing period. The normal growth was hindered (a reduced growth of approximately 3% per year) due to the continuous stress imposed from the SBW defoliation. As a secondary host, black spruce holds the possibility of being less affected by SBW pressure relative to balsam fir and white spruce (Houdon et al., 2021; Nealis & Régnière, 2004). However, some studies previously indicated that the defoliation can lead a growth reduction that could reach up to 50% (Erdle & MacLean, 1999; Krause et al., 2012; Rossi et al., 2018). These studies indicated the direct defoliation impact on growth; whereas, our study highlighted the effect due to the spruce budworm pressure on black spruce during the outbreak period. In addition, the disparity of underestimation could be due to the broad spatial scale of the defoliation data that we averaged over the landscape, but it was the only information available on yearly basis in the province. Though black spruce showed distinct growth declination during outbreak period; the growth increment pattern during the current outbreak period might be due to limited dendrochronological datasets covering the period after 2006. In addition, our study demonstrated that the SBW effect on growth is modulated significantly by climate (Figure 2.5 and Annex E). Climatic variation influences outbreak severity and the extent of defoliation (Gray, 2013), and, the degree of defoliation also determines the extent to which climate affects host tree growth (Boakye et al., 2022). Both the direct climate effect on growth and how climate mediates the effect of defoliation depend on the specific climate variable undergoing

change (e.g., spring–summer temperature and precipitation) and time of the year. Thus, this macro perspective (large scale in space and time) to detect climate effect determining how much black spruce loses growth during a SBW outbreak is hoped to improve our understanding of the disturbance impact in boreal region. Nevertheless, we suggest incorporating multi-year tree-level defoliation estimates, in future studies, that could further widen insect-climate effects on growth, in addition to the result obtained here.

2.5.1 Effect of climate on growth

In years outside of SBW outbreaks, we found black spruce growth to be regulated either positively or negatively depending upon whether the models considered seasonal or monthly climate variables. Temperature (minimum and maximum), precipitation, available water, and winter snowfall have been identified as some of the important factors influencing black spruce growth (D'Orangeville et al., 2018; Hoffer & Tardif, 2009; Marchand et al., 2019). During the period when black spruce achieves peak growth, radial growth release occurs in response to increasing temperature (Rossi et al., 2011). In contrast, warmer temperatures in the late summer negatively affect growth (Fierravanti et al., 2015; Huang et al., 2010). The reduced growth with warmer maximum summer temperatures may relate to the heat stress imposed on trees as temperature increases, leading to lower photosynthetic activity and a water deficit (Fierravanti et al., 2015; Girardin et al., 2016b); this reduced growth may also be explained by carbohydrate loss (Amthor, 2000). Such warmer temperatures also increase water stress during photosynthesis for black spruce, thereby suppressing tree growth (Girardin et al., 2012; Huang et al., 2010). Girard et al. (2011) identified the close association of black spruce growth with precipitation, spring and summer temperature, and snowmelt/snow cover. Our results also support these black spruce

growth responses to seasonal temperature and moisture. Moreover, the carbon isotopic analysis of Walker et al. (2015) identified drought stress, i.e., warm spring temperatures and low CMI, as the underlying cause of reduced black spruce growth through desiccation. Walker et al.'s findings are confirmed in part by our study; the growth was limited by lower spring maximum temperature and spring CMI. Appropriate moisture availability in spring and summer is predicted to help trees compensate for the stresses caused by high temperatures. Chavardès et al. (2021) identified that higher June and July temperatures limited black spruce growth, and increased precipitation in August favored growth. However, July temperature was nonsignificant in our study. This difference can be explained by the geographic location of the sampled trees and differences in the species composition of the two studies; Chavardès et al. (2021) studied either pure spruce or mixed structure stands with trembling aspen in a region around 49°N, whereas our sites had mixed proportions of balsam fir covering a vast ecoregion from 45° to 51°N. Nevertheless, the observed effects of higher monthly (June, July, and August) CMI indicates the need for sufficiently humid conditions to favor radial growth of black spruce. Overall, we found that black spruce growth was driven more by the effect of temperature than precipitation; nevertheless, various other underlying factors could also affect growth, including the soil organic layer (Drobyshev et al., 2010), soil characteristics (Dufour & Morin, 2013; Girardin et al., 2016a, 2016b), latitudinal constraints (D'Orangeville et al., 2016; Huang et al., 2010), and species composition (Chavardès et al., 2021). We recommend incorporating these factors within future growth–climate models to provide additional insight into the response of boreal tree growth to a changing climate.

2.5.2 Effect of climate-defoliation interactions on black spruce growth

Black spruce growth was influenced by the effect of defoliation coupled with climate conditions. Positive climate anomalies of the previous summer can favor SBW activity at all levels of defoliation (Navarro, et al., 2018). The warmer summer minimum temperatures create a favorable window for the earlier emergence of SBW larvae from hibernation/winter-sleeping. Pureswaran et al. (2018a), in an experimental setting, observed a similar pattern of earlier larval emergence from diapause with increasing temperatures; therefore, it can be expected that warmer temperatures enhance SBW infestation that can augment the pressure on black spruce stands. Beyond the active defoliation period, we also observed growth favored by warmer summer minimum temperatures. These warmer conditions that benefit tree growth are reversed during outbreaks of greater SBW severity. Hence, warmer summer minimum temperatures made black spruce significantly more susceptible to SBW during the active defoliation period.

At a monthly scale, June is a critical month for black spruce growth and the SBW life cycle, as changes in climatic conditions affect bud phenology in black spruce and the defoliation behavior of SBW. Increased temperatures favor an earlier budbreak in black spruce (Bellemin-Noël et al., 2021; Pureswaran et al., 2018a; Rossi & Isabel, 2017), whereas regardless of climate-driven bud bursting, host trees that have undergone previous defoliation tend to advance their budbreak phenology approximately by a week in the year following defoliation (Deslauriers et al., 2019). Thus, we observe the narrowing of the phenological offset with the actively feeding phase of SBW larvae. Moreover, greater budbreak in black spruce increases SBW food availability and enhances feeding opportunities for the SBW larvae. Continuously produced fresh foliage limits any feeding competition among larvae when their populations begin to peak. The increasing damage of the foliage results in a loss of tree vigor that can

eventually be lethal to host trees. It also limits the ability of the host trees to expedite photosynthetic processes with the short growing period for boreal coniferous trees (Liu et al., 2019). Hence, increased synchronicity between budbreak in host species and larval emergence heightens SBW effect on growth in successive years (Bognounou et al., 2017; Candau & Fleming, 2005), and this is enhanced further by the warmer temperatures (Pureswaran, et al., 2015).

The growth release due to increase humidity in summer and June was reversed during the active defoliation period, which indicates the higher benefits for the SBW larva i.e., moisture availability favored SBW more than that for the black spruce, during outbreak. Appropriate moisture availability is also recognized to be an important climatic metric contributing to greater insect activity and outbreaks (Weed et al., 2013). With increased humidity of the summer, the larvae are able to obtain appropriate moisture contents from fresh foliage/buds (Carisey & Bauce, 2002). Since SBW don't feed during diapause, their survivability solely depends on the previously accumulated energy reserves during egg lay. Nutritious food increases the energy reserve for eggs which favors the survival of the early instar larva and escape potential mortality (Dickison et al., 1986). This means that the larva tends to get higher nutritive advantage from the humid foliage leading to the higher success of the overwintering larva during the hibernation (Carisey & Bauce, 2002). Eventually, this will lead to the high survival rate of SBW larvae in black spruce (Fuentealba et al., 2017). Besides, the moth dispersal is sometime facilitated by suitable humidity and precipitation (Larroque et al., 2022), which suggests the higher possibility of the extension of defoliating larva and immigrating to a new site in successive year. Such circumstances enhanced SBW population level and favored its expansion by elevating defoliation, consequently, leading to the significant growth reduction in black spruce.

However, the interaction effect of spring minimum temperature, summer maximum temperature, and July temperature with defoliation favored the growth, i.e., SBW-related reductions in growth because of SBW effect on black spruce being less at higher values for these listed climate variables. We can explain this pattern through two possibilities: i) such increased climate values make black spruce less vulnerable to SBW defoliation; or ii) the conditions are less favorable for SBW because of adverse climate conditions for this insect. Fierravanti et al. (2015) identified a reduced vulnerability for black spruce to SBW damage with warmer temperatures. During the spring, when the minimum temperature is almost always below freezing, warmer temperatures can favor greater photosynthesis activity leading to increased growth. Defoliation intensity can be lower with warmer minimum spring temperatures when the temperature increase is insufficient for the larvae to end their diapauses (Han & Bause, 1997; Pureswaran et al., 2018a). Higher summer maximum temperatures not only stress trees and limit growth (Chavardès et al., 2021; Fierravanti et al., 2015) and productivity of black spruce (Girardin et al., 2016a), but also affect SBW performance because the temperatures may be too warm for SBW survival (Régnière et al., 2012). Although some studies have found that high temperatures can limit black spruce growth (D'Orangeville et al., 2018), we found that the coupling of warmer temperatures and defoliating SBW favored growth. Late summer high temperatures can be detrimental to larval survival (Régnière et al., 2012); a heat-related mass mortality of SBW larvae may occur, reducing the SBW effect on growth. Moreover, this SBW mortality from warmer conditions can occur simultaneously with mortality related to predation (Régnière & Nealis, 2007). Nevertheless, even variable temperatures before the onset or during the diapause phase of larvae profoundly affect the development, survivability, and mortality of the SBW larvae (Han & Bause, 1997; 1998). Because warmer conditions heighten the metabolic activity in insects, larval forms could develop faster and proceed earlier through their life stages (Bellemin-Noël et al., 2021; Candau & Fleming, 2005; Parmesan, 2007). Given that black and white

spruce have similar phenological cycles, SBW larvae can feed on the foliage of white spruce to lower the herbivory pressure on black spruce, thereby increasing black spruce growth (Nealis & Régnière, 2004). Similar circumstances could be expected with July temperatures (negative effect without SBW but positive with SBW effect). In July, the biological stages of SBW have already reached the reproductive period; therefore, limited defoliation can be observed. However, we cannot ignore the influence of natural enemies of the SBW (mainly birds, spiders, bugs, ants, and parasitoids) in the boreal forest that limit SBW populations and favor the growth of SBW host trees (Régnière & Nealis, 2007; USDA, 1985; Venier & Holmes, 2010). Thus, the surviving as well as immigrating population of SBW determines defoliation severity over years, and ultimately, the extent of SBW pressure on the growth of host species like black spruce in a landscape. All these complex interrelationships raise questions needing to be addressed to broaden our understanding of climate–insect–host dynamics and their interrelationships in the boreal forest.

2.6 Conclusion

The relationships between defoliation and temperature and precipitation of the current and the past year strongly influence black spruce growth. Our seasonal model explained 70% of the growth variation in black spruce modulated by the additive effect of defoliation (14% growth reduction for a cumulative five-year period) and the interactive effect of spring and summer climate (growth reduction 4%–11%). The increased growth response to summer minimum temperature and CMI during the growing season reversed because of how these climate factors affected SBW defoliation. Our monthly model, explaining 72% of the variation, showed an 18% growth reduction because of defoliation, which varied between 10% and 16% because of the interactions of SBW effect and climate. Heightened growth suppression was

evident with the warmer June temperatures because of a greater vulnerability of black spruce to SBW-related damage. Hence, climate modulates the complex growth–defoliation relationship while also making host trees more vulnerable to warming.

This observed pronounced effect on growth and productivity is expected to be heightened with future climate change. Our identification of the complex relationships between biotic and abiotic factors within the boreal landscape will help the sustainable management of the boreal forest by identifying stands situated in zones vulnerable to defoliation, given the current trends of climate change across large spatial and temporal scales. We suggest incorporating historical data for landscape-level studies, given their broad applicability within ecological research. This long-term knowledge provides an important direction for future research in building predictive forest growth models with the inclusion of defoliation classes and future climate and forecasting disturbance dynamics in the context of altered climate.

2.7 Contribution

Conceptualization: MMG, PM, and AS. Data compilation and curation: AS, MMG, and PM. Methodology design: PM, MMG, and AS. Analysis: AS. Validation: PM and MMG. Original manuscript draft preparation: AS and MMG. Editing and review: AS, MMG, PM, YB, and HM. Supervision: MMG, PM, YB, and HM. Resources: MMG and PM.

2.8 Funding

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2.10 Conflict of interest

All authors declare no conflict of interest.

CHAPTER III

CONCLUSION AND IMPLICATIONS

3.1 General conclusions

The productivity and the growth of boreal trees depend on the climate and the influence of disturbances such as insect outbreaks. Black spruce is an important host for SBW, and successive defoliation over years leads to growth reduction (Hennigar et al., 2008). Our models evidenced changes on the SBW effect with changes in climatic constraints. The growth of black spruce is highly influenced by the defoliation interaction with the prevailing climatic condition —specifically, with the change in temperature and climate moisture state of the previous and the current year. Thus, climate regulates the growth of black spruce as well as the impacts of different cycles of disturbances occurring on the forest surface.

3.1.1 Factors influencing black spruce growth

During non-outbreak periods, greater values of the spring maximum temperature and the spring CMI favor the growth of the black spruce by providing suitable temperature and moisture to initiate photosynthesis. For the summer season, increasing the minimum temperature and CMI (June, July, and August) is favorable to growth (Walker et al., 2015); however, high maximum temperature, specifically for the month

of July, imposes heat stress that limits growth due to carbohydrate loss and decreasing photosynthesis capability (Girardin et al., 2016). At monthly scale, increase in the July temperature limit the growth whereas increasing CMI has positive effect.

During an active defoliation period, when the severity reaches peak, the growth of black spruce is reduced sharply. This SBW effect is highly influenced by the temperature and moisture condition of the previous and current year as these factors favors defoliation. Among climatic predictors included in our models, the influence of summer climate is higher at a time of active defoliation. Specifically, warmer summer minimum temperatures make black spruce significantly more susceptible to SBW. On the contrary, though an increase in spring minimum temperature and summer maximum temperature were less favorable to SBW defoliation, black spruce responded positively, that lowered its vulnerability. Likewise, at the monthly scale, defoliation interaction with June temperature led to higher growth suppression of the spruce trees. The increased June temperature—compared to other variables—can increase SBW activity, even though it has some positive effects on black spruce growth during non-outbreak period. The higher values of the June CMI favored SBW infestation than the black spruce growth itself. Nevertheless, the growth reduction observed with an increase in the June CMI is smaller than that of the June temperature.

Hence, the positive effects of temperature and moisture content on the growth during growing season might be limited and/or reversed due to the effect of defoliation and/or SBW activity. The increase in temperature that enhances the phenological synchrony between budburst and larval emergence means an increase in the defoliation intensity with negative effect on growth. This indicates that climate modulates the SBW effect on the growth of host species in the boreal forest. Since climate is expected to alter rapidly in the 21st century, the impact of the SBW disturbances can be more severe

with the increased warming, which can be an additional threat that warrants consideration for the sustainable forest management in the boreal forest.

3.1.2 Ecological modeling approach

A challenging task in ecological research is to model tree growth that is associated with multiple interacting factors in the forest ecosystem (Girona et al., 2023c). Nevertheless, our study highlights seasonal and monthly models that best describe the black spruce growth variation in the context of increasing disturbance by SBW and the climate change scenario. The models used in the study are the integration of growth, defoliation by SBW, and the climate context. Historical data provides a powerful source of information to develop landscape-level ecological models, that can provide details about past, as well as some insights into the future. The big dendrochronological datasets used in the study assisted in extending the applicability of our models to a wider scale in Quebec. The incorporation of defoliation information from aerial surveys as a proxy for SBW outbreak severity and climatic variables interpolated using BioSIM into the growth models has shown that this modeling approach can be prioritized in upcoming studies. Future ecological models can also be improved by comparing model predictions to observed defoliation annually. The incorporation of multiple confounding variables such as forest compositional structure, associated disturbances like fire, forest harvesting, and soil characteristics can increase the predictability of growth models. Thus, our modeling approach provides direction for developing modeling protocols to reconstruct models from past to make the projection with the different class scenarios of defoliation and climate that are expected in the future, possibly for upcoming outbreaks.

3.2 Implications for forest management

This study will contribute to improve our knowledge about future damage from SBW, which may assist in implementing proactive measures to reduce the impact on forest stands and the associated economic losses due to outbreaks. Hence, these results will contribute to maintain forest health for the attainment of the sustainable forest management goals. The study will also help to better understand the ecology of SBW, the vulnerability of back spruce (the most harvested conifer in Quebec) and the influence of climate in growth during SBW defoliation.

This project provides a multifaceted benefit and support for the sustainable management and planning of the forest in Quebec. The prediction of the impact of climate on host trees is advantageous to the Quebec government for accomplishing its adaptive management strategy in response to insect outbreaks for forest management. For instance, insect control methods can be effective when the predicted climate forecast shows an increasing summer minimum temperature or an increasing June temperature. This is because our study indicates higher SBW activity favored by such climatic condition. It will help to generate a guideline for the implementation of the national forest strategies against the control of loss through SBW infestation. Besides, it broadens the fundamental understanding of SBW outbreak dynamics and to what extent management can alter the intensity and severity of defoliation. From the historical information on defoliation, its fluctuating effect according to the climatic variables is also affected by the site characteristics. This knowledge can aid in the development of more efficient hotspot and outbreak extent monitoring and deploying new or additional tactics for population control which enhances the cost-benefit of the forest.

Aside from SBW management implications, our project will help to improve the reliability of forest productivity and timber supply quantification/projections in a changing climatic scenario. The information obtained about the host-budworm interrelationship can provide a clue about the processes that makes black spruce vulnerable or resistant to defoliation in climate change context. For instance, the increased past summer minimum temperature and current June temperature means higher vulnerability of the black spruce to SBW defoliation in the current year. Whereas, in non-outbreak context, the increasing maximum temperature lowers the growth for upcoming year, so the harvesting plans can be developed accordingly. This can help to develop strategic management intervention aimed at maximizing economic benefit from the forest stand, both at the provincial and national scale.

3.3 Study limitations

A novel methodological approach was used to provide results with higher accuracy through the application of dendrochronological data, independent estimations of outbreak intensity, and generation of the weather data within the wide geographical forest area. However, there are always several constraints that bounds the interpretation of the results and limits the boundary of growth models that are dependent on wide array of predicting parameters.

Indeed, tree growth is interlinked with complex phenomena that are occurring in the forest ecosystem, i.e., it is a result of the interaction with different factors like age, size, gene, microsite factors, climate, soil, competition, composition, species, and disturbances. In this study, tree-specific effects were removed by retaining climate and SBW disturbance from the growth. Even though tree growth can be influenced by other

forest disturbances like fire, the model lacks additional disturbances as potential predictors. Besides, dendrochronological data were more limited for the current outbreak period compared to the outbreak period of 20th century. Whereas, despite having enough study sites located in the northern region of the study area, there was a lower number of sites in the southern region, which also contained host trees other than black spruce i.e., white spruce and red spruce. These species could be considered in further studies to quantify the growth variability due to SBW and climate in a larger ecoregion of Quebec including southernmost sites (Debaly et al., 2022).

Due to the unavailability of defoliation information before 1967, the study period was restricted to cover the last outbreaks of 20th century (1968-1988) and just the part of current (2006-2017) outbreaks. In categorizing the defoliation severity, the sites with tree mortality were classified as sites without active SBW defoliation. There can be some inaccuracies associated with the aerial surveys while categorizing the levels of defoliation (MacLean & MacKinnon, 1996). Nevertheless, these defoliation estimates were broadly averaged within the study sites, which can be one of the reasons that could have underestimated the growth reductions in black spruce due to the SBW effect. Another point of caution is that, since the defoliation survey were primarily targeted at fir stands, they are not a direct measure of the defoliation severity in black spruce stands; so, defoliation was used as a proxy for identifying the presence/absence of SBW around the sites, and its pressure on the black spruce during outbreak periods.

Finally, although software like BioSIM generates precise interpolations with complex model, due to the limited number of weather stations and their great distance from our sites, the interpolated climate variable would still present small differences from the actual climate at the sites. Site-specific weather stations which can record real-time weather variability could generate more accurate insight of climate-defoliation

interaction effects. This means to indicate that there can be some uncertainties in the source climate that could have potentially led to have relatively small climatic effects in this study.

3.4 Perspectives and future research

In eastern Canada, the cyclic outbreaks of SBW have lowered the economic benefit from forest stands (Chang et al., 2012). Recent trend in the climate has altered the extent and the range of SBW disturbances (Pureswaran, et al., 2018b; Seidl et al., 2017). Even though the effect of climate and insect biology is evident to some extent, questions remain on how the interactive effect of insect-caused defoliation and climate influences the growth of host trees like black spruce. To answer these questions, the study outlined climatic factors that can amplify or attenuate the SBW effect on black spruce. We found that climate has a significant role to change the effects of defoliation impact on growth during outbreak. The quantitative growth models presented in the study identify a significant interaction effect between climate and defoliation, meaning that the defoliation impact on growth is also dependent on the seasonal and monthly climatic condition of the previous and current year. Nevertheless, it has given rise to several perspective questions that can be considered and addressed in future research.

The quantification of the growth can help to build the research and managerial guidelines for the boreal forest. The use of the defoliation records in Quebec as an approximation to the outbreak severity was a novel approach applied in this study, which can be extended to other studies. Though the aerial defoliation survey focused on specific outbreak regions, future studies could also rely on the remote sensing strategies to categorize and differentiate outbreak and non-outbreak regions and make a comparative effect on the growth models. Remote sensing data could also provide a

greater resolution of the defoliation variable than the three-level (light, moderate, and severe) scale of defoliation surveys. Moreover, since palaeoecological studies can offer higher temporal scale data than dendrochronological information, ongoing questions can also be approached palaeoecologically in future (Girona et al., 2018b). This will help in making projections of the impact of climate change on the ecological and economic balance of the boreal forest in future outbreaks.

Future landscape-level growth models for forecasting the forest productivity in the boreal forest should incorporate multiple factors that affect growth itself and disturbances cycles. Tree mortality factor, competition, and species compositional factors can improve model performance. While studying SBW disturbances, an essential consideration in these models should be given for the biological happenings of the SBW like diapause mechanism, dispersal, diet, and their demographic features (fertility, population, and mortality).

It is important to estimate the economic valuation of the loss due to SBW disturbance and climate effect in future studies which can be helpful for the cost-benefit analysis of the timber production in the boreal forest. The rate and extent of turnover in the forest-based economic generation, with regard to the disturbance and climate interaction in the forest productivity, can be highlighted. This can give an important insight about the trade-offs between the investment done for controlling insect and the economic return from the forest.

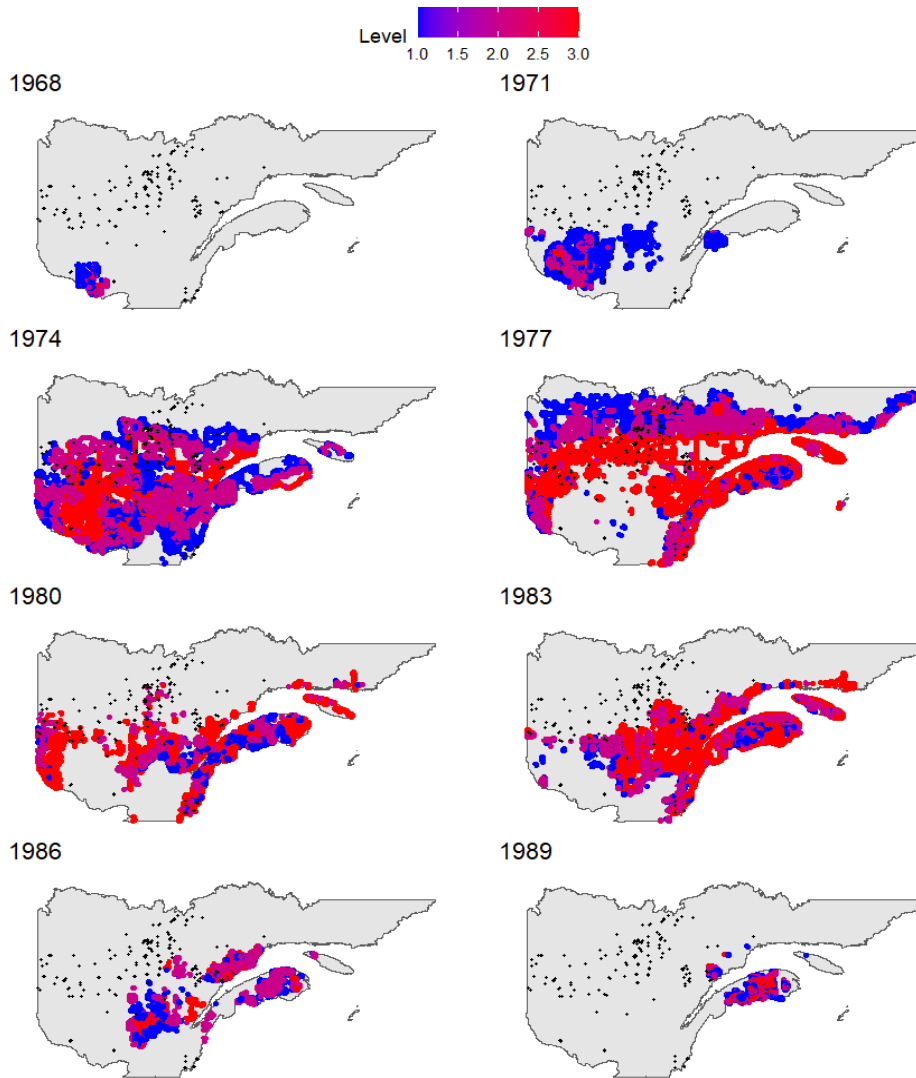
We suggest developing growth models considering historical data to make broad projection summary of defoliation severity and expected climate change scenario including their uncertainty curves, possibly for upcoming outbreaks. This forms an important perspective in building predictive models for the defoliation intensity that could ever happen within expected climate scenarios in the boreal forest. Moreover,

the defoliation severity is ultimately determined by the spruce budworm population level (number of feeding larvae per branch) each year, and this is determined mainly by survival of the local budworm population and immigration via moth dispersal and subsequent egg lay. Having these kinds of information for estimating multi-year defoliation levels, and including in the growth models, could enhance the understanding of insect-climate effects on the growth of host species. Thus, it is recommended to conduct additional studies on the forest growth and insect disturbance regime in changing climate context.

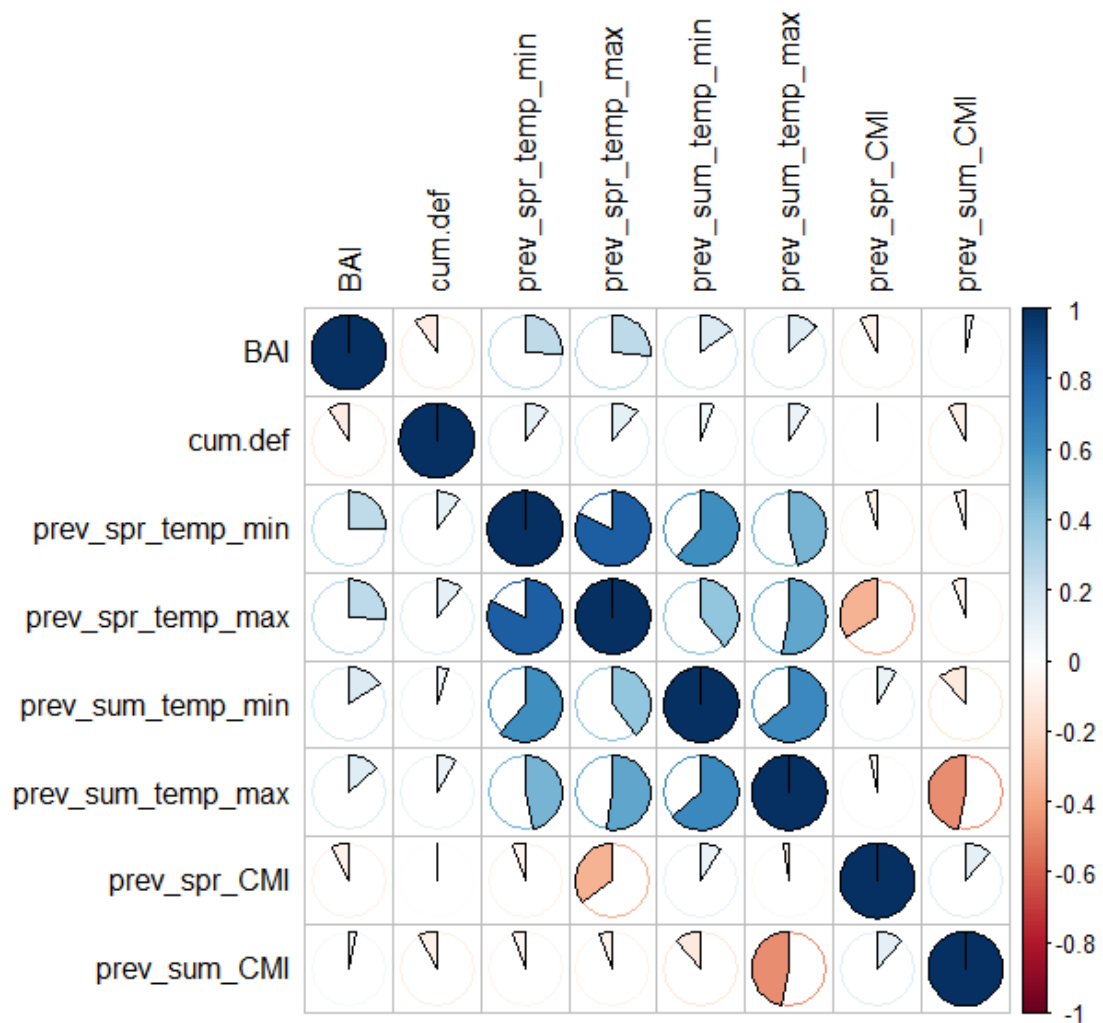
3.5 Scientific contribution

This research has a major scientific contribution in terms of its spatial coverage, temporal scale, datasets used and the methodological approach to answer the complex questions. Does climate and defoliation interact? If so, what are those variables that impact the growth of host-species? This study tried filling-in this research gap by exploring seasonal and monthly scale climate variables linked to the biology of SBW and black spruce growth. The identification of climatic variables that are interacting with the defoliation has provided an interesting clue for initiating additional scientific studies in this regime. An important insight is given by the study to make a comparative interpretation between previous and the upcoming findings, and to develop new research questions. Additionally, some possible discussion put forth in the interpretation of the results is expected to provide researchers with several scientific question for future studies. Moreover, the publication of a scientific paper will contribute to enhance the scientific knowledge about forest growth and the disturbance dynamism in the boreal forest. It is, thus, expected to improve the understanding about the insect disturbance and forest growth in the boreal ecosystem and provide a way to highlight shifting paradigm of scientific research in the field of ecology.

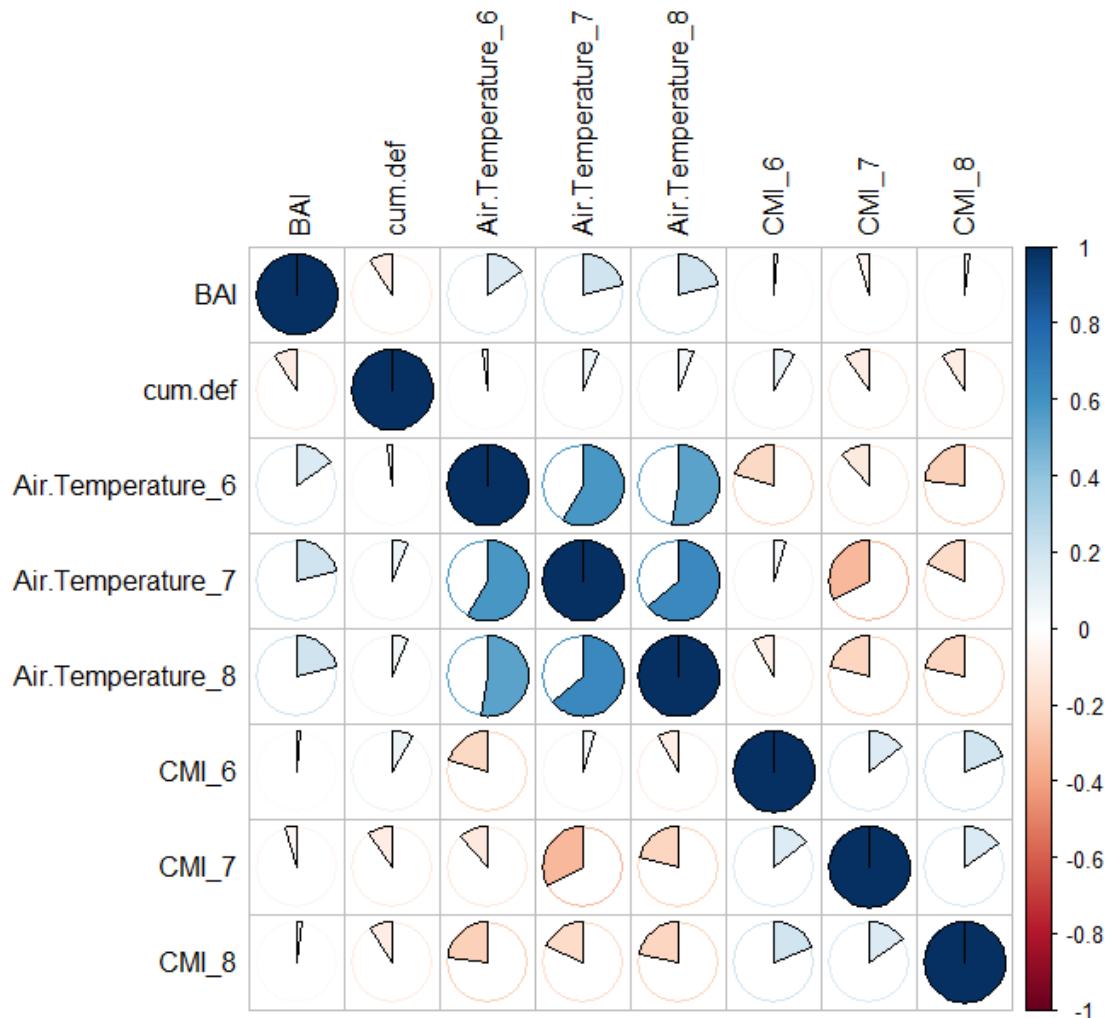
ANNEXES



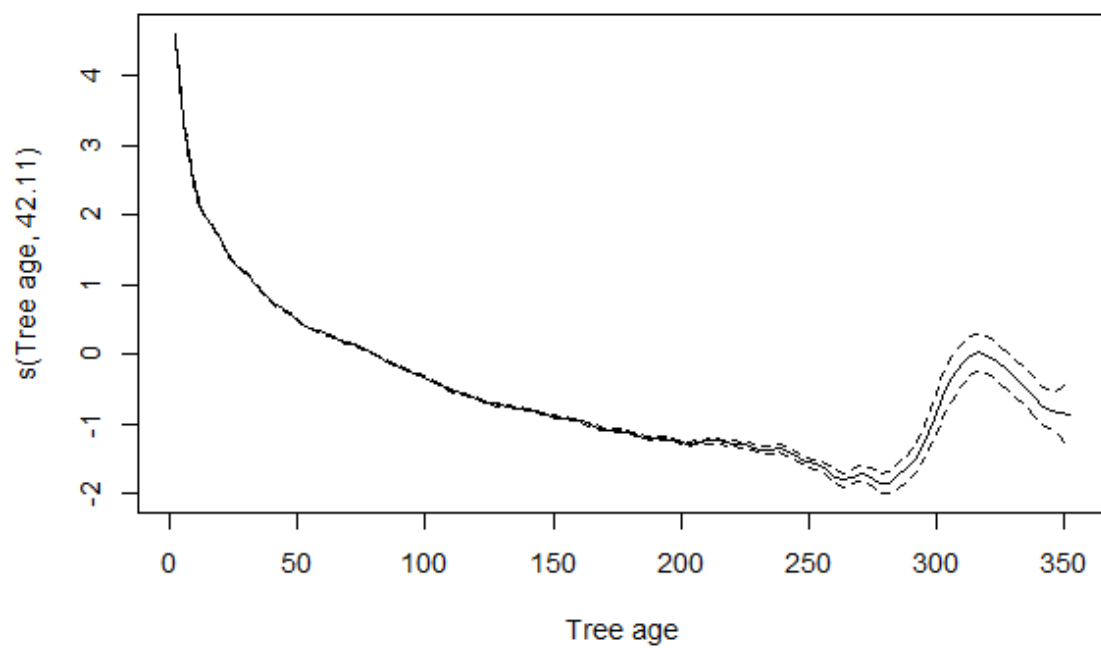
Annex A Spruce budworm defoliation intensity within the study sites from 1968 to 1989 at three-year intervals; levels 1(*blue*) to 3 (*red*) reflect the increase from light to severe defoliation



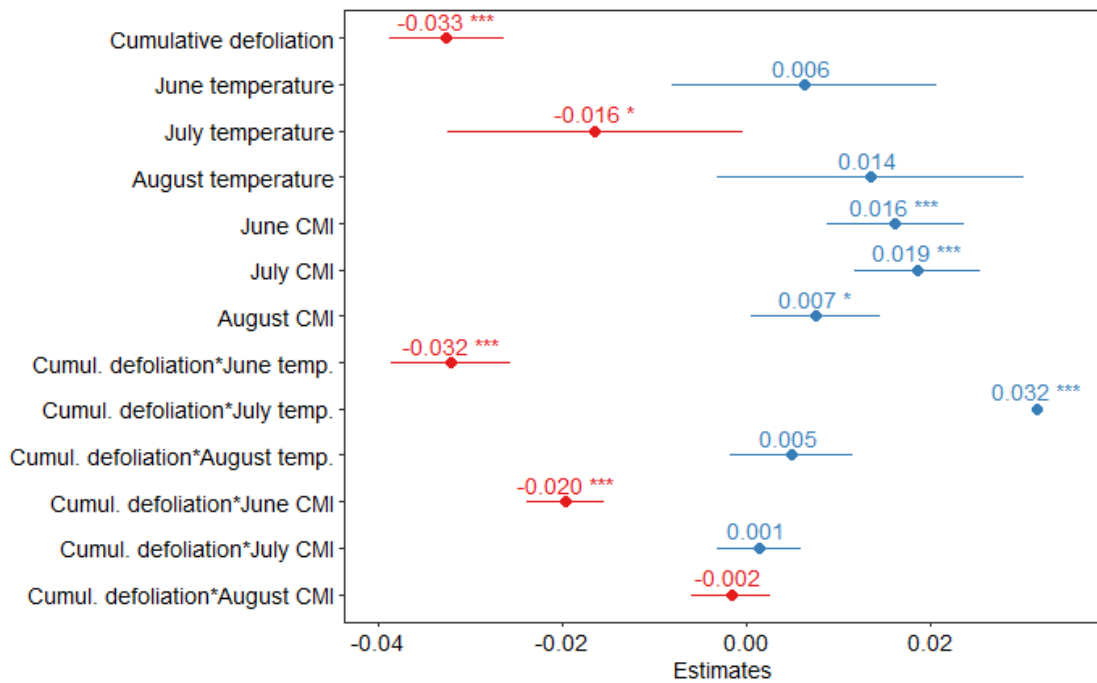
Annex B Correlation matrix for growth, cumulative defoliation, and seasonal climatic variables. The shaded portion within the pie chart denotes the correlation proportion with color indicating the correlation strength and whether the correlation is positive (*blue shades*) or negative (*red shades*)



Annex C Correlation matrix between growth, cumulative defoliation, and monthly climatic variables. Suffixes 6, 7, and 8 represent June, July, and August, respectively. The shaded portion within the pie chart denotes the correlation proportion with color indicating the correlation strength and whether the correlation is positive (*blue shades*) or negative (*red shades*)



Annex D The estimated GAM plot with a 95% confidence interval showing the non-linear relation of age with the basal area increment of black spruce



Annex E Effect of seasonal climate variables and defoliation on the annual growth of black spruce. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity (71-100% defoliation) across a site over the past five years. Significance: *** $P < 0.0001$; ** $P < 0.001$; * $P < 0.01$

Annex F Model sets for the seasonal climatic variables reported with their AICc score. Models were produced using different combinations of seasonal climate and defoliation with a backward selection approach, and the best model was identified using AIC criteria. Note: All these models have the random effect of the site and year in addition to the variables presented

ID	Models	K	AICc	Delta_AICc	AICc Wt	Cum. Wt	LL
1	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	15	-1345.81	0	0.27	0.27	687.9
2	prev_sum_temp_min + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	17	-1344.6	1.21	0.15	0.42	689.3
3	cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI) (BASE MODEL)	17	-1344.6	1.21	0.15	0.57	689.3
4	prev_sum_temp_max + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	17	-1344.6	1.21	0.15	0.72	689.3
5	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	16	-1344.42	1.4	0.14	0.86	688.2
6	prev_spr_CMI + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	16	-1344.27	1.54	0.13	0.99	688.2
7	prev_sum_CMI + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI)	16	-1338.54	7.27	0.01	0.99	685.3
8	prev_spr_temp_min + cum.def *(prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	16	-1337.39	8.42	0	1	684.7
9	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	14	-1337.12	8.69	0	1	682.6
10	prev_spr_CMI + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	14	-1324.18	21.63	0	1	676.1
11	cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	13	-1323.38	22.43	0	1	674.7

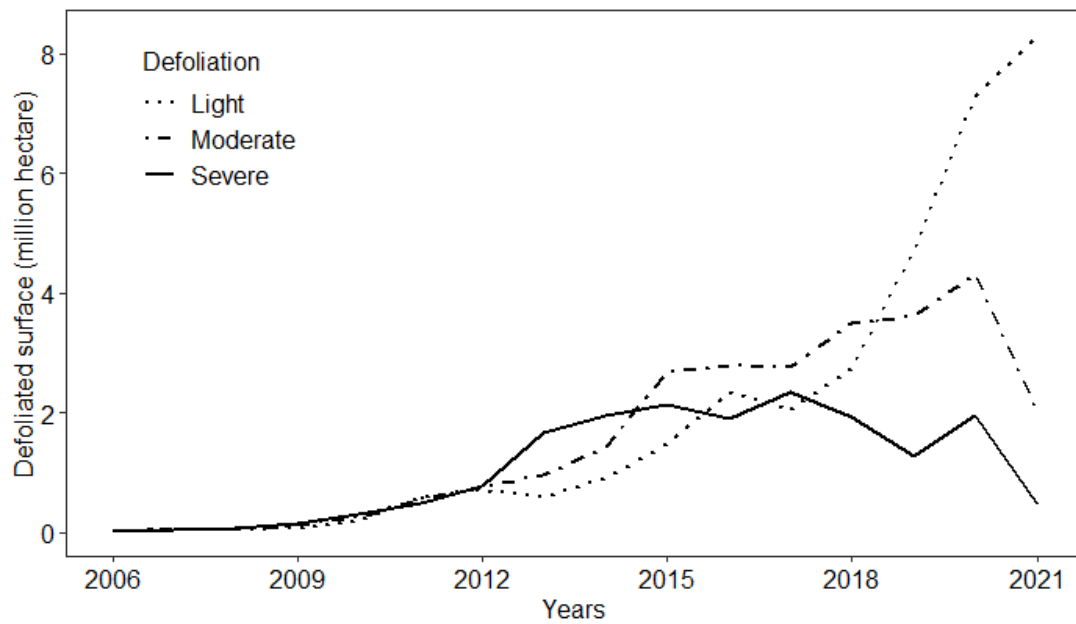
Annex G The detailed parameter estimates for the best model identified after comparing the AIC for monthly predictors. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity (71-100% defoliation) across a site over the past five years. Note: The width of the confidence interval may have been underestimated as we obtained the estimates after the model comparison

Response: LogBAI

			Marginal R2	Conditinal R2
Random effects:			0.032	0.702
	Variance	Std.Dev.		
Site	0.09123	0.302		
Year	0.01387	0.1178		
Residual	0.04525	0.2127		
Fixed effects:				
		Std.	Confidence interval	
Predictors	Coefficients	Error	2.5%	97.5%
Cumul. defoliation (Cum.Def.)	-0.028	0.003	-0.034	-0.022
Prev Spring Temp. Min.	0.009	0.010	-0.010	0.027
Prev Spring Temp. Max	0.051	0.011	0.031	0.072
Prev Summer Temp. Min.	0.019	0.008	0.004	0.035
Prev Summer Temp. Max	-0.053	0.009	-0.071	-0.036
Prev Spring CMI	-0.053	0.009	-0.071	-0.036
Prev Summer CMI	0.016	0.004	0.008	0.024
Cum.Def.:Prev Spring Temp. Min.	0.010	0.003	0.004	0.016
Cum.Def.: Prev Summer Temp. Min.	-0.018	0.003	-0.023	-0.013
Cum.Def.:Prev Summer Temp. Max	0.010	0.003	0.004	0.016
Cum.Def.:Prev Summer CMI	-0.008	0.002	-0.013	-0.004

Annex H Model sets for the monthly climatic variables reported with their AICc score. Models were produced using different combinations of seasonal climate and defoliation with a backward selection approach, and the best model was identified using AIC criteria. Note: All these models have the random effect of the site and year in addition to the variables presented. The numbers 6, 7, and 8 correspond to June, July, and August, respectively

ID	Models	K	AICc	Delta_ AICc	AICcWt	Cum. Wt	LL
1	CMI_7 + CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	15	-1387.6	0	0.33	0.33	708.8
2	CMI_7 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_8)	16	-1386	1.59	0.15	0.47	709.01
3	CMI_7 + Air.Temperature_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + CMI_6 + CMI_8)	15	-1385.9	1.69	0.14	0.62	707.96
4	CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7)	16	-1385.7	1.82	0.13	0.75	708.9
5	CMI_7 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	14	-1385.6	1.93	0.12	0.87	706.84
6	Air.Temperature_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + CMI_6 + CMI_7 + CMI_8)	16	-1384.3	3.26	0.06	0.94	708.18
7	cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8) (BASE MODEL)	17	-1384.3	3.27	0.06	1	709.18
8	CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	14	-1356.5	31.05	0	1	692.28
9	cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	13	-1351.3	36.25	0	1	688.67
10	Air.Temperature_7 + cum.def *(Air.Temperature_6 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8),	16	-1330.8	56.77	0	1	681.42
11	CMI_7 + Air.Temperature_7 + cum.def *(Air.Temperature_6 + Air.Temperature_8 + CMI_6 + CMI_8)	15	-1324.8	62.74	0	1	677.43
12	CMI_7 + CMI_6 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_8)	15	-1302	85.58	0	1	666.01
13	CMI_6 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_7 + CMI_8)	16	-1300	87.57	0	1	666.02
14	CMI_7 + Air.Temperature_6 + cum.def *(Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_8)	15	-1295.3	92.23	0	1	662.69
15	Air.Temperature_6 + cum.def *(Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8)	16	-1293.5	94.07	0	1	662.77



Annex I Area affected by SBW defoliation in Québec from 2006 to 2021, representing the first major SBW outbreak in the twenty-first century (MFFP, 2021)

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