

SHIFTING DISTURBANCES IN A WARMING ENVIRONMENT: THE
WESTERN SPRUCE BUDWORM AND DOUGLAS-FIR BEETLE IN
BRITISH COLUMBIA

by

Amberly Marciniak

B.Sc., The University of British Columbia, 2012

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES
(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

June 2015

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Abstract

Outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman), a native defoliator of Douglas-fir, appear to have been occurring further north in British Columbia (BC) compared to the early 1900s potentially as a result of climate change, but there is a lack of quantitative evidence to support this. I analysed the distribution of western spruce budworm infestation centers in forest health survey data for BC from 1967 to 2011 using a geographic information system (GIS) and linear regression. There was a significant ($p < 0.05$) range shift towards higher latitudes and elevations. I also tested the prediction that this range shift was a result of a climate change-induced northward shift in optimal synchrony between springtime budworm larval emergence and Douglas-fir budburst, since the budworm must feed on newly flushed, highly nutritious needles for the best chance of survival. I simulated the dates of first larval emergence and budburst annually from 1901 to 2011 using phenology models and long-term climate data, then analysed them with GIS and linear regression. The mean difference in dates at higher latitudes and elevations has indeed significantly ($p < 0.05$) converged towards optimal synchrony over the last century, while lower latitudes show divergence from optimal synchrony.

Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), a native bark beetle that infests Douglas-fir in BC, has been associated with stands recently defoliated by western spruce budworm, leading to increased mortality of large-diameter trees. I predicted that moderate defoliation intensity, which reduces tree defenses while leaving thick phloem for optimal Douglas-fir beetle breeding material, will be most closely associated with subsequent Douglas-fir beetle infestation. Evaluation of generalized additive models with long-term insect and biophysical variables showed that moderate cumulative severity of a defoliation event greatly improved model fit for predicting the presence of subsequent Douglas-fir beetle infestation. I concluded that interactions between biotic disturbance agents is an important consideration in future research and forest management because of additive or synergistic effects and how changes in the outbreak dynamics of one species under climate change will affect the other.

Preface

The following work was conducted in collaboration with my supervisor, Dr. Allan Carroll, who provided guidance on the research problems and concepts in Chapters 2 and 3, as well as contributed to the research design and manuscript edits. I resolved the details of the methods, collected, prepared and analysed all data and completed the full write up. Valuable contributions were made by Dr. Sarah Gergel and Dr. Lori Daniels in critiquing the methodology and providing manuscript edits. Chapter 2 and chapter 3 will be submitted to a scientific journal for publication.

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Acknowledgements

I would like to express my sincere thanks to my supervisor, Dr. Allan Carroll, for taking me on as an MSc student and providing me with amazing mentorship and support. Thank you for your unfailing patience and words of encouragement, without which I might never have gotten this far. I would also like to thank Dr. Lori Daniels and Dr. Sarah Gergel for being on my supervisory committee and for their constructive feedback on my methodologies and manuscript.

Many thanks to my fellow lab mates (Debra Wytrykush, Jordan Burke, Anthony Robinson, Romain Belvas, Stanley Pokorny, MarcAntoine Leclerc and Wesley Brookes) for their support, friendship and helpful advice. They were always willing to lend an ear or a hand when I needed it.

I wish to thank the British Columbia Future Forest Ecosystems Science Council, the Natural Sciences and Engineering Research Council of Canada - Alexander Graham Bell Canada Graduate Scholarships (CGS), and the University of British Columbia for funding this research.

And last but certainly not least, I am truly thankful for the unconditional support and love of my friends and family, and especially my parents, Leslie and Terry, who encouraged me to pursue my passion and, whenever difficulties arose, reminded me that I can do anything I put my mind to. To my dear friend, Elaine and my partner, Michael, thank you both for helping me to believe in myself.

1 General introduction

1.1 Forest insect disturbances and climate change impacts

A lot of research concerned with natural and human-driven disturbances has focused on how historical disturbance regimes may be altered due to global climate change. Disturbances, which are commonly defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett & White, 1985, p. 7), occur on a large range of spatial and temporal scales (Turner *et al.*, 1993; Swetnam & Betancourt, 1998). In forested environments, they can include such abiotic and biotic events as droughts, windthrow, wildfires and outbreaks of insects or pathogens, all of which play an integral role in driving forest structure, composition and functional processes (Dale *et al.*, 2001; Wong *et al.*, 2004; Raffa *et al.*, 2008; Marcoux *et al.*, 2015). The extent of damage to the forested landscape depends on the type and severity of disturbances and can range from some changes in the organization and structure of the community to large-scale tree mortality.

Outbreaks of insect pests that feed on tree tissues have had extremely large impacts on forest composition, ecosystem function and socioeconomic value in many parts of the world (Ayres & Lombardero, 2000; Dale *et al.*, 2001; Bale *et al.*, 2002). Such species usually occur naturally at low populations in their preferred forest habitats; for example, defoliators – insects that feed on plant foliage – often act as regulators of forest primary production during endemic (non-outbreak) periods (Larsson & Tenow, 1980; Cedervind, 2003). When certain conditions are met, however, a population may grow rapidly and reach a threshold where the damage they cause is severe and/or widespread enough for the population to be considered an outbreak or epidemic (Carroll *et al.*, 2006; Safranyik & Carroll, 2006). This usually occurs when several of the conditions that promote an insect’s reproduction and survival coincide, such as a particular host age or size class, climate conditions, or other environmental factors, resulting in increased population densities and disturbance (Carroll *et al.*, 2006; Cooke *et al.*, 2007). The rate and extent of mortality of host trees severely increases during outbreaks, which often results in large openings in the canopy, loss of habitat (e.g., mature trees that

cavity nesting birds rely on), or fragmentation of forest stands that impact many other animal, plant, or insect species in the community (Ayres & Lombardero, 2000; Raffa *et al.*, 2008).

Over the past century and a half, the world has experienced significant warming and an increase in climatic variability (IPCC, 2007, 2014). Record high temperatures have occurred since the 1970s, especially at higher latitudes in the northern hemisphere, and it is expected that the mean annual global temperature will increase by 1.8°C to 4.0°C in the 21st century (IPCC, 2007, 2014; Soja *et al.*, 2007). Climate change is a concern for forest management because shifts in temperature, precipitation and atmospheric greenhouse gas concentrations may have significant effects on forest ecosystem processes, including biotic and abiotic disturbances (Bentz *et al.*, 2010; IPCC, 2014). An increasing number of recent studies support that forest insect disturbances are often strongly and directly affected by global climate change (e.g., Ayres & Lombardero, 2000; Dale *et al.*, 2001; Bale *et al.*, 2002; Carroll *et al.*, 2004; Soja *et al.*, 2007; Bentz *et al.*, 2010). One infamous example in western Canada is the mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), which has been expanding its range and maintaining self-sustaining populations in more northern regions that were once climatically unsuitable for the species (Carroll *et al.*, 2004). Other studies have shown similar range expansions or increases in severity, extent, duration, or synchrony of outbreaks for various forest insect pest species, including birch bud moth (*Argyresthia retinella*) in Norway (e.g., Tenow *et al.*, 1999), pine processionary moth [*Thaumetopoea pityocampa* (Denis and Schiff.)] in the Mediterranean (e.g., Hodar & Zamora, 2004; Battisti *et al.*, 2005, 2006), spruce beetle (*Dendroctonus rufipennis*) in Alaska (e.g., Berg *et al.*, 2006; Sherriff *et al.*, 2011), and winter moth (*Operophtera brumata* Bkh.) and autumnal moth (*Epirrita autumnata* L.) in Fennoscandia (e.g., Jepsen *et al.*, 2008, 2011).

In general, it appears that in temperate and boreal forests, the rate of development and reproductive potential of many species are increasing due to rising summer temperatures, while warmer winter temperatures may be reducing winter mortality of insects susceptible to cold weather (Ayres & Lombardero, 2000; Bale *et al.*, 2002; Carroll *et al.*, 2004; Soja *et al.*, 2007). Excessive heat or drought from warmer temperatures and reduced precipitation may also be creating stress on host trees, making them more susceptible to insect attacks (Ayres, 1993; Croise & Lieutier, 1993). Plant fossils from around the Paleocene-Eocene Thermal

Maximum (PETM, 55.8 Ma), a global warming event that occurred at a rate and magnitude comparable to recent climate change, lend historical support for the effects of climate on insect herbivory (Wilf & Labandeira, 1999; Currano *et al.*, 2008; Wilf, 2008). Studies of these fossils found that the diversity and frequency of damage from herbivory increased over the late Paleocene and peaked during the PETM before returning to lower levels again after the PETM. There is overwhelming support that certain outbreaking insects are responding positively to climate change.

1.2 Climate change effects on defoliators and bark beetles

Outbreaking insects in boreal and temperate forests can be divided into two major groups: the defoliators and the bark beetles (Malmström & Raffa, 2000). Defoliators – usually caterpillars in the order Lepidoptera (moths and butterflies) – feed on tree leaves, which can result in reduced growth, top-kill, or even death of smaller trees due to repeated loss of photosynthetic material (Kulman, 1971; Wickman, 1978; Shepherd, 1992). Bark beetles, as their name suggests, breed and reproduce underneath tree bark where the beetle larvae feed on phloem, the living tissue that transports carbohydrates and other organic nutrients to various parts of the tree (Rudinsky, 1962; Wood, 1982; Christiansen *et al.*, 1987). Many bark beetle species only infest weakened or recently dead trees, but certain aggressive species can overcome the defences of large, healthy trees by attacking in large numbers after their population has built up within weaker trees (Rudinsky, 1962; Christiansen *et al.*, 1987; Negrón *et al.*, 2011). Unlike defoliation, which larger trees can generally survive by utilizing stored carbohydrates and relying on photosynthesis from untouched needles (Craighead, 1940; Langstrom *et al.*, 2001a; Cedervind, 2003), successful infestations by aggressive bark beetles always lead to death of the host tree (Rudinsky, 1962). Outbreaks of bark beetles often result in large-scale mortality of trees within a stand or across entire forested landscapes (Rudinsky, 1962; Christiansen *et al.*, 1987; Powell & Logan, 2001; Negrón *et al.*, 2011). Warming temperatures and changes in seasonal and annual precipitation due to climate change have been affecting the outbreak dynamics of both defoliators and bark beetles, although in different ways. Changes in the severity, duration, extent and range of

outbreaks have been observed for several species in both groups (e.g., Swetnam & Lynch, 1993; Dale *et al.*, 2001; Bale *et al.*, 2002; Carroll *et al.*, 2004).

For early-season defoliators that feed primarily on newly flushed foliage, climate change appears to be causing changes in the distribution and frequency of outbreaks as a result of warming induced shifts in phenological synchrony with their host tree (Thomson *et al.*, 1984; Visser & Holleman, 2001; Thomson & Benton, 2007; van Asch & Visser, 2007; Jepsen *et al.*, 2011). The emergence of feeding life stages in synchrony with budburst facilitates access to the highly nutritious young foliage, and is crucial for the survival and population growth of these defoliators (Carroll, 1999; Carroll & Quiring, 2003; van Asch & Visser, 2007). The emergence date of defoliator larvae each year depends directly on temperature, while budburst initiation often has an additional photoperiod requirement, and therefore will not occur until after a certain calendar date, no matter what temperature thresholds are met before that date (Thomson & Benton, 2007). The different requirements for larval emergence and budburst means that the insect responds more rapidly to changes in temperature than the host tree does. As a consequence of warming spring temperatures at higher latitudes, accumulating evidence suggests that larvae of some defoliator species have begun to emerge earlier, leading to closer synchrony with host budburst and a resultant northward shift in outbreaks due to increased larval survival (van Asch & Visser, 2007; Jepsen *et al.*, 2008, 2009, 2011). On the other hand, phenological asynchrony may occur in the southern extent of infestation ranges as defoliator larvae emerge too soon in reaction to increased temperatures and starve from lack of food (e.g., Visser & Holleman, 2001).

Outbreak dynamics of several aggressive bark beetle species have been impacted by climate change through direct and indirect effects of increased tree stress (Raffa *et al.*, 2008). For example, increased drought conditions have led to water stress and reduced vigour of trees, making them more susceptible to bark beetle attacks (Mattson & Haack, 1987; Breshears *et al.*, 2005; Bréda *et al.*, 2006; Negrón *et al.*, 2009). Sub-outbreak populations of bark beetles are attracted to drought-stressed or otherwise weakened trees because stressed trees have less energy to expend on defences (e.g., resin production to flush out attacking insects) (Safranyik & Carroll, 2006). Once the bark beetle populations are able to build up within the weakened trees, they will then mass attack large-diameter, healthier trees that have thicker phloem for

better breeding material (Powers *et al.*, 1999; Safranyik & Carroll, 2006; Negrón *et al.*, 2011).

1.3 Defoliator and bark beetle interactions

Trees stressed by severe or repeated defoliation may also be more susceptible to secondary attacks by bark beetles that share the same host (Berryman & Wright, 1978; Wright *et al.*, 1979; Langstrom *et al.*, 2001b). Bark beetle outbreaks have often been observed in stands where a defoliation event recently occurred (e.g., Cole, 1961; Berryman & Wright, 1978; Hadley & Veblen, 1993; Okland & Berryman, 2004; Steed *et al.*, 2007). Moderate defoliation may weaken the defences of large, otherwise healthy trees (Wright *et al.*, 1984; Fredericks & Jenkins, 1988; Cedervind, 2003), thereby allowing bark beetles to successfully attack with low populations (avoiding competition) while reaping the benefits of a thick phloem that normally would take mass attacks to access (Shrimpton & Thomson, 1985; Gričar & Čufar, 2008). Bark beetle populations may build up more rapidly in defoliated stands, resulting in increased mortality of large trees that may have otherwise survived defoliation. Indeed, several studies have noted higher mortality of overstory trees where a bark beetle infestation followed a defoliation event (e.g., Belyea, 1952; Cole, 1961; Wickman, 1978; Hadley & Veblen, 1993; Langstrom *et al.*, 2001a), suggesting an additive or synergistic effect of interacting defoliators and bark beetles.

If an interaction between defoliators and bark beetles does indeed exist, then in cases where climate change is affecting a defoliator, leading to changes in outbreak distribution or frequency, there is the potential for a “knock-on” effect where increased stress from defoliation could then affect the distribution and frequency of associated bark beetle outbreaks. For example, if warming induced shifts in phenological synchrony are leading to northward shifts in defoliator outbreaks (e.g., Campbell *et al.*, 2006; Jepsen *et al.*, 2008, 2009, 2011), then we might expect to observe a northward shift in associated bark beetle outbreaks as well due to increased areas of stressed, defoliated trees at higher latitudes. Many studies have looked at the effects of a single biotic disturbance agent on forests in terms of climate change impacts, but most have failed to consider how these effects may change if additive or synergistic interactions are occurring between two or more biotic disturbance

agents. My research is intended to shed light on this potentially important interaction by providing quantitative evidence for climate change impacts on a defoliator and its interaction with an associated bark beetle.

1.4 Research questions

1.4.1 Range expansion of western spruce budworm

The western spruce budworm is one of the most destructive and widely distributed defoliators in western North America, where periodic outbreaks have occurred in Douglas-fir forests for centuries (Harris *et al.*, 1985; Fellin & Dewey, 1986; Swetnam & Lynch, 1993; Volney, 1994; Campbell *et al.*, 2006). Reports of episodic infestations of western spruce budworm in western Canada did not occur until the early 1900s when widespread defoliation was observed on Vancouver Island in southwestern British Columbia (BC) (Thomson & Benton, 2007). Since 1930, however, outbreaks have ceased on Vancouver Island, but have been occurring instead within the interior of BC at higher latitudes and elevations (Parfett *et al.*, 1994; MacLauchlan, 2003; Campbell *et al.*, 2006; MacLauchlan *et al.*, 2006; Thomson & Benton, 2007). These observations suggest that there has been a shift of western spruce budworm outbreaks into more northern portions of its host range; therefore, my research will first aim to answer the questions:

1. Have distributional changes in western spruce budworm outbreaks indeed been occurring in recent decades in BC, as observations seem to suggest?
2. Could these changes be a consequence of a warming environment due to recent global climate change?

1.4.2 Douglas-fir beetle infestation subsequent to defoliation

Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) is another important pest of Douglas-fir trees. Sub-outbreak populations of the Douglas-fir beetle restrict attacks to low vigour and recently dead trees. Outbreak populations are often highly destructive by causing large-scale mortality of healthy, large-diameter hosts (Hadley & Veblen, 1993; Powers *et al.*,

1999; Ciesla, 2006; Negrón *et al.*, 2011). Douglas-fir beetle may preferentially and more successfully attack Douglas-fir subsequent to severe defoliation of its host trees by western spruce budworm. These two species have often been observed to reach outbreak level populations within the same regions in western North America (Fredericks & Jenkins, 1988; Gast *et al.*, 1991; Hadley & Veblen, 1993; Ciesla, 2006; Steed *et al.*, 2007). Many of these reports suggest that budworm epidemics may be an important precursor to Douglas-fir beetle outbreaks in regions that have had high host mortality during overlapping budworm and bark beetle outbreaks. However, there are also cases where a defoliation event does not lead to subsequent Douglas-fir beetle attacks (Hadley & Veblen, 1993). Given these observations, my objective is to answer a third question:

3. Does defoliation of Douglas-fir predispose it to subsequent Douglas-fir beetle attack?

1.5 Thesis structure overview

In Chapter 2, I analyse the annual changes in latitude and elevation of western spruce budworm infestation centers, as well as the annual changes in predicted synchrony between western spruce budworm larval emergence and Douglas-fir budburst dates across the province of BC.

In Chapter 3, I use generalized additive models to predict the probability of Douglas-fir beetle presence in a recently defoliated stand with explanatory variables that include defoliation characteristics, as well as other environmental and climatic characteristics.

Chapter 4 contains a summary of the key results of the thesis and a discussion of the implications of my findings in the face of future climate change. It concludes with suggestions for the direction of future research on biotic disturbance interactions in a warming environment.

2 In the pursuit of synchrony: northward shifts in western spruce budworm outbreaks in a warming environment

2.1 Introduction

Over the past century and a half, the world has experienced significant warming and an increase in climatic variability (IPCC, 2007, 2014). Record high temperatures have occurred since the 1970s, especially at higher latitudes in the northern hemisphere, and it is expected that the mean annual global temperature will increase by 1.8°C to 4.0°C in the 21st century (IPCC, 2007, 2014; Soja *et al.*, 2007). Climate change is a concern for forest management because shifts in temperature, precipitation and atmospheric greenhouse gas concentrations may have significant effects on forest ecosystem processes, including biotic and abiotic natural disturbances (Bentz *et al.*, 2010; IPCC, 2014).

One major type of biotic disturbance that will likely increase in extent and severity in the future is that caused by eruptive forest insect pests, such as bark beetles and defoliators (Ayres & Lombardero, 2000; Dale *et al.*, 2001; Soja *et al.*, 2007; Bentz *et al.*, 2010). In temperate and boreal forests, the rate of development and reproductive potential of many insects is expected to increase with increasing summer temperatures, while warmer winter temperatures may reduce winter mortality for species that are susceptible to cold (Ayres & Lombardero, 2000; Bale *et al.*, 2002; Soja *et al.*, 2007). Climate change may also indirectly affect insect herbivores; for example, excessive heat or drought creates stress on trees and lowers their defences, making them less resistant to insect attacks (Ayres, 1993; Croise & Lieutier, 1993; Raffa *et al.*, 2008).

Studies of plant fossils provide strong evidence for a link between climate change and increases in insect herbivory (Wilf & Labandeira, 1999; Currano *et al.*, 2008; Wilf, 2008). During the Paleocene-Eocene Thermal Maximum (PETM), 55.8 million years ago, a sudden spike of high temperature and $p\text{CO}_2$ lasted approximately 100 thousand years (Wilf & Labandeira, 1999; Currano *et al.*, 2008). Fossil angiosperm leaves from that period showed significant increases in insect feeding (e.g., Wilf & Labandeira, 1999; Currano *et al.*, 2008; Wilf, 2008). Furthermore, soon after the PETM ended and temperatures began to cool,

herbivory declined, indicating that the rise in insect feeding associated with rising temperatures and $p\text{CO}_2$ was not coincidental (Currano *et al.*, 2008; Wilf, 2008). These findings concur with predictions of future climate change effects on modern forest insect disturbance (Ayres & Lombardero, 2000; Dale *et al.*, 2001; Soja *et al.*, 2007; Wilf, 2008; Bentz *et al.*, 2010).

Defoliators in general often act as regulators of forest primary productivity, causing up to 10% loss of annual leaf biomass even during endemic (non-outbreak) conditions (Mattson & Addy, 1975; Larsson & Tenow, 1980; Cedervind, 2003). However, outbreaks occur periodically in some species and can cause extensive damage at the stand and/or landscape scale (Kulman, 1971; Shepherd, 1992; Cedervind, 2003). This is especially evident in temperate and boreal forest ecosystems where defoliation is a characteristic ecological disturbance (Cooke *et al.*, 2007; Nealis & Régnière, 2009). Build-up to local outbreak levels results when preferred host species, size class, or other environmental or climatic conditions coincide, thus leading to increasing rates of survival and reproduction (Cooke *et al.*, 2007). Normally for a landscape-scale outbreak to occur, these conditions must be distributed extensively and fairly contiguously over large areas (Roland, 1993; Cooke *et al.*, 2007).

The western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera: Tortricidae) is an eruptive defoliator that feeds mainly on Douglas-fir (*Pseudotsugae menziesii*) (Harvey, 1985; Fellin & Dewey, 1986; Volney, 1994; Nealis & Régnière, 2009). It is univoltine (produces one generation per year) in the majority of its range (Fellin & Dewey, 1986; Nealis & Régnière, 2009). The adults emerge in late July or early August, mate and lay eggs on foliage. Eggs hatch after approximately ten days and the new larvae immediately, without feeding, locate a sheltered place on the tree to spin hibernacula in which to overwinter. They normally emerge from their hibernacula as a second instar in early May to late June and temporarily mine needles and closed vegetative or reproductive buds (Fellin & Dewey, 1986; Nealis & Régnière, 2009). Once vegetative buds begin to flush, larvae preferentially feed on new foliage, which is usually completely consumed or destroyed before older needles will be fed upon (Fellin & Dewey, 1986; Shepherd, 1992; Nealis & Régnière, 2009). Severe or prolonged budworm outbreaks prevent hosts from renewing photosynthetic material, which reduces the tree's growth and vigour and may result in the

death of the top portion of the tree. Top-kill often leads to multiple leaders, stem deformation, predisposition to secondary insects and wood-decaying fungi, or even death of the entire tree (Van Sickle *et al.*, 1983; Fellin & Dewey, 1986; Alfaro & Maclauchlan, 1992).

The western spruce budworm is one of the most destructive and widely distributed defoliators in western North America (Harris *et al.*, 1985; Fellin & Dewey, 1986; Swetnam & Lynch, 1993; Volney, 1994; Campbell *et al.*, 2006). Outbreaks have occurred periodically within the Douglas-fir forests of western Canada and the United States (Harris *et al.*, 1985; Fellin & Dewey, 1986; Campbell *et al.*, 2006). Episodic infestations of western spruce budworm were first reported in the early 1900s in western Canada with widespread defoliation on Vancouver Island, southwestern British Columbia (BC) (Thomson & Benton, 2007). However, since 1930, outbreaks have only occurred at higher latitudes and elevations in the Douglas-fir forests of the interior of BC (Parfett *et al.*, 1994; Maclauchlan, 2003; Campbell *et al.*, 2006; Maclauchlan *et al.*, 2006; Thomson & Benton, 2007). These observations suggest that there has been a shift of western spruce budworm outbreaks into more northern portions of its host range.

This study was initiated to: (i) determine if distributional changes in western spruce budworm outbreaks have indeed occurred in recent decades, and (ii) assess whether changes are a consequence of a warming environment. Synchrony between the emergence of feeding life stages and the onset of budburst by host trees is critical to the survival of many early season insect defoliators, as leaves are easiest to eat and are at their peak nutritional value at this time (Feeny, 1970; Schweitzer, 1979; Larsson & Ohmart, 1988; Quiring, 1992; Carroll, 1999; Visser & Holleman, 2001; Bale *et al.*, 2002; Carroll & Quiring, 2003; van Asch & Visser, 2007). This is true for the western spruce budworm. Emergence by overwintering second-instar larvae approximately 18 days in advance of the onset of Douglas-fir budburst has been shown to be optimal for survival (Beckwith & Burnell, 1982; Thomson *et al.*, 1984; Thomson & Benton, 2007). Although early emergence by young larvae necessitates feeding on potentially suboptimal resources (old needles and unburst buds), it maximizes access to newly flushed foliage by later instars that are more dependent upon a high-quality diet to complete development (Lawrence *et al.*, 1997). The degree of synchrony, and therefore budworm survival, may vary from year to year due to differential responses by insects and

host trees to variations in temperature and precipitation (Shepherd, 1992; Bylund, 1999; Campbell *et al.*, 2006). Annual weather-related variations in the degree of synchrony suggest that the interaction between western spruce budworm and Douglas-fir may be very sensitive to climate change. Therefore, I predict that a northward range shift of western spruce budworm defoliation is a consequence of a climate change-induced shift in the regions with optimal synchrony between spring larval emergence and Douglas-fir budburst. If this prediction is correct, I would expect to observe a shift in the mean outbreak range of western spruce budworm towards higher latitudes and elevations, along with a similar shift in the optimal synchrony between larval emergence and Douglas-fir budburst.

2.2 Methods

An analysis of western spruce budworm outbreak data for BC from 1967 to 2011 was conducted to test the hypothesis that the mean range of outbreaks has shifted northwards. My prediction of a northward shift of optimal synchrony between budworm larval emergence and Douglas-fir budburst was also tested for in a second analysis where the dates of first budworm emergence and first Douglas-fir budburst were simulated across BC from 1901 through 2011 using budworm and host phenology models combined with long-term daily weather data. The following sections describe the data sources, the methods used to extract the relevant data and the statistical analyses that were conducted on the data.

2.2.1 Infestation data

Forest health data for the province of BC have been collected since 1998 by the BC Ministry of Forests, Lands and Natural Resource Operations, and from 1959 to 1995 by the Canadian Forest Service, Forest Insect and Disease Survey (FIDS). These data comprise the annual location, extent and severity of impacts by forest pests as determined from surveys using fixed-wing aircraft over the majority of the forested land in the province, including provincial parks, private land and tree farm licenses, but not federal parks (Van Sickle *et al.*, 2001; BC Ministry of Forests Lands and Natural Resource Operations, 2013). Surveys were conducted from early July through August when herbivory by forest pests was the most visible (BC

Ministry of Forests, 2000). Flight routes varied depending on the topography to ensure coverage of as much of the provincial forested land base as possible. Flight lines were generally flown following a grid pattern with some overlap over level terrain, but over mountainous terrain, flight lines usually followed map contours to increase efficiency, with one or more passes over valleys and watersheds depending on their size and the quality of lighting.

Local budworm populations fluctuate between extreme levels. At high densities, many thousands of larvae occur on a single mature tree, whereas at sub-outbreak levels there may be only a few individuals (e.g., Royama, 1984). As a result only high-density populations cause sufficient defoliation to be detected and mapped and therefore survey data comprise information on outbreak infestations only. Observable infested areas were identified and delineated by two observers and were plotted as either polygons for areas over 1 ha or points for infestations of less than 1 ha. These were drawn on topographical maps at a scale of up to 1:100,000. Afterwards, the mappers compared their respective rough sketch maps and consolidated them into a composite to be used for geographic information system entry. Aerial overview surveys are limited in that the total extent of pest incidence and damage usually cannot be determined without additional checks from the ground, which means that stand level decisions that require more detailed information should not be based on aerial surveys alone. I used the aerial overview survey data to identify the annual distribution and severity of outbreak infestations of the western spruce budworm within the province of BC. Infestations were delimited as polygons of defoliated trees.

2.2.2 Landscape modelling of larval and budburst phenology

The timing of western spruce budworm larval emergence and Douglas-fir bud flush in the spring is determined by the accumulation of thermal units, or degree days, which occurs when temperatures rise above a certain threshold (McMorran, 1973; Thomson & Moncrieff, 1982; Thomson *et al.*, 1984; Thomson & Benton, 2007). The temperature thresholds and degree day requirements differ between the insect and its host due to the difference in the underlying response mechanisms that determine the phenology of each (Chen *et al.*, 2003; Thomson & Benton, 2007; van Asch & Visser, 2007). Western spruce budworm larvae begin

accumulating thermal units as soon as the temperature exceeds the required threshold (Thomson *et al.*, 1984; Thomson & Benton, 2007). In contrast, photoperiod is important for the host to initiate development, and so Douglas-fir do not accumulate thermal units until after a particular calendar date, following which a temperature threshold must also be met (Thomson & Moncrieff, 1982; Thomson & Benton, 2007). The model I used for budworm phenology was based on work by McMorran (1973), Thomson *et al.* (1984), and Thomson and Benton (2007), where larvae begin to emerge after 116 degree-days above a threshold of 5.5°C. For the host phenology, I used March 12 as the date that accumulation begins, and 318 degree-days above 2.78°C to model the start of budburst based on Thomson and Moncrieff (1982) and Thomson and Benton (2007).

The degree-day and temperature threshold requirements for larval emergence and host budburst were used to examine historical synchrony between the two across the province when combined with long-term weather records (Thomson & Benton, 2007). A North American normals database (Canada-USA 1981-2010) and Canada daily databases (Canada 1901-2011 and Canada 2012-2013) were obtained from Régnière (2014). The normals database provided long-term mean and extreme monthly minimum and maximum temperatures and precipitation, while the daily database contained current, real-time observed daily weather based on weather stations across the country (Régnière *et al.*, 2013).

I combined the budworm and host phenology models, along with the long-term weather data, within BioSIM (Régnière, 1996; Régnière *et al.*, 2013) to calculate an estimate of the date of initial budworm larval emergence and Douglas-fir budburst each year from 1901 to 2011, as well as to calculate the relative differences between larval emergence and budburst dates across the Douglas-fir range within BC. BioSIM is a software package created for landscape-wide projections of temperature-driven simulation models in pest management (Régnière, 1996; Régnière *et al.*, 2013). There are four important components to the BioSIM software package: (i) weather databases; (ii) simulation models that allow for a large number of simulations to be run while model parameters may be systematically varied based on the user's needs; (iii) analytical tools for creating graphs, summary tables and fitted regression equations; and (iv) interpolation methods that use DEMs to generate maps of the modelled

events, which then can be used for further geographical information systems (GIS) analyses (Régnière & Logan, 1996; Régnière *et al.*, 2013).

I entered the degree-day and threshold information for the budworm and host, separately, into the Reverse Degree Day (Annual) model provided in BioSIM to calculate the Julian day that the summation of degree-days is reached each year for first larval emergence and host budburst based on the modified Allen method (1976), as described by Thomson and Benton (2007). This is a sine wave method that assumes that the daily temperature cycle takes the form of a sine curve using the maximum and minimum temperatures from each day, with the accumulation of degree-days occurring under the curve between the upper and lower thresholds. The simulation of the Reverse Degree Day (Annual) model was conducted with 3,000 randomly selected points throughout BC, generated by BioSIM. When the simulation was executed, BioSIM selected the “best” sources of weather data (i.e. the 8 nearest georeferenced weather stations) for each location, while adjusting for variation in elevation, latitude and longitude. The 1981-2010 normals database was used if no daily weather data were available.

The two outputs, one containing the yearly dates of larval emergence at each location and the other the host budburst dates, were merged into a single output of the absolute difference between the Julian day of Douglas-fir budburst and the Julian day of western spruce budworm larval emergence. In BioSIM, landscape level maps of BC were created for every year from 1901 to 2011 that displayed a raster grid of pixels with associated absolute difference between the Julian dates of Douglas-fir budburst and budworm larval emergence. The maps were produced using the universal kriging method on the data associated with the 3,000 location points in the final merged output mentioned above, along with elevation as a drift variable and the BC30s DEM provided by BioSIM (Régnière *et al.*, 2013). The maps were viewed and adjusted in ShowMap, an independent application distributed with BioSIM, and then exported for use in GIS analyses.

2.2.3 GIS analyses

2.2.3.1 Range expansion of western spruce budworm outbreaks

To examine the question of northward range expansion of western spruce budworm outbreaks, the insect infestation data from the annual aerial overview surveys was imported into a GIS, ArcMap™ 10.1 (ESRI, 2012). The infestation data in our study comprised vector geographical features in the form of polygons, with each polygon representing an infestation. Attribute information included with individual polygons contained location information, such as region and district, infestation severity, tree species affected and the area of the polygon. Data were truncated to include only the years of 1967 through 2011 to maximize the reliability and inter-annual comparability of the data collected by the aerial overviews (Van Sickle *et al.*, 2001). The years 1996 through 1998 were excluded as these were years during which overview surveys for the entire province of BC were not conducted. The 1999 data also had to be excluded due to a corrupt file that could not be imported properly into ArcGIS. The final data set included 41 layers of western spruce budworm infestation polygons, one for each year from 1967 through 1995 and 2000 through 2011.

To facilitate assessment of changes in the annual location of infestations, centroids were calculated for each polygon. This was done by first determining the latitude and longitude of the centers of the polygons and adding them to the attribute tables using ArcMap's Calculate Geometry tool. Centroids were then calculated with the Make XY Event Layer tool, and added to the map as a new layer containing point features that symbolized the centers of infestation polygons each year. The effective latitude [$\text{Latitude} + (\text{Elevation} / 122 \text{ m})$] (Hopkins, 1919) of the centroids was also calculated and added to the attribute tables. Elevation was obtained from a 30 arc-second DEM of North America (EROS, 2010). The attribute tables for each year containing effective latitude and other information for every polygon were then exported to a spreadsheet program. A total of 19,157 observations (centroids) were available for subsequent statistical analyses.

2.2.3.2 Changes in synchrony of larval emergence and host budburst

To quantify temporal changes in the synchrony of larval emergence and Douglas-fir budburst across BC, the vector polygon data output by BioSIM were imported into ArcMap. The attributes of each of these polygons included the year and a value representing the absolute difference between Douglas-fir budburst date and budworm larval emergence date. Each layer, from 1901 through 2011, was clipped (i.e. restricted) to correspond to the approximate range of Douglas-fir as identified by the provincial forest inventory (BC Ministry of Forests Lands and Natural Resource Operations, 2015a), as the possibility of western spruce budworm emergence timing outside of the range of its host was not relevant to the study. The polygon centroids and the effective latitude of the centroids were calculated and added to the map using the methods described above.

2.2.4 Statistical analyses

Two statistical analyses were conducted: one to test for the occurrence of a range expansion of western spruce budworm outbreaks into higher effective latitudes from the aerial overview survey data, and another to test for annual changes in the synchrony of western spruce budworm larval emergence and Douglas-fir budburst from the BioSIM data. Linear regressions were used in both cases. The R statistical software package (version 3.0.2) was used for all analyses (R Core Team, 2014).

2.2.4.1 Range expansion

To test for northward range expansion of western spruce budworm infestations, I fit a simple linear model which regressed the effective latitude (effLat) of the centroids *versus* year for the period 1967 to 2011: $\text{effLat}_i = \beta_0 + \beta_1(\text{year}) + \varepsilon_i$. A significant, positive relationship would indicate that there has been a shift of infestations northward and to higher elevations. The linear regression was fit with the original data, but the mean effective latitude for each year was plotted along with standard deviation to reduce noise in the final figure.

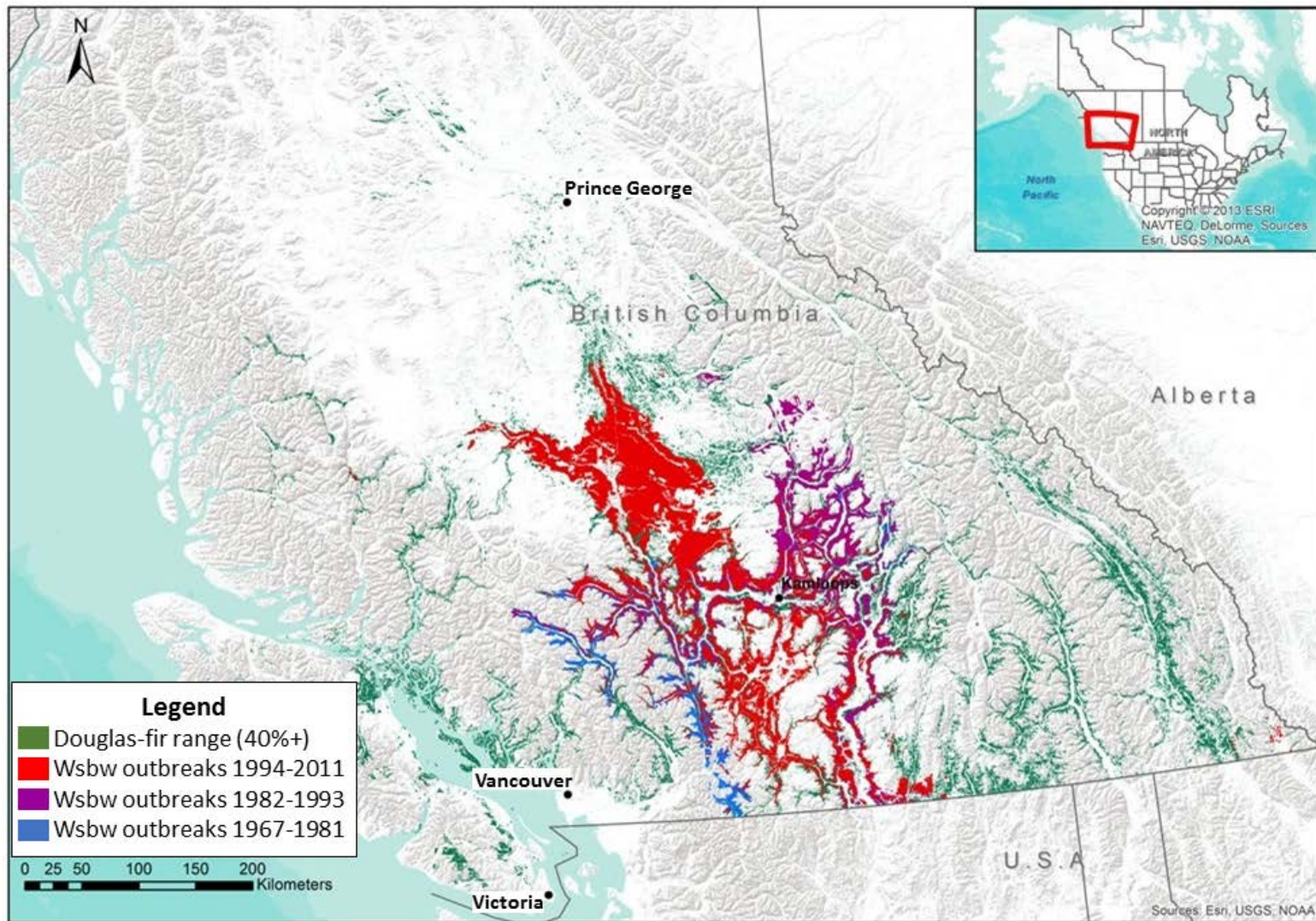
2.2.4.2 Larval emergence and host budburst synchrony

Annual changes in the synchrony of western spruce budworm larval emergence and Douglas-fir budburst were assessed by analysing the difference in Julian date between predicted first budburst and predicted larval emergence at each data point over time. Due to the large number of observations, trends could not be identified in the raw data. However, by grouping the data into categories based on effective latitude, the noise in the data could be reduced and trends became apparent. The dataset was divided into bin sizes of 5° effective latitude, which ranged from 48° to 82°, and within each bin, the annual averages were calculated. The number of days above or below *optimal synchrony* (i.e. larval emergence 18 days ahead of mean budburst) was then computed for each of the data values. Linear regressions were used to determine changes in average annual larval emergence-budburst synchrony (avgDayDiff) through time (year) for each of the effective latitude bins using the model: $\text{avgDayDiff}_i = \beta_0 + \beta_1(\text{year}) + \varepsilon_i$. To facilitate visual assessments of the relationships among larval emergence-budburst synchrony, year and effective latitude, a wireframe surface plot (i.e., a three dimensional representation of the data) was constructed (Mansson, 2010). This was done by fitting the data with loess (locally weighted scatterplot smoothing) regression. A second, coloured surface was overlain on the surface plot using the fields package in R (Fields Development Team, 2006) to indicate where optimal phenology occurred.

2.3 Results

2.3.1 Northward range expansion

Graphical representation of the distribution of western spruce budworm infestations across the province of British Columbia (Figure 2.1) supports the anecdotal assertion that outbreak populations have shifted northward in recent decades. From 1967 to 1981, the majority of defoliation occurred within the south-western range of Douglas-fir. However, by 1994 to 2011, there were large, contiguous areas of defoliation occurring further north than in previous periods. Not surprisingly, there was a significant positive linear relationship between the effective latitude of infestation centroids and year (Figure 2.2).



Data sources: BC MFLNRO. Esri. USGS. NOAA

Figure 2.1: Map of British Columbia, Canada, showing the distribution of western spruce budworm infestations from 1967 to 2011 in relation to the distribution of its primary host, Douglas-fir. Only polygons comprising $\geq 40\%$ Douglas-fir are depicted. Western spruce budworm infestations are grouped into three time steps to provide better visualization of range shifts over time. Data were provided by the BC Ministry of Forests, Range and Natural Resource Operations.

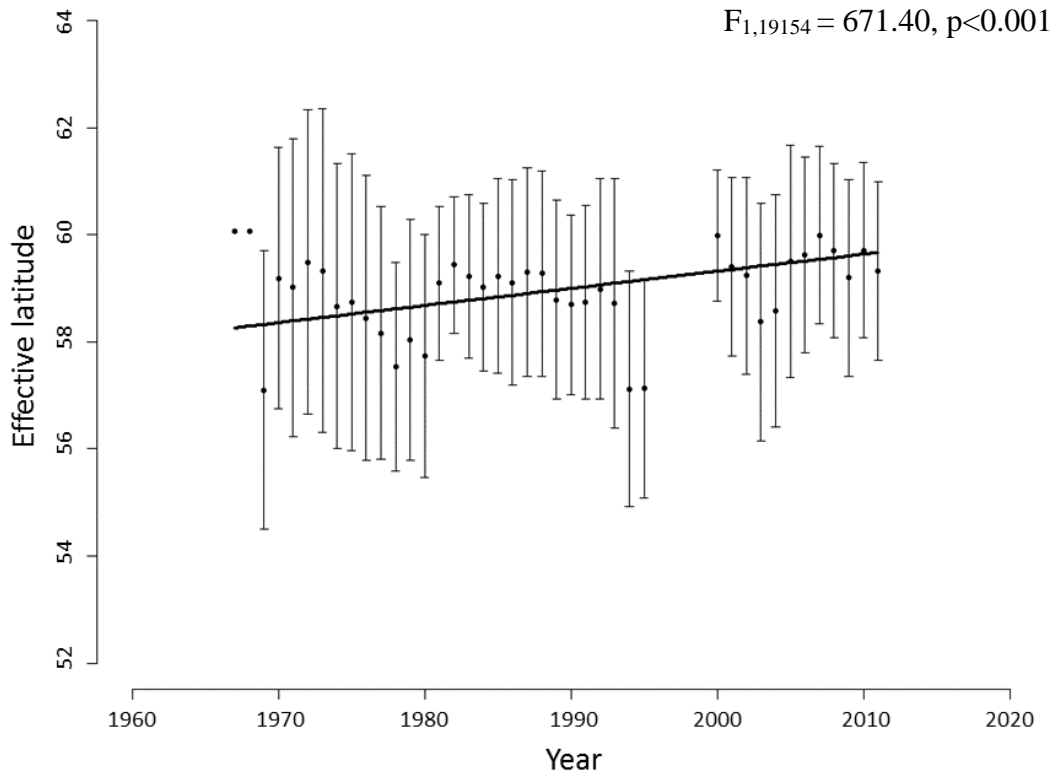


Figure 2.2: Simple linear regression of mean (\pm SD) effective latitude of western spruce budworm infestation centers versus time for 1967 to 2011 in British Columbia, Canada.

2.3.2 Phenological synchrony

Examination of the relationships between average annual larval emergence-budburst synchrony and time along an elevation/latitude gradient revealed an interesting trend (Figure 2.3). At higher elevations/latitudes, the phenology of larval emergence converged toward optimal timing, whereas at lower elevation/latitudes it diverged. At intermediate effective latitudes (between 58 and 62 degrees), the timing of larval emergence was distributed evenly around optimal synchrony and showed no trend through time. During the early 1900s, the average timing between larval emergence and bud flush was further from the optimal timing at higher effective latitudes, and closer to optimal at lower effective latitudes. By the end of the century, the average timing was closer to optimal for the higher effective latitudes, but began to diverge away from optimal at the lower latitudes.

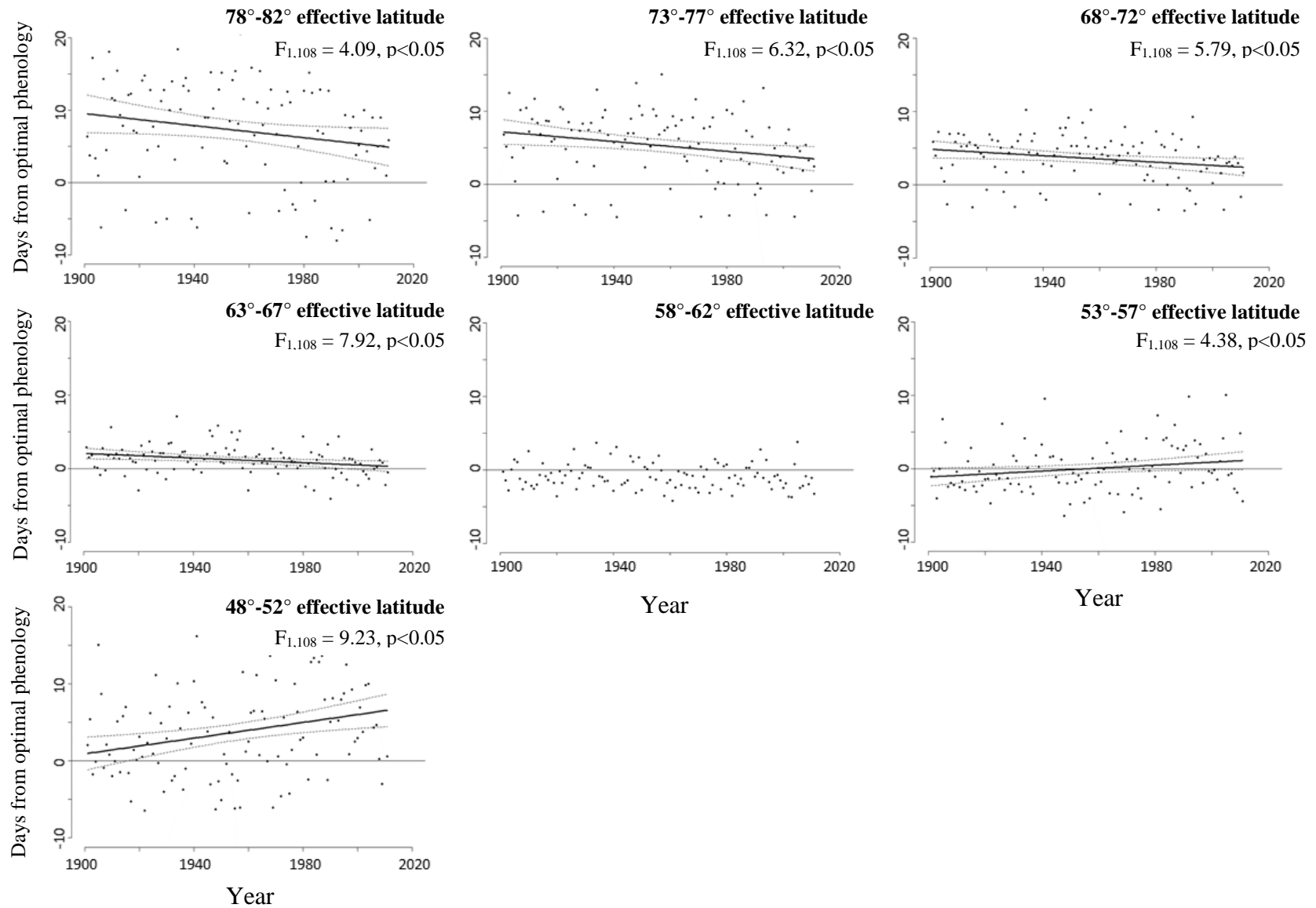


Figure 2.3: Linear regressions, with 95% confidence intervals, of deviation from optimal phenology (i.e. predicted difference between first day of Douglas-fir budburst and larval emergence) versus year for the western spruce budworm in British Columbia, Canada. Data from BioSIM model were binned into equal intervals of 5° effective latitude, and annual averages were calculated within bins, with sample size of 108 in each bin.

Improvements in synchrony are further clarified in Figure 2.4, where the changes in average effective latitude of the 18-day optimal timing between larval emergence and host budburst since the 1900s can be observed in the loess regression. As expected, days from optimal phenology increase with increasing effective latitude; but, it is clear that the difference between phenologies has been improving at higher effective latitudes consistently since about the mid-1900s. Most notable is that the average effective latitude of optimal synchrony is higher in the 21st century compared to any period of the previous century. Western spruce budworm larvae are likely now experiencing optimal synchrony with their host's budburst at higher latitudes and elevations where they would not have in the past.

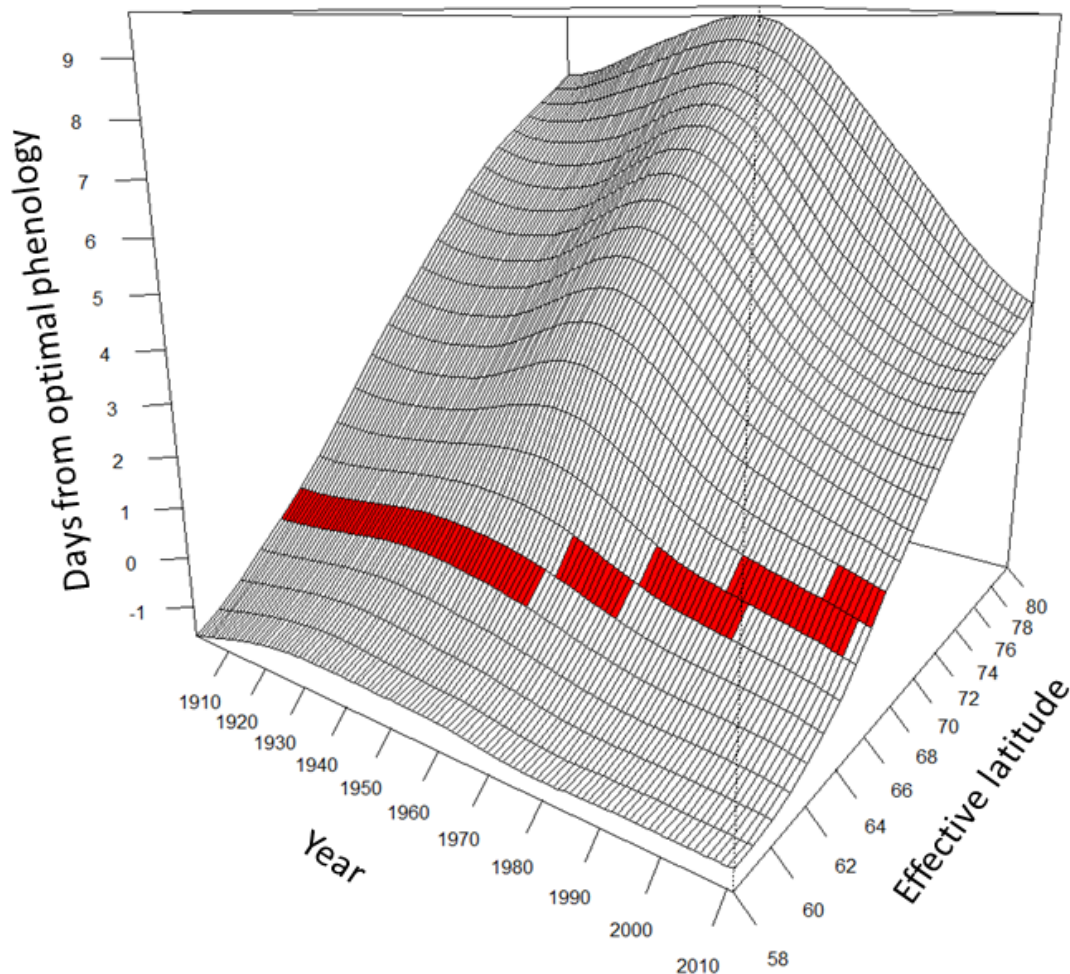


Figure 2.4: Loess regression 3d surface plot of change in phenology (i.e. predicted difference between first day of Douglas-fir budburst and western spruce budworm larval emergence) over year and effective latitude. Solid color indicates where optimal phenology (i.e. 18-day difference between first day of budburst and larval emergence) occurred. Horizontal lines correspond to effective latitude, vertical lines to year, and vertical depth of surface to days from optimal phenology.

2.4 Discussion

2.4.1 Outbreak range shift of western spruce budworm

Western spruce budworm outbreaks in Douglas-fir forests have shifted to higher effective latitudes in BC since the beginning of the previous century. Direct evidence that relatively severe outbreaks have been occurring further northwards within a relatively short time period (1960s to 2010s) is apparent in the results from the analysis of aerial overview survey data for yearly western spruce budworm infestations. Moreover, the long-term phenological analysis of western spruce budworm and its host tree, Douglas-fir, provided further indirect evidence that a northward shift in optimal synchrony between budworm larval emergence and host budburst has been leading to improved survival of western spruce budworm, and thus increased outbreaks, at higher effective latitudes since the early 1900s. The combination of direct and indirect evidence in my study supports my prediction that there has been a northward shift of western spruce budworm outbreaks in BC over the past century as a consequence of climate change-induced northward shift in the regions with optimal synchrony between spring larval emergence and Douglas-fir budburst.

It is important to note that these data do not suggest that western spruce budworm infestations have never historically occurred in Douglas-fir forests at higher effective latitudes. Indeed, several dendrochronological studies have found evidence of western spruce budworm activity throughout the range of Douglas-fir (Swetnam & Lynch, 1989, 1993; Campbell *et al.*, 2006; Axelson *et al.*, 2015). However, my analyses indicate that the propensity for populations to increase to detectable outbreak levels has shifted to higher latitudes and elevations during the previous 100+ years. Dendrochronology is a correlative technique that detects periods during which non-climate related events, such as herbivorous insect activity, may affect tree growth. It cannot be used to estimate herbivorous insect population levels (Swetnam & Lynch, 1993), and therefore may record defoliation events that fall below the level of detectability by aerial survey and, therefore, designation as outbreak. In support of this assertion, Campbell *et al.* (2006) found evidence for two western spruce budworm defoliation events in central BC since 1900, yet only the most recent one in their study, occurring between 1985 and 1995, was documented in aerial overview surveys.

2.4.2 Changes in phenological synchrony

2.4.2.1 Western spruce budworm and Douglas-fir trees in BC

My study supports that there is a strong relationship between northward range expansion of the western spruce budworm and climate-change induced improvements in synchrony between spring emergence of the larvae and the flushing of the host's buds. At higher effective latitudes, the overall trend demonstrates a convergence of larval emergence and host budburst with optimal phenological synchronization (Figure 2.3). In the early 1900s, the average synchrony of the two phenologies at the northern extent of the budworm's range was 5 to 10 days from optimal, which may have led to low western spruce budworm fitness and inability to reach an outbreak level population. Even in years where the climate allowed for optimal synchronization, the insect would have needed a minimum population already present in the area to take advantage of it, but this likely did not happen due to previous years of sub-optimal synchronization (Thomson & Benton, 2007).

Over this last century, the phenologies in the north have begun to converge towards optimal timing for the budworm larvae, which has likely resulted in the observed northward shift of detectable outbreaks. Improved synchrony results in improved budworm development and survival as they gain better access to the more nutritious and edible new spring foliage (Ayres, 1993; Chen *et al.*, 2001, 2003; van Asch & Visser, 2007). Furthermore, it leads to the loss of an important defence mechanism for historically resistant hosts. Chen *et al.* (2001, 2003), for example, found that the phenological window between the budworm and host was larger for resistant trees compared to susceptible ones, and that the resistant trees sustained significantly less defoliation due to this difference. Their studies indicated that western spruce budworm population growth and defoliation can be severely affected when the phenological differences were not optimal for the budworm's survival; therefore, as phenologies between the insect and host continue to converge at higher latitudes and elevations, historically resistant trees may become increasingly susceptible, and result in further expansion of western spruce budworm range into regions where they were not historically identified as an issue when managing the forests for disturbances.

2.4.2.2 Phenological synchrony in a global context

Shifting synchronies as a result of a warming climate have been suggested in studies of other lepidopteran systems. Range expansion of winter moth (*Operophtera brumata*) in Fennoscandia has been linked to improved synchrony between larval emergence and host budburst as a result of climate change (van Asch & Visser, 2007; Jepsen *et al.*, 2008, 2011). Jepsen *et al.* (2008) demonstrated that the winter moth has experienced an expansion of its outbreak range towards the east and north, and attributed part of it to increased winter survival of eggs as winter temperatures increasingly remain above the lethal threshold of -35°C; however, new outbreaks have also occurred at higher altitudes and latitudes in regions where sub-lethal winter temperatures were never reached, apparently due to shifting spring phenology of host-tree budburst (Jepsen *et al.*, 2009, 2011). Likewise, another species of geometrid moth, *Agriopis aurantiaria*, also in Fennoscandia, has undergone northward range expansion due to improved phenological synchrony arising from higher than average spring temperatures (Jepsen *et al.*, 2011).

Warming induced changes in synchrony may not be beneficial to all early season defoliators. For example, Visser and Holleman (2001) found that the average dates of winter moth egg hatch and oak budburst in the UK has diverged over the past 25 years. Warmer temperatures in recent decades have caused increasingly early egg hatch in the spring, which has led to both higher mortality and dispersal of small larvae and significantly lower population densities (Bylund, 1999; Visser & Holleman, 2001; van Asch & Visser, 2007). Similarly, the sudden absence of outbreaks of the larch budmoth, *Zeiraphera diniana*, in the subalpine larch forests of the European Alps has been linked to a period of extreme regional warmth outside the climatic envelope of the past 1200 years that suggests a temperature variation threshold has recently been passed (Baltensweiler, 1993; Esper *et al.*, 2007). Studies suggest that increased winter and spring temperatures have affected the overwintering eggs by inducing early development and egg hatch, leading to increased mortality of eggs when colder weather returns or increased first-instar larvae starvation and mortality when they hatch too early before host budburst. Although the larch budmoth has maintained highly regular outbreaks every 8 to 9 years for over a millennium, recent climate-induced asynchrony between the

phenologies of the insect and host has likely been an important factor in the recent absence of expected outbreaks (Baltensweiler, 1993).

In further support of the above, phenological mismatches in the southern portion of the range of western spruce budworm in BC has resulted in lower populations in that area and emphasised the northward shift in outbreak infestations. Thomson and Benton (2007) demonstrated that a warmer climate on Vancouver Island, BC after 1930 created a departure from optimal phenological synchronization, which resulted in reduced population densities. According to them, the average timing of first budflush of Douglas-fir had remained fairly constant since the early 1900s, with little variation from year to year, whereas the average timing of larval emergence had decreased, with large variations from year to year. Interestingly, I also found that lower effective latitudes (more southern latitudes and lower elevations) have developed a divergence from the mean optimal phenology of western spruce budworm and Douglas-fir (Figure 2.3). If the trend continues, it may be possible that the future will see fewer outbreaks in the most southern parts of BC. In areas where larval emergence and host budburst are becoming increasingly asynchronous, the local population may be reduced to extremely low levels or experience extinction unless the insect is able to adapt through such means as a response to the directional selection if genetic variation is sufficient or switching to a new host with a more suitable phenology (van Asch & Visser, 2007).

2.4.3 Conclusion

My results and those from comparable systems indicate that early-season defoliators which depend on phenological synchrony between emergence of feeding-stages and host budburst have experienced range shifts (contraction and expansion) due to the effects of a warming climate. A positive response to climate change can be expected for these species through an expansion of range into higher latitudes and elevations where host trees are available, as I observed with the western spruce budworm. At the same time, warming temperatures may lead to degraded synchrony and reduced population densities in the southern portion of their range, similar to observed changes in winter moth and larch budmoth dynamics. Further research into life histories of early-season defoliators may aid future outbreak range

predictions, as the impacts and responses will vary from species to species (Bale *et al.*, 2002). My analysis also suggests that western spruce budworm has shown a very rapid response to changes in temperature and synchrony of phenologies of insect and host. This indicates that these systems may react to critical temperature thresholds without warning, such as with the abrupt cessation of larch budmoth outbreaks.

3 Synergistic disturbances in a warming environment: the western spruce budworm and Douglas-fir beetle

3.1 Introduction

Disturbance plays a key role in shaping the composition, structure and function of ecosystem processes within temperate and boreal forests (Malmström & Raffa, 2000; Dale *et al.*, 2001). Natural disturbances, caused by both abiotic (e.g., fire, windstorms and drought) and biotic (e.g., insects and pathogens) agents, range from having limited impacts on an ecosystem's structure and organization to large-scale tree mortality across entire landscapes (Dale *et al.*, 2001). Extensive tree mortality often results in a change of ecosystem function and the loss or fragmentation of important habitats that may positively or negatively affect the survivability, growth and dispersion ability of other plant and animal species (Ayres & Lombardero, 2000). The majority of biotic disturbance in North American forests is caused by herbivorous insects (Fleming *et al.*, 2000; Malmström & Raffa, 2000; Dale *et al.*, 2001; Bale *et al.*, 2002; Hicke *et al.*, 2012a). Insect disturbance is frequently more extensive and severe than fire (Hicke *et al.*, 2012a), and unlike fires and other abiotic agents, it targets specific tree species and often results in continuous damage over several years (Fleming *et al.*, 2000; Dale *et al.*, 2001).

Spatial and temporal predictions of the occurrence of biotic disturbances, such as those associated with outbreaks of forest insects, are critical to forest management, especially given the expectations of increased impacts under climate change (Ayres & Lombardero, 2000; Dale *et al.*, 2001; Bale *et al.*, 2002; Soja *et al.*, 2007; Bentz *et al.*, 2010). Indeed, a growing number of studies have found that warming conditions have affected the extent and severity of recent outbreaks in temperate and boreal forests (e.g., Carroll *et al.*, 2004; Battisti *et al.*, 2005; Jepsen *et al.*, 2008, 2011; Sherriff *et al.*, 2011). Our understanding of the factors affecting forest insect disturbances has been largely derived from the isolated study of individual insects; however, forests are complex ecosystems prone to disturbance from multiple sources. For example, insect outbreaks often coincide with droughts that putatively lead to increased tree stress and lower tree defences (Mattson & Haack, 1987; Croise &

Lieutier, 1993; Negrón *et al.*, 2009). Similarly, herbivory-related fuel loading can facilitate wildfire spread and severity (Raffa & Berryman, 1987; Hummel & Agee, 2003; Parker *et al.*, 2006). Moreover, disturbances that lead to an increase in dead, injured, or stressed host material, such as windthrow, logging and landslides, are known to aid in rapid population growth of certain insects and pathogens (e.g., Furniss *et al.*, 1979; Jenkins *et al.*, 1998; Carroll *et al.*, 2006; Dodds *et al.*, 2006). Therefore, broader studies of the potential interactions between disturbance agents may allow for a better understanding of how and when significant additive or synergistic disturbances may occur.

The majority of insect-related disturbance events within temperate and boreal forests are caused by eruptive bark beetles and defoliators. Bark beetles (Coleoptera: Curculionidae: Scolytinae) are subcortical insects that feed and reproduce within the phloem tissues of living host trees. Successful colonization of the bole of trees by aggressive bark beetles often leads to tree death (Wood, 1982). Defoliating insects, most commonly found in the order Lepidoptera, feed externally on plant foliage as larvae. Consumption of the leaves or needles removes photosynthetic tissue that is essential for maintenance and growth of trees. As a result, trees with prolonged or severe defoliation may experience growth loss, increased susceptibility to secondary insect or pathogen attacks, or even mortality (Craighead, 1940; Cooke *et al.*, 2007). Periodic landscape-scale outbreaks by various defoliator and/or bark beetle species have affected every forest type within the boreal and temperate zones of North America (Ayres & Lombardero, 2000).

Severe defoliation reduces tree vigour through depletion of carbohydrate reserves required for growth and defence processes that are relevant to bark beetles (Christiansen *et al.*, 1987; Raffa & Berryman, 1987; Langstrom *et al.*, 2001b; Cedervind, 2003). As a result, there has been a long-standing general expectation that infestations of tree-killing bark beetles are closely linked to defoliator outbreaks (Dewey *et al.*, 1974; Wright *et al.*, 1979; Wallin & Raffa, 2001). Indeed, aggressive bark beetle species from several genera (*Dendroctonus*, *Ips*, *Scolytus*) have been found to colonise their conifer hosts during and/or after a defoliation event (e.g., Wright *et al.*, 1984; Berryman, 1988; Hadley & Veblen, 1993; Langstrom *et al.*, 2001a; Cedervind, 2003). However, not all defoliation events are followed by bark beetle attacks and not all bark beetle outbreaks are preceded by defoliation (Hadley & Veblen,

1993), therefore the conditions under which these two disturbance types interact remain unclear.

The western spruce budworm (*Choristoneura occidentalis*) is the most widely distributed defoliator of coniferous forests in western North America, with a long history of periodic outbreaks in many regions (Fellin & Dewey, 1986; Campbell *et al.*, 2006). Douglas-fir beetle (*Dendroctonus pseudotsugae*) is another important eruptive disturbance agent in Douglas-fir forests and has often been observed to reach outbreak levels following western spruce budworm defoliation (Fredericks & Jenkins, 1988; Lessard & Schmid, 1990; Gast *et al.*, 1991; Hadley & Veblen, 1993; Sturdevant & Kegley, 2006; Steed *et al.*, 2007). Although Douglas-fir beetle is considered aggressive due to its ability to kill large, healthy trees during outbreak conditions (Furniss *et al.*, 1979; Fredericks & Jenkins, 1988; Powers *et al.*, 1999), it generally prefers to attack stressed, low vigour trees, which have reduced resistance and are therefore more susceptible to attack (Fredericks & Jenkins, 1988; Gast *et al.*, 1991; Powers *et al.*, 1999). When stressed host material is abundant, a Douglas-fir beetle population can build up quickly to reach outbreak levels.

The purpose of my study was to quantify the potential for two biotic disturbance agents to interact over large forested landscapes. Forest insect pests, including the Douglas-fir beetle and western spruce budworm, have been thoroughly monitored in western Canada since the early 1900s (Van Sickle *et al.*, 2001; BC Ministry of Forests Lands and Natural Resource Operations, 2013), which makes this system an ideal one to critically evaluate the role of defoliators in subsequent bark beetle infestation. More specifically, using long-term detailed forest health survey data together with a vegetation resource inventory dataset for the province of British Columbia (BC), Canada, I assessed the Douglas-fir – western spruce budworm – Douglas-fir beetle interaction to determine the potential for a defoliator outbreak to predispose conifer stands to attack by a primary, tree-killing bark beetle. Evidence suggests that repeated defoliation events have differential impacts to conifer resin defense systems and phloem quantity, whereby defenses decline in response to defoliation (acute effects) earlier than reductions in phloem thickness (chronic effects) (Wright *et al.*, 1984; Shrimpton & Thomson, 1985; Gričar & Čufar, 2008). Therefore, given that a localized bark beetle population eruption is more likely when impaired tree defenses coincide with a large

supply of thick phloem (Safranyik & Carroll, 2006), I tested the prediction that moderate defoliation intensity (i.e., reduced tree defenses, without thinning phloem) will be most closely associated with subsequent Douglas-fir beetle infestation.

3.2 Methods

Detailed data pertaining to the spatial and temporal distribution of western spruce budworm and Douglas-fir beetle impacts, together with information regarding various site, environmental and climatic variables were obtained for analyses. Each data source and the methods used to extract the relevant data are described below.

3.2.1 Insect infestation data

Annual aerial overview surveys of forest health conditions for BC were conducted by the Canadian Forest Service, Forest Insect and Disease Survey (FIDS) from 1959 to 1995, and then by the BC Ministry of Forests, Lands and Natural Resource Operations from 1998 onward. Fixed-wing aircraft were used to assess the entire province for the annual location, extent and severity of impacts by forest pests (Van Sickle *et al.*, 2001; BC Ministry of Forests Lands and Natural Resource Operations, 2013). To ensure a methodical survey, flight routes were conducted either in a grid pattern (level terrain) or following map contours (mountainous terrain) (BC Ministry of Forests, 2000). Two observers in each aircraft identified and delineated infested areas based on evidence of herbivory on topographical maps at a scale of up to 1:100,000. Their respective rough sketch maps were later compared and consolidated into a composite that could be entered in a geographical information system (GIS).

Aerial overview survey data were used to identify the annual distribution and characteristics of Douglas-fir beetle and western spruce budworm infestations. These were distinguished visually from the air based on the appearance of tree damage and the time of year it occurred (BC Ministry of Forests, 2000). Douglas-fir beetle infestations were identified from mid-June to late August by Douglas-fir trees with foliage that had turned entirely red, indicating they had been attacked and killed the previous year. Infestations of greater than 50 trees were

mapped as polygons and classified by the percentage of mortality of trees within the polygon: light (1-10%), moderate (11-29%), or severe (30%+). For western spruce budworm, the peak period for damage was from late June to mid-August and current year's feeding damage was mapped based on the appearance of thinning foliage and a reddish tinge to the trees, stands, or hills as a result of active feeding on the foliage. Only "outbreak" infestations with sufficient defoliation to be detected from the air were mapped. Infestations were attributed a defoliation severity class of light (1 – 25%), moderate (26 – 50%), or severe (51 – 100%) based on visual assessment of affected trees (BC Ministry of Forests, 2000).

3.2.2 Modelling probability of Douglas-fir beetle presence

The probability of Douglas-fir beetle infestation presence or absence in stands defoliated by western spruce budworm was tested in generalized additive models (GAMs). Potential predictor variables included western spruce budworm defoliation severity and duration, precipitation deviations, and several other host and environmental variables. The following sections describe the methods of obtaining Douglas-fir beetle presence/absence information along with the predictor variables and the variable selection procedure using GAMs to find the best model fit.

3.2.2.1 Fishnet grid

A fishnet, or grid of rectangular cells, was overlaid upon the Douglas-fir beetle distribution map in ArcMap, using the Create Fishnet tool in the Arc Toolbox. The fishnet cells were polygons of 1 km x 1 km and each labelled with a unique value. Each cell was counted as a single observation.

3.2.2.2 Douglas-fir beetle distribution

Annual Douglas-fir beetle distribution was examined in a geographical information system (GIS), ArcMap™ 10.1 (ESRI, 2012), by importing the aerial overview survey infestation data, which comprised vector geographical features in the form of polygons. Each polygon

represented a single infestation and contained attribute information, including location, severity, affected tree species and polygon size. Data were truncated to include only the years of 2000 through 2013 to increase reliability due to more complete and standardized survey methods compared to older surveys (BC Ministry of Forests, 2000; Gray, 2008). The final data set included 14 layers of Douglas-fir beetle infestation polygons for 2000 through 2013.

The infestation polygons were then rasterized into pixels of 50 m x 50 m. The presence or absence of Douglas-fir beetle raster pixels within each fishnet cell was calculated for each year using the intersect polygons with raster (`isectpolyrst`) command in Geospatial Modelling Environment (GME) (Beyer, 2014). Cells were scored a 0 when Douglas-fir beetle was absent, and a 1 when the beetle was present.

3.2.2.3 Western spruce budworm infestation variables

Western spruce budworm infestation data from aerial overview surveys for 2000 through 2013 were added to the Douglas-fir beetle distribution map in ArcMap. Polygons in each year were rasterized based on the midpoints of the severity percentage ranges (uninfested = 0%, low = 12%, moderate = 37%, severe = 75%). Raster cells were 100 m x 100 m.

The weighted mean severity of western spruce budworm infestations within each of the fishnet grid cells was calculated in GME with the `isectpolyrst` command. From this, I obtained the annual summarization of raster cell values contained within the polygons, including the mean, minimum, maximum, standard deviation, count, and sum of raster cell values, which represented infestation severity. GME attached the output to the attribute table of the fishnet layer in ArcMap, and I exported the mean values to a spreadsheet. This resulted in a table with weighted mean defoliation severity percentage for every 1 x 1 km fishnet cell yearly for 2000-2013.

I determined the beginning of a budworm outbreak in each 1 x 1 km fishnet cell to be where a non-zero mean severity value was preceded by five or more consecutive values of zero, and the end of an outbreak to be the most recent non-zero value that was followed by five or more consecutive zero values (Gray, 2008). There could be some zero values within an outbreak period, likely due to a short-term density-independent perturbation such as an early

frost followed by population recovery, which could lead surveyors to record a defoliation level of zero for that time (Gray, 2008). As a whole, however, these outbreaks were considered to be single, multi-year events. In each fishnet cell, the characteristics of the most recent outbreak to be tested in later analyses were *duration* (last year of outbreak – first year of outbreak + 1), *maximum severity* (maximum mean severity percent), *average severity* (average of all mean severity percentages), *severity standard deviation* (standard deviation of all mean severity percentages), and *cumulative severity* (Table 3.1). To calculate *cumulative severity*, the mean severity in each year of the outbreak were assigned a value: 0.1-25% (low severity) = 1, 25.1-50% (moderate) = 2, and 50-100% (severe) = 3. *Cumulative severity* was the sum of these values for the duration of the outbreak. The longer the outbreak and the more years with moderate and severe defoliation, the higher the cumulative severity would be.

Table 3.1: List of all explanatory variables tested in generalized additive models for predicting the probability of Douglas-fir beetle attacks subsequent to western budworm defoliation in 1 x 1 km fishnet cells.

Type	Variable	Name	Description
Disturbance (wsbw outbreak)	Duration (years)	sev_dur	Duration of the most recent western spruce budworm outbreak = final outbreak year – first outbreak year + 1
	Maximum severity (%)	sev_max	Highest percent value of mean severity in a year over the course of the most recent western spruce budworm outbreak.
	Average severity (%)	sev_avg	Mean severity percent averaged over all years of most recent western spruce budworm outbreak.
	Severity standard deviation	sev_std	Sample standard deviation of mean severity percent values over all years of most recent western spruce budworm outbreak.
	Cumulative severity	sev_cum	Cumulative severity over all years of most recent western spruce budworm outbreak. Sum of severity values where 1 = low severity (0.1-25%), 2 = moderate (25.1-50%), and 3 = severe (50-100%).
Precipitation	Total spring precipitation deviation	tsp_dev	Deviation of the total spring precipitation 3-year average from the 30-year normal mean (1971-2000).
	Total annual precipitation deviation	tap_dev	Deviation of the mean total annual precipitation 3-year average from the 30-year normal mean (1971-2000).
Host and site characteristics	Crown Closure (%)	site_crmclos	Mean tree crown closure: percentage of ground area covered by vertically projected crowns of tree cover. Categorical variable, where 0-5% crown closure = 0, 6-15% = 1, 16-25% = 2, 26-35% = 3, 36-45% = 4, 46-55% = 5, 56-65% = 6, 66-75% = 7, 76-85% = 8, 86-95% = 9, 96-100% = 10.
	Host projected age (years)	fd_age	Age projected for 01/01/2009 for the leading species (Douglas-fir). Categorical variable, where 1-20 years stand age = 1, 21-40 yrs = 2, 41-60 yrs = 3, 61-80 yrs = 4, 81-100 yrs = 5, 101-120 yrs = 6, 121-140 yrs = 7, 141-250 yrs = 8, 251+ yrs = 9.
	Site Index (m)	site_ind	Estimate of site productivity for tree growth (height in metres at breast height of 50 years), based on normalized set of coefficients calibrated to reflect the range of heights for a given tree species.
	Host mean percent (%)	fd_perc	Mean percent of Douglas-fir trees based on relative basal area in older stands, and number of stems/ha in younger stands. Estimated to nearest percent for all living trees above a specified diameter.
	BEC zone	bec_zone	The dominant biogeoclimatic zone – highest level of ecosystem classification in BC; represents areas of broad macroclimate and named mainly after dominant late-successional tree or plant species. 14 BEC zones have been identified in BC.
	BEC subzone	bec_sub	Dominant biogeoclimatic subzone – divisions of BEC zones that further define an area's climate. Classification is based on a combination of precipitation and temperature.
	Spatial (Longitude, Latitude)	long,lat	Spatial or (Longitude, Latitude) is included as a variable to address any spatial trends in the data.

3.2.2.4 Climate variables

Climate and weather data were obtained as instrumental records from weather stations collected and managed by Environment Canada, while BioSIM, which includes a stochastic weather generator, was used to increase the spatial extent and/or temporal detail of the data (Régnière, 1996; Régnière *et al.*, 2013). BioSIM is a software package created for landscape-wide projections of temperature-driven simulation models in pest management (Régnière, 1996; Régnière & Logan, 1996; Régnière *et al.*, 2013). There are four important components to the BioSIM software package: (i) weather databases, which were included with BioSIM; (ii) simulation models that allow for a large number of simulations to be run while model parameters may be systematically varied based on the user's needs; (iii) analytical tools for creating graphs, summary tables, and fitted regression equations; and (iv) interpolation methods that use DEMs to generate maps of the modelled events, which then can be used for further GIS analyses (Régnière & Logan, 1996; Régnière *et al.*, 2013).

Mean annual and monthly weather variables were calculated for 3000 random point locations throughout BC from 1970 through 2013 using BioSIM (Régnière, 1996; Régnière *et al.*, 2013). The program calculated minimum, maximum and mean temperature (°C), total precipitation (mm) and various other variables from existing daily weather data from BC weather stations, and then simulated daily weather data for the random point locations based on the eight closest weather stations. Adjustments were made to account for differences in latitude, longitude and elevation. Additionally, any gaps in daily weather data were filled with data from the 1981-2010 Environment Canada Normals Database that includes long-term monthly statistics calculated over 30-year standard normal generating periods. Total annual precipitation (mm) and total spring precipitation (mm) (March-June) were also determined given the assertion by earlier studies that low precipitation or drought-conditions improve the colonization success of the Douglas-fir beetle (Jantz & Rudinsky, 1966; Schmitz & Gibson, 1996; Powers *et al.*, 1999).

A series of annual landscape-level precipitation maps for BC were generated with the event mapping analysis in BioSIM using the universal kriging method with elevation as a drift variable and the BC30s DEM (Régnière *et al.*, 2013). The maps were imported into ArcMap

where they were rasterized using the maximum-area method with 100 x 100 m cells. The yearly rasters and fishnet grid were run through the `isectpolyrst` analysis in GME. This generated a summary of mean, maximum, minimum, count and sum total annual and total spring precipitation raster values within each of the fishnet cells. The mean total annual and mean total spring precipitation for each of the cells and years were exported as a table from ArcMap.

Total annual and spring precipitation deviations were calculated for each year from 2000 through 2013 by averaging the values from each year and the two previous years and subtracting the three-year average from the 1971-2000 average. The mean of the precipitation deviation results for 2000 through 2013 were then recorded for each of the fishnet cells to be used in subsequent statistical analyses (Table 3.1).

3.2.2.5 Host and site variables

Host and site data were obtained from the BC Vegetation Resources Inventory (VRI) Forest Vegetation Composite Polygons and Rank 1 Layer using the program ArcMap (B.C. Ministry of Forests, Lands and Natural Resource Operations 2013b). To predict Douglas-fir beetle presence, I selected variables related to the abundance of Douglas-fir trees with complete or near-complete records from the VRI attribute table in ArcMap (e.g., Furniss *et al.*, 1981; Schmitz & Gibson, 1996; Negrón, 1998; Powers *et al.*, 1999; Shore *et al.*, 1999). The final selected variables were the mean percentage, projected age and crown closure of Douglas-fir, as well as the average site index and dominant biogeoclimatic (BEC) zone and subzone (Table 3.1). The method used to calculate the values for each Douglas-fir and site variable in a 1 x 1 km fishnet was similar to the method I used to obtain the western spruce budworm defoliation severity and total annual and spring precipitation deviation values. Each layer was rasterized with the maximum area method, and then brought into GME to be summarized within the fishnet cells using the `isectpolyrst` command. The average projected host age and crown closure values for each cell were converted into class categories (Table 3.1).

BEC zone and subzone are not entirely independent from other vegetative, environmental and climatic variables; however, the BEC system is designed to integrate the interactions between climate and soil to determine the vegetation potential of a site (Pojar *et al.*, 1987). BEC zones, the highest level of climatic classification in the BEC system in BC, represent areas of broad macroclimate and are named after the dominant late-successional tree or plant species. While Douglas-fir dominates late-successional forests of the Interior Douglas-fir (IDF) and Coastal Douglas-fir (CDF) BEC zones, it also commonly grows in parts of the Ponderosa Pine (PP), Bunchgrass (BG), Montane Spruce (MS), Interior Cedar-Hemlock (ICH), Sub-boreal Spruce (SBS), Coastal Western Hemlock (CWH) and Sub-boreal Pine Spruce (SBPS) zones (Centre for Forest Conservation Genetics, 2015); therefore, these zones also include potential infestation sites of Douglas-fir beetle.

BEC subzones may be even better predictors as they provide refined descriptions of the climate within BEC zones, as the subzones are divided based on precipitation and continentality on the coast and by temperature and precipitation in the interior. Since the subzones summarize multiple aspects of climate in a broader, integrative way compared to the precipitation variables I developed for testing in the model, they may be useful for predicting the presence of Douglas-fir beetles. However, subzones are not equivalent across BEC zones (BC Ministry of Forests Lands and Natural Resource Operations Research Branch, 2015). For example, the climate of the dry-cool subzone of the IDF zone is different from the dry-cool subzone of the MS zone. Therefore, I tested for the effect of BEC subzone in a separate analysis within the IDF BEC zone only, as the IDF zone was most associated with western spruce budworm defoliation due to the host, Douglas-fir, being the most abundant in this zone.

3.2.2.6 Final set-up of variables

In the end, I had a summary of the values of the independent variable (Douglas-fir beetle presence/absence) and the 13 predictor variables listed in Table 3.1 within 545,376 fishnet cells that covered the approximate range of Douglas-fir in BC. As I was testing for the importance of western spruce budworm disturbance on the presence or absence of Douglas-fir beetle attacks within defoliated stands, I reduced the data to only those fishnet cells where

a western spruce budworm outbreak has occurred since year 2000. Furthermore, any fishnet cells that were missing values for predictor variables were not used. A total of 30,756 observations were analysed in the generalized additive models described in the following section.

3.2.2.7 Predicting Douglas-fir beetle presence: generalized additive model

I employed binomial generalized additive models (GAMs) (Hastie & Tibshirani, 1987, 1990; Wood & Augustin, 2002) to test the importance of defoliation variables, along with site, host and climatic variables, on the ability to predict the presence of Douglas-fir beetle subsequent to a western spruce budworm defoliation event. As a nonparametric (i.e., nonspecific) extension of generalized linear models (GLMs), GAMs have some advantages that make them useful in ecological research (Hastie & Tibshirani, 1990; Yee & Mitchell, 1991; Fewster *et al.*, 2000; Guisan *et al.*, 2002), including studies on insect pest species distribution and population dynamics (e.g., Gallego *et al.*, 2004; Yamasaki & Futai, 2012; Haynes *et al.*, 2014). GAMs offer better flexibility in that the relationships between the dependent and predictor variables do not need to be decided on beforehand (Hastie & Tibshirani, 1990; Wood & Augustin, 2002). The shape of the response curves are determined by the data rather than an a priori model through the application of nonparametric regression splines (smoothers) to the predictor variables and then the additive calculation of the component response. The mean response to the x variables are related by GAMs via:

$$g(E(y_i)) = \beta_0 + s_1(x_{1i}) + s_2(x_{2i}) + \dots s_p(x_{pi}) \quad (1)$$

where g is a known link function that relates the linear predictor with the expected value of the response variable y , β_i are the parameters to be estimated, s_p are the unknown smoothing functions, and x_{pi} are the predictor variables. To avoid the potential problem of overfitting the data in a GAM, each spline in the model is penalized by the effective degrees of freedom so that simple linear relationships are preferred, rather than complex, non-linear ones (Wood & Augustin, 2002; Wood, 2004; Haynes *et al.*, 2014).

First, correlation between pairs of predictor variables was tested using a Pearson's correlation matrix in R (version 3.1.2) (R Core Team, 2014). GAMs were then fit with penalized

likelihood estimation in R using the ‘mgcv’ package (Wood, 2004). The function ‘bam’ was used, which is similar to ‘gam’, but able to fit a generalized additive model to a very large data set containing tens of thousands of data (Wood *et al.*, 2015). The GAMs were fit with a binary distribution and logit link as the dependent variable was either 1 (Douglas-fir beetle present) or 0 (Douglas-fir beetle absent). The smoothed variable $s(Long, Lat)$ was also included in the models to address any spatial trends in the data.

Variable selection was conducted by way of a backwards selection method, similar to that proposed by Wood and Augustin (2002). A full model was fit and then a variable would be removed and the new reduced model would be compared to the full model. The reduced model was a better fit compared to the full model if (1) the Akaike Information Criterion (AIC) was lower (Akaike, 1974; Guisan *et al.*, 2002), (2) the deviance was significantly reduced ($p < 0.05$), allowing a better fit, as measured by a chi-square (χ^2) difference test (Guisan *et al.*, 2002), and (3) the majority of the 95% confidence region for the variable in question contained zero (Wood & Augustin, 2002). Highly correlated variables were tested in separate models, and then the one that showed the best fit according to the above criteria was selected to remain in the model. The final model was a balance between simplicity in fewer predictor variables and the best fit, and so a variable could be removed even if it was significant if there was only a relatively small increase (e.g. <100) in AIC for the reduced model.

3.3 Results

3.3.1 Variable selection

The variables associated with western spruce budworm defoliation were generally highly and positively correlated ($r > 0.5$) (Table 3.2). The only pair that were not as highly correlated ($r < 0.5$) was duration of defoliation (sev_dur) and average severity (sev_avg). Total annual precipitation deviation (tap_dev) was also highly and positively correlated with total spring precipitation deviation (tsp_dev) ($r = 0.96$). An increase in tap_dev is correlated with an increase in tsp_dev and vice versa. Other site and host variables were relatively less

correlated with each other and with the defoliation and precipitation variables ($r < 0.3$). One interesting observation, however, was that the mean age class of Douglas-fir (fd_age), site index (site_ind) and crown closure of the site (site_crnclos) all had a negative correlation with variables related to western spruce budworm defoliation. For example, as fd_age increased, there was a decrease in defoliation duration (sev_dur), maximum severity (sev_max), average severity (sev_avg) and cumulative severity (sev_cum).

Table 3.2: Pearson correlation matrix assessing the relationships among variables used to predict the probability of Douglas-fir beetle infestation subsequent to western spruce budworm defoliation in a 1 x 1 km fishnet (grid) cell within the Douglas-fir range of British Columbia. Variables that are closer to 1 or -1 are more highly positively or negatively correlated, respectively. Variables are the duration (sev_dur) and maximum (sev_max), average (sev_avg), standard deviation (sev_std) and cumulative (sev_cum) severity of western spruce budworm defoliation, as well as mean percent of Douglas-fir (fd_perc), site index (site_ind), and total annual (tap_dev) and spring (tsp_dev) precipitation deviation.

	Sev_ dur	Sev_ max	Sev_ avg	Sev_ std	Sev_ cum	Fd_ mnperc	Fd_ age	Site_ index	Site_ crnclos	Tap_ dev	Tsp_ dev
Sev_dur	1										
Sev_max	0.51	1									
Sev_avg	0.13	0.77	1								
Sev_std	0.33	0.93	0.84	1							
Sev_cum	0.83	0.73	0.45	0.55	1						
Fd_perc	0.29	0.17	0.10	0.11	0.31	1					
Fd_age	-0.03	-0.05	-0.03	-0.05	-0.02	0.13	1				
Site_ind	-0.19	-0.15	-0.09	-0.12	-0.18	-0.21	-0.22	1			
Site_crnclos	-0.14	-0.14	-0.09	-0.13	-0.15	-0.10	0.18	0.29	1		
Tap_dev	0.11	0.07	0.02	0.05	0.09	0.19	0.13	-0.21	0.02	1	
Tsp_dev	0.16	0.13	0.06	0.10	0.15	0.18	0.10	-0.22	0.02	0.96	1

Due to high correlation, the variables associated with western spruce budworm defoliation and with precipitation deviation were tested in separate generalized additive models (GAMs). Full GAM models with all site and host variables (except biogeoclimatic subzone and total annual precipitation deviation) plus either sev_dur, sev_avg, sev_max, sev_std, or sev_cum were tested against reduced models that included the same predictor variables without defoliation (Table 3.3). Both the AIC and deviance were significantly reduced ($p < 0.05$) when each of the defoliation variables were included in the GAM. Cumulative severity (sev_cum) and defoliation duration (sev_dur) each reduced the AIC and deviance by about 2 to 4 times more than the others. Furthermore, the majority of the 95% confidence intervals of these two defoliation variables did not contain zero, whereas the confidence intervals of the

other variables more often contained zero (Figure 3.1). There was also a clearer pattern in the additive effect of these variables on the presence/absence of Douglas-fir beetle infestation. The probability of Douglas-fir beetle being present increased as defoliation duration and cumulative severity increased, up to a point – the probability slowed down or stopped increasing after about 11 years duration or a cumulative severity score of 10. The other three variables did not affect the probability as strongly, as the probability only changed a relatively small amount as the measures of the variables increased. Since sev_dur and sev_cum were highly correlated (Table 3.2) due to the calculation of cumulative severity using duration as well as severity, sev_cum was selected to remain in the model due to it producing a lower AIC and deviance compared to sev_dur.

Table 3.3: Results of generalized additive models assessing the probability of Douglas-fir beetle infestation subsequent to western spruce budworm defoliation. Variables related to defoliation, including the duration (sev_dur), average severity (sev_avg), maximum severity (sev_max), standard deviation of severity (sev_std) and cumulative severity (sev_cum), were generally highly correlated with one another and so compared in separate models for best fit through the lowest AIC and highest reduction in deviance. Variables associated with precipitation, including the total annual (tap_avg) and spring (tsp_avg) precipitation deviation averaged over 2000-2013, were also highly correlated and selected for in the same way. A lower AIC and deviance indicates a better model fit.

	Variable	AIC	AIC difference	Resid. df	Resid. deviance	Change in df	Change in deviance	p-value
Defoliation	No defol.	15525.81		30691	15392			
	Sev_dur	14496.91	-1028.90	30683	14348	7.89	-1043.00	<0.0001
	Sev_avg	15252.18	-273.63	30684	15106	7.03	-285.80	<0.0001
	Sev_max	15060.02	-465.79	30686	14917	5.22	-474.42	<0.0001
	Sev_std	15230.90	-294.91	30683	15083	7.43	-308.24	<0.0001
	Sev_cum	14364.32	-1161.49	30683	14217	7.39	-1174.10	<0.0001
Precipitation	No precip.	14364.32		30692	14366			
	Tsp_dev	14361.54	-2.78	30683	14217	8.32	-148.68	<0.0001
	Tap_dev	14279.05	-85.27	30685	14135	6.96	-231.35	<0.0001

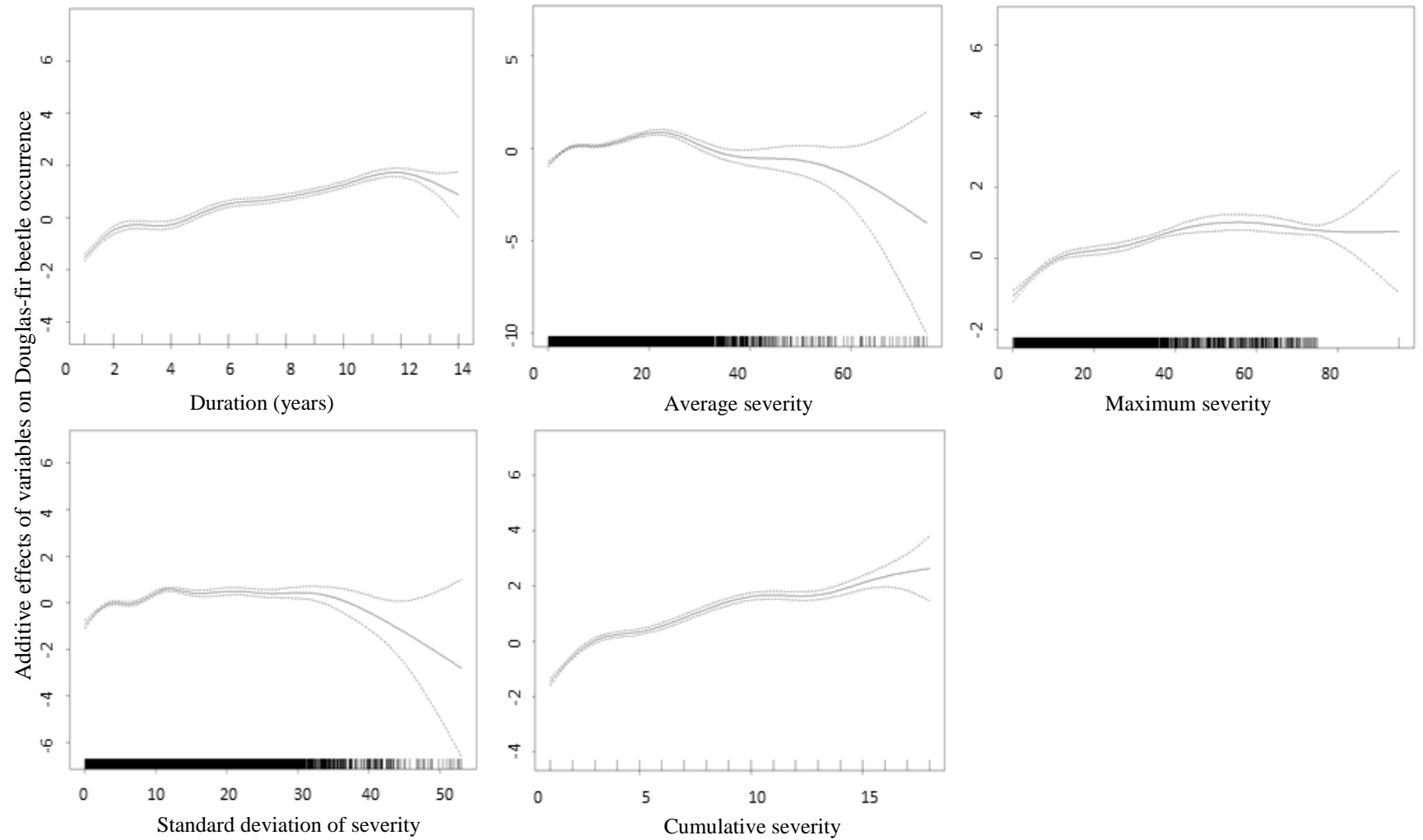


Figure 3.1: Results of generalized additive models showing the additive effect of each variable on the presence/absence of Douglas-fir beetle subsequent to western spruce budworm defoliation in 1 x 1 km fishnet (grid) cells over the Douglas-fir range in British Columbia. The five models with either defoliation duration, average severity, maximum severity, standard deviation of severity or cumulative severity were tested separately due to high correlation among these variables, along with several other site, host and precipitation deviation predictor variables. Dotted lines represent the 95% confidence intervals around the main effects, and the vertical dashes along the x-axis show the distribution of points entering into the model.

Similar to the defoliation variables, total spring precipitation deviation (tsp_dev) and total annual precipitation deviation (tap_dev) were tested in separate GAMs due to their high correlation (Table 3.3). Including tap_dev in a model with cumulative defoliation and other site and host variables reduced the AIC and deviance by a little more than 1.5x as much as tsp_dev. Neither tsp_dev or tap_dev had the majority of their 95% confidence intervals containing zero; however, the additive effects of each on the probability of Douglas-fir beetle presence showed different patterns (Figure 3.2). The highest probability of Douglas-fir beetle infesting after a western spruce budworm defoliation event occurred at a total spring precipitation deviation of about -50 mm and at a total annual precipitation deviation of between 0 and 150 mm. The very broad confidence bands at the beginning of tsp_dev and tap_dev and at the end of tsp_dev made the influence less clear. Total annual precipitation deviation was selected to remain in the model given that it produced the lowest AIC and deviance.

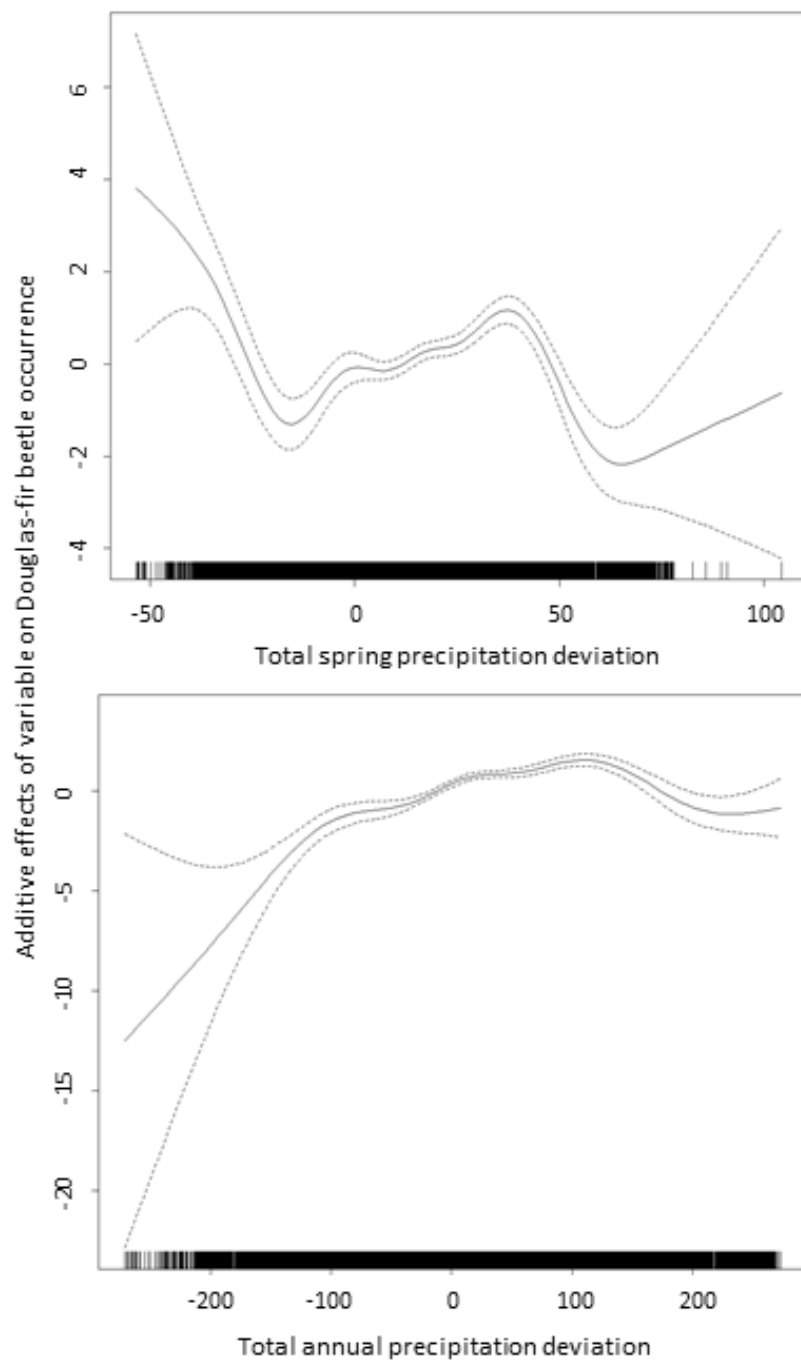


Figure 3.2: Results of generalized additive models showing the additive effect of each variable on the presence/absence of Douglas-fir beetle subsequent to western spruce budworm defoliation in 1 x 1 km fishnet (grid) cells over the Douglas-fir range in British Columbia. The two models with either total spring precipitation deviation or total annual precipitation deviation were tested separately due to high correlation between these variables, along with several other site, host and precipitation deviation predictor variables. Dotted lines represent the 95% confidence intervals around the main effects, and the vertical dashes along the x-axis show the distribution of points entering into the model

The full model then included cumulative severity of defoliation, total annual precipitation deviation and the other site and host variables, excluding dominant BEC subzone, which would be tested later within the Interior Douglas-fir (IDF) zone alone. Restricted GAMs, each with the removal of either dominant biogeoclimatic zone (bec_zone), site index (site_ind), site crown closure class (site_crnclous), projected age class of Douglas-fir (fd_age), mean percent of Douglas-fir (fd_perc), or spatial (long,lat) all showed significant ($p < 0.05$) increases in AIC and deviance (Table 3.4). Removing bec_zone and site_ind, however, increased the AIC and deviance by only a relatively small amount (< 50 , together) compared to the others, and so were removed to simplify the model without sacrificing too much fit.

Table 3.4: Results of generalized additive models predicting the probability of Douglas-fir beetle infestation subsequent to western spruce budworm defoliation. GAMs with one or more predictor variables removed (i.e., restricted models) were compared to a full model with all variables, including cumulative severity of defoliation, total annual precipitation deviation, dominant biogeoclimatic zone (bec_zone), site index (site_ind), site crown closure (site_crnclous), and projected age class (fd_age), mean percent (fd_perc) of Douglas-fir trees, and a spatial variable (long,lat). A lower AIC and deviance indicates a better model fit.

Variable	AIC	AIC difference	Resid. df	Resid. deviance	Change in df	Change in deviance	p-value
Full	14279.05		30685	14135			
Without bec_zone	14287.15	+8.10	30694	14161	-8.97	+26.25	<0.01
Without site_ind	14323.28	+44.23	30686	14181	-1.12	+46.42	<0.001
Without site_crnclous	14374.97	+95.92	30692	14242	-7.06	+107.53	<0.001
Without fd_age	14394.75	+115.70	30693	14266	-7.96	+131.79	<0.001
Without fd_perc	14585.66	+306.61	30686	14443	-0.84	+308.60	<0.001
Without long,lat	16521.07	+2242.02	30708	16423	-23.05	+2288.10	<0.001
Without bec_zone + site_ind	14326.03	+38.88	30695	14202	-1.02	+40.77	<0.001
Without bec_zone + site_ind + site_crnclous	14465.95	+139.92	30704	14360	-8.89	+158.01	<0.001

A final GAM analysis was conducted with only the fishnet cells where the Interior Douglas-fir (IDF) zone was the dominant BEC zone. A restricted model with BEC subzone (bec_sub) removed was compared to the full model with bec_sub, cumulative severity of defoliation (sev_cum), total annual precipitation deviation (tap_dev), site crown closure class (site_crnclous), projected age class (fd_age), mean percent (fd_perc) of Douglas-fir and the spatial variable (long,lat) (Table 3.5). Removing bec_sub increased the AIC by > 100 and

significantly increased the deviance as well; therefore, the model is a better fit with *bec_sub* included.

Table 3.5: Generalized additive model results for predicting the probability of Douglas-fir beetle infestation subsequent to western spruce budworm defoliation within the Interior Douglas-fir (IDF) biogeoclimatic (BEC) zone of British Columbia. A restricted model with BEC subzone (*bec_sub*) variable removed was compared to a full model with BEC subzone, cumulative severity of defoliation, site index, site crown closure, projected age and mean percent of Douglas-fir and total annual precipitation deviation. A lower AIC and deviance indicates a better model fit.

Variable	AIC	AIC difference	Resid. df	Resid. deviance	Change in df	Change in deviance	p-value
Full	14196.14		30672	14027			
Without <i>bec_sub</i>	14326.03	+129.89	30695	14202	+22.46	+174.65	<0.001

3.3.2 Final variables to predict Douglas-fir beetle presence

The model that best predicted the presence of Douglas-fir beetle based on the tested variables included cumulative severity of western spruce budworm defoliation (*sev_cum*), site crown closure class (*site_crnclos*), mean percent of Douglas-fir trees (*fd_perc*), projected age class of Douglas-fir (*fd_age*), total annual precipitation deviation (*tap_dev*), and a spatial variable (*long,lat*) indicating that variables tended to be clustered in space. BEC subzone improved the model within the IDF zone.

To understand how the individual variables in this model affected the prediction of subsequent Douglas-fir beetle infestation in a budworm defoliated stand, the number of fishnet cells where Douglas-fir beetle was present (“attacked” cells) were totaled and then plotted as a percentage of the total against each of the predictor variables. The plots showed which values or categories of the predictor variables were associated with the highest and lowest proportion (or probability) of “attacked” cells. The same was done for observations where subsequent Douglas-fir beetle attacks were absent (“unattacked” cells), shown on the same plot. In Figure 3.3, the percentage of “unattacked” cells declined exponentially with increasing cumulative severity of western spruce budworm defoliation, so that the highest proportion of “unattacked” cells (76%) were associated with a cumulative severity of less than 4 or 5. Conversely, 67% of the total “attacked” cells had a cumulative severity of greater

than 7. The percentage of “attacked” cells increased rapidly after a cumulative severity of 7 and peaked at a cumulative severity of 10, before declining.

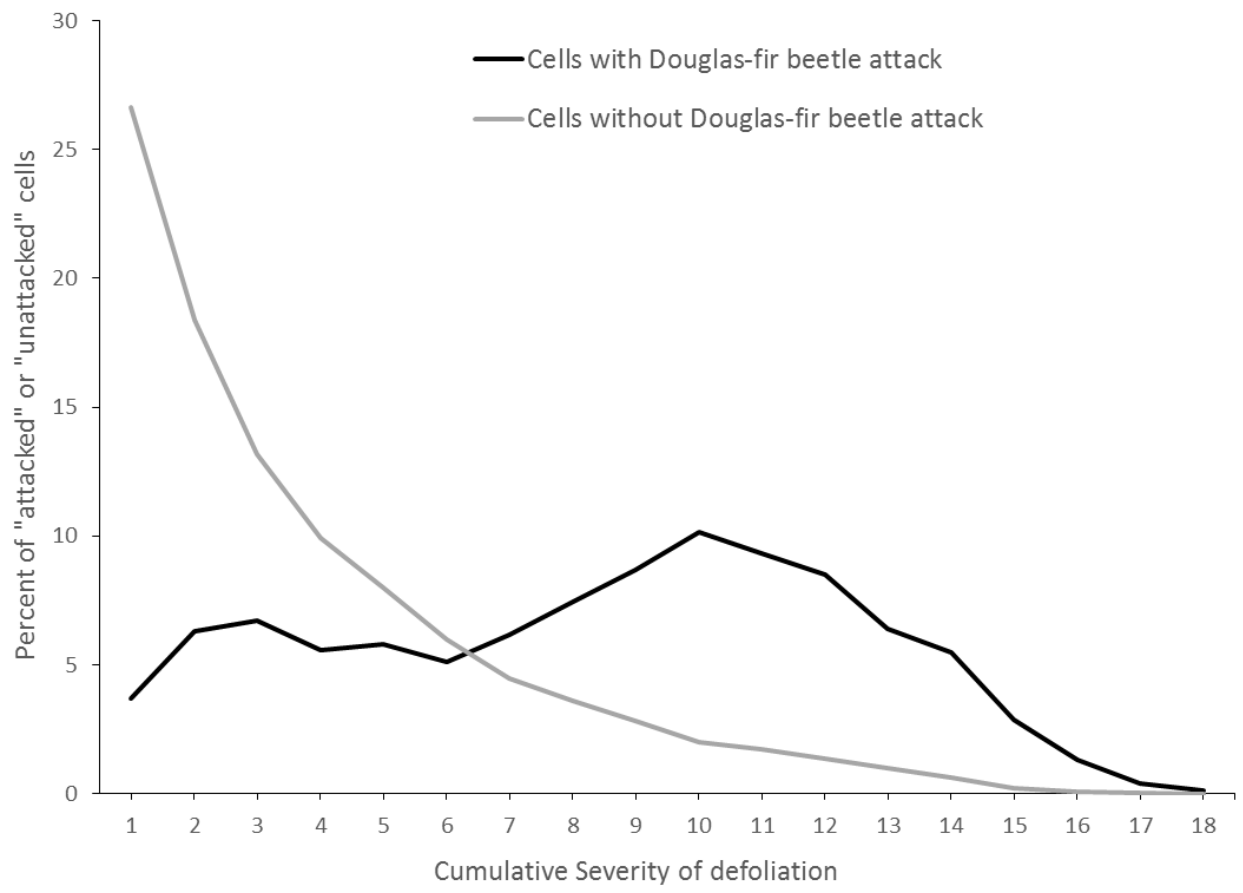


Figure 3.3: Percentage of “attacked” cells (experienced Douglas-fir beetle attacks subsequent to western spruce budworm defoliation) (N = 4,553) versus the cumulative severity of defoliation and percentage of “unattacked” cells (experienced no Douglas-fir beetle attack subsequent to defoliation) (N = 26,203) versus cumulative severity of defoliation. The sum of the points in each individual plot will be 100%. Cells were 1 x 1 km fishnet (grid) cells laid over the range of Douglas-fir trees in British Columbia, Canada, where recent (2000-2013) western spruce budworm defoliation occurred. Cumulative severity was calculated by assigning a value to the mean severity of defoliation in a cell (1 = low, 2 = moderate, 3 = high) and summing the values across the number years of the defoliation event.

The proportion of “attacked” cells also increased exponentially as the mean percent of Douglas-fir increased (Figure 3.4). The pattern was similar for the “unattacked” cells, although the rate of increase occurred a different rate. Of the total “attacked” cells, the highest proportion (88%) was associated with a mean percent of Douglas-fir trees of 60-80% or greater. Conversely, of the total “unattacked” cells, the highest proportion (70%) occurred where the mean percent of Douglas-fir was <60-80%. In comparing the mean age class of

Douglas-fir, the pattern was even more similar for both where the beetle was present and where it was absent (Figure 3.5). Overall, the percentage of cells exponentially increased with increasing age class and peaked at age class 8 (141-250 years), before rapidly declining. The proportion of the total “unattacked” cells was higher in age classes 1 to 6 (age ≤ 120 years) compared to the proportion of the total “attacked” cells that fell within the same Douglas-fir age range. After age class 7 (121-140 years), this relationship was reversed. Over 75% of the “attacked” cells fell within age class range of 7 to 9, whereas only 65% of the “unattacked” cells were associated with a Douglas-fir age class of 7 or greater.

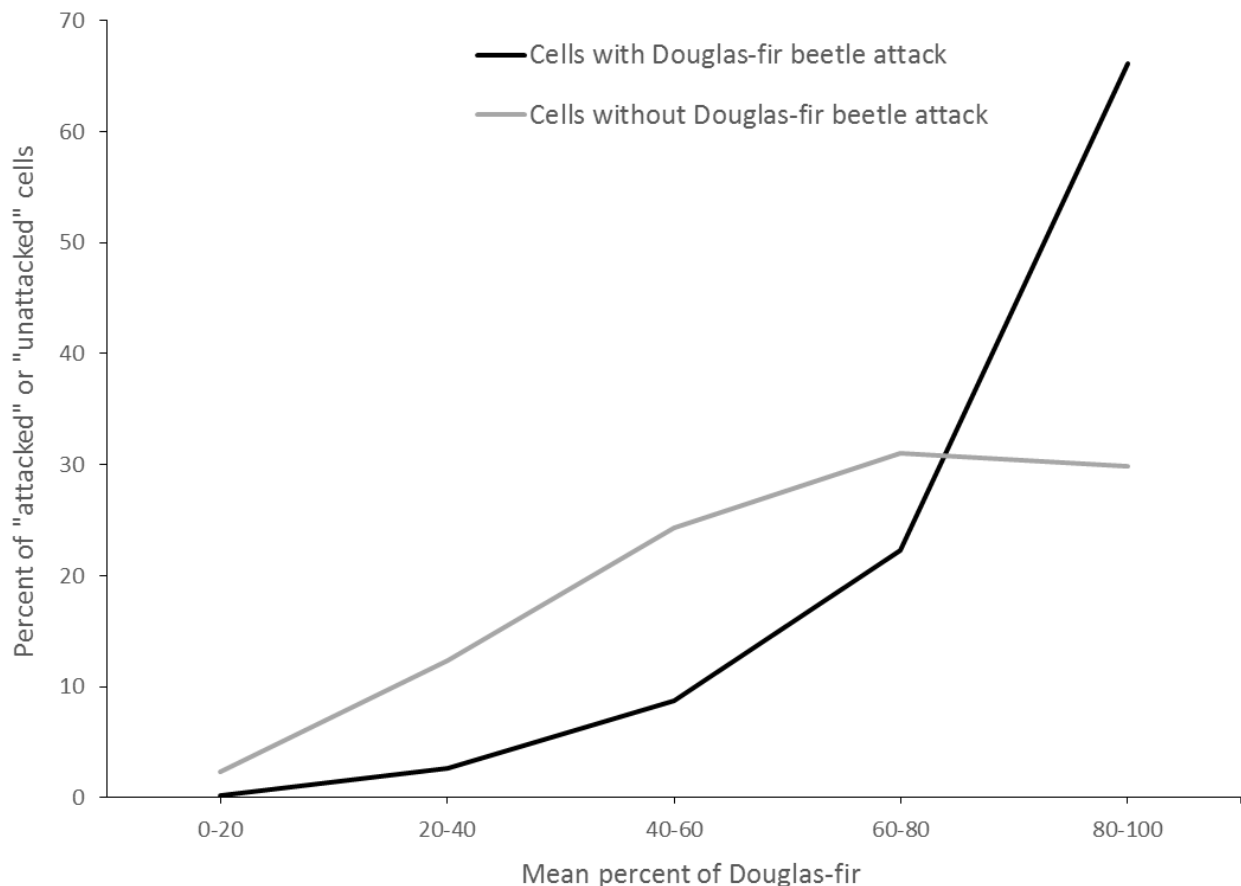


Figure 3.4: Percentage of “attacked” cells (experienced Douglas-fir beetle attacks subsequent to western spruce budworm defoliation) (N = 4,553) versus the mean percent of Douglas-fir trees and percentage of “unattacked” cells (experienced no Douglas-fir beetle attack subsequent to defoliation) (N = 26,203) versus the mean percent of Douglas-fir trees. The sum of the points in each individual plot will be 100%. Cells were 1 x 1 km fishnet (grid) cells laid over the range of Douglas-fir trees in British Columbia, Canada, where recent (2000-2013) western spruce budworm defoliation occurred.

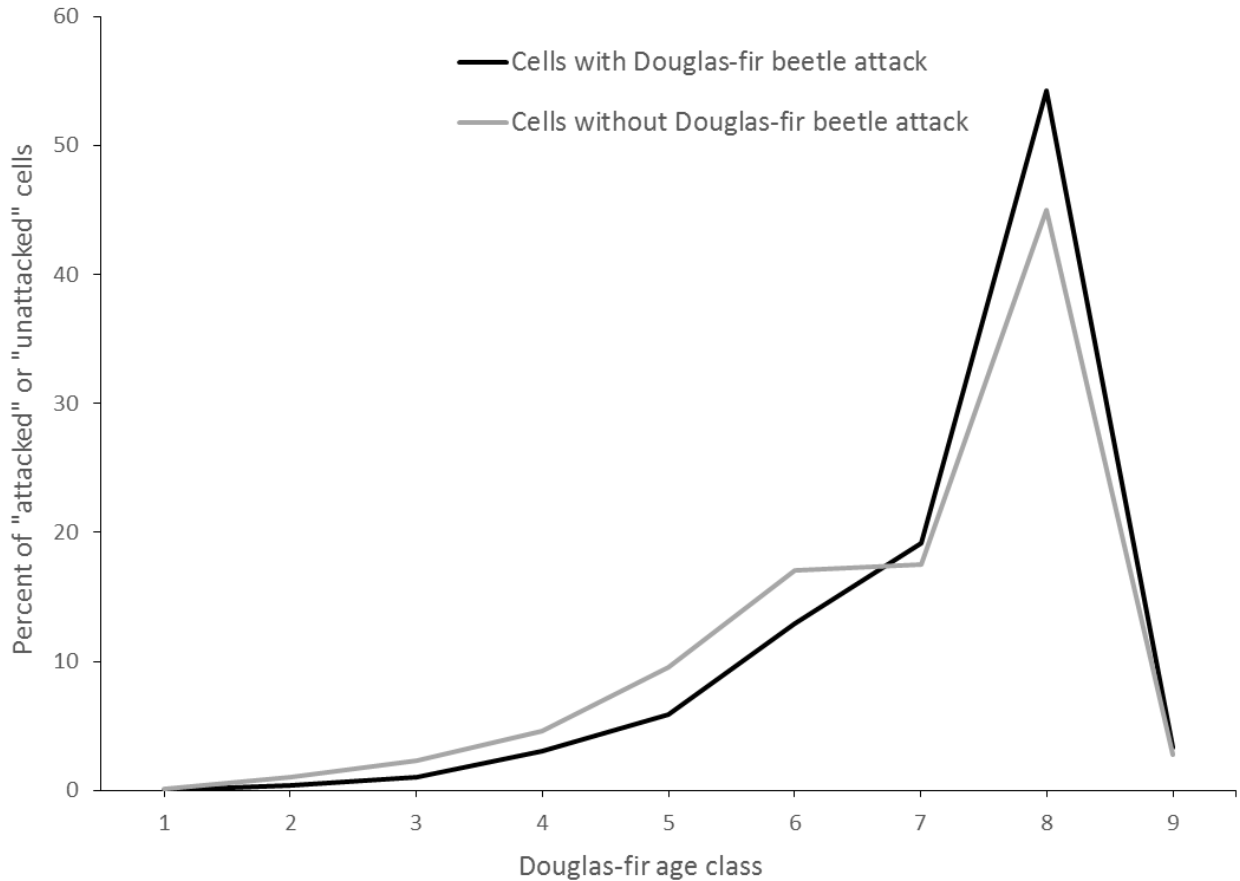


Figure 3.5: Percentage of “attacked” cells (experienced Douglas-fir beetle attacks subsequent to western spruce budworm defoliation) (N = 4,553) versus the 01/01/2009 projected age class of Douglas-fir trees and percentage of “unattacked” cells (experienced no Douglas-fir beetle attack subsequent to defoliation) (N = 26,203) versus the 01/01/2009 projected age class of Douglas-fir trees. The sum of the points in each individual plot will be 100%. Cells were 1 x 1 km fishnet (grid) cells laid over the range of Douglas-fir trees in British Columbia, Canada, where recent (2000-2013) western spruce budworm defoliation occurred. Age classes are: 1 = 1-20 years, 2 = 21-40 years, 3 = 41-60 years, 4 = 61-80 years, 5 = 81-100 years, 6 = 101-120 years, 7 = 121-140 years, 8 = 141-250 years, and 9 = 251+ years.

The distribution of “attacked” and “unattacked” cells in regards to the crown closure class within the fishnet cells followed the same pattern (Figure 3.6). The percentage increased with increasing crown closure class, then peaked midway before decreasing. A higher proportion of the “attacked” cells were associated with slightly lower crown class, peaking at class 3 (26-35% closure), whereas the percentage of “unattacked” cells peaked at a class of 4 (36-45% closure).

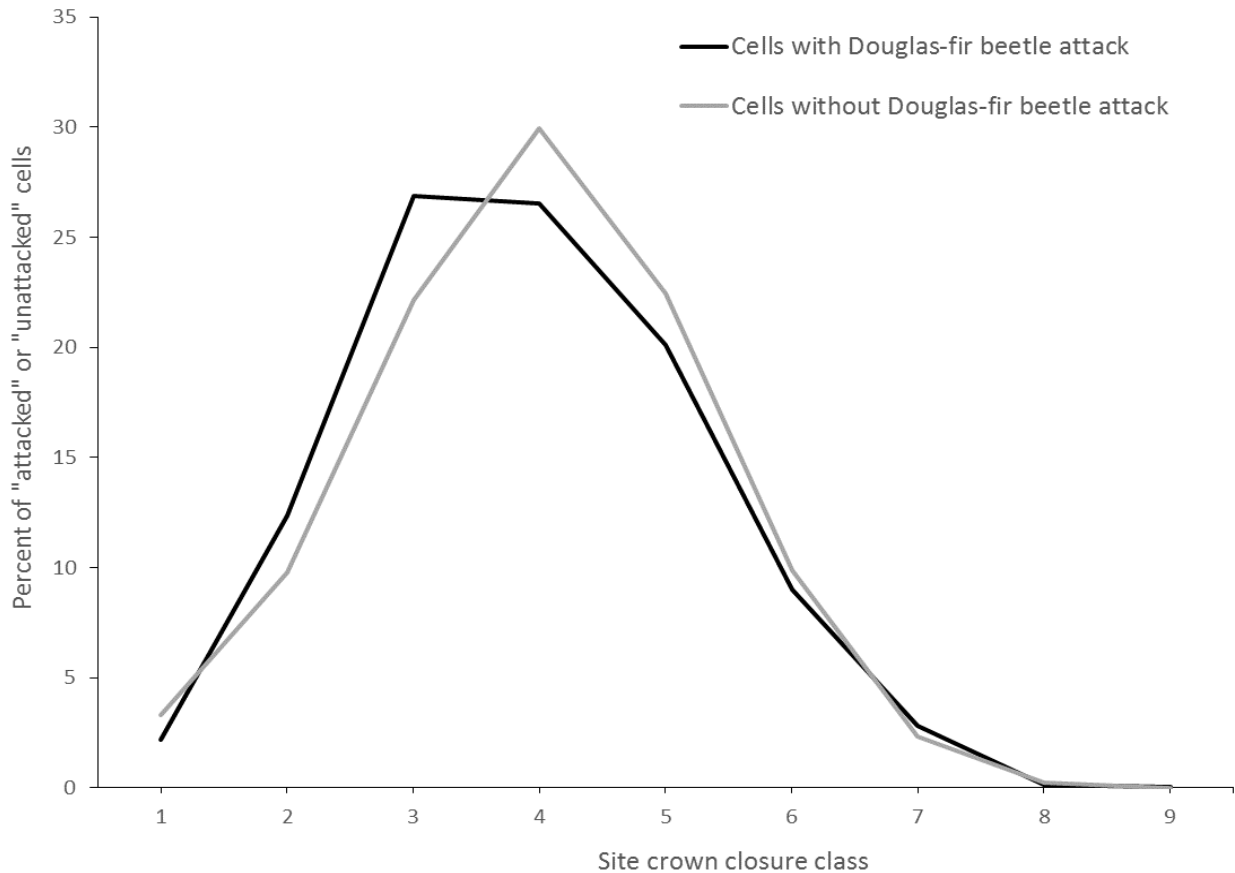


Figure 3.6: Percentage of “attacked” cells (experienced Douglas-fir beetle attacks subsequent to western spruce budworm defoliation) (N = 4,553) versus crown closure class of the site and percentage of “unattacked” cells (experienced no Douglas-fir beetle attack subsequent to defoliation) (N = 26,203) versus crown closure class of the site. The sum of the points in each individual plot will be 100%. Cells were 1 x 1 km fishnet (grid) cells laid over the range of Douglas-fir trees in British Columbia, Canada, where recent (2000-2013) western spruce budworm defoliation occurred. Crown closure classes are: 0-5% = 0, 6-15% = 1, 16-25% = 2, 26-35% = 3, 36-45% = 4, 46-55% = 5, 56-65% = 6, 66-75% = 7, 76-85% = 8, 86-95% = 9, and 96-100% = 10.

Interestingly, of the “attacked” cells, a higher percentage were associated with a total annual precipitation deviation of about -29 mm to 114 mm, compared to “unattacked” cells which had the highest proportion associated with a deviation of about -117 mm to 48 mm (Figure 3.7). In other words, cells were more likely to be attacked if the average total annual precipitation for 2000 to 2013 was around or higher than the 30 year mean (1971-2000).

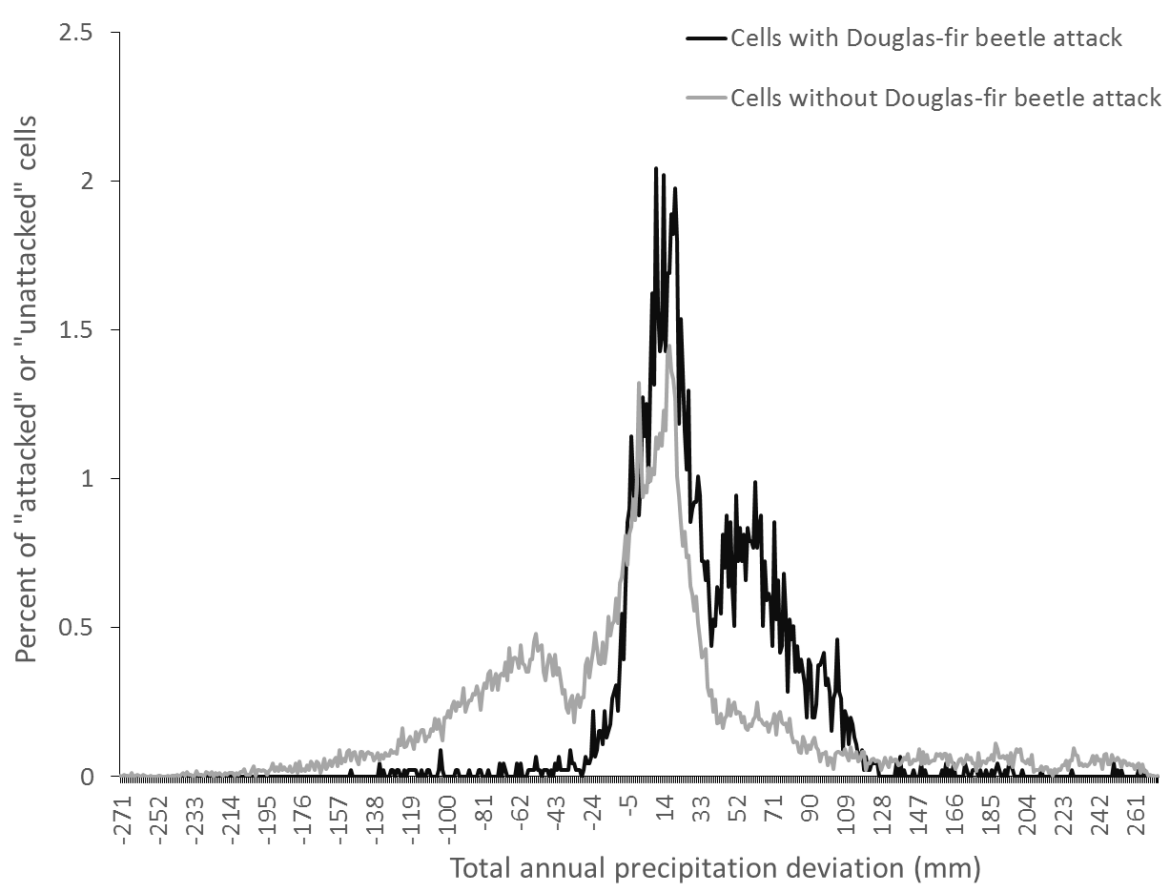


Figure 3.7: Percentage of “attacked” cells (experienced Douglas-fir beetle attacks subsequent to western spruce budworm defoliation) (N = 4,553) versus the total annual precipitation deviation from the 30 year mean (1971-2000) and percentage of “unattacked” cells (experienced no Douglas-fir beetle attack subsequent to defoliation) (N = 26,203) versus the total annual precipitation deviation from the 30 year mean (1971-2000). The sum of the points in each individual plot will be 100%. Cells were 1 x 1 km fishnet (grid) cells laid over the range of Douglas-fir trees in British Columbia, Canada, where recent (2000-2013) western spruce budworm defoliation occurred.

3.4 Discussion

3.4.1 Summary of key findings

Defoliation of Douglas-fir by western spruce budworm increases the probability of subsequent infestation by the Douglas-fir beetle, even after controlling for the influence of a number of host, site and climatic variables. These results concur with observations that these two biotic disturbance agents often reach outbreak levels together in the same regions (Gast *et al.*, 1991; Hadley & Veblen, 1993; Ciesla, 2006; Steed *et al.*, 2007). Cumulative

defoliation severity had the largest influence on the probability of subsequent Douglas-fir beetle impacts. Furthermore, in keeping with my prediction, the highest probability of bark beetle infestation occurred following moderate levels of cumulative defoliation. The Douglas-fir beetle tended to be absent from cells with low cumulative severity, but present once substantive defoliation accumulated, indicating that both severity and duration of a western spruce budworm outbreak had an important influence on Douglas-fir beetle presence. Several years of stress on the host trees through loss of their photosynthetic material would likely be attractive to the Douglas-fir beetle due to increased susceptibility to bark beetle attacks (Berryman & Wright, 1978; Wright *et al.*, 1979, 1984; Negrón, 1998). However, after cumulative severity of defoliation reached a certain level, it became less likely again for Douglas-fir beetle to be present, indicating that only moderate, not high, levels of cumulative severity increased the probability of subsequent Douglas-fir beetle attacks in defoliated stands.

Although western spruce budworm defoliation was shown to be an important factor in predicting the eruption of subsequent Douglas-fir beetle infestation, the inclusion of several other aspects of the biotic and abiotic environment were required to construct a predictive model that may be useful to forest managers. Host, site and climatic conditions within the defoliated stands were all important components of the final model, which emphasizes the complexity of forest insect population dynamics. The Douglas-fir beetle preferred to attack stands with large diameter, mature trees (Furniss *et al.*, 1979, 1981), which generally have thicker phloem and a decline in defensive capacity due to senescence. Also, not surprisingly, the probability of infestation increased with increasing proportion of Douglas-fir compared to other species, thereby facilitating host location and reducing intra-specific competition (Rudinsky 1962, Negrón 1998, Wermelinger 2004). Climatic factors, as indicated by biogeoclimatic variables and precipitation deviation, were also important to Douglas-fir beetle infestation dynamics. Although Douglas-fir beetle and other bark beetles have been observed to outbreak more often in stands that have experienced prolonged dry periods or severe drought (Rudinsky, 1962; Christiansen *et al.*, 1987; Powers *et al.*, 1999), this seems to be contrary to my results, which show that a higher percent of the cells attacked by Douglas-fir beetle were associated with annual precipitation that was somewhat higher than the 30-year mean (**Figure 3.7**). It may be that the combined stress of defoliation and drought leads to

more rapid thinning of the phloem than either stressor individually, thereby making those trees less attractive to the Douglas-fir beetle (e.g., Gieger & Thomas, 2002). Finally, including the spatial variable (longitude, latitude) was significant for predicting Douglas-fir beetle infestations in defoliated stands. It suggests that spatial correlation existed, which is unsurprising given the nature of the data. A stand is more likely to experience a bark beetle outbreak if an outbreak occurs in an adjacent stand, given there is a high proportion of suitable host trees and decent connectivity between stands (Raffa *et al.*, 2008). Furthermore, synchronous outbreaks may occur even over long distances if homogenous processes occur over a wide area, such as drought, stand-replacing disturbances, or temperature changes (Aukema *et al.*, 2008; Raffa *et al.*, 2008).

3.4.2 Mechanism behind Douglas-fir beetle attacks after defoliation

Conifer defences against bark beetle attacks include the release of resin from preformed resin ducts or blisters that are severed as beetles bore through the bark, along with secondary induced resins by tissues surrounding the point of penetration (Berryman & Wright, 1978; Reid & Robb, 1999; Franceschi *et al.*, 2005; Raffa *et al.*, 2005). The induced response is often the most effective at repelling or killing bark beetles (Raffa *et al.*, 2005), but it is also energetically expensive, and therefore only vigorous trees containing sufficient energy reserves are able to express it to its fullest capacity (Christiansen *et al.*, 1987; Franceschi *et al.*, 2005; Six & Skov, 2009). Repeated defoliation impairs photosynthetic capacity, as well as leads to a decline in stored carbohydrates and a prioritization of resource allocation to the maintenance of living tissues at the expense of defences (Christiansen *et al.*, 1987). Low density Douglas-fir beetle populations are mainly restricted to stressed or weakened trees, and even outbreaks cannot be sustained for too long in vigorous stands (Six & Skov, 2009); however, bark beetle brood success is related to the available quantity and nutritive quality of the host's phloem (Amman, 1972; Larsson *et al.*, 1983; Haack *et al.*, 1987; Reid & Robb, 1999), which is positively correlated to tree size and vigour (Cole, 1973; Hawksworth *et al.*, 1983; Waring & Pitman, 1985; Reid & Robb, 1999). Therefore, both the food value (i.e., phloem quantity and quality) and the defensive ability of the hosts will contribute to the distribution and abundance of bark beetles within a stand.

Moderate cumulative defoliation by the western spruce budworm may increase the susceptibility of trees to subsequent Douglas-fir beetle attacks by suppressing host resistance, but not causing the phloem resource to diminish as would be expected under higher levels of cumulative defoliation (Wright *et al.*, 1984; Fredericks & Jenkins, 1988; Negrón, 1998; Cedervind *et al.*, 2003; Sturdevant & Kegley, 2006). Indeed, several studies have shown that there may not be a significant reduction in phloem thickness for many years during stress conditions, even as tree growth diminishes (Shrimpton & Thomson, 1985; Gričar & Čufar, 2008). Conversely, chronic, high levels of defoliation will lead to reductions in the quantity and quality of phloem (Kozlowski, 1969; Kulman, 1971; Wright *et al.*, 1984; Conway *et al.*, 1999; Dobbertin & Brang, 2001), and thereby decrease the probability of Douglas-fir beetle infestation.

3.4.3 Importance of interactions between biotic disturbance agents

This study emphasizes the importance of recognising the interactions that can take place between biotic disturbance agents. This is a crucial consideration when managing for healthy forests as the combined effects of two interacting disturbance agents, such as defoliation followed by a bark beetle infestation, may lead to higher amounts of mortality in a stand than if either event had occurred alone (Belyea, 1952; Wickman, 1978). This suggests that such interactions may result in additive, or even synergistic, impacts on the ecosystem. An additive impact refers to the effect of two stressors or disturbances on plant growth that is equal to the sum of the effects of the two stressors taken separately, whereas if the effect of the two stressors taken together is greater than the sum of their separate effects, then it is said to be a synergistic impact (Bansal *et al.*, 2013; Hauser *et al.*, 2013). An interaction may also have an antagonistic impact on the ecosystem, which means that the effect of the two stressors is actually less than the sum of the effect of the two stressors taken independently of each other (Bansal *et al.*, 2013; Hauser *et al.*, 2013). The type of impact may vary with factors associated with the geography, environment, climate and plant response (McCullough *et al.*, 1998; Bebi *et al.*, 2003; Hauser *et al.*, 2013), but there have been several examples in literature of additive and synergistic effects as a result of abiotic and biotic disturbance agent

interactions (McCullough *et al.*, 1998; Desprez-Loustau *et al.*, 2006; Parker *et al.*, 2006; Dobbertin *et al.*, 2007; Raffaele *et al.*, 2011; Bansal *et al.*, 2013).

The interaction between western spruce budworm and Douglas-fir beetle found in my study leads to high mortality in both the smaller and larger size classes of trees during overlapping infestations, as severe western spruce budworm defoliation causes mortality of understorey trees, while a subsequent outbreak of Douglas-fir beetle cause early mortality in large diameter trees that normally can survive multiple years of defoliation (Hadley & Veblen, 1993). This suggests that there may be an additive effect on the forest environment when defoliators and bark beetles in similar systems interact. Furthermore, without moderate western spruce budworm defoliation (or some other disturbance) to weaken the defences of optimal hosts, Douglas-fir beetle populations would likely not build up so quickly or have the ability to kill large, healthy trees, and so the effect of such a defoliator and bark beetle interaction may even be synergistic at times (Craighead, 1940; Belyea, 1952; Wickman, 1978; Cedervind, 2003). Several occurrences of high mortality in both the smaller and larger size classes of stands within North America and Europe have supported the idea of additive or synergistic effects resulting from interactions between defoliators and bark beetles (e.g., Belyea, 1952; Cole, 1961; Berryman & Wright, 1978; Hadley & Veblen, 1993; Langstrom *et al.*, 2001a; Wallin & Raffa, 2001; Cedervind *et al.*, 2003; Sturdevant & Kegley, 2006). Cole (1961), for example, suggested that about 14% of the mortality of ponderosa pines in one outbreak was caused by bark beetle attacks following pine butterfly defoliation in the Northwest, and Berryman and Wright (1978) advised a forest manager that timber losses would likely increase due to bark beetles during and shortly after a Douglas-fir tussock moth epidemic. In Scandinavia, more than 80% of dead defoliated Scots pine had been attacked by the pine shoot beetle and it was concluded that this beetle likely played a role in the mortality process (Langstrom *et al.*, 2001a; Cedervind *et al.*, 2003).

Not only does increased mortality result from defoliation followed by bark beetle attacks, but any changes in the outbreak dynamics of one biotic agent will affect those of the second. Anthropogenic interventions, for example, have actually increased the potential for synergistic effects between biotic disturbance agents. Past forest management practices have led to changes to forest stand structure and composition, and are thought to be responsible for

the 20th century increases in duration, extent and intensity of western spruce budworm in some regions of western North America (Anderson *et al.*, 1987; Hadley & Veblen, 1993; Swetnam & Lynch, 1993). Fire suppression and certain logging methods have resulted in forest conditions that favour the budworm, such as denser, multilevel stands dominated by Douglas-fir. In turn, the increased western spruce budworm outbreak extent and intensity has increased the vulnerability and susceptibility of the forest stands to subsequent Douglas-fir beetle outbreaks. Douglas-fir beetle populations have been observed to reach outbreak levels in defoliated stands where western spruce budworm outbreaks have become more severe and synchronous due to past anthropogenic impacts on the forest (Hadley & Veblen, 1993). Consequently, it is not only the direct impacts on forest health that need to be considered when changes are observed in the outbreak dynamics of a defoliating insects, but also the effect on other biotic disturbance agents, such as bark beetles, which may amplify the disturbance impact.

3.4.4 Climate change impacts on biotic disturbance interactions

The interaction between biotic disturbance agents may become an even more important consideration with future climate change. With rising temperatures and temperature and precipitation extremes, it is predicted that outbreaks of many pest species will continue to increase (Ayres & Lombardero, 2000; Soja *et al.*, 2007; Bentz *et al.*, 2010; IPCC, 2014). Several major defoliator species in North America and Europe have experienced increases in outbreak range and severity due to climate change (e.g., Tenow *et al.*, 1999; Hodar & Zamora, 2004; Battisti *et al.*, 2006; Jepsen *et al.*, 2008, 2011), including the western spruce budworm (Swetnam & Lynch, 1993; Maclauchlan, 2003; Maclauchlan *et al.*, 2006; Cooke *et al.*, 2007). Climate change has played a significant role in the range expansion of outbreak-level populations of western spruce budworm that has occurred from Vancouver Island, BC into other regions to the east and north since the early 1900s (Volney, 1994; Campbell *et al.*, 2006; Maclauchlan *et al.*, 2006; Thomson & Benton, 2007; Marciniak & Carroll, in prep). Within the areas where the western spruce budworm outbreak range has recently expanded, Douglas-fir beetle will have been more likely to successfully infest due to an increase in cumulative severity of defoliation. This may lead to more severe or expanded range of

Douglas-fir beetle outbreaks as well. On the other hand, severe defoliation that occurs over an extended period of time may result in chronic effects (e.g., reduced host phloem) that reduce the probability of subsequent Douglas-fir beetle infestations; therefore, managing for these disturbances will require knowledge of the defoliator outbreak history.

Similar responses may occur in the outbreak dynamics of other eruptive bark beetles where there is an additive or synergistic interaction with a defoliator, such as the European spruce bark beetle, *Ips typographus* L., which exhibits periodic outbreaks in Central and Northern Europe that has resulted in extensive mortality of Norway spruce (Okland & Berryman, 2004; Wermelinger, 2004). Studies have mainly focused on the direct effects of climate change on the bark beetle (Jönsson *et al.*, 2011), such as extreme weather events that result in large amounts of windfelled host material (Okland & Berryman, 2004; Wermelinger, 2004); however, warming temperatures have also been leading to an increase in defoliation of Norway spruce by web-spinning sawflies of the genus *Cephalcia* Panzer (Führer & Fischer, 1991; Marchisio *et al.*, 1994; Meterc *et al.*, 2014), which may increase the susceptibility of Norway spruce stands to European spruce bark beetle attacks, as has been seen with the western spruce budworm and Douglas-fir beetle. Therefore, it is necessary for forest managers to take into account the synergistic interactions and effects of biotic disturbance agents, together with other abiotic elements of the environment, when planning for future climate change impacts.

4 General conclusions

This research demonstrates the complexity of biotic forest disturbances and the need for a better understanding of both the life history of, and interactions between, biotic disturbance agents to successfully manage forests for such disturbances. The following sections summarize the key findings of the studies conducted in the previous two chapters, their implications for forest management under future climate change, and suggestions for the direction of future research.

4.1 Key findings

Chapter 2 demonstrated the northward range shift that has occurred over the past century in western spruce budworm outbreaks in British Columbia, Canada, and linked it to climate change-induced shifts in optimal synchrony between spring larval emergence and Douglas-fir budburst. The timing between larval emergence and host budburst is crucial to the survival and population growth of the western spruce budworm due to the fact that it is an early-season defoliator that relies on newly flushed foliage for its high nutritional value (Feeny, 1970; Carroll, 1999; Carroll & Quiring, 2003; van Asch & Visser, 2007). Warming temperatures due to climate change at higher latitudes and elevations have resulted in a convergence towards optimal timing, thus increasing the survival and growth rate of larvae and probability of western spruce budworm populations reaching outbreak levels. It was concluded that other early-season defoliators in temperate and boreal forests may also experience northward range shifts with climate change and, in fact, this has been observed already in some geometrid moth species, such as the winter moth, in Fennoscandia (van Asch & Visser, 2007; Jepsen *et al.*, 2008, 2009, 2011).

In chapter 3, I found that moderately-severe western spruce budworm defoliation in a Douglas-fir stand increased the probability of a subsequent Douglas-fir beetle infestation. The loss of current year foliage over multiple years putatively reduced the defensive abilities of large, healthy host trees, but still allowed the trees to maintain a thick phloem as suitable breeding material (Wright *et al.*, 1984; Fredericks & Jenkins, 1988; Negrón, 1998;

Sturdevant & Kegley, 2006). This allowed the Douglas-fir beetle to successfully attack the hosts even at low populations when they would normally be limited to recently dead or smaller, weaker trees (Six & Skov, 2009). On the other hand, chronic, highly-severe defoliation would lead to trees using up their stored resources to offset the loss of photosynthetic material, ultimately leading to thin, poor quality phloem that is less optimal for Douglas-fir beetle reproduction (Kozlowski, 1969; Kulman, 1971; Dobbertin & Brang, 2001). The interaction between these two biotic disturbance agents can lead to increased stand mortality as younger, understory trees die from defoliation while, at the same time, bark beetle infestations build up in and kill weakened overstory trees that would normally survive defoliation or low frequency bark beetle attacks separately (Belyea, 1952; Wickman, 1978). The increased mortality suggests an additive or synergistic effect among such biotic disturbance agents that should be an important consideration in future research on forest disturbances. Rather than focusing on the effects of a single disturbance agent, future studies have to look more into the complex relationships that can occur between biotic disturbance agents that may have unexpected impacts on forest ecosystems compared to if they occurred individually.

4.2 Implications for forest management with future climate change

Interactions between defoliators and bark beetles, where defoliation weakens large, otherwise healthy trees and facilitates attacks by secondary (i.e., non-aggressive) bark beetles, have been observed in several systems. Fir engraver beetles (*Scolytus ventralis* LeConte) have been known to outbreak subsequent to heavy defoliation by the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) (Berryman, 1973; Wright *et al.*, 1984) and western spruce budworm (Gast *et al.*, 1991). Jack pines defoliated by jack pine budworm are more likely to be attacked by five-spined engraver beetles (*Ips grandicollis* Eichhoff) or the pine sawyer beetle (*Monochamus carolinensis* Olivier) (Wallin & Raffa, 2001). In eastern North America, a positive correlation was found between the success of the four-eyed spruce bark beetle (*Polygraphus rufipennis* Kirby) in colonizing black spruce and the preceding damage caused by the eastern spruce budworm (*Choristoneura fumiferana* Clem.) (Bowers *et al.*, 1996). Successful attacks by western balsam bark beetle (*Dryocoetes confuses* Swaine), a

destructive pest of subalpine fir in BC, have also been observed in stressed, defoliated trees (Bleiker *et al.*, 2003).

Such interactions are also seen to occur between forest insects other than defoliators and bark beetles. Defoliators, beetles and even pathogens may weaken a tree and lead to secondary attacks by other insect species. Buprestid beetles, such as *Agrilus biguttatus*, which are wood borers associated with oak decline in several countries in Europe, have been known to infest and kill defoliated trees that normally could repel attacks (Moraal & Hilszczanski, 2000). The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) appears to be more attracted to lodgepole pine infected by Armillaria (*Armillaria mellea* (Vahl. Ex. Fr.) Krummer) or comandra blister rust (*Cronartium comandrae* Pk.) (Rasmussen, 1987; Colgan & Erbilgin, 2010). General bark beetle colonization was also found to be more likely to occur in ponderosa pine in Arizona that had been heavily affected by south western dwarf mistletoe (*Arceuthobium vaginatum*[Willd.] Presl subsp. *Cryptopodum* [Engelm.] Hawksw. & Wiens) (Kenaley *et al.*, 2006, 2008; Colgan & Erbilgin, 2010). In addition, defoliation may increase host susceptibility to pathogens. For example, herbivory by the cottonwood leaf beetle (*Chrysomela scripta* Fabricius) has been linked to increased mortality of *Populus* species in 2002 by *Septoria musiva* Peck stem canker (Coyle *et al.*, 2002). The blue-stain fungus *L. wingfieldii* may also take advantage of the reduced defences of its host, Scots pine, after defoliation by the pine looper (*Bupalus piniaria* L.) (Langstrom *et al.*, 2001b; Colgan & Erbilgin, 2010).

It is obvious that interactions occur between many different species of biotic disturbance agents in boreal and temperate forests. The implications of this are that changes in the dynamics of one biotic disturbance agent will lead to changes in one or more others. Several insect species have already been demonstrating changes in outbreak extent, severity, duration, and/or synchrony as a result of climate change during the last century (e.g., Blais, 1983; Volney, 1988; Roland, 1993; Carroll *et al.*, 2004; Berg *et al.*, 2006; Jepsen *et al.*, 2008). Many of the major periodic defoliators have responded positively to warming temperatures and changes in precipitation. Western spruce budworm outbreaks have been expanding northward and to higher latitudes, as well as increased in severity, duration and synchrony in some areas of western North America (Swetnam & Lynch, 1993; Campbell *et*

al., 2006; Maclauchlan *et al.*, 2006; Cooke *et al.*, 2007; Marciniak & Carroll, in prep). There has also been an expansion of the core outbreak area of winter moth (*Operophtera brumata* Bkh.) towards the north and east in Norway (Jepsen *et al.*, 2008, 2011) and of the pine processionary moth (*Thaumetopoea pityocampa* [Denis & Schiffermuller]) to higher latitudes and altitudes in France and Italy (Battisti *et al.*, 2005; Hoch *et al.*, 2009). Bark beetles, as well, have been responding positively to warmer summers and winters, increased average temperatures, and/or decreased precipitation. The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), for example, has expanded its range northward towards the Yukon and westwards into Alberta in the last century as warming temperatures have allowed it to successfully infest regions that were historically climatically unsuitable for it (Powell & Logan, 2001; Carroll *et al.*, 2004; Safranyik & Carroll, 2006). Range expansion and increases in outbreak frequency and severity of these biotic disturbance agents in reaction to climate change increases the susceptibility of forest stands to subsequent outbreaks by secondary biotic disturbance agents. As western spruce budworm, for example, expands northward, it is likely that there will be northward shifts or more frequent outbreaks of Douglas-fir beetle populations as result of the increased defoliation disturbance in those regions.

Furthermore, the effects of the biotic disturbance agents on the ecosystem will be compounded when they interact. Higher levels of tree mortality have been observed where two biotic disturbance agents, such as defoliators and bark beetles, interact (Belyea, 1952; Wickman, 1978; Hadley & Veblen, 1993; Cedervind *et al.*, 2003). When a defoliator outbreak occurs alone, generally the smaller, understorey trees experience the highest mortality (Fellin & Dewey, 1986; Cooke *et al.*, 2007), while large-diameter, overstorey trees often survive (Craighead, 1940; Langstrom *et al.*, 2001a; Cedervind *et al.*, 2003). However, bark beetles may quickly build up within the large trees that were weakened by defoliation, and then kill those trees that would normally have been able to recover from the defoliation event (Hadley & Veblen, 1993).

Stand or landscape-levels of mortality from the combined attacks of defoliators and bark beetles could lead to a number of further impacts on the environment. For example, widespread tree mortality can change a forest from a net carbon sink to a large net carbon source as carbon is released from hundreds of thousands of dead tree stems (Kurz *et al.*,

2008a,b). This is a concern because the released carbon may exacerbate global warming even further. The build-up of both fine and coarse woody surface fuels can also affect forest fire behavior, such as increasing the rate of spread and intensity of ground fires (Jenkins *et al.*, 2008, 2012; Hicke *et al.*, 2012b). Finally, increased tree mortality will affect the forest ecosystem in terms of structure and biodiversity (Dale *et al.*, 2001). Widespread loss of one or more tree species to biotic disturbance can significantly reduce the overall biodiversity of forests. On the other hand, gaps created in the canopy by fallen trees also allow more light to reach the forest floor, which will increase understorey growth and diversity of shrubs, grasses and shade-intolerant tree species. This may create a food source for animals and insects that would not normally frequent those areas, and thus cause a shift in the abundance and diversity of predators, parasitoids and detritivores.

Future research should not only consider the effects of climate change on individual biotic disturbance agents, but also gather more information on the interactions between biotic disturbance agents and how those interactions may impact the overall level of disturbance to be expected. It is important to determine what the outcomes of such interactions between biotic disturbance agents will be, such as whether the effects will be additive, synergistic or antagonistic. These disturbance systems are complex and difficult to predict, but increasing our knowledge regarding interactions will go a long ways in helping to properly manage forests for disturbances with climate change.

4.3 Future research directions from this thesis work

The studies in this thesis utilized one of the most comprehensive forest disturbance data sets in the world. The periodicity, wide coverage and rigorous standards of the aerial overview surveys make it possible to observe annual changes in disturbances at the landscape level across the entire province of BC with high accuracy. There remain, however, some limitations in this research that can be addressed by future investigations. Broad scale spatial and temporal data sets collected using remote sensing techniques can present some issues in identifying specific patterns and interactions due to the scale and resolution of the data (Levin, 1992; Schneider, 1994; Qi & Wu, 1996).

“It is argued that the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology. Applied challenges... require the interfacing of phenomena that occur on very different scales of space, time, and ecological organization. Furthermore, there is no single natural scale at which ecological phenomena should be studied; systems generally show characteristic variability on a range of spatial, temporal, and organizational scales.” (Levin, 1992, p. 1943)

The above quote implies that while I found biotic disturbance range shifts and interactions to be occurring at the provincial scale, it is important to supplement these results with field work at smaller scales to get a better sense of the full story. Thus, data collection and analyses at different scales should be the direction of future studies. Landscape-scale aerial surveys or other high-resolution remote sensing are useful for detecting and understanding overarching patterns and long-term changes (e.g., Ciesla, 2006; MacIaughlan *et al.*, 2006; Gray, 2013), while stand-level or region-level field measurements aid in identifying causes and effects and other information missing from the broad-scale data. Forest managers will also benefit from more localized data in that it will provide them with more precise knowledge of how biotic disturbances might change or interact, thereby allowing them to better manage for future disturbances.

Additionally, effects of climate change on range expansion and biotic disturbance agent interactions were considered only in the context of the current and historical behaviour of the insects, as well as in the context of the current forest structure, composition and range. We assumed, for example, that the range of western spruce budworm is mostly restricted to the range of its main host, which is Douglas-fir in BC; however, it has been observed to feed at low levels on a wide variety of conifers (Harvey, 1985; Fellin & Dewey, 1986; Volney, 1994; Nealis & Régnière, 2009). There are situations where biotic disturbance agents may extend outside of their historical range by accepting and adapting to other tree species, as seen by the example of the mountain pine beetle that has been moving east and to higher elevations where lodgepole pine, its main host in BC, is not abundant (Safranyik *et al.*, 2010). The ability of certain forest insects to expand further outside of their historical host

range should be considered in future research, as well as how such expansions may affect other biotic disturbance agents that interact with them.

Not only can biotic disturbances expand outside of their historical range, but the geographical ranges of many tree species may shift in the longer term due to climate change, as predicted by climate-based species distribution models and ecosystem-based climate envelope modeling (Hamann & Wang, 2006; Aitken *et al.*, 2008). Some tree populations will die out in certain regions that are becoming less climatically favourable and some will migrate to new, more climatically favorable locations (Williams & Liebhold, 1995). Fossil records and genetic data providing evidence for past glacial and postglacial migrations demonstrate the robust capacity of tree species to shift range (Davis & Shaw, 2001; Hamrick, 2004; Aitken *et al.*, 2008). Other research shows that forests have been affected already over the last century by droughts and other effects of climate change (Breshears *et al.*, 2005). Such tree species range shifts and die-offs complicate attempts to predict eruptive forest insect responses, especially because range shifts of insects and range shifts of their hosts occur on different time scales. Insects can respond in a relatively short period of time, such as years, due to rapid reproduction and dispersal abilities, while the response time of forests may be on the scale of centuries (Williams & Liebhold, 1995). This is important because forest insects require an expansion in the range of susceptible forest if they are to expand as well. Future research could consider the ability of biotic disturbances to extend beyond the current range of their hosts, as well as how the host range itself may respond to future climate change. There is still a lack of information for many forest insect disturbances in regards to whether they can be expected to shift with their host species, expand or contract their range, adapt to novel host species that come into their historic range, or respond in other unforeseen ways.

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