

**SPREAD AND IMPACT OF AN ERUPTIVE HERBIVORE IN A NOVEL HABITAT:
CONSEQUENCES OF CLIMATE CHANGE - INDUCED RANGE EXPANSION**

by

Anthony Robinson

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Abstract

The Mountain Pine Beetle (MPB) has now affected more than 16 million hectares of forest in western Canada causing significant economic, social and ecological impact to the provinces of British Columbia and Alberta. Recent findings suggest that pine trees lacking historical exposure to MPB impacts are evolutionary naive, resulting in unprecedented impacts in previously unoccupied areas. MPB can also reproduce successfully in jack pine, the most abundant species of *Pinus* in the boreal forest which provides a potential conduit for further range expansion eastwards. Current understanding of MPB outbreak dynamics is based largely on research from its original habitat in lodgepole pine. As MPB expand their range, population dynamics are expected to differ from that of the originating habitat due to novel trophic interactions.

I assessed the speculation that tree depletion by MPB in novel pine habitat is more severe than in evolutionarily experienced habitat. I utilized a landscape-level analysis of MPB infestation data across BC in relation to forest characteristics and climatic suitability. This required the use of several different data sources including a climate suitability model, province wide vegetation inventory and annual aerial overview survey data. Additionally I evaluated how potential host availability varies across the boreal forest of Canada and how this affects rates of spread under varying levels of climatic suitability and host susceptibility. Habitats only recently invaded by the MPB experienced impacts that were 1.7 to 3.9 times greater than those with long-term exposure to MPB impacts. Predicted MPB spread was rapid under conditions of high climatic suitability. Only under conditions of both low climate suitability and low host susceptibility did host availability limit spread.

The challenge to forest management is large given the recently documented changes to insect population dynamics in naive environments. Priority should be given to the development of predictive tools supporting strategic landscape planning intent on minimizing additional impacts to naive ecosystems into the future. Despite continued uncertainty as to community and ecosystem trajectories under global change, this thesis exposes a coherent pattern of ecological change across a broad system at two distinct spatial scales.

Preface

This thesis is original, unpublished, independent work by the author, A. Robinson

Chapter 2 is based on work conducted in the Forest Insect Disturbance Ecology Lab (FIDEL), Department of Forest and Conservation Science, Faculty of Forestry, UBC, under the directions of Dr Allan Carroll. I was responsible for all analysis in this chapter, with supervision and mentorship provided by Allan Carroll. Manuscript edits provided by Dr Sarah Gregel and Dr Mike Wulder.

Chapter 3 is based on work completed at the Pacific Forestry Centre, Canadian Forest Service, Victoria BC under the joint direction of Dr Michael Wulder and Dr Allan Carroll, with added assistance from Dr Joanne White. I was responsible for all analysis in this chapter, with supervision and mentorship provided by Mike Wulder, Joanne White and Allan Carroll.

All writing was conducted by me, with review from my research committee consisting of Dr Allan Carroll, Dr Mike Wulder and Dr Sarah Gregel.

Identification and design of the research program was a joint effort between myself, Allan, Mike and Sarah. All research data analysis was conducted by me.

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List of Abbreviations

MPB - Mountain Pine Beetle

TSI -Total severity index

AveSevT₀ - Average severity T₀ – Data standardized for infestation initiation point

MaxSev - Maximum severity

T₀ – Data standardized for infestation initiation point

T_{max} – Time to maximum severity

T₂₅ - Time to a summed severity of $\geq 25\%$

T₂₀ - Time to a summed severity of $\geq 20\%$

T₁₅ - Time to a summed severity of $\geq 15\%$

T₁₀ - Time to a summed severity of $\geq 10\%$

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Dedication

To my partner Taylor Monk and my parents Peter and Vicki Robinson

Chapter 1: Introduction

Warming of the global climate system is unequivocal, and since the 1950's many of the observed changes are unprecedented (IPCC 2014). Each of the last three decades has been successively warmer at the earth's surface than any preceding decade since 1850 (IPCC 2014). The Earth's climate has warmed by approximately 0.6 °C over the past 100 years with two main periods of warming, 1910 - 1945 and 1976 onwards. The 2014 International Panel on Climate change (IPCC) summary report suggested 1983-2012 was likely the warmest 30 year period of the last 1400 years in the northern hemisphere.

There is now ample evidence of the ecological impacts of recent climate change, from polar terrestrial to tropical marine environments, from local to landscape and in some cases even continental scale. The responses of both flora and fauna span an array of ecosystems and organizational hierarchies, from species to communities (Walther et al. 2002). Common changes in response to climate change include earlier breeding or first singing of many bird species, earlier appearance of migratory birds and mismatch of peak food availability and emergence of young (Parmesan 2006, Hitch and Leberg 2007, Chen et al. 2011). Understanding how organisms respond to environmental changes and describing the underlying mechanisms behind responses are key research components in the fields of ecology and biogeography.

One of the most common effects of a warming climate has been changes to the spatial distribution/ range of many species. Biological and physical constraints constantly affect the rate of range expansions and contractions, altering the distribution of species in space and time. Ranges expand as individuals colonize new areas and contract as populations become locally

extinct. Climatic thresholds are one of the most important factors in constraining the geographic boundaries of species and was first explored by (Grinnell 1917), with additional work conducted by Andrewartha and Birch, (1954). Robertson et al. (2009) described a species' range as a geographical manifestation of a species' response to spatial and temporal variation in a range of environmental influences. Observations of range shifts in parallel with climate change have been particularly rich in bird species. Hitch and Leberg, (2007) showed bird species had a northward shift of 2.35 km/year in response to climate change. One meta-analysis estimated species distributions have recently shifted to higher elevations at a median rate of 11.0 meters per decade, and to higher latitudes at a median rate of 16.9 kilometers per decade Chen et al. (2011), rates approximately 2 to 3 times larger than previously reported by Parmesan and Yohe (2003).

In addition to bird species, range shifts are frequently detected in insects, due largely to their short life cycles, high reproductive potential and mobility, and physiological sensitivity to temperature changes (Parmesan 2006, Musolin 2007, Deutsch et al. 2008). Climate can impact mortality, growth rate, and development. Herbivorous insects, with distinct life-history strategies to exploit plants of varying growth forms and strategies, can be expected to be affected by climate change through impacts on vegetation (Bale et al. 2002). Temperature may induce changes in plant life cycle duration (rate of development), population density, size, genetic composition. Temperature increases may also affect the extent to which host plants are exploited as well as impact local and geographical distribution of host plants (Bale et al. 2002). For insect herbivores, the ability to complete a life cycle represents successful adaptation to both the host plant/tree and to the climatic environment in which they are found. While impacts of a warming environment on insect populations vary, in most cases distributional changes, both range

expansions (Parmesan et al. 1999, Battisti et al. 2005, Hickling et al. 2005, 2006), and contractions (Wilson et al. 2005) occur.

Since the early part of the twentieth century, the sensitivity of insects to spring and summer temperatures (Uvarov 1931, Ford 1945, Dennis 1993) has gained more attention. Historically, natural constraints prevent many species from erupting into wide-scale epidemics; although more recently, several instances of insect eruptions have occurred largely as a consequence of a warming environment. Eruptive herbivores have significant impacts on the landscape, affecting timber production, wildlife habitat, wildfire dynamics, forest composition and structure, biogeochemical cycling, and biogeophysical processes (Dymond et al. 2010, Bentz et al. 2010, Edburg et al. 2012). Warm winters in western North America have increased winter survival of the larvae of bark beetles, helping drive large-scale forest infestations and forest die-off since the early 2000's (Bentz et al. 2010).

Insect species that regularly experience positive feedback are considered eruptive insects, owing to their ability to surpass multiple stand level development thresholds when conditions are conducive (Raffa et al. 2008, Boone et al. 2011). This occasionally results in wide scale ecological, economic and social impacts (Kurz et al. 2008, Schoennagel et al. 2012, Edburg et al. 2012, Collins et al. 2012). Recently mountain pine beetle *Dendroctonus ponderosae* Hopkins (MPB hereafter) outbreaks have severely affected over 16 million hectares of pine forests in western Canada alone (Westfall and Ebata 2013). Outbreaks are also expanding further east, north and to higher elevations than observed previously (Carroll et al. 2004, Safranyik et al. 2010). Following an unprecedented expansion over the Rocky Mountains (a previously

recognized biogeoclimatic barrier to expansion), MPB has spread east to within 120km of Saskatchewan and crossed the borders of the Yukon and Northwest Territories in the north.

Infestation by MPB has been shown to influence biophysical and biogeochemical processing, affecting water quality and supply, carbon storage and nutrient cycling in forests for many years following infestation (Edburg et al. 2012). In terms of carbon stores alone, MPB outbreaks have the potential to turn forests into carbon sources (Kurz et al. 2008, Hicke et al. 2012). Currently the risk to economic, social and ecological functioning of western Canadian forests is elevated due to MPB range expansion and consequently a high priority to forest managers (Nealis and Peter 2008, Nealis and Cooke 2014). Understanding these systems requires a complex knowledge of how processes interact at different biological and spatiotemporal scales.

1.1 Mountain pine beetle life stage dynamics

Throughout most of their range, MPB populations have one generation per year (univoltine), with larvae development closely linked to temperature. This characteristic suggests that in environments with temperature regimes outside a narrow optimal range, population synchrony may degrade over time (Safranyik and Carroll, 2006). In cooler summers, such as those that often occur at high elevations, some or all of the brood may require two years to mature (Safranyik and Carroll, 2006). Extreme winter temperatures are important mortality factors for MPB, while microclimate may also strongly influence the timing of crucial life history events (Bentz et al., 1991; Safranyik and Carroll, 2006).

Beetles colonize trees via a pheromone-mediated mass attack that combined with phytopogenic symbiotic blue stain fungi, effectively exhausts host defenses (Aukema et al. 2006, Roe et al. 2011). Females select host trees and are joined by males as they bore into the phloem, copulate and excavate galleries along which they oviposit in vertical galleries. Females deposit their eggs (approximately 60 per female on average) singly into niches cut in the sides of the gallery and cover them with boring dust (Safranyik and Carroll, 2006). The larvae feed and develop passing through four instars as they construct galleries that terminate in a pupal chamber, from which brood adults emerge (Amman 1982, Bentz et al. 1991, Bentz and Mullins 1999, Safranyik 2004). Beetles overwinter as late instar larvae before completing development the following spring (Bentz and Mullins 1999). Fungi in the family Ophiostomataceae play a number of beneficial roles for the beetle host by providing nutrition, protection against tree defences, and modifying environmental conditions within the tree (Solheim and Krokene 1998, Roe et al. 2011). Fungal spores are inoculated into trees as beetle bores through the bark, they germinate quickly and penetrate living cells in both phloem and xylem, causing desiccation and disruption of transpiration, effectively terminating resin production by the tree (Safranyik and Carroll, 2006).

MPB has evolved life stage-specific temperature thresholds that promote phenological synchrony between critical temperature tolerances and the appropriate season (Bentz et al., 1991; Logan and Bentz, 1999; Safranyik and Carroll, 2006; Safranyik, 1978). Small changes in temperature can increase or decrease development rates. For example, increases in temperature due to climate change have been shown to synchronize emergence of beetles, leading to population outbreak (Carroll et al., 2006a; Logan and Powell, 2001; Logan et al., 2003). However, above a certain temperature threshold, increasing temperature is detrimental to

synchronous emergence and outbreak (Logan and Powell, 2001). Furthermore, when cold-intolerant life stages (e.g., egg, pupa, and teneral adult) are exposed to extremely cold weather, populations may contract. Temperatures of -40° C can cause 100% mortality, particularly if occurring out of season (Safranyik and Linton, 1998).

1.2 Populations dynamics

The historical range of MPB in western Canada rarely extended past southern British Columbia where its preferred host is lodgepole pine (*Pinus contorta var. latifolia*). MPB population exist in one of four states; endemic, incipient endemic, epidemic-outbreak and post-epidemic (declining) (Safranyik and Carroll, 2006). These phases are defined by rates of increase, host selection behavior, and the presence/absence of positive feedbacks in host colonization success (Safranyik and Carroll, 2006; Raffa et al. 2008). The population exists in an endemic state when conditions are sub-optimal and prefer weakened and dying trees because they lack sufficient population densities to mass attack well defended healthy trees (Safranyik et al. 1974, Safranyik and Carroll 2006). Populations in this endemic phase typically experience generation mortality of approximately 98%; thus their long-term average rate of increase remains at unity. Factors responsible for such a high level of mortality include tree resistance, interspecific competition, and predation and parasitism (Safranyik and Carroll, 2006). Although the density-dependent effects of parasitism/predation by natural enemies are important in the regulation of endemic populations, once populations build in numbers to the incipient epidemic the effects of regulation by natural enemies becomes insignificant.

During the incipient epidemic phase, populations have grown in size to a level where behavior shifts to seeking out large diameter trees (Boone et al., 2011; de la Giroday et al., 2012; Raffa et al., 2008; Safranyik and Carroll, 2006). Such large diameter trees are generally the most highly resistant trees within a stand. Thus, the main factors that drive a shift in population behavior are those that either cause either a decline in tree resistance (climate, management, indirect control) or an increase in beetle population size (weather and climate, direct control) (Safranyik and Carroll, 2006). Rapid expansion in populations is observed once critical life stage thresholds are overcome, described by Boone et al, (2011) as density dependent behavioral shifts.

Episodically populations transition from endemic to incipient-epidemic, whereas if conditions allow, populations reach an epidemic state. In this state, MPB will attack and kill large tracts of live standing pine. The transition from endemic to epidemic is typically fueled by a change in one or a number of abiotic factors such as drought, fire damage or an unusually hot summer (Raffa et al. 2008). As beetles transition from the endemic to epidemic state, host tree defenses become irrelevant and beetles actively seek out bigger, healthier, better defended hosts (Boone et al., 2011). The increase in population is followed by an increase in food availability as beetles no longer need to persist on dead and dying trees as at an increased density of attack they are able to seek out the best possible food source. Thus the small disturbance on a system results in an increase in the magnitude of the perturbation, indicative of a positive feedback loop. At this point the availability, quantity and quality of food resources (host trees) become the primary density dependent factors (Safranyik and Carroll, 2006). Safranyik and Carroll 2006 provide a schematic representation of the interaction among lodgepole pine, secondary bark beetle species, and the MPB populations cycle through all phase of development, I provide a generalized feedback loop

diagram modified from Safranyik and Carroll (2006) below (Figure 1). Following amplification to landscape level eruption in the absence of cold induced mortality, these populations will persist until host resources are depleted. Epidemic populations typically exist for a number of years, until a point where critical limiting factors are reached. Cold weather (causing over-winter mortality or limiting summer flight periods) or exhausted supplies of host material are two major reasons populations may subside to lower levels. Given favourable conditions over a number of years, epidemic dynamics at the stand scale can amplify to a landscape level event, where extensive mortality of large diameter trees occurs. Such conditions have been seen in British Columbia over the past decade. Because of this broad spatial scale of impact has great ecological and economic impacts, I chose to focus this thesis on ways of understanding landscape level dynamics of MPB outbreaks.

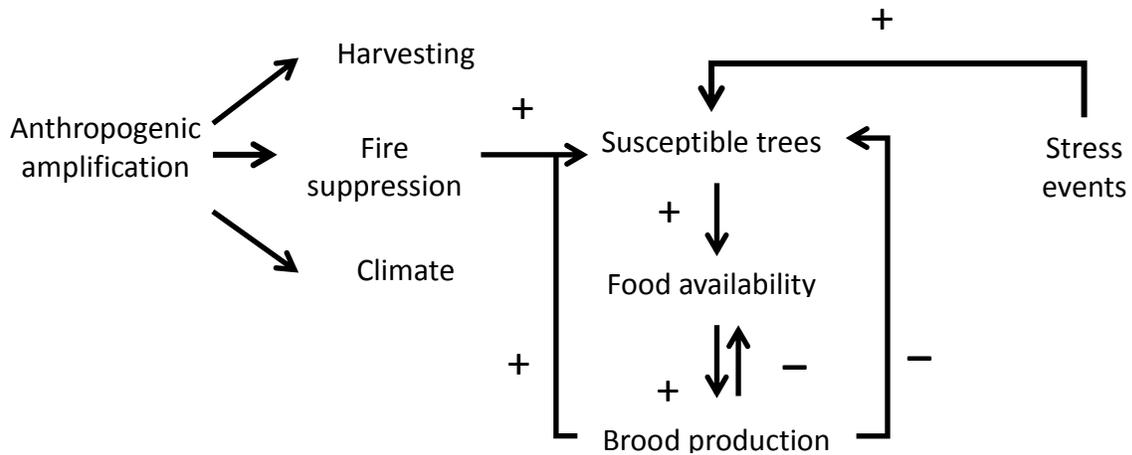


Figure 1. Modified from (Safranyik and Carroll 2006). A schematic representation of the interaction among susceptible hosts and the mountain pine beetle during the epidemic population phase. Anthropogenic amplification (described below) and natural stress events are included as

factors contributing to an increase in susceptible trees. Arrows accompanied by ‘+’ and ‘-’ indicate positive and negative feedback loops, respectively.

1.2.1 Anthropogenic exacerbation of population dynamics

Anthropogenic factors also play a major role in the likelihood of eruptions. The propensity for MPB populations to spread from an individual stand to a landscape scale outbreak also depends on the availability of susceptible host trees throughout the landscape. Factors affecting availability and susceptibility of host trees are considered indirect drivers of population eruptions and include fire suppression and harvesting (as well as climate). In the context of the recent BC outbreak, such anthropogenic drivers likely exacerbate the epidemic phase, promoting the breach of the threshold between single tree mass attack and a synchronous landscape scale outbreak (Raffa et al. 2008). Thus, the even-aged, contiguous lodgepole pine forests in central British Columbia formed the basis for unprecedented levels of MPB-induced mortality following range expansion beyond the historical bounds of the species.

Forest management (fire suppression)

Fire is the most influential landscape scale disturbance mechanism post-Pleistocene glaciation, and is a major driver of forest structure, species composition, heterogeneity and ecosystem function and services (Barclay et al., 2009; Bergeron et al., 2002; Weir et al., 2000). The advent of modern suppression practices in the mid 1940’s has resulted in a marked reduction in wildfires which ultimately determines the abundance of mature trees across the landscape. Broad scale fire suppression has led to an age structure highly susceptible to beetle attack. Taylor and

Carroll, (2004) suggest approximately 17% of pine stands were in age classes susceptible to MPB attack in early 1900s, compared to approximately 55% in 2004. Thus, the notable reduction in wildfire as a result of fire suppression has increased the average age of pine stands (Taylor and Carroll, 2004), catalyzing unprecedented levels of mortality following large, synchronous emergence of beetles attacking highly susceptible host trees spread across a contiguous landscape.

Forest management (harvesting)

While climatic changes may be responsible for increasing the geographic range of MPB, increases in outbreak severity and frequency are in part due to forest management activities over the past 100 years. Forests have been managed for development and extraction of timber, resulting in an overabundance of large diameter trees leading to an even aged monospecific forest structure (Barclay et al., 2009). Taylor and Carroll (2004) report between 1910 and 1990 there was a threefold increase in the amount of pine in the most susceptible age classes to MPB attack, a result of selective harvesting and fire suppression. The development of positive feedback mechanisms has occurred in this system as beetles preferentially attack large diameter trees during epidemic periods (Boone et al., 2011; Safranyik and Carroll, 2006). An overabundance of large diameter trees results in notably larger numbers of beetles as these trees produce notably more beetles per tree. These large MPB populations are highly resilient to normal levels of mortality and are able to overcome the most highly defended hosts, thus host availability is increased and resultant impacts increase. Safranyik and Carroll (2006) suggest 40 times the number of beetles will emerge from a 40-cm tree when compared with a 10-cm tree. Combine this with favorable climatic conditions driving synchronous emergence and the

likelihood of landscape level outbreak is high. As early as 1974, Safranyik et al. suggested that large areas of lodgepole pine approaching maturity create significant opportunity for continued losses through MPB outbreaks. Despite this, forest continued to be managed for high value timber resources which led to extensive areas of large diameter highly susceptible trees.

Weather and climate (host susceptibility)

Drought stressed trees have been shown to exhibit reduced defensive mechanisms (Carroll et al., 2004). The decline in tree resistance can be either temporary, such as following a period of drought, or it could be a permanent consequence of senility, disease or damage (Safranyik et al., 1975). An index of aridity was used by Carroll et al., (2004) in formulation of a model of the impacts of climatic condition on the establishment and persistence of MPB populations. This model is particularly relevant as declines in host resistance combined with favorable conditions for beetle establishment and survival are regarded as primary factors for the development of incipient infestations.

1.2.2 Co-evolution - A defense free space in western Canada

The relationship of co-evolution between plants and phytophagous insects occurs most commonly when insect life stages, single or multiple exert direct pressure on host plants through consumption of tissue. Host plants are not passive contributors and defend themselves against attack through chemical, physical and structural adaptations (Ehrlich and Raven 1964, Ylloja et al. 1999, Awmack and Leather 2002, Franceschi et al. 2005). Reciprocal selective responses occur through a continuous loop of evolutionary feedback between offense and defense (Ehrlich and Raven 1964, Berryman et al. 1987). Plants strive to develop more effective defenses while

insects adapt to circumvent or exploit them by any means necessary (Ehrlich and Raven 1964, Berryman et al. 1987). Over time this process regulates both insect population dynamics and selects for hosts with increased defensive capacity.

Regulation of insect population dynamics by host plants can best be explained by the influence of feedback processes. It has been suggested that secondary plant substances have the leading role in feedback to patterns of host utilization in phytophagous insects (Ehrlich and Raven 1964, Royama 1992). For example, host quality and defensive chemicals can feedback negatively to insect fecundity, in some cases affecting all stages of an insect's development (Price 2000, Awmack and Leather 2002). Evolutionarily this has restricted certain groups of insects to a narrow range of food plants (Ehrlich and Raven 1964). Alternatively positive feedback can occur as increasing population density increases food availability; host defense or avoidance mechanisms are cooperatively overwhelmed or circumvented as the herbivore population grows in size (Boone et al. 2011). Insect species that regularly experience positive feedback are considered eruptive insects, owing to their ability to surpass multiple stand level development thresholds when conditions are conducive (Raffa et al. 2008, Boone et al. 2011). This occasionally results in wide scale ecological, economic and social impacts (Kurz et al. 2008, Schoennagel et al. 2012, Edburg et al. 2012, Collins et al. 2012).

Anthropogenic climate change coupled with alteration of natural disturbance regimes through extensive forest management have manifested positive feedback resulting in the invasion of areas outside of the beetles' historical range (Raffa et al. 2008, Bentz et al. 2010, Safranyik et al. 2010). Resulting in changes to MPB population dynamics, seen at unprecedented scales, the

most concerning of which are interactions with novel hosts. Recent work indicates that populations of lodgepole pine that reside outside the historic range of MPB are better quality hosts than those that live inside the historic range. Cudmore et al.(2010), found that trees living in areas that were historically climatically unsuitable for MPB produced more brood per female than trees living in historically suitable areas. Trees outside the historic range also have higher constitutive and lower induced defensive chemical compositions (Clark et al. 2010, 2012a). Thus it has been suggested that host tree populations in historically unsuitable areas are at a disadvantage, being considered evolutionarily naive. This comes as result of a lack of selection pressure from MPB, meaning range expansion into these areas is an invasion of a novel habitat. Unlike perhaps the more common invasion of an exotic species, this is an invasion of a native species, only previously restricted in range by unsuitable climatic conditions. MPB has entered a defense free space, a term coined by Gandhi and Herms, (2009). Exotic invasive insects such as gypsy moth (*Lymantria dispar* L.), hemlock woolly adelgid (*Adelges tsugae* Annand), and emerald ash borer (*Agrilus planipennis* Fairmaire) have caused wide scale damage in eastern North America through defoliation and decline or mortality of their hosts. Gandhi and Herms (2010) suggests that some of the most devastating species are spreading in “defense free space”, where due to a lack of co-evolutionary history with their invader, hosts are inherently more susceptible. Given the unprecedented levels of tree mortality the range expansion of MPB north and east in western Canada constitutes an invasion of a “defense free space”.

1.3 Thesis overview

A number of recent studies have predicted continued impacts as climatic conditions reorganize, occurring not only in newly favorable lodgepole pine habitats, but also in lodgepole × jack pine

hybrids, and ultimately the jack pine forests that occur across the North American boreal region (Nealis and Peter 2008, Safranyik et al. 2010, Nealis and Cooke 2014). Range expansion from west of the North American continental divide into the “defense free space” of the eastern boreal forest threatens to provide a conduit to naive pine hosts in eastern North America (de la Giroday et al. 2012), adding significant burden to the already major effects of the recent MPB range expansion. As MPB expands into naive lodgepole pine, then to hybrid lodgepole/jack pine, and then into boreal jack pine stands, beetle-host tree interactions and colonization dynamics are expected to change at each step. This may in turn affect the level of impacts and rate of spread into subsequent habitats. There is also a great deal of uncertainty in how the changing climate will affect the susceptibility of naive pines.

To date little research has been done to quantify both the dynamics of MPB populations in naive habitats’ and the potential for spread across Canada. Thus the purpose of this thesis is to assess the dynamics of MPB in naive vs. experienced habitats, first looking back in time at the dynamics of MPB in naive vs. experienced across much of BC. Following on from this, I assess the potential for MPB to spread across the boreal by modeling the influence of host availability on spread under varying scenarios of climate and host conditions. Given that current understanding of outbreak dynamics and their relationships to drivers of MPB range expansion are based largely on research from climatically suitable habitats of lodgepole pine, this research forms one of many steps towards better understanding MPB population dynamics in novel environments at the landscape scale.

This thesis is sectioned into four chapters. Following this first chapter, in Chapter 2 I address the speculation that depletion of trees by MPB in novel pine habitat is more severe than in experienced pine habitat. I test the hypothesis that due to an insufficiently evolved defensive response, naive trees will be more susceptible, resulting in increased impacts (more severe and rapid) compared to experienced habitats. I examined infestations from 1996 to 2011, in relation to forest characteristics and a climatic suitability model (by Safranyik 1975 and later refined by Carroll et al. 2004). Beetle population dynamics, forest characteristics and climate suitability readily-available landscape scale data sets were used to test my hypothesis. This work covered a much larger area than any previous work in an effort to broaden knowledge of MPB population dynamics at the landscape scale.

Building on Chapter 2 and recent findings that MPB reproduce successfully in jack pine (the most abundant species of *Pinus* in the boreal forest), in Chapter 3 I assessed the potential for MPB spread at a continental scale. I examined the impact of host availability given the lack of landscape scale information with regards to MPB population dynamics in the previously unoccupied boreal forest. In Chapter 4, I integrate my research and conclusions in light of current research in the field in the context of my specific goals and hypotheses. I comment on strengths and limitations of the thesis research and discuss the potential applications of these research findings.

The focus of my thesis work is on two vastly different scales, firstly at the landscape scale, then at the continental scale. In this thesis I assess both the multi-year dynamics of MPB in naive and experienced habitats and the potential for spread of MPB through the boreal forest, with

particular emphasis on the potential constraints provided by host availability. In collaboration with my research committee I use geographic information systems (GIS) and remote sensing tools with the objective of answering three different questions about past and future spread of MPB. 1) Is the rate of depletion of trees as a result of MPB infestation greater in naive vs. experienced habitats? 2) What is the potential for MPB to spread across Canada? 3) Can forest structure constrain spread eastwards?

Chapter 2: Exacerbated impacts by an eruptive herbivore in evolutionarily naive habitats: consequences of range expansion by the mountain pine beetle.

2.1 Introduction

Direct effects of anthropogenic climate change have now been documented on every continent, in every ocean and within most major taxonomic groups (IPCC 2013). Changes are frequently detected in insects due to their short life cycles, high reproductive potential and mobility, and physiological sensitivity to temperature changes (Parmesan 2006, Musolin 2007, Deutsch et al. 2008). The effects of a warming environment on insect populations vary, but in most cases include distributional variations, comprising both range expansions (Parmesan et al. 1999, Hickling et al. 2005, 2006), and range contractions (Wilson et al. 2005). Range shifts by insects have resulted in altered species interactions, such as reduced mortality from natural enemies (Menéndez et al. 2008) and novel herbivore-host plant associations (Braschler and Hill 2007, Cullingham et al. 2011). Where novel herbivore-plant interactions have arisen, evidence suggests herbivore impacts may be greater than expected due to insufficiently co-evolved plant defenses (Cudmore et al. 2010, Raffa et al. 2012).

Long-term co-evolutionary interactions between plants and herbivores give rise to natural constraints that keep most herbivore populations from increasing to outbreaks (Ehrlich and Raven 1964, Karban and Baldwin 1997, Ylloja et al. 1999, Awmack and Leather 2002, Gandhi and Herms 2010). In systems where insect herbivore outbreaks are common, they are often essential aspects of plant life histories and are therefore considered normative (Herms and Mattson 1992, Logan and Powell 2001). In some cases, normative outbreaks may result from

eruptive population dynamics, especially among bark beetles. Population eruptions result when densities exceed key thresholds, prior constraints cease to exert influence, and positive feedbacks amplify across scales (Raffa et al. 2008). When a series of years with weather that favors herbivore survival coincides with an abundance of susceptible hosts, population eruptions can lead to spectacular landscape-scale outbreaks.

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hereafter MPB) is an eruptive forest insect that occurs across the coniferous forests of western North America from northern British Columbia to Mexico. The most recent outbreak has resulted in the mortality of trees over approximately 20 million ha [ca. 16 million ha in Canada (Westfall and Ebata 2014), 4 million ha in the US (USDA Forest Service 2013)]. Although it is oligophagous within the genus *Pinus*, lodgepole pine (*Pinus contorta* var. *latifolia*) is its main host through most of its range (Safranyik and Carroll, 2006). MPB is an aggressive bark beetle that feeds and reproduces within the phloem tissue of its host trees. Successful colonization by MPB is conditional upon the death of the tree (Safranyik and Carroll 2006). This intense selection pressure has resulted in the evolution of a complex array of defenses that enable trees to resist attack. Defenses include resins released from constitutive resin ducts severed as beetles bore through the bark and secondarily-induced resins released by tissues surrounding the wound (reviewed by Franceschi et al. 2005, Safranyik and Carroll 2006, Raffa et al. 2008). If the expression of these defensive mechanisms occurs with sufficient rapidity and magnitude, the beetles and their associated microorganisms will be confined and killed within a lesion of dead tissue and the tree may survive.

Even with its extensive spatial distribution, the historic latitudinal and elevational range of MPB was not restricted by the availability of suitable host trees. In fact, lodgepole pine in Canada extends north into the Yukon and Northwest Territories and east across much of Alberta (Farrar 1995), far beyond the reach of historical MPB populations (Safranyik and Carroll 2006).

Historically the potential for MPB to expand north and east was limited by climate (Logan and Powell 2001, Carroll et al. 2004). In recent decades, climatic restrictions to MPB distribution have relaxed. Carroll et al. (2004) showed that the amount of climatically suitable habitat for MPB has increased dramatically since 1970 and beetle populations have been expanding at an increasing rate into newly suitable areas. A large portion of the most recent outbreak in western Canada has occurred in areas that were historically unsuitable for MPB (Carroll et al. 2004, Taylor et al. 2006, Cudmore et al. 2010). Expansion by MPB into formerly climatically unsuitable areas has allowed the beetle contact with populations of lodgepole pine in which selection for specific defensive responses may not have occurred. Support for this assertion was recently provided by Cudmore et al. (2010), who found that MPB had higher reproductive success in lodgepole pine trees growing in areas that had only recently become climatically available. Similarly, Raffa et al. (2012) documented inferior defenses to MPB attacks by whitebark pine (*Pinus albicaulis* Engelmann) growing in high-elevation areas that were largely climatically unsuitable to the beetle in the past. Less effective host-tree defenses and higher overall beetle productivity in evolutionary naive pine habitats suggests that the dynamics of MPB in newly invaded regions may differ from its native range.

This study assessed the dynamics of MPB infestations in novel versus native habitats. More specifically, I evaluated the hypothesis that due to an insufficiently evolved defensive response,

naive trees will be more susceptible to attack resulting in higher levels of tree mortality and stand depletion compared to experienced habitats. I combined a landscape level analysis of MPB infestation data across BC in relation to forest characteristics and climatic suitability.

2.2 Materials and methods

2.2.1 Study area

The study area comprises nearly 24 million hectares extending from the Kamloops in the south 50°6'N, to 55°3'N, north of McKenzie. The eastern border comprises the Rocky Mountains (i.e. the BC/ Alberta provincial boundary), while the western border corresponds to a line over the Coastal Mountains 126°8'W (Figure 2). This area was chosen based on the availability of detailed data pertaining to forest characteristics, MPB outbreak conditions, and climatic suitability.

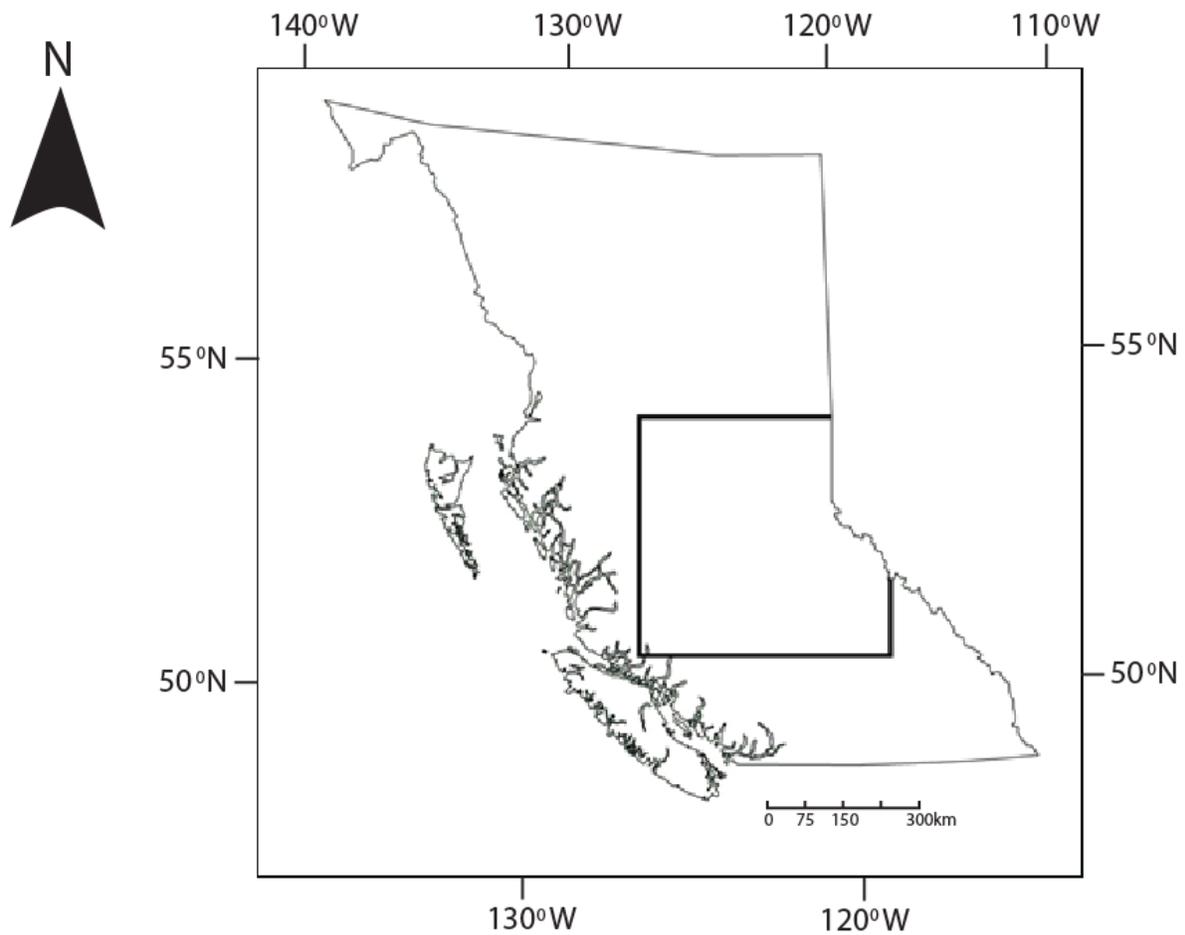


Figure 2. Location of the study area in relation to the province of British Columbia. The study area covers an area of 23,719,000 hectares spanning from the Coast Mountains in the west to the BC/Alberta provincial boundary in the east.

2.3 Data collection and assembly

2.3.1 Forest characteristics

Forest structure and composition can have a substantial influence on the infestation characteristics of MPB. For example, stands of trees that are between 60 and 160 years-old, dominated by lodgepole pine growing at a moderate density (i.e. 1500 stems/ha) are considered to be optimal habitat for MPB (Shore and Safranyik 1992) due to the quantity and quality of the phloem resource (Safranyik and Carroll 2006). I utilized a vegetation resources inventory (VRI) provided by BC Ministry of Forests, Lands and Natural Resource Operations to quantify the role of forest characteristics on MPB infestation dynamics. VRI data are acquired using a photo-based, two-phased vegetation inventory consisting of phase photo interpretation and ground sampling. In this process each forest stand is delineated as a separate polygon and labeled with a unique identification number and a series of attributes such as species composition (up to six species recorded for each stand), age (in years), total stand basal area (m² / ha) and canopy closure (in 5% intervals) (British Columbia Ministry of Sustainable Resource Management 2002).

2.3.2 MPB dynamics

Annual aerial overview surveys of forest health conditions have been conducted by the BC Ministry of Forests, Lands and Natural Resource Operations for the entire province since 1999 and for portions of the province since 1996. Since the distribution and abundance of dead pine trees is considered to be an accurate representation of the distribution and abundance of MPB populations during outbreaks (Safranyik and Carroll 2006), annual changes in the occurrence and severity of mapped infestations were assumed to be an accurate proxy of MPB infestation dynamics at the stand and landscape scale. The aerial overview survey is generally conducted

from early July through to August every year in fixed-wing aircraft flying at 150 to 170 km/hour and at 500 to 1,000 meters above the terrain (BC Ministry of Forests, Lands and Natural Resource Operations, 2013). During aerial surveys, areas of infestation identified from the red foliage of newly dead trees are delineated on base maps (1: 250,000 NTS topographic maps) and later digitized into geo-referenced vector data sets. One of five severity classes based upon the percentage of newly killed trees in an infestation (Table 2) is assigned to each polygon in the annual infestation data. This analysis utilized infestation polygons within the study area from 1996 to 2011, inclusive (Figure 3). Potential limitations of this data include the inability to preclude alternative causes of tree death without extensive ground truthing. However the Ministry of Forest data base shows no evidence of extensive mortality to lodgepole pine caused by anything other than MPB exists during the selected years, within the selected study area.

Table 1. Severity classes assigned to each polygon in the annual infestation data set. Midpoint value assigned for the purpose of analyses (Ministry of Forests, Lands and Natural Resource Operations, 2013).

Severity rating	% of attacked trees	Severity code	Midpoint
Trace	< 1%	T	1
Light	1%-10%	L	5
Moderate	11% to 30%	M	20
Severe	31% to 50%	S	40
Very Severe	> 50%	V	75

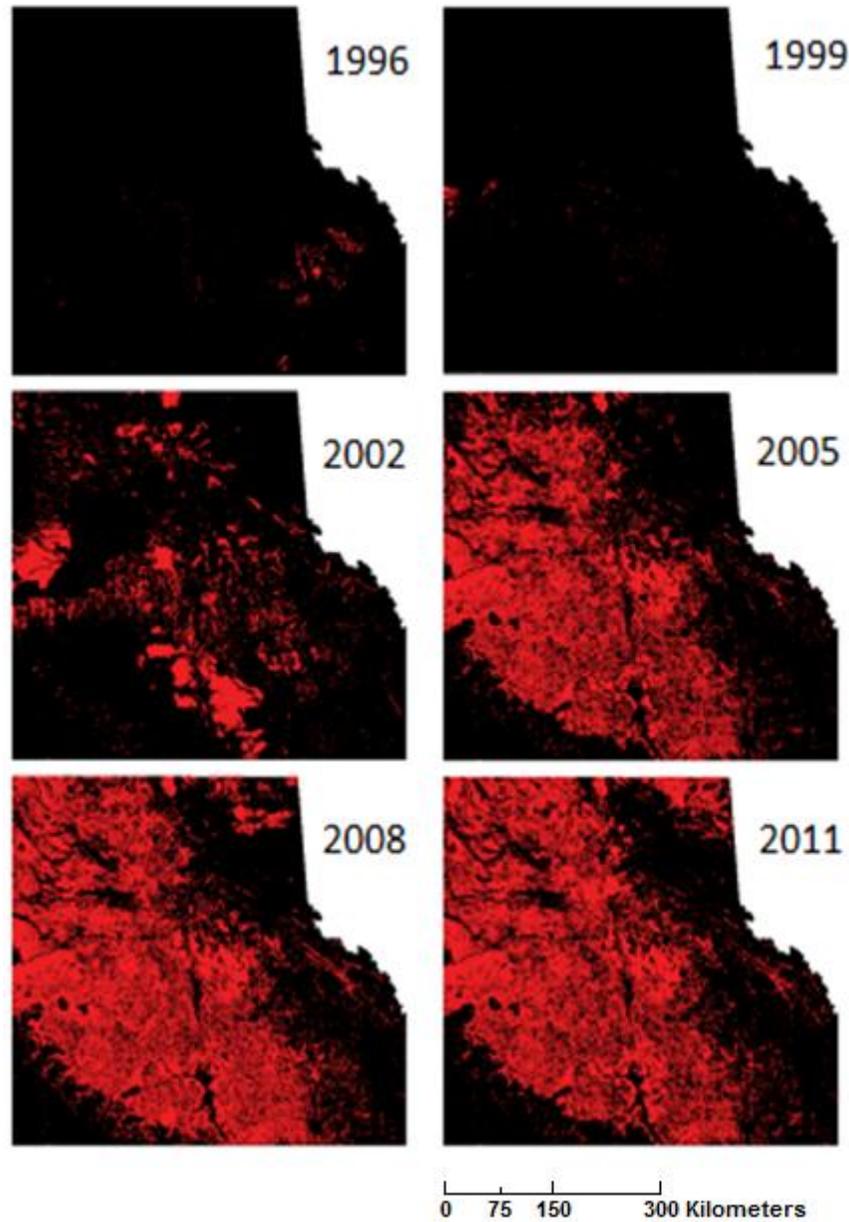


Figure 3. Areas of tree mortality (all severity classes) caused by the mountain pine beetle in the study area from 1996-2011. Data projected from aerial overview survey conducted yearly in fixed-wing aircraft flying (BC Ministry of Forests, Lands and Natural Resource Operations, 2013). Areas of infestation identified from the red foliage of newly dead trees are delineated on base maps (1: 250,000 NTS topographic maps) and later digitized into geo-referenced vector datasets.

2.3.3 Climatic suitability

Estimates of historic climatic suitability (Carroll et al. 2004) were used as a proxy for the degree of selection pressure imposed by MPB on lodgepole pine defensive capacity (Figure 4). Pine forests that were historically available and occupied by MPB were considered evolutionarily experienced, whereas habitats that were historically unsuitable to MPB, but recently invaded due to warming-induced range expansion (Carroll et al. 2004) were considered evolutionarily naive. This dichotomy is supported by studies of tree defensive chemistry (Clark et al. 2010, 2014) and MPB productivity (Cudmore et al. 2010). Historic climatic suitability classes (HCSC) were developed by Carroll et al. (2004) based on an empirical model of the influence of weather on the establishment and persistence of MPB populations (Safranyik et al. 1975), combined with a spatially explicit, climate-driven simulation tool (BioSIM; Regniere et al. 1995). Historic weather records were used to produce maps of the distribution of previously climatically suitable habitats for the period 1941 to 1970 for the mountain pine beetle in British Columbia. The map outputs comprise grid coverage of HCSC values for ≈ 1.2 million 64-ha cells (Carroll et al. 2004). All information was projected in a GIS layer and used during analysis. MPB infestations were well represented in all historic climate suitability classes within the study area (Figure 4).

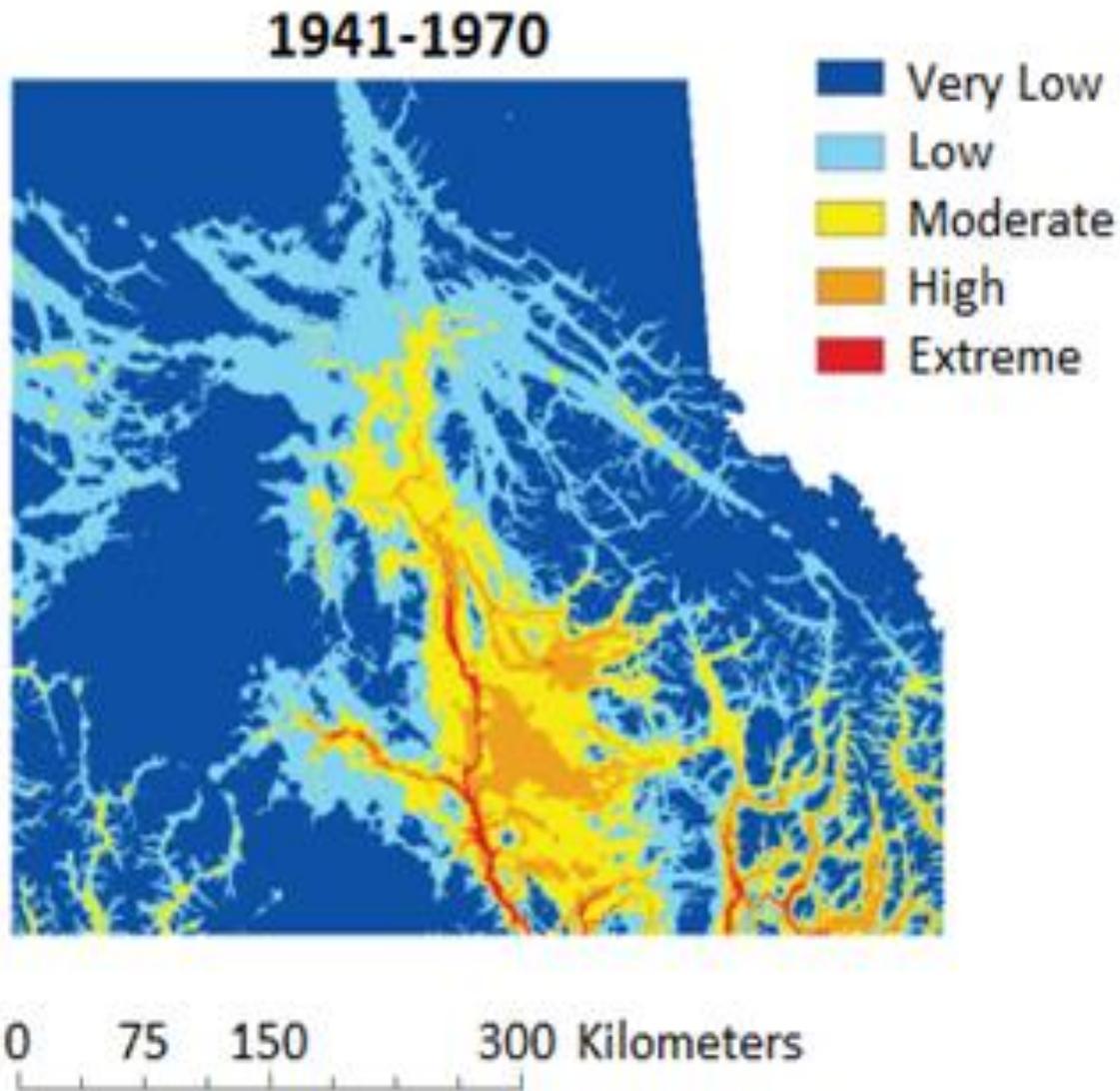


Figure 4. The distribution of historically climatically suitable classes (HCSCs; Carroll et al. 2004) derived from 1941-1970 climate normals (30 year monthly means and extreme minima and maxima) . “Extreme” HCSCs are considered to be climatically optimal habitats with long-term exposure to MPB, whereas “low” and “very low” HCSC’s are considered to be evolutionarily naive to MPB infestations (Carroll et al. 2004; Cudmore et al. 2010).

2.3.4 Data manipulation and analyses

2.3.4.1 Data manipulation

In order to summarize the three sources of data across the study area and assess the hypothesis of increased impacts in naive environments, a total of 237,190 1km x 1km cells covering an area of 23,719,000 ha were placed in a uniform grid pattern extending from the Coast Mountains in the west to the BC/ Alberta provincial boundary in the east (Figure 2, Figure 5). All data were compiled at a common spatial resolution, projected in ESRI Arc GIS® using the datum D_North_American_1983. This grid allowed me to summarize my data at a common spatial scale and control for error within the data set, in relation to climate and host availability. The 1km x 1km (100ha) grid overlay was derived using the Fishnet Function in Arc GIS, with forest characteristics, MPB infestation information and historic climatic suitability quantified within each cell. To extract information for each 1km x 1km grid cell I used the program Geospatial Modelling Environment (GME) (Beyer 2001), to calculate an area weighted mean for individual attributes of forest characteristics, MPB dynamics (i.e. annual infestation severity from 1996 – 2011) and climatic suitability. The area weighted mean climatic suitability was computed for each cell and then partitioned into classes according to Carroll et al. (2004) ranging from very low to extreme climatic suitability. Additionally the area weighted mean infestation severity was computed for each cell across 16 years for use in statistical analysis. Prior to analysis with GME both polygon-based data sources (aerial overview survey and VRI data) were converted to 100m x 100m raster coverage to facilitate computer processing while retaining the spatial detail of the polygon data (see Appendix 1). Area weighted mean climatic suitability for each grid cell was calculated for historic climatic conditions (1941-1970) and recent climatic conditions (1981-2010) (Carroll et al. 2004), to facilitate assessments of changes through time.

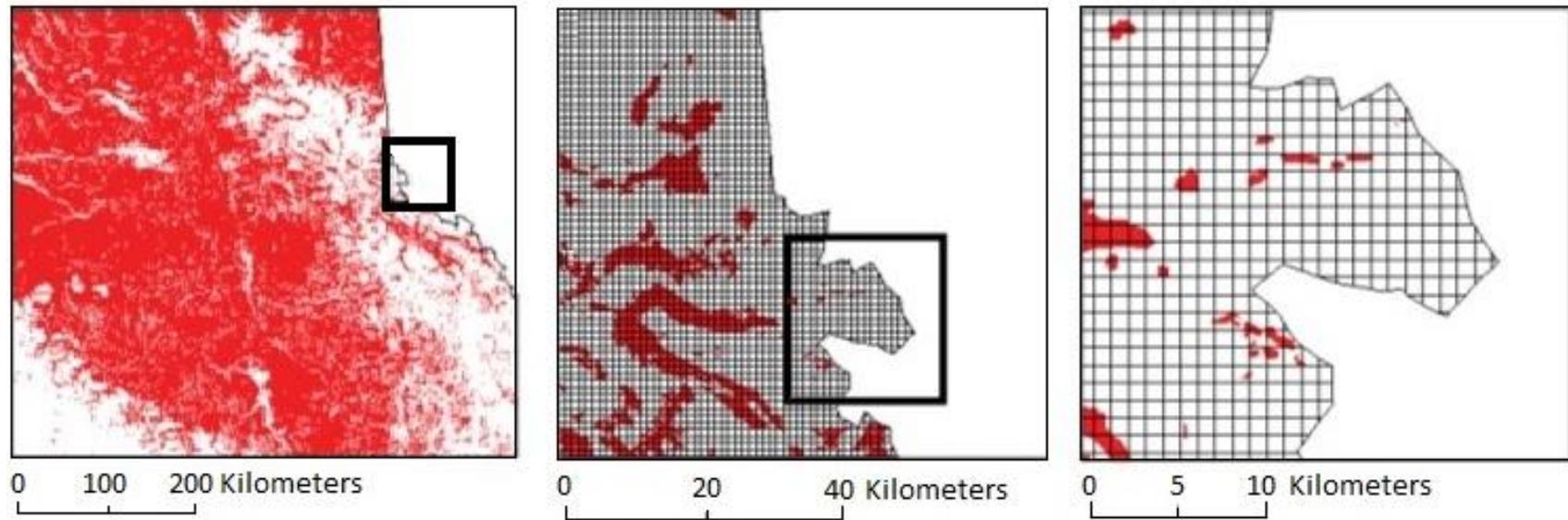


Figure 5. Area of study in British Columbia and a representation of a 1km x 1km (110ha) grid overlay applied using Arc GIS. Data were obtained for annual locations of mountain pine beetles from 1996 – 2011, inclusive. All infestation severity classes are presented.

Several proxies of MPB impacts were derived from the annual aerial overview survey data: minimum and maximum severity, mean annual severity and average severity across the 16 year time period using the area weighted mean function in GME. To refine this analysis I partitioned the 237,190 cells by presence or absence of MPB infestation across the 16 years, excluding those cells that failed to have at least one positive value. Severity values for each cell were standardized for the initiation of infestation (the first positive value in each cell). Defining the beginning of an infestation for each cell was important given that populations may undergo significant declines for one or more years in the midst of several years of otherwise high population levels (Safranyik and Carroll 2006). Furthermore standardizing data for a common start point (T_0) allowed for the analysis of patterns of infestation severity across the time period, regardless of actual year of initiation. Thus I excluded cells in which a clear initiation point was not observed; defined as an infestation level of less than 20% in the first year of observation. In cells with an initial infestation greater than 20%, infestations may have commenced prior to the time period considered in this study and were hence excluded. I calculated a total severity index (TSI) as the sum total of trees killed (severity %) in a cell (i.e. annual tree mortality estimates) in each cell since the beginning of infestation, an average severity for each cell since infestation initiation ($AveSevT_0$) and maximum severity or maximum % of trees killed in a given cell ($MaxSev$). In addition, I calculated mean “time to event” variables from data standardized for T_0 , these included the time (years) to maximum severity (T_{max}) and the time to a summed severity of $\geq 25\%$, 20%, 15% and 10%, (T_{25} , T_{20} , T_{15} and T_{10} respectively).

Following the area weighted mean calculation, the amount of susceptible pine (i.e. ≥ 60 years old) was determined for each 1x1km cell for use as a covariate in analyses. Using the VRI data I

calculated the % cover of the dominant species (i.e. > 50%) for each cell. The proportion of susceptible pine (PropSp) occupying each cell was calculated using the area weighted mean function in GME. Cells with <1% pine were excluded from subsequent analyses. Additionally I partitioned cells to include only those in which a clear increase in historic climatic suitability was observed, excluding cells that remained unsuitable (very low and low HCSC) between the two time periods, 1941-1970 and 1981-2010 according to Carroll et al., (2004).

2.3.4.2 Statistical Analysis

All statistical analyses were conducted using R software (Everitt and Hothorn 2006). Analyses of covariance (ANCOVA) was used to assess the influence of historic climatic suitability class on the impacts (TSI, AveSevT0 and MaxSev) caused by MPB (Table 3), with the proportion of susceptible pine in each cell used as a covariate. Impact variables were square root transformed, while proportionally derived data (PropSP) was arcsine square root transformed to meet the assumptions of ANCOVA.

I tested the hypothesis that time to a given severity level across all HCSC are the same over the range of observations, versus the alternative that at least one pair of the HCSC classes have a different survival rate/curve. Survival Analysis (Everitt and Hothorn 2002) was used to assess differences in the rate of impacts (i.e. time in years to reach some level of impact) among historic climatic suitability classes. Kaplan-Meier estimates were computed by the survfit function from package survival (Everitt and Hothorn 2002) which takes a model formula of the form: $\text{Surv}(\text{time}, \text{event}) \sim \text{group}$. Where time is the “time to event” data, event is a logical variable being TRUE when the event has been observed, for example a summed severity level of 25%

(T_{25}) and FALSE when the event has not occurred or a given level not reached within the 16 year time period in this case. Those cells that did not reach the event are termed “censored”. A key assumption of survival analysis is that censoring is uninformative (Everitt and Hothorn 2002, Klein and Moeschberger 2003). Survival times, or rate of impacts, were compared graphically by plotting the Kaplan-Meier estimates. Using a series of log rank tests, I quantified the difference between Kaplan-Meier survival curves associated with each HCSC. The basic concept behind the Log-Rank test is to test the null hypothesis that Kaplan-Meier hazard functions are equal for all groups by testing the variance and co-variance between the observed and expected values (Klein and Moeschberger 2003).

2.4 Results

Exclusion of cells without a clear increase in historic climatic suitability, a defined infestation initiation point, and/or with <1% susceptible pine reduced the total number of cells for analysis from 237,190 to 41,229 (Table 2). The total % of trees killed in a cell (TSI), the maximum % killed in a given cell (MaxSev) and the average severity for each cell since infestation initiation (AveSevT0) were highest in cells that were putatively evolutionarily naive to MPB impacts (HCSC = very low and low) when compared with cells that were historically optimal and considered evolutionarily experienced (HCSC = high and extreme; Table 2). In evolutionarily naive habitats (very low and low HCSCs), MPB infestations peaked rapidly and then declined (Figure 6). By contrast, much lower levels of mortality, and no clear peak of beetle activity was evident in habitats that were considered evolutionarily experienced (high and extreme HCSCs). Not surprisingly, the moderate HCSC was intermediate (Figure 5). In addition, in the extreme HCSCs no infestations were recorded after 10 years of activity, despite the relatively low annual

levels of tree mortality, whereas some level of infestation was detected in each of the 16 years post infestation initiation in the other climatic suitability classes.

Table 2. Total % of lodgepole pine trees killed (TSI), maximum % killed in a given cell (MaxSev) and mean annual rate of mortality (AveSevT₀) caused by the mountain pine beetle in relation to the historic climatic suitability class (HCSC: 1941-70) of 100ha cells with at least 1% susceptible (≥ 60 years old) lodgepole pine in central British Columbia, Canada.

HCSC (1941-70)	TSI	MaxSev	AveSevT₀	n
Very Low	52.5	25.7	5.9	12827
Low	51.2	25.9	5.6	10690
Moderate	47.9	21.9	4.8	13871
High	38.6	16.8	3.7	3619
Extreme	16.4	7.7	1.7	222
Total				41229

Both historic climatic suitability and the proportion of susceptible pine in each cell significantly affected each measure of MPB impact. Furthermore, the influence of historic climatic suitability on MPB impacts was dependent upon the proportion of susceptible pine (Table 3, Figure 7).

Regardless of the metric of impact, the lowest values were always associated with habitats that were historically optimal to MPB. In addition, in keeping with my hypothesis, the severity of MPB impacts increased with decreasing historic climatic suitability; however, impacts were lower than expected in the very low HCSC (Figure 7). Interestingly, the relative difference in impacts between putatively experienced (extreme HCSC) and naive (low HCSC) habitats diminished with increasing amounts of susceptible pine. In cells dominated by susceptible pine

(81-100%), the total % trees killed, the annual rate of tree mortality and the maximum annual mortality were 1.7 – 1.8 times greater in naive versus experienced habitats, whereas in cells with small amounts of susceptible pine (0-20%) they were 3.3 – 3.9 times greater in naive compared to experienced habitats (Figure 7).

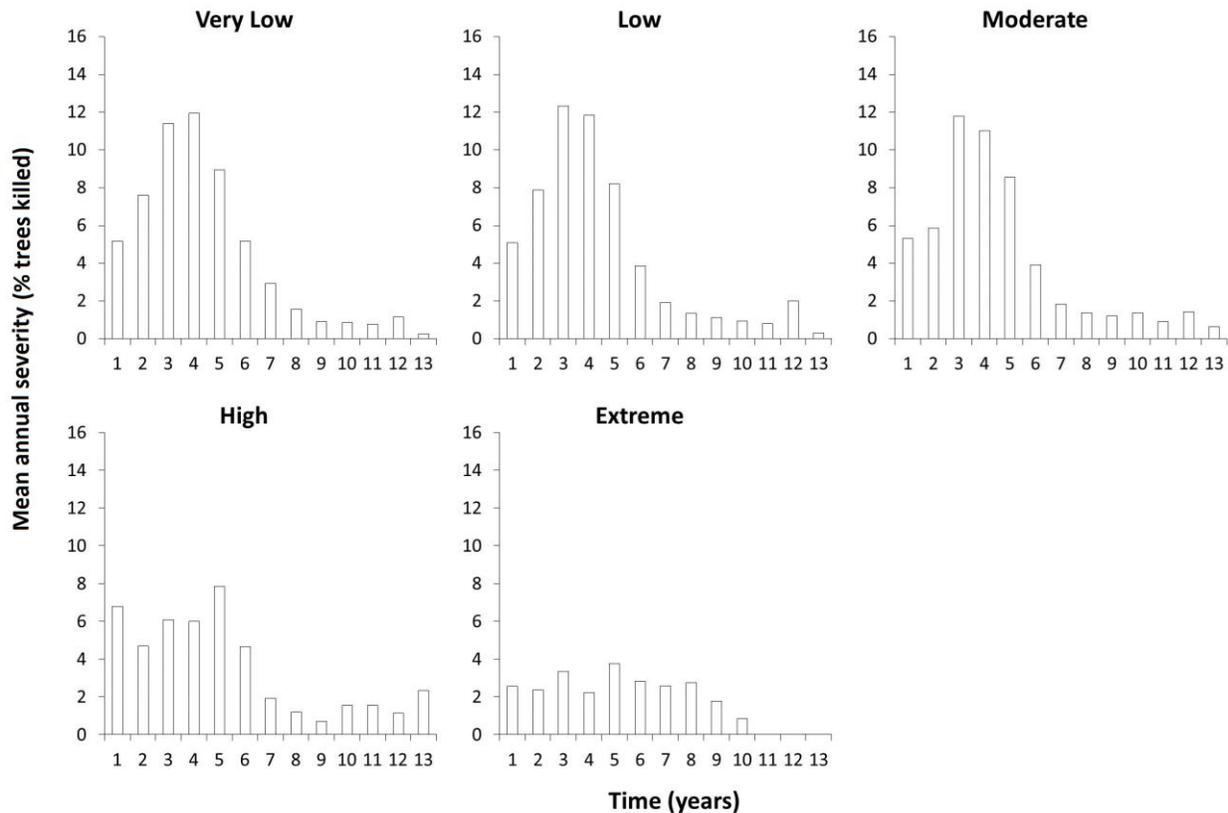


Figure 6. Relationship between mean annual severity (% of trees killed) and time (normalized for the infestation initiation point T^0) for pine dominated habitats with historically (i.e. 1941-70) very low, low, moderate, high and extreme climatic suitability to the mountain pine beetle in British Columbia, Canada. Areas with “very low” and “low” climatic suitability historically had conditions unsuitable for mountain pine beetle survival and development whereas areas with “extreme” climatic suitability are those with historically optimal conditions.

Table 3. Summary of analyses of covariance assessing the independent and interacting influences of historic (i.e. 1941-70) climatic suitability (HCSC) and availability of susceptible pine (proportion ≥ 60 years old; PropSP) on total % of lodgepole pine trees killed (TSI), maximum % killed in a given cell (MaxSev) and average annual rate of mortality (AveSevT₀) caused by the mountain pine beetle from 1996-2011 within 100ha cells in central British Columbia, Canada.

Impact Variables	Df	TSI†				AveSevT ₀ †				MaxSev†			
		Sum Sq	Mean Sq	F value	Pr	Sum Sq	Mean Sq	F value	Pr	Sum Sq	Mean Sq	F value	Pr
HCSC	4	3133	783	116.22	<0.000 1	177.2	44.3	67.21	<0.000 1	1270	317	94.82	<0.000 1
PropSP*	1	86632	86632	12855.2 5	<0.000 1	9499.5	9499.5	14410.3 2	<0.000 1	37322	3732 2	11148.5 9	<0.000 1
PropSP*:HCS C	4	1453	363	53.89	<0.000 1	104.9	26.2	39.78	<0.000 1	638	159	47.61	<0.000 1
Residuals	41219	27777 7	7			27172. 3	0.7			13798 8	3		

*Arcsine Transformation performed prior to analysis

† Square Root transformation performed prior to analysis

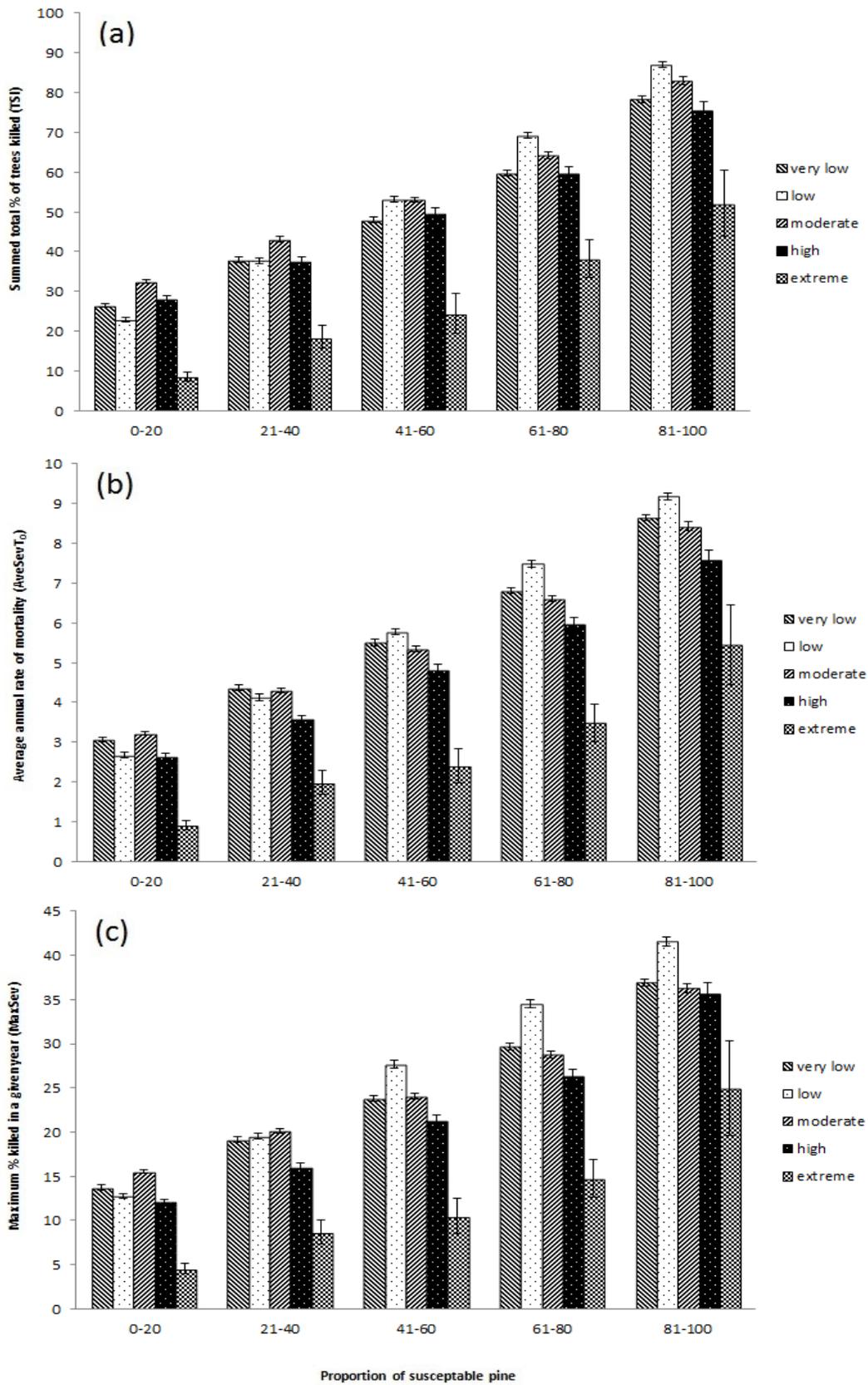


Figure 7. Relationship between (a) summed total % of trees killed , (b) average annual rate of severity, (c) maximum % trees killed by the mountain pine beetle from 1996-2011 and historic climate suitability within 100ha cells in central British Columbia, Canada, containing different proportions of susceptible lodgepole pine (trees ≥ 60 years old). Historic climatic suitability was derived from 1941-1970 climate normals (30 year monthly means and extreme minima and maxima) *sensu* Carroll et al. (2004). Data are presented as means \pm SE. The degree of evolutionary exposure of lodgepole pine populations to the mountain pine beetle is assumed to be highest in historically climatically optimal (i.e. “extreme”) habitats and lowest in historically climatically poor (i.e. “very low” and “low”) habitats.

There was no clear influence of historic exposure to MPB on the time to reach the maximum percentage of trees killed in any given year (T_{max}) in a cell. By contrast, the time required to reach cumulative mortality percentages of 25, 20, 15 or 10 was nearly twice as long in the most experienced (extreme HCSC) versus the most naive (very low HCSC) habitats (Table 4, Figure 8). Log rank tests identified significant differences between group (HCSC) survival curves in the T_{25} , T_{20} , T_{15} and T_{10} variables (Table 4).

Table 4. Log-rank comparisons of mean time (years) to maximum % (T_{\max}), 25% (T_{25}), 20% (T_{20}), 15% (T_{15}) and 10% (T_{10}) mortality of mature (≥ 60 years old) lodgepole pine caused by the mountain pine beetle over 16 years (1996-2011) within 100ha cells in central British Columbia, Canada, grouped by historic (1941-70) climatic suitability (HCSC) to the beetle. The degree of evolutionary exposure of lodgepole pine populations to the mountain pine beetle is assumed to be highest in historically climatically optimal (i.e. “extreme”) habitats and lowest in historically climatically poor (i.e. “very low” and “low”) habitats.

HCSC	T_{\max}	T_{25}	T_{20}	T_{15}	T_{10}
Very Low	2.9	2.9	2.7	2.5	2.3
Low	3.0	3.1	2.8	2.6	2.3
Moderate	3.5	3.7	3.5	3.1	2.7
High	3.1	3.8	3.4	3.0	2.6
Extreme	2.9	5.4	4.8	4.5	4.1
P value	>0.05	<0.0001	<0.0001	<0.0001	<0.0001

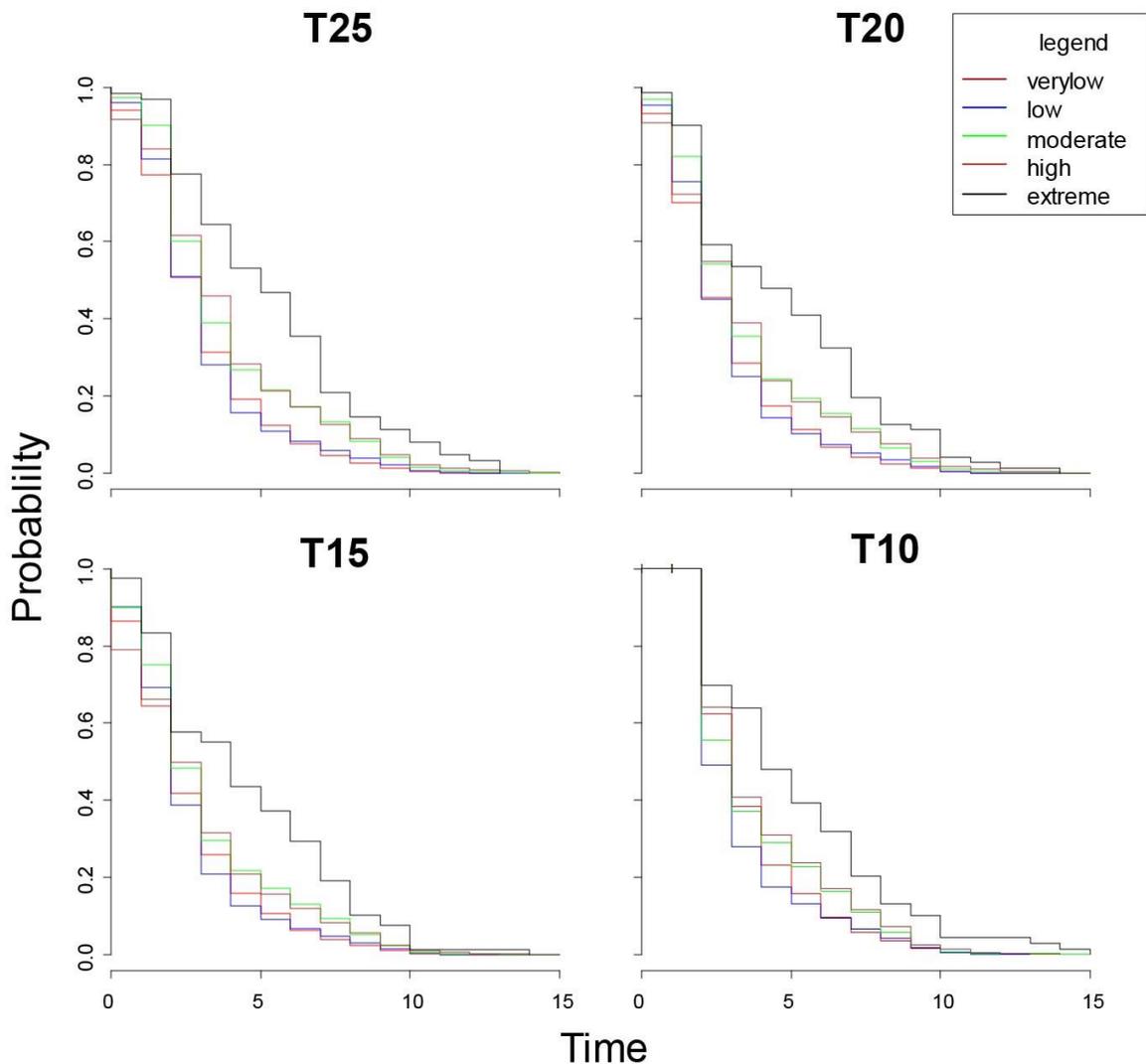


Figure 8. Kaplan-Meier survival curves indicating the probability over time (years) of the summed mortality of mature (≥ 60 years old) lodgepole pine caused by the mountain pine beetle within 100 ha cells in central British Columbia, Canada not exceeding 25% (T25), 20% (T20), 15% (T15) and 10% (T10). Data for grid cells are presented by historic (1941-70) climatic suitability. The degree of evolutionary exposure of lodgepole pine populations to the mountain pine beetle is assumed to be highest in historically climatically optimal (i.e. “extreme”) habitats and lowest in historically climatically poor (i.e. “very low” and “low”) habitats.

2.5 Discussion

Historic herbivory by MPB has selected for reduced susceptibility among populations of lodgepole pine. The rate of mortality and total proportion of trees killed was consistently lowest in putatively evolutionarily experienced habitats and generally increased with declining historic exposure to MPB as determined from historic climatic suitability. Although the impacts by MPB within the most naive habitats (“very low” HCSC) tended to be less than expected, it was not surprising, and no reason to reject my hypothesis, for several reasons. First, even though I considered only those grid cells that had experienced notable warming since 1941-70, the cells that were historically “very low” in terms of climatic suitability were still the least suitable habitats in my analysis, and were therefore more prone to weather and climate capable of higher levels of MPB mortality and lower impacts (Safranyik et al. 1975, Carroll et al. 2004). Second, despite warming in recent years in the areas that were historically the least suitable to MPB, mature trees in these habitats were chronically exposed to cold winters and cool summers conditions associated with reduced tree growth, thinner phloem and lower suitability to MPB (Shrimpton and Thomson 1985). Third, the habitats in which MPB impacts were consistently greatest, i.e. “low” HCSCs, are arguably equivalent to the “very low” habitats in terms of their limited historic exposure to MPB. Indeed, there are no records of impacts by MPB in either “very low” or “low” HCSCs in western Canada prior to 1970 (Carroll et al. 2004).

Although the influence of historic climatic suitability on MPB impacts was consistent regardless of the metric of habitat susceptibility, the magnitude of the influence was dependent on the amount of mature lodgepole. This outcome is consistent with the expectation of selection for increased defensive capacity by lodgepole pine with increasing exposure to MPB through

evolutionary time. MPB in the epidemic phase preferentially colonizes the most defensive trees in a given stand (Boone et al. 2011) due to the links among tree vigor, tree defenses and phloem quantity/quality (Safranyik and Carroll 2006). In fact, this provides the basis for positive feedbacks within MPB populations and landscape-scale outbreaks (Raffa et al. 2008). With increasing amounts of potential host trees in habitats considered evolutionarily experienced to MPB, and therefore higher defensive capacity, the preference to colonize the most defensive trees likely lead to relative increases in their aggregation and impacts, thereby diminishing (but not negating) the magnitude of the differences in impacts between experienced and naive habitats. In habitats with low amounts of susceptible pine, the scarcity of host trees precludes the potential for positive feedback (Raffa et al. 2008).

The rate at which MPB impacts accrued was also inversely related to the degree of historic exposure of lodgepole pine populations to MPB. Considering the lower defensive capacity of pines in novel habitats (Raffa et al. 2012, Clark et al. 2014) and higher productivity of MPB in these trees (Cudmore et al. 2010), these results are not surprising. It is expected that these two factors together will exacerbate population increases and MPB epidemics (Safranyik and Carroll, 2006). Thus, my results support the postulation by Cudmore et al. (2010) that the extremely high levels of tree mortality in the northern portions of the ongoing MPB outbreak in western Canada were a consequence of trees being evolutionarily “naive” to MPB herbivory.

2.5.1 Evolutionary selection pressure and MPB impacts

Exposure to herbivory by bark beetles has led to the evolution of multiple defense mechanisms among conifers (Christiansen et al. 1987, Franceschi et al. 2005). Indeed selection pressures on populations of lodgepole pine in areas considered historically suitable for MPB attack have produced adaptation in two ways: 1) Constitutive levels of terpenes particularly α -pinene have been reduced, so as to reduce their apparency to pioneering female beetles during mass attack (Clark et al. 2010) and 2) induced levels are higher and mobilize more quickly to better defend against attack once it has been initiated (Clark et al. 2012b) thus experienced host populations have a competitive advantage over their generally more northern (climatically unsuitable) equivalents. Undeniably a tree can afford to lose some needles from insect herbivores, although when organisms such as the MPB land and excavate brood chambers into the phloem of the tree, the effect on tree fitness has a direct and almost immediate influence. This rapid attack by MPB on the essential vascular tissue of pine trees is something that only a few species of aggressive primary bark beetles can achieve. For this reason the influence on the evolution of host resistance and allocation of strategies for plant defense occurs at vastly different temporal scales when comparing an aggressive bark beetle such as MPB to less aggressive insect herbivores. Undoubtedly long term attack by less aggressive insect herbivores can effect plant architecture, growth rates, cone production and even cause shifts in plant sexual expression (Whitham and Mopper 1985), although their potential to rapidly affect tree fitness is minimal at best. While long-lived plants are expected to allocate more resources to defensive mechanisms (Herms and Mattson 1992), defenses used by conifers against bark beetle are physiologically very expensive (Christiansen et al. 1987) consequently if a lack of evolutionary pressure exists (i.e. no selection, naive habitats), host populations are unlikely to evolve such costly adaptations (i.e. strong

selection, experienced habitats), a simple genetic trade-off between growth and defense and a process of reciprocal evolutionary change or co-evolution. This analysis supports the evidence by Clark et al. (2010, 2012) for evolution of populations of lodgepole pine in areas experiencing a long temporal interaction with MPB. I extend this analysis across an area covering more than 23 million hectares of British Columbia showing further evidence for increased impacts of MPB in putatively inexperienced populations of lodgepole pine, supporting the apparent lack of co-evolutionary pressure among host and insect in these environments.

2.5.2 Assumptions and limitations

The assumption that the historic climatic suitability estimates of Carroll et al. (2004) are representative of the evolutionary association between MPB and lodgepole pine in western Canada is supported by several lines of evidence. First, population genetic studies have revealed that MPB has undergone a post-Pleistocene demographic expansion northward (Mock et al. 2007, Bentz et al. 2011), following behind an earlier expansion by lodgepole pine (MacDonald and Cwynar 1985, Cwynar and MacDonald 1987). Second, lodgepole pine still occurs at much higher latitudes than does MPB (Safranyik and Carroll 2006), indicating that it has greater capacity to tolerate cold climates than does the beetle. Third, lodgepole pines in naive habitats, as indicated by historic climatic suitability (Carroll et al. 2004), exhibit higher apparency (Clark et al. 2010), lower induced defensive responses (Clark et al. 2014), and higher susceptibility to MPB (Cudmore et al. 2010). Fourth, as indicated above, there is no evidence in recorded history of MPB infestations in pine habitats with poor historic climatic suitability prior to 1970 (Carroll et al. 2004). Thus, it is unlikely that lodgepole pine populations growing in areas of low climatic

suitability experienced MPB impacts sufficient to select for effective defensive responses even during transient post-glacial climatic warming events preceding recorded history.

Whilst the numerical distribution of HCSC's is irregular across this data set, regardless of the metric of impact, the influence of historic climatic suitability was consistent. The "extreme" HCSC had consistently reduced impacts compared all other HCSC's, whilst this class had a notably reduced number of samples, the impact of MPB infestation in the "high" HCSC was also consistently less compared to the "very low", "low" and "moderate" suitability classes, particularly as the proportion of susceptible pine approached its maximum.

This research had several limitations. Firstly the reliance on forest inventory data used to describe forest characteristics in my assessment of MPB population dynamics in naive vs experienced habitats. I utilized VRI made available by BC Ministry of Forests. The limitations proposed throughout this data include: it can be highly subjective even though it requires well-trained interpreters and in some cases not cover important areas such as forest parks or conservation regions. Secondly is use of annual aerial insect survey data showing the distribution and abundance of dead pine trees across the province. This data is provided again provided by the BC Ministry of Forests. While these surveys provide valuable strategic data, they are most useful for broad scale analysis. Again time consuming and unprotected to biases introduced by different surveyors and interpretation. Also the potential limitations of this data include the inability to preclude alternative causes of tree death without extensive ground truthing. The limitations of MPB aerial surveying techniques and vegetation inventory data have been

suggested throughout the literature (Coops et al. 2006, Coggins et al. 2008, Morgan et al. 2010, Meddens et al. 2012).

To overcome the limitations with both forest inventory and aerial overview data I employed an area weighted mean function across my data set. The area weighted mean permits the final average number to reflect the relative importance of each number that is being averaged. What this equates to spatially is that the mean value for each 1 x 1km cell within my study area are the most realistic representation of what actually occurred within each cell, whether it be forest characteristics or MPB population dynamics. For example, a 1x1km cell that is made up of pine that is 60 years or older under the function of the area weighted mean it must be averaged across the 1x1km cell. This mean that the majority of the cell has to be equal to or above 60 years in age in order to reach this averaged value. In the same vein, a cell that has an infestation severity rating in the severe rating class (31 – 50%) must have a weighted average across the 100ha area of greater than 31%. This process smooths the available data considerably and is thus a conservative estimate of infestation severity across my study area.

2.6 Conclusion

The direct effects of anthropogenic climate change have now been documented worldwide. Insects are commonly reported to have been impacted, due to their short life cycles, reproductive potential, high mobility and physiological sensitivity to temperature. Resulting range shifts by insects have opened up novel associations. In western North America, climate warming coupled with extensive forest management have changed MPB dynamics across large areas (Raffa et al. 2008, Bentz et al. 2010, Safranyik et al. 2010). The amount of climatically suitable habitat has

grown since 1970, and beetles living in newly suitable lodgepole pine habitats are more successful (Carroll et al. 2004, Cudmore et al. 2010). It is expected that due to an insufficiently evolved defensive response in naive trees, the susceptibility of these trees will be higher, resulting in more rapid and severe host depletion. This landscape level analysis supports this evidence indicating that MPB is causing more rapid and severe impacts in those areas that have not historically experienced periodic infestation. Given that past and current impacts of herbivorous insect eruptions as a result of a warming climate are well documented and expectations are that continued climate warming will likely lead to further expansion of the range of MPB, further north, east and to higher elevations (Logan and Powell 2001, Carroll et al. 2004, Safranyik et al. 2010), priority should be given to the development of predictive tools supporting strategic landscape planning intent on minimizing additional impacts to naive ecosystems into the future.

Chapter 3: Host availability could limit the spread of mountain pine beetle into Canada's eastern boreal forest

3.1 Introduction

Documented impacts of a warming environment on insect populations vary but often involve both range expansions (Parmesan et al. 1999, Battisti et al. 2005, Hickling et al. 2005, 2006), and range contractions (Wilson et al. 2005). When combined with extensive alteration of natural disturbance regimes due to forest management, a warming climate can impact herbivorous insect dynamics across large areas (Raffa et al. 2008, Bentz et al. 2010, Safranyik et al. 2010). Climate change is expected to increase the extent and severity of outbreak events, given the sensitivity of herbivorous insects to variations in climate and given the historical increases in herbivory associated with warming environments (Currano et al. 2008). The mountain pine beetle (*Dendroctonus ponderosae*; hereafter MPB) is one such insect that has taken advantage of favorable climatic conditions. It has responded quickly to a warming climate by expanding its range to higher latitudes and elevations (Carroll et al. 2004, Safranyik et al. 2010), likely aided by an abundance of highly susceptible trees within a contiguous forested landscape (Taylor and Carroll 2004, Li et al. 2005, Raffa et al. 2008, Barclay et al. 2009). The most recent outbreak resulted in tree mortality over approximately 20 million ha of pine forest in North America [ca. 16 million ha in Canada (Westfall and Ebata 2013), 4 million ha in the US (USDA Forest Service 2013)].

An important component of this unprecedented outbreak are the dramatic long-distance dispersal events undertaken by MPB populations (de la Giroday et al. 2011, 2012). Historically, MPB in Canada were restricted to pine forests west of the Rocky Mountains and south of 56° N (Safranyik and Carroll 2006). In recent years, infestations have expanded over 500km northward and are now situated near the Yukon border (i.e. >60° N) in British Columbia (Westfall and Ebata 2014). Moreover, since 2002 dispersing beetles have breached the geoclimatic barrier of the Rocky Mountains, spreading east across northern Alberta (Nealis and Peter 2008, Robertson et al. 2009, Safranyik et al. 2010). At present, invading populations have been detected as far north as southern Northwest Territory and east within 50km of the Alberta – Saskatchewan border (i.e. <110° W) (Nealis and Cooke 2014). Persistent populations are now situated within the lodgepole × jack pine hybrid zone at the western margin of the transcontinental boreal forest. Jack pine (*Pinus banksiana*), the principal pine species of Canada's boreal forests is a successful host for MPB (Furniss and Schenk 1969). As climatic conditions continue to change, there is concern that MPB will spread unhindered through the boreal jack pine forests of Canada, eventually reaching the Great Lakes region of North America (Logan and Powell 2001, Carroll et al. 2004, Nealis and Peter 2008, Bentz et al. 2010, Safranyik et al. 2010).

Several studies have examined the risks to northern and eastern pine forests associated with invasion by MPB (Nealis and Peter 2008, Safranyik et al. 2010, Cullingham et al. 2011, Coops et al. 2012, Erbilgin et al. 2013, Nealis and Cooke 2014, Taft et al. 2015). Spread is only possible if MPB populations can persist in novel pine habitats following invasion and manifest the eruptive population dynamics characteristic of its native habitat (Safranyik et al. 2010). Within its historic range, MPB's predictable eruptive dynamics arise as a function of a distinct suite of trophic

interactions associated with endemic and epidemic population phases (Safranyik and Carroll 2006). Small endemic populations comprise too few beetles to overcome the defenses of a single large-diameter, healthy tree, and are therefore confined to trees with impaired defenses. In contrast, epidemic populations have exceeded the threshold population density for successful attack of healthy, highly-defensive mature trees (Boone et al. 2011). Once a population reaches the epidemic phase, conducive weather conditions and adequate host availability help support positive feedbacks within the population leading to potential landscape-scale outbreaks (Safranyik and Carroll, 2006; Raffa et al., 2008). Host availability has been recognized as a primary factor driving eruptive population spread (Carroll et al. 2006, Barclay et al. 2009, Safranyik et al. 2010, Boone et al. 2011). Taylor and Carroll (2004) report a threefold increase in the amount of pine in the most susceptible age classes to MPB attack between 1910 and 1990, a result of selective harvesting and fire suppression. This forms a catalyst for the development of positive feedback mechanisms in this system as beetles preferentially attack these highly susceptible, larger diameter trees during epidemic periods (Boone et al. 2011; Safranyik and Carroll 2006). Healthy well defended hosts have been shown to amplify beetle population growth during epidemic conditions (Boone et al. 2011). The complex eruptive dynamics of MPB in its native habitat are highly heterogeneous in time and space. As such, it is currently unknown whether similar dynamics might occur in a boreal forest setting given potential differences in host availability, host susceptibility, and climatic suitability (Bentz et al. 2010, Safranyik et al. 2010).

Given the importance of the abundance of susceptible hosts to the eruption and spread of a MPB (Safranyik and Carroll, 2006), I asked the following questions:

- 1) How does potential host availability (i.e. mature *Pinus* spp.) vary across the boreal forest of Canada; and
- 2) Assuming various levels of climatic suitability and host susceptibility, how will host availability affect the rate of spread of MPB through the boreal forest of Canada?

To measure continental host availability I constructed 100km wide, geographically distinct zones east from the Alberta/BC border quantifying data developed by Yemshanov et al. (2011) within each zone. Using a simple model of population growth parameterized from the present MPB outbreak in western Canada, I present a series of four scenarios of MPB spread across the boreal forest over the next 50 years. These scenarios aim to examine key areas of disagreement among scientists about how the rate of spread of MPB may vary.

3.2 Materials and methods

3.2.1 Study area

The study area comprised the near entirety of Canada's boreal forest (270 million hectares), stretching from the BC/ Alberta provincial boundary in the west to the Maritime Provinces in the east (Figure 9). Available data (spanning the continent) included: boreal forest characteristics provided by Yemshanov et al. (2011).

3.2.2 Host availability analysis

Data developed by Yemshanov et al. (2011) provided species-level maps of pine volume for 1 x 1 km grid cells across Canada (Figure 9). This dataset combined data from the Canadian National Forest Inventory (CanFI) and Earth Observation for Sustainable Development of

Forests (EOSD; Wulder et al. 2008) satellite derived land cover data. CanFI provides detailed information, including forest type, canopy age, and species-composition data (i.e., a numeric species code and stand volume calculated in absolute and per-hectare units), ranging from 7-56 species per record. The EOSD coverage employs multi-spectral Landsat satellite data and classifies three basic forest vegetation types; mixed-wood, coniferous, and broadleaf-dominated forests (Wulder and Nelson 2003). Yemshanov et al. (2011) used a spatial randomization technique to map the species-level information in CanFI to the land cover classes in EOSD. In so doing, a finer spatial resolution species map was produced, supporting the allocation of volume for each grid cell using similar down-scaling processes. To measure continental host availability in relation to MPB spread, I constructed 100km wide, geographically distinct zones east from the Alberta/BC border using ArcGIS® software version 10.3.1 (ESRI©, Redland CA, 2014), splitting the study area from west to east. For example Zone 1 from 0 – 100 km, zone 2 is from 101 km to 200 km (Figure 9). I considered this split of 100km to be a relevant distance based on 1) the beetles' ability for long-distance dispersal (Jackson et al. 2008), 2) the consistent eastward spread of the beetle in recent years (Nealis and Cooke 2014), and (3) the relatively constrained north-south distribution of forests across the boreal region (see Figure 9). The location of zonal boundaries was based on the start point of the Alberta/BC border and for the purpose of this analysis spread is assumed to be in a west to east direction. I used the ZONAL STATS function in ArcGIS SPATIAL ANALYST to extract information relating to MPB host availability, including pine volume, and area of pine for each species, within each 100km wide zone) (Figure 9). I used total pine volume within each zone in this modelling analysis, while total pine area data provided additional information into host distribution in the boreal, it was not integrated into modeling efforts. I consider pine volume to be the best indicator of host availability within each

zone as it provides a more detailed account of the forest landscape than just pine area alone and has been used in several other similar research efforts (White et al. 2005, Safranyik et al. 2010, Cullingham et al. 2011). Additionally pine volume is the best indicator of host availability for the scale of this analysis given the difficulty with quantifying other metrics when considering the entirety of the Canadian boreal.

3.2.3 Modeling continental spread

In order to model spread across the continent in relation to host availability I combined a growth model with a spatial analysis of host availability across Canada (pine volume with each 100km zone). I did this by first modelling population growth under 4 separate scenarios in order to capture the range of predicted conditions, I then measure the potential cumulative distance of MPB spread over 50 years based on the 4 growth model curves. This allowed me to incorporate a spatial element into the research when assuming spread from west to east. Requirements for this model include fixed values; measure of host availability as obtained from (Yemshanov et al. 2011), an upper limiting value of MPB spread achievable under epidemic conditions (Jackson et al. 2008) and modifier values, which were supported by the range of predicted conditions (Bentz et al. 2010, Safranyik et al. 2010, Coops et al. 2012).

3.2.3.1 Rationale for Gompertz growth model

I utilized a modified Gompertz growth model (Gompertz 1825) to predict the relationship between availability of susceptible host trees (pine volume m^3/ha) and rate of spread in to the boreal. The Gompertz model has been used extensively in population studies to represent the course of biological growth (Weymouth and McMillin 1931, Winsor 1932, Ricklefs 1967,

Brunton and Wheldon 1980, Riffenburgh and Johnstone 2001). It is a practical approach as the sigmoid growth curve can be manipulated by defining an upper limiting value (or upper asymptote), a rate constant and a lag value (or point at which growth rate is equal to zero) (Winsor 1932). The effective growth rate and the inflection point (when the overall rate of growth starts to decline) are determined by simple parametrization of these values. Four parameters in this simple model: y , A , b and c , were adapted to create useful comparisons among scenarios of MPB growth and spread through the transcontinental boreal forest, primarily based upon host availability using host susceptibility and climatic suitability as modifiers.

The Gompertz growth model is described below

$$y(t) = Ae^{-be^{-ct}}$$

In my analysis, y represents the rate of spread (km/year) and t represents the availability of susceptible host trees (pine volume m³/ha), A is the ultimate limiting value (km/year) or upper asymptote. These are fixed parameters. By assessing the availability of hosts at a continental scale across Canada, I was able to control for (t) and measure the rates of spread (y) (km/year) across the country in west to east direction, thus a spatial measure is incorporated. c is the “rate constant” which determines the spread of the curve along the x axis and the magnitude of b , the lag value, reflects the choice of the point at which the rate of spread is equal to zero. These variables are non- fixed, thus I term them modifiers in this analysis.

3.2.3.2 Fixed parameters

The upper asymptote A , or maximum rate of spread, was derived from Jackson et al. (2008). This study used direct observation of emergence, weather radar imagery, and aerial capture to assess MPB spread during epidemic conditions in central BC. Results show MPB as far as 800m above the forest canopy with an estimated density of 4950 beetles/ha and an estimated transport distance of 30–110 km/day⁻¹. Aerial transects were completed during peak emergence periods, approximately 22km southwest of Prince George, BC. Not only was this area dominated by lodgepole pine trees within highly susceptible age classes (Taylor and Carroll 2004), but trees within this area are considered evolutionarily naive to MPB impacts (Carroll et al. 2004, Cudmore et al. 2010). Such naivety has been linked with increased production of MPB (Cudmore et al. 2010) and increases in associated impacts (Robinson and Carroll, unpublished). I expressed pine volume in each west to east zone as a percentage of the maximum pine volume observed in my analysis of host availability, equating maximum pine volume to the volume of pine trees within the study area used in Jackson et al. (2008) by using stand volume estimates from Yemshanov et al. (2011). As a reference I used a maximum pine volume approximated at 300m³/ha from (Yemshanov et al. 2011) (Figure 9). Thus I was able to form a baseline for maximum spread achievable (110km/year) during the most ideal of situations for a MPB outbreak; high climatic suitability and an abundance of highly susceptible (naive) hosts.

3.2.3.3 Scenario development

To capture the range of predicted conditions I created four different scenarios of the Gompertz growth curve in relation to climate suitability and host susceptibility, presented in the table below (Table 5). In this population growth model c is the “rate constant” determining the spread

of the curve along the x axis. Justification for modification of these parameters is supported by several lines of evidence. While some predict it unlikely that MPB will be limited by climate in the near future (Safranyik et al. 2010) and show a significant increase in areas with suitable climatic conditions (Coops et al. 2012) others disagree and reason that climate will limit the probability of range expansion across the boreal jack pine in the near future (Bentz et al. 2010). Additionally, although past research indicates negligible difference between MPB development in jack pine and its primary host lodgepole (Safranyik and Linton 1982, Cerezke 1995), brood production in naive lodgepole pine was recently found to be more than twice that of experienced hosts (Cudmore et al. 2010). This is coupled with the suggestion that a lack of contiguous forest exists throughout the boreal (Safranyik et al. 2010). Thus, I make a case for modifying model parameters to create alternative scenarios based on the range of potential conditions derived from the published literature. I integrate these scenarios with a measure of pine volume to examine the influence of host availability on MPB dynamics at the landscape scale

Safranyik and Carroll (2006) related yearly population change to generation mortality factors, illustrating small changes in mortality can have large effects on the rate of population change. During an epidemic associated with optimal climatic conditions, they predict potential rates of population increase of two to eight-fold each year. Only when generation mortality reaches a level of 97% or above does the rate of population increase become less than or equal to 1 (Safranyik and Carroll 2006). I chose a rate constant “ c ” of 2 for high climatic suitability and 1 for low climatic suitability, a conservative number considering populations can grow by eight times or more in a single year when generation mortality reduces to a level of 80% or lower

(Safranyik and Carroll 2006). Additionally Safranyik and Carroll (2006) suggest based on past outbreaks a doubling in population is most common over large landscapes.

Table 5. Scenarios derived from the range of predicted conditions of climatic suitability and host susceptibility used to explore mountain pine beetle spread in relation to host availability.

The parameters A , b and c define the shape of the gompertz growth curves. The maximum spread achievable (110km/year) represents the maximum estimated spread during peak emergence in epidemic conditions in naive lodgepole pine in central, BC (Jackson et al. 2008). c is the “rate constant” determining the spread of the curve along the x axis and relates directly to the impact of climatic suitability on MPB epidemics (Safranyik and Carroll 2006). Variation in host susceptibility largely a function of age class, climate and co-evolutionary history (Cudmore et al. 2010) is used to parameterize b , the lag value.

Scenario	Description	A (<i>km/year</i>)	b	c
1	High climate suitability + High host susceptibility	110	10	2
2	Low climatic suitability + High host susceptibility	110	10	1
3	High climate suitability + Low host susceptibility	110	50	2
4	Low climate suitability + Low host susceptibility	110	50	1

Variation in host susceptibility is used to parameterize b , the lag value, reflecting the choice of the point at which the rate of spread is equal to zero. Host susceptibility is made up of several components, including but not limited to the individual trees ability to defend itself against attack, largely a function of age class (Taylor and Carroll 2004, Safranyik and Carroll 2006) but also its co-evolutionary history (Cudmore et al. 2010, Clark et al. 2012b). The influence of indirect drivers of temperature and moisture also have significant influence on host resistance (Safranyik and Carroll 2006). During sub-outbreak conditions host susceptibility significantly affects MPB growth rates (Safranyik and Carroll 2006, Boone et al. 2011). Effectively better defended trees are able to resist attack, thus there is a lag effect in the growth curve of a given MPB population. The magnitude of this “lag effect” is insignificant in outbreak conditions, once critical thresholds are overcome and positive feedback mechanisms promote rapid population expansion, trees’ defenses prove to be inconsequential (Boone et al. 2011). The potential for spread is also directly affected by the rate at which MPB populations exhaust their immediate hosts. Smaller epidemic infestations within a stand will not spread when an abundance of available hosts exist, as these populations grow in to large scale epidemics they rapidly exploit their hosts and spread (Safranyik and Carroll 2006). Representative of high host susceptibility conditions I use a lag value of 10 (Table 5), alternatively in a scenario where host susceptibility is low, I use a lag value 5 times that value.

3.2.3.4 Cumulative distance

Using these 4 scenarios of future conditions for the boreal forest and the estimated host availability I determined the potential cumulative distance of MPB spread over 50 years based on the Gompertz growth model. I restrict my future scenarios to 50 years as my approach assumes

host availability will not change appreciably in that time span. Additionally, while Bentz et al. (2010) predicts climatic suitability for the remainder of the century, Safranyik et al. (2010) and Coops et al. (2012) only go as far as the mid 2000's. Cumulative distance was based on spread east from the BC Alberta provincial border.

3.3 Results

3.3.1 Host availability

Estimated pine volume within each 100-km zone was highest in the west (zones 1 to 3), reaching a value more than 2,300,000 m³, where the predominant species is lodgepole pine (Figure 10).

Approximately 400km east of the BC-Alberta border the availability of pine declines to less than half of the volume of the areas to the west (zones 4 to 5) and is associated with a transition from lodgepole to jack pine (Figure 10). Relatively low volumes of jack pine exist throughout eastern Alberta, Saskatchewan and central and western Manitoba (zones 5 to 15) where values average less than 500,000 m³ (indicative of smaller more sparse trees). The availability of pine increases in eastern Manitoba (zone 15 to 19), and again in and western Ontario (zones 23 through 27) where a transition into a high-volume mixed jack pine/eastern white pine/red pine dominated forest is observed (Figure 10).

A relatively low area of pine in western Alberta (50,000 – 60,000 km²) associated with high-volume pine (2,300,000m³) (Figure 10, Figure 11) indicates a more dense forest cover compared too much of the boreal. Comparatively the same forested area exists in zones 1 through 5 and zone 6 through 10, although the latter are correlated with reduced volume (~ 500,000m³)

associated with a transition from lodgepole pine to jack pine. The notable increase in the area (Figure 11) of pine in eastern Ontario (zones 16 to 30) is associated with relatively high pine volumes (Figure 10), indicating that average density is high across a large area. The same cannot be said for the province of Quebec (zones 30 to 40), where especially in the east, low volumes are associated with large areas of pine indicating a relatively sparse forest cover over a large area of the province (Figure 11). Both area and volume of pine species decreases markedly further in eastern Quebec, New Brunswick, Nova Scotia, Newfoundland and Labrador (zones 34 to 40) (Figure 10, Figure 11).

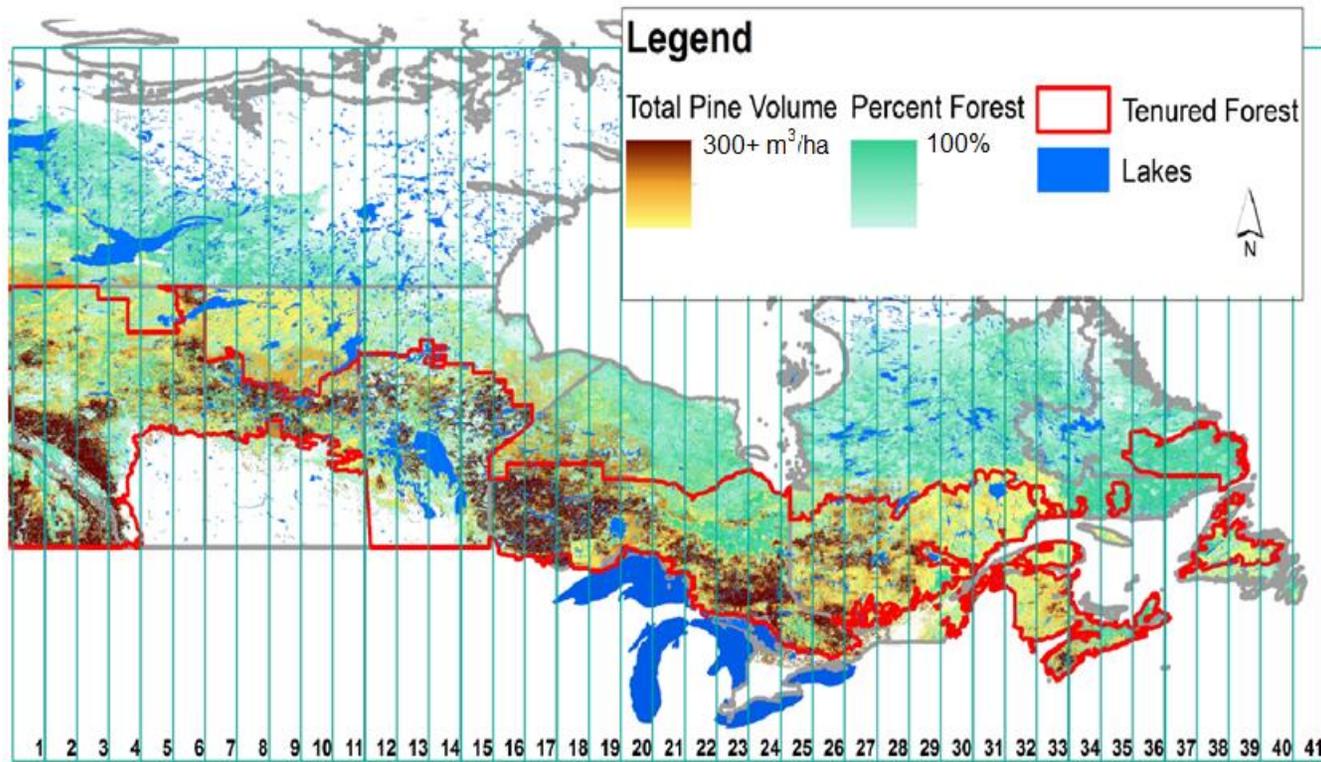


Figure 9. 100km-wide zones for which statistics were calculated for both pine volume and area. The study area covers the majority of Canada spanning from the BC/Alberta provincial boundary in the west, to the eastern Maritime Provinces (Newfoundland, Labrador, New Brunswick, Nova Scotia). Tenured forest areas (indicated in red) show the administrative boundary of a range of timber license agreements, for the extraction and utilization of forests and forest resources. Percent forest, indicated in green shows forested land under natural or planted stands of trees of at least 5 meters in situ, whether productive or not.

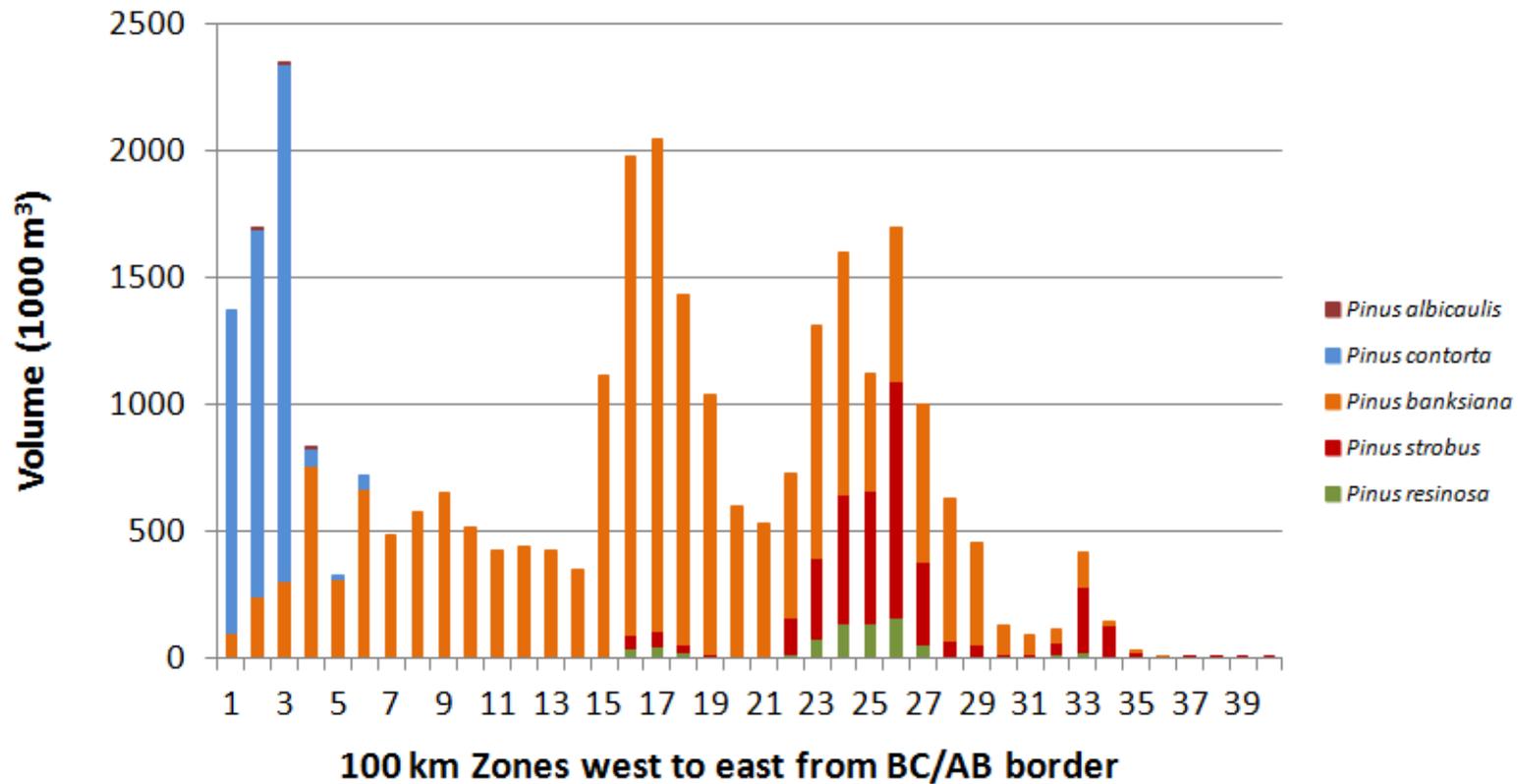


Figure 10. Estimated pine volume ($m^3 \times 1000$) by species (Yemshanov et al., 2011), partitioned within 100km-wide zones, west to east from the BC-Alberta Border. For example Zone 1 from 0 – 100 km, zone 2 is from 101 km to 200 km. Information relating to forest characteristics including pine volume and area for each species was extracted using zonal statistics function in ARC GIS spatial analyst.

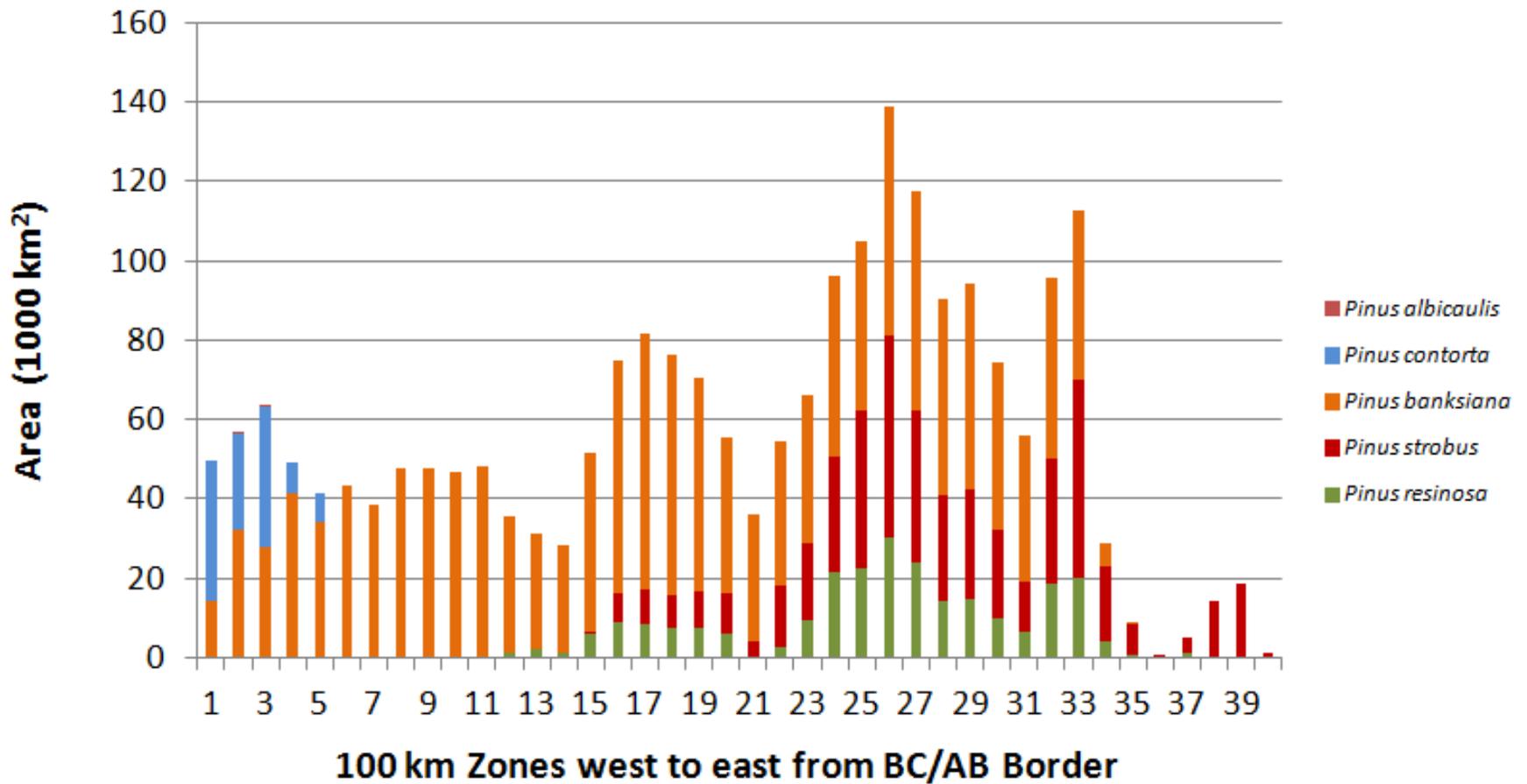


Figure 11. Estimated forested area ($\text{km}^2 \times 1000$) by species from (Yemshanov et al., 2011), partitioned within 100km-wide zones, east from the BC-Alberta Border. For example Zone 1 from 0 – 100 km, zone 2 is from 101 km to 200 km. Information relating to forest characteristics including pine volume and area for each species was extracted using zonal statistics function in ARC GIS spatial analyst.

3.3.2 Modelling continental-scale spread

In ideal conditions MPB, are able to spread large distances regardless of pine volume. In scenario 1: MPB population epidemic conditions [with a rate constant of 2 (high host susceptibility) and lag value of 10 (high climatic suitability)], these ideal circumstances produces a curve that accelerates rapidly from zero and quickly reaches its upper asymptote at 110km/year (Figure 12). In contrast, scenario 4, representative of low host susceptibility and poor climatic suitability, is much slower to reach a spread rate greater than zero, and only approaches *A* in 75th percentile of pine volume. It is evident from the curves that as growth rates slow, pine volume becomes much more influential on spread distance. For example in scenario 1 a spread rate of 60km per year is achievable at a volume of 75m³/ha, while in scenario 4 the volume of pine required to reach this rate is almost twice that value. By contrast, the volume of pine required to reach this rate is almost twice that value for scenario 4.

Cumulative distance is based on the summed annual spread of MPB east from the BC-Alberta border, and determined directly in relation to host availability under the 4 scenarios (Figure 13). When host availability is high as is the case in zones 1 - 3, the rate of spread was predicted to be high in all scenarios, thus it is expected that initial spread could be as much as 110km per year. However, if the susceptibility of novel pine habitats and the suitability of the climate are both low as in scenario 4, then MPB spread will not only cease around 1500 km from the BC Alberta border (zone 15), but a lack of pine volume may force it to spread slowly and remain in one zone for a number of years before reaching the next zone (Figure 13). By contrast, when high climatic suitability and high host susceptibility coincides (scenario 1), then variable host availability

proves little barrier to spread throughout eastern Alberta, Saskatchewan and western Manitoba (Figure 13). Indeed, scenario 1 predicts the arrival of MPB in eastern mixed pine forests (i.e. zones >20) in less than 20 years (Figure 13). It is important to note that low volumes of pine throughout the Maritime Provinces fail to support MPB population under all scenarios.

Varying host susceptibility and climate suitability in scenario 2 and 3 produced both slightly different curves in the growth model and the analysis of cumulative distance. In scenario 2 where host susceptibility is high and climate suitability is low, the upper asymptote A is reached at a volume close to $200\text{m}^3/\text{ha}$, in comparison in scenario 3 A is reached at a value of approximately $150\text{m}^3/\text{ha}$ (Figure 12). A less contrasting difference when comparing scenario 1 and 4, but none the less a difference. This difference carries over into the calculation of cumulative distance, where in approximately 25 years, scenario 3 is predicted to reach as far as zone 30 versus zone 25 for scenario 2 (Figure 13). Thus it appears according to this conceptual growth model that climate suitability has comparatively more influence on population growth.

In Figure 13 I provide three points of interest derived from the analysis of host availability. These include: (i) transition from high-volume lodgepole pine to low-volume jack pine in west/central Alberta (zone 4, ~ 400km from BC/Alberta border); (ii) transition from low-volume jack pine to high-volume jack pine with some mixed pine species in eastern Manitoba (zone 15, ~ 1500km from BC/Alberta border); (iii) transition from high-volume mixed species stands to low-volume pine in the Maritime Provinces (zone 30, ~ 3000km from BC/Alberta border) (Figure 9). In scenario 4 (Figure 13), the maximum cumulative distance of spread is achieved in approximately 25 years and halts at the transition from high-volume pine to low-volume of

eastern Alberta, Saskatchewan and western Manitoba (zones 5 to 15). In this case spread fails to reach the higher volume jack pine areas of eastern Manitoba and Ontario. In scenarios 1 through 3, it is clear that the sparseness through zones 5 to 15 is not enough to limit MPB population growth, with spread reaching the higher volume jack pine areas of eastern Manitoba and Ontario (zones 16 through 33) in approximately 20 years. In scenario 1 the lack of pine in zones 34 onwards forms a barrier to MPB, while in scenario 2 and 3, spread ceases in the higher volume areas eastern Manitoba and Ontario (zones 16 to 33).

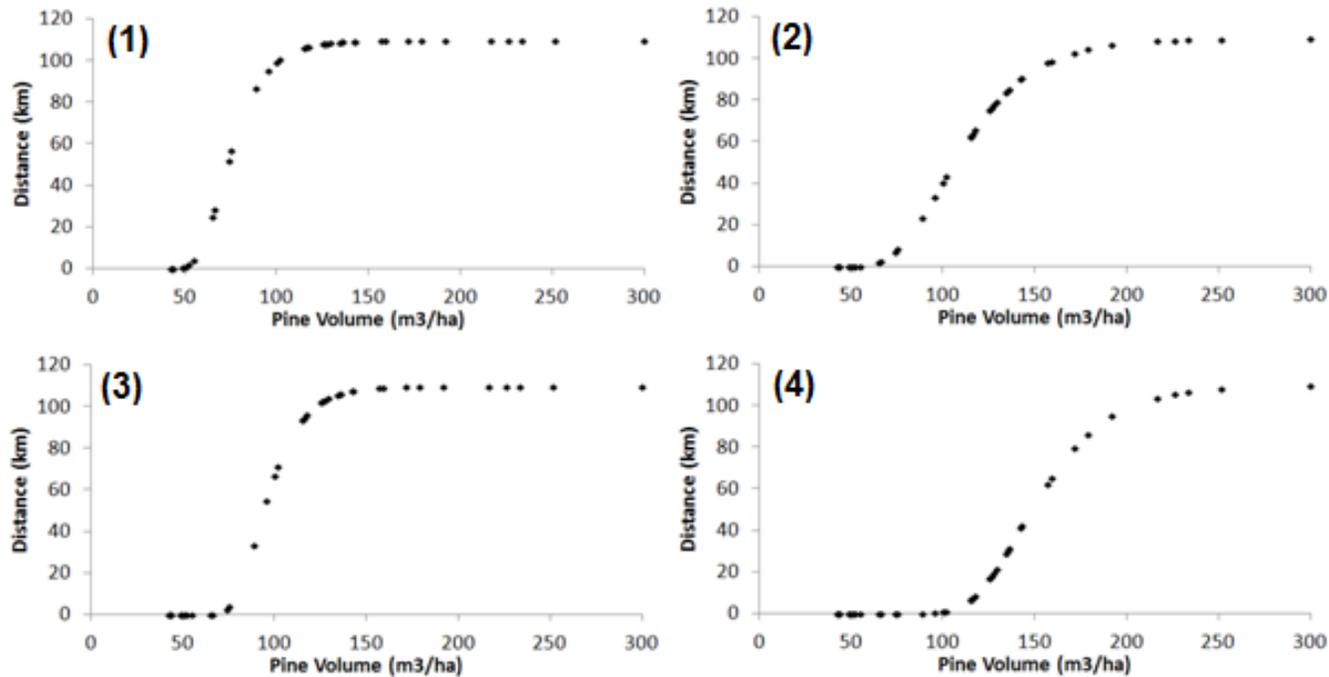


Figure 12. Scenario results showing annual spread distance (km) by epidemic mountain pine beetle in relation to the volume of available host trees. The upper asymptote (110km/year) is derived from the maximum dispersal distance for the mountain pine beetle (Jackson et al. 2008) under ideal conditions [mean host availability = 300m³/ha (Yemshanov et al., 2011), high host susceptibility (Cudmore et al., 2010), and high climatic suitability (Carroll et al., 2004)]. The scenarios are: (1) high climate suitability + high host susceptibility; (2) low to moderate climatic suitability + high host susceptibility; (3) high climate suitability + moderate host susceptibility, and; (4) low to moderate climate suitability + moderate host susceptibility (Table 1).

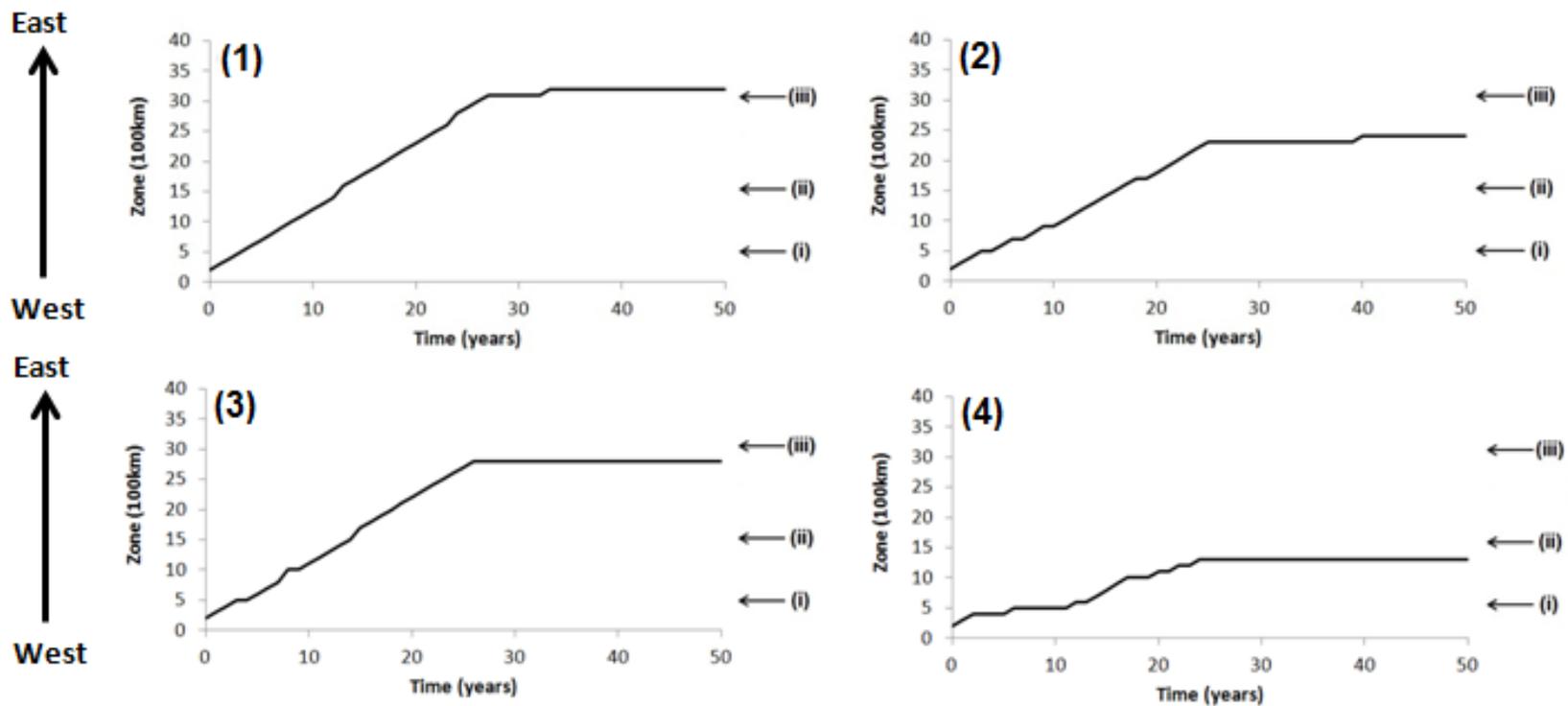


Figure 13. Predicted annual cumulative distance based on the sum of predicted annual dispersal events of mountain pine beetle east from the BC-Alberta border, assuming one dispersal event per year, predicted by Gompertz growth model analysis under the 4 scenarios of host susceptibility and climatic suitability (1) High climate suitability + High host susceptibility . (2) Low climatic suitability + High host susceptibility. (3) High climate suitability + low susceptibility. (4) Low climate suitability + low host susceptibility. Arrows to the right indicate points of interest regarding host availability. (i) transition from high-volume lodgepole pine

to low-volume jack pine in west/central Alberta (zone 4, ~ 400km from BC/Alberta border); (ii) transition from low-volume jack pine to high-volume jack pine with some mixed pine species in eastern Manitoba (zone 15, ~ 1500km from BC/Alberta border); (iii) transition from high-volume mixed species stands to low- volume pine in the Maritime Provinces (zone 30, ~ 3000km from BC/Alberta border).

3.4 Discussion

3.4.1 Host availability

Modelling results from this analysis suggest if climatic conditions remain suitable, the relative sparseness of pine throughout eastern Alberta, Saskatchewan and central and western Manitoba may be little barrier to MPB range expansion under epidemic conditions even if host trees are less susceptible to attack. Regardless of low host availability across Alberta and Saskatchewan, under the most favorable conditions of climatic suitability and host susceptibility regions of high-volume jack pine in eastern Manitoba and western Ontario are reached as quickly as 20 years.

My findings demonstrate that large tracts of susceptible host trees are much less common in the boreal forest compared to the native range of MPB in western Canada. Certainly the availability of large tracts of susceptible hosts has been shown as a catalyst for eruptive dynamics leading to positive feedback in bark beetle populations (Raffa et al. 2008, Boone et al. 2011). In three out of four of the scenarios host availability shows little influence on predicted spread rates with MPB arriving at the transition between low and high-volume jack pine in 20 years or less. In unfavorable conditions not only does spread cease approximately 1500 km from the BC/Alberta border, but a lack of pine volume may force MPB to remain in one zone for a number of years before reaching the next.

This model indicates as MPB population growth rates slow, pine volume becomes more influential on the rate of spread, a result consistent with the suggestion that host availability is a primary driver of population dynamics. This trend can be contextualized within the theory of

feedback mechanisms published in schematics by Safranyik and Carroll (2006). As population growth rate slows, secondary bark beetles begin to compete with MPB for the same resources. Thus negative feedback exists between beetle population decline and food availability. The opposite is true in favorable conditions, as populations increase in size, food availability increases due to the ability of large populations to take out the biggest healthiest trees (Boone et al. 2011). Beetles that access larger trees can produce 40 times the amount of brood when comparing 40cm DBH hosts to 10cm (Safranyik and Carroll 2006), combine this with suitable climatic conditions and landscape scale amplification can occur. This types of feedback can occur on a range of temporal scales, with varying implications (Raffa et al. 2008).

Whilst the availability of host trees is considered a primary driver of extensive outbreaks where positive feedbacks facilitate rapid spread over large landscapes (Safranyik and Carroll, 2006; Aukema et al., 2008, 2006; Raffa et al., 2008). Results from this modeling analysis suggest other factors are in effect when considering the predicted rates of spread through the area of low-volume jack pine through eastern Alberta, Saskatchewan and western Manitoba.

3.4.2 Climatic suitability

Results from this analysis indicate the scarcity of pine throughout eastern Alberta, Saskatchewan and central and western Manitoba remains little obstacle to MPB range expansion under favorable climatic conditions. Moreover climate suitability had relatively more influence on population growth compared to host susceptibility in three out of the 4 scenarios presented. This result is not surprising given that historic latitudinal and elevational range of MPB was not restricted by the availability of suitable host trees but by climate (Logan and Powell 2001,

Carroll et al. 2004). MPB's primary host lodgepole pine, extends north and east far beyond the reach of historical beetle populations (Farrar 1995, Safranyik and Carroll 2006). In recent decades Carroll et al. (2004) showed that the amount of climatically suitable habitat for MPB has increased dramatically since 1970 and beetle populations have been expanding at an increasing rate into newly suitable areas.

Distinction of my growth model parameters relating to climate suitability was supported by variation in future predictions. While Coops et al. (2012) show a significant increase in the areas with suitable climatic conditions and Safranyik et al. (2010) predict it unlikely that MPB will be limited by climate in the near future, Bentz et al. (2010) disagree and reason that climate will limit the probability of range expansion across the boreal jack pine in the near future. Owing to this disparity in predicted conditions I vary the rate constant in the gompertz growth model by doubling the value for conditions representative of high climatic suitability. This I consider a conservative number as populations have been shown to grow by eight times or more in a single year when generation mortality reduces to a level of 80% or lower (Safranyik and Carroll 2006). Moreover a large portion of the most recent outbreak in western Canada has occurred in areas that were historically unsuitable for MPB (Carroll et al. 2004, Taylor et al. 2006, Cudmore et al. 2010). Areas where increased impacts (Robinson and Carroll. unpublished) and production of brood has been demonstrated (Cudmore et al. 2010). Thus the predicted influence of climate suitability in naive environments such as the boreal may be underestimated in this particular case. Although further investigation should be undertaken to properly quantify these possible relationships.

3.4.3 Host susceptibility

Host susceptibility had little influence on rates of spread across the boreal in three out of four predictive scenarios. Only when combined with poor climatic conditions did reduced host susceptibility cause notable reduction in the rate of spread across the boreal. Combining these conditions with a reduction in available hosts slows spread and shows beetles being forced to stay in one zone for a number of years before reaching the next. While climate suitability appears to be having more influence on rates of spread under the parameters of this predictive model, one should not discount the influence of host susceptibility in relation to spread.

Spread is only possible in the boreal if MPB populations can persist in novel pine and demonstrate the same eruptive population dynamics as in the native range. Susceptibility of trees can be both a function of the individual trees ability to defend itself against attack (Taylor and Carroll 2004, Safranyik and Carroll 2006) and its co-evolutionary history (Cudmore et al. 2010, Clark et al. 2012b). Under conditions such as those depicted in scenario 1 it might be assumed that the threshold for mass attack will be overcome driven by an increase in the average susceptibility of trees causing landscape level mortality of boreal hosts. Trees' defenses prove to be inconsequential once critical thresholds are overcome and positive feedback mechanisms promote rapid population expansion (Boone et al. 2011). Whereas in sub-outbreak conditions such as those depicted in scenario 4, host susceptibility significantly affects MPB growth rates (Safranyik and Carroll 2006, Boone et al. 2011). At this point the influence of indirect drivers of temperature and moisture have significant influence on host resistance (Safranyik and Carroll 2006).

While host susceptibility has been the basis for a number of susceptibility models applied to MPB populations in its native range (Waring and Pitman, 1985; Amman et al., 1988; Shore and Safranyik, 1992; Shore et al., 2000; Li et al., 2005) less attention has been applied to the boreal forest (Safranyik et al., 2010; Cullingham et al., 2011). Recent evidence for higher productivity (Cudmore et al., 2010) and increased impacts (Robinson and Carroll. unpublished) of MPB in naive pine suggests the threshold (defined by tree defenses) between endemic and epidemic states appears to be lower in novel habitats. Although the potential for eastern pine species (including jack pine, eastern white pine and red pine species) to support populations to a level of mass attack is largely unknown.

Jack pine, just like naive lodgepole pine in the northern regions, has not coevolved with MPB and therefore is unlikely to have evolved any natural specific defense. It contains higher levels of α -pinene than do coevolved lodgepole pine (Wallin and Raffa 1999, Clark et al. 2010, 2012b), α -Pinene being the precursor to trans-verbenol the main aggregation pheromone synthesized by pioneering female MPB (Borden et al. 1987, Hunt et al. 1989). Successful attacks and reproduction are occurring in individual jack pine (Cullingham et al. 2011), but what that means at the landscape scale is uncertain. Exploitation of the chemical similarity between historical and novel hosts for pheromone production and aggregation has facilitated host expansion of MPB in jack pine forests (Erbilgin et al. 2013). Until further research quantifying the potential for MPB range expansion at a both the fine and broad scale is conducted, a full understanding of the complex system will not exist.

3.4.4 Assumptions and limitations

Inside the historic range of MPB, eruptive dynamics are a result of a distinct suite of trophic interactions associated with endemic and epidemic population phases (Safranik and Carroll 2006). Endemic populations contain insufficient numbers to overcome the resistances of a single healthy, large-diameter tree. These populations are generally confined to trees with weakened defenses that provide relatively lower nutrition value and resultant brood productivity (Safranyik and Carroll 2006). In contrast, epidemic populations have exceeded the threshold population density for successful attack of healthy, highly-defensive mature trees (Boone et al. 2011). Conducive weather conditions and adequate host availability help support the epidemic phase in which positive feedback occurs within the population leading to the potential for landscape-scale outbreaks (Safranyik and Carroll, 2006; Raffa et al., 2008).

Owing to the fact that endemic population dynamics have not yet been observed in novel pine forests (Carroll pers comm.) I assume epidemic like conditions throughout this predictive growth model. This assumption is supported by the fact that to date only epidemic behavior has been observed in novel pine forests – including areas with low climatic suitability (Carroll pers comm.). Until such time as published data reveals endemic behavior in the boreal, I must assume range expansion is driven by dramatic long-distance dispersal events undertaken by MPB populations (de la Giroday et al. 2011, 2012). Such events that have seen dispersing beetles breach the geoclimatic barrier of the Rocky Mountains and spread east across northern Alberta (Nealis and Peter 2008, Robertson et al. 2009, Safranyik et al. 2010).

While rapid range expansion as a consequence of MPB outbreak is driven largely by climatic suitability and the availability of susceptible hosts supporting positive feedback at the landscape scale (Taylor and Carroll 2004, Aukema et al. 2006, 2008, Raffa et al. 2008), major uncertainty exists as to whether the pine species of the boreal forest can prove to be suitable hosts to MPB populations. It has been suggested that increased productivity from naive lodgepole pine was the catalyst for unprecedented outbreak (Cudmore et al. 2010) and increased impacts confirmed (Robinson and Carroll. unpublished), although these numbers may not prove relevant to the boreal forest. Given high levels of host availability epidemic MPB preferentially colonizes the most defensive trees in a given stand (Boone et al. 2011) due to the links among tree vigor, tree defenses and phloem quantity/quality (Safranyik and Carroll 2006). However these studies have focused on a species that is physiologically different from those of the eastern boreal system. Detailing MPB population dynamics in pure jack pine stands again requires more detailed experimentation, while in progress (Burke and Carroll in press.) published results have yet to been shown within the scientific community.

In areas with contiguous forest conditions, suitable age classes for infestation, and large populations of synchronously emerging beetles (as seen in British Columbia), MPB have reportedly spread from 30-110 km in a single outbreak event (Jackson et al. 2008). This upper limiting value based on Jackson et al. (2008) may overestimate MPB spread in naive habitats as this value was derived from outbreak populations developed in naive lodgepole pine. The flight period under investigation in this study indicated that beetles were caught in convective wind currents, a situation that should be considered a chance event requiring temporal coincidence with mass outbreak populations. Also given that emergence and flight occurs over a short time

period regulated by daily temperatures it is unlikely that passive dispersal of beetles in advective wind current would occur every year. Cooke and Carroll (n.d.) did find the rate of spread northward and eastward between 2006-2010 was particularly swift, averaging 80km/year, dominated by annual jumps exceeding 100km in 2006-07 and 2008-09. This was again achievable during outbreak conditions in naive lodgepole pine, not jack pine. In addition lower levels of connectivity in the boreal forest described by Safranyik et al. (2010) are likely to force a shift in the mechanisms of dispersal from predominantly short distance to long distance dispersal due to large open tracts of forest that need to be overcome by MPB.

Regardless of the simple nature of this growth model, there is significant uncertainty on both the parameters governing its curve and the results under varying scenarios. The selection of this equation does not imply biological significance, or that they are accurate models of the growth process, but merely that it is well suited for a comparative descriptive purpose using a growth model that has been found to approximate the growth curve of many kinds of organisms

3.4.5 Implications for managers

Predicted rates of spread suggest that in conditions favorable to MPB (both suitable climate and susceptible hosts) forest managers may face large challenges. Alternatively in unfavorable conditions forest managers should concentrate their efforts on the low-volume areas in Alberta, Saskatchewan and western Manitoba. Unfavorable conditions are associated with high levels of generation mortality due to variations in climate suitability, beetle phenology, forest structure, connectivity and host susceptibility, all of which creates an uncertain risk of establishment and local persistence in the naive habitat. Many large-scale direct control efforts aimed at mitigating

the effects of MPB epidemics have been undertaken in the past century throughout North America. Tactics include cultural and mechanical treatments, chemical insecticides and semio-chemical manipulation of beetle populations (Carroll et al. 2006). Essentially direct control applications are aimed at reducing generational survival within populations, to minimize their rate of increase/spread and the mortality of high-value trees. Programs target newly attacked trees, with the objective of destroying the host tree before the beetles emerge and disperse. As current projections of MPB locations see the beetles as far east as 50km from the Saskatchewan border (Nealis and Cooke 2014) it is clear that control efforts should be located in this area.

If MPB populations are kept at low levels by a combination of direct control efforts and/or a failure to meet critical threshold levels due to interactions with direct and indirect drivers, rates of spreads are directly proportional to size of source population. Direct control activities during endemic conditions have been shown to significantly reduce population numbers, diminishing the likelihood of development of future outbreaks (Carroll et al. 2006). Although the success at population suppression by direct control is limited (Carroll et al. 2006), it has been suggested that any level of direct control intervention will slow the spread and impacts of an epidemic population (Nelson et al. 2007). Although facilitating successful control programs is challenging as efforts require prompt and thorough application of the most appropriate treatments, in order to maximise results, with the quality of survey activities serving to limit the effectiveness of direct control activities (Coggins et al. 2008).

3.5 Conclusion

There is little consensus on the susceptibility and climatic suitability of the boreal pine forests for MPB. Results from my analysis indicate that the predicted spread of MPB could be rapid under conditions of high climatic suitability. Only under conditions of both low climate suitability and low host susceptibility did host availability become a limiting factor affecting spread. Currently, we cannot assume equivalency between western and eastern pine species in their ability to support MPB eruptive dynamics which lead to major range expansion events. Altered chemical composition of hosts may help MPB overcome some of the potential restraints for establishment and spread in the boreal forest due to low pine volume and connectivity. Although without solid quantification of all of the factors influencing MPB population dynamics in the boreal forest following a major host change, this predictive growth model is only able to provide limited insight into the possible outcome of continued spread of MPB east into the boreal system. Implications from this study are broad as climate induced range expansion represents significant potential for similar outbreak events to occur across a range of insect species and habitats as a result of a warming climate.

Chapter 4: Conclusion

This study assessed the dynamics of MPB infestations in novel (naive) versus native (experienced) habitats, and the influence of host availability on the potential for MPB spread across the boreal forest of Canada. First, I evaluated the hypothesis that naive trees will be more susceptible to attack due to an insufficiently evolved defensive response resulting in higher levels of tree mortality and stand depletion than experienced habitats. I combined a landscape-level analysis of MPB infestation data across BC in relation to forest characteristics and climatic suitability. This required the use of several different data sources including a climate suitability model, province wide vegetation inventory and annual aerial overview survey data. Additionally I assess the potential for MPB to spread across the boreal by modeling the influence of host availability on spread under varying scenarios of predicted climate and host conditions. I combine a continental scale assessment of host availability, utilizing data developed by Yemshanov et al. (2011) with a simple model of population growth parameterized from information pertinent to the present MPB outbreak in western Canada.

4.1 Overall conclusions and integration with current research

The MPB has responded quickly to take advantage of favorable conditions, expanding its range in more northern latitudes and higher elevations as a result of a warming climate (Carroll et al. 2004, Raffa et al. 2008, Safranyik et al. 2010) and abundant highly susceptible trees within a contiguous forested landscape (Taylor and Carroll 2004, Li et al. 2005, Raffa et al. 2008, Gillanders et al. 2008, Barclay et al. 2009). Much of the most recent outbreak in western Canada occurred in areas historically unsuitable for MPB (Carroll et al. 2004, Taylor et al. 2006, Cudmore et al. 2010). Not only has MPB expansion enabled contact with populations of

lodgepole pine lacking defensive responses, but also with boreal jack pine, a species extending throughout Canada. Cudmore et al. (2010) found MPB had higher reproductive success in lodgepole pine trees in areas only recently becoming climatically suitable. Similarly, Raffa et al. (2012) documented inferior defenses to MPB attacks by high-elevation whitebark pine (*Pinus albicaulis* Engelmann). Less effective host-tree defenses and higher overall beetle productivity in evolutionary naive pine habitats suggests that MPB dynamics in newly invaded regions may differ from that in its native range. As climatic conditions restructure, a conduit for further range expansion into the eastern boreal may be provided by naive pine hosts in eastern North America, (de la Giroday et al. 2012).

My work shows that recently invaded habitats experienced impacts 1.7 to 3.9 times greater than those habitats with long-term exposure to MPB. In addition, the rate at which impacts accrued in “naive” habitats was significantly greater than that associated with “experienced” habitats. Furthermore my study identified a major gap in host tree availability throughout Saskatchewan and Manitoba, which may provide a barrier to MPB spread in unfavorable climatic and host conditions. This simple growth model exploring factors relevant to MPB population eruption suggests that MPB impacts are highly dependent on pine volume. As growth rates slow or population dynamics decline, pine volume becomes more influential on the rate of spread. According to this model, however, in epidemic conditions MPB can spread large distances regardless of pine volumes. In suboptimal conditions, spread ceased around 1500 km from the BC/Alberta border. Low pine volume forced MPB to remain in one 100km wide zone for several years before expanding. This result (combined with recent research) supports the idea that MPB

dynamics may differ greatly in boreal jack pine. Without further research it is difficult to make spatially accurate predictions as to how this insect responds to a major shift in host.

4.2 Limitations

This research had several limitations. First the reliance on forest inventory data used to describe forest characteristics in my assessment MPB population dynamics in naive vs experienced habitats. I utilized a vegetation resources inventory (VRI) provided by BC Ministry of Forests, Lands and Natural Resource Operations. Data are acquired using a photo-based, two-phased vegetation inventory consisting of phase photo interpretation and ground sampling. The limitations suggested with this data source is that it does not cover areas such as forest parks or conservation regions, can be highly subjective, and can require well-trained interpreters (Morgan et al. 2010). Additionally these inventories are of variable vintages and often prioritized by merchantability thus change is often not captured through cyclical updating resulting in a failure to properly assess forest susceptibility.

Secondly the use of annual aerial insect survey data used to assess the spread of MPB across the study area. I utilized annual aerial overview surveys of forest health conditions which have been conducted by the BC Ministry of Forests, Lands and Natural Resource Operations for the entire province since 1999 and for portions of the province since 1996. The distribution and abundance of dead pine trees is considered to be an accurate representation of the distribution and abundance of MPB populations. While these surveys provide valuable strategic planning data, they are most useful for broad scale analysis, with limitations at the stand level. They can also be time consuming and exposed to biases introduced by different surveyors and interpretation

(Goodwin et al. 2008, Morgan et al. 2010, Meddens et al. 2012). Additionally potential limitations of this data include the inability to preclude alternative causes of tree death without extensive ground truthing.

To address these shortcomings and overcome the limitations with both forest inventory and aerial overview data I utilized an area weighted mean function across the study area to summarize data within each 1 x 1km cell. The benefit of using a weighted average is that it allows the final average number to reflect the relative importance of each number that is being averaged. What this means spatially is that the final mean values for each 1 x 1km cell within my analysis is a reflection of the spatial importance of each value being averaged. This in effect, standardizes the data at a common spatial scale and provides a smoothing effect to any inherent deficiencies in the data.

In the second part of my thesis research I assessed how host availability varies across the boreal forest of Canada and how host availability affects the rate of spread of MPB under variable climatic suitability and host susceptibility. Whilst this approach is broad in its spatial extent and is likely to somewhat oversimplify the phenomenon of spread across the boreal, it extends the simple fact that MPB need both climatic conditions suitable for spread and an abundance of susceptible hosts. One of the greatest uncertainties is suggested by Safranyik et al (2010), who imply that MPB populations may persist for a numbers of years in an endemic state until eventually favourable climatic conditions combined with the availability of susceptible host trees may enable populations to build up to such numbers that mass attack is possible.

While my study cannot rule out the influence of a highly favorable climate, it does quantify the lack of pine throughout the Canadian prairies (Alberta, Saskatchewan and Manitoba). With pine volumes in these areas 3 to 4 times less than volumes seen in western Alberta and BC, high volume areas known to support endemic populations throughout the last decade, one might suggest the Prairies pose a significant barrier to MPB spread into the boreal. Indeed this study's approach was spatially broad and other factors independent of host availability including climate, disease, predation, history, and human impact can have significant impacts on species distribution and rate of spread. Although the strength of this work was its ability to address a larger area than much prior work and use readily-available landscape scale data sets to extrapolate potential future conditions.

There is little doubt that MPB will face a chemically different phloem environment when locating and colonizing jack pine and other naive pines in its new geographic range. Successful reproduction has now been observed in jack pine stands in western Alberta (Cullingham et al. 2011). Modeling assessments of stand susceptibility indicate that western Alberta is susceptible, although a reduction in susceptible habitat due to lower pine volume and less connectivity in the east may prove a significant barrier to further expansion (Safranyik et al., 2010; Robinson et al., unpublished data). Although higher reproductive success in naive lodgepole (Cudmore et al. 2010), documented inferior defenses by high-elevation whitebark pine (Raffa et al. 2012), lower induced defenses (Clark et al. 2014) and readily generated trans-verben (Erbilgin et al. 2013) in jack pine may provide sufficient feedback to MPB population dynamics to enable population eruption.

By combining modelled spread rate determinants with a continental scale assessment of host availability, this study provides further understanding of the risk to the novel forests across Canada. Despite the study's limitations, the information it produced provides researchers with data and measures that can be used to guide future research on the MPB and other natural disturbance and forest-related issues.

4.3 Implications for management

4.3.1 Future challenges in managing for MPB range expansion

In recent years, the impacts of changing climate on herbivorous insects have manifested as increases in thermally benign habitats and changes in phenological synchrony with the environment. These outbreaks have substantial ecological and economic ramifications, and have provoked calls for policy change ranging from more aggressive harvesting and fire suppression to mitigation of global emissions (Raffa et al. 2008). The most consistently observed response by eruptive forest insects to climate change has been shifts in their distribution. In BC, MPB has significantly expanded its range to more northerly latitudes and higher elevations (Logan and Powell 2001; Carroll et al. 2004; Aukema et al. 2008; Safranyik et al. 2010; Shore, Riel, and Fall 2010). A change in an insect's range constitutes an invasion of a new habitat, as such increases in insect-caused forest disturbance beyond the long-term range of natural variability is expected to significantly reduce forest carbon reservoirs, increase rates of heterotrophic respiration and cause feedback to future climate change.

The adverse impacts of MPB outbreaks to the timber and recreation industries are well documented. Projections for the current epidemic include a \$2.5 billion decrease in manufacturing activity, a loss of 27,000 direct jobs, and a loss of \$250 million in government stumpage and royalty revenues in British Columbia alone (Sims et al. 2010). This phenomenon creates a large number of difficult management scenarios to government agencies, industry and managers across a number of areas. Management requires a multidisciplinary approach to facilitate generalization of common objectives throughout western North America. Interactions between MPB and forest management involve an important feedback loop: MPB populations affect forest-management decisions and forest-management decisions affect MPB population dynamics (Sims et al. 2010).

Hence as climatically benign habitats increase allowing further range expansion by MPB, demonstrated in several publications, the scope of management broadens. The complexity of the issue is exemplified when considering influences of management on forest structure. For example forest structure plays a vital role in determining a susceptibility at a range of scales (e.g. stand, landscape scale), as forest structure is determined by the decisions of numerous forest service managers and timber tenure holders each who manage a small part of the forest as a whole, it can be a less than easy task synthesizing management plans to maintain timber supply and forest resilience. The literature recognizes that while climatic changes may be responsible for increasing the geographic range of MPB, increases in outbreak severity and frequency are in part due to the structure of public forest management over the past 100 years. Results from this study confirm that impacts of MPB in newly invaded habitats are a consequence of a lack of co-evolutionary history among beetles and trees. In areas with new or no current MPB attack,

especially in areas within the expanding range, there is relatively high uncertainty of how the MPB may spread. Based on recent and past literature some strong predictions of MPB spread and impact can be made, although the challenge may lie in communicating these management strategies to relevant decision makers.

4.4 Recommendation for effective direct and indirect control in novel habitats:

Extensive review of direct and indirect control tactics in the native range has been published in (Safranyik and Wilson 2006) providing managers with valuable insight into the control of MPB populations. However, recently the attention of forest managers has shifted, given the current context of beetle invasion into naive environments following breach of the Rocky Mountains. Much attention has been placed on long and short term planning for managing and mitigating the MPB infestation in Alberta, a province where a transition in an easterly direction from lodgepole pine to lodgepole x jack pine hybrids to jack pine is observed. In 2007 Alberta Sustainable Resource Development (ASRD) developed both a MPB Action Plan (ASRD 2007a) and Management Strategy (ASRD 2007b). The management strategy defines two prime provincial objectives: 1. To contain infestations and minimize spread of MPB north and south along the eastern slopes of Alberta, 2. To prevent the spread of MPB eastward into the boreal forest of lodgepole x jack pine hybrid and jack pine. Concurrently the action plan details actions for managing and mitigating infestations, research requirements and implementation issues in the context of mass movement of beetles into Alberta.

Mathey and Nelson, (2010) suggest the success of any management strategy is linked to the timing of the attack and how it affects the growing stock, subsequently impacting timber and

revenue flows. Although from an ecological point of view management should aim to minimize impacts of epidemic populations on ecosystem function, achieved through treatments aimed at limiting the amount of susceptible trees or reducing the numbers of beetles. It has been suggested for effective control of beetles the two approaches (direct control and preventive management) should be used in combination when implementing a landscape-level management plan.

Preventive management can be considered a proactive approach as it is primarily executed prior to outbreak development, aiming to reduce the susceptibility of stands on the landscape using various forestry practices. Conversely direct control tends to be a reactive approach aimed at reducing beetle populations by various means following observation of tree mortality.

Based on the principles set out in the 2007 management strategy, ASRD has split MPB management into three priority zones (Leading-edge zone, Holding zone, Salvage Zone) aiming to encompass all levels of MPB infestations and determine levels of management and control. For example the leading edge zone presents the greatest risk to future spread and thus receives the bulk of attention. While ASRD current objectives are based on timely detection of beetles, effective and expedient responses to infestation and useful communications and liaison between stakeholders, both short term and long term goals must be taken in to account. Assessments of susceptibility, a precursor to preventative management are typically derived from conventional forest inventory data; however, this information often represents only managed forest areas and may not cover areas such as forest parks or conservation regions which can cause some problems (Coggins et al. 2013). Whilst not a focus of this study, I did quantify managed and unmanaged pine volume and area across the extent of the Canadian boreal in my analysis developed from (Yemshanov et al. 2011). Considering the factor of managed and unmanaged, results indicate the

majority of the total pine volume in any given 100 km zone is found in forest under some form of tenure (considered managed forest).

McFarlane et al. (2012) suggests understanding perceptions of risks, awareness, and trust in management agencies is critical to effective management of large-scale forest insect disturbance. Thus it may be more effective for researchers and forest manager to formulate management plans and scenarios of MPB range expansion when the generalized forest stand characteristics are known. For example in western Alberta pine volumes are high, associated with a small area (high density) the majority of which is considered managed forest. Projections of MPB range expansion through this area may be more easily forecasted using mechanistic models compared to unmanaged areas of the boreal jack pine forest where forest stand characteristics are associated with a high level of uncertainty. Models may require notable interpolation of data sources contributing to error margins and predictive power.

Prior to the unprecedented MPB outbreak experienced over the past decade the landscape in western Canada included an abundance of largely undeveloped older lodgepole pine stands, that matured without active silviculture influence. This landscape proved to be highly susceptible to development of landscape scale outbreaks of MPB (Taylor and Carroll 2004, Taylor et al. 2006). Major landscape level disturbances including forest management and extensive fire suppression have similar effects on ecosystem functioning in the novel range. Fire and forest management have been recognized as a major driver of age class distribution giving an indication of forest structural complexity, stand volume and habitat potential (Weir et al. 2000, Fall et al. 2004) a

surrogate for landscape level susceptibility to MPB (Shore and Safranyik 1992, Li et al. 2005, Barclay et al. 2009).

Should the invasion of MPB continue in novel habitats it may be pertinent to further explore the ecological, economic and social impacts on a broader scale. Ayres and Lombardero, (2000) suggest it is probable that climatic effects on some herbivores and pathogens will have an impact on biodiversity, recreation, property value, forest industry and water quality. Adverse impacts of MPB outbreaks to the timber and recreation industries are well documented. Projections for the current epidemic include a \$2.5 billion decrease in manufacturing activity, a loss of 27,000 direct jobs and a loss of \$250 million in government stumpage and royalty revenues in British Columbia alone (Sims et al. 2010). The boreal forest was considered to be on the edge of what is economically operable by (Safranyik et al. 2010), hence it may be assumed that loss of these forest due to invasion by MPB may be of less economic importance to forest managers. Regardless of inherent ecological, economic and social values effective management should aim to minimize any potential damage caused by MPB.

4.5 Future research

Although this is only the early stage in the projected trends of global warming, ecological responses to recent climate change are already clearly visible (Price et al. 2013). The past and current impacts of herbivorous insect eruptions as a result of a warming climate are well documented and expectations are that continued climate warming will be likely to lead to further expansion of the range of MPB, further north, east and to higher elevations (Logan and Powell 2001, Carroll et al. 2004, Safranyik et al. 2010). Understanding the influence of various factors

driving MPB spread into novel environments is multifaceted, even when the immediate causes of this destructive phenomenon are clear there is often a deeper and more far reaching driving mechanism behind population dynamics and ultimately spread. Undeniably the arrival of MPB into north eastern Alberta creates significant concern as potential for this destructive species to spread further east has been demonstrated (Nealis and Peter 2008, Safranyik et al. 2010, Cullingham et al. 2011), although uncertainty exist in the magnitude of spread and impact in this novel system. In order to fully assess the risk to novel forests of Canada we need to take into account a range of unknowns.

To date we do not know how exactly MPB will reproduce in jack pine, granted there is confirmation that MPB can successfully reproduce in jack pine (Cullingham et al. 2011), however the level of production (brood per female) is largely unknown. This may be a function of host susceptibility, or simply the fact that jack pine are generally smaller than lodgepole pine may result in there being thinner bark and therefore proportionately less trees available for MPB colonization. The influence of elevated α -pinine levels on MPB dynamics in jack pine compared to lodgepole pine is another major question. Furthermore what is the likelihood that these naive trees are more at risk to mass attack by MPB due to a higher production of karimones which may catalyze MPB aggregation (Clark et al. 2010, 2012a).

Increases in the variability of climate produce both favorable and unfavorable conditions for MPB outbreak (Bentz et al. 2010, Safranyik et al. 2010), and how this effect population dynamics and ultimately spread into the novel environments is unknown. The lack of contiguous forest stands may effect spread and impacts of MPB (Safranyik et al. 2010). Additionally long

range dispersal events, where MPB can travel vast distances in wind currents may promote long distance spread (Jackson et al. 2008). It has been shown that the boreal forest has a different forest structure which may influence dispersal (Safranyik et al. 2010). This may influence short distance dispersal as flight under the canopy from tree to tree may be forced over larger distances due to low pine volumes. In order for beetle infestations to spread through the forests at endemic or incipient beetle population levels, patches of susceptible forest must exist, and these patches must be close enough together that beetles can disperse from one to another (Barclay et al. 2009). Additionally to date endemic behavior has not been observed in the boreal forest. This is a major topic of interest and should attract significant research efforts given the beetle may persist in the endemic state for several years until favorable conditions promote transition to incipient and epidemic population states.

Several authors have predicted range expansion into the boreal forest, while the mechanistic relationships between MPB and climate are well known and may predict climate suitability in the boreal with a high level of accuracy, we can only make limited predictions of spread and impact until such time as beetle host interactions are more rigorously explained. Accurate assessment of the threat of MPB spread and impact in the boreal requires an integrated approach that draws on the entirety of knowledge sources. Many of the predictions for MPB range expansion into the boreal have been based almost entirely on lodgepole pine systems which has given rise to considerable uncertainty of the accuracy of predictions as beetle host dynamics in the boreal are investigated. However understanding differences in population behavior as a consequence of range expansion, and formulation of projections of spread into currently unaffected pine forests

in the boreal is crucial to strategic landscape planning intent on minimizing additional impacts to naive ecosystems.

If left unabated the invasion of MPB into the boreal system may lead to impoverishment and degradation of ecosystem services and economical and social values of the systems. Uncertainty exists with reference to MPB spread into the novel as risk or susceptibility systems are yet to be tested on boreal forests because of the simple fact that MPB has only recently arrived. Hence understanding those factors that drive this dynamic in the boreal system is a first step in integrating implications for social, economic and ecological systems. Improving the system of understanding of MPB spread and impacts into naive environments will aid in estimating resilience to perturbations, help predict likely responses to changing climate, and aid in design of mitigation strategies. Hence priority should be given to the development of predictive tools supporting strategic landscape planning intent on minimizing additional impacts to naive ecosystems into the future. Notably a better understanding of the processes that determine spatial patterning in host availability throughout the boreal is needed in order to properly assess both the impacts of shorter duration and longer term MPB infestation events and trends throughout this expansive system.

Despite continued uncertainty as to community and ecosystem trajectories under global change, this thesis exposes a coherent pattern of ecological change across a broad system at two distinct spatial scales. Based upon the lessons learned and communicated in this thesis, implementation of the elements of the proposed future research will provide further understanding of how herbivorous insects operate in environments where hosts may be lacking in defensive capability.

Bibliography

- Amman, G.. 1982. The mountain pine beetle - identification, biology, causes of outbreaks, and entomological research needs. *Edited by* D.M. Shrimpton (editor). Fairmont Hot Springs, British Columbia. Environment Canada, Canadian Forestry Service. pp. pp. 7–12.
- Andrewartha, H.G., and Birch, L.C. 1954. *Distribution and Abundance of Animals*. University of Chicago Press; 1st Edition edition (December 1954).
- ASRD. 2007a. Mountain Pine Beetle Action Plan, Alberta Sustainable Resource Development. Alberta Sustainable Resource Development. Available from http://www.mpb.alberta.ca/AlbertasStrategy/documents/MPB_action_plan.pdf.
- ASRD. 2007b. Mountain Pine Beetle Management Strategy, Alberta Sustainable Resource Development. Alberta Sustainable Resource Development. Available from http://www.mpb.alberta.ca/AlbertasStrategy/documents/MPB_man_strategy.pdf.
- Aukema, B., Carroll, A., Zheng, Y., Zhu, J., Raffa, K., Moore, D., Stahl, K., and Taylor, S. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography (Cop.)*. **31**: 348–358. doi: 10.1111/j.2007.0906-7590.05453.x.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., and Taylor, S.W. 2006. Landscape level analysis of mountain pine beetle in British Columbia , Canada : spatiotemporal development and spatial synchrony within the present outbreak. *Ecography (Cop.)*. **3**.
- Awmack, C.S., and Leather, S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Ecol. Evol. Syst.* **47**: 817– 844.
- Ayres, M.P., and Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* **262**: 263–286.
- Bale, J.S., Masters, G.J., Hodkinson, I., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., and Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Chang. Biol.* **8**: 1–16.
- Barclay, H.J., Schivatcheva, T., Li, C., and Benson, L. 2009. Effects of fire return rates on traversability of lodgepole pine forests for sustainable forest management. *J. Ecosyst. Manag.* **10**: 115–122.

- Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., and Larsson, S. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* **15**: 2084–2096.
- Bentz, B.J., Bracewell, R.R., Mock, K.E., and Pfrender, M.E. 2011. Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae*. *Evol Ecol* **25**: 1269–1288. doi: 10.1007/s10682-011-9474-x.
- Bentz, B.J., Logan, J.A., and Amman, G.D. 1991. Temperature dependent development of the mountain pine beetle (Coleoptera:Scolytidae) and simulation of its phenology.
- Bentz, B.J., and Mullins, D.E. 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the intermountain west. *Environ. Entomol.* **28**: 577–587.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J. a., Kelsey, R.G., Negrón, J.F., and Seybold, S.J. 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. *Bioscience* **60**: 602–613. doi: 10.1525/bio.2010.60.8.6.
- Berryman, A.A., Stenseth, N.C., and Isaev, A.S. 1987. Natural regulation of herbivorous forest insect populations. *Oecologia* **71**: 174–184. doi: 10.1007/BF00377282.
- Beyer, H.L. 2001. Geospatial Modelling Environment. Spatial Ecology LLC. Available from <http://www.spatial ecology.com/gme/>.
- Boone, C.K., Aukema, B.H., Bohlmann, J., Carroll, A.L., and Raffa, K.F. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Can. J. For. Res.* **41**: 1174–1188. doi: 10.1139/X11-041.
- Borden, J., Ryker, L., and Chong, L. 1987. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. *Can. J. For. Res.* **17**: 1987.
- Braschler, B., and Hill, J.K. 2007. Role of larval host plants in the climate-driven range expansion of the butterfly *Polygona c-album*. *J. Anim. Ecol.* **76**: 415–23. doi: 10.1111/j.1365-2656.2007.01217.x.
- Brunton, G.F., and Wheldon, T.E. 1980. The Gompertz equation and the construction of tumour growth curves. *Cell Tissue Kinet.* **13**: 455–460.
- Carroll, A.L., Shore, T.L., and Safranyik, L. 2006. Chapter 6, Direct Control: Theory and Practice. *In* The Mountain Pine Beetle - A synthesis of Biology, Management and Impacts of Lodgepole Pine: pp. 155–172.

- Carroll, A.L., Taylor, S.W., Régnière, J., and Safranyik, L. 2004. Effects of Climate Change on Range Expansion by the Mountain Pine Beetle in British Columbia. *In* Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium. Kelowna, British Columbia, Canada October 30 - 31, 2003. *Edited by* and J.E.S. T.L. Shore, J.E. Brooks. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 p. 223. pp. 223–232.
- Cerezke, H.. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts. *Can. Entomol.* **127**: 995–965.
- Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B., and Thomas, C.D. 2011. Rapid range shifts of species of climate warming. *Science* (80-.). **333**: 1024–1026. doi: 10.1126/science.1206432.
- Christiansen, E., Waring, R.H., and Berryman, A.A. 1987. Resistance of Conifers to Bark Beetle Attack : Searching for General Relationships. *For. Ecol. Manage.* **22**: 89–106.
- Clark, E.L., Carroll, A.L., and Huber, D.P.W. 2010. Differences in the constitutive terpene profile of lodgepole pine across a geographical range in British Columbia, and correlation with historical attack by mountain pine beetle. *Can. Entomol.* **142**: 557–573. doi: 10.4039/n10-022.
- Clark, E.L., Huber, D.P.W., and Carroll, A.L. 2012a. The Legacy of Attack : Implications of High Phloem Resin Monoterpene Levels in Lodgepole Pines Following Mass Attack by Mountain Pine Beetle , *Dendroctonus ponderosae* Hopkins. *Env. Monit Assess* **41**: 392–396.
- Clark, E.L., Pitt, C., Carroll, A.L., Lindgren, B.S., and Huber, D.P.W. 2012b. Comparison of constitutive and induced resin chemistry between lodgepole and jack pine stands in British Columbia and Alberta: Potential role in mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae), range expansion.
- Clark, E.L., Pitt, C., Carroll, A.L., Staffan-Lindgren, B., and Huber, D.P.W. 2014. Comparison of lodgepole and jack pine resin chemistry : implications for range expansion by the mountain pine beetle , *Dendroctonus ponderosae* (Coleoptera : Curculionidae). *PeerJ* **240**: 1–18. doi: 10.7717/peerj.240.
- Coggins, S., Wulder, M.A., Coops, N.C., and White, J.C. 2008. Linking survey detection accuracy with ability to mitigate populations of mountain pine beetle. Victoria, BC Canada.
- Coggins, S.B., Coops, N.C., Hilker, T., and Wulder, M. a. 2013. Augmenting forest inventory attributes with geometric optical modelling in support of regional susceptibility assessments to bark beetle infestations. *Int. J. Appl. Earth Obs. Geoinf.* **21**: 444–452. Elsevier B.V. doi: 10.1016/j.jag.2012.06.007.

- Collins, B.J., Rhoades, C.C., Battaglia, M. a., and Hubbard, R.M. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *For. Ecol. Manage.* **284**: 260–268. Elsevier B.V. doi: 10.1016/j.foreco.2012.07.027.
- Cooke, B.J., and Carroll, A.L. (n.d.). The risk of mountain pine beetle spread to eastern pine forests : what can we predict ? : 1–41.
- Coops, N.C., Wulder, M. a., and Waring, R.H. 2012. Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest. *For. Ecol. Manage.* **274**: 161–171. Elsevier B.V. doi: 10.1016/j.foreco.2012.02.011.
- Coops, N.C., Wulder, M.A., and White, J.C. 2006. Integrating remotely sensed and ancillary data sources to characterize a mountain pine beetle infestation. *In Mountain Pine Beetle Initiative Working Paper 2006-07*. Victoria, BC Canada.
- Cudmore, T.J., Björklund, N., Carroll, A.L., and Staffan Lindgren, B. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. *J. Appl. Ecol.* **47**: 1036–1043. doi: 10.1111/j.1365-2664.2010.01848.x.
- Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J., and Coltman, D.W. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Mol. Ecol.* **20**: 2157–71. doi: 10.1111/j.1365-294X.2011.05086.x.
- Currano, E.D., Wilf, P., Wing, S.L., Labandeira, C.C., Lovelock, E.C., and Royer, D.L. 2008. Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc. Natl. Acad. Sci. U. S. A.* **105**: 1960–4. doi: 10.1073/pnas.0708646105.
- Cwynar, L.C., and MacDonald, G.M. 1987. Geographical Variation of Lodgepole Pine In Relation to Population History. *Am. Nat.* **129**: 463–469.
- Dennis, R.L.. 1993. *Butterflies and Climate Change*. Manchester University Press, Manchester.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., and Martin, P.R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude Thermal Safety margin. *PNAS* **105**: 6668–6672.
- Dymond, C.C., Neilson, E.T., Stinson, G., Porter, K., MacLean, D.A., Gray, D.R., Campagna, M., and Kurz, W.A. 2010. Future spruce budworm outbreak may create a carbon source in eastern Canadian forests. *Ecosystems* **13**: 917–931. doi: 10.1007/s10021-010-9364-z.
- Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D., and Meddens, A.J. 2012. Cascading impacts of bark beetle-caused tree

- mortality on coupled biogeophysical and biogeochemical processes. *Front. Ecol. Environ.* **10**: 416–424. doi: 10.1890/110173.
- Ehrlich, P.R., and Raven, P.H. 1964. Butterflies and plants: A study in coevolution. *Evolution* (N. Y.) **18**: 586–608.
- Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najjar, A., and Evenden, M. 2013. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naive host ecosystem. *New Phytol.* **201**: 940–950.
- Everitt, B.S., and Hothorn, T. 2002. Chapter 9 Survival Analysis : Glioma Treatment and Breast Cancer Survival. *In A Handbook of Statistical Analyses Using R — 2nd Edition.* pp. 143–158.
- Fall, A., Fortin, M.-J., Kneeshaw, D.D., Yamasaki, S.H., Messier, C., Bouthillier, L., and Smyth, C. 2004. Consequences of various landscape-scale ecosystem management strategies and fire cycles on age-class structure and harvest in boreal forests. *Can. J. For. Res.* **34**: 310–322. doi: 10.1139/X03-143.
- Farrar, J.L. 1995. *Trees in Canada.* Natural Resources Canada, Canadian Forest Service, Ottawa, Ontario, Canada. Copublished by Fitzhenry and Whiteside Limited, Markham, Ontario, Canada.
- Ford, E.. 1945. *The New Naturalist: Butterflies.* Collins, London.
- Franceschi, V.R., Krokene, P., Christiansen, E., and Krekling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* **167**: 353–376. doi: 10.1111/j.1469-8137.2005.01436.x.
- Furniss, M.M., and Schenk, J.A. 1969. Sustained Natural Infestation by the Mountain Pine Beetle in Seven New Pinus and Picea Hosts. *J. Econ. Entomol.* **62**: 518–519.
- Gandhi, K.J.K., and Herms, D.A. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions* **12**: 389–405. doi: 10.1007/s10530-009-9627-9.
- Gillanders, S.N., Coops, N.C., Wulder, M. a., Gergel, S.E., and Nelson, T. 2008. Multitemporal remote sensing of landscape dynamics and pattern change: describing natural and anthropogenic trends. *Prog. Phys. Geogr.* **32**: 503–528. doi: 10.1177/0309133308098363.
- Gompertz, B. 1825. On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philos. Trans. R. Soc. London* **115**: 513–583.

- Goodwin, N.R., Coops, N.C., Wulder, M.A., Gillanders, S., Schroeder, T.A., and Nelson, T. 2008. Estimation of insect infestation dynamics using a temporal sequence of Landsat data. *Remote Sens. Environ.* **112**: 3680–3689. doi: 10.1016/j.rse.2008.05.005.
- Grinnell, J. 1917. The Niche-Relationships of the California Thrasher. *Auk* **34**: 427–433. University of California Press on behalf of the American Ornithologists' Union. Available from <http://www.jstor.org/stable/4072271>.
- Hermes, D.A., and Mattson, W.J. 1992. The Dilemma of Plants: To Grow or Defend. *Q. Rev. Biol.* **67**: 283–335.
- Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Ted Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., and Vogelmann, J. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Glob. Chang. Biol.* **18**: 7–34. doi: 10.1111/j.1365-2486.2011.02543.x.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R., and Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Chang. Biol.* **12**: 450–455. doi: 10.1111/j.1365-2486.2006.01116.x.
- Hickling, R., Roy, D.B., Hill, J.K., and Thomas, C.D. 2005. A northward shift of range margins in British Odonata. *Glob. Chang. Biol.* **11**: 502–506.
- Hitch, A.T., and Leberg, P.L. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conserv. Biol.* doi: 10.1111/j.1523-1739.2006.00609.x.
- Hunt, D.W.A., Borden, J.H., Lindgren, B.S., and Gries, G. 1989. The role of autoxidation of α -pinene in the production of pheromones of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. J. For. Res.* **19**: 1275–1282.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by B.V. and M.P.M. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.
- Jackson, P.L., Straussfogel, D., Lindgren, B.S., Mitchell, S., and Murphy, B. 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Can. J. For. Res.* **38**: 2313–2327. doi: 10.1139/X08-066.
- Karban, R., and Baldwin, I.T. 1997. Induced responses to herbivory. *In* Induced responses to herbivory. Available from <Go to ISI>://BIOSIS:PREV199800102710.

- Klein, J.P., and Moeschberger, M.L. 2003. Survival Analysis: Techniques for Censored and Truncated Data. *In* Springer, Second Edi. *Edited by* K. Dietz, M. Gail, K. Krickeberg, J. Samet, and A. Tsiatis. Springer, New York.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**: 987–90. doi: 10.1038/nature06777.
- De la Giroday, H.-M.C., Carroll, A.L., and Aukema, B.H. 2012. Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. *J. Biogeogr.* **39**: 1112–1123. doi: 10.1111/j.1365-2699.2011.02673.x.
- De la Giroday, H.-M.C., Carroll, A.L., Lindgren, B.S., and Aukema, B.H. 2011. Incoming! Association of landscape features with dispersing mountain pine beetle populations during a range expansion event in western Canada. *Landsc. Ecol.* **26**: 1097–1110. doi: 10.1007/s10980-011-9628-9.
- Li, C., Barclay, H.J., Hawkes, B.C., and Taylor, S.W. 2005. Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle attack. *Ecol. Complex.* **2**: 232–239. doi: 10.1016/j.ecocom.2005.03.001.
- Logan, J.A., and Powell, J.A. 2001. Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera:Scolytidae). *Am. Entomol.* **47**: 160–172.
- MacDonald, G.M., and Cwynar, L.C. 1985. A Fossil Pollen Based Reconstruction of the Late Quaternary History of Lodgepole Pine (*Pinus contorta* ssp *latifolia*) in the Western Interior of Canada. *Can. J. For. Res.* **15**: 1039–1044.
- McFarlane, B.L., Parkins, J.R., and Watson, D.O.T. 2012. Risk , knowledge , and trust in managing forest insect disturbance. *Can. J. For. Res.* **42**: 710–719. doi: 10.1139/X2012-030.
- Meddens, A.J.H.M., Hicke, J.A.H., and Ferguson, C.A.F. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol. Appl.* **22**: 1876–1891.
- Menéndez, R., González-Megías, A., Lewis, O.T., Shaw, M.R., and Thomas, C.D. 2008. Escape from natural enemies during climate-driven range expansion: a case study. *Ecol. Entomol.* **33**: 413–421. doi: 10.1111/j.1365-2311.2008.00985.x.
- Mock, K., Bentz, B., O’neill, E., Chong, J., Orwin, J., and Pfrender, M.. 2007. Landscape-scale genetic variation in a forest outbreak species , the mountain pine beetle (*Dendroctonus ponderosae*). *Mol. Ecol.* **16**: 553–568.
- Morgan, J.L., Gergel, S.E., and Coops, N.C. 2010. Aerial Photography: A Rapidly Evolving Tool for Ecological Management. *Bioscience* **60**: 47–59. doi: 10.1525/bio.2010.60.1.9.

- Musolin, D.L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Glob. Chang. Biol.* **13**: 1565–1585. Blackwell Publishing Ltd. doi: 10.1111/j.1365-2486.2007.01395.x.
- Nealis, V.G., and Cooke, B.J. 2014. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests.
- Nealis, V.G., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests Compiled by Vince Nealis. Victoria, British Columbia.
- Nelson, T.A., Boots, B., Wulder, M.A., and Carroll, A.L. 2007. Environmental characteristics of mountain pine beetle infestation hot spots. *BC J. of Ecosystems Manag.* **8**: 91–108.
- Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583. Available from <http://dx.doi.org/10.1038/21181>.
- Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42. doi: 10.1038/nature01286.
- Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R. a, Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., Mckenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J. a, and Venier, L. a. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems 1. *Environ. Rev.* **21**: 322–365.
- Price, P.W. 2000. Host Plant Resource Quality, Insect Herbivores and Biocontrol. *In* Proceedings of the X International Symposium on Biological Control of Weeds. pp. 583–590.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *Bioscience* **58**: 501–517.
- Raffa, K.F., Powell, E.N., and Townsend, P.A. 2012. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proc. Natl. Acad. Sci.* **110**: 2193–2198. doi: 10.1073/pnas.1216666110.
- Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* **48**: 978–983. doi: 10.2307/1934545.

- Riffenburgh, R.H., and Johnstone, P.A.S. 2001. Survival patterns of cancer patients. *Cancer* **91**: 2469–2475. doi: 10.1002/1097-0142(20010615)91:12<2469::AID-CNCR1282>3.0.CO;2-U.
- Robertson, C., Nelson, T.A., Jelinski, D.E., Wulder, M.A., and Boots, B. 2009. Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. *J. Biogeogr.* **36**: 1446–1458. doi: 10.1111/j.1365-2699.2009.02100.x.
- Roe, A.D., James, P.M.A., Rice, A. V, Cooke, J.E.K., and Sperling, F.A.H. 2011. Spatial community structure of mountain pine beetle fungal symbionts across a latitudinal gradient. *Microb. Ecol.* **62**: 347–60. doi: 10.1007/s00248-011-9841-8.
- Royama, T. 1992. Analytical population dynamics. *Edited by* M.B. Usher. Chapman and Hall, New York.
- Safranyik, L. 2004. Mountain Pine Beetle Epidemiology in Lodgepole Pine. *In* Mountain Pine Beetle Symposium: Challenges and Solutions, 30–31 October 2003. Kelowna, British Columbia, Canada. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Information Report BCX-399. pp. 33–40.
- Safranyik, L., and Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In* The Mountain Pine Beetle – A Synthesis of Biology, Management, and Impacts in Lodgepole Pine. pp. 3–66. doi: 10.1673/031.011.12701.
- Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Peter, B., Cooke, B.J., Nealis, V.G., and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *Can. Entomol.* **142**: 415–442. doi: 10.4039/n08-CPA01.
- Safranyik, L., and Linton, D.A. 1982. Survival and development of mountain pine beetle broods in jack pine bolts from Ontario. *Can. For. Serv. Res. Notes* **2**: 17–18.
- Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1974. Management of Lodgepole Pine to Reduce Losses From The Mountain Pine Beetle. Government of Canada, Department of the Environment, Canadian Forest Service Forestry Technical Report 1. (pp.) Victoria, BC: Pacific Forest Research Centre.
- Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle, and its associated blue stain fungi in western Canada. *In* Management of Lodgepole Pine Ecosystems. *Edited by* E.M. Baumgartener. Washington State University Cooperative Extension Service, Pullman WA. pp. 406–428.
- Safranyik, L., and Wilson, B. (*Editors*). 2006. The Mountain Pine Beetle. A Synthesis of Biology, Management, and Impacts on Lodgepole Pine. *In* The mountain pine beetle : a

synthesis of biology, management, and impacts on lodgepole pine / by Les Safranyik and Bill Wilson. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC Canada.

Schoennagel, T., Veblen, T.T., Negron, J.F., and Smith, J.M. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. *PLoS One* **7**: e30002. doi: 10.1371/journal.pone.0030002.

Shore, T.L., Riel, W.G., and Fall, A. 2010. Geographic Spread of the Mountain Pine Beetle. *In* Victoria.

Shore, T.L., and Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Pacific and Yukon Region Information report, Pacific Forestry Centre, Victoria, BC, Canada.

Shrimpton, D., and Thomson, A.J. 1985. Relationship between phloem thickness and lodgepole pine growth characteristics. *Can. J. For. Res.* **15**: 1004–1008.

Sims, C., Aadland, D., and Finnoff, D. 2010. A dynamic bioeconomic analysis of mountain pine beetle epidemics. *J. Econ. Dyn. Control* **34**: 2407–2419. Elsevier. doi: 10.1016/j.jedc.2010.06.010.

Solheim, H., and Krokene, P. 1998. Growth and virulence of mountain pine beetle associated blue-stain fungi, *Ophiostoma clavigerum* and *Ophiostoma montium*. *Can. J. Bot.* **76**: 561–566.

Taft, S., Najar, A., Godbout, J., Bousquet, J., and Erbilgin, N. 2015. Variations in foliar monoterpenes across the range of jack pine reveal three widespread chemotypes: implications to host expansion of invasive mountain pine beetle. *Front. Plant Sci.* **6**. doi: 10.3389/fpls.2015.00342.

Taylor, S.W., and Carroll, A.L. 2004. Disturbance, Forest Age, and Mountain Pine Beetle Outbreak Dynamics in BC: A Historical Perspective. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. pp. 41–51.

Taylor, S.W., Carroll, A.L., Alfaro, R.I., and Safranyik, L. 2006. Forest, Climate and Mountain Pine Beetle Outbreak Dynamics in Western Canada. *Mt. Pine Beetle – A Synth. Biol. Manag. Impacts Lodg. Pine*: 67–94.

USDA Forest Service. 2013. Major forest insect and disease conditions in the United States: 2012. Forest Health Protection, Washington, D.C., USA. Washington, D.C., USA.

Uvarov, B.. 1931. Insects and climate. *R. Entomol. Soc. London* **79**: 174–86.

- Wallin, K.F., and Raffa, K.F. 1999. Altered constitutive and inducible phloem monoterpenes following natural defoliation of jack pine : Implications to host mediated interguild interactions and plant defense theories. *J. Chem. Ecol.* **25**: 861–880. Springer. Available from <http://cat.inist.fr/?aModele=afficheN&cpsidt=1836433>.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395. doi: 10.1038/416389a.
- Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in Western Canada. *Ecol. Appl.* **10**: 1162–1177.
- Westfall, J., and Ebata, T. 2013. 2013 Summary of forest health conditions in British Columbia. Victoria, BC, Canada.
- Westfall, J., and Ebata, T. 2014. 2014 Summary of Forest Health conditions in British Columbia. Victoria, BC Canada.
- Weymouth, F.W., and McMillin, H.C. 1931. The relative growth and mortality of the pacific razor clam (*Siliqua patula*, Dixon), and their bearing on the commercial fishery. *Bull. U.S. Bur. Fish.* **46**: 543–567.
- White, J., Wulder, M., Brooks, D., Reich, R., and Wheate, R. 2005. Detection of red attack stage mountain pine beetle infestation with high spatial resolution satellite imagery. *Remote Sens. Environ.* **96**: 340–351. doi: 10.1016/j.rse.2005.03.007.
- Whitham, T.G., and Mopper, S. 1985. Chronic Herbivory: Impacts on Architecture and Sex Expression of Pinyon Pine. *Science* **228**: 1089–1091.
- Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., and Monserrat, V.J. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**: 1138–1146. doi: 10.1111/j.1461-0248.2005.00824.x.
- Winsor, C.P. 1932. The Gompertz Curve as a Growth Curve. *Proc. Natl. Acad. Sci. U. S. A.* **18**: 1–8. doi: 10.1073/pnas.18.1.1.
- Wulder, M.A., and Nelson, T.A. 2003. EOSD Land Cover Classification Legend Report Version 2. Victoria BC. Available from <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:EOSD+Land+Cover+Classification+Legend+Report+Version+2#0>.
- Yemshanov, D., Mckenney, D.W., and Pedlar, J.H. 2011. Mapping forest composition from the Canadian National Forest Inventory and land cover classification maps. *Env. Monit Assess.* doi: 10.1007/s10661-011-2293-2.

Ylloja, T., Roininen, H., Ayres, M.P., Rousi, M., and Price, P.W. 1999. Host-driven population dynamics in an herbivorous insect. *Proc. Natl. Acad. Sci.* **96**: 10735–10740.

Appendices

Appendix A

4.1.2 Sensitivity analysis

In using the area weighted mean function in GME I found that processing times were extremely slow when using the polygon based approach, thus I converted polygon infestation and VRI data to 100m raster data. I choose the conversion to 100m in an effort to retain the detail of the information contained in the data sets, although allowing a much faster processing time in GME. Using the “insectpolyrast” command in GME I calculated for each raster in a 'zonal' polygon dataset (in this case the 1km grid cell layer) that defines the area over which a summary is to be made. I provide a comparison of the “insectpolyrast” (Raster) command over the “insectpolypoly” (Polygon) in Figure 14. In this case the tool summarizes the categorical severity raster (Trace to Very Severe, ranging from midpoint of 1 to 75, Table 1) computing the results to the attribute table of the zonal polygon dataset. The accuracy of predictions using the Polygon and Raster commands showed no difference, with an R^2 value of 0.9997, indication of no bias towards one method or the other, allowing for shorter processing times using the raster command.

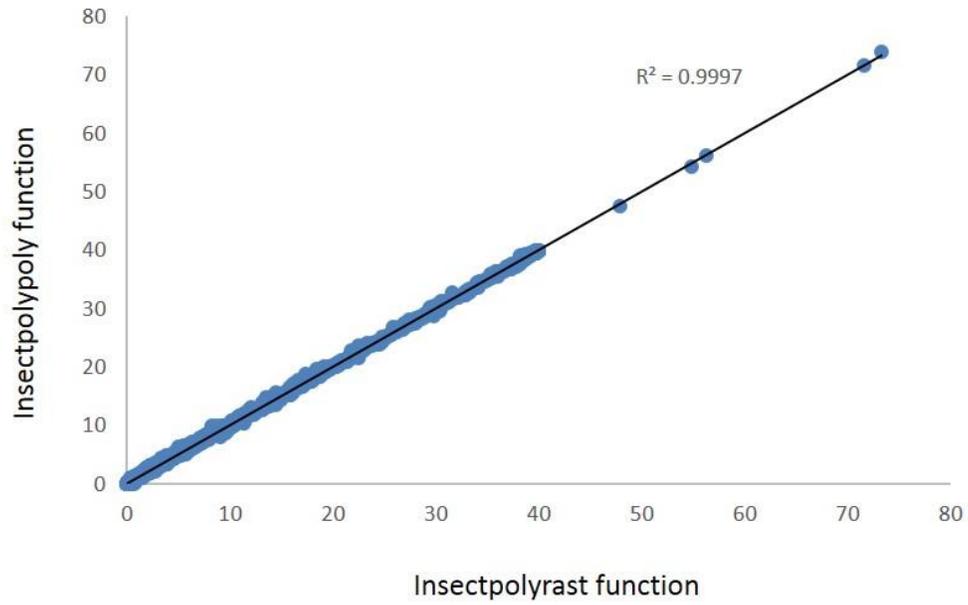


Figure 14. Comparison of the “insectpolyrast” (Raster) command over the “insectpolypoly” (Polygon). In this case the tool summarizes the categorical severity raster (Trace to Very Severe, ranging from midpoint of 1 to 75). R2 value of 0.9997, indicates no bias towards one method or the other.