4-2019

Habitat Suitability of the Mountain Pine Beetle in Alberta, Canada under Future Climate Scenarios

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HABITAT SUITABILIY OF THE MOUNTAIN PINE BEETLE IN ALBERTA, CANADA UNDER FUTURE CLIMATE SCENARIOS

by

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A thesis submitted to the Graduate College in
partial fulfilment of the requirements
for the degree of Master of Science
Geography
Western Michigan University
April 2019

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ACKNOWLEDGEMENTS

My first wave of gratitude is due to my family, particularly my mother – who surrounded us with the pursuit of education and whose exhausted naps on her textbooks after dinner instilled a determined nature in each of us. To Tyler Corbin, my partner, without whom this adventure may have never begun! Thank you for your constant support, encouragement and timely reminders that this is for our family and our future.

I would also like to express my most sincere gratitude to my committee chair, Dr. Gregory Veeck. From the day I received a response to my initial letter of inquiry about the program until the day I submitted my completed thesis, Dr. Veeck presented a consistent enthusiasm and inspiring dedication to learning. Thank you for the countless impromptu discussions, for your wise words of counsel, and for tirelessly correcting my pronouns. I would like to thank my committee members, Dr. Kathleen Baker, Dr. Lisa DeChano-Cook and Dr. Laiyin Zhu, for their helpful advice and encouragement throughout this research. Finally, thank you to the Department of Geography of Western Michigan University, for their support during my studies.

I would like to acknowledge the Alberta Department of Agriculture and Forestry for initiating this research with the gracious sharing of data. Finally, I would also like to thank the staff of the Waldo Library, for their reliable assistance during my research.

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Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the most destructive insect currently devastating North American forests (Safranyik & Carroll, 2006). Native to western North America, the mountain pine beetle has recently expanded beyond its historic range, into the novel territory of Alberta, Canada. Since its arrival in the mid-2000s, the mountain pine beetle has diffused eastward at an average rate of 80km/year (Cooke & Carroll, 2017). Poised at the doorstep of the boreal forest, current concern anticipates the potential diffusion of the mountain pine beetle to eastern North America.

The Maxent (maximum entropy) model, a presence-only spatial distribution model, is used to assess changes to future habitat suitability for the mountain pine beetle under future climate scenarios. Both a moderate (RCP 4.5) and extreme (RCP 8.5) emissions scenario are considered for the years 2050 and 2070. Through the application of the Maxent model, this research finds that a changing climate will dramatically decrease mountain pine beetle habitat suitability in Alberta, Canada, regardless of the emissions scenario under consideration. By examining the historical spatial distribution of mountain pine beetle infestation, this research identifies key environmental variables that might be used to predict the future diffusion patterns associated with the mountain pine beetle.

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ABM – Agent-based Model

ASCII – American Standard Code for Information Interchange

AUC – Area Under the Receiver Operating Characteristic (ROC) Curve

BRT – Boosted Regression Tree

CA – Cellular Automata

CMD – Climate Moisture Deficit

CSV – Comma Separated Value

DBH – Diameter at Breast Height

DEM – Digital Elevation Model

FFP – Frost Free Period

FHSD – Forest Health Spatial Data

FIDS – Forest Insect and Disease Survey

GIS – Geographic Information Systems

GCM – General Circulation Model

GLM – General Linear Model

GPS – Global Positioning System

LULC – Land Use and Land Cover

Maxent – Maximum Entropy Model

MPB – Mountain Pine Beetle

PAS – Precipitation as Snow

RCP- Representative Concentration Pathway

ROC – Receiver Operating Characteristic

SAHM – Software for Assisting Habitat Modeling

SDM – Species Distribution Model

SI – Swarm Intelligence

STAMP – Spatial Temporal Analysis of Moving Polygons

CHAPTER 1

INTRODUCTION

The purpose of this chapter is to provide a brief introduction to my thesis research assessing factors that covary with the continuous expansion of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) into the eastern forests of North America. Native to western North America, and having coevolved with western coniferous forests, mountain pine beetles play an important ecological role which, at endemic, or normal, levels positively influences many natural processes. At epidemic levels, however, these small beetles can cause monumental damage, destroying widespread swaths of forest, causing significant economic, ecological and social impact (Figure 1.1).

Epidemic levels of mountain pine beetle infestations have grown significantly over the past several decades in many areas of western North America. This increase is due to a combination of both anthropogenic and environmental factors. Anthropogenic factors, particularly historic land use practices, such as livestock grazing, logging as well as forest and wildfire management strategies, such as full suppression tactics (Morris et al., 2017), coupled with environmental factors of warming climatic trends and drier growing seasons (Bentz et al., 2010) have contributed to the increase in frequency of mountain pine beetle epidemics.

Full suppression is a wildland fire management strategy which seeks to extinguish any wildland fire, preferably within the first forty-eight hours of its ignition. This strategy was instated following increasingly devastating wildland fires between 1950 and 1988. Ignored, however, was the reality that fire plays an integral role to many of the forest ecologies in question. Ultimately, these tactics led to increasingly dense forests with over-mature trees and high accumulations of brush at the forest floor level. Ironically, with more fuel, the tactic led to fires of such intensity that they were impossible to engage, let alone control. Another outcome was the creation of a stressed forest structure which engineered the perfect habitat for the mountain pine beetle, so that under the right climatic conditions, explosive population increases occurred year after year.

Figure 1.1: Epidemic levels of mountain pine beetle near Bonaparte Lake, British Columbia, Canada. Source: K. Buxton, BC Ministry of Forests, Lands and Natural Resource Operations.

The impacts of these epidemic outbreaks have been far-reaching and deeply damaging to the forests which provide a range of goods and services. These goods and services incorporate ecological, economic and social values, often referred to most broadly as ecosystem services (MA, 2005). Impacts are seen in each western state (Figure 1.2) of the US as well as in Canada, where in

British Columbia alone, 710 Mm^3 of lodgepole pine (*Pinus contorta* Douglas) have been killed by mountain pine beetle over the last decade. This devastation represents a loss of more than 50% of the total merchantable pine (British Columbia Ministry of Forests, 2012). Such mortality rates also impact the ecosystem services provided by these forests, including air purification, management of water run-off and soil erosion, production of wood and other forest products, climate regulation through carbon storage and other biophysical processes which affect the planetary energy balance (Morris et al., 2017). Further complicating this issue is the fact that wildfire management strategies may be modified due to real or perceived increased wildfire risk (Jenkins et al., 2014) (Figure 1.3). Societal impacts are also felt at local to regional scales, affecting property values, recreational experiences, tourism, and landscape aesthetics (Flint et al., 2009), which remain to be completely quantified economically (Maguire et al., 2015).

Figure 1.2 : Bark beetle impacted forest in the Gila National Forest , New Mexico
Source: Credit Tyler Corbin, 2018

Figure 1.3: Significant wildfire near the Gila National Forest, New Mexico
Source: Credit Tyler Corbin, 2018

Though the range of mountain pine beetle was historically (pre-2000) bounded by the Rocky Mountains, several events coalesced to give the mountain pine beetle's traditional range opportunity to expand. These specific events were, first, peak outbreaks of mountain pine beetle during the 2000s in British Columbia, Canada and, second, changes to atmospheric conditions which were capable of carrying mountain pine beetles up and over the Rocky Mountains on convective updrafts, successfully displacing the mountain pine beetle into the novel environment of Alberta, Canada. This displacement of the mountain pine beetle led to a series of outbreaks with millions of hectares of forest left dry and dying.

The beetle, now established east of the Rocky Mountains, faces no other obvious geographic barriers to the Atlantic Ocean. Their diffusion in this novel environment has been steadily expanding eastward at an average rate of 80km/year (Cooke & Carroll, 2017). Though their preferred host, lodgepole pine (*Pinus contorta*), becomes less dense and more scattered moving east across Alberta, jack pine (*Pinus banksiana*), a naïve species, despite having not coevolved with the mountain pine beetle, has recently shown genetic evidence as a suitable host for mountain pine beetle colonization (Cullingham et al., 2011). Jack pine is the predominant species of the continental boreal forest, stretching west to east, across all of northern North America. Cudmore et al. (2010) show that mountain pine beetle brood success performed much higher in regions with naïve lodgepole pine than in lodgepole pine extant within the beetle's historical native range. Additionally, a study conducted by Rosenberger et al. (2017), assessed mountain pine beetle reproductive success in species of tree common in eastern North America (jack, *Pinus banksiana*; red, *Pinus resinosa*; eastern white, *Pinus strobus*; and Scots, *Pinus sylvestris*). Mountain pine beetle reproductive success was documented in each species, suggesting that these novel hosts will pose no barrier to further range expansion (Rosenberger et al., 2017). Has an ecological bridge been established for the eastward spread of mountain pine beetle? If so, what are some of the environmental conditions that make this diffusion possible? Looking forward, how does habitat suitability for the mountain pine beetle change under future climate scenarios? These are the issues addressed in this thesis and are articulated in greater detail in the following chapters.

CHAPTER 2
BACKGROUND

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an eruptive herbivorous bark beetle native to western North America. One of 600 species in the United States, bark beetles, aptly named, spend most of their lives beneath the bark of trees. To subsist, bark beetles mine the water and nutrients within the phloem layer of several pine species. While the majority of bark beetle species live in dead, weakened or dying hosts the mountain pine beetle is one of several which, unfortunately, targets, attacks and survives within living trees (USFS, 2014).

Biology and Behavior

Adult mountain pine beetles are dark brown to black, rather stout and cylindrically shaped, at about 5mm in length – about the size of a grain of rice (Taylor & Carroll, 2004), as seen in Figure 2.1. Beetles develop through four life stages, called instars: egg, larva, pupa, and adult (Bentz et al., 2009). Development rates are geographically variable, being highly dependent on ambient temperature. Temperatures must exceed 16°C to allow flight, or emergence, to occur (Reid, 1962; Schmid 1972; Billings & Gara, 1975). Safranyik and Jahren (1970) found that rates of daily emergence were proportional to cumulative degree-days beginning at about 14.4 °C (Figures 2.2 and 2.3).

Figure 2.1: Closeup of an adult mountain pine beetle

Source: (NPS, 2018)

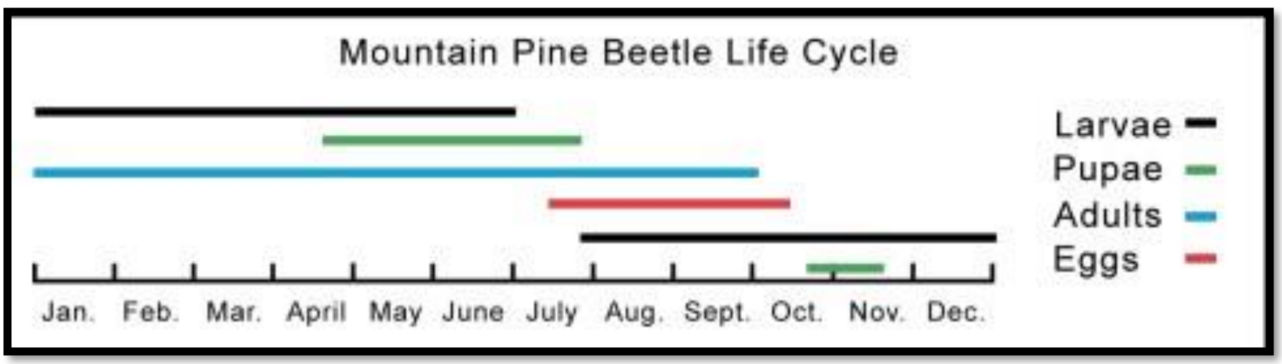

Figure 2.2: Mountain pine beetle life cycle
Source: Johnson, 1982

Most commonly, the mountain pine beetle is a univoltine species (hatching one generation per year). However, cases of bivoltinism have been documented with findings of simultaneous conditions of warmer winters and warmer summer temperatures at higher elevations (Mitton & Ferrenberg, 2012). Current knowledge of mountain pine beetle phenology comes largely from studies conducted within their historic range in British Columbia and in the United States (Bleiker & Hezewijk, 2016).

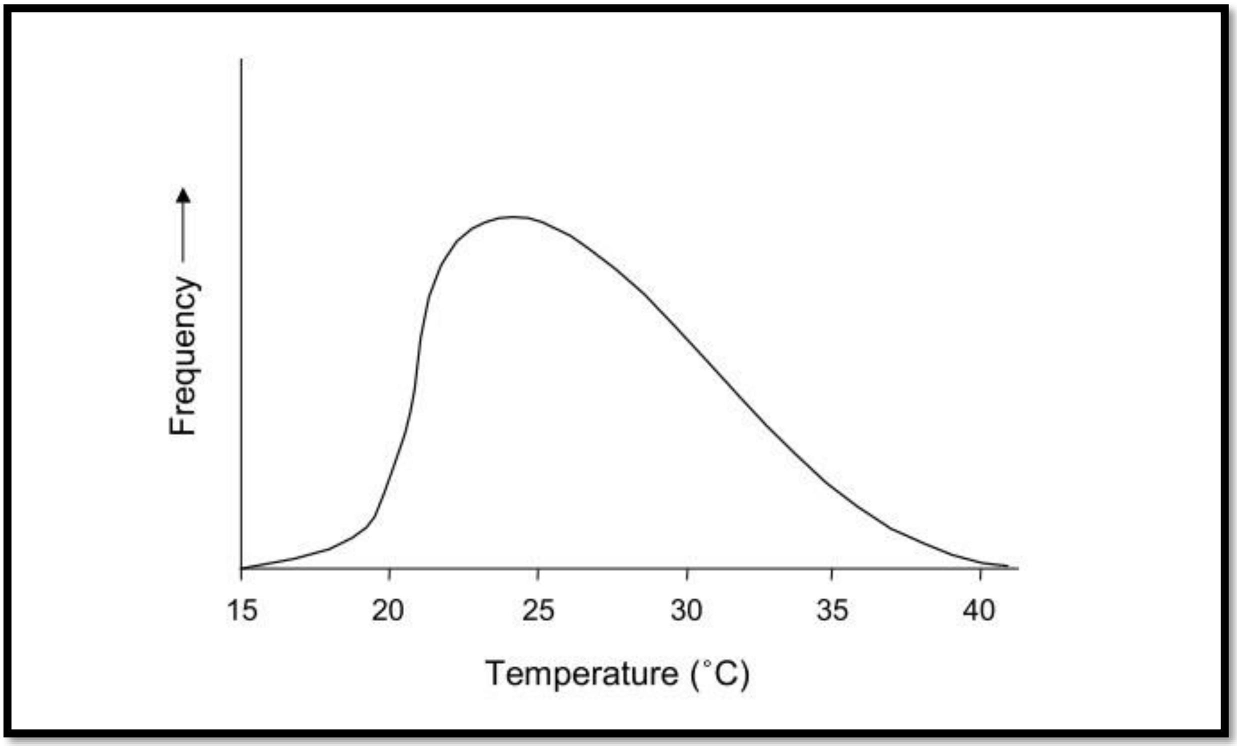

Figure 2.3: Frequency of emergence of mature mountain pine beetle in relation to temperature
Source: Safranyik & Carroll, 2006

With the exception of adult emergence from brood trees in search of new host trees, all life stages are spent in the phloem layer immediately beneath the tree bark. Adult emergence, or flight, typically occurs in late July through August. Flight has been found to start later and be more temporally contracted at higher latitudes (Bleiker & Hezewijk, 2016). Both in the historic and new ranges, flight periods for the mountain pine beetle have been found to be synchronous. This synchronous behavior, also called mass attack, is defined by hundreds of beetles descending upon a tree within a several, often less than two, days - a key strategy which results in successfully overwhelming the tree's defenses. Female beetles initiate attacks, employing a combination of random landings and visual orientation (Hynum & Berryman, 1980) while assessing host suitability based on chemical compounds present in the bark (Raffa & Berryman, 1982). Although the phase beginning with emergence and ending with the selection of, and colonization of, new host trees is one of the most important phases of mountain pine beetle ecology, it is likely the least understood, as well (Safranyik & Carroll, 2006).

According to Safranyik and Carroll (2006), tree characteristics which are selected by female beetles are trees with neither too thin a bark or too small a diameter (DBH – diameter at breast height) old trees - requiring a minimum bark thickness as well as the presence of bark scales and ridges. This preference for larger trees is due to the positive relationship between DBH and phloem thickness (Amman, 1969; Shrimpton & Thomson, 1985), which the larval broods feed upon. Once emerged, adults typically locate suitable host trees within two days of emergence, but are capable of searching for several days beyond that if no appropriate hosts are found prior to this time (Safranyik & Carroll, 2006).

If the tree is acceptable, beetles begin to bore through the bark in order to construct galleries, within which they lay their eggs. As a female beetle penetrates the bark, it releases aggregating pheromones which instigate a mass attack, attracting hundreds of male and female beetles to the same tree within several (often less than two) days. Males also release an antiaggregating pheromone which prevents overcrowding by regulating the number of attacks on one tree. This leads to attacks on nearby trees, leading to groupings of dead trees across a landscape (Bentz, Kegley & Gibson, 2009), an important factor in interpretations of my research.

Also, upon boring into the bark, beetles release spores of blue stain fungi, carried into the tree by the beetles. These spores germinate rapidly, killing living cells in both the phloem and xylem of the tree (Safranyik et al., 1975). The presence of this fungi greatly aids the success rate of an attack by incapacitating the ability of the tree's sap to run freely. For more information about the symbiotic relationships between blue stain fungi and the mountain pine beetle, please refer to the excellent article, "Integrating models to investigate critical phenological overlaps in complex ecological interactions: The mountain pine beetle-fungus symbiosis" (Addison et al., 2015).

The process of boring into the phloem, the inner bark, essentially starves the tree of water and nutrients as the phloem acts as a matrix of food supply lines, carrying sap from the leaves to the rest of the tree and moisture and nutrients from the roots and trunk to the leaves. These bore holes serve as the first visible symptom that a tree has been attacked. These external signs are usually found on the lower bole of the tree trunk and are a mixture of (i) pitch tubes surrounding entry holes; (ii) boring dust scattered and piled at the base of the trunk; (iii) patches of missing bark picked off by woodpeckers in pursuit of bark beetle brood; and (iv) a pattern of tiny round emergence holes, about 2.5mm in diameter, through which newly developed adults emerge (Safranyik & Carroll, 2006). It is important to note that less healthy trees may not produce pitch tubes and that the remaining symptoms could be due to a variety of other causes. Therefore, these signs cannot stand as reliable indicators of mountain pine beetle attack by themselves (Safranyik & Carroll, 2006).

Crown symptoms follow, when needles of successfully invaded trees begin to change color within several months to a year following the initial attack due to a loss of moisture. The visible symptoms of crown fading, first from green to greenish-yellow and later, yellow, to bright red to brown by the following year, depend on factors such as the timing of the attack, attack density, tree vigor and weather conditions (Safranyik & Carroll, 2006). Needles turn grey within three years of being attacked. Crown symptoms alone also cannot reliably serve as a precise timeline of mountain pine beetle attack. At the tree level, only sub-bark symptoms are definitive indicators (Safranyik & Carroll, 2006). For a description of sub-bark symptoms, please see the informative article, “Mountain Pine Beetle: A synthesis of its biology, management and impacts on Lodgepole Pine” (Safranyik & Carroll, 2006).

Range – Past and Present

Pre-2000, the historic biogeographical range of the mountain pine beetle extended from northern Mexico (31°N), west to the Pacific Coast, east to the Black Hills of South Dakota, USA and into northern British Columbia (BC), Canada (56°N) – with small detached populations in Alberta and south-east Saskatchewan. This south to north boundary has been correlated historically with the –40°C isotherm (Safranyik, 1978). In terms of elevation, mountain pine beetle habitat ranges from near sea level in British Columbia to 11,000 feet (3,353 m) in southern California. Figure 2.4 shows that prior to 2000, the northern part of the mountain pine beetle's range was restricted to the west of the Rocky Mountains (Safranyik et al., 2010).

Unfortunately, however, the range of the mountain pine beetle has recently expanded significantly. There are three predominant modes of mountain pine beetle dispersal:

(i) emergence of beetle attack occurs in the nearest suitable host trees;

(ii) beetles emerge to attack suitable hosts after a periods of flight exercise (Safranyik at al., 1992); and

(iii) beetles become caught in atmospheric convective upward drafts, where they are transported long distances by wind (Furniss & Furniss, 1972).

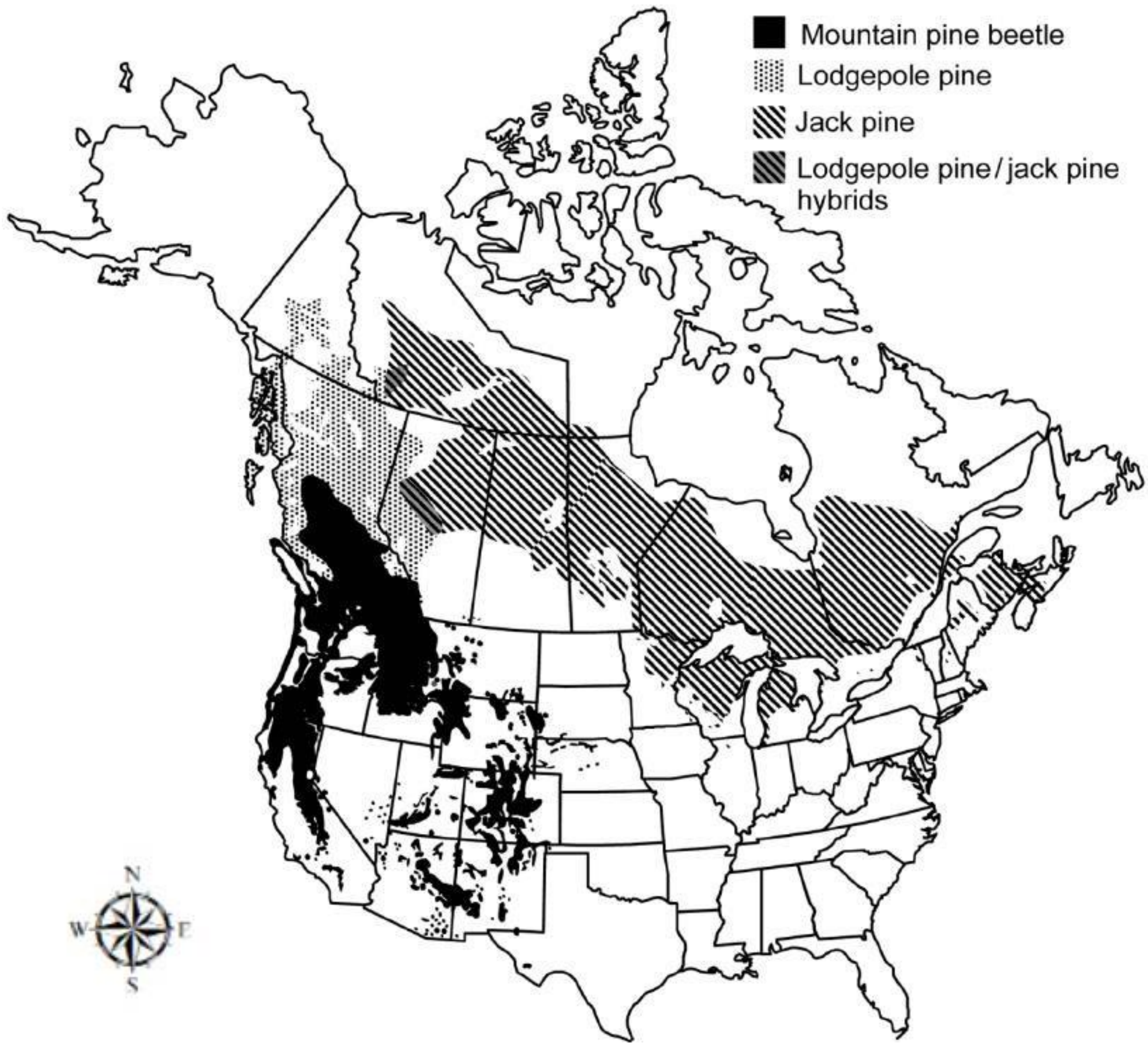

Figure 2.4: Historical distribution of mountain pine beetle (*Dendroctonus ponderosae*) and the distribution of lodgepole pine (*Pinus contorta*) and jack pine (*P. banksiana*); regions where lodgepole pine and jack pine hybridize are also indicated (adapted from Mu and Powell, 2001). Source: Safranyik et al., 2010.

Since the 2000s, the mountain pine beetle historic range has expanded when beetles from a massive epidemic which erupted in central British Columbia then blew over the Rocky Mountains on upper atmospheric winds and spread to northeastern British Columbia and northcentral Alberta (Jackson et al., 2008; Safranyik et al., 2010). This transference was confirmed by genetic analysis (Bartell, 2008). This diffusion event allowed the mountain pine beetle to clear the Rocky Mountains, previously an effective major geographic barrier (Robertson et al., 2009; de la Giroday et al., 2012). Now, east of the Rocky Mountains, with no other obvious topographic barrier, theoretically, no obstacles inhibit continued range expansion to the Atlantic coast (Safranyik et al., 2010).

Long-range dispersal of mountain pine beetle for hundreds of kilometers is uncommon but not unprecedented. Previous documentation of mountain pine beetle dispersal range from the Rocky Mountains across the southern grasslands region as far as the Cypress Hills of southeastern Saskatchewan, Canada (Hiratsuka et al., 1982). The range expansion that is the focus of this thesis research, however, is novel in that the ecosystem to which mountain pine beetle has now expanded is contiguous boreal forest, stretching eastward and northward across Canada and into northeastern United States.

Factors Affecting Range Expansion

Numerous studies identify the many factors that can contribute to or impede the diffusion of the mountain pine beetle. These factors include temperature, elevation, precipitation, topography, latitude, the availability/continuity of host tree species, competition and predators. Climate conditions that are most favorable for conditions promoting mountain pine beetle diffusion and infestation include:

(i) seasonal temperatures which allow synchronous adult emergence and attack (Bentz et al., 1991; Safranyik et al., 2010),

(ii) univoltine (one year life cycle) development, allowing the most cold-hardy brood stages to overwinter (Logan and Bentz 1999),

(iii) a mild winter, promoting survival (Bentz and Mullins, 1999), and

(iv) reduced precipitation during the growing season, negatively impacting host resistance (Safranyik et al., 1975).

According to Bleiker (2017), cold winter temperatures have been identified as the most important factor limiting the diffusion and abundance of the mountain pine beetle (Safranyik, 1978; Safranyik et al., 2010).

The world's climate warmed by 0.6 ± 0.2^{o}C during the last century, with the mean global temperature projected to increase by 1.4 – 5.8^{o}C by 2100 (IPCC, 2007) as a result of human induced increases in atmospheric greenhouse gas emissions (Bentz et al., 2010). According to the Intergovernmental Panel on Climate Change (IPCC) the rise in temperatures is projected to exceed global mean increases, particularly at high latitudes and elevations. These increasing temperatures also have the potential to promote drought stress on host forests, reducing their defensive capacity to fend off mountain pine beetle colonization (Faccoli, 2009; Kolb et al., 2016). Still, despite the excellent work already completed, increased understanding of bark beetle-climate interactions, specifically the role of increasing fire frequency, wind and drought disturbances, is needed (Morris et al., 2017).

In Alberta specifically, two different climate scenarios are considered. First, a scenario with increased international effort to promote reductions in greenhouse gas emissions and the second, where humanity continues to emit increasing amounts of greenhouse gases. The Prairie Climate Centre (2017) reports the following:

1. Regardless of the scenario, all of Canada is projected to get warmer in the future (Figure 2.5);
2. Canada's Artic will warm much faster than Canada's south – with some months projected to experience a 12 ^{o}C increase;
3. December and January are expected to warm much faster than the other months of the year;
4. Southern Canada is projected to get much more precipitation in the spring, fall and winter months but much less in summer months.

These projections are directly related to the diffusion and impacts of mountain pine beetle infestations in new regions, but there is great uncertainty of outcomes given the uncertainty involved in predicting future climatic conditions in Canada.

Mountain pine beetle populations are highly sensitive to variation in mean annual temperature (Logan & Powell, 2001). In outbreak and non-outbreak years alike, mountain pine beetle populations that have been documented to establish and persist in new areas are slowly but steadily becoming climatically adapted due to a warmer environment (Logan & Powell, 2001; Carroll et al., 2004).

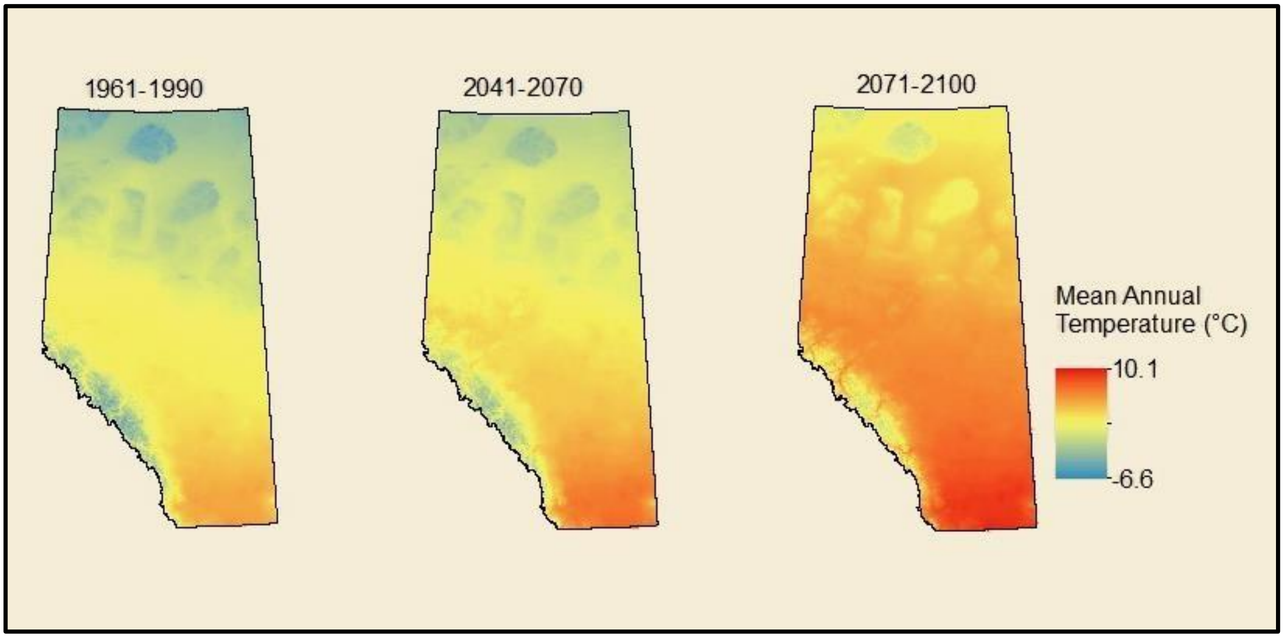

Figure 2.5: Alberta observed (left) and predicted climate change (center and right)
Source: BMCAA (2019)

As climate changes, so do the geographical ranges of many species. Numerous studies show that climate change-induced range migration – that of forests (Aitken et al., 2008), forest plants (Fitzpatrick et al., 2008) and bird migrations (Jenni & Kery, 2003), particularly, indicate a shift to higher elevations and higher latitudes (Parmesan & Yohe, 2003; Parmesan, 2006; Root et al., 2003;). These examples demonstrate the association between migrating geographical ranges, topography, and a warming climate. Direct climatic factors are generally believed to impose the cool boundaries of a species, while the interaction between species (host/predator, etc.) determines the warm limits of a species' distribution (MacArther, 1972; Parmesan, 2005). Therefore, as cool boundaries for the mountain pine beetle continue to extend northward, so too does the potential for the species' range expansion over time, especially in the absence of natural predators. The long-term rate of spread, or diffusion, of mountain pine beetle is thus intrinsically intertwined with the rate of climatic warming, in turn dependent on climate sensitivity to greenhouse gas levels, which in itself carries uncertainty, as well as levels of anthropogenic greenhouse gas prediction, which is equally unpredictable (Cooke & Carroll, 2017).

Hosts

The preferred host of the mountain pine beetle is lodgepole pine (*Pinus contorta*) though most species of pine that grow within its range are readily attacked. These include: Ponderosa *(P. ponderosa* C. Lawson), western white *(P. monticola* Douglas), whitebark *(P. albicaulis* Engelm.), and limber pines (*P. flexilis* James) (NRCAN, 2017). Six eastern species of North American pine have also been attacked: eastern white pine (*P. strobus* L.), pitch pine (*P. rigida* Mill.), red pine (*P. strobus* L.), and jack pine (*P. banksiana* Lamb.) (Safranyik et al., 2010). Recently confirmed by genetic evidence, jack pine (*P. banksiana* Lamb.), the predominant species of the boreal forest, also is now a viable host for both attack and reproduction (Cullingham et al., 2011).

As expected, the geographic ranges of the traditional hosts of the mountain pine beetle mimics that of the mountain pine beetle's historic range (Figure 2.6). Since the summer of 2005, the rate of expansion has increased at an average rate of 80km/year eastward across Alberta (Cooke & Carroll, 2017). Some possibility of a slowing of this rate of spread exists as the mountain pine beetle population moves farther from traditional host populations in the dense pine stands of the Rocky Mountain foothills to the scattered, naive pine of the boreal plains. It is reasonable to expect, for example, that a 10-fold decrease in available trees per hectare would lead to a 10-fold decrease in the number of insects (Cooke & Carroll, 2017). Now, however, that jack pine, the predominant species of the boreal forest, appears to be an acceptable host, future predictions regarding mountain pine beetle diffusion remains uncertain. Other factors, such as

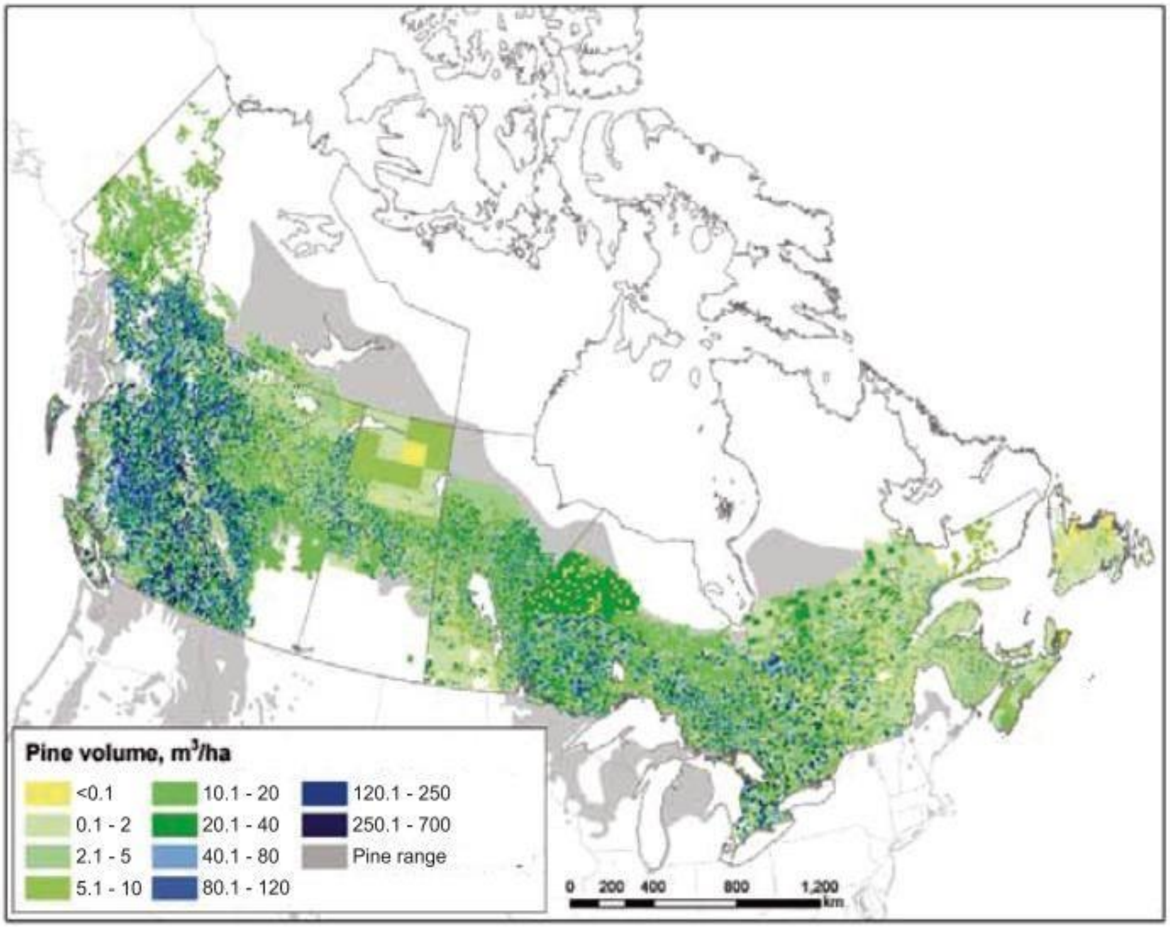

Figure 2.6: Estimated volumes of pine species in Canada showing host connectivity (data from the Canadian Forest Service forest inventory). Source: Safranyik et al., 2010

how the mountain pine beetle responds to relatively novel environments, the unpredictability of future weather and climatic conditions, and human efforts to limit colonization of new ecological areas also contribute to this uncertainty (Cooke & Carroll, 2017).

Impact

The mountain pine beetle is considered by researchers to be the most aggressive, persistent and destructive insect found within mature pine (Pinaceae) forests in western North America. According to Dale et al. (2001), it is estimated that insect disturbances affect an area that is almost

45 times as great as that affected by fire, resulting in an economic impact nearly five times as great. The mountain pine beetle has already had the greatest economic importance of all insects in the forests of western North America (Samman & Logan, 2000). The reason for this is that the mountain pine beetle is one of a few bark beetles that is a true predator that must kill its host in order to successfully reproduce (Heavilin et al., 2007). Although most of North America's bark beetles are native and play an integral ecological role in forest dynamics (Fleming et al., 2002; Sanchez-Martinez & Wagner, 2002), researchers believe recent outbreaks are increasing in frequency, severity and extent (Westfall, 2006; Kurz et al., 2008; Raffa et al., 2008).

According to research by Safranyik and Carrol (2006), mountain pine beetle populations can be considered as having four distinct states: (1) endemic; (2) incipient epidemic; (3) epidemic; and (4) post-epidemic or collapse. Endemic populations are scattered and restricted to damaged or weakened pine trees. Incipient-epidemic populations have increased sufficiently to overcome the defenses of average diameter host tree species. Once the incipient epidemic phase has been reached, adding favorable climatic conditions to beetle survival, rapid spread across a landscape can occur, reaching the epidemic phase. Once the majority of large-diameter host species have been killed, the collapse phase initiates (Carroll et al., 2006).

Epidemic phases of the mountain pine beetle have occurred in different regions at different times. According to Pedersen (2003), the two key factors that have contributed to the expansion of the mountain pine beetle epidemic are:

1. the threefold increase since 1910 of the number of hectares of mature, susceptible lodgepole pine forests that are 80 years of age and older (Taylor & Carroll, 2004); and
2. warmer climate conditions expanding the beetle's range into previously unsuitable areas, particularly reaching higher latitudes and elevations (Carroll et al., 2004).

Historical outbreaks previously documented in central British Columbia, Canada occurred in the 1930s, 1970s, early 1980s and mid-1990s with a peak in 2005. In the mid-1990s, an outbreak affected more than 14 million ha of pine forests, an area more than ten times the size than any previously recorded outbreak (Safranyik et al., 2010). In 2003, a 100% increase in rate of spread and attack intensity since 2002 was recorded through aerial overview surveys (BC Ministry of Forests, 2004). According to Walton (2012), by 2011, over 700 million m^3 of trees distributed over 18.1 million hectares of pine forests had been killed, representing approximately 50% of the total merchantable pine volume in the province. This is expected to grow to more than 57% by 2021 (British Columbia Ministry of Finance, 2013). According to aerial surveys, by 2014, 51,804 hectares were documented as being affected by mountain pine beetle, down from 63,102 hectares in 2013. Economic impact is significant as the forest and logging sector is a long-standing significant industry in British Columbia, with a direct contribution of CAN $1.65 billion to gross GDP in 2012 (British Columbia Ministry of Finance, 2013). One study predicts that between 2009 – 2054, a cumulative loss of CAN $57.37 billion (US $44.63 trillion) (1.34%) to GDP will result from the impacts of mountain pine beetle damage (Corbett et al., 2016).

The extent of mountain pine beetle infestation in Alberta is variable. Mountain pine beetle outbreaks first appeared in the province of Alberta, Canada during the summer of 2005. Since then, the mountain pine beetle has spread eastward across Alberta at an average rate of 80km/year (Cooke & Carroll, 2017). In 2005, in attempts to reduce its spread, Alberta began an annual program to detect and eliminate mountain pine beetle populations along the presumed leading front. As of 2016, the mountain pine beetle continues to be the primary bark beetle causing tree mortality (Alberta Agriculture and Forestry, 2016).

Aerial beetle-kill forest surveys are completed annually by provincial governments in Canada. These surveys monitor locations of “red-attack” trees. Table 2.1 describes of attack phases of mountain pine beetle while Figure 2.7 illustrates the red and grey attack phases.

Table 2.1: Phases of mountain pine beetle attack and descriptions

Attack Phase	*Description*
Green Attack	Currently infested; pine needles begin to shift from green to yellow. Difficult to assess from aerial surveys
Red Attack	Infested the year prior; pine needles turning red; highly visible – most aerial surveys monitor red attack. Timber is salvageable for a short time period.
Grey Attack	Tree is now dead – needles have turned grey. Timber is largely unsalvageable.

Source: Created by the author

Scotia and Brown (2017) recorded a three-fold increase, from 11,853 red trees in 2016 to 46,000 red trees in 2017 in the Edson Forest Area. According to the 2017 Bugs & Diseases Report for Alberta, Canada, while some areas are seeing increased rates of infestation, others are seeing significant declines (Scotia & Brown, 2017). For example, in 2015, 22,011 red trees were detected in the survey area. By 2017, however, only 2,601 red trees had withstood attack - presumably due to aggressive and sustained control efforts.

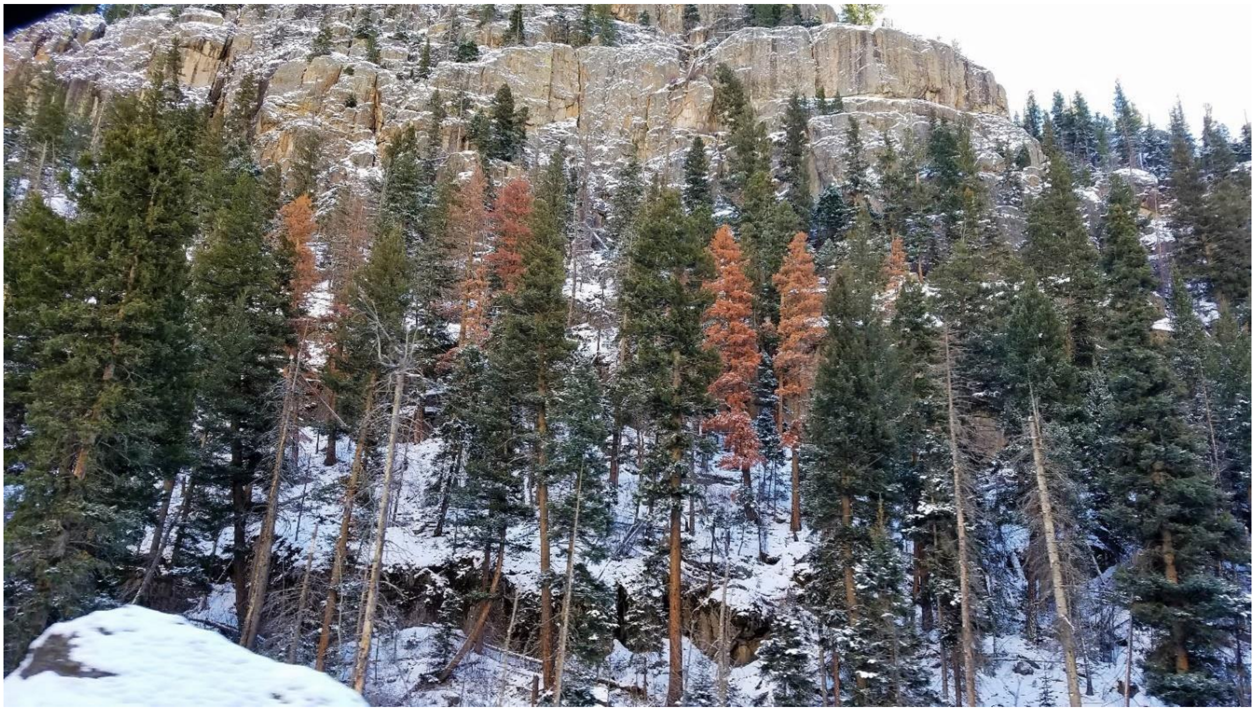

Figure 2.7: Mountain pine beetle red attack phase near Wolf Creek Pass, Colorado.
Source: Photo taken by author, 2018

In the United States, according to US Forest Service (USDA Forest Service, 2011), infestations of mountain pine beetle outbreaks have also been quite extensive, particularly in the states of Colorado and Wyoming. It is thought that these outbreaks were initially triggered by extended drought in the region during the late 1990s and early 2000s. More than 1.5 million acres of forest in northern Colorado are affected. Again, as in Canada, the infestation is a major threat to regional economies and public safety – due to falling trees and an increase in fuel loading for wildland fires. Another statistic provided in the Colorado State University (Colorado State University, 2017) documents a mortality rate of 1 in 14 trees in Colorado due to mountain pine beetle. The effects present themselves in numerous sectors of society. Excessive timber losses are perhaps the most obvious result but this level of landscape-level change also impacts the forest's ability to purify air and water, protect against soil erosion, and also drastically change a region's wildland fire regimes by increasing fuel loading. Wildlife composition, recreational values, aesthetics and safety are also heavily effected (Safranyik et al., 1974; McGregor, 1985; Safranyik & Carroll, 2006). According to the Aerial Survey Highlights for Colorado for 2017 (USDA Forest Service, 2015; USDA Forest Service, 2017), epidemic levels of the mountain pine beetle have ended, for the time being, within Colorado. Since 1996, nearly 3.4 million trees have been affected by mountain pine beetle. In 2017, however, less than 900 acres newly attacked trees were reported. This decline is believed to be due to a depletion of available host trees. Figure 2.8 shows recent remnants of beetle attack trees near Big Meadows Reservoir, Colorado. In contrast, Figure 2.9 shows the recent high level of impact in a National Forest in Montana, where hiking trails and camping were forbidden during the 2018 season due to concerns of public safety.

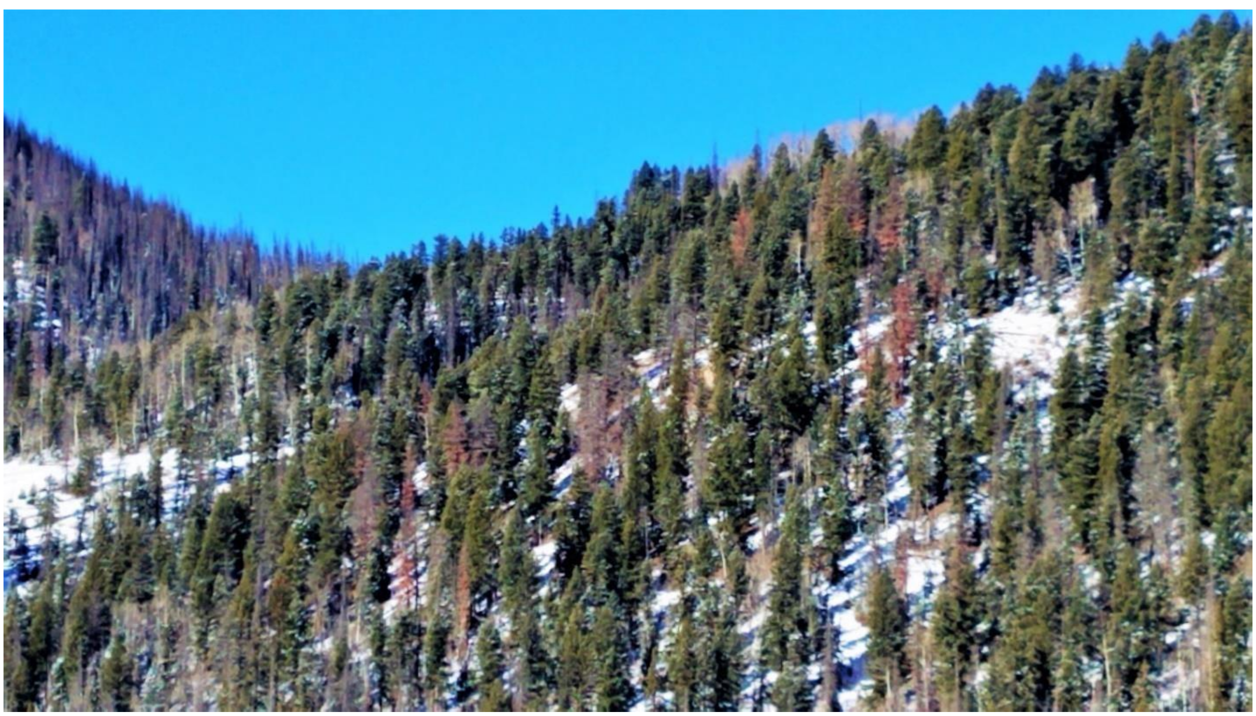

Figure 2.8: Remnants of beetle attacked trees, this photo shows a mixture of red and grey attack trees located near Big Meadows Reservoir, Colorado. Trees with white trunks are aspen (*Populus tremuloides*) – not to be mistaken for grey attack conifers. Source: Photo taken by author, 2018

Figure 2.9: Mountain pine beetle has led to such extensive damage in the Big Snowy Mountains, Montana (a) that campsites and hiking trails remained closed throughout the 2018 season due to risk of falling trees (b). Source: Taken by the author, 2018

CHAPTER 3

LITERATURE REVIEW

This chapter will introduce previous research on the mountain pine beetle and the methods employed to analyze this remarkable diffusion. Biological invasions follow four common phases: arrival, establishment, spread and impact (Venette, 2015). In the mid-2000s, mountain pine beetle diffused beyond its native range into novel territories in Alberta, Canada. Since then, the mountain pine beetle has successfully established and spread at an average rate of 80km/year (Cooke & Carroll, 2017). Findings from this research is of particular interest with respect to the diffusion of mountain pine beetle as it stands poised at the doorway of the boreal forest, forming an ecological corridor from western North America to eastern North America.

The mountain pine beetle epidemic, having reached an unprecedented scale and intensity, has successfully expanded and established itself far beyond its native range. Now, stretching before the mountain pine beetle are the novel habitats of naïve forest species stretching from western North America to the Atlantic. Naïve host species, those which have not co-evolved with the disturbance agent in question, such as jack pine, have been confirmed as suitable for mountain pine beetle colonization (Cullingham et al., 2011). Again, the intent of this research is to assess the habitat suitability and potential diffusion of mountain pine beetle populations into these new ecosystems in order to both better understand the changing climatic variables which may be most relevant within this new terrain while also providing new information for forest managers and policy makers about the new potential risk to these valuable forests.

It is essential to obtain a thorough understanding of prior research in terms of both the methodologies used to explore the diffusion patterns of invasive species and the actual findings related to mountain pine beetle. A researcher must be adequately informed as to the succession of methods used in the past as well as current best practices which allows for the identification of gaps in the research and/or methodologies. This review has three related goals: 1) summarize work meaningful to the importance of establishing the rate of spread, or diffusion, of an invasive species; 2) review a variety of the methodologies used to map and model such diffusion and; 3) review all methodologies previously used to model the spread of the mountain pine beetle. The studies related to the modeling methodologies will be briefly summarized with a focus upon the data collection procedures, the most significant variables identified by this previous work, and the data analyses methods, results, conclusions, and noted limitations of prior studies.

Rate of Spread

Before generating projections of species diffusion, the rate of spread of the species must be estimated. There are numerous factors that influence this rate, including: presence and density of suitable habitats most vulnerable to invasion, suitable climatic conditions, interspecies competition, predation (Boone, Six, & Raffa, 2008) and host susceptibility and vigor (Cooke & Carroll, 2017). Once established, species begin to expand their geographic range in a process known as stratified diffusion where local growth and dispersal is paired with long distance movement (Shigesada, Kawasaki, & Takeda, 1995). If successful, these long-distance dispersed colonies eventually coalesce with the point of origin, greatly increasing the rate of spread and the colonized territory (Hengeveld, 1989; Shigesada & Kawasaki, 1997). Cycles of dispersal and establishment continue until all of the susceptible habitat is occupied (Liebhold & Tobin, 2008). Stratified dispersal has been observed and documented for numerous non-native species, including the Argentine ant (*Linepithema humile)* (Suarez, Holway, & Case, 2001), Africanized honeybee (*Apis mellifera scutellate)* (Winston, 1992), horse-chestnut leaf miner (*Cameraria* *ohridella)* (Gilbert, Gegoire, Freise, & Heitland, 2004), emerald ash borer (*Agrilus planipennis)* (Muirhead, et al., 2006) and the gypsy moth (*Lymantria dispar)* (Liebhold, Haverson, & Elmes, 1992).

Insect disturbances are considered to have significantly damaging effects on the ecology and economy on Canadian forests. Successful establishment of an invasive species beyond its native range poses a significant threat to native ecosystem structure, productivity, diversity and function (Tobin et al., 2016). It is crucial to monitor, simulate, and predict insect disturbance processes in order to gain insights into past, present, and future forest ecosystem scenarios (Liang et al., 2017). Estimating the rate of spread of the species and modeling future projections of potential range expansion are integral components for the development of land and resource management plans and policies (Tobin et al., 2015).

Methodologies used to Model Diffusion

Diffusion models "build a simplified mathematical representation of the main features of the process as a time series of indicators describing the phenomenon of interest" (Jaakkola, 1996, p. 65). There are numerous analytical methods used to model diffusion, each carrying an associated list of assumptions and therefore presenting differing strengths and weaknesses. This complex process incorporates manipulation of a variety of variables and, depending on what phenomenon is being modeled, some methods are more appropriate than others for particular species and biomes. The study of diffusion has a rich history, being used for a wide breadth of topics ranging from biological to the adoption of technologies, such as the spread of: political ideologies and mobile phones (Jaakkola, 1996), marketing (Mahajan, Muller, & Bass, 1990), disease (Rahmandad & Sterman, 2008), and invasive plant and animal species (Ferrari, Preisser,

& Fitzpatrick, 2014; Hastings et al., 2005; Reeves & Usher, 1989; Safranyik, Silversides, McMullen L H, & Linton, 1989; Shigesada et al., 1995; West et al., 2016; Raghavan et al., 2019).

Common Challenges in Modelling

Three common challenges to quantitative modelling were identified by Venette (2015). First, developing a model which offers a more meaningful prediction of spread and impact than would be derived from random chance or intuitive models, (i.e. plant pests spreading to where suitable hosts are found). When models are made for areas in which the subject of interest has not yet arrived, extrapolations from what is known about the species in its native range are made and applied to the new locations. Further, simplifying assumptions about the invading population, such as individuals being the genetic equivalent of individuals in their native range will also mimic those of future generations. This, of course, is not the case specifically with the mountain pine beetle, whose larvae has shown to present varying cold tolerance based on geography (Régnière & Bentz, 2007). For example, a cold tolerance difference of 10^{o}C in late-instar larvae between north-central Alberta and southern British Columbia, Canada was found by recent research (Bleiker, Smith, & Humble, 2017). Second, validating the model – physical, conceptual, statistical or mathematical – presents a challenge as models are always an abstraction and simplification of reality. As our knowledge of biological invasions remains incomplete, models are intended to capture enough of reality in order to be useful (Venette, 2015). Lastly, Venette identifies portraying the results in a useful manner for the intended audience, often decision makers, as the third challenge. Scope, resolution, information loading and presentation offer just a glimpse of considerations the researcher should undertake throughout the modeling process.

Modeling Diffusion of Invasive Species

Diffusion describes the means by which a species redistributes itself, passively or actively, in an area of concern after it has established (Venette, 2015). Numerous quantitative models have been developed in order to measure and forecast diffusion (Shigesada & Kawasaki, 1997; Hastings et al., 2005). Later in this chapter, Table 3.2 offers a summary and comparison of many diffusion models.

Species Distribution Models

Species distribution models (SDMs), also known as bioclimatic envelopes, correlative niche models, or ecological niche models, are commonly used in the fields of macroecology, biogeography and biodiversity research to model the geographic distributions of species based on correlations between known occurrence locations and their associated environmental conditions (Gomes et al., 2018). SDMs are probabilistic models which statistically correlate species' known occurrences within its present environment in order to estimate distribution and predict changes in their distribution under changing climates (Guisan & Zimmermann, 2000). SDMs are popular models due to the increase of availability of species location data as well as the ease of implementation of some of the modeling methods (Gomes et al., 2018).

SDMs have been criticized for lacking mechanisms for independent validation (Araujo & Peterson, 2012). Further, two assumptions of SDMs are violated when modelling invasive species. First, SDMs assume the species' ecological niche is stable in both time and space (the invasive species in its adventive area has similar environmental conditions of its native range) (Gallien et al., 2012). This assumption is not always met as the naturalized climatic niche of an invasive species can differ from their native climatic niche (Medley, 2010; Early & Sax, 2014; Parravicini et al., 2015). Second, SDMs assume that the species is at semi-equilibrium within its environment, meaning the species has already spread to all suitable locations and is absent from all unsuitable locations (Guisan & Thuiller, 2005). Equilibrium of an invasive species is not met until the latest state of invasion (Barbet-Massin et al., 2018).

Despite these limitations and while more studies are needed, SDMs of invasive species have been shown to adequately predict spread. Barbet-Massin et al. (2018) used SDMs to model the diffusion of the Asian hornet (*Vespa velutina nigrithorax*) which is invading Europe and is climatically driven. Their results show predictive accuracy was slightly, but significantly, better when their model was calibrated with invasive data only, excluding native data (Barbet-Massin et al., 2018).

Comparing Interpolation Methods

A study conducted by Tobin et al. (2015) demonstrated the application of three methods of interpolation, (square-root area regression, distance regression and boundary displacement) to estimate the diffusion rate of the gypsy moth, *Lymantria dispar*. The moth is a non-native invasive defoliator insect which currently occupies nearly three-quarters of the forested land considered to be susceptible in the USA (Tobin et al., 2015). In this study, both point and polygon data were used. Findings suggest that estimates for the rate of spread between the three methods were similar while using polygon data. Point data, however, generally provided greater spatial resolution in the verification of species presence (Tobin et al., 2015) (Table 3.1). Tobin et al. (2015) further describe the point data for this species, collected with pheromone baited trapping systems, as having the additional advantage of delineating measurements of abundance, or density. This is particularly valuable knowledge for management efforts as lower density populations may be more reactive to control tactics. This study shows that even with low-quality spatial records of infestation, relatively simple mathematical approaches can be used to accurately estimate rates of diffusion (Tobin et al., 2015).

Table 3.1: Comparison of point and polygonal data when estimating gypsy moth spread (*Lymantria dispar*) using three analytical methods

		Spread rate estimate (± SE), km/year		
Data Source	Moth threshold	Square-root area regression	Distance regression	Boundary displacement
Polygon data	NA	1.1 (1.9)	9.6 (2.0)	9.9 (5.0)
Point data	1	13.5 (2.3)	15.7 (0.3)	7.3 (3.0)
	10	21.2 (1.2)	19.3 (0.5)	9.7 (2.8)
	100	23.8 (2.2)	22.8 (0.6)	14.7 (10.5)
	Overall	19.5 (3.1)	19.3 (2.0)	10.6 (3.7)

Adapted from Tobin et al., 2015

There are countless diffusion models in existence. Models continue to evolve to better fit their subject matter but many have come far from early, generic versions. Table 3.2 summarizes a variety of models varying from approaches focusing on population dynamics, using statistical forecasting to incorporating spatial heterogeneity, to incorporating competition and evolution of the species in question – the mountain pine beetle, for example. Concerning the incorporation of evolution, Garcia-Ramos & Rodriguez (2002) modeled the influence of local adaptation on invasion in a spatially heterogeneous environment, and found that the rate of adaptation to local conditions can be the key limiting factor to spread, especially where large differences between habitat patches exist.

Table 3.2: Descriptions of diffusion models with examples

Modeling Method	Description of Model	Examples
Approaches using analytical methods		
Square-root regression	Distance-to-time analysis using successive measurements of invaded area	
Distance regression	Regresses the distance from an infested location from a reference point on the year it first became infested (Gilbert & Liebhold, 2010)	
Boundary displacement	Estimates rate of spread by considering displacement distances between pairs of consecutive invasion boundaries (Tobin et al., 2015).	(Tobin et al., 2015)
Approaches using population dynamics: (most common)		
Integro-difference	Estimates spread velocity	House finch of North America (Veit & Lewis, 1996), the Holocene spread of trees (Clark, 1998; Clark et al., 2001); Oak trees across Britain after the last glaciation (Skellam, 1951); Earth worms in an agricultural field (Marinissen & van den Bosch, 1992)
Approaches using statistical forecasting:		

Table 3.2 - Continued

Modeling Method	Description of Model	Examples
Survival analysis	Used to predict how long a location will remain free of an invading species	Phytophthora lateralis, a root pathogen of a riparian tree (Jules et al., 2002)
Incorporating Spatial Heterogeneity:		
Reaction-Diffusion	Models spread of a single species is examined in an environment with periodic variation in diffusivity and/or growth rate	*Gleditsia triacanthos* *Lithraea ternifolia* in Argentine forests (Marco & Paez, 2000; Shigesada et al., 1986; Shigesada & Kawasaki, 1997)
Gravity	Movements are not random but are biased by the attractiveness of destinations; invasions mimic satellite introductions instead of a moving wave	Zebra mussel spread (Bossenbroek, Kraft, & Nekola, 2001); Spatial spread of a genetically modified microbe with presence of a competitor (Cruywagen, Kareiva, Lewis, & Murray, 1996)
Individual-based	Incorporate detailed information about individual fecundity, dispersal and landscape structure	Landscape level predictions of *Pinus radiata* in S. Africa (Higgens et al., 1996)
Data-based stochastic	Incorporates corridors	Spread of rabies on heterogeneous landscapes (Smith et al., 2002)
Percolation Theory	How spatial heterogeneity affects not only the rate of spread, but its final outcome; Relationship between disturbance and the spread of invaders (With, 2002)	

Source: Created by the author

Diffusion Modeling of Mountain Pine Beetle (MPB)

Forest insect disturbances, the mountain pine beetle included, remain a particular challenge to prediction efforts due to the highly dynamic nature of insect behavior (Liang et al., 2017). Listed and described below are several of the many approaches that have been used to depict, predict, assess and manage mountain pine beetle outbreaks in the following order: remote sensing, general linear models, equation-based models, agent-based models (ABM), cellular automata (CA), ForestSimMPB, STAMP (spatial-temporal analysis of moving polygons) followed by a comparison of three popular contemporary SDM models, Maxent, boosted regression trees (BRT), and generalized linear models (GLM). Please refer to Table 3.2 for a summary of these modeling methods for mountain pine beetle.

Remote Sensing

Wulder et al. (2006) found that analyses of Landsat imagery in conjunction with diffusion models used to predict red attack damage in a mixed-stand forest had an accuracy of 86% (Wulder et al., 2006). Remote sensing, in combination with ancillary spatial data, has been used to create a mountain pine beetle red attack likelihood surface which accurately identifies damaged forest stands at the landscape scale (Perez & Dragicevic, 2010). Landsat imagery, though coarse at 30-meter^2 resolution, was also used to map outbreak locations and tree mortality (Meigs et al., 2015). Liang et al. (2014) analyzed a decade-long Landsat time-series stacked with the aid of automatic attribution of change detected by the Landsat-based Detection of Trends in Disturbance and Recovery algorithm (LandTrendr) in order to characterize mountain pine beetle outbreak patterns. These change-detection analysis maps have an overall accuracy ranging from 87% to 94% (Liang et al., 2014). These maps are coupled with predictor variables (anthropogenic, biologic and physical) in a general linear model (GLM) framework and the findings are discussed in the GLM section. Other researchers have utilized a range of additional remotely sensed products, such as GeoEye-1 (Dennison, Brunelle, & Carter, 2010), which provide high-resolution (0.46 meter) satellite imagery. Although GeoEye-1 provides detailed spatial and temporal information, unfortunately, the high cost and difficult accessibility make it less than practical for repeat management applications (Morris et al., 2017). However, remotely sensed images extracted from the use of drones presents a promising technique for high-value, smaller areas, although it is not yet understood how these images will be integrated with satellite and aerial imagery (Morris et al., 2017).

Equation-based Models

Equation-based models represent the most popular approach for insect diffusion models (Perez & Dragicevic, 2010). These mathematical equations, however, fail to take into account some of the spatial dynamics which influence the phenomenon (Perez & Dragicevic, 2010). Spatial distribution of the mountain pine beetle has been studied through the lens of many spatial statistic methods (Campbell, Alfaro, & Hawkes, 2007). Perez & Dragicevic (2010) utilized agent-based modeling (ABM) paired with the analytical capabilities of geographic information systems (GIS) to model mountain pine beetle infestation at two spatial scales – at the local, treelevel scale and the landscape scale – to study how micro-level mountain pine beetle outbreaks create infestation patterns which affect macro scale forest health. These authors developed this GIS-AB approach, notably freely available (http://repast.sourceforge.net/download.html), to simulate mountain pine beetle infestation over forest landscapes primarily consisting of lodgepole pine (*Pinus contorta*) with Douglas-fir (*Pseudotsuga mensiesii)* at smaller proportions and White Spruce (*Picea glauca*) distributed throughout the landscape. Aerial overview survey data and five different raster GIS datasets showing forest cover attributes of tree species, age, height, health state and diameter at breast height (DBH). Their results from the simulation for a landscape scenario over a 10-year period, using both moderate and extreme winter tree-mortality rates, showed mountain pine beetle infestation locations remain in close proximity to previous attack sites during the first four years, but are more dispersed over longer periods of time.

Cellular Automata

Liang et al. (2017) employed an insect-CA (cellular automata) modeling framework, integrating remote sensing, GIS and cellular automata to predict the mountain pine beetle mortality patterns. Results ranged from 88% to 94% accuracy, showing this method has a high degree of effectiveness for modeling forest insect dynamics. Additionally, results showed that a small neighborhood size is the most effective in simulating the actual movement of mountain pine beetle, indicating short-distance as the predominant dispersal mode of the mountain pine beetle.

ForestSimMPB

ForestSimMPB is a novel model approach which integrates Swarm Intelligence (SI) theory and agent-based model within a GIS framework in order to determine the spatial pattern associated with mountain pine beetle attacks (Pérez & Dragićević, 2011). Inclusion of swarm intelligence theory presents a strength to this model in that it incorporates the unique biological behavior of the mountain pine beetle, with specific regard to emergence, aggregation and attack behavior. The use of an agent-based model is also a strength as it allows incorporation of a heterogeneous forest landscape. Further, these authors operated the model over three sites: 1) pure lodgepole; 2) geographic barrier scenario; and 3) mixed forest scenario. Results suggest that the forest composition, artificial barriers, and the trees' health status influence the spatial distribution of insects and their general behavior during an outbreak (Pérez & Dragićević, 2011). These authors also note that including wind and elevation data would contribute an improved understanding with respect to the effect of these variables on mountain pine beetle behavior. The main drawback of this approach at this time is that it remains to be validated due to the difficulty of gathering sufficient forest data over a wide temporal range for the study areas. Cost may also be a significant issue given the extent of post-2000 mountain pine beetle outbreaks and the limited resources of the agencies charged with mitigation efforts.

STAMP – Spatial-temporal analysis of moving polygons

STAMP, a recently developed pattern-based approach, was used by Robertson et al., (2009) to illustrate fine-scale spatial dynamics of processes associated with mountain pine beetle range expansion. These scholars studied the movement patterns of mountain pine beetle infestations in areas where range expansion was occurring across three regions in the Canadian Rocky Mountains. Based on aerial survey data from 1999-2005, Robertson et al. (2009) found that dispersal patterns of the mountain pine beetle vary with geography and host/beetle population dynamics. While habitat connectivity was found to facilitate successful colonization, long range dispersal patterns to new distant locations was found to be common during periods of low overall range expansion whereas a locally connected dispersal pattern was found during periods of rapid invasion (Robertson, et al., 2009). Through the use of STAMP, trends in the number and size of the polygons by year were determined, revealing both fine- and coarse-scale patterns of changes in mountain pine beetle biogeographical range over time.

Cooke & Carroll (2017) used a synthetic framework which modeled future spread rates across Canada as a function of coupled nonlinear recruitment dynamics that arise from the distinct population phases of the mountain pine beetle, and correlated thermal response functions that are characteristic of the influence of climate and climate change on ecosystem processes. Population growth dynamics, they state, are relevant to dispersal in that population levels determine the number of diffusers able to travel long distances. Their study differs from previous studies, which have examined spread risk factors individually, by “providing a synthetic perspective on the role of synergistic nonlinear process interactions in expected rates of population growth and spread” (Cooke & Carroll, 2017, p. 13). This study uses normalized insect survey data from British Columbia and Alberta, Canada, pine volume density maps, and three indices of mountain pine beetle climatic suitability (an index of seasonality, winter survival, and summer and winter climatic suitability). Climatic suitability maps were computed using BioSIM, a standard tool used to generate spatial maps of mountain pine beetle climatic suitability (Bentz et al., 2010; Cooke & Carroll, 2017). Two climate models (drying climate and warming climate) and one forest health scenario (an increase in the ratio of stressed to vigorous trees) are combined with the goal of predicting the possibility of eruption from endemic to epidemic phases. “This synthetic model shows a classic “tipping point” model that is capable of identifying sudden, unanticipated behavior due to nonlinear determinacy, multivariate causality, stochasticity, and uncertainty in model parametrization and specification” (Cooke & Carroll, 2017, p. 19). Results show that warm, dry conditions lead to an increased probability of severe mountain pine beetle outbreaks. Five sources of uncertainty are identified:

(1) The incompleteness of precise knowledge of all drivers, interactions and functional parameters which affect eruptive behavior;

(2) The potential for variations in drought may lead to region-specific impacts;

(3) Adaptive seasonality (life cycle events occurring synchronically with ephemeral resources (Logan & Powell, 2003) will degrade and may cause a sudden decline in climatic suitability;

(4) Large areas of jack pine through eastern Alberta and Saskatchewan are already infected with dwarf mistletoe and its impact on the trees defense capabilities;

(5) Finally, the authors acknowledge that mountain pine beetle brood success is higher in naïve lodgepole pine hosts, but it is not known how jack pine, another naïve host species, will affect mountain pine beetle brood success.

Importantly, the study also reflects upon the unpredictability of a long-term spread rate, as it is reliant on the rate of climate warming, which is related to uncertain greenhouse gas emissions, of which the share of anthropogenic activities producing greenhouse gas is equally uncertain. For additional research suggestions, see the article.

Comparing Three SDMs

Sidder et al. (2016), compared the suitability of three species distribution models (SDMs) – Maxent, boosted regression trees, and generalized linear models – to evaluate how the climate niche, potential distribution, and climatic drivers of the mountain pine beetle have changed across three time periods. The climate niche is defined as the range of climatic conditions conducive to mountain pine beetle outbreak (e.g. upper and lower temperature thresholds found in occupied habitat). Potential distribution is defined as the spatial extent where suitable topography and climate exists for mountain pine beetle outbreak. Lastly, climate drivers refer to those climate variables which are identified as most influential with respect to mountain pine beetle outbreaks. Forty-five initial variables were narrowed down to fourteen through testing for significant correlations based on Pearson, Spearman, and Kendall coefficients. Highly correlated variables were filtered using expert knowledge of mountain pine beetle ecology and were selected to represent seasonal climatic influences (Table 3.3). Summaries of the comparisons of the three models used in this study follow.

Maxent. Maxent (maximum entropy or closest to uniform), freely available and hosted online at https://biodiversityinformatics.amnh.org/open_source/maxent/, is one the most popular recent SDMs (Renner & Warton, 2013). It is a self-contained Java application for species distribution modeling based on occurrence (locations of presence of the species) while also incorporating environmental variables (temperature and rainfall) for a surrounding area (Phillips et al., 2006; Phillips & Dudik, 2008). This presence-only model is advantageous as it allows for the use of the plentiful data sources from archived natural history collections, greatly reducing the cost, in both time and money, of sampling a species throughout its geographic extent (Gomes et al., 2018). While presence data may be abundant, absence data are more difficult to obtain and often less reliable, due to the required high field survey efforts. To account for this, "Maxent uses a background sample to contrast the distribution of presences along environmental gradients against the distribution of background points, randomly drawn from the study area" (Gomes et al., 2018, p. 4; Sidder et al., 2016). Therefore, modeling techniques that require only presence data are extremely useful (Graham et al., 2004). Evangelista et al., (2011) also employed the Maxent model in order to estimate forest vulnerability and potential distribution across three bark beetle species (mountain pine beetle (*Dendroctonus ponderosae*), western pine beetle (*Dendroctonus brevicomis*), and pine engraver (*Ips* pini)) across a study area of eight states in the interior west, equaling 2.2 million km^2 of

Table 3.3: Predictor variables used in the three niche models by Sidder et al. (2016).

Variables	Description	Rationale
CMD	Hargreaves climatic moisture deficit (CMD). Sum of the monthly difference between reference atmospheric evaporatie demand and precipitation. A higher CMD reflects a greater moisture deficit.	Drought affects the host tree's ability to defend itself against bark beetle attack (Safranyik, 1978). Belowaverage precipitation across the growing season correlates with an increased MPB (Carroll et al., 2006).
PAS	Precipitation as snow (PAS, mm) between August of previous year and July of current year.	
PPT_sp	Spring precipitation between March-May.	
PPT_sm	Summer precipitation between June-August.	
PPT_at	Autumn precipitation between SeptemberNovember.	Reduction in autumn moisture immediately following attack benefits larval overwinter survival (Amman, 1978).
bFFP	Julian date on which the frost-free period (FFP) begins.	Spring temperature affects the larval development (Aukema et al., 2008).
eFFP	Julian date on which the frost-free period ends.	Early onset of frost period in the late summer and autumn may affect the egg and larval development (Safranyik, 1978).

Table 3.3 – Continued

Variables	Description	Rationale
Tmin_wt	Winter mean minimum temperature (°C).	Severe winter temperatures can reduce overwinter survival and cause widespread beetle mortality (Safranyik, 1978; Sambaraju et al., 2012).
DD_0_wt	Winter-degree days below 0°C.	
DD_0_sp	Spring degree-days below 0°C.	Spring temperature affects larval development (Aukema et al., 2008).
DD18_sm	Summer degree-days above 18°C.	Summer heat accumulation affects many aspects of the MPB life cycle, including emergence, flight, and egg hatch (Sambaraju et al., 2012)
elevation	Digital elevation model (DEM) at 1-km resolution	Topographic variables roughly define a suitable topography for host species (Safranyik, 1978; Sambaraju et al., 2012).
slope	Maximum change in elevation between each cell and its eight neighbors.	
aspect	Downslope direction of a grid cell.	

Adapted from Sidder et al., 2016

the interior Rocky Mountains. Using both moderate and extreme climate projection scenarios for both 2020 and 2050, results from Evangelista et al., (2011) showed that suitable habitats for both the mountain pine beetle and pine engraver will stabilize or decrease. Habitat for the western pine beetle was shown to increase, however.

Boosted Regression Trees (BRT). Boosted regression trees are "an ensemble method for fitting statistical models that use regression trees and boosting to combine many simple models and improve performance" (Sidder et al., 2016, p. 7). The authors fitted the BRT model with SAHM (Software for Assisted Habitat Modeling) and experimented with parameters for the learning rate and tree complexity with the goal of having at minimum 1000 trees and biologically senisble response curves (Sidder et al., 2016).

General Linear Models (GLM). General linear models are based on maximum likelihood regression principles and use standard linear regression techniques (Long & Lawrence, 2016). GLM is a regression approach which fits parametric terms using some combination of linear, quadratic, and/or cubic terms (Elith et al., 2006). Liang et al. (2014) analyzed a decade-long Landsat time-series generated maps to characterize mountain pine beetle outbreak patterns. The research coupled these maps with a general linear model (GLM) and a set of anthropogenic, biologic, and physical predictor variables. After a stepwise removal of insignificant variables, findings indicated neighborhood mortality, winter mean temperature anomalies, and residential housing densities are positively correlated with mountain pine beetle morality while summer precipitation was found to be negatively correlated (Liang et al., 2014). Additionally, Sidder et al. (2016) found that generalized linear models reduced omission error and had greater predictive success when compared to Maxent or boosted regression trees, though each of the three models generated reasonable predictions.

Significant results of Sidder et al. (2016) include an indication of expansion of climatically suitable habitat for mountain pine beetle over the last fifty years – particularly with an upward shift in the mean elevation across the US Rocky Mountain region. Additionally, their models indicate drought is a more prominent driver for current mountain pine beetle outbreaks than temperature, suggesting a climatic signature change from historic to current outbreaks. Results also show a reduction in climatically suitable habitat although it appears that high elevation forests have an increase in potential susceptibility. In addition, a comparison of the three methods in this same article resulted in reasonable accuracy for all three, though these authors state that the simpler, generalized model predicted a higher percentage of current outbreak locations with a reduced omission error while both Maxent and BRT were the topperforming historical models. The next chapter, based on this review of literature, will outline the data and methods used in my research.

CHAPTER 4
DATA AND METHODS

The recent diffusion of the mountain pine beetle (MPB) well beyond its native range coupled with changing global climate regimes has made future predictions regarding this troublesome species quite difficult. Areas that were once thought inhospitable and safe from invasions now have the potential to become ideal habitat as winters become increasingly warm, precipitation becomes more variable and host forests experience increased stress as they adapt to these fast-changing climatic conditions. While previous research has analyzed mountain pine beetle distributions across the interior west of the United States using Maxent, Alberta remains uncharted territory for these type of analyses over the time period selected for the project and it is hoped information derived from the application of Maxent models will contribute to a general understanding of the current threat and challenge. This chapter will describe the research methods and data used for this thesis intended to assess habitat suitability across Alberta, Canada for the mountain pine beetle.

Study Area

Again, the location for this thesis research is Alberta province of Canada. Alberta, a land locked, western province of Canada, is situated within the square of British Columbia to the west, the Northwest Territories to the north, Saskatchewan to the east and the US state of Montana to the south (Figure 4.1). Alberta has an area of nearly 661,848 square kilometers (255,500 square miles). Elevation ranges from 3,747m (12,293 ft) in the southwest of the province to 152m (499 ft) in the northeast. Mountains and foothills range along the southwestern boundary (Figure 4.2). The Great Plains, composed of largely treeless areas in the eastern and southern regions, sweep eastward across the province, representing part of Canada's great "grain belt". In contrast, the northern half (57% of the province) is covered in boreal forest that is predominantly composed of aspen (*Populus tremuloides*) and white birch (*Betula papyrifer*) in the south shifting to white spruce (*Picea glauca*), larch (*Larix occidentalis*) and black spruce (*Picea mariana*) to the north. Lodgepole pine (*Pinus contorta*) and alpine fir (*Abies lasiocarpa*) are found in the west while the previously discussed jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) are found in the east.

Figure 4.1: Alberta, Canada. Source: Created by author

Figure 4.2: Landscape in mountainous southwest Alberta, Canada with grey-attack trees Source: Taken by author, 2018

Alberta experiences a humid continental climate with four distinct seasons. Due to Alberta's great extent, ranging over 1,200km (750 mi) from north to south and from east to west, climate varies greatly. Average winter extremes range from -54°C in northern Alberta to -46°C in southern Alberta. Average winter temperatures, however, vary from 0°C in the southwest to -24°C in the north. Winter temperatures in the southwest are often moderated by incoming chinook winds from the Rocky Mountains. Average summer temperatures range from 21°C in the Rocky Mountains and in areas north, to 28°C in the prairies of the southeast. Alberta experiences a significant number of sunny days – totals ranging from 1900 to 2500 hours per year - and summer experiences 18 hours of daylight. Due to the presence of the Rocky Mountains, precipitation is often deposited on the windward side of the mountains, creating a rain shadow which extends over the majority of Alberta. Annual precipitation ranges from 300 mm (12 in) in the southeast to 450 mm (18 in) in the north. The leeward foothills of the Rocky Mountains record a mean annual precipitation of 600 mm (24 in). To the point for this thesis, thirty-eight million hectares of Alberta are forested, resulting in Alberta's third largest industry, and contributing $5.3 billion to the economy (Alberta Chambers of Commerce, 2016). Approximately 60% of coniferous forest in Alberta is composed of trees aged 80 years or older (Alberta Agriculture and Forestry, 2018). Between the 2004/2005 fiscal year and 2012, the government of Alberta devoted $336 million for mountain pine beetle control and mitigation (Government of Alberta, 2013). If current projections hold true, this sum will get much greater before it declines due to intermittent infestation-driven deforestation.

Research Design

Maxent (Maximum Entropy Modeling) was selected for this study to create a species distribution model for the mountain pine beetle across Alberta. As mentioned in Chapter 3, species distribution models (SDMs) are widely used in biogeography, macroecology and biodiversity research. Maxent, one of the most commonly used contemporary SDMs, is a machine-learning algorithm which calculates a species' probability distribution based on outcomes predicting maximum entropy, or in other words, that which is closest to a uniform solution.

Again, as noted in Chapter 3, Maxent is a presence-only model, allowing for the incorporation of a wide range of types of date sources, from natural history collections to field collected data, to be utilized by scientists while avoiding the high costs of sampling a species throughout its range (Gomes et al., 2018). The model is nonlinear, nonparametric and is not sensitive to multicollinearity (Evangelista et al., 2011). Such modeling techniques which require only presence data are of extreme value due to data limitations and available resources in terms of both cost and time for surveys and data analyses (Graham et al., 2004). Maxent has become increasingly popular since its introduction in 2004. Using presence, or occurrence, data, Maxent is designed to allow researchers to model a species' geographic distribution based on correlations between known occurrence records and the associated environmental conditions at those localities (Phillips et al., 2006). When applied to presence-only species data, the pixels of the study area constitute the space over which the Maxent probability distribution is defined (Phillips et al., 2006).

While presence data may be abundant, spatially registered absence data are much more difficult to obtain and as noted earlier, are often unreliable due to insufficient survey effort or resources (Gomes et al., 2018). In response to the lack of absence data, Maxent uses a background sample to contrast the distribution of occurrences along environmental gradients against the distribution of background points, selected at random from the study area (Gomes et al., 2018). Thus, to create a model, Maxent generates background points randomly for comparison against observed presence data. Maxent also requires data that reflect actual environmental conditions as inputs. These variables are most often sourced from the WorldClim BioClim list of 19 climatic variables, noted previously, which contain a range of moderate to high resolution climatic data and have been used by many researchers in conjunction with the Maxent model (Baldwin, 2009; Evangelista et al., 2011; Rochlin et al., 2013; DellaSala et al., 2011; Dowling, 2015; Abrhaet al., 2018; Zhang et al., 2018; Raghavan et al., 2019). This study follows the conventions established in this previous research and discussed extensively earlier in the thesis.

Maxent software version 3.4.1 is freely available online (www.cs.princeton.edu/%7Eschapire/ maxent). A complementing tutorial with accompanying test data is also provided, with thorough instructions for data preprocessing as well as useful introductions to Maxent's features and capabilities. Numerous university faculty as well as scientific researchers have posted additional tutorials to further illustrate the previous uses of Maxent. In addition, an active Google group exists for Maxent, providing a live forum for past, current and potential users of the software to help new adopters troubleshoot many potential problems. As more and more work is completed using this software, the resources represented by the Google group (https://groups.google.com/forum/#!forum/MAXENT) will become ever-more valuable.

The use of the Maxent model produces several outputs, one of which is an html file, which allows the editing of results. In addition to modeling a species' current distribution, Maxent has built-in capabilities to project potential future distributions by incorporating two sets of environmental conditions as two unique sets of variables. To be clear, current environmental conditions build the model while environmental conditions sourced from climate models projecting future changes using the MESS (Multivariate Environmental Similarity Surface) analysis tool, incorporated in the model.

Maxent output produces several charts, including the Area Under the Receiver Operating Characteristic (ROC) Curve, or the AUC. For each run, the AUC returns a number between zero and one, indicating how well the model performs. A value of 0.5 indicates the results may be near to random whereas confidence increases as the AUC value nears 1.0. The output also produces results which test the contribution of each incorporated environmental variable in two different ways – jackknife tests and analysis of variable contributions. Jackknife tests identify the most significant variables by rank order by testing each variable in isolation and comparing its relative contribution to explanatory prediction power to that of all the incorporated variables. The analysis of variable contributions also provides the percent of total prediction that each variable contributes to the model.

In addition, the Maxent model also produces a raster file which displays habitat suitability on a 0 – 1 range. The habitat suitability threshold is defined by the user. In this study, a sensitivity criterion of 90% is used to discern between suitable and unsuitable habitat for diffusion of the mountain pine beetle. Maxent outputs this graphic in an ASCII file (.asc) which can be converted, using the ArcGIS ASCII to Raster tool in Spatial Analysis. This feature allows for further analysis of mountain pine beetle habitat suitability across the study area through the production of raster-based maps for each time period under investigation.

Data for the Analysis

Several forms of data are required for Maxent analysis. Presence data for the mountain pine beetle, kindly provided by the Forestry Division of Alberta Agriculture and Forestry, serves as the biological data that constitutes the core of the model. Nineteen current climatic variables, detailed in Table 4.1, are required in order to train the model to accurately reflect conditions within all areas where the mountain pine beetle is known to reside within the study area. Bioclimatic variables are sourced from the monthly temperature and rainfall values in order to generate more biologically meaningful variables (Hijmans et al, 2005). Finally, future climate scenario data are also required so that future habitat suitability for the mountain pine beetle can be projected into the future.

Table 4.1: WorldClim's 19 bioclimatic variables

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (mean of monthly (max temp – min temp))
BIO3	Isothermality (BIO2/BIO7) (*100)
BIO4	Temperature Seasonality (standard deviation * 100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5 – BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Source: Adapted from Hijmans et al., 2005

Presence Data

Point data for mountain pine beetle presence in Alberta, Canada were graciously provided through the Forestry Division of the Alberta Agriculture and Forestry Department. Until 1995, forest pest surveys were conducted annually by the Forest Insect and Disease Survey (FIDS) unit of the Canadian Forest Service. In these early years, surveys were conducted from fixed wing aircraft, based on the services of a trained sketch-mapping surveyor who delineated affected polygons and rated associated damage levels. In 1997, provincial governments took control of the responsibility of conducting all insect surveys within their provinces. Methodologies used across provinces then diverged. Once infestation spread to Alberta in 2005, Alberta developed a "zero tolerance" policy to the mountain pine beetle. From this point forward, the methodology used in Alberta to conduct the insect surveys used helicopters equipped with GPS (global positioning systems) to more accurately locate individual clusters of attacked trees, with identification resolution for these surveys often down to a single tree. These methods are considered to have produced much more accurate results in terms of the identification of infestation locations and infestation levels all with spatial georeferencing as compared to the previous fixed wing survey efforts, whereby location was often only roughly estimated (Cooke & Carroll, 2017). Though there are known limitations to the data, the data has been used numerous times to make reliable large-scale inferences for studies referenced previously in Chapter 3 in this thesis (Aukema et al., 2006; Chen et al., 2015). For further description of how this data is obtained and its known limitations, please see Appendix A.

Regardless of the methods for collection, point data for the presence of the mountain pine beetle has been collected on a nearly annual basis, going back to 1975. For the purpose of this study, point data from year 2017 is used to train and test the model. Upon investigating the data, it was found that many years contained point locations for red attack trees that were sourced from other causes than mountain pine beetle attack. Using ESRI's ArcMap 10.6.1, only records that were designated as mountain pine beetle attack were retained from the original annual aggregated datasets. Also, this point data was further processed in order to match the geographic extent, coordinate system and pixel size of the climate data – a strict requirement for Maxent. Ultimately, all occurrence data was converted to CSV files to include only three columns, in this order: species, longitude and latitude. The 2017 dataset incorporated 17,628 records of mountain pine beetle occurrence within the study area.

Environmental Data

Environmental variables of interest include both current climatic variables (Table 4.1) and projections of these climatic variables in the future as well as elevation above sea level (m) and a binary variable reflecting the presence/absence of forest land use/land cover across the study area. All climatic variables were obtained through WorldClim version 1.4 (http://worldclim.org/) which are already downscaled and bias corrected. These bioclimatic variables have been shown to support more effective model development as compared to monthly data alone, as insects are easily affected by fluctuations in temperature (Kumar & Stohlgren, 2009).

Data for current climate conditions were obtained from WorldClim's 19 bioclimatic variables (see Table 4.1) as GeoTIFF files. Climatic variables based on future climate scenarios were obtained from the CCSM4 climate model, based on CMIP5, for the years (2050 and 2070). Moderate Representative Concentration Pathway (RCP) 4.5 as well as the identical variables generated using a less optimistic scenario of RCP 8.5 were downloaded for both time frames, 2050 and 2070. RCP 4.5 predicts that emissions will peak in 2040 and then stabilize. In contrast, RCP 8.5 predicts that emissions will continue to grow past 2100. All climatic variables were selected at a 30-second resolution, equal to roughly $1km^2$, or 0.00833333333 degrees.

Maxent requires that all environmental variables be of the same geographic extent, spatial resolution and projection coordinate system (Evangelista et al., 2011). Therefore, all environmental variables were also processed using ArcMap 10.6.1 to create a consistent and appropriate dataset within a common scale. To accomplish this, the Extract by Mask tool was used, setting the variable BIO1 as the mask and altering the Environment settings so that each operation matched the exact geographic extent, resolution and projection system of BIO1. ModelBuilder was then utilized to expedite the process and ensure that each layer (each variable) was generated in precisely the same manner for exactly the same pixel and scale. Figure 4.3 details the data development steps used to prepare all data for inclusion in the model.

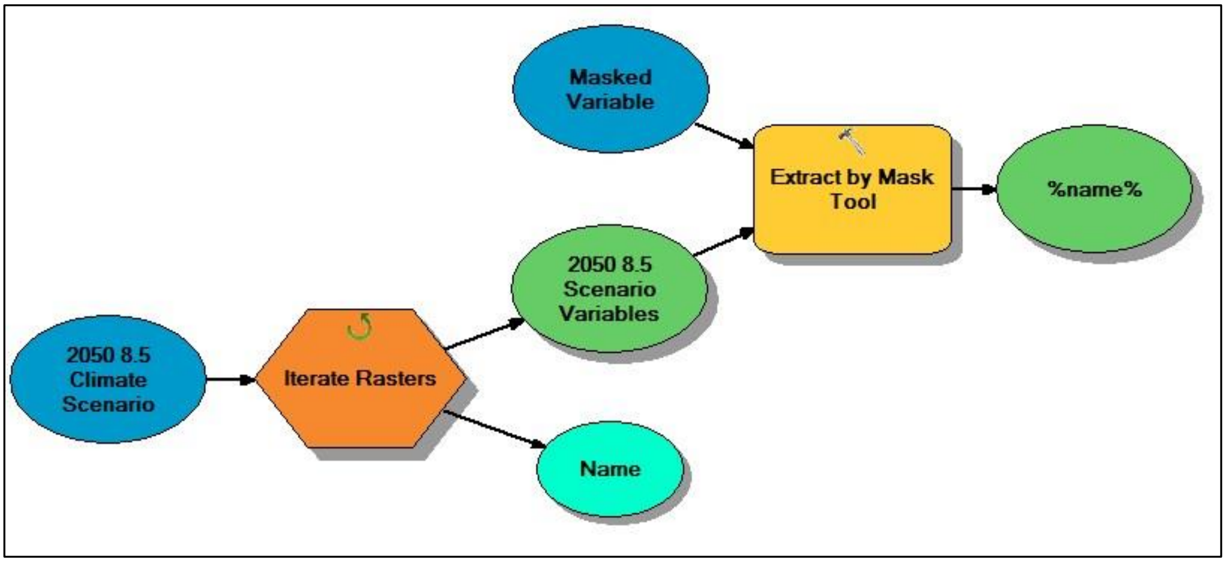

Figure 4.3: Extract by Mask operation ModelBuilder used in ArcGIS 10.6.1 Source: Created by the author

Once all data were standardized, using ArcMap, all resulting layers were converted from

GeoTIFF files to ASCII files using: Toolbox > Conversion Tools > From Raster > Raster to ASCII, ensuring the resulting output file ended in .asc. All resulting datasets are sent to a unique directory for subsequent use in the Maxent model runs (Figure 4.4).

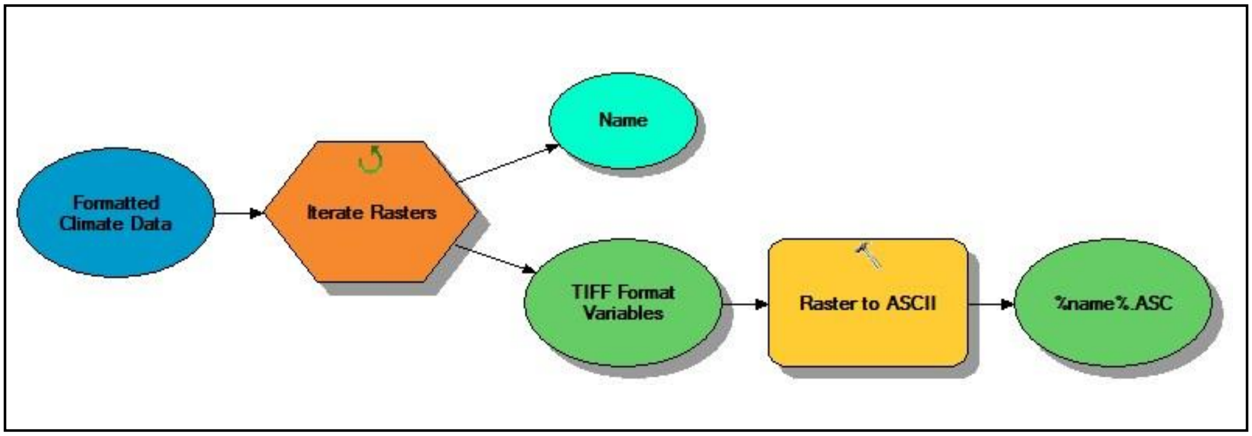

Figure 4.4: Process used to convert raster files to ASCII files in ArcGIS 10.6.1. Source: Created by the author

Finally, elevation data and land cover data were obtained through Geospatial Data Extraction (http://maps.canada.ca/czs/index-en.html). A larger land cover dataset was reclassified to include only three land use/land cover (LULC) categories: (1) conifer forests (code 210); (2) broadleaf forests (code 220); and (3) mixed forest (code 230). The remaining land use/land cover categories were classified as no data and masked out of the study analyses. The resulting raster dataset representing only forested areas was then converted to an ASCII file for use in Maxent and subject to the same data processing procedures as the steps used to process the climatic variables that are described above.

Model Inputs and Parameters

This section will outline the inputs and all parameters that were tuned for use in the

Maxent user interface. Mountain pine beetle presence data for 2017 is linked to the "Samples" file. The bioclimatic variables for the current climate scenario are linked to "Environmental Layers". A unique output folder is designated for each model run and then the prepared future climate projection data is individually linked to "Projection layers directory/file". The output type is Logistic and file type is .ASC.

Parameters are tuned to include a 10 percentile training presence threshold rule. By doing this, suitable habitat is defined to include 90% of the data, the portion used to develop the model. This was designated under Settings > Advanced > Apply threshold rule > 10 percentile training presence as suggested by previous successful research efforts (Evangelista et al., 2011; Dowling, 2015). Each analysis included 10 replications, using a different set of randomly selected (bootstrap) occurrence points for training and validating the model. These results were then averaged across the 10 replicates for a single results model. AUC values and associated estimates of variable contributions in percentage values were recorded for each model. 30% of the occurrence points are typically withheld for model validation, in accordance with Evangelista et al. (2011). The number of iterations for each run was increased from the default value of 500 to 5000 in order to allow smoothing and improve model performance. This is done so that the model is permitted an adequate number of iterations to assure convergence. Without adequate iterations for convergence, the model may over or under-predict. All other parameters remained set at the default settings.

The first Maxent run includes the current climate data. A separate run is conducted for each of the two emissions scenarios, 4.5 and 8.5, for each 2050 and 2070, resulting in a total of five models (Table 4.2). Each model was run in two sets. Initially, all 21 environmental variables are included. Finally, a second set of models is run, using only the top four contributing variables, as recommended by previous research (Papes, 2018). These four top contributing variables were recorded, including their numeric contribution, given in percent.

Table 4.2: Summary of five Maxent models

Model Run	Description
A	Current climatic variables only
B	Projection for climate scenario 2050, RCP 4.5
C	Projection for climate scenario 2050, RCP 8.5
D	Projection for climate scenario 2070, RCP 4.5
E	Projection for climate scenario 2070, RCP 8.5

Source: Created by the author

Graphic representations of results are also included in the Maxent output. Analysis of the graphic results can be conducted in ArcGIS by importing the .ASC file and converting it to a raster file (Arc Toolbox > Conversion Tools > To Raster > ASCII to Raster). The preset, "Integer" needs to be changed to "Float", allowing the results to range from 0 to 1. In order to display the results as binary - suitable and unsuitable habitat – the raster values need to be reclassified using the Reclassify tool. Under 'Classify', designate the classification method to be 'Manual' with two 'Classes'. The break value used for the first class should be gleaned from the threshold value, which is found in the Maxent 'Results' CSV under "10 percentile training presence logistic threshold". In ArcGIS, a range of the lowest number to this threshold is classified as zero (unsuitable), while the range above this threshold is classified as one (suitable). The resulting raster displays the two classes, zero and one, unsuitable and suitable habitat for the species at hand, in this case, the mountain pine beetle. The area of land infested by the beetle (and not infested) can be calculated by exploring the raster count in the attribute table. Results of all analyses are presented in Chapter 5.

CHAPTER 5

RESULTS

In this chapter, Maxent model results are depicted both numerically and graphically. Overall model performance is evaluated using the Area Under the Receiver Operating Characteristic (ROC) Curve, or the AUC. As described in Chapter 4, AUC values range from 0 to 1, with a result of 0.5 indicating that results may be random with confidence increasing as the value nears 1.0. Again, binary maps created to show suitable versus unsuitable habitat under current and future climatic conditions are provided as figures, followed by the quantified area and percent reduction in habitat suitability. Environmental variables are assessed both by their percent contribution and a jackknife test of variable importance. The jackknife test of variable importance sifts through the environmental variable in two ways - where first, the model eliminates one variable at a time and reporting the most important variable. Second, the jackknife test runs each variable independently, reporting which variable has the most information not present in any other variable. Again, 21 total environmental variables are used as dependent variables for introduction into the Maxent models. Prior to model results, descriptive statistics are provided to contextualize the resulting models. Table 5.1 provides the descriptive statistics for all variables under the current climate scenario used in the baseline model. As will be clear later in the chapter, the four variables that are retained in the model are shown in Table 5.2.

Descriptive Statistics

Table 5.1 provides the mean, range and standard deviation of elevation and the 19 bioclimatic variables (forests, the 21st environmental binary variable, is categorical, not continuous and is excluded from the statistical analysis). The study area incorporates a wide spectrum of elevation, with a low ranging from 171 meters in the Slave River to a high of 3,523 meters at Mount Columbia (Figure 5.1). Average annual precipitation (Bio12) ranges from a low of 270mm to a high of 836mm while precipitation of the warmest quarter (June, July, August) (Bio18) has a range from 118mm to 310mm (Figure 5.2). Annual mean temperature (Bio1) ranges from a low of -8.6℃ to a high of 6.2℃. Mean temperature of the warmest quarter (Bio10) ranges from a low of 0.2℃ to a high of 18.7℃ while the minimum temperature of the coldest month (Bio6) ranges from a low of -31.8℃ to a high of -12.0℃ (Figure 5.3). Figures 5.1 – 5.3 offer insight into the spatial distribution of each variable in Alberta, Canada and are helpful in understanding the final habitat suitability maps produced by Maxent.

Model Performance

Maxent model performance is evaluated using the Area Under the Receiver Operating Characteristic (ROC) Curve, or the AUC. As described in Chapter 4, AUC values range from 0 to 1, with a result of 0.5 indicates the results may be random with confidence increasing as the value nears 1.0. All models performed reasonably well, with AUC values ranging from a minimum of 0.715 to a maximum of 0.794. Individual model AUC values are reported in parentheses in Table 5.4.

Table 5.1: Descriptive statistics of the current climate variables used in the analysis

Variable	Description	Unit	Mean	Minimum	Maximum	Standard Deviation
Bio1	Annual Mean Temperature	°C	0.29	-8.60	6.20	2.16
Bio2	Mean Diurnal Range (mean of monthly (max temp – min temp))	°C	12.22	8.20	15.30	1.02
Bio3	Isothermality (BIO2/BIO7) (*100)	%	2.65	1.90	3.60	4.01
Bio4	Temperature Seasonality (standard deviation * 100)	%	1157.87	684.40	1468.30	183.96
Bio5	Max Temperature of Warmest Month	°C	22.28	7.30	28.80	2.13
Bio6	Min Temperature of Coldest Month	°C	-23.42	-31.80	-12.00	4.42
Bio7	Temperature Annual Range (BIO5 – BIO6)	°C	45.71	27.90	53.00	47.09
Bio8	Mean Temperature of Wettest Quarter	°C	13.94	7.40	18.60	2.14
Bio9	Mean Temperature of Driest Quarter	°C	-6.98	-21.30	12.20	3.54
Bio10	Mean Temperature of Warmest Quarter	°C	14.17	0.20	18.70	1.91
Bio11	Mean Temperature of Coldest Quarter	°C	-15.36	-23.90	-5.50	4.30
Bio12	Annual Precipitation	mm	453.66	270.00	836.00	7.88
Bio13	Precipitation of Wettest Month	mm	77.14	52.00	116.00	1.33
Bio14	Precipitation of Driest Month	mm	18.29	7.00	47.00	0.52
Bio15	Precipitation Seasonality (Coefficient of Variation)	%	52.07	16.00	72.00	1.08
Bio16	Precipitation of Wettest Quarter	mm	205.84	128.00	309.00	3.74
Bio17	Precipitation of Driest Quarter	mm	61.23	28.00	174.00	1.78
Bio18	Precipitation of Warmest Quarter	mm	205.08	118.00	310.00	3.79
Bio19	Precipitation of Coldest Quarter	mm	69.49	28.00	214.00	2.17
DEM	Digital Elevation Model	m	750.82	171.00	3523.00	409.62

Source: Calculated by author

Table 5.2: Descriptive statistics of the four variables retained in the final model for each future climate scenario.

Climate Model	**Variable**	**Description**	**Unit**	**Mean**	**Range**	**Standard Deviation**
B: 2050, RCP 4.5 Moderate Emissions	Bio18	Precipitation of the warmest quarter	mm	199.02	110.00 – 303.00	3.80
	Bio12	Annual precipitation	mm	464.25	270.00 – 846.00	8.31
	Bio10	Mean temperature of warmest quarter	°C	16.91	3.80 – 21.9	1.93
C: 2050, RCP 8.5 Extreme Emission	Bio18	Precipitation of the warmest quarter	mm			3.78
	Bio12	Annual precipitation	mm	462.79	267.00 -856.00	8.17
	Bio10	Mean temperature of warmest quarter	°C	17.70	44.00 – 22.80	2.00
				20.20	-27.80 – -9.40	
Scenario	Bio6	Minimum temperature of coldest month	°C	-193.85	100.00 – 304.00	4.06
Scenario	Bio6	Minimum temperature of coldest month	°C	-20.01	-27.60 - -9.10	4.13
D: 2070, RCP 4.5 Moderate Emissions Scenario	Bio18	Precipitation of the warmest quarter	mm	200.89	107.00 – 318.00	4.12
	Bio12	Annual precipitation	mm	476.09	273.00 – 869.00	8.62
	Bio10	Mean temperature of warmest quarter	°C	17.29	4.10 – 22.40	1.96
	Bio6	Minimum temperature of coldest month	°C	-20.00	-27.90 - -8.300	4.43
E: 2070, RCP 8.5 Extreme Emissions Scenario	Bio18	Precipitation of the warmest quarter	mm	191.19	103.00 – 304.00	3.59
	Bio12	Annual precipitation	mm	475.18	273.00 – 864.00	8.10
	Bio10	Mean temperature of warmest quarter	°C	19.21	6.10 – 24.50	2.03
	Bio6	Minimum temperature of coldest month	°C	-18.27	-25.30 – -7.10	3.99

Source: Calculated by the author

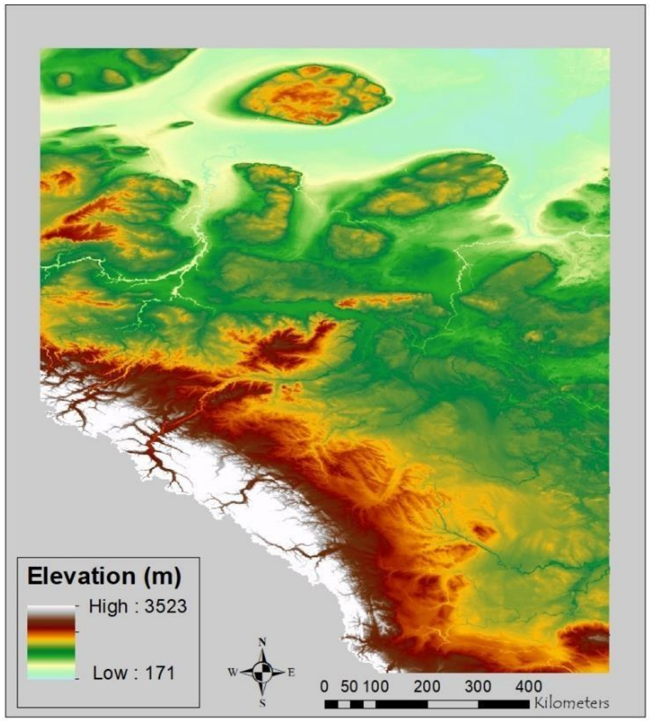

Figure 5.1: Topographic map of Alberta, Canada
Source: Created by the author

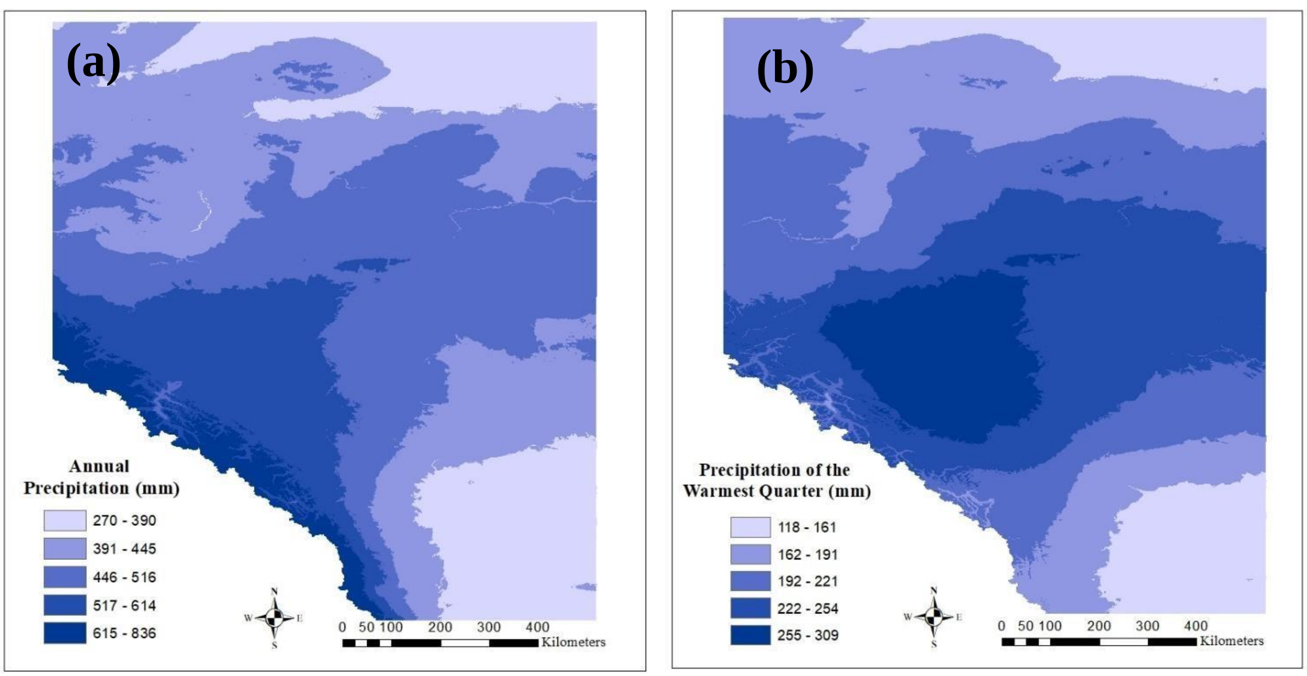

Figure 5.2: Annual precipitation (Bio12) (a) and precipitation of the warmest quarter (June, July, August) (Bio18) (b) in Alberta, Canada during current climate conditions. Source: Created by author

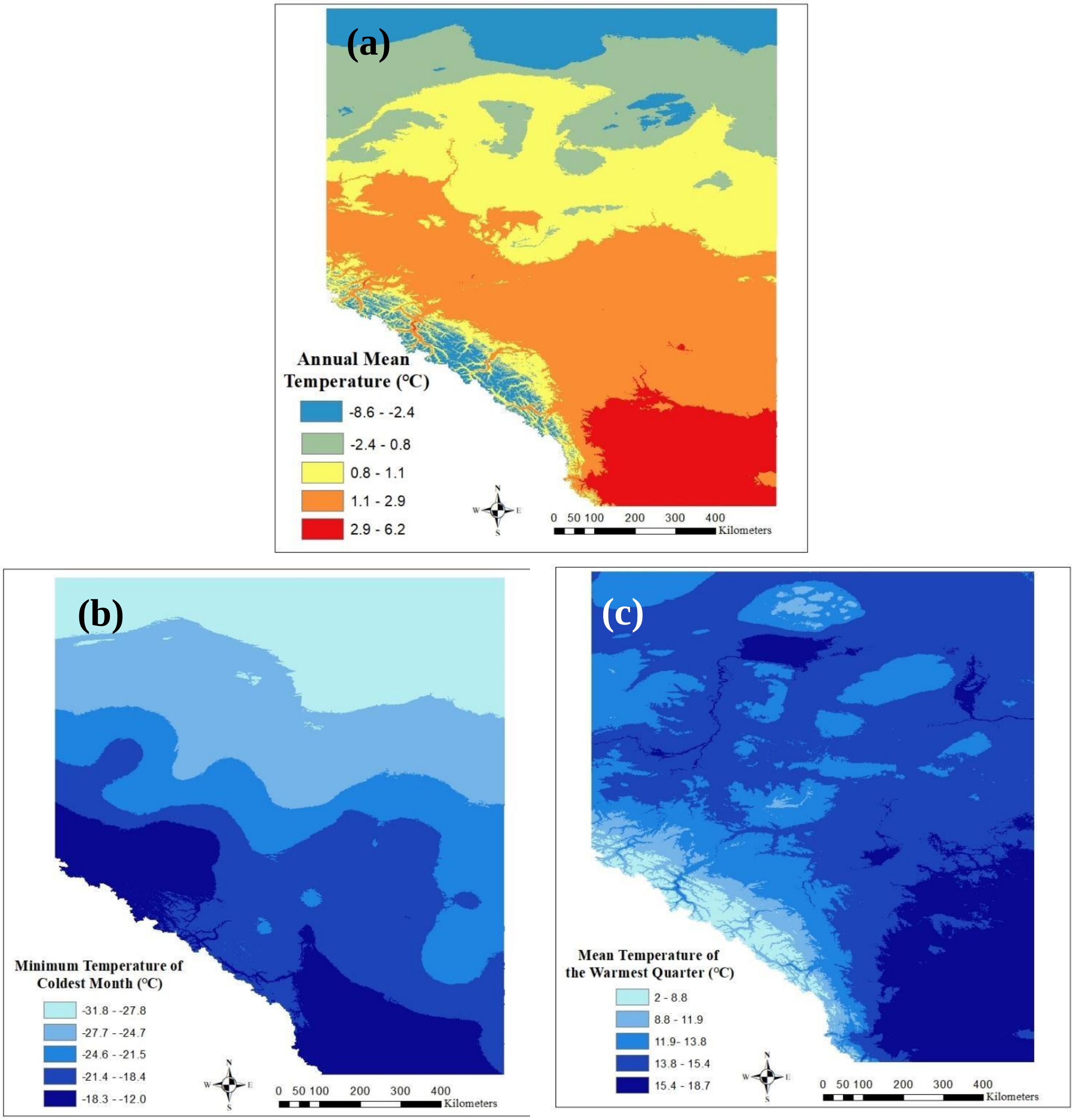

Figure 5.3: Annual mean temperature (Bio1) (a); minimum temperature of the coldest month (January) (Bio6) (b); and mean temperature of the warmest quarter (June, July, August) (Bio10) in Alberta, Canada under current climate conditions. Source: Created by the author

Habitat Suitability Distribution Maps

Turning to the visualizations of the Maxent results depicted in Figures 5.4 and 5.5, these maps show some very interesting results. The maps for future scenarios clearly indicate a continuous spatial reduction in habitat for the mountain pine beetle over time. The binary maps shown in Figure 5.5 were created using a sensitivity criterion of 90% to discern between suitable and unsuitable habitat for the future diffusion of the mountain pine beetle, as described in Chapter 4.

Model A, incorporating only current climatic conditions, identifies suitable habitat for the mountain pine beetle located along the eastern slopes of the Rocky Mountains with an additional concentration that has broken out in central Alberta. Figure 5.4 shows a comparison between the Division of Forestry's mapped results of the 2017 annual mountain pine beetle survey (a) and the Maxent model output for the distribution of mountain pine beetle in 2017 under current climate conditions (b) (Model A). This comparison provides validity to the Maxent model's performance as the extent and location of infestation in both maps is nearly identical. The aggregate sum of suitable habitat is to approximately 68,368 km^2 for 2017 (Table 5.3). This habitat is considered to represent the current location and extent of mountain pine beetle infestation and is used as a baseline for future comparison. Model A performed reasonably well, with an average test AUC of 0.793. Counter-intuitively, and perhaps the most important finding of the study, future projection models, again, show a decline in suitable habitat for the mountain pine beetle.

All independent models using future climate projections (models B, C, D and E) predict decreasing habitat suitability for the mountain pine beetle (Figure 5.5). Model B, incorporating the climate scenario for 2050 RCP 4.5, reports a habitat suitability decrease of 68%, to 21,604

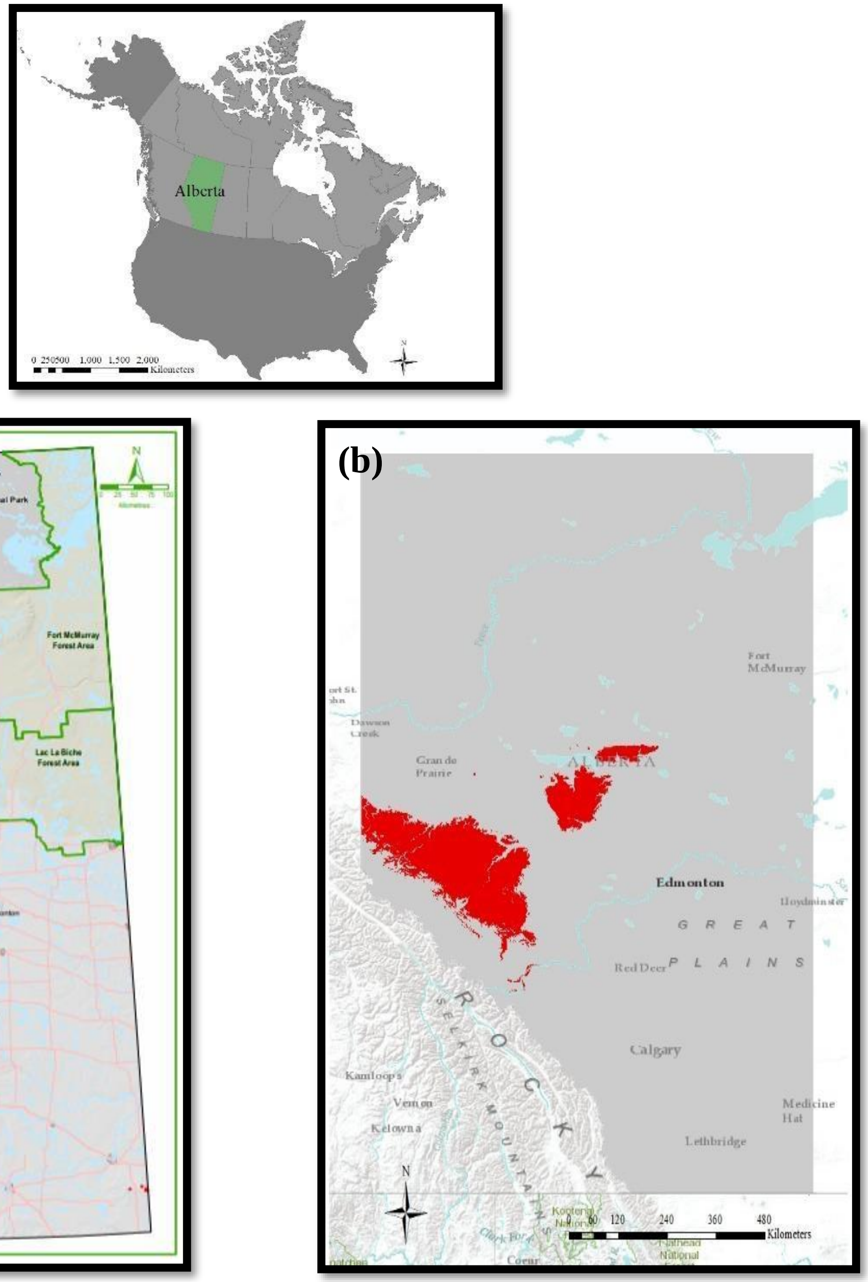

Figure 5.4: Forestry Division of the Alberta Agriculture and Forestry Department's annual mountain pine beetle survey map for 2017 (a) showing their representation of mountain pine beetle infestation compared to the Maxent output (b) representation of infestation extent under current climate conditions (Model A). Geographic coordinate systems differ. Source: (a) (Alberta Agriculture and Forestry, 2017), (b) Created by the author

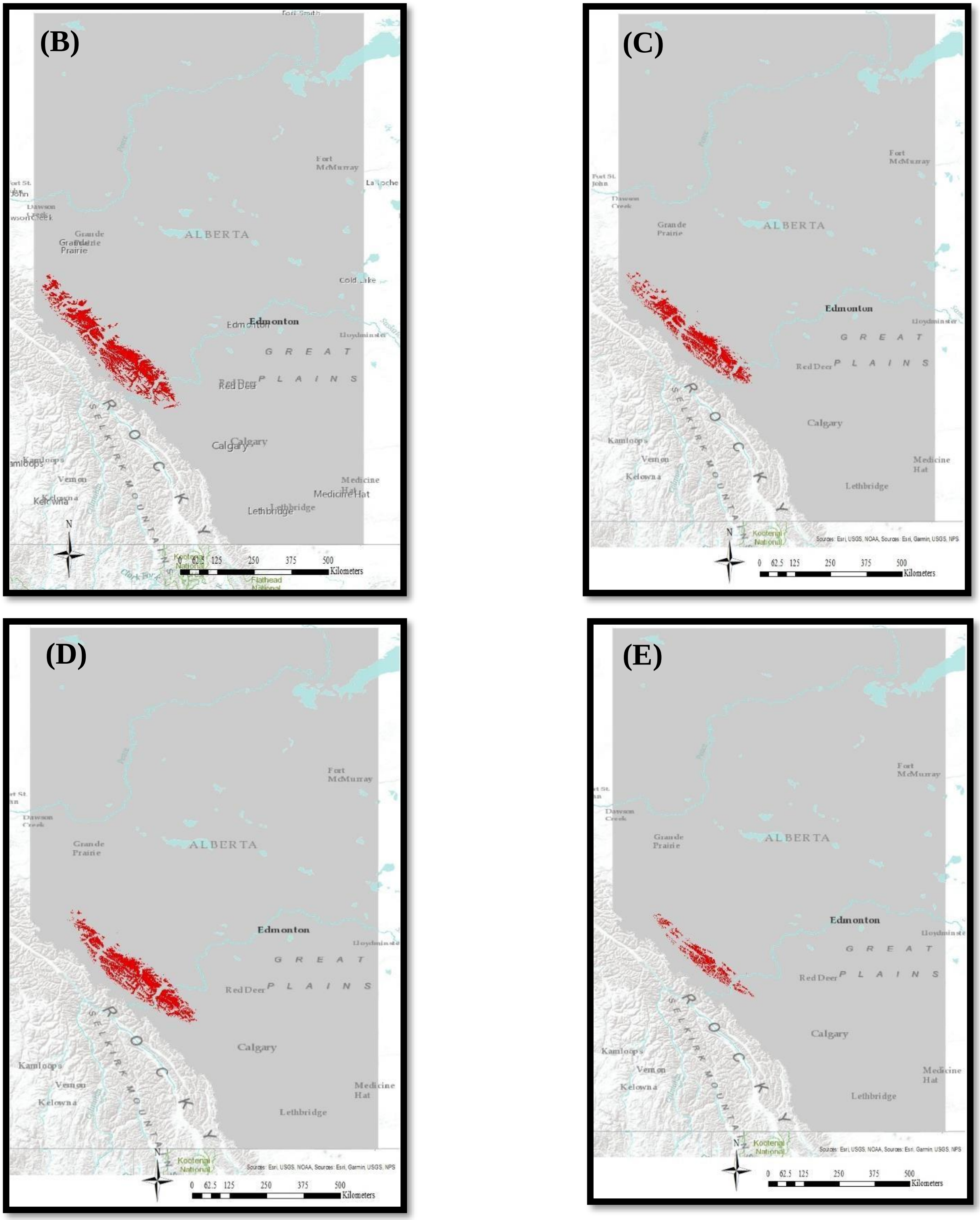

Figure 5.5: Predicted habitat suitability of the mountain pine beetle future climate projections. Two emissions scenarios, RCP 4.5 (B and D) and 8.5 (C and E), were modeled for each 2050 (B and C) and 2070 (D and E), respectively. RCP 4.5 represents a moderate emissions scenario; RCP 8.5 represents an extreme emission scenario. Red areas show suitable habitat and gray areas show unsuitable habitat. Average test AUC was 0.778.

km^2. Model C, incorporating the climate scenario for 2050 RCP 8.5, reports a habitat suitability decrease of 78%, to 15,156 km^2. Model D, incorporating the climate scenario for 2070 RCP 4.5, reports a habitat suitability decrease of 75%, to 17.038 km^2. Finally, Model E, incorporating the climate scenario for 2070 RCP 8.5, reports a habitat suitability decrease of 92%, to 5,729 km^2 (Table 5.3).

These results, and their consistency across scenarios, are both interesting and important. If results of Maxent are valid, several conditions may be developing over time. Of course, there is no way of knowing, based on these results, which of the outcomes is most probable but they do offer baseline insights into future possibilities.

Table 5.3: Predicted area (km^2) of suitable habitat for mountain pine beetle.

Model	Total Area (km^2)	Area Decrease (km^2)	Percent Decrease (%)
A	68,368		
B	21,604	46,764	68
C	15,156	53,212	78
D	17,038	51,330	75
E	5,729	62,639	92

Note: Model A uses current climate data, representing the current extent of the mountain pine beetle and serves as a baseline for comparison; Model B uses climate projection data for 2050, RCP 4.5 (moderate emissions); Model C uses climate projection data for 2050, RCP 8.5 (extreme emissions); Model D uses climate projection data for 2070, RCP 4.5 (moderate emissions); and Model E uses climate projection data for 2070, RCP 8.5 (extreme emissions). Source: Created by the author

Variable Contributions and Relative Importance

The Maxent model analyzes environmental variables both by considering their percent contribution to model performance (Table 5.4) and also by performing a jackknife test of variable importance (Figure 5.6). Of the 21 total environmental variables included, four climatic variables consistently rose to the top as having the highest percent contribution. Precipitation of the warmest quarter (Bio18), typically representing the months from June to August, is the variable with the highest contribution, with an average contribution of 31.6% (Table 5.4). Annual precipitation (Bio12) has the second highest predictive power with an average contribution of 13.5%. Throughout all five models, variable Bio18 consistently outperforms all other variables, accounting for the highest percent contribution for each model.

Table 5.4: Top four predictor variables and their average percent contribution (from 10 replicates) from the Maxent model. AUC values for each model are reported in parentheses. Variables are ranked to show the order of importance per model.

Predictor Variables	Contribution (%)	Rank
Model Run A: Current variables only (0.793)		
Precipitation of the warmest quarter (Bio18)	31.6	1
Annual precipitation (Bio12)	13.5	2
Mean temperature of warmest quarter (Bio10)	10.3	3
Minimum temperature of coldest month (Bio6)	9.9	4
	Σ 65.3	
Model Run B: 2050 RCP 4.5 Projection (0.793)		
Precipitation of the warmest quarter (Bio18)	30.6	1
Annual precipitation (Bio12)	15.5	2
Mean temperature of warmest quarter (Bio10)	7.8	4
Minimum temperature of coldest month (Bio6)	12.2	3
	Σ 66.1	
Model Run C: 2050 RCP 8.5 Projection (0.715)		
Precipitation of the warmest quarter (Bio18)	32.5	1
Annual precipitation (Bio12)	10.7	3
Mean temperature of warmest quarter (Bio10)	11.2	2
Minimum temperature of coldest month (Bio6)	9.9	4
	Σ 64.3	
Model Run D: 2070 RCP 4.5 Projection (0.794)		
Precipitation of the warmest quarter (Bio18)	37	1
Annual precipitation (Bio12)	7.1	4
Mean temperature of warmest quarter (Bio10)	9.7	2
Minimum temperature of coldest month (Bio6)	9.5	3
	Σ 63.3	
Model Run E: 2070 RCP 8.5 Projection (0.794)		
Precipitation of the warmest quarter (Bio18)	31.6	1
Annual precipitation (Bio12)	13.8	2
Mean temperature of warmest quarter (Bio10)	7.5	4
Minimum temperature of coldest month (Bio6)	7.9	3
	Σ 60.8	

Source: Created by the author

Finally, Maxent performs a jackknife test of variable importance. Again, the jackknife test of variable importance sifts through the environmental variable in two ways - where first, the model eliminates one variable at a time and reporting the most important variable. Second, the jackknife test runs each variable independently, reporting which variable has the most information not present in any other variable. Model B shows annual precipitation (Bio12) as the environmental variable with the highest gain when used in isolation, indicating that it has the most useful information by itself. Minimum temperature of the coldest month (Bio6) is the environmental variable which decreases the gain the most when it is omitted, indicating Bio6 as having the most information that is not present in any other variable (Figure 5.6). Each future model's jackknife test report similar findings (Appendix B).

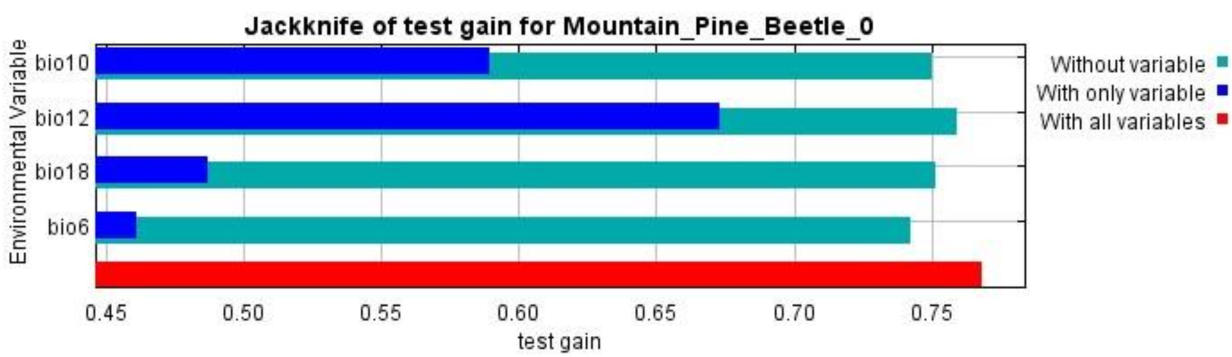

Figure 5.6: Jackknife test evaluating relative importance of environmental variables for mountain pine beetle in Alberta, Canada. Note: "Bio10" is mean temperature of the warmest quarter; "Bio12" is annual precipitation; "Bio18" is precipitation of the warmest quarter; "Bio6" is minimum temperature of the coldest month.

CHAPTER 6

DISCUSSION

The Maxent model analyses results indicate that a changing climate will lead to significant changes in habitat suitable for the mountain pine beetle. Climatic variables based on future climate scenarios were obtained from the CCSM4 climate model, based on CMIP5, for the years 2050 and 2070. Moderate Representative Concentration Pathway (RCP) 4.5 as well as the identical variables generated using a less optimistic scenario of RCP 8.5 were downloaded for both time frames, 2050 and 2070. RCP 4.5 predicts that carbon emissions will peak in 2040 and then stabilize. In contrast, RCP 8.5 predicts that carbon emission will continue to grow past 2100. Interestingly, these results depict a resounding decrease in overall habitat over time, regardless of the emissions scenario under consideration. These results contrast with current concerns by the Forestry Division of Alberta and much of the current literature anticipating the continued eastward diffusion into the boreal forest.

It is important, however, to remember that like all models, Maxent models are simplifications and abstractions of reality. These model results contain numerous untested and untestable assumptions about changing environmental conditions over space and time (Evangelista et al., 2011). Furthermore, these models rely on projected climate scenarios and although global climate models have significantly improved, they continue to contain numerous uncertainties, whether considering the model structure, the unpredictability of future carbon emissions, and natural variability that may occur in the future (Woldemeskel et al., 2015).

Temperature and precipitation are projected to change significantly within Canada under future climate scenarios. Importantly, precipitation is known to be one the most difficult variables to accurately predict as GCMs do not include the full range of real-world precipitation-forming processes that occur over the extent of the province of Alberta, much less for the North American continent (Legates, 2014). Finally, the data used for this analysis shows only the spatial distribution of the mountain pine beetle in Alberta, Canada. This spatial distribution does not include the full range of climate variability for mountain pine beetle habitat.

Thus, the Maxent results, which recognized precipitation of the warmest quarter (Bio18) as having the highest contribution to model construction, should be interpreted with caution. There are copious additional natural and anthropogenic variables that are known to facilitate or regulate mountain pine beetle habitat, range and intensity (Evangelista et al., 2011). Interspecific interactions, predation, adaptation, forest management practices, localized climatic conditions and extreme weather events all contribute to the evolution or change in habitat suitability for the beetle but simply cannot be confidently incorporated into current versions of Maxent models (Heikkinen et al., 2006; Evangelista et al., 2011). The wind event, for example, which successfully displaced mountain pine beetle populations over the Rocky Mountains in 2005, while not unprecedented, is a rare and unpredictable event that simply cannot be anticipated. This displacement into entirely novel terrain allowed alarming population growth leading to monumental ecological change which is poised to continue. Finally, the WorldClim data used for the current climate models represents averaged measurements gathered between 1970 and 2000. Therefore, these results represent a hypothesis of a potential future scenario of mountain pine beetle habitat suitability, their possible distribution and forest vulnerability.

Despite the varying degrees of uncertainty, these model results and similar studies provide valuable insights to forest managers to the potential effects of climate change on biodiversity (Heikkinen et al., 2006; Evangelista et al., 2011). Mountain pine beetle is a climate driven species. While future carbon emission rates are unpredictable, even under moderate emission scenarios, future changes in climate and budding infestations are expected to continue to have significant impacts on forest composition, carbon sequestration and cycling, fire regimes and hydrology (Evangelista et al., 2011). Some researchers consider the silver lining and speculate upon the long-term, positive effects that mountain pine beetle infestations may inflict by default. One particular hypothesis of interest is that mountain pine beetle outbreaks may indeed act as a natural selection event, eliminating trees that are most susceptible to the beetle and the least adapted to the anticipated warmer, drier conditions (Six, Vergobbi, & Cutter, 2018) while improving forest heterogeneity and revitalizing ecosystem functions (Evangelista et al., 2011). While these factors are not included in the model, changes in the 19 bioclimatic variables that were included in the model seem to predict declines in suitable trees and forested regions. Analyses such as those completed in this thesis may aid in the development of early warning systems for outbreaks in novel areas, providing increased opportunities to plan management and research priorities in efforts to make forests more resilient while reducing negative impacts of potential mountain pine beetle outbreaks. The study also moves the debate forward in terms of potential methods to be applied by other researchers in the future.

CHAPTER 7
CONCLUSION

The results presented in this research predict a significant decrease in future suitable habitat susceptible to the mountain pine beetle under both moderate and extreme carbon emission scenarios. Minimum cold temperatures of the coldest month, Bio6, contains information that is present in no other variable, in agreement with research conducted by Bleiker et al., (2017), identifying cold temperatures being the most important variable in limiting both distribution and abundance of the mountain pine beetle. These Maxent results successfully identified Bio6 as being significant while also successfully identifying precipitation as a meaningful variable. Summer and winter drought have also been identified by previous research as driving factors initiating the spread of mountain pine beetle (Carroll et al., 2006; Seidl et al., 2016; Sidder et al., 2016) and other bark beetle species (Hart et al., 2017), a significant success of the Maxent model.

Further study is recommended to continue to refine these results in order to better understand possible impacts at higher spatial and temporal resolutions. These future projects would include studies of the relationships between the mountain pine beetle and climate at smaller and larger spatial resolutions. At smaller scales, it may be possible to include variable forest composition, continuity and density which may produce results more informative for natural resource managers. At larger scales, this study could be expanded to include Saskatchewan, the neighboring province and next potential candidate for mountain pine beetle infestation. Including an examination of how climate change may impact the boreal forest is needed to better understand potential changes in this novel ecological region. In particular, a greater understanding of how drought effects the boreal forest would also improve further research. Finally, while the general circulation model CCSM4 is powerful in isolation, averaging this model with two to five additional models would help include a broader variance, potentially strengthening the model results.

Finally, turning to the mountain pine beetle and its future range, it is clear steady improvement in predictions are essential for the future preservation of boreal forest regions and the important forest product industries that are essential to the provinces' economy. It is hoped that this research will advance these goals and promote the invention of more effective monitoring procedures.

APPENDIX A

MOUNTAIN PINE BEETLE PRESENCE DATA

Provided from the Forestry Division of Alberta Agriculture and Forestry Department, Forest Health Spatial Data (FHSD) provides information on forest health pests across Alberta, Canada. The mountain pine beetle heli-GPS data surveys are carried out by observers in rotary wing aircraft flying at low elevation and are conducted in known areas of mountain pine beetle activity. Heli-GPS surveys are used to intensively cover a specific area where management action is being contemplated. The aim is to record the boundaries of disturbance either by sing GPS or large-scale maps (1:50,000).

The heli-GPS surveys are generally competed on an annual basis, between August 15 and September 15. The data is delivered to Edmonton, Alberta by September 30. The survey data is generally collected using a computer tablet though paper maps and a hand held GPS unit may be utilized as a back up. Each year, the Forest Health Officer (FHO) will determine where to conduct Heli-GPS surveys based on where management action is considered for that specific year. Al Heli-GPS candidate areas in the Province are categorized into either Primary or Secondary Areas based on the anticipated level of control work for the year in question. The data standards for each Area are as follows:

For all heli-GPS surveys, the data is checked to ensure the following:

- Surveys are completed by September 15th
- GPS locations of points are within +/- 30 meters
- Polygon boundaries encompass all fading/red trees
- Polygon infestation severity is within +/- 10% of actual severity

Primary Areas (Generally in the leading edge zones)

- Only patches of three or more trees are GPSed unless the FHO directs surveyors to GPS patches of single or two red or fading trees. This can vary between years.
- The accuracy of the red tree counts are:

  ○ 1 or 2 trees - +/- 0 trees ○ 3 – 10

  trees - +/- 1 trees ○ 11 – 24 trees - +/- 4

  trees ○ 25+ - +/- 10 trees

- 95% of all patches of >3 red trees are captured

Secondary Areas (usually in the active holding zones)

- Only patches of five or more trees are GPSed unless the FHO directs surveyor to GPS sites with less or more red trees. This varies from year to year.
- The accuracy of the red tree counts are:

  ○ 5 – 25 trees - +/- 5 trees ○ 25+ trees

  - +/- 10 trees ○ 95% of all patches of

  >25 red trees are captured ○ 80% of all

  patches of >5 <25 red trees

Known Limitations of the Data:

- The areas surveyed each year (Primary/Secondary) can be different and therefore, year over year comparisons may be difficult.
- The surveyors do not ground truth all of the red trees identified. Therefore, it is not guaranteed that all of the red trees mapped are the result of MPB attack.

- The surveyors may not map tree patches less than three red trees in Primary areas and may not map patches smaller than five trees in Secondary areas. As a result, the dataset does not include all of the MPB killed trees.
- Grey attacked trees are not captured.
- The surveyors attempt to distinguish between “new” faders and “old” faders but the accuracy of this distinction is not guaranteed and therefore, the data may reflect several years and several generations of MPB attack.

APPENDIX B

MAXENT JACKKNIFE TEST RESULTS

Appendix B provides the jackknife test of variable importance results for each of the five Maxent models in this research.

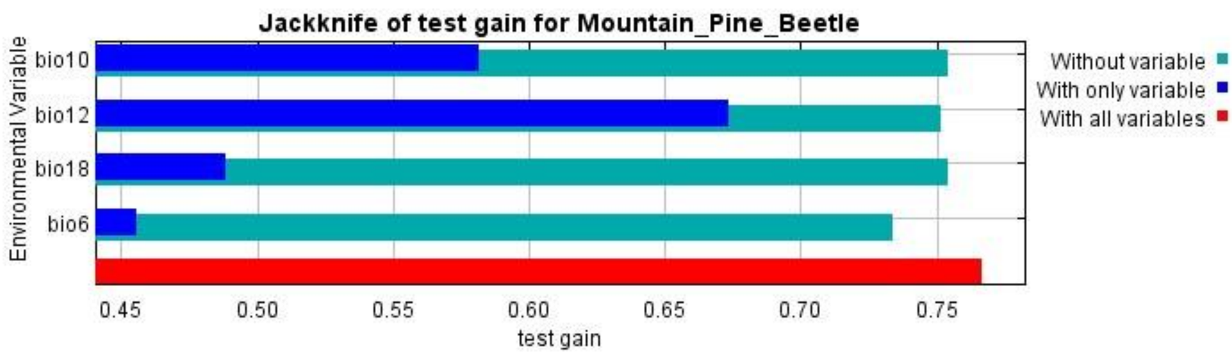

Figure B.1: Jackknife results for Model A, based on the current climate

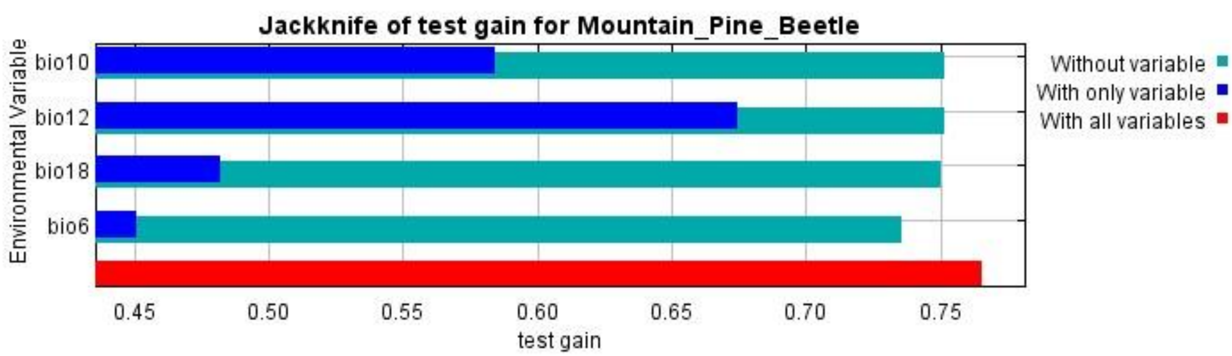

Figure B.2: Jackknife results for Model B, 2050, RCP 4.5 (moderate) climate scenario

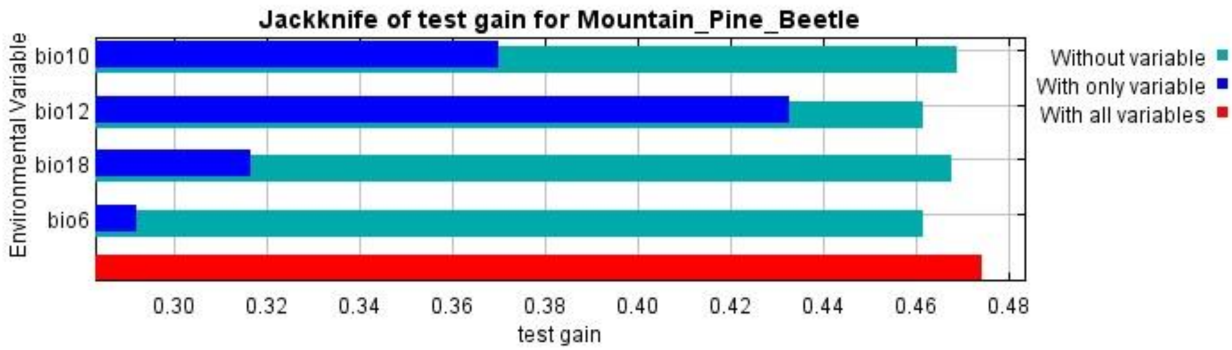

Figure B.3: Jackknife results for Model C: 2050, RCP 8.5 (extreme) climate scenario

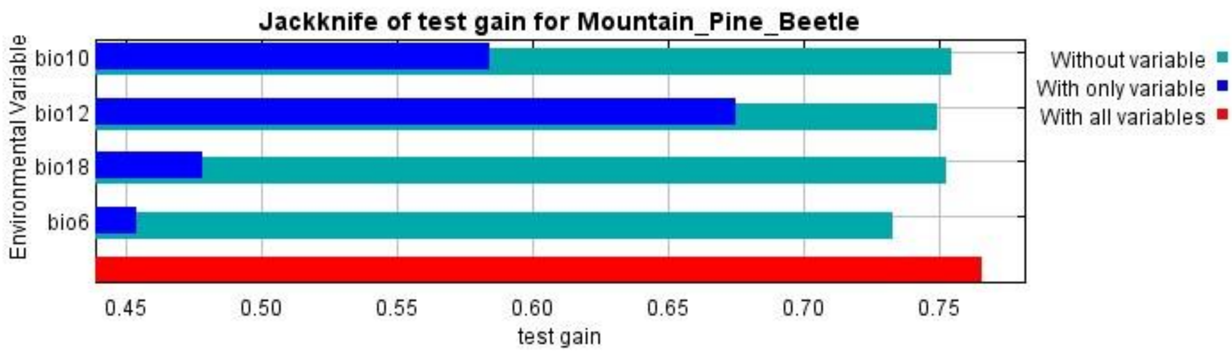

Figure B.4: Jackknife results for Model D: 2070, RCP 4.5 (moderate) climate scenario

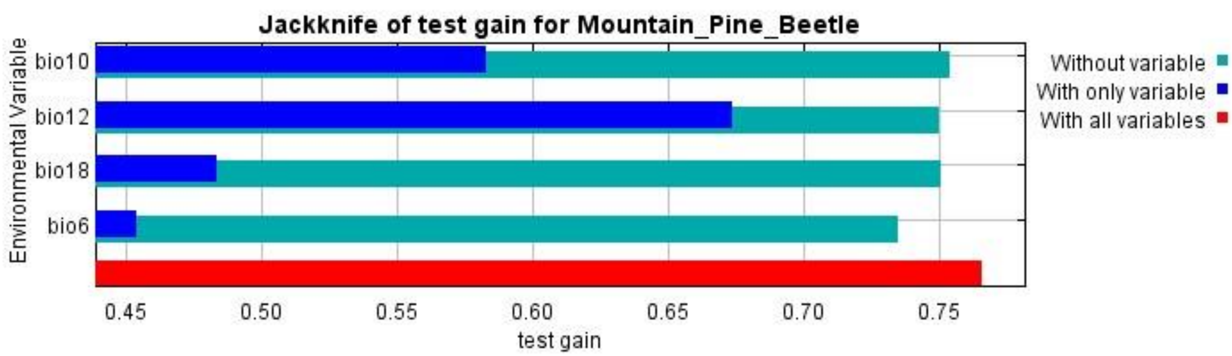

Figure B.5: Jackknife results for Model E: 2070, RCP 8.5 (extreme) climate scenario

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