

**A REVIEW OF THE EFFECTS OF CLIMATE AND WEATHER ON
MOUNTAIN PINE BEETLE POPULATION DYNAMICS AND IMPACTS
OF CLIMATE CHANGE ON RANGE EXPANSION IN CANADA**

by

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ABSTRACT

The recent past and future range expansion of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), are reviewed on the basis of the review of the direct and indirect effects of climate and weather on beetle population dynamics. The recent warming has resulted in decreased cold-induced mortality, increased adaptive seasonality, and reduced host-tree defense, and has increased climatically benign habitats for the beetle. There has been a significant range expansion of mountain pine beetle in western Canada in the recent decades, posing a risk of future infestation in the adjacent boreal jack pine (*Pinus banksiana* Lamb.) forests.

KEYWORDS

Climate change, mountain pine beetle, global warming, range expansion, climatic suitability

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1. Introduction

The global average temperature has risen by roughly 0.6 °C in the past 30 years and is predicted to increase by 1.4-5.8 °C by 2100 due to a combination of global changes such as growing greenhouse gas concentrations, deforestation, and loss of glaciers (Hansen et al., 2006; Houghton, 2001). The change in temperature across North America has been projected to be more significant than the global average increases and may result in a greater frequency of extreme weather events (Bentz, 2010). Moreover, the associated effects on precipitation patterns will result in longer dry seasons and more frequent droughts (Seager & Vecchi, 2010). The assortment of changes in climate can influence not only human activities but also the other living organisms in ecosystems. Consequently, some species may be forced out of their habitats, whereas some are flourishing (Parry, 2007).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), an eruptive bark beetle, is the most significant agent of mortality in lodgepole pine (*Pinus contorta* Douglas) forests in North America. The current mountain pine beetle epidemic is more significant than any previously recorded, extending from northern Mexico (latitude 31° N) to northwestern British Columbia (latitude 56° N) (Safranyik & Carroll, 2006). In the recent decades, there has been a significant expansion in the geographical range of mountain pine beetle in Canada (Safranyik et al., 2010), affecting trees at higher elevations and latitudes than ever before (Mitton & Ferrenberg, 2012). According to the B.C. Ministry of Forest, Lands and Natural Resource Operations (2014), the cumulative area of infestation in British Columbia is estimated at 18.1 million hectares, with 710 million cubic meters of cumulative timber loss since the current outbreak began in the early 1990s. In addition to extensive timber losses, the epidemic also significantly impacts fuel loading, watershed quality, biodiversity, recreation, etc. (Safranyik et al, 1974; McGregor 1985).

Several studies have suggested that the mountain pine beetle outbreak is primarily a consequence of climate change. According to Carroll et al. (2006), two major conditions are required for an outbreak to occur. First, there should be a large amount of large, mature pine trees that mountain pine beetles prefer to attack. Second, favorable weather for beetle survival must last for several years; specifically, hot summers that facilitate reproduction, and mild winters that allow for offspring survival (Safranyik & Carroll, 2006). As the lodgepole pine forests are widely distributed in western Canada, the range expansion by the beetle in Canada is not restricted by the availability of host trees. Therefore, the outbreaks can only be explained by climate change (Carroll et al., 2004). To analyze the past and current range expansion and to predict the future range expansion, the effects of climate change on range expansion by the mountain pine beetle have been extensively studied (Logan & Powell, 2001; Carroll et al., 2004, 2006; Bentz et al., 2010; Safranyik et al., 2010).

The purpose of this report is to 1) review the direct and indirect effects of climate and weather on mountain pine beetle population dynamics, and to 2) examine the impacts of climate change on range expansion by the mountain pine beetle in Canada. It is essential to understand how climate influences the beetle populations prior to the analysis of the impact of climate change on range expansion. This report provides a detailed look into three major effects of climate, including cold-induced mortality, adaptive seasonality, and tree vigor and defenses. The past and current mountain pine beetle range expansions in response to climate change are discussed; the future range expansion predicted by using three different models under certain climate change scenarios are reviewed as well.

2. Background

2.1. Geographic distribution and host trees

The mountain pine beetle, a small bark beetle approximately 4.0-7.5 mm in length, is native to the forests of western North America from Mexico to British Columbia (Taylor et al., 2006). Mountain pine beetle infestations have been documented in western Canada for over 85 years (Safranyik & Carroll, 2006). In western Canada, the principle hosts of mountain pine beetle are lodgepole pine. However, other species of *Pinus* are also susceptible such as jack pine (*Pinus banksiana* Lamb.), ponderosa pine (*Pinus ponderosa* Dougl.), and whitebark pine (*Pinus albicaulis* Engelm.). The mountain pine beetle prefers to attack large mature trees, which have thick bark to protect their offsprings and provide superior nutritional benefits to developing larvae. Normally, mountain pine beetle populations are innocuous, infesting a small amount of trees in a forest. However, when desirable host trees are sufficient and climatic conditions are favorable, the small endemic populations can dramatically increase and lead to large-scale outbreaks that may destroy millions of hectares of forests (Safranyik & Carroll, 2006).

2.2. Life cycle

The mountain pine beetle has four life stages including egg, larva, pupa and adult (Figure 1). All of the life stages occurred within the subcortical tissues of the host trees except for the dispersal period by mature adults during the summer (Safranyik & Carroll, 2006). The attacks are initiated by female adults; they overcome the tree's defenses, bore through the bark into the phloem tissue and release pheromones, which attract more beetles to the same tree and the adjacent trees. Once a tree is successfully colonized, egg galleries are constructed parallel to the direction of the stem. The larvae emerge in late August and feed on the phloem tissue. The beetle typically stays as third- or fourth-instar larvae over the winter and resumes development in the spring. In early

summer, pupation occurs shortly before the adult emergence (Bentz et al., 1991). A brood is defined as a group of individuals that develop from eggs. Brood that emerges from a host tree in one year is termed “univoltine”, whereas “semivoltine” requires two (or more) years of development (Logan & Powell, 2001).

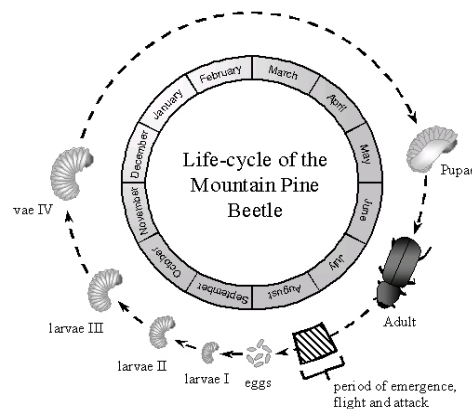


Figure 1. Mountain pine beetle life-cycle (adapted from Regional District of Okanagan-Similkameen, 2014).

3. Climate and Mountain Pine Beetle

3.1. Temperature

Temperature is a key indicator of climate change and is the most significant climatic factor affecting mountain pine beetle outbreak progression. Because the mountain pine beetle is a poikilotherm, every aspect of its life cycle is dependent upon temperature (Bentz et al., 1991; Carroll et al., 2006). Temperature determines the beetle’s survival and the rates and limits of development. In general, cold temperatures restrict the rate of growth and spread of beetle populations, whereas warm temperatures benefit beetle development.

3.1.1. Cold-induced mortality

Cold-induced mortality is a major factor driving the population dynamics of mountain pine beetle (Safranyik, 1978; Régnière & Bentz, 2007). Significant mortality is usually found during

the cold season when the temperatures are low enough to kill the beetles, including winter, late fall and early spring. However, the mortality threshold of beetles is not fixed; it varies by daily temperature fluctuations which influence the larvae's response.

Insects may die in the cold because the water in their bodies freezes (Lee, 1989). To survive and thrive in low temperatures, insects have developed several ways to deal with cold weather (DiFonzo et al., 2012). The first strategy is to escape freezing conditions altogether by insect migrations. For example, the monarch butterfly (*Danaus plexippus*) migrates from southern Canada in the fall to central Mexico to overwinter, and the population eventually moves back north in the spring (Urquhart & Urquhart, 1978). However, many insects cannot avoid low temperature exposure and they adjust physiological and biochemical processes to enhance their tolerance to freezing temperatures. Freeze tolerant species can withstand ice formation in the extracellular body fluid, whereas freeze intolerant species, such as mountain pine beetle, must avoid freezing of body tissues (Salt, 1961; Bentz & Mullins, 1999).

Mountain pine beetle larvae are able to metabolize an alcohol called glycerol, which is most abundant antifreeze polyol in their bodies, to avoid the water in their bodies from freezing (Sømme, 1964). The supercooling point refers to the lethal temperature that spontaneous freezing occurs in the beetle's body tissues. According to Sømme (1964), the supercooling points of insects decrease as the concentration of glycerol increases. To prepare for the winter, the beetles start to produce and accumulate anti-freeze in the late fall. Cold-hardiness of mountain pine beetle increases with the accumulation of glycerol. The amount of antifreeze peaks during the winter and helps beetles keep from freezing (Sømme, 1964).

Regardless of the natural anti-freeze, exposure to cold temperature is still the primary cause of beetle mortality (Safranyik, 1978; Cole 1981). In winter, sustained temperatures below -35°C for several straight days can effectively kill the beetles (BC Ministry of Forest, Lands and Natural Resources Operations, 2012). Mountain pine beetle eggs, pupae and young larvae are the most susceptible to freezing temperatures (Amman, 1973; Reid, 1962; Safranyik, 1978). All of the unhatched eggs are killed during the winter; therefore, the beetles primarily overwinter as larvae which are vulnerable to cold temperatures in the early stages (Amman, 1985). Unlike late-stage larvae which can survive in the cold, young larvae have high mortality rates when the temperature is close to -40°C . However, a deep layer of snow may insulate mountain pine beetles in the base of the tree. Therefore, cold temperatures are more effective before it snows (BC Ministry of Forest, Lands and Natural Resources Operations).

Sambaraju et al. (2012) has suggested that cold snaps and large, sudden drops in daily winter temperatures are detrimental to mountain pine beetle survival. A cold snap is a period of intensely cold temperature. In the early fall and late spring, significant beetle mortality may result from temperature consistently below -25°C (BC Ministry of Forest, Lands and Natural Resources Operations). A cold snap is most effective in the fall, before the beetles have accumulated sufficient amount of anti-freeze, and before insulation of the base of host trees by snow (Carroll et al., 2004).

The southern and central British Columbia has experienced an increase by 1.1°C in average annual temperatures from 1895 to 1995 (Gayton, 2008). Milder winters resulted from the recent warming, with less lethal temperatures for mountain pine beetle, have resulted in higher overwinter survival (Logan et al., 2010). Historically, mountain pine beetle population growth in British Columbia has been significantly limited by cold snaps between -30°C and -40°C in early

winter that result in high mortality rate of larvae. However, such cold snaps are effective before beetles produce natural antifreeze, or before insulation of the base of host trees by snow. The central B.C. has not met these conditions for three decades (Carroll et al., 2004).

3.1.2. Adaptive seasonality

Unlike parasitic insects, mountain pine beetles have to kill their hosts to reproduce successfully. However, pine trees are not passive victims; they have significant chemical (i.e. toxic resin) and physical (i.e. bark) defenses to protect them from beetle attacks. Therefore, the beetles have evolved a mass-attack strategy to overcome these defenses through extensive amounts of attacking beetles (Raffa & Berryman 1987). Increased temperatures encourage beetles to meet three conditions to mass attack their hosts. First, synchronous emergence of adult beetles from hosts is required to provide the maximum number of beetles to attack and kill the hosts and, further, to maintain an outbreak (Amman, 1985; Logan and Bentz, 1999). Second, timing of synchronous emergence is crucial for beetles to maximize their fitness because emergence must occur early enough to maximize time for oviposition but late enough to minimize mortality from lethal spring (or early summer) temperature (Hicke, 2006). Third, synchronous univoltinism, which is achieved with sufficient heat accumulation, is considered important for mass attack (Amman, 1973; Safranyik, 1978). The term “adaptive seasonality” refers to optimally timing life stages to synchronize adult emergence, which allows for mass attack (Logan & Bentz, 1991).

Diapause is a mechanism often used by insects as a means to survive predictable and unfavorable environmental conditions, and to maintain an adaptive seasonality (Tauber et al., 1986; Logan & Powell, 2001). It can reset and synchronize the seasonal clock annually. However, the mountain pine beetle does not have diapause or any other physiological timing mechanism for

synchronizing development (Logan & Bentz, 1999). Instead, every aspect of seasonality is directly controlled by temperature variability (Logan & Bentz, 1999; Logan & Powell, 2001).

Bentz et al. (1991) showed that each life stage of mountain pine beetle has a specific optimal temperature regime and threshold for development (Figure 2). The interaction between temperature and beetle development results in an inherent mechanism for synchronizing larval instar molts and adult emergence. Instars III and IV usually halt development in the fall due to the high temperature thresholds, which avoids progression to pupae that are susceptible to winter mortality. Eggs, and instars I and II have lower temperature thresholds of development, they can continue to develop. Synchrony is completed when late-hatching eggs catch up in development.

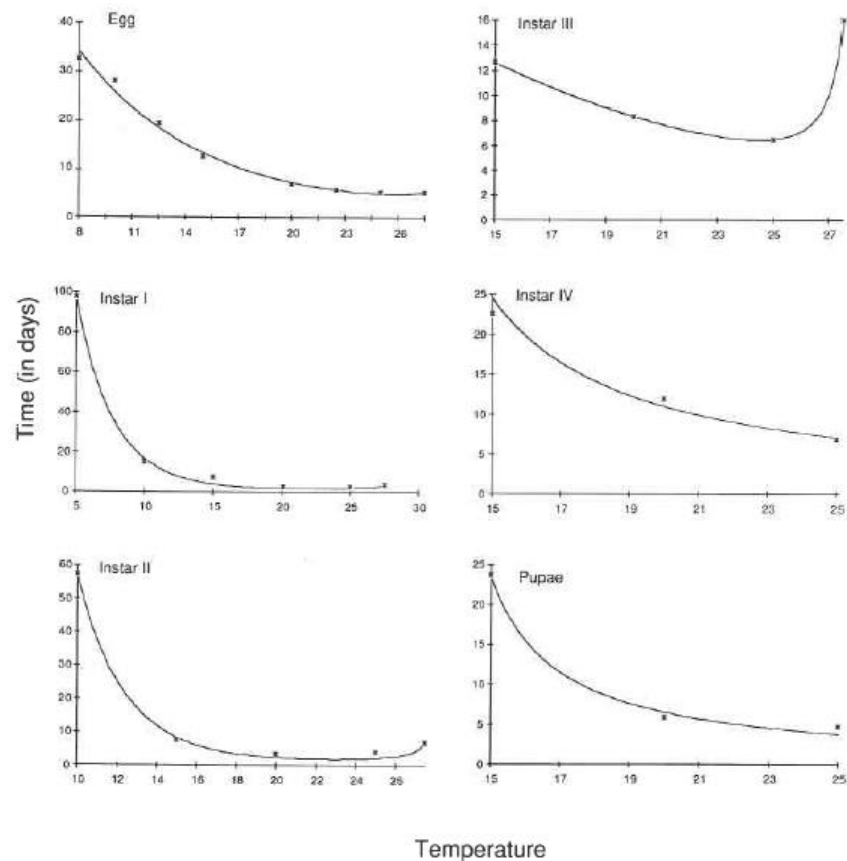


Figure 2. Developmental time functions for eggs, larval instars, and pupae fit to median times at constant temperatures. Curves represent the time (in days) to complete the life-stage at each constant temperature (adapted from Benz et al., 1991).

Temperature affects voltinism of the mountain pine beetle by controlling specific life stage development rates (Logan & Bentz, 1999; Logan & Powell, 2001; Safranyik & Carroll, 2006). The mountain pine beetle usually completes its life cycle in one year with sufficient heat accumulation; however, more years may be required in cool environment. In general, each of the beetle life stage's development can be accelerated by an increase in the ambient temperature. However, Logan & Bentz (1999) and Logan & Powell (2001) suggested an adverse effect of warmer temperatures on mountain pine beetle populations during summer. Due to excessive heat accumulation, beetle populations can be forced into partial multivoltinism (i.e. have more than one generation per year) that cause cold-susceptible stages (i.e. eggs, pupae, adults) to overwinter. Consequently, fly synchrony is interrupted and mass attack success is reduced in the following year (Taylor et al., 2006).

Climate change has resulted in increased temperatures and longer growing seasons that generally facilitate mountain pine beetle population growth (Bentz et al., 2010). Logan et al. (2010) suggest that the warming climate creates sufficient thermal energy for the mountain pine beetle to complete its life cycle in one year. Due to longer growing seasons, more larvae are able to reach the late larval stage before winter sets in, avoiding early larval stages that more susceptible to cold temperatures. Therefore, an increased number of beetles survive to emerge in the following year (Gayton, 2008). Collectively, the recent warming has resulted in increased the likelihood of adaptive seasonality in the beetle's range.

3.2. Drought

Global warming has increased the frequency and intensity of droughts in western Canada during the summer, and will continue to do so in the future (Hogg & Bernier, 2005). The reduction in precipitation associated with droughts has reduced available moisture for host trees (Kipfmue

& Swetnam, 2002). In addition, the increases in temperatures are increasing evaporative demand on host trees (Williams et al., 2013). Collectively, host trees are under moisture stress that limits their capacity of defense to the beetles, increasing the beetle attack success. Kipfmüller and Swetnam (2002) found host trees under moisture stress during the drought periods throughout most of the beetle range in the United States. In lodgepole pine forests, warm and dry conditions created by droughts may cause a reduction in tree resistance to beetle attacks, which increases host susceptibility to beetle attacks, and, therefore indirectly facilitates beetle population growth (Thomson & Shrimpton, 1984, Safranyik et al., 2010).

Available soil moisture has been considered the most significant factor governing tree vigor which determines host resistance to beetle attacks (Hopping & Mathers, 1945). Increased host vigor can increase the capacity of host tree defense to beetle attacks (Mitchell et al., 1983). However, the moisture availability largely depends on the amount of precipitation (Hopping & Mathers, 1945). Droughts often cause a reduction in precipitation, resulting in moisture stress on host trees. When trees are moisture-stressed, their stomata close to restrict transpiration and, therefore, to conserve water. However, the stomata closure restricts carbon assimilation and cause carbon starvation (McDowell et al., 2008). Due to changes in carbon assimilation, fewer carbohydrates are available for host trees to produce chemical defenses (i.e. resin) and to repair tissue (Hermes & Mattson, 1992). Therefore, moisture-stressed trees are more susceptible to mountain pine beetle invasions. Moreover, the symbiotic fungi carried with beetles can amplify hydraulic failure and accelerate tree death. Ultimately, drought-induced reduction in tree defensive capacity results in a decreased threshold number of beetles for a successful mass attack (Bentz et al., 2010).

However, the impacts of drought on host trees are more pronounced at lower outbreak levels than higher levels (Creeden, 2014). Endemic mountain pine beetle population usually grows slowly by overwhelming the defenses of individual trees with weakened by other abiotic or biotic agents such as root diseases, dwarf mistletoe, and storm damaged (Tkacz & Schmitz, 1985; Amman & Schmitz, 1988; Schowalter & Filip, 1993; Nebeker et al., 1995). Vigorous trees are able to repel most beetle attacks if tree-growing conditions are suitable and beetle populations are sufficiently low. However, droughts may cause moisture stress on host trees over a large region, leading beetle populations to expand dramatically to epidemic proportions. During that population phase, the beetles are able to overcome the defenses of vigorous trees, diminishing the role of host stress from drought (Creeden, 2014).

4. Range expansion

4.1. Past range expansion

Historically, the range of mountain pine beetle was limited by climate, restricted to the southern regions of BC and the extreme south-western regions of Alberta, between 800 and 1400 m in elevation (Carroll et al., 2006). The high elevations of the Rocky Mountains and non-forested prairies were natural barriers which have limited the geographic distribution. However, climate change has resulted in an increase in climatically benign habitats for mountain pine beetle (Logan & Powell, 2001; Carroll et al., 2004).

Carroll et al. (2004) have suggested a notable shift in climatically suitable beetle habitats toward higher latitude and elevation in the past few decades. They adapted a climate-suitability model developed by Safranyik et al. (1975) and used weather data to simulate the distribution of habitat with different levels of climatic suitability to mountain pine beetle (Figure 3). Between 1970 and

2000, BC experienced a relatively sudden increase in the amount of extremely suitable habitats for mountain pine beetles, particularly in south-central and southeastern areas of the province. The dramatic increase in the amount of extremely suitable habitat has been explained as a result of the increase in average annual temperature (more than 1°C) of central BC during the same period. Interestingly, the distribution of climatically suitable habitats delineated the area affected by mountain pine beetle before 2000 (Carroll et al. 2004).

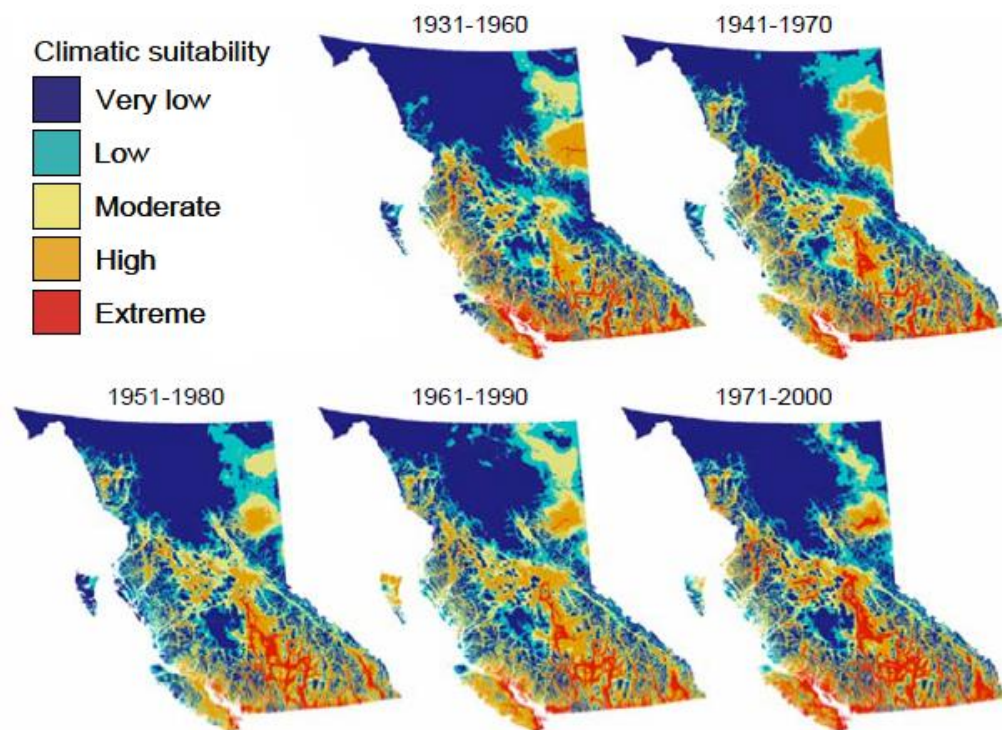


Figure 3. Historic distribution of climatically suitable habitats for the mountain pine beetle in BC derived from real weather data and empirical model of the influence of climate on the establishment and persistence of beetle populations. Areas with “very low” suitability are unsuitable for mountain pine beetle whereas “extreme” areas are those considered climatically optimal (adapted from Carroll et al., 2006).

Mountain pine beetle populations have followed the shift in climatically suitable habitats between 1970 and 2000 (Carroll et al., 2004). Before 1970, there were no infestations observed in climatically unsuitable habitats. However, the amount of infestations has been increasing in

those formerly unsuitable habitats since then. The invasion of new climatically benign habitats indicated that infestations have been encouraged by the changes in climatic conditions.

Interestingly, mountain pine beetle populations experienced a significant decline in those historically most suitable habitats in the 1980s. It has been explained as a consequence of the excessive heat accumulation which led to partial multivoltinism (i.e. a loss of adaptive seasonality) and made more beetles overwinter in cold-intolerant stages (Carroll et al., 2004).

The current latitudinal and elevational range of mountain pine beetle has been primarily restricted to BC Interior by climate rather than the availability of susceptible host trees (Bentz et al., 2010). In fact, lodgepole pine extends into Yukon, Northwest Territories, and Alberta. However, temperatures become colder at higher elevations and latitudes, limiting beetle overwinter survival and synchrony and therefore beetle population growth (Logan & Powell, 2001).

4.2. Future range expansion

Previous outbreaks collapsed due to the adverse effects of climate (i.e. over-heat accumulation) in the combination with disturbance-induced decreases in the amount of host trees; however, a number of studies have suggested that the current outbreak may not entirely collapse as in the past due to climate change (Logan & Powell, 2001; Carroll et al., 2004). Sambaraju et al. (2012) reveals that an increase in mean temperature by 1°C to 4°C can increase the risk of outbreak, particularly at higher elevations and northern latitudes. For instance, the area at -120.8°W/58°N was formerly considered as low-risk area of infestation in BC; however, a new occurrence of infestation was observed in this area, associated with an average increase of 1.5°C in latitude and 4°C in elevation. As Carroll et al. (2004) has provided evidence that climate conditions in western Canada have been changing and the beetle has expanded its range to historically unfit

habitats during the last thirty years of the 20th century, scientists believe that the mountain pine beetle will expand its range into northern latitudes.

To predict range expansion in the future, we have to assess two factors over the landscape, 1) the availability of host trees and 2) the existence of long-term favorable weather conditions, which are important regarding the development of mountain pine beetle outbreaks (Carroll et al, 2004; Safranyik, 1978).

As the mountain pine beetle is able to attack a wide range of pine species, this insect may move northward and eastward to establish and persist in the boreal forest of Canada where numerous trees are susceptible to infestation. The range of lodgepole pine extends into Yukon and Northwest Territories, posing a risk of future infestation into these areas. In Alberta, infested lodgepole pine forests intermingle with boreal jack pine forests (Figure 4). Jack pine, a viable host for the beetle (Furniss & Schenk, 1969), is the most abundant tree species in the boreal forest of Canada that extends across the continent. According to Safranyik et al. (2010), the beetle can attack and breed in jack pine hosts as successfully as in lodgepole pine hosts. In addition, the hybrids of these two pine species (i.e. jack and lodgepole pine) across the northern Alberta forms a bridge between the western and eastern pine forests that may help beetle populations move eastward to invade the boreal forest. Therefore, the boreal forest satisfies the first requirement, providing abundant host trees for the beetle in the future outbreak.

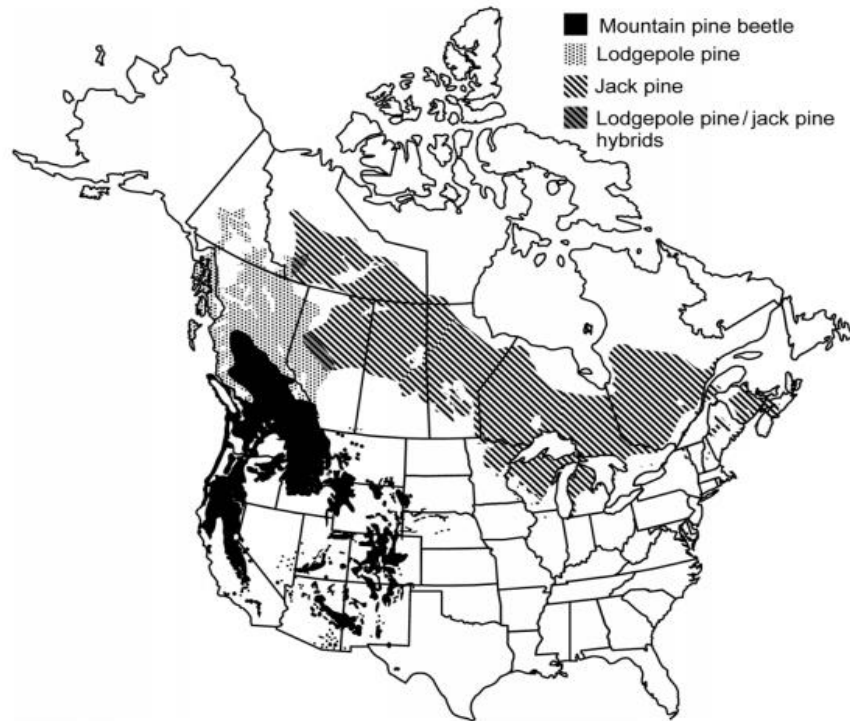


Figure 4. Historical distribution of mountain pine beetle and the distribution of lodgepole pine and jack pine; regions where lodgepole pine and jack pine hybridize are indicated (adapted from Logan & Powell, 2001).

However, the structure of pine stands in the boreal zone will influence the forest susceptibility to mountain pine beetle (Safranyik et al., 2010). There are two major differences in stand structure between jack pine stands in the boreal zone and lodgepole pine stands that have been infested in western Canada, which may result in different characteristics of future mountain pine beetle infestation. First, jack pine trees in the boreal forest are smaller than lodgepole pine trees in which outbreaks have been observed. Second, jack pine stands are less contiguous (Safranyik et al., 2010). These two differences result in smaller volumes within pine stands in the boreal zone. A stand where the volume of pine is greater than 40m³/ha has been determined to be highly susceptible to outbreaks (A.L. Carroll, unpublished). Apparently, most of the eastern boreal forests are below this level of susceptibility, except for the southern Ontario and several small isolated areas (Figure 5). Therefore, the growth and spread of beetle populations will be

generally slower in the boreal forest than in the pine stands that have been infested in western Canada (Safranyik et al., 2010). However, it is important to note that the pine stands in the southern Ontario where stand volume exceed 40m³/ha may be more susceptible and may accelerate the future range expansion (Safranyik et al., 2010).

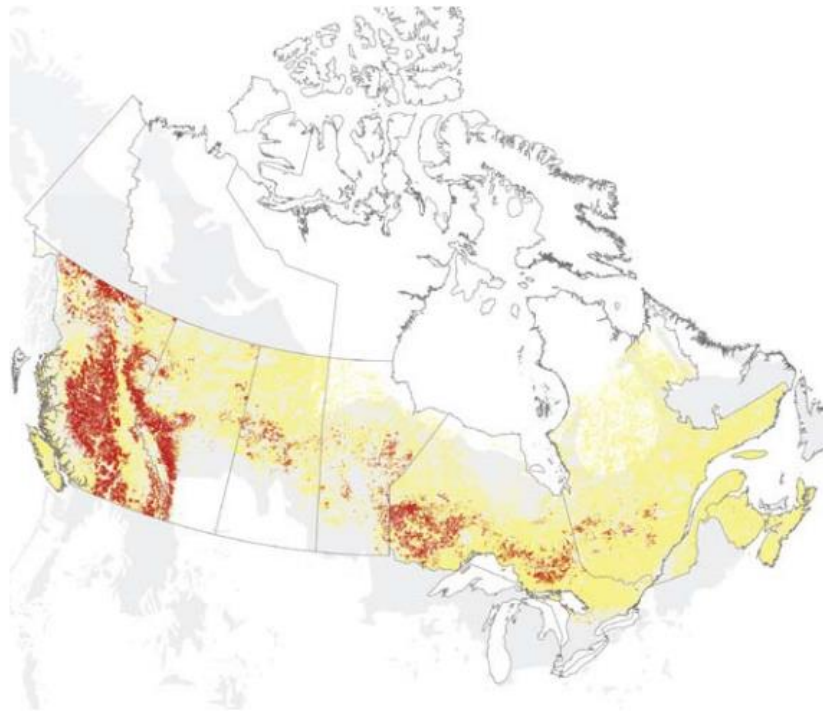


Figure 5. Pine stands in Canada where stand volume exceeds 40m³/ha are shown in red. At a given level of susceptibility of individual pine trees, such stands are much more susceptible. Yellow areas have less than 40m³/ha of pine (adapted from Nealis & Peter, 2008).

To determine whether the boreal forest can satisfy the second requirement (i.e., sustained favourable weather), Safranyik et al. (2010) developed three climate-suitability models to assess climatic suitability of the boreal forest for the establishment and spread of beetle populations.

1) The Safranyik et al. model of climate suitability determines the likelihood of beetle attack success, optimal development, and over-winter survival based on several climatic variables (Safranyik et al., 1975; Carroll et al., 2004); 2) the Logan et al. model of adaptive seasonality is

based on stage-specific development rates to estimate the likelihood of a synchronized univoltine life cycle (Bentz et al., 1991; Logan & Powell, 2001); 3) Régnière and Bentz model determines the beetle survival over winters (Régnière & Bentz, 2007). These models were run under BioSIM that integrates biological models with climate and weather data (Régnière et al., 1995; Régnière, 1996). A moderate climate change scenario with an annual 1% increase in CO₂ starting in 2000 was used. It is important to note that the models predict not only increases in temperatures but also extreme weather events. Two maps were produced for each model to illustrate climatic suitability in Canada in 1971-2000 and 2001-2030 respectively.

The map produced by using the Safranyik et al. model illustrates that climatically suitable habitats are mainly distributed in the north-south direction in western Canada and the Maritime Provinces. In the recent past (1971-2000), as expected, the climate suitability was highest in southern and central BC (Figure 6a). The suitability was moderate in the south of the boreal forests, excluding Ontario and the Maritime provinces. In the near future (2001-2030), under the moderate climate change scenario, the suitability intensifies across the landscape, with an apparent increase in climatically areas to the north in western Canada (Figure 6b).

The result of the Logan et al. model shows climatic conditions conducive to adaptive seasonality in the recent past (1970-2000) was extremely suitable in the regions that have been infested in the current outbreak, especially in central BC as well as Alberta foothills (Figure 6a). In central Alberta and Saskatchewan, current climate condition is relatively suitable but the area of suitability declines eastward. In the near future (2001-2030), under climate change, the area of suitability will increase in BC, whereas Alberta will experience a general decrease (Figure 6b). Yukon and North West Territories are predicted to have an increased area of suitability that

allows for adaptive seasonality. In the rest of boreal forests, the area of climatic suitability will decline slightly and shift northward.

Régnière and Bentz model of winter mortality suggests that, except in south-central British Columbia and on the extreme west and east coast, the likelihood of winter survival for mountain pine beetle is extremely low, in both the past (Figure 6e) and the future (Figure 6f). The area of suitability will slightly increase in central Alberta and in southern Saskatchewan, whereas the rest of landscape does not have significant changes.

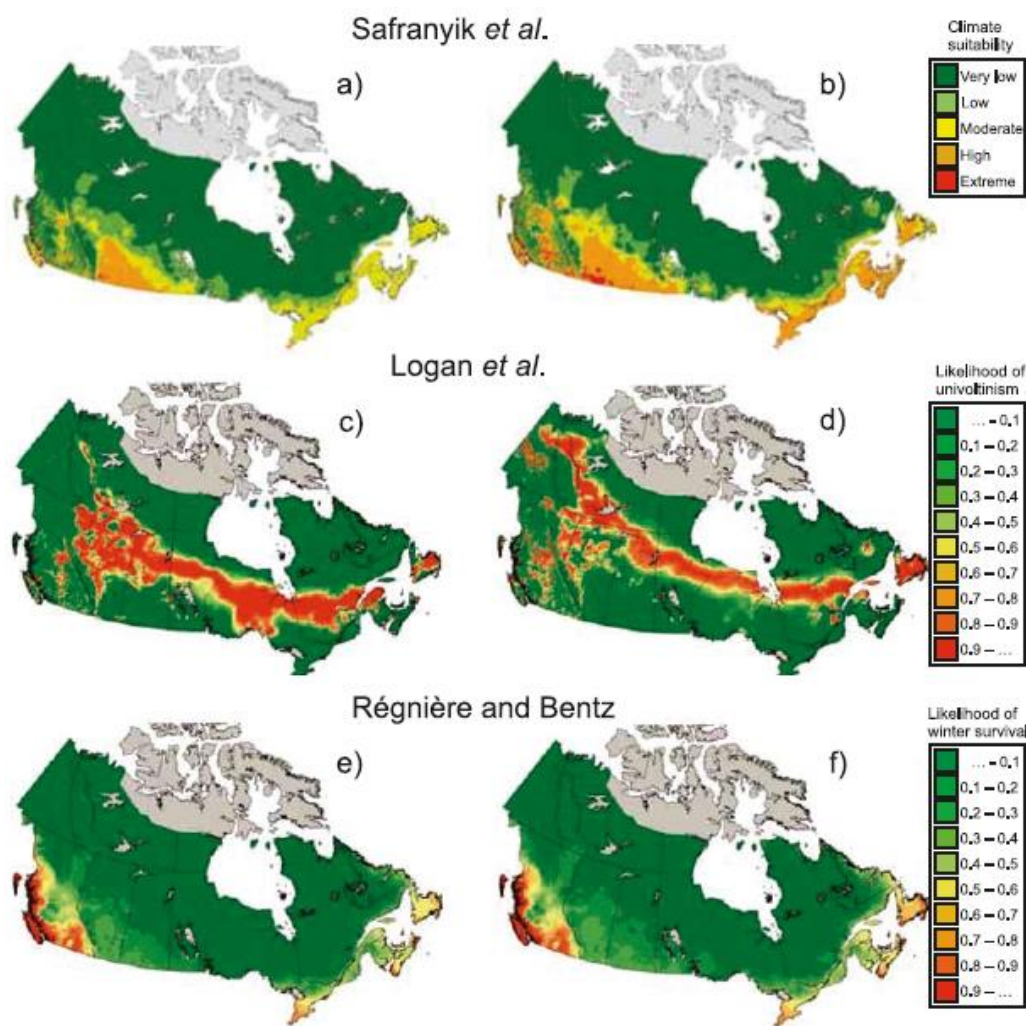


Figure 6. Distribution of relative climatic suitability for mountain pine beetle in the recent past (1971-2000) and the near future (2001-2030), as defined by the Safranyik et al., Logan et al., and Régnière and Bentz models (adapted from Safranyik et al., 2010).

Safranyik et al. (2010) suggests that the climatically optimal habitats for mountain pine beetle will be in the areas with high values for climate suitability and likelihood of winter survival overlap the band of adaptive seasonality. Based on the results of three models (Figure 6), the climatically optimal habitats were mostly in southern and central British Columbia, southern and west central Alberta, and southern Saskatchewan in the recent past (1971-2000). From 2001 to 2030, climate suitability will generally increase in southern and central British Columbia and move northward to the western boreal region. The rest of the boreal forest has been predicted to stay unsuitable for mountain pine beetle in the near future, although beetle univoltinism is possible (Figure 6).

5. Conclusion

The recent climate change has encouraged mountain pine beetle outbreaks to occur due to the direct and indirect effects of warming on beetle population dynamics, including decreased cold-induced mortality, increased adaptive seasonality, and reduced host trees' defensive capacity (Logan et al., 2010). As the recent warming has resulted in milder winters with less lethal temperatures for the beetle, cold-induced mortality has increased. In addition, longer growing seasons associated with the warming have increased adaptive seasonality that encourages mass-attack success. Moreover, increased frequency and intensity of droughts resulted from climate change have caused an increased amount of moisture-stressed host trees which are more susceptible to beetle attack (Bentz et al., 2010). Despite the possibility that beetle populations may collapse due to the adverse effect of excessive heat accumulation in areas with extremely warm temperatures (Logan & Bentz, 1999), climate change generally facilitates beetle

population growth and creates more suitable habitat for the beetle (Logan & Powell, 2001; Carroll et al., 2004).

Climate change could alter the distribution of mountain pine beetle outbreaks in Canada (Sambaraju et al., 2012). Due to climate change-induced temperature increases, mountain pine beetle has dramatically expanded its geographical range in western Canada in the recent decades (Safranyik et al., 2010). The previous range of mountain pine beetle was restricted in southern BC and extreme south-western regions of Alberta (Carroll et al., 2006). In the recent past, beetle populations have followed the shift in climatically suitable habitats resulted from the warming, particularly in central British Columbia and western Alberta, where the current climate suitability is greatest (Carroll et al., 2004; Safranyik et al., 2010). The current mountain pine beetle outbreak has affected a susceptible portion of Boreal Plains Ecoregion and is likely to invade the adjacent boreal jack pine forests in the near future. As climate suitability decreases eastward across the boreal forest, there is a determinate but decreasing likelihood that climate will continue to favour a rapid eastern expansion of beetle populations (Safranyik et al., 2010). However, susceptibility will increase again due to the increased volume and contiguity of pine forests in the southern regions of Ontario (Safranyik et al., 2012; Sambaraju et al., 2012).

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