

CLIMATIC EFFECTS ON SPRUCE BEETLE AND MOUNTAIN PINE BEETLE DISTURBANCES IN WESTERN NORTH AMERICA

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ABSTRACT

Spruce beetle (*Dendroctonus rufipennis*) and mountain pine beetle (*Dendroctonus ponderosae*) are both primary bark beetles native to the forests of western North America. Both species have experienced extensive outbreaks in the past two decades, which are partially attributed to climate change. Although both species are affected by climate change, the manner in which they are affected differs. Mountain pine beetles disturbance levels are predominately influenced by climate change through range expansion as more pine-dominated areas become climatically suitable for their life cycles. Spruce beetles however are already found throughout the entire range of their host spruce trees and are affected through a change in development time rather than range expansion. In either case, regardless of the mechanism, climate change provides opportunities for increased disturbance levels from both spruce beetles and mountain pine beetles in western forests, creating future forest management challenges.

KEYWORDS

Climate change, mountain pine beetle, natural disturbance, spruce beetle

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INTRODUCTION

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins and spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae: Scolytinae) are both primary bark beetle species native to North America (Bentz et al. 2010). Present throughout many forests, populations are usually kept at endemic levels through limitations in host availability, predators, and climate. Both species have eruptive potential, allowing them to reach epidemic levels causing extensive damage when suitable conditions persist for several years. The damage inflicted during these outbreaks has large impacts on the forest, affecting hydrologic cycles, stand structure, fire behavior, and overall composition.

Forest ecosystem processes and their resulting state and structure are highly dependent on complex relationships between endogenous and exogenous factors interacting through varying spatial and temporal scales. Small changes in one aspect of any contributing factor can result in large system shifts (Hayes et al. 2007). The large number of valuable goods and services provided by forests makes possible shifts in forest structure and processes of high concern. With the onset of climate change there is a growing potential for large changes in forests and their supporting ecosystems. Forest disturbances, both biotic and abiotic, play important and healthy roles in forest processes when operating within the range of natural variability. However with climate change bringing more favourable conditions for a variety of disturbances for longer time periods over a larger land base, the stage is set for epidemic disturbance levels, putting the world's forests at risk.

Although climate change's effects may be seen in alterations to a variety of disturbances, one of the most notable potential risks to western North America's forests comes from the effects of climate change on bark beetle populations. Bark beetles are present in virtually all forests in North America and when population levels are high, have the ability to cause 60% or higher stand mortality (80-90% mortality in larger diameter trees) (Raffa et al. 2008). In many years bark beetles affect larger areas than forest fires and with their ability to cause such extensive mortality have large impacts on forest structure, composition, and function (Raffa et al. 2008).

These alterations to the forest affect visual quality, recreation, hydrology, habitat, carbon sequestration, fire hazards, timber quality, and timber supply.

Like any disturbance agent, there is vast variability between species, host ecosystems, and the impacts produced. To illustrate how climate change will affect species differently depending on a variety of factors including current range, life cycle requirements, and preferable environmental conditions, a comparison will be drawn between spruce beetle and mountain pine beetle, two primary bark beetles whose recent outbreaks have been linked to climate change.

Climate change is highly dependent on many contributing factors, and the degree of warming and other climatic alterations is still largely unknown. Climate change will not only cause alterations in temperature, but also changes in UVB radiation, precipitation, atmospheric CO₂ and nitrogen deposition (Hayes et al. 2007). These factors will interact directly with disturbance agents like bark beetles, but also have indirect effects on disturbances through interactions with hosts and predators. There is also potential for alterations to disturbance levels to produce a feedback effect on climate change through alterations to conifer biomes, increased decay levels from tree mortality, and lower sequestration rates from fewer living, vigorous trees, further altering our natural systems (Kurz et al. 2008; Raffa et al. 2008).

BACKGROUND

CLIMATE AND PRIMARY BARK BEETLES

In the past decade, British Columbia's average annual temperatures have risen 0.7°C (Hamann et al. 2006). This warming has coincided with significant increases in bark beetle activity in both the United States and Canada (Hayes et al. 2007). The Intergovernmental Panel on Climate Change (IPCC) has predicted average annual temperature rises of 2-4° in the next 100 years with the largest effects occurring in northern and polar regions, like Canada (Eastaugh 2008). The rising temperatures will affect areas differently depending on factors including topography, soil, exposure, and groundwater resources; some areas may experience little change but in many areas dramatic alterations will occur (Hamann et al. 2006). Along with a general warming,

many other factors including extremes in weather will also increase. This widening variability of climatic and weather events will have widespread impacts on forests and their disturbances.

Natural systems, in large, have coevolved over thousands of years into balanced relationships (Raffa et al. 2008). Under new anthropogenic modifications to the environment, factors in this balanced relationship are shifting. These shifts create advantages for certain species in particular areas, especially for those near critical thresholds to increased vigour, breaking the stability in the relationship (Raffa et al. 2008). This change causes the potential for explosive alterations to disturbance regimes and other natural systems such as those seen with bark beetles in North America.

As previously noted, bark beetles play very important roles in North America's forests. The potentially eruptive nature of several species makes them of high concern due their ability to cause widespread mortality (Raffa et al. 2008). Bark beetles are always present in forests, but usually only at endemic levels. When populations are low, most bark beetles do not attack healthy trees, but rather select stressed trees, slash, or recent blow down (Garbutt et al. 2006). These less vigorous trees have lower defenses and can overcome by fewer beetles. The presence of endemic bark beetle populations creates many benefits including increased biodiversity, varied forest structure, faster stand structure progression, and food sources for several species (Raffa et al. 2008).

Bark beetles life cycles are dependent on host availability, as development occurs in the phloem tissues. Adults emerge from their host tree, locate new suitable hosts and emit aggregate pheromones to induce a mass attack. Beetles then mine beneath the tree's bark and begin the construction of egg galleries in the phloem. Eggs are laid throughout the egg gallery. The eggs hatch into larvae and create feeding channels (often constructed at right angles to the egg gallery). The larvae develop through several instars (varies between species) before pupating and developing into adults. The adults then emerge from the bark and once again locate new suitable hosts. The presence of blue stain fungi, which aids in blocking translocation in trees, is important in the ability of the beetles to overwhelm the host trees defenses. The fungi can be transmitted on the mycangia of invading beetles, phoretically, or through other means and

picked-up by the young adults in the pupal chamber before dispersal (Raffa et al. 2008). In a successful attack the beetles, along with the blue stain fungi, are able to overwhelm the trees defenses and kill the tree. In an unsuccessful attack the tree's defenses, predominantly resins, are able to kill or pitch out enough beetles to prevent all translocation from being cut off. Even in unsuccessful attacks beetles have large effects on the host tree, altering terpenoid and phenolic levels, inducing autonecrosis and traumatic duct formation, and lowering the tree's resin levels (Raffa et al. 2008).

Temperature controls many parts of a bark beetle life cycle including all life stage development, dispersal, survival, reproduction, and symbiotic relationships (Raffa et al., 2008, Bentz et al., 2010). Other climatic factors, including precipitation, have dramatic impacts on host susceptibility and therefore attack success (Raffa et al. 2008). Due to these factors climate change has a large potential to alter bark beetle disturbance frequency and severity.

Although temperature is the driving factor behind bark beetle life cycles, several other factors beyond numerous years of suitable weather need to be present for outbreaks to occur including active beetle populations and extensive areas of host trees of appropriate size, species, and age (Hayes et al. 2007). Similarly the severity of the attack and its impacts is dependent on stand health, species composition, structural composition, and stand age (Garbutt et al. 2006). All of these factors together with individual species characteristics create several possible outcomes to climate change's effects on bark beetle disturbances: geographic alterations of disturbance levels as areas become climatically suitable or unsuitable, increased or decreased rates in damage as species vigour or reproductive rates change, species expansion to new host species, or a combination of several of these effects (Raffa et al. 2008). The outcome for any specific species is reliant on species-specific life cycle processes and requirements.

MOUNTAIN PINE BEETLE

Mountain pine beetle's historic range spreads from Mexico (31°N) up to central British Columbia (56° N), and from the Pacific Ocean east to North Dakota (Taylor et al. 2006). The northern range is limited by extremely cold winters (events below -40° C) and summer temperatures, not the distribution of its host species whose range spreads north into Alaska and the Yukon and east to the Atlantic Ocean (Figure 1) (Taylor et al. 2006).

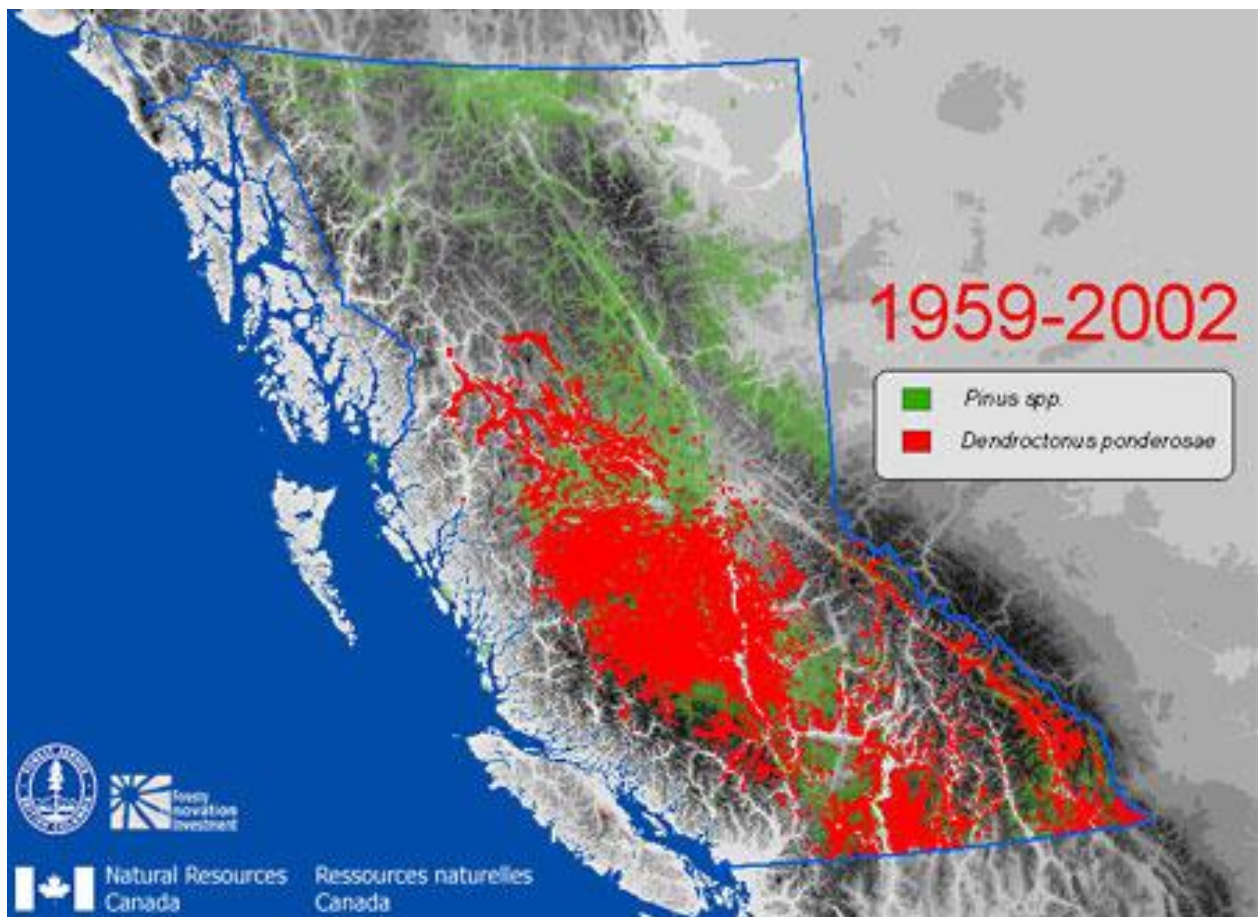


Figure 1: Distribution of *Pinus spp.* and 2002 mountain pine beetle outbreak in British Columbia (Beetle Kill, n d) from Natural Resources Canada, Canadian Forest Service (Natural Resources Canada- Canadian Forest Service).

Mountain pine beetle is the most destructive agent of mature pine in British Columbia (Safranyik et al. 2010). The current mountain pine beetle outbreak has caused extensive damage in British Columbia's interior, killing over 675 million m³ of pine from 1999-2009 (Figure 2), with estimates of 67% of the provinces merchantable pine falling victim to the epidemic by

2020 (Natural Resources Canada 2009; Walton 2010). The outbreak peaked in 2004, but the area affected has continued to grow in the northern regions of the outbreak, with the largest effected area in the Northern Interior Forest Region occurring in 2009 (Westfall et al. 2010). Although four other outbreaks are on record in British Columbia, none have affected such a large area (Taylor et al. 2004). Many factors have contributed to the onset of the epidemic, but two factors in particular created the required suitable environmental conditions to produce an outbreak of this magnitude; warming climates and the increased proportion of susceptible pine created through fire suppression (Taylor et al. 2004).

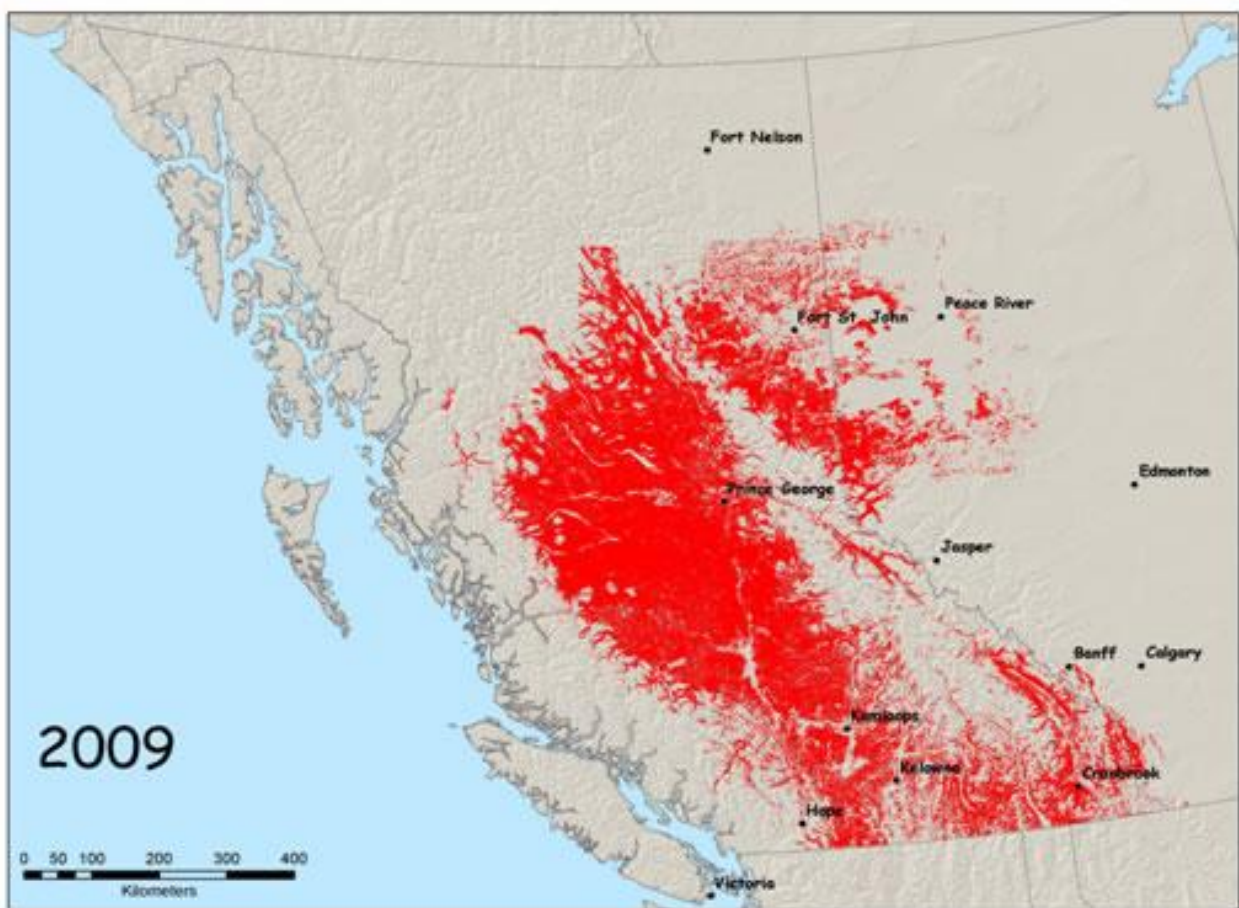


Figure 2: Area infested by the mountain pine beetle as of 2009 (from Natural Resources Canada (<http://canadaforests.nrcan.gc.ca/article/mountainpinebeetle>) compiled from data from BC Ministry of Forests, Lands and Natural Operations aerial surveys (<http://www.for.gov.bc.ca/hfp/health/overview/overview.htm>)).

Mountain pine beetle, like all bark beetles, develop in and feed on trees' phloem. Since the thickness of phloem increases with age and size, older larger trees with thicker phloem are usually preferred hosts (Safranyik et al. 2006; Raffa et al. 2008). Host selection is still not fully understood but is thought to be partially random, visual, and odor/stress driven coupled with a gustatory assessment upon possible selection (Safranyik et al. 2006). These factors make lodgepole pine, *Pinus contorta* Douglas, mountain pine beetle's primary host in British Columbia, above 80 years in age the most susceptible trees to mountain pine beetle attack. Historically 17-25% of the province's pine was considered susceptible to mountain pine beetle attack, but currently more than 55% is susceptible (Taylor et al. 2004). This substantial increase in susceptible pine is due to the large success of British Columbia's forest fire suppression, which began in the early 1900's (Taylor et al. 2004). This increased level of susceptible host species coupled with higher temperatures has created one of the largest natural disturbances in British Columbia's recorded history.

Although both mountain pine beetle and spruce beetle disturbances are altered by climate change, the way each disturbance is impacted is very different. Mountain pine beetle is not distributed throughout the entire range of its host pine trees. Its range is not limited by host availability, but rather by climatic factors (Carroll et al. 2004). The northern edge of the mountain pine beetle's range falls in central British Columbia at 56° N. This range has historically been determined by -40° wintertime events and summer temperatures (Taylor et al. 2006). These cold weather events not only limited mountain pine beetle in its northern distribution, but also limited its elevation distribution, usually 800-1400 meters in British Columbia (up to 3300 meters in southern California) (Taylor et al. 2006; Williams & Liebhold, 2002).

After the 1950s, mountain pine beetle populations began to occur outside of its historic range (Taylor et al. 2006). In extreme cases mountain pine beetle are able to disperse 30-110 km/day through the aid of wind, allowing populations to establish in areas far from their previous location if conditions permit (Aukema et al. 2006; Jackson et al. 2008). Small populations have developed previously, but not persistent populations like those currently occurring. Small, but

sustained populations have been located along the northeast slopes of the Rocky Mountains and as far east as Slave Lake, Alberta (with an isolated population in Cypress Hills, Alberta) (Safranyik et al. 2006; Carroll et al. 2004; Safranyik et al. 2010). Insects are very quick to populate new areas as regions become climatically suitable, making them excellent indicators of climate change (Elias 1991). Logan and Powell (2001) have projected a 7° northward shift in mountain pine beetles range for every 2.5°C increase in temperature; making migration much further north very probable with the projected 2-4° C warming in the next 100 years.

Lodgepole pine is present north of the current range, but its distribution ends just east of mountain pine beetles current range. Mountain pine beetle has the ability to feed on 22 pine species including species outside of its current range (Safranyik et al. 2010; Bentz et al. 2001). This ability creates the opportunity for mountain pine beetle to spread east into the boreal taking jack pine, *Pinus banksiana* Lambert, as a new host as climatic limitations diminish. Safranyik et al. (2010) have put the risk of expansion into the boreal at a moderate level. If this threat becomes a reality, over 35 million ha of pine-dominated stands in Canada will be at risk.

Safranyik et al. (1975) and Carroll et al. (2004) developed a model to project the climatic suitability of areas for mountain pine beetle, which could be used to track the suitability of specific areas as climate change increases. Six primary factors were developed as model inputs; >305 degree days above 5.5° from August to the end of growing season and >833 degree day from August 1st to July 31st, minimum temperatures >-40°, average August temperatures >18.3°, total precipitation in April to June < long term average precipitation levels, variability of growing season precipitation, and aridity (Taylor et al. 2006). These factors are the primary controls over climatic suitability for mountain pine beetle and will all vary with climate change.

Phenology is central to mountain pine beetle population dynamics (Bentz et al. 1991). Winter temperatures below -40° C are one of the primary constraints on range and population growth. Cold hardiness varies by population, season, and individual (Bentz et al. 1991). Beetles rid their bodies of large proteins and food prior to winter and produce antifreeze proteins and polyhydric alcohols to cold harden (Régnière et al. 2007). Regardless, high mortality occurs at -

40° C; large amounts of snow can help insulate the beetles from winter temperatures, allowing for higher survival rates during extreme cold weather events.

Cold weather has serious implications for the survival and vigour of mountain pine beetles, but hot weather can also have negative impacts on survival and development. Warm weather increases the development rate of all life stages. The lower development time, although it provides the potential for multiple generations in a year or multivoltinism, can also put development out of synchrony with important seasonal events, increasing mortality (J.A. Logan et al. 2001). Mountain pine beetle has different cold tolerances for all of its development stages with the 3rd and 4th instars being the most cold hardy (Bentz et al. 1991). Therefore, when development stages other than instars 3 and 4 occur during cold periods of the year, mortality rates increase. Multivoltinism can also reduce flight synchrony and mass attack success (Taylor et al. 2006); this only occurs when temperatures are very warm. Warm weather producing severe drought may stress trees too much, lowering the moisture level in the phloem below the optimum range for mountain pine beetle development.

Moderately warm temperatures have been shown to increase survival and vigour through improved synchrony of flight, dispersal, and increased mass attack success (Aukema et al. 2008). The optimal temperature for all life stage development is 23-25°C with the entire life cycle taking only 30 days to complete in this temperature range (Bentz et al. 1991).

Temperatures that provide suitable conditions for a univoltine life cycle give the best synchrony with seasonal events, and decrease mortality (Safranyik et al. 2010). Hence, the degree of warming will be very important in the alterations to mountain pine beetle disturbance levels. Raffa et al. (2008) have suggested that bark beetle populations contain enough genetic variability to adapt quickly to climatic cues and factors that may diminish the negative impacts hot weather and other factors have on populations in several generation periods.

Female mountain pine beetles lay approximately 60 eggs per year, $\frac{2}{3}$ of which are female (Carroll et al. 2006). Due to the high fecundity of bark beetle species a 2.5% drop in generational mortality, usually 97.5-98.6 % could cause the population to double (Régnière et al. 2007). The extreme sensitivity of population size to alterations in mortality creates

enormous potential for climate change to promote explosive population growth if ample host species are available. Cold temperatures are considered the primary control on mortality levels, but food availability and the presence of predators also affects mortality rates (Safranyik et al. 2010).

The vigour of host trees is another primary constraint on bark beetle survival. Drought and other environmental stresses play important roles in lowering trees' defense systems, allowing for higher attack success and survival of beetles, predominantly from the effects on resin production (Raffa et al. 2008). The efficacy of blue-stain fungi, often driven by environmental triggers, is another factor that can affect survival rates (Safranyik et al. 2006). With such small alterations in generation survival causing such large impacts to the overall population, changes to either host tree or blue-stain fungi vigour could have enormous consequences.

Lower levels of mortality due to climatic factors are a central aspect of climatic effects on mountain pine beetle disturbance levels, but the implications of this increased survival and range expansion together is where the real potential for change occurs. In the past three decades mountain pine beetle infestations have started to occur in areas previously deemed climatically unsuitable (Carroll et al. 2004; Logan et al. 2009). Populations have moved into high elevation whitebark pine forests in Canada and the United States, having serious impacts on the entire ecosystems due to their fragility. Small but persistent populations are also present in Alberta along the northeast slopes of the Rocky Mountains; populations are now spreading to central Alberta east of Slave Lake (Carroll et al. 2003; Alberta Sustainable Resource Development, 2009).

Past outbreaks in British Columbia lasted between 3 and 20 years, collapsing as available hosts decreased or climatic events caused extensive mortality (Carroll et al. 2006), but with an expanding range and warmer climates these two control factors may no longer have the same efficacy (Carroll et al. 2004). As the beetle depletes its available hosts, new hosts will be provided as the range expands north and east with the warming climates, not forcing the populations back to their historic endemic levels for decades to come (Carroll et al. 2004).

If the mountain pine beetle does make a successful break into the boreal forest, which probability is increased with small populations persisting outside of the historic range, the lower levels of beetle competition between British Columbia and Manitoba could allow even larger attack success than in the present range (Safranyik et al. 2010). Similarly Safranyik et al. (2010) have predicted the potential invasion further into Alberta and the boreal may be aided by an increased role of blue-stain fungi and its symbiosis with the mountain pine beetle. Brood production in Jack pine, the principal pine in the boreal, is found to be equal to that in lodgepole pine, implicating similar reproductive levels possible in the boreal to those in lodgepole pine dominated regions in British Columbia (Safranyik et al. 2010). The lower percentage of pine in most parts of the boreal may help lower the overall potential impact of the mountain pine beetle in Canada's northern forests.

SPRUCE BEETLE

Spruce beetles can be found in endemic levels throughout the range of its host spruce trees, distributed across North America. All spruce trees are potential hosts, but *Picea glauca* Voss (white spruce) and *Picea engelmannii* Parry (Engelmann spruce) are the preferred hosts with *Picea mariana* Miller (black spruce) being the least preferred host species (Government Of Canada 2010; Schmid et al. 1977). Usually spruce beetles outbreaks can be linked to a clearly identifiable disturbance (fire, drought, wind, or harvest) that enable the populations to build up in less vigorous hosts; such an event has not been identified to explain the recent outbreaks (Berg et al. 2006).

Unlike mountain pine beetles, spruce beetles have two diapauses in their development. The first diapause is a facultative pre-pupal diapauses; the second diapause is obligatory and occurs during the adult development stage (Bentz et al. 2010). Spruce beetles typically develop through a semivoltine lifecycle lasting two years, but under favourable environmental conditions are able to progress to a univoltine (one year) life cycle; this is due to warmer temperatures prevention of the pre-pupal diapause (Bentz et al. 2010). It is this phenomenon that has been linked to the 1990's outbreak in Alaska and the Yukon. Over 1.2 million ha in Alaska and 350,000 ha in the Yukon have experienced extensive mortality in the past two

decades (Figure 3) (Berg et al. 2006). Smaller outbreaks have occurred in Utah and Colorado (Hansen et al. 2001). Spruce beetle levels in British Columbia are not as high as in the Yukon or Alaska, but British Columbia's infested hectares grew by 25% from 2008 to 2009, and rising temperatures may keep British Columbia's spruce beetle populations on this course (Westfall et al. 2010).

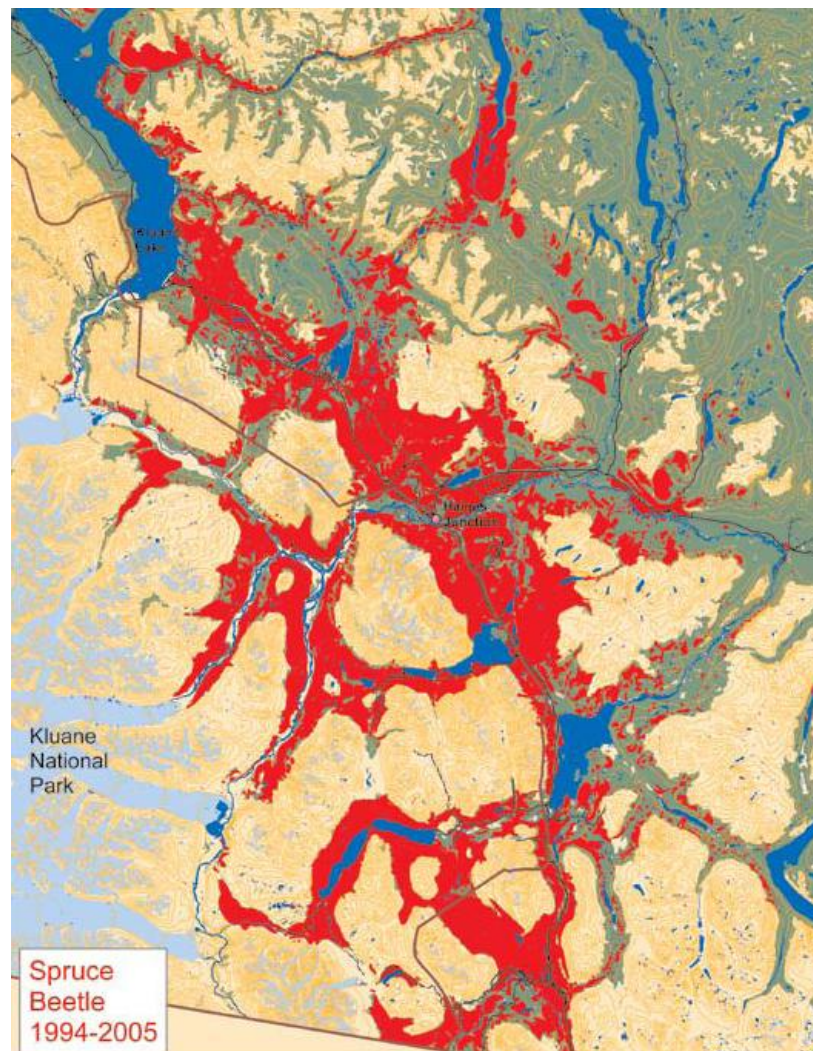


Figure 3: Areas with over 50% mortality caused by the spruce beetle from 1994-2005 in southern Alaska and the south-west Yukon (from Garbutt et al., 2006).

Spruce beetles are present throughout the entire range of spruce trees. Climate change does not provide opportunities for spruce beetle range expansion, only alterations in herbivory

severity both temporally and spatially within its existing range. Increases in damage can be caused by more frequent disturbances like windthrow, flooding, drought, or harvest, which produce higher levels of stressed trees, allowing spruce beetle populations to build-up more frequently (Garbutt et al. 2006). Another reason for increased herbivory rates stems from the alteration in voltinism seen in many spruce beetle populations. Climate is the driving force behind many of these causes of increased damage (Berg et al. 2006; Raffa et al. 2008).

Spruce beetles are the most destructive agent of mature spruce in Canada, with mortality reaching as high as 90% in large spruce in some stands (Herbertson et al. 2008). The population size of spruce beetles is largely responsible for mortality induced, but other factors are also of importance. The mortality inflicted is also dependent on host vigour, the vigour of the symbiotic blue-stain fungi (most commonly *Letographium abietinum*) carried by the spruce beetle, the number of beetle attacks on an individual tree, and the presence of other bark beetles (Werner et al. 2006). *Ips perturbatus* and *Dryocetes affaber*, both secondary bark beetles, lower spruce beetles attack success when present in the same stands (Werner et al. 2006). Drought, heat stress, and age are among the main contributors to tree and stand vigour. Many of the factors controlling attack success are highly influenced by climatic factors, host vigour in particular (Berg et al. 2006; Raffa et al. 2008).

Climate also controls spruce beetle phenology and therefore population dynamics.

Development time of all life stages is temperature dependent. Spruce beetle's lifecycle can range from univoltine to semivoltine either taking 2 years, the most common, or 3 years.

Warmer temperatures result in univoltine lifecycles while cooler weather leads to semivoltine lifecycles, with the coldest weather resulting in 3-year development time (Hansen et al. 2003).

The duration of the lifecycle is environmentally regulated, not genetically regulated, with brood production and survival not being impacted by the varying lifecycle durations (Hansen et al.

2003). Univoltine lifecycles were rare in northern spruce beetle populations prior to the 1990's when temperatures rose significantly (Berg et al. 2006). Figure 4 shows projected probabilities of univoltine life cycles in spruce beetles across North America over three time periods (Bentz

et al., 2010); univoltinism is projected to increase substantially across North America in the next century, increasing the probability of spruce beetle outbreaks.

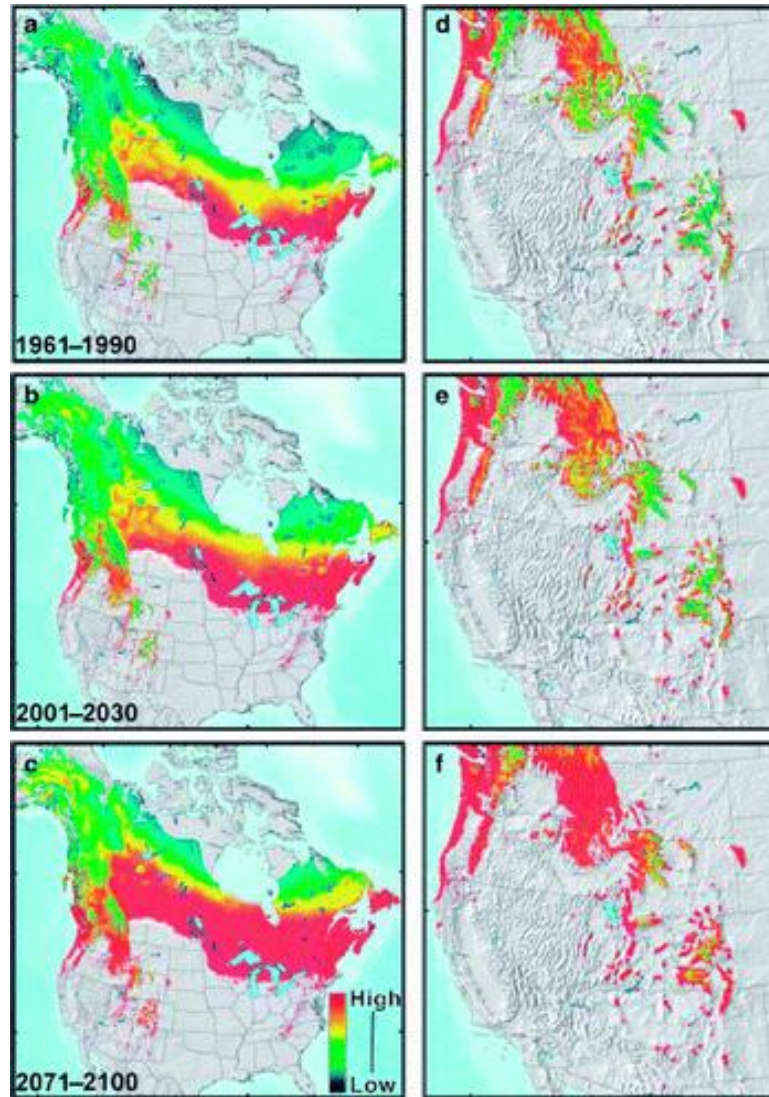


Figure 4: The predicted probability of univoltine life cycle in North America during three periods: (a) 1961–1990, (b) 2001–2030, and (c) 2071–2100, and only in the western United States in (d) 1961–1990, (e) 2001–2030, and (f) 2071–2100 (from Bentz et al., 2010).

Summer temperatures and drought in the previous half decade are the chief factors in predicting outbreaks (Herbertson et al. 2008). According to Berg et al. (2006) average summer temperatures above 10.3°C for five consecutive years increases the probability of an outbreak

by 50%. This is largely due to higher temperatures producing univoltine life cycles; temperatures above 16.5°C in the phloem tissues during mid June to mid July promote univoltinism (M. Hansen et al. 2001). The number of cumulative hours with temperatures above 17°C 40-90 days after adult flight has also been described as an indicator of voltinism (with more hours above this temperature resulting in higher levels of univoltinism) (Hansen et al. 2001). These specific temperature requirements cause voltinism to vary by aspect, elevation, location on the bole, aspect of the bole, and canopy cover (Hansen et al. 2001).

Univoltinism brought on by warm weather is an important aspect of increased herbivory by spruce beetles, but winter temperatures also bind population levels. Spruce beetles ambient temperature threshold for mortality is -24°C, unless protected by substantial amounts of snow (Berg et al. 2006). Overwinter survival is dependent on individual and population's ability to supercool through the production of glycerol and other cryoprotectants and general chemistry, but -24°C is a common threshold, sometimes going down to -34°C (Herbertson et al. 2008). Cold temperatures are required to fulfill a spruce beetle's diapause, a dormancy driven by environmental conditions and the beetle's endocrine system, but they are also a major constraint on survival (Werner et al. 2006; Bentz et al., 2010). Warming temperatures may not provide temperatures cold enough to induce the required diapause as frequently, leading to increased development time and lower reproductive rates or higher mortality levels through increased chance of predation and extreme weather events. Many bark beetles do not have a required diapause and with time spruce beetles may be able to evolve to develop without one.

The Yukon's Kluane region and Alaska's Kenai Peninsula have both suffered severe spruce beetle attacks during the past two decades. Over 1 million ha of Alaska's Kenai Peninsula have experienced extensive spruce beetle induced mortality (Hansen et al. 2001). Although both regions have had outbreaks in the past 20 years, only one of these areas, the Kenai Peninsula, has historically had spruce beetle outbreaks (Berg et al. 2006). The Kenai Peninsula's average winter temperature is -14.6° C while the Kluane regions average winter temperature is -23.7° C (Berg et al. 2006). The colder temperatures in the Kluane region are believed to have kept spruce beetle populations at endemic levels until the climatic warming in the recent decades.

Now, due to climate change, the cold temperatures previously limiting spruce beetle populations are no longer occurring as frequently, allowing beetle populations to grow. This coupled with the increase in univoltine development is causing explosive population levels.

IMPLICATIONS FOR FOREST MANAGEMENT

With so many values at risk, proper land and forest management is critical to the vitality and functionality of future forests. The risk posed by increased bark beetle disturbances is not the only threat to the forest; this risk is coupled with increased frequency of many other forest disturbances, including pathogens, extreme weather events, and fire, as climate change continues (Petzoldt et al. 2008; Stocks et al. 1998; Wotton et al. 2010). Bark beetles alone have vast impacts on the forest, but when joined with other natural disturbances, the effects are even greater.

One of the largest impacts bark beetle outbreaks can cause is land cover change, or regeneration delays. Spruce beetle outbreaks can change land cover types, as seen in the Kenai Peninsula of Alaska, where spruce beetle attacks are changing forests into shrub and grassland complexes (Eastaugh 2008). These shifts in ecosystem type have implications for wildlife, hydrology, timber supply, carbon sequestration and many other important factors (Volney et al. 2000). In some cases land cover change does not occur, but delayed regeneration and poor stocking may result. This is especially true in northern spruce stands where the dense branches and fine branchlets remain on dead standing and downed trees for years, blocking the amount of sunlight reaching the forest floor and impeding regeneration (Garbutt et al., 2006). This regeneration delay has impacts on the land's processes as well as timber supply implications. Large areas of poorly stocked and slow regenerating forests can substantially change annual allowable cut (AAC) levels and non-timber forest objectives feasibilities. These phenomena show how disturbances affect not only the current forest, but also future forests and their dependents.

The increased level of dead or dying timber prompts another management dilemma, possible increased forest fire risk. The lower moisture content of beetle-killed wood may drastically

increase the fire potential in those stands. This is a topic of some debate, with a number of studies yielding different findings regarding the impacts of bark beetle disturbance on forest fire risk. Lynch et al. (2006) found that stands hit by mountain pine beetle outbreaks 13-16 years prior to a fire were 11% more likely afflicted by the forest fire than stands not affected by mountain pine beetle. However, the same study found that outbreaks 5-8 years old did not increase the likelihood of a forest fire. Another study by Bebi et al. (2003) found that spruce beetle outbreaks caused no increase in forest fires. The drastically varying views and their supporting research shows this topic needs further investigation to understand its potential implications to forests and forest management especially with the large areas of dry forests, in the face of warming temperatures being an issue of high concern to many. The potential forest fires from these conditions not only have very serious implications on forests and other ecosystems, but also put communities, individuals, and infrastructure at high risk.

Due to the enormous effects bark beetles have on forests, prompt and thorough management is required to minimize potentially catastrophic effects. Both direct control and indirect control provide promising tactics to meeting mitigation strategies. Carroll et al. (2006) outlined three tactics for direct control; cultural and mechanical, chemical, and semiochemical. Additional tactics include suppression, holding, salvaging, and monitoring. For any of these tactics to be efficient, there needs to be a thorough knowledge of population processes. Early detection increases the efficacy of any control tactic. The use of remote sensing tools and models can give management personnel the benefit of early detection (Coops et al. 2010; Wulder et al. 2006).

Indirect control in the form of stand and forest management and tending is another avenue in bark beetle disturbance management. Activities that increase the vigor of trees, which in turn better their defenses, aid in lowering beetle attack success (Whitehead et al. 2006). Planting species mixes instead of monocultures can also lessen outbreak severities. Management practices that minimize other disturbances, like windthrow, provide other ways to lower beetle population levels. Prompt attention to other disturbances that do occur which lower trees

defenses or provide downed trees for habitat also assists in keeping population levels low, and lessens outbreak potential.

With any strategy or tactic, ensuring that the necessary institutions have the capacity to make knowledgeable timely decisions and fully implement the required actions is very important. In almost all scenarios fast and complete action is crucial to success and without the framework and background knowledge pre-established, the necessary actions will not be made as easily.

Currently in British Columbia, provincial bark beetle management takes place in four steps: stand rating for susceptibility, surveys to detect infestations, assessments of the spread of infestation, and management actions (British Columbia Ministry of Forests and Range 2003). The province is broken up into provincial zones that are placed into one of three categories: aggressive management for stands that can have substantially reductions in infestation rates and spread through aggressive control within 2 years, containment zones where direct control is deemed biologically feasible to hold the infestation level, and salvage zones where salvage will occur when possible. Within the provincial zones there are smaller beetle management units (BMUs). BMUs are divided into four categories; prevention/suppression for stands where aggressive direct control can keep infestation rates low, holding in stands where adequate resources are unavailable for suppression or in stands with chronic outbreaks, and salvage in stands where management would be ineffective, or monitor in stands where salvage is not possible in the short term (British Columbia Ministry of Forests and Range 2003). Through the use of these zones and units, stands and areas can be prioritized and resources allocated appropriately to optimize resource use efficacy.

One of the largest downfalls of the provincial management guidelines is the lack of true preventative management. All efforts are focused on areas already suffering from some form of infestation, rather than creating a landscape overall less prone to infestation. Whitehead et al. (2006) highlights management practices that lower forest and landscape susceptibility through lowering the contiguity of pine forests, using silvicultural practices including thinning to promote tree vigour, and lowering the forest age through shorter rotations. Without long-term landscape level management of forests to lower susceptibility direct control will always be

costly and difficult to implement successfully especially in the face of climate change (Whitehead et al. 2006).

Thorough knowledge of population processes and how they are affected by varying events is imperative for successful control of populations, especially as new factors come into play (Carroll et al. 2006). Since the relationship between bark beetles and their host tree species is so central to the disturbance frequency and severity, the effects on bark beetle disturbances produced by climate change will depend not only on the direct effects on bark beetle life cycles and vigour, but also on the effects on trees and their vigour. Phenology is fundamental in tree's vigour and survival, and as climate shifts important seasonal cues, trees growth and dormancy cycles will become out of sync with the environment (Aitken et al. 2008). This will put many species at increased risk of frost damage, heat damage, and general stress, reducing overall vigour.

In the short-term future many trees will be under the stress discussed above, but in the mid to long-term future, adaptations will occur. Aitken et al. (2008) have developed three possible fates of tree populations in the face of climate change: persistence through migration, tracking its ecological niche; persistence through adaptation in current locations; or extirpation. Due to the longer life cycles of trees, any of these outcomes will take decades to play out, but the outcomes will play important roles in disturbance levels in the future. Adaptations could develop that favoured bark beetles' survival, or increase their mortality. The migration of tree species could also expand or shrink the ranges of bark beetles. A recent study by Coops and Waring (2010) has projected that during the last 30 years of the twenty-first century climatic changes will have extirpated lodgepole pine from almost its entire current range. Although warmer and drier climate pine species including ponderosa pine, *Pinus ponderosae* Douglas, may expand their ranges to area previously dominated by lodgepole pine, the dramatic changes to the ecosystems will still provide adaptive challenges to bark beetles and other forest pests along with the trees themselves. These potentials need to be considered carefully when managers are developing strategies in aiding species vigour and survival in the face of climate change, especially through aided migration.

With the increased potential for epidemic disturbance rates driven by climate change, it is critical for foresters and land managers to maintain a comprehensive knowledge of all disturbances and their contributing factors. The required level of monitoring and action can only be attained through comprehensive landscape level management. Drivers behind specific disturbances may vary, but the strategies and tactics to properly monitor and control them are by and large the same. To attain the required level of management, comprehensive and frequent inventories of forests and disturbances are required. Without these, tracking the changes required to properly monitor disturbance levels will prove impossible.

For increased success in management of these disturbances and their impacts on forests, further research and resources are required. Studies are currently being done using remote sensing techniques to monitor beetle outbreaks, but without implementation and widespread usage the possible benefits from these technologies will be underdeveloped. Further development of models for stand susceptibility and beetle life cycles can also lend very useful information to managers. However, with all strategies, tactics, and research appropriate ecological policies, rather than political or economic policies need to carefully govern their applications.

CONCLUSION

Climate change is already affecting the world's forests and their disturbances. As the level of warming continues to increase, so will the magnitude of alterations to the natural world, including forest disturbances. Not all disturbances will increase from the alterations provided by climate change like bark beetles in western North America, but many will. The mechanisms behind increases to disturbance levels may vary from increased rates of damage from higher reproductive rates as seen with the spruce beetle to range expansion like that of mountain pine beetle, but no matter what the mechanism the risks to the forests remains the same. To provide the best opportunities to combat future disturbances, thorough inventories and comprehensive models need to be in place to locate and prioritize potential outbreaks. Preventative management rather than disturbance management provides excellent opportunities to lower potential outbreak risks before they occur. Further understanding of

bark beetle life cycles and their interactions with host species and climatic factors will provide valuable insights into future disturbance levels and increase model prediction capabilities. Clearer projections on changes in climatic factors will increase projection accuracy and management efficacy. The same principals of understanding life cycles, host interactions, and climatic interactions are important in efficiently managing all disturbances both now and in the future.

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