Canadian Council of Forest Ministers

Conseil canadien des ministres des forêts

# Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests

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# RISK ASSESSMENT OF THE THREAT OF MOUNTAIN PINE BEETLE TO CANADA'S BOREAL AND EASTERN PINE FORESTS

Prepared for the Canadian Council of Forest Ministers, Forest Pest Working Group

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# Executive Summary

Since 2000, mountain pine beetle (MPB) has spread relatively rapidly east across the Rocky Mountains, through northeastern British Columbia, across much of Alberta, and northward towards Yukon and the Northwest Territories (Figure 1). The risk of farther northward spread is low in the near future due to poor climatic suitability and the subsiding of large populations in northern British Columbia. However, an area of highly susceptible pine in southeastern Yukon is expected to be at risk by 2050 due to the anticipated effects of climate change. Spread into the boreal forest is comparatively slower than spread across western and central Alberta. Slower spread rates are likely due to (i) aggressive control efforts in eastern and central Alberta; (ii) lower pine volumes in eastern Alberta compared to farther west; and (iii) a lack of massive long-distance immigration events into eastern Alberta. The current climate of Canada's southern boreal forest can likely support MPB, and there is an opportunity to improve climatic suitability indices to assess future risk.

The greatest threat of eastward spread currently comes from populations around Lesser Slave Lake, which are persisting and slowly spreading through high volume pine stands in the area (Figure 2). Provincial inventory data used in this assessment show more pine at risk across Alberta, Saskatchewan, Manitoba and Ontario than national data sources used in previous assessments (Figure 3). While climate regulates MPB populations at a landscape scale, stand characteristics are the main determinant of population dynamics at the local scale. A detailed forest inventory, including a quantification of the phloem resources available, is necessary to better assess the potential threat posed by MPB to eastern pine forests.

In addition to the persistent, slowly spreading populations around the Lesser Slave Lake area, there are two other avenues for eastward spread. In 2018, there is evidence of long-distance dispersal of beetles from large source populations in western Alberta into susceptible pine stands south of Lesser Slave Lake. If populations build to uncontrollable levels in central Alberta in the near future, they would provide a source of beetles that could disperse the 300 km into Saskatchewan, fueling eastward spread. The threat will likely persist several years until the large outbreaks in western Alberta collapse. The second avenue for eastward spread is through the long-term threat posed by extremely low density MPB populations that may be established in eastern Alberta. Such low-density populations could increase under favourable conditions, threating eastward spread and requiring special monitoring efforts.

MPB spread requires both dispersal (or movement) and the subsequent establishment of the founding population in a new environment. Spread will likely be positively correlated with beetle population size. Spread of endemic (or low density) populations is likely to be negligible, while untreated spot and incipient infestations could spread at a rate of tens of metres up to several kilometres per year. Massive populations could result in a spread of 100–300 km in the direction of the prevailing wind. Spread via the human-assisted pathway is unlikely due to the low volume of wood moved and provincial policies, but specialty users present a specific and higher risk. Overall, there is relatively high uncertainty associated with the rate of MPB spread in Canada, which highlights (i) the need for a better understanding of dispersal; (ii) the importance of annual surveys and annual review of control decisions; (iii) the need for a better understanding of MPB population dynamics in novel habitats; and (iv) the extremely volatile nature of the situation and how quickly it can change.

Populations can be suppressed through management actions, but control of large populations is not feasible. The relationship between MPB's annual population growth rate, the size of the infestation and the proportion of the population that can be treated will determine whether or not it is a "winnable" battle. Detection of infested trees and control efficacy are dependent on available resources. Successful suppression requires early detection and aggressive control that is sustained until the cause or causes of the outbreak are no longer operative. These principles should apply in the new range, although there is higher uncertainty of specific treatment thresholds due to novel beetle-host-climate interactions. Small perturbations in the system can also manifest in sudden changes, which means that management decisions and allocation of resources must be reviewed annually.

Quantifying MPB's expected impact on novel pine forests is key to determining the socio-economic and ecological consequences of MPB spread. Impact in the boreal forest is expected to be lower than in British Columbia due to comparatively lower pine volumes: stands that have many large mature pine trees are expected to suffer the highest mortality rates. Overall, MPB's impact is expected to negatively affect stand merchantability, forest-dependent communities, Indigenous communities, carbon storage, and ecosystem services values. The potential impact of MPB in boreal and eastern pine forests is far greater than that of any other forest insect in Canada. Wildfire risk in the fire-prone boreal ecosystem is expected to increase with tree mortality, but it will change over time. There may be the potential to recover some losses by harvesting beetle-killed trees; however, value will be reduced and it may be more beneficial to leave stands with good secondary structure and understory for their mid-term timber supply and ecological values.

Canada's boreal and eastern pine forests are novel habitat for MPB. MPB is exposed to substantial variation in hosts within its historic range in western North America, and it is likely that the behaviour and population dynamics of MPB in its new habitat will fall within the range of that observed on the variety of pine hosts attacked in the beetle's historic range. However, the uncertainty associated with this statement is high and there is a need for empirical stand-level field studies. The vast majority of introduced species tend to perform similarly across their native and invaded ranges. In assessing the threat MPB poses to boreal and eastern forests, it is critical to consider that MPB possesses at least two key traits of highly successful species: (i) high reproductive capacity; and (ii) widespread dispersal ability (but only during outbreaks). These characteristics will likely make MPB a significant disturbance agent in any pine-dominated ecosystem.

# Background

### Current State of the MPB Threat

Mountain pine beetle (MPB) is a native disturbance agent of pine forests in western North America. Periodic eruptions generally occur every 25–40 years in lodgepole pine-dominated ecosystems in British Columbia's interior and cause notable tree mortality. The recent epidemic that started in the mid-1990s surpassed any previous outbreak in recorded history by an order of magnitude. Over 730 million $m^3$ or approximately 55% of the merchantable pine in British Columbia was killed resulting in significant economic, social and ecological impacts. Just as the epidemic was peaking in the mid-2000s, large numbers of beetles moved long distances across the Rocky Mountains on upper atmospheric winds. The beetles were deposited east of the Continental Divide in northeastern British Columbia and northwestern Alberta where they quickly established and spread through a region where infestations had not been previously recorded.

Prior to 2000, MPB infestations in Alberta were limited to around Banff and the southern Rocky Mountains, Kananaskis region and an isolated pocket of lodgepole pine spanning the southern Alberta-Saskatchewan border called the Cypress Hills (Figure 1). Since about 2006, MPB has spread through lodgepole pine forests in western and central Alberta aided by several long-distance dispersal events. Spot infestations have been recorded near 60° N for the first time in recorded history and close to the Saskatchewan border in Alberta.

There still appears to be no impervious biological barrier to prevent eastern spread, although the rate of spread in eastern Alberta has been slowing. The slower rate of spread is attributed to lower pine volumes, poor connectivity of susceptible pine stands, lower probability of long-distance dispersal events as distance to a large source population increases, and aggressive control efforts sustained to date by the province in eastern Alberta. Eastern Alberta, where infestations are relatively small and control can be effective, has been identified in Canada's MPB National Response Plan and Containment Strategy as the best place to employ slow-the-spread tactics.

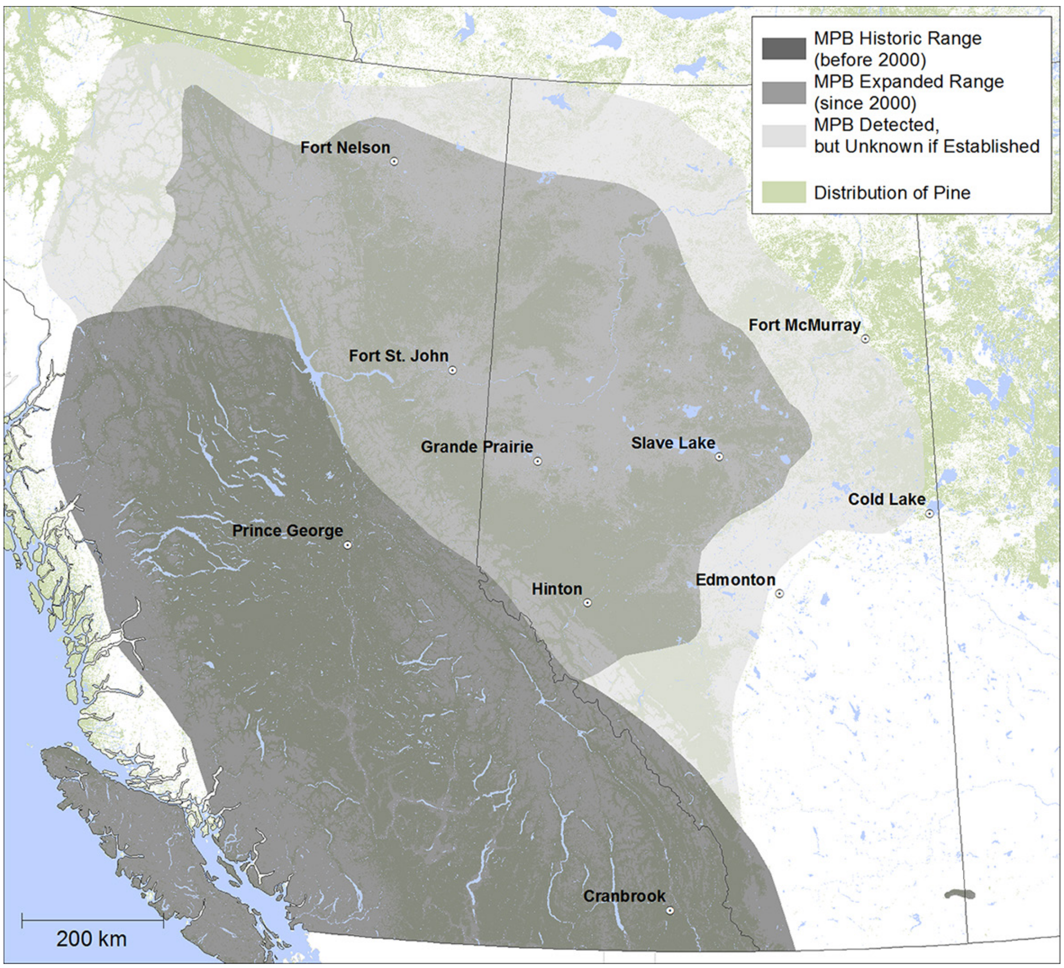



**Figure 1.** The historic range (before 2000) and expanded range (after 2000) of MPB in Canada. Outside the expanded range is a region where MPB has been infrequently detected at low densities in aerial surveys (British Columbia) or in pheromone-baited trees (Alberta, Northwest Territories). Currently, it is unknown whether MPB is established in this outer region or in parts of it. That is, it is unknown whether the beetles detected in this outer region are produced locally from established (resident) low-density populations or whether they are from larger established populations farther west that occasionally disperse into the region but fail to establish.

There is very high uncertainty around the potential for large populations of MPB in western Alberta to contribute to eastward spread in the near future. Large populations along the eastern slopes of the Rockies could spread through the corridor of susceptible pine forest that runs south of Lesser Slave Lake and build up on the eastern edge of the Foothills Region; this scenario would position large populations that could potentially disperse the 300 km directly into Saskatchewan. Regardless, increasing populations along the foothills of the Rocky Mountains has prompted the province of Alberta to reallocate control resources from eastern Alberta to the foothills to protect key watersheds and commercial forests. This reallocation of resources will manifest in reduced control in eastern Alberta, which may leave small active infestations to percolate, build over time and spread if left untreated.

## Risk Analysis Process

Risk analysis involves assessing what is known to characterize risk (risk assessment) and developing an appropriate response (risk response); communication to foster adaptation and transparency occurs through the iterative and adaptive process. This Risk Assessment, like previous assessments, follows the general Risk Analysis Framework developed under the National Forest Pest Strategy for the Canadian Council of Forest Ministers (Nealis 2015). Affirmative provocative statements are used to elicit scientific evidence and expert opinion to reveal new knowledge. For each statement, associated uncertainties and the research needed to reduce the level of uncertainty are identified. It is an integrated and adaptive approach where new knowledge, uncertainty, and appropriate responses are repeatedly assessed as new information becomes available.

### 2007 Initial Emergency MPB Risk Assessment

(Nealis and Peter 2008) http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/28891.pdf

In 2007, alarming levels of tree mortality from MPB east of the Rocky Mountains prompted the Canadian Forest Service (CFS) to conduct an emergency risk assessment of the potential threat to Canada's boreal and eastern pine forests. The assessment determined there were no host-related impediments to the spread of MPB farther east or north, but that spread rates and the severity of infestations were expected to be less than in central British Columbia due to differences in forest structure and a relatively unfavourable climate in the near future. Natural extinction of MPB was deemed unlikely, and the threat of persisting populations erupting and spreading into the boreal forest and causing socio-economic and ecological impacts was highlighted. The assessment advised the development of a comprehensive response, including both short-term direct control and longer-term preventative management. The most critical immediate information needs identified were the effectiveness of management responses in controlling MPB, refinement of MPB monitoring and detection, and a detailed forest inventory. The 2007 assessment focused additional questions on risk related to the vulnerability of boreal and eastern pine species to attack, expected MPB survival rates in novel climates, dispersal rates and directions of spread, and ecological and socio-economic impacts.

### 2010 MPB Risk Assessment (update)

(Nealis and Cooke 2014) http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/35406.pdf

The 2010 update was requested by the Canadian Council of Forest Ministers Forest Pest Working Group through the National Forest Pest Strategy due to the rapid changes in the distribution of MPB and the significant investments being made by forest managers in response to the threat. The 2010 update included data up to 2011/2012 and focused on new scientific evidence produced since the initial emergency assessment and followed the same general framework. Socio-economic impacts were not reassessed. The reassessment found that between 2007 and 2011, MPB continued to expand its geographic and host ranges and was persisting in areas previously thought to be climatically unsuitable. The significant contribution and erratic nature of long-distance dispersal of beetles from high density populations on eastward spread were recognized, and the frequency of long-distance dispersal events was predicted to decline after 2011. The 2010 update also found that MPB could locate and attack sparse clusters of pine trees in mixed wood stands and that population growth and spread were potentially less constrained by the low connectivity of susceptible stands than initially predicted; there was high uncertainty regarding MPB behaviour on the leading edge. Additionally, jack pine and lodgepole pine populations in the new range may have lower resistance to MPB, and beetle reproduction may be higher in these hosts due to their putative naiveté. Overall, wildfire risk was predicted to increase. The need for an informed analysis of response options incorporating the latest survey and research results was reiterated.

**2012–2013 The Canadian Forest Service's MPB Strategy and Research Plan**
(Burke and Sankey 2013) Internal Canadian Forest Service Document

Given the assessment that the risk of MPB spread east into Canada's boreal forest was real and imminent, the CFS developed a strategy to provide a framework for future CFS decisions and activities concerning MPB using an integrated science-policy approach. Scientists and policy analysts identified key policy questions and priority research areas for the CFS. The policy questions related to (i) the level of risk posed by MPB to Canada's boreal forest, including its potential impacts on fibre supply, communities and ecosystem services; (ii) the likely pathways of spread and potential opportunities for, and benefits of, intervention; (iii) the lessons learned to date and communication practices for sectors regarding future risk; and (iv) the maintenance and further development of an integrative science-policy approach. Five research themes relevant to the policy issues were identified in the Research Plan: novel habitat ecology; dispersal and spread; impacts (biophysical, socio-economic, forest resilience, community adaptive capacity); mitigation and decision support systems; and integration and synthesis. The Strategic and Research Plan defines the role of the CFS in delivering expertise, knowledge and tools to forest practitioners and stakeholders related to MPB.

**2017 MPB Response Plan (A Strategic Approach to Slow the Spread of MPB Across Canada)**
(Hodge et al. 2017) https://www.ccfm.org/pdf/2017-MPBStrategicContainmentApproach.pdf

A Response Plan (containment strategy) with options to slow the eastward spread of MPB was developed in response to a request from the Canadian Council of Forest Ministers Forest Pest Working Group. The plan uses research and field observations from both Alberta and British Columbia to inform management actions and practices. The importance of early detection of infestations while populations are relatively small and of aggressive control actions sustained through time until populations are pushed below a critical threshold are highlighted. The draft containment strategy includes the technical aspects of MPB population management, the science behind spread control, and a discussion of the economic challenges and realities of MPB management. Collaborative multi-jurisdictional management actions are required for successful management, and eastern Alberta is identified as a suitable region to apply slow-the-spread practices outlined in the strategy.

**2018 MPB Risk Assessment (reassessment of the threat)**

As in 2010, the Forest Pest Working Group of the Canadian Council of Forest Ministers initiated the 2018 Risk Assessment. Over 7 years of new research and information has accumulated and a forthcoming proposal from Alberta for federal assistance to control MPB in eastern Alberta warranted a reassessment of the threat. This assessment includes evidence from previous risk assessments that is still relevant and amalgamates a number of previous statements with the objective of providing a stand-alone, comprehensive discussion of evidence around general topics. Eastward spread has slowed due to aggressive control efforts as well as stand and climatic factors. The greatest threat of eastward spread comes from persistent populations east and south of Lesser Slave Lake that are persisting and spreading slowly in susceptible pine (Figure 2). There is more susceptible pine at risk in Alberta and farther east than initially assessed. In the near future, large populations in western Alberta may stoke populations in central Alberta, which could fuel farther eastward spread. Over the course of an extensive outbreak, MPB may spread 100–300 km. The current management strategy and control efforts in Alberta have reduced the area impacted by MPB. Tools remain limited for detection and control such that the main way to increase control efficacy is through greater allocation of resources. There is still a need to quantify potential socio-economic impacts, including ecological services values, although the values at risk to MPB in Canada's boreal and eastern pine forests are arguably greater than for any other forest insect.

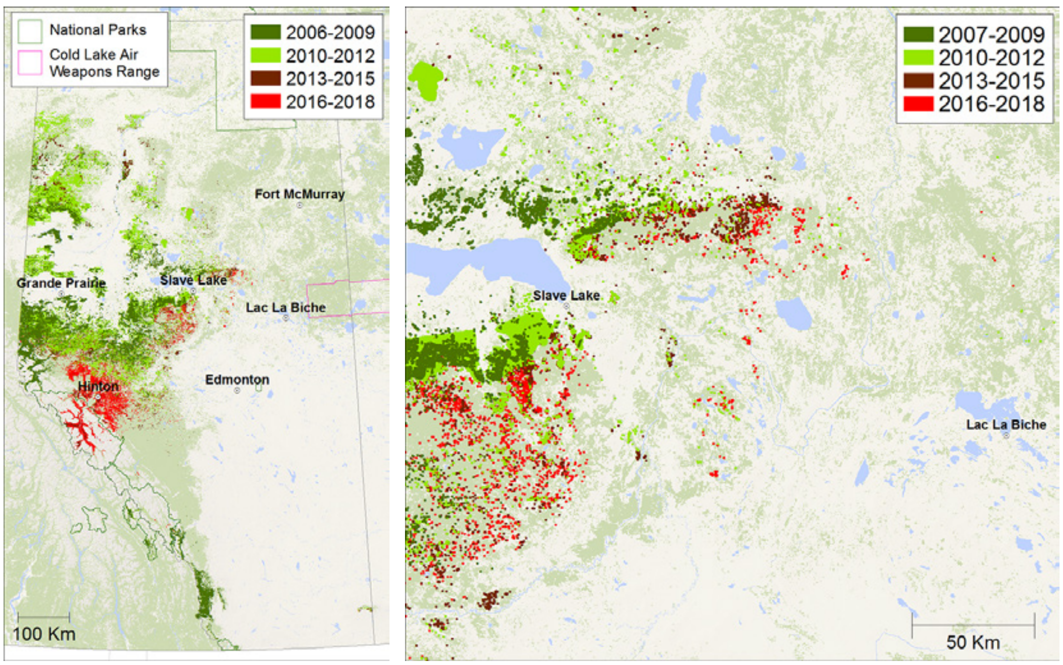



**Figure 2.** Progression of MPB spread through Alberta over time. Older infestations are plotted on top of more recent infestations, such that a site is coloured for the earliest year of infestation. The bright red areas are where MPB is actively spreading, with infestations recorded only within the 2016–2018 time period. The map of the province on the left shows the two areas in Alberta where MPB is currently spreading: western Alberta around Hinton and central Alberta around Slave Lake. The map on the right is a closeup of the area around Slave Lake where there is the greatest threat of MPB spreading east to Saskatchewan. Intensive control activities are conducted in central and eastern Alberta to reduce the rate of eastward spread.

# Likelihood of Spread

## 1. A SIGNIFICANT PORTION OF CANADA'S BOREAL FOREST IS AT RISK TO MPB ATTACK. (K. Bleiker)

### EVIDENCE

Mountain pine beetle (MPB) is a specialist on *Pinus* but a generalist within the genus. It has been recorded as successfully attacking 22 species of pines (Safranyik et al. 2010). To date, of the native North American pines, only Jeffrey pine and Great Basin bristlecone pine are described as unsuitable for MPB development (Wood 1982; Bentz et al. 2016, Eidson et al. 2017, 2018). A number of pine species whose natural distributions are outside the range of MPB were attacked in arboreta in the western United States during an MPB outbreak in the mid-1960s (Furniss and Schenk 1969; Smith et al. 1981). Successful attacks were reported on the four species of pine native to eastern North America, i.e., jack pine, red pine, eastern white pine and pitch pine. The susceptibility of jack pine, and the non-native species Scots pine, was reconfirmed during a 1981 Canadian Forest Service survey of shelterbelt trees in the non-forested grasslands region of southern Alberta (Hiratsuka et al. 1982). Successful attack on a pure jack pine tree in the tree's native range was reported in 2011 in central Alberta (Cullingham et al. 2011).

While some individual trees are susceptible to attack, MPB outbreaks only occur in stands with a high proportion of old, large-diameter pine trees (Safranyik and Carroll 2006). This is linked to increased productivity of MPB in large trees with thick phloem and the fact that host resistance declines after age 60, which lowers the threshold density of beetles required to mount a successful attack (see Statements 3 and 4). A stand susceptibility index (SSI), which accounts for stem density, species composition, age as well as climatic suitability of a location, has proven to be a useful long-term indicator of potential losses should a beetle epidemic occur in lodgepole pine stands in British Columbia (Shore and Safranyik 1992; Shore et al. 2000). A stand susceptibility analysis for Alberta and Saskatchewan using a modified SSI found that the eastern slopes of the Rocky Mountains contained well-connected stands of susceptible pine; however, stand susceptibility was low in eastern Alberta and throughout Saskatchewan (Safranyik et al. 2010). There is also a large area of highly susceptible pine in southeast Yukon (Hodge 2012).

Safranyik et al. (2010) highlighted that the susceptibility of jack pine stands in Canada's western boreal forest may not be the same as for lodgepole pine stands in central British Columbia if there are differences in MPB epidemiology in the two species (see Statements 3 and 4). Despite potential differences, the general maxim that "more big pine trees are better for MPB" will likely apply across species so that pine volume can be used as a surrogate to assess stand susceptibility for any species.

Estimates of pine volume vary with the source of data. Figure 3a shows nationally available CanFI and EOSD data from Yemshanov et al. (2011), which was used in previous risk assessments (Nealis and Peter 2008; Safranyik et al. 2010; Nealis and Cooke 2014; Cooke and Carroll 2017). Figure 3b shows the successor of CanFI, which are data derived from k nearest neighbours (kNN) interpolation methodology, attribute values from the photo plots of Canada's National Forest Inventory (NFI) (Gillis et al. 2005; Stinson et al. 2016) as reference data, and 2001 MODIS imagery as the main source of predictive variable (Beaudoin et al. 2014). Figure 3c is collated forest inventory data obtained from each province overlaid on kNN data to fill in areas not covered by provincial data.

From Alberta through Ontario, pine volumes estimated from provincial inventory data are much higher than volumes calculated from nationally available data (Figures 3a-c). Provincial data from British Columbia show lower pine volumes in central British Columbia than national data because the provincial data are more recent (2016) and reflect losses incurred during the recent MPB epidemic. Pine volumes are highest along the eastern slopes of the Rocky Mountains, decrease in central Alberta and then drop again in eastern Saskatchewan and western Manitoba before substantially increasing again in Ontario. Detailed predictions cannot be made based on the resolution of these data, but based on provincial data, pine volumes through much of Saskatchewan and Ontario are comparable or higher than pine volumes in central Alberta where the beetles spread relatively quickly (Figure 3c).

The accuracy and availability of detailed forest inventory data and issues related to using substitute variables presents challenges for quantifying forests at risk to MPB in Canada (Nelson et al. 2006). There are also inherent difficulties in changing the scale of models or indices like the SSI because key drivers of a system may change when certain thresholds are surpassed or system drivers may vary with scale (Nelson et al. 2006, Raffa et al. 2008). There are challenges with respect to collating provincial data, e.g., collection methods differ among the provinces leading to inconsistencies and the data are available only for the working forested landbase. With those caveats in mind, the composite map of pine volume using provincial and national kNN data presented here is an advancement in the assessment of pine at risk in Canada: there is more pine at risk in Canada than previously thought.

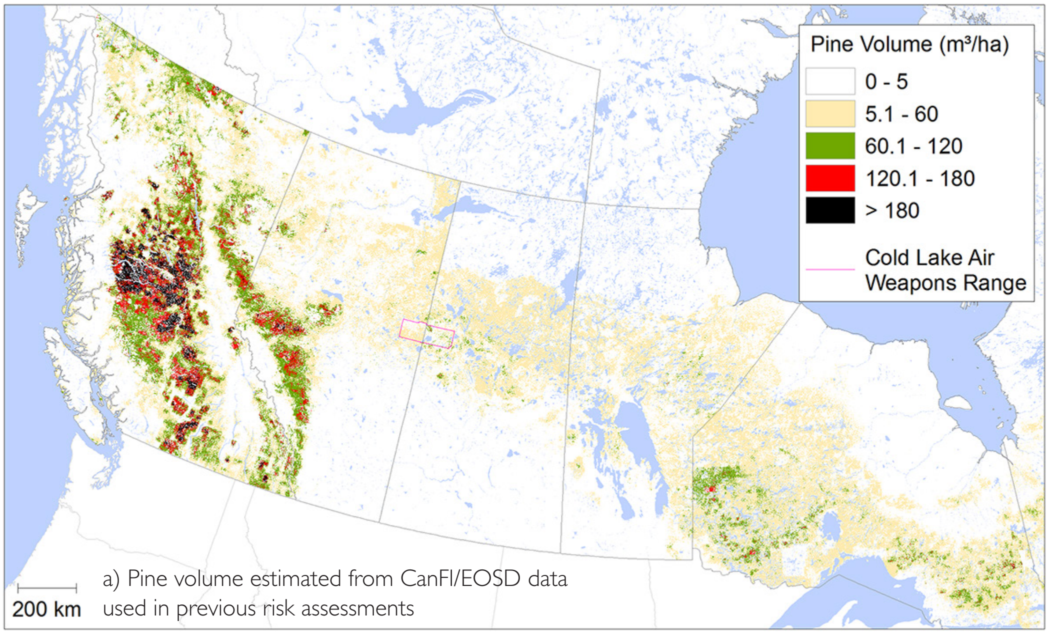
Almost 50 years ago, Furniss and Schenk (1969) asked why MPB had not spread yet from lodgepole pine in British Columbia to jack pine in central Alberta and east across the boreal forest. Almost 20 years ago, Logan and Powell (2001) postulated that a climate-facilitated range expansion of approximately 7° N from a 2.5 °C warming could lead to MPB moving into previously unoccupied lodgepole pine forests in northern British Columbia and an eastward invasion through jack pine. Host availability is the main determinant of MPB population levels at the stand or site level, but climate is the primary driver of MPB epidemics at the larger landscape scale (Goodsman et al. 2018) (Statement 2).

## UNCERTAINTY

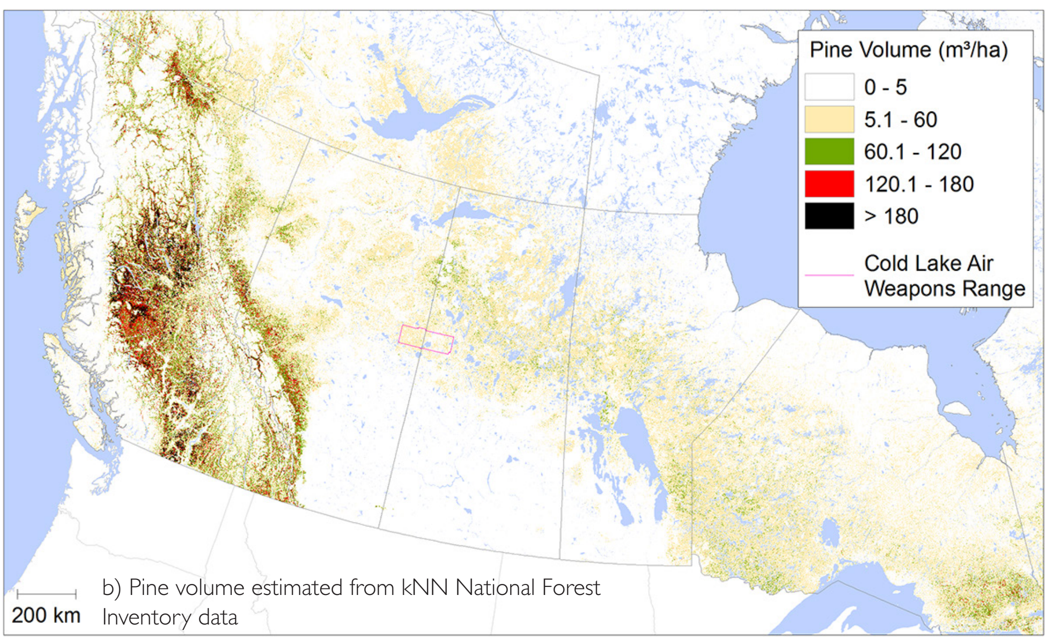
1. Low uncertainty that eastern pine species in Canada are suitable hosts for MPB.
2. Moderate uncertainty regarding the abundance and distribution of susceptible pine stands in Canada.
3. Moderate uncertainty that the stand susceptibility index developed for lodgepole pine stands in British Columbia applies east of the Rocky Mountains. (Low uncertainty that "more big pine is better for MPB" will apply across species.)

## RESEARCH NEEDS

1. Quantification of factors affecting the susceptibility of jack pine stands to MPB to validate, re-parameterize or adapt the stand susceptibility index developed for lodgepole pine stands in British Columbia for use in other regions.
2. Collation of the best available inventory data and standardization of mensuration data to improve estimates of pine volume and variables used to assess stand susceptibility.




a) Pine volume estimated from CanFI/EOSD data used in previous risk assessments




b) Pine volume estimated from kNN National Forest Inventory data

Figure 3. *(Continued).*

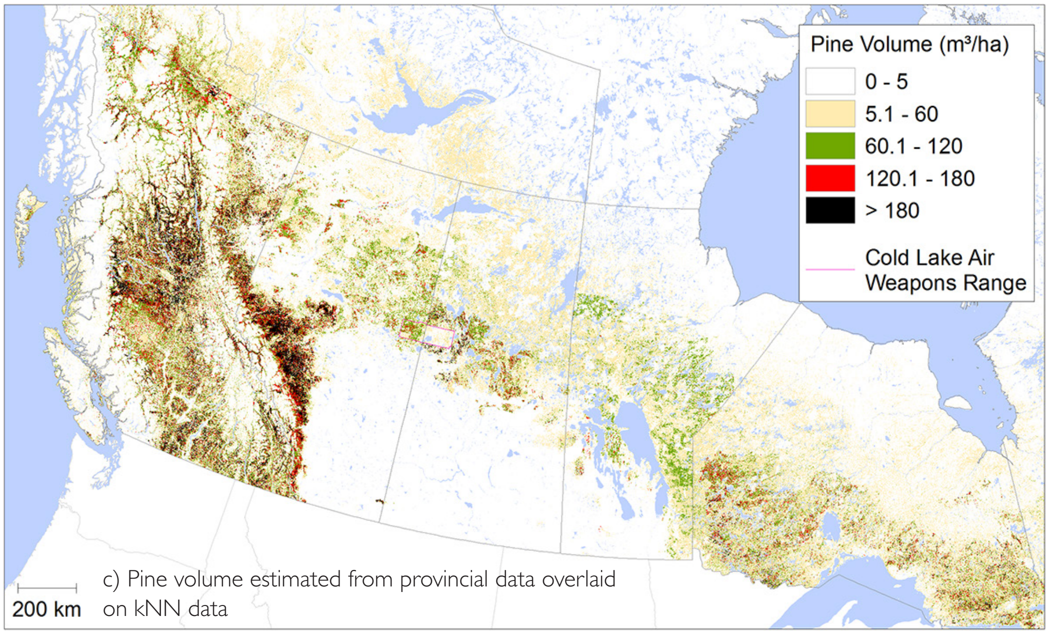



**Figure 3.** *(Continued)* Estimated volume ($m^3$/ha) of all species of *Pinus* in western Canada using (a) national CanFI and EOSD data from Yemshanov et al. (2011), which was used in previous risk assessments; (b) national kNN data from Beaudoin et al. (2014); and (c) provincial data obtained from each province for the working landbase overlaid on national kNN data. The provincial data for British Columbia are more recent (2016) than the national data sources and reflect volume losses in the province to MPB during the recent epidemic (see Figure 5). *(Concluded)*

## 2. A SIGNIFICANT PORTION OF CANADA'S BOREAL FOREST IS CLIMATICALLY SUITABLE FOR MPB. (K. Bleiker)

### EVIDENCE

Climate and weather are the key determinants of the distribution and demography of MPB (Safranyik 1978). Mild winters and warm summers have been linked to increases in the area infested, tree mortality and beetle productivity (e.g., Aukema et al. 2008, Sambaraju et al. 2012, Creeden et al. 2014, Goodsman et al. 2018). Synchronous outbreaks over extensive landscapes support climate as the main factor driving MPB epidemics at large spatial scales (e.g., Aukema et al. 2008; Goodsman et al. 2018). Once outbreaks are initiated, they usually end when insects run out of host trees (Safranyik and Carroll 2006); populations in stands collapse due to intraspecific competition and host depletion (Aukema et al. 2008; Goodsman et al. 2018). Extreme weather events can also reduce populations and in rare cases even arrest outbreaks. The burgeoning 1970s and early 1980s MPB outbreak in central British Columbia ended after back-to-back early season cold events in 1984 and 1985 (Safranyik and Linton 1991). More than one extreme temperature event may be required to push large populations below eruptive thresholds.

The range of MPB in Canada is limited by cold winter temperatures and not by the distribution of available host trees (Safranyik 1978). The northern limit of MPB's distribution coincides with the -40 °C isotherm, which has migrated northward with climate change (Safranyik et al. 1975; Carroll et al. 2004). Cold temperatures are the largest single source of mortality in the life cycle of MPB (Safranyik 1978, Amman and Cole1983). Cold tolerance varies with life stage. Eggs will not survive winter anywhere in Canada and adult beetles are unlikely to survive most winters in

Canada's boreal forest, but some late instar larvae can survive temperatures approaching -40 °C in mid-winter when they are most cold hardy (Reid and Gates 1970; Bentz and Mullins 1999; Cooke 2009; Bleiker and Smith 2016; Bleiker et al. 2017; Rosenberger et al. 2018). Results vary as to whether early larval instars are actually as cold tolerant as late larval instars and the current overwinter survival model does not include stage specific mortality among larval instars (Safranyik and Linton 1998; Bentz and Mullins 1999; Régnière and Bentz 2007; Cooke 2009; Régnière et al. 2012).

Growing season temperatures determine MPB's developmental rate and the life stage(s) that enter winter (Bentz et al. 1991). In most of Canada, a synchronous one-year life cycle with late-instar larvae entering winter is probably best for MPB survival. The beetle can complete its life cycle in two years, but infestations are limited in regions with insufficient degree-days for a one-year life cycle (<833 degree-days above 5.6 °C) (Safranyik et al. 1975). In fact, successive years of above-normal summer temperatures allowing MPB to complete its life cycle in one year likely contributed to an MPB outbreak in cool high elevation whitebark pine forests in the Rocky Mountains in the 1930s (Logan and Powell 2001). Fractional life cycles that are less than one year are possible but would be maladaptive in the boreal forest if non-cold-tolerant life stage(s) entered winter.

In addition to the direct effects on winter survival and developmental rate, weather also impacts MPB indirectly through effects on the host tree. For example, long-lasting drought increases host susceptibility by compromising the resin defences of trees and lowering the number of beetles required to mount a successful attack (Safranyik et al. 1975, Raffa et al. 2008; Kolb et al. 2016). This has significant implications for colonization success and MPB's ability to transition from endemic to epidemic tree-killing behaviour (Boone et al. 2011; Cooke and Carroll 2017). Furthermore, interacting factors and non-linear dynamics in this system can manifest in "tipping points," such that a seemingly minimal change in climate or a small perturbation in the system can have sudden and unpredictable impacts on MPB populations and tree mortality (Kolb et al. 2016; Cooke and Carroll 2017).

The amount of climatically suitable habitat for MPB has increased dramatically over the last century in North America, largely due to milder winters, and the beetle has responded by expanding its range northward, moving into higher-elevation forests and increasing the number and frequency of infestations (e.g., Carroll et al. 2004; Powell and Bentz 2009; Safranyik et al. 2010; Cooke and Carroll 2017). In spite of favourable summer conditions for MPB development, the threat to Yukon and the Northwest Territories is predicted to be low at least through to 2030 due to cold winter temperatures (Hodge 2012, 2014).

Assessments of the climatic suitability of Canada's central boreal forest range from low to moderate depending on the climatic suitability index examined (Nealis and Peter 2008; Bentz et al. 2010; Safranyik et al. 2010; Nealis and Cooke 2014). Bentz et al. (2010) state that the probability of MPB spreading across Canada this century is low even with the anticipated effects of climate change due to the harsh winter climate in certain areas through which the beetle must pass. In contrast, Safranyik et al. (2010) conclude that winter conditions along the southern edge of Canada's boreal forest are currently sufficient to allow MPB to persist and that spread through central Canada will largely hinge on the importance of MPB maintaining a synchronous one-year life cycle such that the most cold-tolerant life stage overwinters.

In the period 2001–2030, the MPB phenology model predicts that the latitudinal band in which MPB can maintain a one-year life cycle will shift northward such that there will be a limited region in which both winter and summer temperatures are conducive to MPB outbreaks. However, recent research indicates that MPB can regulate its life cycle to a certain degree (Bleiker and Smith 2017;

Bentz and Hansen 2018); field data from central Alberta show that MPB can maintain a one-year life cycle even with an advanced flight period and where developing insects receive 40% more degree-days than needed for a one-year life cycle (Bleiker and Van Hezewijk 2016; Bleiker and Smith 2017). There is a need to elucidate parameters and thresholds associated with an adaptive life cycle and create a climatic suitability index that incorporates the potential impact of both summer and winter temperatures.

### UNCERTAINTY

1. Low uncertainty regarding the cold tolerance of eggs, young adults, and late-instar larvae, and moderate uncertainty regarding the cold tolerance of the other life stages.
2. High uncertainty regarding the temperature thresholds and the timing of cold events required for significant early (spring) and late (fall) season mortality (acquisition/loss of cold tolerance), and low uncertainty regarding cold tolerance in mid-winter.
3. High uncertainty regarding the extent of temperature conditions under which MPB can maintain an adaptive one-year life cycle.
4. Moderate uncertainty regarding the overall climatic suitability of the boreal forest through central Canada for MPB and how rapidly it will change over time.
5. Moderate uncertainty over using climate or weather-based models, which work well at large spatial scales, to predict mortality at smaller spatial scales where stand-level factors (e.g., interspecific competition, host depletion) can obscure the effects of weather.
6. High uncertainty regarding how the MPB system will be impacted by minor perturbations, such as small changes in weather.

### RESEARCH NEEDS

1. Quantification of conditions (e.g., temperature and time thresholds) that lead to the acquisition and loss of cold tolerance in MPB.
2. Identification of climatic factors and relevant parameters that regulate MPB's life cycle.
3. Development and/or refinement of current climatic suitability indices into a composite index that is parameterized to the current available knowledge.

## 3. MPB CAN LOCATE AND SUCCESSFULLY COLONIZE JACK PINE OR POPULATIONS OF LODGEPOLE PINE THAT OCCUR OUTSIDE THE BEETLE'S HISTORIC RANGE. (K. Bleiker, N. Erbilgin)

### EVIDENCE

Given a suitable climate, the establishment and persistence of MPB in a habitat largely depend on the beetle's interaction with the host tree: MPB must locate and successfully colonize suitable host trees. Tree constitutive and induced defensive chemistry plays a significant role in host location, selection and colonization (Raffa et al. 2008; Erbilgin et al. 2017a; Erbilgin 2019). MPB must kill its host tree, or at least a strip of the tree, to successfully reproduce and pines have evolved chemical defence systems to resist attack by herbivores and fungal pathogens. The constitutive or preformed resin defences of pines are always present, and the induced resin defences are initiated once an attack occurs. Both defence systems contain terpenes and other compounds, such as phenolics, that can be attractive and toxic to bark beetles, depending on their concentration (Erbilgin et al. 2017a).

Plant volatile compounds may be used by MPB to locate and select suitable host trees for attack (Moeck and Simmons 1991). When populations are low or at endemic levels, beetles typically locate and colonize stressed and moribund hosts with severely compromised defences (Boone et al. 2011; Bleiker et al. 2014). When populations are high, beetles preferentially attack large vigorous host trees that have better resources but are also well defended (Boone et al. 2011). MPB overwhelms the defences of healthy trees by attacking en masse: initial attacking beetles produce aggregation pheromones de novo (male pheromone) and through oxidation of the host monoterpene $\alpha$-pinene (female pheromone) to coordinate a rapid mass attack (Erbilgin et al. 2017a). Anti-aggregation pheromone is produced through autoxidation of $\alpha$-pinene as additional beetles arrive to reduce competition.

The increased susceptibility of naïve species/populations hypothesis posits that pine populations and species populations that have had no co-evolutionary interactions, or limited interaction, with MPB lack the chemical defences of species and populations that have putatively coevolved with MPB (as evidenced by Sturgeon (1979) for western pine beetle and populations of ponderosa pine). Studies have tested this hypothesis for lodgepole pine populations west of the Rockies with mixed results. Some studies use the climatic suitability rating of a site for the period 1941–1970 to infer the selective pressure exerted by MPB over evolutionary time. Using this method, an analysis of constitutive defence chemistry found support for the hypothesis in central British Columbia, but not in southern British Columbia, or in a latitudinal comparison of sites (Clark et al. 2010). Total monoterpenes in the induced response were higher at sites with a high climatic suitability rating compared to sites with a lower rating, which supports the hypothesis (Burke et al. 2017); however, there is emerging evidence that it is the relative concentration of certain monoterpenes, rather than the total level, that is most critical for tree defence (reviewed in Erbilgin 2019). Interestingly, limonene, which is very toxic to MPB at low concentrations (Chiu et al. 2017; Reid et al. 2017), is found in higher concentrations in putatively experienced lodgepole pine compared to naïve lodgepole pine and it is also positively correlated with MPB attack density (Clark et al. 2010; Burke et al. 2017).

A confounding factor in some of these studies is that MPB had killed a significant proportion of the mature trees at some of the study sites and the defences of surviving trees were assumed to be representative of the beetle-killed pine population. However, MPB may preferentially attack trees with certain chemical traits, and this can change with beetle density; certain host chemotypes are also more likely to succumb to, resist, or avoid attack such that the character of surviving or non-attacked trees may not represent MPB-killed trees (Raffa and Berryman 1983; Boone et al. 2011; Erbilgin et al. 2017a).

Climatic fluctuations which occur over time—historical, dendrochronological and geologic time—have also led to changes in the distribution and abundance of both bark beetles and their conifer hosts (Brunelle et al. 2008). The historic suitability of a site based on a 30-year period in the 1900s may not be indicative of the evolutionary history between lodgepole pine and MPB, especially when pine is relatively long-lived and coevolution may require hundreds or thousands of years. Interestingly, whitebark pine was postulated to be a naïve species with weakly coevolved defences for MPB because it grows in areas of low climatic suitability for the beetle (Raffa et al. 2013); however, an analysis of whitebark pine chemistry indicates a coevolutionary history (Bentz et al. 2015). There may also be trade-offs as once attacked by MPB, whitebark pine appears to be less defended than lodgepole pine, but whitebark might also be less apparent because lodgepole is more likely to be attacked when the two species co-occur (Raffa et al. 2013, 2017; Bentz et al. 2015). There is also evidence of MPB outbreaks occurring in high elevation whitebark pine forests based on lake cores suggesting a relationship that dates back over 8,000 calendar years before present to the early

Holocene, if not earlier (Brunelle et al. 2008). The outbreaks occurred during a cool wet period (the 8,200-year event) that would have promoted whitebark pine forests, but a short warming during the event may have facilitated the MPB outbreaks recorded in the lake cores. Similarly, a warming trend from 1920 to 1940 likely led to an MPB outbreak in high elevation whitebark pine forests (Logan and Powell 2001). The mixed results highlight the complexity in the systems and the potential influence of other factors. Indeed, the amount of selective pressure exerted by MPB may vary by species or population, but secondary metabolites, plant life history strategies, and resources involved in defence are also likely affected by abiotic and environmental stresses. Herbivore pressure is only one potential factor affecting tree defences.

Like whitebark pine, jack pine has also been hypothesized to be a naïve species with respect to MPB. A study of tree defences found that compared to lodgepole pine, jack pine has: (i) higher total and relative levels of α-pinene; (ii) lower total and relative levels of myrcene (synergist to the aggregation pheromone); (iii) lower total and relative levels of several terpenes that are toxic to MPB (limonene, 3-carene, β–phellandrene), although results for some compounds depended on chirality; and (iv) lower total combined terpenes (Hall et al. 2013; Clark et al. 2014; Erbilgin et al. 2017b). Results of other studies varied for some terpenes and enantiomers, e.g., only relative levels of α-pinene varied between the two species, and the trends for induced defences changed over time, but most of the general trends prevailed (Hall et al. 2013; Erbilgin et al. 2014, 2017b; Taft et al. 2015, Burke and Carroll 2016; Lusebrink et al. 2011, 2016; Cale et al. 2017; Rosenberger et al. 2017).

Similar to the putatively naïve species and populations discussed previously, the implications for jack pine are difficult to discern due to complex and dynamic interactions. For example, concentrations and combinations of compounds that may increase aggregation and the likelihood of successful colonization may lead to decreased brood productivity due to intraspecific competition. Aggregation (and anti-aggregation) pheromone production and attack density are positively correlated with α-pinene in cut logs (Erbilgin et al. 2014; Taft et al. 2015; Burke and Carroll 2016), although similar attack rates have been recorded on cut logs of lodgepole, ponderosa, limber, jack, red, eastern white and Scots pine (Cerezke 1995; Rosenberger et al. 2017). Like jack pine, whitebark pine has higher levels of α-pinene and lower levels of myrcene, toxic compounds and β -phellandrene compared to lodgepole pine, and attack density is higher on whitebark than on lodgepole pine, but brood production per female is greater in lodgepole pine in living trees (Statement 4; Bentz et al. 2015; Raffa et al. 2017). Less toxic compounds in jack pine compared to lodgepole pine could lower tree resistance and presumably the number of attacks required to overwhelm jack pine defences, resulting in more resources and increased per capita productivity (Statement 4). Lower levels of β -phellandrene, which while toxic is also attractive to MPB, could make jack pine less apparent and less likely to be attacked similar to whitebark pine, although with adequate beetle pressure any difference could become inconsequential (Bentz et al. 2015; Raffa et al. 2017). Interestingly, the most abundant monoterpenes in lodgepole pine are not the most toxic to MPB and certain minor monoterpenes may be more important than some major compounds (Chiu et al. 2017). Adding a layer of complexity are the microbial symbionts of MPB that tolerate some of the most toxic compounds to the insect better than the less toxic compounds (Adams et al. 2011; Cale et al. 2017).

Throughout its extensive latitudinal range, MPB has been exposed to substantial chemical plasticity in its hosts (e.g., Sturgeon 1979; Forrest 1980; Smith 1983; von Rudloff and Lapp 1987; Clark et al. 2010, 2014; Erbilgin 2019). Although pines exhibit impressive variation in the quality and quantity of their defensive compounds at the species, population and even tree level, pines are actually similar in terms of the overall types of compounds in their resin because the secondary metabolites likely evolved in response to a suite of herbivores and pathogens (von Rudloff and Lapp 1987; Keeling and Bohlmann 2006). In fact, the chemical similarity of jack pine to lodgepole pine has been cited as a factor facilitating MPB range expansion in central Alberta (Erbilgin et al. 2014; Erbilgin 2019). Although certain compounds and concentrations may be more toxic or attractive to MPB and differ between jack and lodgepole pine or other hosts, it is unknown whether such differences will actually manifest at the tree level, let alone the stand and landscape levels. Two prominent historical hosts, ponderosa pine and lodgepole pine, may vary in their chemistry and even their susceptibility (e.g., Rosenberger et al. 2017; Keefover-Ring et al. 2016), yet MPB causes significant losses in stands of each species and to date there appears to be little practical significance of any differences. The non-linear relationships and interactions in the system are affected not only by the composition and concentration of defensive compounds but also by beetle density, the stage of the colonization process, microbial symbionts, and environmental or abiotic factors.

A recent review by Erbilgin (2019) identified two phytochemical mechanisms that have likely facilitated MPB's host range expansion. First, overall jack pine chemistry is similar to that of MPB's historical hosts and is compatible with beetle pheromone production, aggregation on host trees, as well as development of MPB brood and associated microorganisms. Second, compared to some of the well-defended historical hosts, jack pine has lower concentrations of some toxic and repellent defence chemicals, and comparatively high concentrations of chemicals promoting host colonization. While there is a need for tree and stand level studies, evidence to date indicates that tree chemistry should not inhibit MPB's ability to locate and colonize jack pine.

### UNCERTAINTY

1. Low uncertainty regarding the effect of most of the individual monoterpenes that have been studied to date on individual beetle behavior when tested in isolation, and moderate to high uncertainty regarding some of the chemicals not studied yet.
2. High uncertainty regarding how (or if) chemical plasticity or morphological differences at the tree, population, or species level will affect MPB populations dynamics in jack pine. High uncertainty regarding MPB population dynamics in boreal forests at the stand and landscape level.

### RESEARCH NEEDS

1. Empirical field data on MPB host selection and colonization behavior in jack pine at different spatial scales, particularly the stand level.
2. Quantification of the threshold density of beetles required for populations to overcome tree resistance and transition from endemic to outbreak (tree-killing) behaviour in jack pine in forest stands.

## 4. MPB PRODUCTIVITY IN JACK PINE WILL BE WITHIN THE RANGE OBSERVED IN PINE SPECIES FROM ITS HISTORIC RANGE. (K. Bleiker)

### EVIDENCE

Once host defences are negated and MPB has established in a tree, productivity within the tree is strongly correlated with tree diameter and the quantity of resources (Amman 1972; Raffa et al. 2008; Carroll et al. 2017). Beetles lay more eggs, suffer less intraspecific competition, develop faster, and grow larger in lodgepole pine trees with thick phloem compared to thin phloem (Safranyik and Carroll 2006). The number of brood increases linearly with phloem thickness in lodgepole pine; the density of beetles emerging from lodgepole pine slabs increased from 160 to 940 per square metre, or 16 to 59 offspring per female, as phloem thickness increased from 2.2 mm to 5.8 mm (Amman 1972). Phloem thickness and tree diameter are positively correlated, although stand conditions and tree age affect this relationship; however, in general, phloem thickness explains MPB's preference for large trees (Safranyik and Carroll 2006).

Reproduction appears to be low at endemic population levels when beetles colonize suppressed and stressed hosts with compromised defences, presumably due (at least in part) to the thin, poor quality phloem in these hosts (Boone et al. 2011; Bleiker et al. 2014). As populations increase, beetles can coordinate the successful mass attack of larger diameter stressed trees. Productivity increases when beetle densities are sufficient to mass attack more than two trees at a site (Carroll et al. 2017); this may be related to the quality of host that can be accessed by that beetle density. As beetle populations continue to increase, they can successfully colonize larger and more vigorous trees with thicker phloem, which in turn produce more beetles allowing access to even better-quality hosts: this leads to positive feedback and explosive population growth (Safranyik and Carroll 2006). At very high population levels, host defences become largely inconsequential as enough beetles are available to overwhelm the defences of the most vigorous trees in a stand (Raffa et al. 2008). At this time, the main determinant of population growth is host tree and stand characteristics: eruptions occur in stands with a high proportion of large diameter trees with thick phloem (Statement 1).

Interspecific generalizations for phloem thickness are challenging because of the confounding effect of environmental, site, and stand conditions (Bentz et al. 2015). Jack pine phloem may be thinner than lodgepole pine phloem because it grows on poorer quality sites (Lusebrink et al. 2016; Rosenberger et al. 2017); however, a minimum total bark thickness of only 1.5 mm is required for successful MPB development (Safranyik and Carroll 2006). Females will abandon galleries if they break through the outer bark while constructing them. Successful MPB reproduction has been reported in jack pine logs with a mean phloem thickness of only 1.1 mm (Lusebrink et al. 2016). In a study using cut bolts of lodgepole and ponderosa pine as well as several eastern pine species, including jack pine, phloem thickness had a stronger (positive) effect than pine species on both the likelihood of successful brood establishment and the number of successful galleries (Rosenberger et al. 2017). The positive relationship between phloem thickness and MPB productivity will very likely apply to jack pine such that reproduction will increase with the thickness of jack pine phloem, which is expected to be positively correlated with diameter. Larger diameter trees may also provide some level of protection from cold snaps due to the greater thermal mass of the tree (Carroll et al. 2017).

Phloem quality, e.g., nutritional and chemical differences, could also affect developing brood (Erbilgin 2019). Overall, MPB productivity in cut logs or naturally infested trees in the field appears to be relatively similar across pine species, with some exceptions. Initial studies indicated that ponderosa pine is a better host than lodgepole pine, producing larger beetles that emerge faster, but there was no difference in emergence time, productivity or size in subsequent studies that controlled for the effects of tree diameter and phloem thickness (Wood 1963; Amman 1982; West et al. 2016; Rosenberger et al. 2017). Limber pine appears to be a better host than lodgepole pine in terms of MPB reproduction and survival (Langor 1989; Langor et al. 1990). In contrast, MPB productivity in whitebark pine and lodgepole pine in either cut logs or naturally infested trees is similar and the effect of host species on beetle size is inconsistent (Amman 1982; Raffa et al. 2013; Dooley et al. 2015; Bentz et al. 2014, 2015). Adult beetle size is positively correlated with fecundity, survival and dispersal potential (Safranyik and Carroll 2006; Graf et al. 2012; Erbilgin et al. 2014; Evenden et al. 2014), but being small is advantageous in tree species with thin phloem (Safranyik et al. 2010). MPB can successfully reproduce in a variety of hosts, including spruce and other non-pine hosts (Safranyik and Linton 1983; Huber et al. 2009; McKee et al. 2013). The point is that MPB can tolerate and have a positive population growth rate in a wide variety of host environments that vary in their chemistry and quality.

The chemical defence system may affect attack density and whether beetles successfully overwhelm tree defences (Statement 3). This in turn can affect phloem quantity per female, intraspecific competition, and per capita brood production. Tree species can differ in stored resources that influence beetle size (Lahr and Sala 2014; Roth et al. 2018), but whether these effects scale up to the stand or landscape level given the significance of other factors, including phloem thickness and weather, are currently unknown (Bentz et al. 2015). Site or environmental factors, e.g., drought, site index, could potentially affect host quality and thus MPB developing in the phloem, but a factor such as drought may also have larger implications for MPB population dynamics through its effect on host tree resistance and the threshold density of beetles needed for populations to transition from endemic to outbreak behaviour (Cooke and Carroll 2017).

MPB productivity and attack rates in jack pine are similar to lodgepole pine in studies using cut logs (Safranyik and Linton 1982; Cerezke 1995; D.W. Langor, unpub. data, cited in Safranyik et al. 2010; Rosenberger et al. 2018). In some studies, but not in all, gallery lengths and size of offspring vary between jack pine and lodgepole pine and in some cases, results differ among years. Unfortunately, many did not control for phloem thickness, which likely contributed to some of the differences. Analysis of fat content (a fitness indicator) are puzzling: female beetles reared in jack pine bolts have a higher fat content than those reared in lodgepole pine, despite higher nitrogen levels in lodgepole pine phloem, while male beetles reared in jack pine have a lower fat content than those reared in lodgepole (Erbilgin et al. 2014; Lusebrink et al. 2016). MPB can successfully reproduce in living jack pine trees as evidenced by attacks on trees in shelterbelts in southern Alberta, in an arboretum in Idaho, and in central Alberta, but unfortunately no measures of productivity were reported (Furniss and Schenk 1969; Hiratsuka et al. 1982; Cullingham et al. 2011).

Beetle productivity may vary among host environments and affect MPB's potential growth rate and outbreak potential; however, to date studies have not found a consistent difference in brood production among host species, including in lodgepole and jack pine. MPB can successfully reproduce in a wide variety of hosts that vary greatly in their chemistry and quality. Evidence to date indicates that it is reasonable to expect that MPB's productivity in jack pine will fall somewhere in, or very near, the range of that observed in the different pine hosts that occur in the beetle's historic range.

### UNCERTAINTY

1. Low uncertainty that the relationship between phloem thickness and MPB productivity will apply to jack pine as it applies for multiple host species in the historic range.
2. High uncertainty regarding the amount of phloem resources in the boreal forest available for MPB.
3. Moderate uncertainty regarding the effect of host species on the nutritive value of phloem and whether any potential differences will scale up and impact MPB population dynamics at the stand or landscape level.

### RESEARCH NEEDS

1. Quantification of host variation, including jack pine phloem resources, in the boreal forest.
2. Empirical field data on MPB reproduction in jack pine trees in relation to phloem, tree, and stand characteristics.

## 5. THE NATURAL SPREAD RATE OF MPB WILL VARY AND DEPEND ON BEETLE POPULATION SIZE. MPB CAN SPREAD LONG DISTANCES (e.g., 100–300 km) WHEN POPULATION LEVELS ARE EXTREMELY HIGH. (K. Bleiker)

### EVIDENCE

Adult beetles emerge from the natal host and disperse in search of new trees in the summer. Temperature determines the timing of emergence and flight, but usually the main flight period starts the second or third week of July in central Alberta and lasts several weeks (Bleiker and Van Hezewijk 2016). Ideal conditions for flight include warm temperatures and winds that do not exceed MPB's maximum flight speed (Safranyik and Carroll 2006). Female beetles emerge slightly ahead of males and the largest females tend to emerge first (Safranyik and Carroll 2006). Based on flight mill experiments, individual capacity and propensity to fly vary significantly with fit beetles flying an average of 6 km and the longest flight being 24 km (Evenden et al. 2014). Flight velocity on the mill is approximately one-third the speed of that estimated by a field study suggesting that flight may be impaired on mills, so mills likely provide a conservative reference point. The direction of flight is downwind until an attractive odour plume is encountered (Safranyik et al. 1992).

MPB dispersal is characterized as either: (i) short-range, in which beetles fly under the canopy; or (ii) long-range, in which beetles fly above the canopy and potentially travel long distances assisted by upper atmospheric winds (Jackson et al. 2008). The process of dispersal is not well understood. The proportion of the population engaging in long-distance dispersal is thought to be positively correlated with beetle population density and negatively correlated with host availability, but this has not been tested. Other factors, e.g., weather, stand, and site characteristics, may also affect flight behaviour and capacity. Only one study to date has attempted to empirically quantify the proportion of beetles that disperse above the canopy under field conditions, and the result was 2.5% (Safranyik et al. 1992). This study released beetles in a stand with many available host trees and a low beetle population, so it likely represents the minimum percentage of a population that has the potential to disperse over long distances.

The spread of MPB depends not just on beetles dispersing from a site but also on their ability to establish upon arriving at a new location. Endemic beetle populations are restricted to colonizing moribund or weakened trees because there are inadequate numbers of beetles to mass attack and overcome the defences of healthy trees. Beetles presumably search under the canopy until they locate a suitable weakened host, although a small proportion (2.5%) may disperse longer distances above the canopy (Safranyik et al. 1992). The probability of a small number of beetles dispersing long distances and establishing at a new site is presumably low. Thus, for endemic populations, dispersal is most likely to occur within and between adjacent stands and to be largely driven by the spatial distribution of extremely weakened host trees (Logan et al. 1998).

As populations increase to incipient levels, beetle densities become sufficient to coordinate the successful mass attack of large diameter defended trees, although senescing or stressed trees may be the initial target or focus. An incipient population is characterized by small numbers of mass attacked trees occurring in discrete patches, or "spot" infestations, in susceptible stands. One of the trees in the spot may be a "focus tree", a highly susceptible tree that is attacked first, while adjacent attacked trees may be "spillover attacks" and only attacked because they are next to the focus tree. This "switching" behavior at close range may be due to spatial-temporal differences between the aggregation and anti-aggregation pheromones (Geiszler and Gara 1978).

At incipient population levels, new mass-attacks may occur proximate to old attacks resulting in the growth of a spot infestation; however, a large number of beetles apparently disperse and initiate new spots in the same stand some distance from the old attacks or in nearby stands despite the presence of closer suitable hosts (Safranyik et al. 1992; Borden 1993; Robertson et al. 2007; Carroll et al. 2017). Even though beetles will attack cut logs in the laboratory without flight exercise, some beetles, potentially the most physiologically fit beetles, are more likely to attack a host after flight exercise (Shepherd 1966; Borden et al. 1987). A propensity for flight exercise before orienting to a host could reduce or delay intraspecific competition in a population and also help beetles escape natural enemies. New spot infestations are often 30–50 m from the original spot, but distances of several hundred metres to several kilometres are also common (Safranyik et al. 1992; Borden 1993; Robertson et al. 2007). An analysis of isolated infestations in Alberta supports this range in dispersal distances for spot infestations: most new infestations were within 2 km of an infestation recorded the previous year, but almost 20% of new infestations were more than 4 km from a potential parent infestation (Carroll et al. 2017). A small proportion of incipient populations may still engage in long-distance dispersal above the canopy, but beetles may not establish at a new site if the population density is insufficient to successfully colonize available hosts. Collectively, these studies indicate that at incipient population levels, spread and successful establishment via natural dispersal will commonly occur within and between stands that may be several kilometres apart, although longer distances cannot be ruled out, especially as populations build.

At high population densities, even very vigorous trees are susceptible to attack. As populations increase and host trees are depleted, the proliferation of new spot infestations that dominated at the incipient stage gives way to the growth of individual spots as the beetle more thoroughly infests existing spots (Robertson et al. 2007). Infested areas eventually coalesce and populations collapse at a site due to intraspecific competition and host depletion (Aukema et al. 2008; Goodsman et al. 2018). To date, all records of long-distance dispersal events have been associated with extensive outbreaks, and thus host tree depletion. Large populations supply the source of migrants and dispersal occurs above the canopy where it is aided by wind. Dispersing beetles may purposely fly above the canopy, or be inadvertently lifted by convective air currents (Furniss and Furniss 1972). Regardless of whether the proportion of a population dispersing long distances increases with density, even a small proportion (e.g., 2.5%) of a massive population may be an adequate density to establish at a new site.

Factors leading to the termination of long-distance dispersal events are largely unknown. Beetles could drop out of the atmosphere in response to inadequate resources to support loft (e.g., fold their wings), a cue signalling available host material, or contact with cool air. Beetles could also be forcibly expelled from the atmosphere by storm cells and downdrafts. Factors leading to the arrest of long-distance dispersal will affect distance travelled and the number of beetles arriving at a site. This has important implications for the fate of "satellite populations" and whether or not they successfully locate and colonize hosts and reproduce at a new site. Incipient and outbreak populations can be detected at new sites based on the examination of dead trees which become apparent from the air one year after attack; however, very low, or endemic, populations that are below tree-killing densities are challenging to detect.

Wind will determine the direction of travel and the distance travelled. In 2005, during the peak of the epidemic in central British Columbia, beetles travelled 30–110 km per day in flight above the canopy (Jackson et al. 2008). Within the same time period, atmospheric dispersion models estimated potential dispersal distances of 40 km (Ainslie and Jackson 2011). Multiple long-distance dispersal events happened in the 2000s and 2010s between British Columbia and Alberta as well as within Alberta (M. Undershultz, pers. com.). There are records of long-distance dispersal events during past outbreaks as well. The 1970s–1980s outbreak in British Columbia and Montana led to the infestation of the Cypress Hills area on the southern Alberta-Saskatchewan border and records of attacks on pine trees in shelterbelts in the non-forested grasslands region of southern Alberta indicate dispersal distances of 200–300 km (Cerezke 1989; Hiratsuka et al. 1981). A number of bark beetle species, including MPB, have been recovered from snowfields some distance from the nearest host tree or infestation, demonstrating that beetles can be vertically displaced by over 1,200 m (Furniss and Furniss 1972). Similarly, MPB was observed at 1,500 m above sea level, or 900 m above ground level, in central British Columbia during the recent epidemic (K. White cited in Jackson et al. 2008). These records also demonstrate MPB's ability to disperse over non-host landscapes.

The potential for wind-assisted long-distance dispersal of MPB dates back at least to the early 1940s in Canada. Two Dominion employees, G.R. Hopping, Entomologist-in-Charge, Vernon, and H.L. Holman, District Forestry Officer, Calgary, exchanged letters politely arguing over the plausibility of Holman's idea that the rather spontaneous eruption of MPB in Banff National Park was due to beetles from British Columbia dispersing over mountain passes versus an increase in endemic populations. Holman writes "I doubt if anyone would agree with me that insects could be carried that far [by wind] … but the dispersion of timber species and plants in this region proves that their seeds have been blown long distances in an easterly direction and the adult beetle is not as large as some of these" (Holman H.L. in a letter dated 22 January 1942 to the Department of Mines and Resources, Ottawa). Hopping initially resisted the idea, but he suggested several ways for Holman to test his theory, including dragging nets from airplanes, flying tanglefoot-covered kites on 300-m cords, and placing tanglefoot traps on fire towers and tree tops in mountain passes.

The risk of MPB arriving and establishing in a new stand is a function of the distance to a source population and the size of the source population. Spread and successful establishment in a new habitat by endemic populations will likely be limited due to the low numbers of beetles involved. Incipient populations can be expected to spread at a rate of tens of metres to several hundred metres per year, to several kilometres per year. Long-distance dispersal events with successful establishment in a new habitat likely require large source populations and conditions, particularly wind, that favour long-distance movement. When these conditions are present, successful establishment of populations 100–300 km from the source population can be expected. Spread will occur in the direction(s) of the wind during the dispersal period (eastward spread in Alberta) and can occur over unsuitable intervening habitat, such as prairie grassland.

### UNCERTAINTY

1. High uncertainty regarding processes involved in dispersal, particularly long-distance dispersal, at all population levels.

### RESEARCH NEEDS

1. Quantification of factors affecting dispersal, particularly how beetle population density, host availability, and environmental factors may affect beetle behavior and the proportion of the population dispersing long distances.

### 6. IN THE ABSENCE OF MANAGEMENT, MPB WILL CONTINUE TO EXPAND ITS RANGE EASTWARD IN CANADA'S BOREAL FOREST BY THE NATURAL PROCESS OF A DISPERSAL. OUTBREAK POPULATIONS IN WESTERN ALBERTA COULD FUEL FARTHER EASTWARD SPREAD IN THE NEAR FUTURE (2–8 YEARS). (K. Bleiker)

#### EVIDENCE

Given the nature of MPB dispersal discussed previously (Statement 5), spread east is likely to continue, although the rate of spread is unknown and there is the potential for management efforts to dramatically slow the spread. Since the notable invasion event in 2006, MPB spread through western and central Alberta has been faster than originally anticipated (Nealis and Peter 2008). The main factors contributing to the faster than anticipated rate of spread are (i) several long-distance dispersal events that occurred after 2006, most notably in 2009 and 2012 (M. Undershultz, pers. com.); (ii) more susceptible pine in central Alberta than initially assessed (Statement 1, Figure 3); and (iii) favourable weather for survival promoting source populations for migrants.

Eastward spread in Alberta has slowed in the last 6 years compared to the 2006–2011 time period. Slower eastward spread is likely due to several factors. Firstly, pine volumes are lower in eastern Alberta compared to western Alberta and spread rate is expected to be positively correlated with pine volume (Statement 1). Based on pine volumes estimated from provincial inventory data presented in this risk assessment (Figure 3c), spread rate could actually increase through western Saskatchewan should the beetle cross the border, or at least be comparable to that observed in east-central Alberta. Once MPB is established in an area, the impact of stand characteristics on MPB population levels and its persistence (Statement 1) is worth highlighting. MPB has slowly, but persistently, spread east and south of Lesser Slave Lake since 2012 despite aggressive control efforts in this region and the lack of apparent recent long-distance dispersal events; the resolution of the spatial data is somewhat limited, but these areas both contain relatively high volumes of pine (Figures 1, 3c).

Another factor contributing to slower eastward spread is Alberta's aggressive control program which targets spot infestations in eastern Alberta (Statement 8). Spot infestations can spread up to several kilometres a year if left untreated (Statement 5). Some larger populations in west-central Alberta that could be a source of long-distance migrants are also controlled. As distance to large source populations grows, the probability of long-distance dispersal contributing to eastward spread declines. Currently, the leading edge in eastern Alberta is >300 km from the extremely large source populations in Jasper in western Alberta. Based on these factors, eastward spread rates should remain static or continue to decline in the future; however, there is new evidence that large populations in western Alberta threaten to fuel eastward spread in the near future.

Large populations in western Alberta may affect eastward spread rates in two ways. First, and most certain, is control efforts will be reduced in eastern Alberta as provincial resources are reallocated to higher priority areas in the foothills and along the eastern slopes of the Rocky Mountains. This may allow some infestations near the eastern edge to potentially establish, proliferate, and spread. Beetles are dispersing out of Jasper along two west-east corridors: the Athabasca River valley (Highway 16), which is contributing to population increases around Hinton; and, as of 2018, east along the Saskatchewan River (Highway 11). Minimizing north-south spread of MPB along the eastern slopes of the Rocky Mountains to minimize impacts on key watersheds is a higher priority for the province of Alberta than slowing eastward spread, which will trigger a reallocation of provincial resources in 2018/2019 (E. Samis, pers. com.).

Second, and much less certain, is how the large source populations in Jasper and Hinton may lead to populations building up in susceptible pine on the edge of the Lower Foothills south of Lesser

Slave Lake and then dispersing long distances into eastern Alberta and western Saskatchewan. There is a corridor of susceptible pine that runs northeast from Hinton to south of Lesser Slave Lake (Figure 3c). Historically, the climatic suitability of the Upper Foothills Region (and Jasper) has been low for MPB, but a few successive years of favourable weather could see populations rapidly spread along this corridor to the Lower Foothills. Alternatively, MPB could disperse long distances from source populations in western Alberta to the eastern edge of the foothills, as evidenced by reports of new infestations around Whitecourt and Swan Hills in early August 2018 following a storm event (E. Samis, pers. com.). MPB has been actively managed by the province in much of this area, but large numbers of migrants in combination with favourable weather could allow for populations to dramatically increase in the region. A build up of populations in this region would position source populations within 300 km of the Saskatchewan border. Reports dating back to the 1940s indicate that MPB can disperse 100–300 km across a variety of landscapes during large outbreaks. Thus, MPB could disperse long distances from south of Lesser Slave Lake directly into Saskatchewan if large source populations are allowed to build in this region.

Considering how rapidly and unexpectedly MPB spread across Alberta in only 12 years, it is reasonable to assume that in the absence of control it will continue to spread east. Other than stating that spread will be faster during outbreaks which occur periodically in stands over time, it is difficult to predict a rate of spread. The uncertainty around spread highlights (i) the need for a better understanding of long-distance dispersal; (ii) the importance of annual surveys and annual review of control decisions; (iii) the need for a better understanding of MPB population dynamics in jack pine forests; and (iv) the extremely volatile nature of the situation.

#### UNCERTAINTY

1. Low uncertainty that MPB will continue to spread east in the absence of management but high uncertainty regarding the rate and extent of spread.
2. High uncertainty regarding MPB population dynamics in jack pine forests and the potential for spread, including long distance dispersal and establishment in a new area.
3. High uncertainty regarding how large populations in western Alberta may push eastward spread in the near future (2–8 years).

#### Research Needs

1. Quantification of stand- and landscape-level factors on MPB population dynamics, spread, and dispersal. This includes (i) the effects of climate, the distribution and abundance of susceptible stands, and other factors affecting spread and dispersal in the boreal forest; and (ii) beetle density thresholds associated with transitions in population phases and quantification of factors affecting these thresholds.
2. Analysis of susceptible pine in the Lower Foothills Region, particularly the area south of Lesser Slave Lake.

### 7. FARTHER NORTHWARD EXPANSION OF MPB'S RANGE WILL BE LIMITED IN THE NEAR FUTURE DUE TO LOW CLIMATIC SUITABILITY. (K. Bleiker)

Historically, climate has limited MPB's distribution to south of approximately 56° N in British Columbia until the recent epidemic when MPB expanded its range northward by approximately 3° of latitude (Safranyik et al. 2010). Spot infestations have been mapped close to the Yukon border in British Columbia on both sides of the Continental Divide: in the northern Rocky Mountain trench and in the Liard Basin in northeastern British Columbia (Figure 1). MPB was confirmed north of 60° in 2012 in baited trees in the Northwest Territories near the British Columbia-Alberta border (K. Bleiker, pers. obs.). A check of attacked trees in March 2013 found live larvae but only below the snowpack; this was also true for trees in spot infestations that were assessed in the northern Rocky Mountain Trench in British Columbia in June 2012 (K. Bleiker, pers. obs.). A wildfire burned through the area where MPB was detected in the Northwest Territories in the summer of 2013. There have been no reports of MPB north of 60° since 2013.

Yukon and the Northwest Territories both completed their own Risk Assessments for MPB (Hodge 2012, 2014). The current risk in both territories is considered low due to poor climatic suitability and the low likelihood of long-distance dispersal into the Territories in the immediate future because the large populations have subsided in adjacent British Columbia. Under a number of projected climate change scenarios, the suitability of southeast Yukon and the southwest Northwest Territories becomes quite favourable for MPB by the middle of this century. The climatic suitability of that region is predicted to be moderate around 2050, which is significant as MPB spot infestations have persisted in areas rated as low climatic suitability in the northern Rocky Mountain trench for a number of years.

Significant spread in a northerly direction is likely to be limited in the near future by an unsuitable winter climate, specifically extreme winter minimum temperatures. However, in just a few decades the estimated impact of climate change will make southeast Yukon and the southwest Northwest Territories favourable for MPB and the region will be at risk of invasion if there are MPB outbreaks in adjacent northern British Columbia or Alberta to provide a source of migrants.

### UNCERTAINTY

1. Moderate uncertainty regarding the rate of warming in the north, which will determine the climatic suitability for MPB.
2. Moderate uncertainty regarding the distribution and abundance of susceptible pine stands in Yukon and the Northwest Territories.

### RESEARCH NEEDS

1. Composite analysis of pine volume and climatic suitability of the north under the most recent and widely accepted climate change scenario(s) when an updated climatic suitability index is available (Statement 2).

## 8. SUSTAINED APPLICATION OF THE CURRENT AGGRESSIVE MANAGEMENT PRACTICES IN ALBERTA'S EASTERN LEADING-EDGE ZONE WILL SLOW EASTWARD SPREAD. (K. Bleiker, C. Whitehouse)

### EVIDENCE

Effective control of MPB depends on early detection of infestations and rapid application of aggressive intensive control measures that are maintained annually until populations are suppressed to the desired level and the factors leading to population growth are no longer operative (Carroll et al. 2006, 2017; Six et al. 2014). If control activities are delayed for a year, favourable weather may allow populations to quickly escalate beyond a controllable level. Management efforts can also be facilitated by unfavourable weather, as the combined effects may be more likely to decrease populations to endemic levels (Cooke and Carroll 2017).

The effort required to suppress an infestation will depend on the annual population growth rate, the proportion of infested trees (a.k.a. green attack) controlled in the area, and the initial size of the population (number of infested trees). A population with a high annual population growth rate will require a higher percentage of the infested trees be treated to be effective compared to a population with a lower growth rate (Figure 4). For example, populations with annual growth rates of 3% and 5% will only start to decline if more than 67% and 80% of the infested trees that occur on the landscape are controlled, respectively (Figure 4; Carroll et al. 2006). In terms of years, it will take longer to suppress a large infestation than a small one with the same growth rate and proportion of trees controlled. An extensive infestation could run out of host trees before control could effectively suppress the outbreak. Theoretically, any population may be suppressed with enough effort; however, it may not be operationally possible due to funding or logistical issues.

Are control efforts in Alberta effective at slowing eastern spread? The data available to address this question are not perfect, so there are important caveats associated with every answer. One study indicates that control efforts in the leading-edge management zone reduced the area colonized by MPB to approximately 70% of that predicted under a "do nothing" scenario (i.e., ~30% reduction) (Carroll et al. 2017). The same study estimated that detection and treatment rates at the landscape level in eastern Alberta in the years examined were only 54–68% in the absence of immigration, such that control would only be effective for populations with annual growth rates under three-fold. However, it should be recognized that available funding strongly affects these numbers. For example, control efficacy could be increased by conducting more intensive ground surveys, which have a 98.5% detection rate for green attack, and by controlling a higher proportion of infested trees (see Statement 9).

Large populations that cover extensive areas and have a high annual growth rate are not feasible to control; however, control of smaller spot infestations in eastern Alberta created by long-distance dispersers is feasible if the rules of early detection and aggressive and sustained control are followed. Moderate infestations in central Alberta, which may be source populations for migrants dispersing east, may be feasible to control depending on their size, growth rate, and the resources available. The challenge is identifying "winnable" and "unwinnable" battles and when "winnable" battles become "unwinnable," or vice versa, given the dynamic and stochastic nature of the system. Surveys and review of control decisions are required annually to ensure resources are strategically and effectively allocated. The Strategic Approach to Slow the Spread of MPB Across Canada is a comprehensive containment strategy developed under Canada's National Forest Pest Strategy and it identifies eastern Alberta, where populations are small and annual growth rates usually low, as the best place to focus control efforts to minimize eastward spread (Hodge et al. 2017).

The province of Alberta annually surveys for MPB infestations. To date, survey points with three or more attacked trees in the leading-edge management zone (Figure 5) are fed into the province's Decision Support System and prioritized for treatment because resources are not available to extensively survey and control all sites. Within the leading-edge management zone is an area that falls under the Spread Management Action Collaborative (SMAC). SMAC is an inter-provincial Memorandum of Agreement signed in 2012 between Alberta and Saskatchewan. The agreement formalizes a joint strategy that combines resources from both provinces to conduct control where there is the highest risk of MPB entering Saskatchewan, which currently is the region east of Lesser Slave Lake in the Lac La Biche Forest Area. Areas for action are prioritized based on annual survey results and discussion among SMAC members. In the SMAC area, sites with one or two trees may be actioned if resources are available.

In 2017, the province of Alberta moved the border of its eastern leading-edge zone from just west of Fort McMurray to the Saskatchewan border, which includes the region where endemic MPB populations may be established and vigilant monitoring is required (Figure 1). Low numbers of beetles have been detected in trees baited with MPB aggregation pheromone near the eastern border of Alberta (e.g., within the Cold Lakes Weapons Range in 2017), well in advance of the nearest spot infestations identified in aerial surveys (Figure 5). Saskatchewan established a similar network of baited trees sites along its western border, but MPB has not been detected in Saskatchewan as of 2018.

Currently, it is unknown whether the beetles detected in eastern Alberta near the Saskatchewan border are: (i) dispersing long distances into the region each year from infestations in central Alberta (e.g., migrants from infestations south or east of Lesser Slave Lake), which are over 100 km away; (ii) dispersing even longer distances from very large source populations in western Alberta (i.e., migrants from Hinton or Jasper over 300 km away); (iii) established resident populations that dispersed into the area in the past during one of the big immigration years; or (iv) some combination of i–iii. Ongoing research suggests that "…the paucity of susceptible host material and altered competitive interactions may be a biological barrier to [MPB] persistence and spread in the boreal forest" (Pokorny and Carroll 2018, unpub. data). The study was conducted at a handful of sites in eastern Alberta, so spatial inference is limited, but it highlights the need to understand the dynamics of different population levels in novel habitats. Interestingly, MPB has been detected at some baited tree sites in eastern Alberta multiple times, even though it is akin to "looking for a needle in a haystack." Once beetles are detected at sites for a few consecutive years, sites are moved one township east to delimit the farthest eastern edge of infestation (F. McKee, pers. com.). Determining whether low density MPB populations have established in eastern Alberta is important because endemic populations could erupt under favourable conditions. This region should be monitored in any initiative to slow eastward spread to ensure that MPB infestations do not arise in an area to the east of where survey and control activities are conducted.

One lesson from MPB's historic range is that as long as there are susceptible stands of pine and MPB is endemic, outbreaks will occur. The use of control to slow or limit eastward spread of MPB in Canada is unique though because MPB is not endemic in eastern Canada: it is a novel environment for MPB with much uncertainty around beetle-host-climate interactions. Regardless, the following rules for successful suppression of infestations in the historic range are expected to apply to slowing eastward spread into new habitats: (i) practice vigilant monitoring and detection so that infestations are controlled at the first sign of increase (or occurrence in a new area); (2) apply sustained control efforts until the cause(s) of the outbreak is no longer operative; and (3) treat a high proportion of infested trees with the ideal objective being 100% treatment over the entire area (Carroll et al. 2006). The only long-term control for MPB is indirect control: preventative management that increases the resiliency of forests and reduces stand susceptibility to MPB by altering stem density, age classes and species composition across the landscape (Fettig et al. 2014; Gillette et al. 2014; Fettig and Hilszczański 2015).

## UNCERTAINTY

1. Low uncertainty that control can be effective at suppressing small spot infestations that are detected early and treated aggressively under a sustained management plan.
2. Low uncertainty that control efficacy could be increased with a higher rate of green attack detection (e.g., increased ground surveys) and controlling of a greater proportion of green attack.
3. Moderate uncertainty regarding the size of MPB populations and annual growth rates where control can be effective in jack pine forests.

4. High uncertainty regarding whether beetles caught in baited trees in Alberta near the Saskatchewan border (e.g., Cold Lake Air Weapons Range) are part of an established (resident) population or whether they disperse long distances into the region annually. High uncertainty regarding their potential to persist and eventually erupt and spread.
5. High uncertainty regarding the ability to implement response action, if required, inside the Cold Lake Air Weapons Range in Saskatchewan.

### RESEARCH NEEDS

1. Determination of the impact of large populations in western Alberta and smaller spot infestations in central Alberta on eastward spread (see Statement 5).
2. Quantification of control efficacy in jack pine stands, including determining beetle and attacked tree density thresholds where control can be effective.
3. Quantification of the extent and the potential persistence (residency) and threat posed by low density MPB populations detected in baited trees in eastern Alberta near the Saskatchewan border.
4. Development of new tools to increase detection rates for green attack and new options for control and/or ways to increase the feasibility of control (see Statement 9).

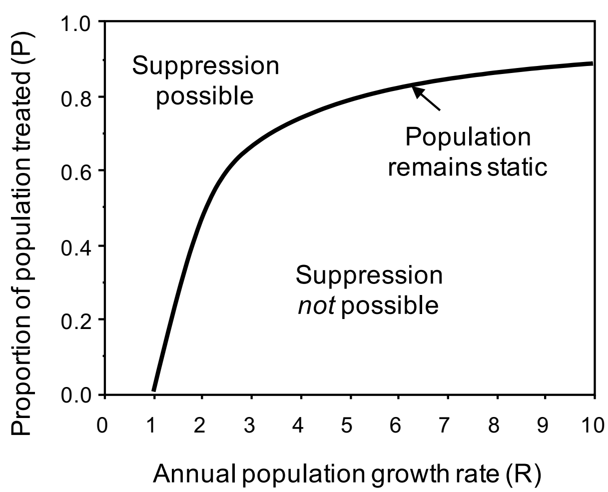



**Figure 4.** Relationship between MPB's annual population growth rate (R) and the proportion of the population (P) that must be treated for control to suppress population growth. The curve (P=1-1/R) represents a static population. Suppression is possible above the curve but is not possible below the curve. Adapted and redrawn from Carroll et al. 2006.

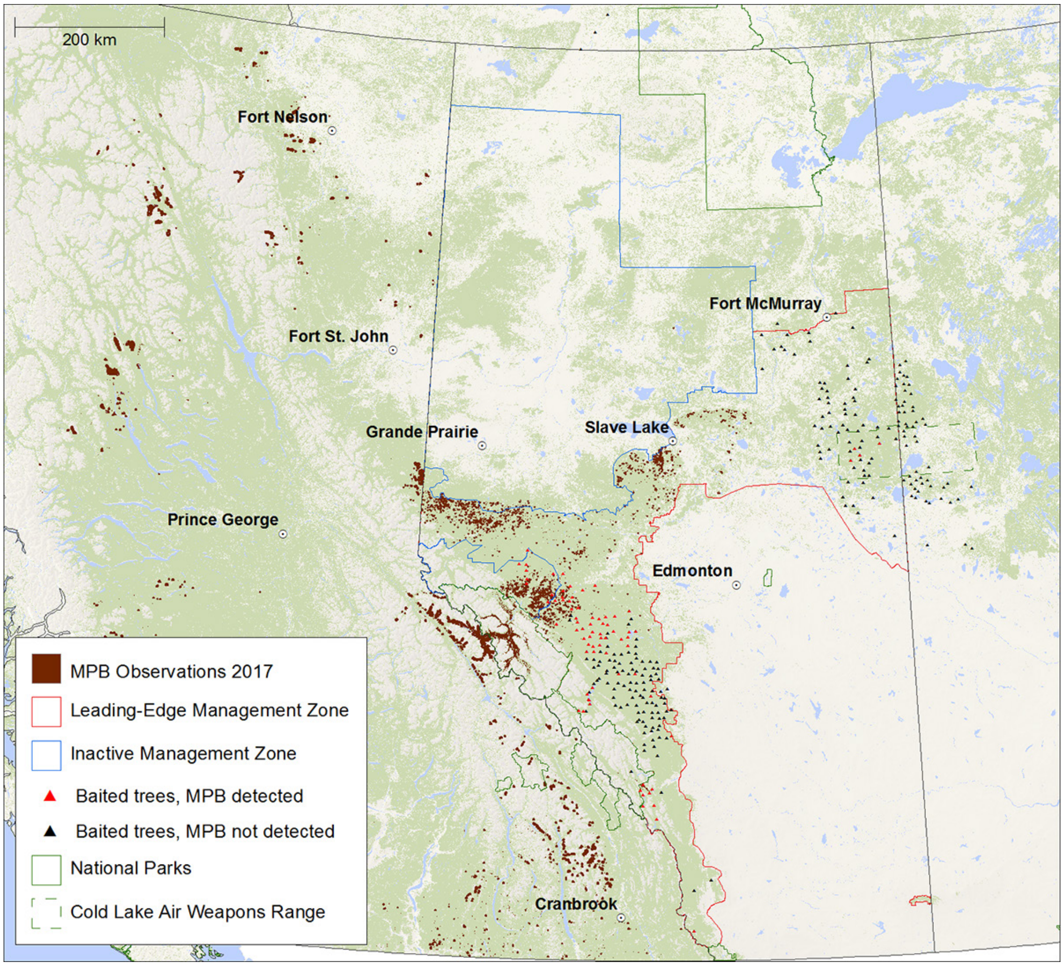



**Figure 5.** MPB observations and Alberta's management zones in 2017. Attacked trees identified during aerial surveys that were conducted in some regions in 2017 are shown in brown. Infestations in Alberta's leading-edge management zone are prioritized for potential control action. Infestations in the province's inactive management zone are not controlled for a variety of reasons. In northwestern Alberta aerial surveys and control actions are not conducted because infestations have largely subsided in this region. Aerial surveys and control are not conducted in the western part of the smaller inactive management zone polygon adjacent to the British Columbia border (Kakwa-Willmore Wilderness Area) because beetle survival is generally low in this high elevation region. Aerial surveys are conducted in the eastern portion of this area (east of Jasper, around Hinton) to map MPB, but infestations are not controlled because populations are too large for treatment to be effective. Triangles are sites where the provinces of Alberta or Saskatchewan detected MPB in trees baited with the aggregation pheromone of MPB. See text for more detail.

## 9. THERE ARE FEW TOOLS TO DETECT AND CONTROL MPB AND THEIR EFFICACY IS LIMITED. (K. Bleiker, B. Cooke)

### EVIDENCE

Measures to manipulate and reduce MPB populations require the timely detection and treatment of infested trees (green attack) (Fettig and Hilszczański 2015). Control activities can reduce the severity and spread of infestations (e.g., Trzcinski and Reid 2008; Wulder et al. 2009b). The main options to control MPB infestations are cultural and mechanical treatments that kill insects by destroying the bark. Aggregation pheromones can be used to concentrate or hold beetles in a stand prior to applying a cultural or mechanical treatment: this tactic has been used successfully in an area within the Cypress Hills Provincial Park in Saskatchewan (R. McIntosh, pers. com.). The use of anti-aggregation pheromones or inhibitors to manage MPB has had mixed success to date, especially when beetle population levels are high (Gillette et al. 2014; Fettig and Hilszczański 2015). New research on using acoustics to manipulate beetle behaviour may generate a new tool in the future. Chemical insecticides for MPB are no longer widely used in Canada, especially at the stand or landscape level, and there are no effective large-scale biological control options (Carroll et al. 2006). Prescribed fire, or letting wildfires burn, is a potential tactic for remote locations where a high fire intensity can be achieved; however, it is not appropriate in most situations, including large infestations (Carroll et al. 2006).

Treatments that destroy the bark are very effective at killing MPB. This can be achieved during milling if it is feasible to harvest and process infested trees before the beetles emerge. A number of methods can be used to destroy insects on site in the field, including solar radiation, bark peeling devices, and chipping whole trees, but by far the most widely used and efficacious method is falling, piling and burning infested trees (a.k.a. fall and burn) (Carroll et al. 2006; Fettig and Hilszczański 2015). Although fall and burn is very effective at killing insects, a big challenge lies in early detection of green attack so that control activities can be conducted before beetles complete development, emerge and disperse to new host trees. In the typical one-year life cycle, MPB flight and the colonization of new hosts occur in July and August, but the foliage does not usually fade until the following spring or summer (Bleiker and Van Hezewijk 2016). Fall and burn activities need to be executed over the winter and early spring when brood are under the bark and piles of infested wood can be burned safely. Thus, infested trees are usually not visible from the air in the timeframe needed for control work.

Green attack can be reliably detected during ground surveys when a person in the field inspects the trunk of each tree for pitch tubes, which are indicative of attack. The exception may be "blind attacks" where trees fail to produce pitch tubes and the only sign of attack is boring dust on the trunk, which is more difficult to see. The labour-intensive ground surveys require a starting point, which comes from helicopter surveys that are conducted in Alberta in areas that have been prioritized for management. Aerial surveys are used to geolocate red attack, which are trees with red crowns that were attacked the previous year and no longer contain insects. Ground surveys to locate green attack are then conducted in the location of the red attack as a starting point. Operational procedures for the ground surveys are prioritized based on available resources and the density and distribution of beetles in a given stand. The trunk of every tree in a 50-m radius plot centred on the red attack tree(s) is assessed for signs of attack (e.g., pitch tubes, boring dust, or galleries under the bark). Additional plots are surveyed adjacent to the original plot depending on the distribution and density of green attack in the original plot and available resources. The efficacy of green attack detection in ground survey plots is extremely high at 98.5%; however, on a larger scale, detection efficacy is much lower because of the difficulty in finding green attack that is not closely associated with red attack (C. Whitehouse, pers. com; also see Statement 5).

A large-scale analysis of aerial survey data for lodgepole pine in Alberta found that approximately two-thirds of green attack are likely to occur near red attack (Carroll et al. 2017). This provides a rough estimate for the total efficacy of combined helicopter and ground surveys and is important in terms of the efficacy of control and whether an infestation can be suppressed (Statement 8; Figure 4). An analysis of the same detection method used by Saskatchewan to control MPB in Cypress Hills Provincial Park found that the method was efficient. However, the study found that efficacy could be improved, especially over a large spatial area, by using an approach such as a machine learning classification tree to identify areas to conduct additional ground surveys to look for green attack that are not associated with red attack (Kunegel-Lion et al. 2019). The same conclusion was reached by Strohm et al. (2016) in an analysis of MPB control in Banff National Park. Basically, at a certain spatial scale, it is more beneficial to detect a lower percentage of green attack over a larger area than to detect almost 100% of the infested trees in a smaller area. This is largely due to the nature of MPB dispersal and that populations below a certain threshold density are unable to kill trees and do not require control (Statements 2, 5). The detection rate for green attack at the landscape scale in jack pine is unknown and may differ from that in lodgepole pine forests due to potential differences in beetle attack density, drought or site conditions that may affect the rate of foliage fade, and the visibility of red attack in mixed species stands. It is also unknown whether "blind attacks" are more common in jack pine.

While combined aerial and ground surveys can detect green attack, they are either not feasible or fail to detect MPB in areas where populations are extremely low and beetles are restricted to colonizing moribund or downed trees. In these areas, baits releasing synthetic aggregation pheromones can be used to detect MPB. Baits are stapled to trees prior to the beetle's flight and checked for pitch tubes in the fall and the presence, or absence, of MPB recorded. The provinces of Alberta and Saskatchewan use baited trees along their border in an effort to delimit the current eastern edge of MPB in Canada. MPB has not been detected in the Saskatchewan boreal forest since the province started a monitoring program in 2012 in stands with a high susceptibility rating; however, MPB has been recorded in baited trees at sites very close to the border in Alberta in a number of years (e.g., 2017 shown in Figure 5). In an effort to delimit the eastern edge of occurrence, baited tree sites are moved farther east once beetles have been detected at a site for a number of consecutive years (F. McKee, pers. com.). The ability to accurately detect and delimit the eastern edge of MPB's range in Canada depends on how effective the bait is and the network and density of baited trees on the landscape. Studies are underway to develop protocols for monitoring the presence of MPB using baited tree sites and to use baits to determine beetle population density (N. Erbilgin, unpub. data; Klutsch et al. 2017).

There has been little advancement in tools available for MPB detection and control at an operational level. Direct control options to suppress populations remain limited, with fall and burn being the most widely used and effective tool in Canada. Timely detection of green attack remains a challenge, yet it is key to an effective control program. To date, remote sensing technology cannot meet the information needs and operational constraints for the timely detection and control of MPB (Wulder et al. 2009a). Advancements in drone technology may improve detection at the stand level. There is the possibility to increase detection efficacy using environmental variables through the use of machine learning or models, depending on the values, management objectives, and cost (Kunegel-Lion et al. 2019). An increase in green attack detection efficacy at a large spatial scale would greatly increase control efficacy: it would be a game-changer in terms of the size and growth rate of infestations that could be suppressed and the number of years during which control actions would need to be applied to achieve suppression.

### UNCERTAINTY

1. Low uncertainty that tools are limited for the detection and control of MPB at an operational level.
2. Low uncertainty that the fall and burn control treatment is efficient and effective at killing insects.
3. Low uncertainty that green attack detection efficacy is extremely high in ground plots and this should apply to most pine species (although moderate uncertainty if "blind attacks" on jack pine are more common and will affect detection efficacy of ground surveys).

4. Moderate uncertainty regarding green attack detection efficacy at the stand and landscape level, especially in forests with jack and eastern pine species.
5. Moderate uncertainty regarding the efficacy and attractive radius of pheromone baits in jack pine and eastern pine forests and at different beetle population densities.

### RESEARCH NEEDS

1. Technology or methods that increase detection efficacy for green attack, especially at a large spatial scale. An advancement at the stand level that is more economical and extensive than ground surveys could also improve control efficacy.
2. New cost-effective tools for direct control of MPB.
3. Improved estimates of current detection and control efficacy, particularly in jack pine.

## 10. MPB COULD SPREAD TO EASTERN PINE FORESTS THROUGH THE TRANSPORT OF INFESTED WOOD BY HUMANS. (K. Bleiker)

### EVIDENCE

In addition to potentially spreading east through the natural process of beetle dispersal (Statement 6), MPB could be introduced to eastern Canada through the transport of infested wood by humans. This could occur either in untreated shipments of commercial logs, in firewood, or in wood debris imported into oil development areas that have intact bark coming from infested areas in western Canada (including the Cypress Hills) and the United States. The human-assisted movement pathway has not been considered in previous risk assessments because it was considered to have a low probability of occurrence due to the putatively low volume of wood moved long distances. However, we consider it in this update because of the examples reported below, in addition to the fact that the consequences could be very high as it could result in very rapid spread of MPB to eastern regions which are ill-prepared to deal with its sudden arrival.

Bark beetles are good candidates to spread through the movement of infested wood because insects are protected under the bark during transport. Establishment of MPB at a new location depends on the presence of suitable hosts and climate, both of which exist in eastern Canada (Statements 1, 2), as well as the number of insects introduced. Given that one mass-attacked tree can produce enough beetles to successfully attack several trees, one truckload of infested logs poses a significant threat for the introduction and establishment of MPB in a new habitat.

The following examples demonstrate that, from a biological perspective, it is plausible that MPB could spread via the movement of infested wood.

- In 1999, a log home builder in Whitecourt, Alberta received shipments of lodgepole pine that were heavily infested with live MPB larvae (E. Samis, pers. com.); the logs and insects were destroyed following identification.
- During the 2010s in Minnesota, a voluntary inspection of several mills found galleries and dead MPB adults under the bark of imported pine logs; galleries were also found in lodgepole pine logs imported by a furniture maker in the state (B. Aukema, pers. com.).
- Live Douglas-fir beetles (*Dendroctonus pseudotsugae*) were moved from infested areas in Oregon to Minnesota where they were caught in funnel traps in 2001 up to 17 km from the point of introduction (Dodds 2010). The Douglas-fir beetle likely did not establish in the east because it is outside the range of its primary host, Douglas-fir (K. Dodds, pers. com.).

- Red turpentine beetle (*D. valens*) was introduced to China likely in the 1980s through the movement of infested pine from the western United States (Yan et al. 2005). Other bark beetles, including spruce beetle (*D. rufipennis*), recently arrived in China in logs exported from western North America. Preventative measures and extensive protocols are in place in China to prevent introduction and establishment, including having receiving ports in areas with no potential hosts within 100 km or more, intensive inspections upon arrival, and the application of treatments in the receiving port.
- Human transport of infested wood facilitated range expansion of the great spruce beetle (*Dendroctonus micans*) in Europe (Fielding et al. 1991).
- There are numerous examples of non-*Dendroctonus* bark beetles and wood borers being moved in infested wood with the most palpable examples for Canada being emerald ash borer (*Agrilus planipennis*), Asian long-horned beetle (*Anoplophora glabripennis*) and brown spruce longhorn beetle (*Tetropium fuscum*).

In terms of MPB's biology, spread through the movement of infested wood is highly plausible. Therefore, it is largely the volume of infested wood with bark moved to non-infested areas that will affect the probability of MPB spreading via human transport. There is little information available on the movement of pine logs with bark intact, and it will vary over time with market fluctuations. Overall, log movement from infested to non-infested regions is likely low; however, specialty markets, such as log home builders or furniture makers, represent a specific risk. The probability of MPB movement in infested firewood is likely very low because major producers in British Columbia heat treat firewood prior to export, although exceptions could occur, and provincial and territorial campgrounds usually stock locally sourced firewood (Gagné et al. 2017). Firewood disposal bins are located along some provincial borders and the transport of firewood over long distances from infested to non-infested regions for personal use is likely limited due to transportation costs and regulations enacted for other species.

Several provinces have policies to prevent the movement of MPB-infested wood in Canada.

- Saskatchewan, under the Forest Resources Management Act, restricts the importation, transportation and storage of pine logs and pine forest products from infested areas, including the Cypress Hills of Saskatchewan, British Columbia, Alberta and the United States.
- Manitoba, under the Forest Health Protection Act, restricts the importation of untreated pine wood with intact bark from infested provinces or states in Canada, the United States, and Mexico.
- Ontario has no restrictions currently in place for MPB, but it is considered an invasive forest pest and it will likely become regulated in the near future under the Ontario Invasive Species Act. Ontario conducted a Risk Assessment and developed a Risk Response Plan for MPB. Some relevant tools for MPB management (e.g., fall and burn control, bait trees for monitoring) are also included in Ontario's updated Forest Management Planning Manual.

There are no specific regulations for MPB in the other provinces and territories in Canada; however, many have the ability to designate pests or invasive species and enact restrictions under various legislative acts. Similar to Canada, there is no federal regulation of the movement of MPB-infested wood in the United States and limits on wood movement are state-by-state. The states of Minnesota and Wisconsin both have exterior quarantines for all untreated or uninspected pine logs with attached bark coming from MPB-infested areas of Canada or the United States.

MPB's life cycle makes it easy to transport in infested wood. Although specific data on wood movement are not available, it appears wood movement from infested provinces and states to non-infested provinces and territories in Canada is low due to market factors. Furthermore, several provinces have restrictions on importing pine wood with intact bark to limit the risk of MPB spread. Despite this, specialty users, such as log home builders and furniture makers, may represent a specific risk.

### UNCERTAINTY

1. Moderate uncertainty regarding the frequency and volume of pine wood with intact bark moved from infested areas to non-infested regions, including by specialty users such as log home builders.

### RESEARCH NEEDS

1. Information on the movement of pine wood with bark intact in North America, especially high-risk specialty users.

# *Consequences of Spread*

## 11. FIBRE LOSSES ASSOCIATED WITH MPB-CAUSED TREE MORTALITY WILL VARY ACROSS THE LANDSCAPE AND WILL AFFECT THE MERCHANTABILITY OF SOME STANDS IN THE BOREAL FOREST. SOME LOSSES MAY BE MITIGATED BY SALVAGE HARVESTING, BUT A RAPID DECLINE IN WOOD QUALITY FOLLOWING BEETLE ATTACK WILL LIMIT THE POTENTIAL USES AND/OR VALUE. (K. Bleiker, K. Lewis)

### EVIDENCE

Fibre losses associated with MPB will depend on the level of tree mortality, which in turn will be determined by stand characteristics (primarily pine volume) and the severity of the infestation. While MPB killed an estimated 54% of the merchantable pine in the province of British Columbia, losses at the stand level varied widely. In the hardest-hit region of central British Columbia, many stands fell in the highest mortality class of 71–100%; pine mortality was lower in other regions, but, overall, MPB caused a significant reduction in pine volume in the interior of British Columbia.

Total pine volume loss from MPB in Alberta is expected to be less than in British Columbia because of lower pine volumes in Alberta and the characteristics and climate of boreal stands may not be as conducive to large outbreaks (Statements 1, 2). However, there are already notable cases where MPB has killed 90% of the mature pine in some high-volume pine stands in western Alberta in the Peace River and Grande Prairie regions (D. Letourneau, R. Hermanutz, pers. com.). More typically though, data from 3.6 million ha of affected area that was examined in north-west and west-central Alberta show that as of 2015–2016 approximately 20% of the pine leading stands (>50% pine) lost 30% or more of the basal area to MPB (B. Horne, unpub. data). Losses can be expected to accrue annually in stands where MPB is still active and in new areas as it continues to spread. In stands and areas where MPB has already run its course, populations are likely to persist at low levels, below the tree-killing (and detection) threshold, until the next outbreak. In British Columbia, outbreaks generally occur every 25 to 40 years. Stands that experience moderate levels of mortality (30%) from MPB in the early 2000s may be susceptible to another infestation in several decades.

Potential losses may be mitigated by an opportunity to salvage beetle-killed trees for an extended period of time following death (sometimes referred to as "shelf life"). Salvage logging continues in some ecosystems in British Columbia more than 20 years after the end of the outbreak, but it is only economic in stands that also have healthy higher value trees, where hauling costs to the mill are low, and when the selling price of the product is high enough to offset losses due to waste. The ultimate factor limiting salvage potential is how long trees remain standing, which is a function of butt rot that develops at the base due to the passive absorption of moisture from the ground (Lewis and Thompson 2011). Carpenter ants can also cause trees to fall in addition to promoting butt rot. Once a tree falls to the ground and absorbs moisture, decay sets in quickly. Site moisture affects sap rot at the base, but it is not a good predictor of decay and degradation (Lewis and Thompson 2011).

In British Columbia, the sapwood of MPB-killed trees is fully blue-stained by six months post-mortality, which seriously affects marketability of J-grade lumber. Two years after death, trees have sufficient checks to affect production and marketability of larger dimension lumber. Trees continue to develop checks over time due to seasonal wetting and drying cycles, although depending on market conditions and operating costs, it may be possible to produce smaller dimension lumber for several years post-mortality. For pulp and some other uses, the wood may be useful for decades (Lewis and Thompson 2011). The use of beetle-killed wood may come with additional unforeseen challenges, including fire and mill safety issues associated with processing the very dry wood.

In Alberta the rate of drying and checking is higher in trees in the mixed wood region than trees in the Foothills Region in the first two years following death (Lewis and Hrinkevich 2013). The generally dry nature of jack pine forests in the Prairie boreal forest will advance checking, especially in stands with smaller diameter trees, and the aggressive nature of wood borers in the boreal forest may reduce volume. In the long-term, wood fibre may persist over an extended period of time if trees remain standing, potentially allowing a longer period for salvage logging for certain uses (Lewis and Hrinkevich 2013). In British Columbia, trees began to fall around 8 years following death (Lewis and Thompson 2011).

While there is the potential to salvage beetle-killed trees for a number of years, their value and use will be reduced. The timber industry, infrastructure and landscape of the boreal forest are also different from British Columbia. Limited road access in undeveloped parts of the boreal forest may affect salvage opportunities, and the ability to use affected fibre will be determined by economics.

### UNCERTAINTY

1. High uncertainty regarding the level of mortality to expect in jack pine stands from MPB in the boreal forest. This is due to the uncertainty associated with MPB productivity, population dynamics, spread potential, tree resistance and stand susceptibility described in previous statements.
2. High uncertainty regarding the impact of MPB on the merchantability of jack pine stands in the boreal forest due to dynamic factors affecting merchantability (e.g., market prices) and the uncertainty of MPB's impact.
3. Low uncertainty regarding how wood quality is likely to change over time following attack but moderate uncertainty regarding wood quality changes for jack pine (and eastern pines), particularly for small trees.

## RESEARCH NEEDS

1. Anticipated mortality (impact) from MPB at the stand level for different stand types and ecosystems within the boreal forest.
2. Determination of the salvage window for jack pine, especially smaller diameter trees, in the boreal ecosystem.
3. Analysis of the economics of jack pine salvage in the boreal forest.

## 12. FOREST MANAGEMENT PRACTICES IMPLEMENTED TO REDUCE OUTBREAK SPREAD AND RECOVER ECONOMIC VALUE FROM STANDING DEAD PINE WILL INFLUENCE MID-TERM FIBRE SUPPLY AND OTHER FOREST VALUES, AND AFFECT THE VULNERABILITY OF FORESTS TO FUTURE DISTURBANCES AND CLIMATE CHANGE. (E. Campbell)

## EVIDENCE

History tells us that careful consideration of forest management responses to insect outbreaks is needed to reduce the risk of exacerbating their socio-economic consequences. Management responses to large-scale MPB outbreaks can affect mid-term timber supply, forest resilience to future disturbances or climate change, and the continued flow of ecosystem services (Campbell et al. 2009; Dhar et al. 2016a). Both remedial (sanitation or salvage logging) and proactive actions that are guided by landscape-level management policies are needed to enhance forest recovery rates and mitigate vulnerability to outbreaks through the maintenance of complex forest structure and dynamics across landscapes (Campbell et al. 2009; Fettig et al. 2014; Seidl et al. 2016).

Extensive MPB outbreaks, which are not feasible to control (Statement 8), may lead to large-scale salvage logging operations to recover some economic value and mitigate losses (Statement 11). A number of factors should be considered before the decision to salvage beetle-killed wood is made. Large-scale salvage logging operations can lead to the homogenization of forests and adversely impact certain forest values and ecosystem services. Many stands that suffered high levels of pine mortality in British Columbia contained substantial post-outbreak secondary structure: residual canopy trees, and saplings and seedlings of commercially acceptable species, including surviving and putatively resistant hosts (Astrup et al. 2008; Hawkins et al. 2012; Campbell and Antos 2015; Axelson et al. 2018). Left intact and not harvested, stands with an abundant and well-spaced secondary structure offer an opportunity to retain certain forest values and ecosystem services while contributing to the mid-term timber supply.

Forest thinning by MPB outbreaks enhances the growth of secondary structure, but rates of growth increase will vary among stands depending on the level of beetle-induced pine mortality, site and regional climate conditions, as well as the health of secondary structure (Campbell et al. 2007; Hawkins et al. 2012; Amoroso et al. 2013). In British Columbia, research indicates that 75–80% of the beetle-affected stands in the managed forest land base that were not logged are likely to recover merchantability 25–50 years post MPB outbreak (Astrup et al. 2008; Hawkins et al. 2012; Amoroso et al. 2013). Management decisions to leave some stands unsalvaged, or to selectively log dead pine from mixed species stands, could shorten stand rotation ages substantially compared to stands reforested after salvage logging, in addition to promoting structural complexity needed to maintain socio-ecological resilience of forests to outbreaks (Dhar et al. 2016a; Axelson et al. 2018).

In the boreal forests where MPB outbreaks are novel and expanding northward and eastward, the capacity of affected stands to recover and contribute to mid-term fibre supply without management intervention is not as well understood as in British Columbia. McIntosh and MacDonald (2013) report the near absence of secondary structure in pure lodgepole pine forests of Alberta and suggest that salvage logging and reforestation may be necessary. Two other studies in mixed species stands in boreal forests, one in northeastern British Columbia (Campbell and Antos 2015) and the other in western Alberta (Oboite and Comeau 2018), found abundant, well-spaced, healthy secondary structure. Both white and black spruce in Alberta exhibited substantial post-outbreak increases in height and diameter growth, indicating the potential for some stands to recover mid-term harvestable volumes without management intervention. However, responses varied according to tree species (black vs. white spruce), tree size, and among sites; as such, a better understanding of this variability is needed to guide appropriate management action in heavily infested regions. As the geographic range of MPB expands eastward into jack pine forests, appropriate management responses will depend on the levels of pine mortality, the characteristics of secondary structure in impacted stands, ecological values at risk, and the economic significance of these potential fibre losses (Statement 13). Managers in boreal and eastern forests could start implementing proactive approaches now, such as harvest scheduling and silvicultural practices, which would maintain boreal forest complexity and limit the social, economic, and ecological consequences of MPB spread to eastern Canada.

Climate change interjects a great deal of uncertainty regarding appropriate management interventions for mitigating the socio-economic consequences of MPB outbreaks. Boreal forest trees are already exhibiting drought stress and reduced growth (Girardin et al. 2016), and relying on the increased growth of secondary structure to provide the mid-term fibre supply may become increasingly risky. In regions of the boreal forest where an increasingly warm, moist climate is driving increased growth (Girardin et al., 2016), forests could recover faster than in the past; however, D'Orangeville et al. (2018) suggest the beneficial effects of climate warming on boreal tree growth may be transient. Salvaged stands reforested with the same species or populations of the same genetic stock as in the past are at risk to fail, as they are already maladapted to the current regional climate (Aitken et al. 2008). Understanding tree species and their genetic-based responses to a changing climate is an active area of research that is only beginning to provide information that could guide post-disturbance reforestation activities (e.g., Six et al. 2018).

### UNCERTAINTY

1. High uncertainty regarding the impact of MPB on jack pine stands.
2. Moderate to high uncertainty regarding the capacity of beetle-affected stands to recover mid-term economic value without salvage logging.
3. High uncertainty regarding the effects of climate change on rates of recovery in different stands, sites, and biomes, including the effect of climate change on reforestation after logging or on the growth of advance regeneration in stands that are not harvested.

### RESEARCH NEEDS

1. Estimate of fibre losses due to MPB in the boreal forest.
2. Improved forest inventory for the boreal forest. This includes better data on the distribution and volume of pure and mixed jack pine stands, and on advance regeneration (i.e., secondary structure) in pine stands.
3. A better understanding of boreal forest dynamics, including long-term trends in tree growth, stand response to tree mortality, and the effect of regional climates on tree growth.
4. Projections over time of boreal forest dynamics at the landscape level that consider major forest disturbances (e.g., MPB outbreaks, climate change, wildfire) under a range of potential management and mitigation scenarios.

## 13. THE IMPACT OF MPB-CAUSED TREE MORTALITY ON TIMBER FLOWS IN THE BOREAL FOREST WILL BE HIGHLY VARIABLE. (B. Stennes)

### EVIDENCE

The impact of MPB-caused tree mortality on timber flows and forest sector activity will vary depending on regional fibre supply and demand. Between 1994 and 2004, which were relatively strong fibre demand years, the forest sector in Saskatchewan and Manitoba averaged a harvest of 57% and 27% of the softwood annual allowable cut, respectively (Canadian Council of Forest Minister's National Forest Database, http://nfdp.ccfm.org). Currently, it is estimated that the forest industry in Saskatchewan has the mill capacity to use 80% of the annual allowable cut, leaving timber available for 2 or 3 new mills. The Government of Saskatchewan reports that softwood is approximately 50% of the merchantable growing stock, with pine comprising almost half of that volume. In 2017 it was estimated that Saskatchewan's forest industry supported over 8,400 direct and indirect jobs and totalled nearly $1.2 billion in forest product sales; full development of the sector could support over $2 billion in sales and 13,000 jobs (Government of Saskatchewan 2018). Ontario's harvest averaged 65% of capacity over the strong fibre demand years of 2003–2007. While these statistics may indicate some capacity to absorb MPB-related timber supply impacts, utilization needs to be examined at the management-unit level to determine the actual risk to wood supply.

In the short-term and when MPB spread rates are slow, we expect harvesting to be redirected to salvaging or pre-emptive harvesting in vulnerable areas, potentially allowing harvest rates to remain largely unchanged (Phillips et al. 2007). In the medium and longer term, the forest industry could adapt by focusing on non-pine harvesting (including hardwoods) and through forest management such as salvaging and planting non-pine to reduce future vulnerability to MPB. Forest managers in Ontario and Quebec, where timber values are relatively high, should have additional time to anticipate the arrival of MPB and work towards mitigating supply impacts with appropriate forest management.

Looking at evidence from the recent MPB outbreak in British Columbia, approximately 731 million $m^3$ or 54% of the merchantable pine in the province was killed (BC FLNRO 2016). One of the hardest hit regions was the Quesnel Timber Supply Area where pine comprised approximately 70% of the timber harvesting landbase. AACs in this district were more than doubled to facilitate salvage, and then subsequently reduced to near pre-uplift levels (~11% above); in the near future, AACs may fall to 65–70% of pre-uplift levels (Nicholls 2017). Some regions of British Columbia were able to mitigate the effect of losses to MPB through salvage logging and recovery of beetle-killed pine stands, reforestation efforts, and directing harvests towards pine instead of other tree species. There was little effect of MPB in areas of British Columbia where pine mortality was low or other tree species comprise a significant component of the timber supply.

### UNCERTAINTY

1. Moderate uncertainty regarding the inventory of merchantable pine in the boreal forest, especially at the management-unit level. This includes uncertainty associated with inter-provincial differences in collection methods.
2. High uncertainty regarding the rate or spread and mortality of MPB in the boreal forest, with and without management and control.
3. Moderate uncertainty regarding the salvage period for MPB-killed jack pine in the boreal forest.

## RESEARCH NEEDS

1. Consistent inventory data of merchantable species and timber supply utilization by management unit across the boreal forest.
2. Rate of spread (with and without control) and anticipated mortality (impact) of MPB in the boreal forest.
3. Salvage period for MPB-killed jack pine and eastern pine species in the boreal.

## 14. COMMUNITIES IN THE BOREAL FOREST WILL VARY IN THEIR CAPACITY TO ADAPT TO MPB-CAUSED TREE MORTALITY. (R. Friberg)

## EVIDENCE

The vulnerability of boreal forest communities to MPB impacts varies considerably based on factors that determine local susceptibility to MPB and the capacity to cope and adapt (Thornes 2002; Adger 2003; Engle 2011; Williamson et al. 2007). The proportion and susceptibility of pine across local forested landscapes, the degree of economic reliance on pine, and the availability of alternate timber species are important determinants of vulnerability for communities reliant on the forest industry (Parkins and MacKendrick 2007). The timing and magnitude of economic impact on forest industry activities are difficult to predict and will vary considerably for different boreal forest communities due to factors including timber harvesting strategies in response to MPB (e.g., adjustments to short- and longer-term harvest rates), markets for salvage wood, etc. This uncertainty is concerning for communities along the front lines of MPB expansion, and those that may be impacted in future (R. Friberg et al., unpub. data). In British Columbia and the Foothills Region of Alberta, vulnerability to MPB was found to also vary significantly with the social dimensions of community capacity, and political dimensions of risk awareness and leadership (Parkins and MacKendrick 2007).

The nature of impacts from MPB will vary among boreal forest communities. Many communities rely on the forest industry for local employment, while others rely to a differing, and in some cases significant extent, on tourism. There is concern and uncertainty among boreal communities about the timing and magnitude of impacts to the tourism sector as forest landscapes are altered by MPB (Friberg et al., unpub. data). An additional uneasiness emerging currently among Alberta communities facing MPB is the potential for increased risk to public safety and infrastructure from wildfire (e.g., Kulig and Botey 2016), and the nature of these concerns can differ from the municipal level to broader scales such as county or region (Friberg et al., unpub. data). Again, there is both concern and uncertainty among communities about how MPB may impact their susceptibility to wildfire. Other immediate challenges to boreal communities include damage, disruption, reduced visual appeal, and public safety risks related to town infrastructure, such as recreational trail networks, golf courses, and parks. The additional financial burden to municipalities for MPB mitigation and hazard tree removal is potentially significant where treatments must be carried out in the vicinity of existing infrastructure such as homes and power lines.

Adaptive capacity, viewed as "the ability of a system to evolve in order to accommodate perturbations or to expand to the range of variability with which it can cope" (Adger 2003), is important to mitigate the vulnerability of communities to disturbances like MPB. Adaptive capacity is also viewed as a key factor in community resilience (Engle 2011), which in the context of forest-based communities is defined as "the existence, development, and engagement of community resources by community members to thrive in an environment characterized by change, uncertainty, unpredictability, and surprise" (Magis 2010). Regarding the resilience of boreal forest communities, however, an important consideration emerges around findings of significant inequities in the adaptive capacity of urban versus rural communities in British Columbia (Burch 2010). There are commonly shortages in financial and human resources in rural communities, especially in remote First Nations communities (Krishnaswamy et al. 2012). This increases community vulnerability and reduces resilience to MPB impacts.

Additional knowledge about the vulnerability and resilience of boreal forest communities is emerging from work in the Alberta Foothills Region (Friberg et al., unpub. data) through the application of an integrated assessment framework involving factors that include biophysical, social and economic exposure to MPB (e.g., Parkins and MacKendrick 2007); stability factors including biophysical and economic diversity, redundancy, social cohesion and latitude for response (e.g., Kerner and Thomas 2014; Walker et al. 2004); community assets for adaptation or transformation (e.g., Berkes and Ross 2016; Kulig and Botey 2016; Tyler and Moench, 2012); institutional adaptive capacity at local, provincial and federal scales (e.g., Emerson et al. 2012; Gupta et al. 2010); and factors such as leadership that facilitate the activation of existing adaptive capacity (e.g., Burch 2010). Areas of potential concern emerging from the assessment include the close proximity of some rural, boreal forest communities to financial thresholds below which some municipal services could no longer be provided. In addition, MPB presents a considerable degree of uncertainty for communities in terms of the timing, duration and extent of economic impact on forest and tourism-based industries. Changes to timber supply, for example, that might not have a substantial impact on their own might in combination with other local factors such as timber supply reductions for woodland caribou, and global factors, including market price and trade barriers, contribute to a cumulative impact on local employment and municipal tax base.

### UNCERTAINTY

1. Low uncertainty that MPB will result in negative social and economic impacts to human communities reliant on boreal forests in Canada.
2. Moderate to high uncertainty regarding the geographic extent of MPB impacts.
3. High uncertainty regarding the extent of impact on individual communities due to uncertainty in the timing and magnitude of MPB impact on local landscapes, high uncertainty regarding the timing and extent of socio-economic impacts, and high uncertainty regarding the cumulative effect of these and other factors.
4. Low uncertainty that the vulnerability of some rural and First Nations communities will be adversely affected by inequities in adaptive capacity.

### RESEARCH NEEDS

1. Increased knowledge about the potential timing and severity of economic impacts on forest and tourism industries, both regionally and on specific communities (e.g., through scenario development).
2. Increased knowledge about potential key weaknesses in existing adaptive capacity among diverse boreal forest communities and relevant, context-specific strategies for increasing adaptive capacity and resilience.
3. Identification of opportunities for strengthening institutional adaptive capacity at local, provincial, and federal levels.
4. Knowledge about context-specific MPB impacts on British Columbia communities and the effectiveness of local, provincial, and federal responses.

## 15. THE ECOSYSTEM SERVICES VALUES AT RISK IN EASTERN PINE FORESTS EXCEED THOSE OF TRADITIONAL COMMERCIAL TIMBER VALUES. (B. Cooke)

### EVIDENCE

Commercial timber values are determined by the total price that could be commanded for all timbers procured from a forest by bringing them to market. This is a number that is not easily calculated, although it is arguably easier to calculate than non-timber values. Because the procurement of timber takes time and is expensive, and because market prices fluctuate, it is insufficient to sum the merchantable volume total and multiply by a current lumber price to obtain a total valuation. One could do this for the entire province of Saskatchewan and produce an economic valuation for jack pine of $2 billion. However, there is insufficient milling capacity to access all this timber in the long-run as well as insufficient road infrastructure in the short-run. Therefore, this latent value represents an overvaluation. Moreover, the net present value of all future timbers requires discounting to achieve a proper valuation.

Forest ecosystem services are valued flows of outputs or commodities from a forested ecosystem that may be disrupted when the ecosystem is disturbed, for example, by fire, insects, disease, harvesting, or other forest land uses such as agricultural or suburban development. These are frequently valued byproducts of timber production (Dhar et al. 2016b) and they include, but are not limited to

- groundwater purification / surface water quality;
- provision of subsistence and luxury foods (mushrooms, nuts, berries);
- provision of biodiversity and habitat for endangered or threatened species;
- provision of specific habitats for subsistence and sport hunting and fishing;
- provision of tourism, spiritual and recreation opportunities;
- regulation of climate (via carbon sequestration); and
- regulation of fire behaviour (via fuel abundance, quality, and distribution).

Some of these ecosystem services can, like timber, be readily priced because there are markets for them. Others are non-commodities whose values are intrinsic and must be assessed at the level of a political negotiation. For example, biodiversity, which encompasses genetic variation at all levels of organization from the gene pool to individual species to entire communities, may have a latent value that becomes of high commercial value only when an element of the system becomes a critical ingredient for the pharmaceutical industry (e.g., Taxol is derived from the Canada yew and is now used to treat certain cancers). Traditionally, the timber production function has been the focus of forest economics research, but non-timber values are increasingly being studied. Even if these ecosystem services have intrinsic value that is non-quantifiable, they are still amenable to policy analysis through the study of trade-offs associated with varying forest management scenarios.

To our knowledge, there has never been (i) a formal commercial valuation of the timber assets across Canada at risk of MPB attack; or (ii) an ecosystem services valuation of the eastern pine forests in Canada. Consequently, any statement about the timber and non-timber values at risk are highly uncertain. However, there are two sources (Dhar et al. 2016b; Troy and Bagstad 2009) that could serve as a basis for extrapolation to address ecosystem services values at risk, which taken together demonstrate that it is, in theory, possible to quantify the non-timber values of the eastern pine forests.

A literature review reported both positive and negative impacts of MPB on ecosystem service values in British Columbia (Dhar et al. 2016b). The total change in value resulting from MPB was not estimated in this study, the focus being on qualitative effects of the co-production functions. The most severely negatively impacted regulating service was water quality. For supporting services, terrestrial habitat services showed positive responses, while aquatic habitat showed negative responses, and nutrient cycling showed a short-term negative effect. Salvage logging following MPB outbreak can increase negative impacts on ecosystem services compared to MPB outbreak without salvage logging (Statement 12). There were no effects on cultural services, such as tourism and recreation, reported to date in British Columbia. Similar qualitative responses might be expected in Alberta and provinces eastward, although pine comprises a lower percentage of the eastern forest, so the magnitude of impacts might be a fraction of that experienced in British Columbia.

The most comprehensive study in Canada was conducted in southern Ontario where standing forests as a whole were estimated to be worth $7.4 billion in ecosystem service values (Troy and Bagstad 2009). Per-hectare values are highest where human population densities are highest, and in those cases ecosystem service values are higher for keeping trees standing than for cutting them down. The average values identified in this study would not extrapolate well to rural and northern Canada, although this would be less of a concern for values identified in the northern part of the study area, where white pine is one of the more dominant tree species. It is not possible to easily translate this number into a pine ecosystem service value for all Ontario or eastern Canada, but it does illustrate how it may be possible to do so, in theory. It also shows why urban red and white pines will have greater value than commercial pine timber. The value of pine in this southern Ontario valuation will be a fraction of the total $7.4 billion estimated for all forests and that number would grow after including red and white pines in central Ontario, and then jack pine in northern Ontario. That number would rise again with the inclusion of red, white and jack pine in the rest of Canada.

In New Brunswick, the eastern spruce budworm has been characterized as a "$15 billion problem" for the threat it poses to spruce and fir. Given the extent of pine at risk to MPB over nine provinces—an area 100 times larger than New Brunswick—the values at risk are at least as high as this and probably considerably higher. Although calculating a precise number is difficult without additional data, there are clearly multiple billions of dollars of timber and non-timber assets at risk of MPB attack in eastern Canada.

## UNCERTAINTY

1. High uncertainty regarding applicability of known ecosystem impacts in British Columbia to different pine ecosystems.
2. High uncertainty regarding how MPB will affect the flow of multiple ecosystem services.
3. High uncertainty regarding the relative value of commercial timber values versus non-timber values.

## RESEARCH NEEDS

1. Ecosystem services data to better quantify impacts of MPB at a regional (e.g., Prairie boreal), provincial, and national level.
2. Return on investment analysis to differentiate between those that benefit and those that bear the cost.

## 16. MPB WILL HAVE A SIGNIFICANT IMPACT ON THE CARBON BALANCE OF CANADA'S BOREAL FORESTS. (C. Boisvenue)

### EVIDENCE

The carbon sequestered by a forest stand in a given year is mainly determined by the balance between two large carbon fluxes: carbon uptake via Net Primary Productivity (NPP) and carbon release to the atmosphere via ecosystem respiration (Kurz et al. 2013). Small differences between these two large fluxes determine whether the system is a carbon source or sink in a given year. Tree mortality from MPB transfers biomass from the live carbon pools (leaves, branches, trunks, roots) to the dead carbon pools (fine litter, coarse woody debris, soil carbon). This reduces the photosynthetic capacity and NPP and increases respiration in a forest (Maurer et al. 2016). The more biomass transferred from live carbon pools to dead pools, the larger the carbon emissions to the atmosphere (Kurz et al. 2008). Recovery of the carbon stocks will follow the trajectory of vegetation recovery and will depend on the severity of infestation, forest type, and initial carbon stocks (Pfeifer et al. 2011; Hicke et al. 2012; Raymond et al. 2015).

Recent research indicates that post-disturbance $CO_2$ and $H_2O$ dynamics are driven by the level of tree mortality as well as the response of the remaining and new regenerating vegetation (Reed et al. 2014). Residual understory trees and new growth may be stimulated after the death of large mature trees due to decreased competition and increased nutrient availability, such that forest regeneration may actually offset some of the losses incurred from MPB-caused tree mortality; this may allow carbon stocks to recover faster than initially predicted (Edburg et al. 2012; Hansen 2014; Seidl et al. 2016). Other factors may help counteract the negative effect of MPB-caused mortality on carbon stocks and yearly dynamics. For example, increased $CO_2$ levels in the atmosphere (i.e., $CO_2$ fertilization) associated with a changing climate may lead to faster vegetation growth and increased carbon sequestration. As a result of these interacting factors, carbon uptake by the land following the recent MPB epidemic in British Columbia may overcome carbon losses by 2020 (Arora et al. 2016). Drought, which influences decomposition rates, and wildfire will also affect the carbon balance of forest stands (Bourbonnais et al. 2014; Garrett et al. 2016; Stinson et al. 2011; Edburg et al. 2012).

Current estimates of forest carbon largely use tree and stand allometric equations that rely solely on dominant large tree data. Unfortunately, there are very few data on the carbon content of other vegetation types. Imperatives to commodify carbon are based on the contribution of $CO_2$, the most prominent greenhouse gas, to increasing global temperatures. MPB outbreaks may also contribute to increasing global temperatures through effects on the regional and global energy balance via changes in surface albedo (O'Halloran et al. 2011; Edburg et al. 2012). The impact of current and potential future levels of MPB infestation on the energy balance of the boreal forest are not well quantified.

### UNCERTAINTY

1. Low uncertainty that MPB-caused tree mortality leads to the release of carbon from killed trees.
2. Moderate to high uncertainty regarding the effects of MPB-caused tree mortality on the overall carbon budget and global temperatures in the long-term. This includes vegetation recovery and new growth following MPB outbreaks, the potential interaction between tree mortality and wildfire, and impacts on surface albedo.

3. Moderate to high uncertainty regarding the overall amount and severity of MPB disturbances (i.e., the monitoring data used to estimate MPB impacts on the national forest carbon budget are coarse and based on visually assessed categories of mortality).

### RESEARCH NEEDS

1. Quantification of the impact of MPB-caused mortality on live and dead carbon pools over time. This includes the percent of trees in the red and grey attack stages.
2. Temporal quantification of decomposition rates of dead biomass following MPB outbreaks in different ecosystems and conditions (e.g., drought), including jack pine stands in the boreal forest.

## 17. MPB INFESTATIONS WILL INCREASE WILDFIRE RISK THROUGHOUT WESTERN CANADA. (C. Stockdale)

### EVIDENCE

There is growing concern and evidence that MPB epidemics are significantly increasing landscape-level wildfire risk. Wildfire risk is defined as the likelihood of fire occurrence combined with the impact of a fire if it does occur (Finney 2005). Given that MPB affects vegetation, and therefore fuel, it should be expected to change both the likelihood and impact of fires; however, there is considerable controversy regarding the precise nature of these effects (Klutsch et al. 2011; Moran and Cochrane 2012; Jenkins et al. 2014; Hart et al. 2015; Nelson et al. 2016). The disagreements largely stem from whether one is investigating how MPB affects fire occurrence (number of fires per unit area and time), size, rate of spread, intensity (heat produced by the fire), severity (mortality caused by the fire), smoke production, or short- and long-range ember transport (which can start new fires). Further complicating the matter is that the effects of the different stages of beetle attack (red, grey, downed) have varying temporally limited effects.

At its most basic, stands of dead trees with needles still attached (red attack) should burn at a higher intensity, ignite more easily, and spread faster than fires in live trees (Perrakis et al. 2014). This has been observed in many wildfires. Once the needles fall off the tree (grey stage), the effects on wildfire become complex and difficult to predict. As needles fall, they accumulate on the forest floor; forest floor fuels make fire ignition more likely. However, as the needles fall, the canopy bulk density decreases, which lowers the likelihood of crown fires. The effect of these falling needles is difficult to predict because of these opposing forces, and is likely site-specific. Furthermore, as the amount of dead versus live fuel increases, fire initiation should become more likely. As the dead trees begin to fall, coarse woody debris increases the surface fuel load; at this stage, the probability of ignition is low, but should a fire start, it will have a high intensity. A number of studies have questioned these general relationships (Kulakowski and Veblen 2007; Simard et al. 2011; Harvey et al. 2014; Hart et al. 2015); their application is limited as they were conducted in areas with a specific fire regime (small-sized, low-frequency fires) under a small range of potential fire weather or they failed to account for factors such as fuel moisture and loading in stands with red- and grey-attacked trees (see critiques by Moran and Cochrane 2012; Meigs et al. 2015; Nelson et al. 2016). In general, it is likely that there will be short-term increases in wildfire extent, severity, and probability of ignition following MPB-caused tree mortality when the time lags of the various attack stages are taken into account (Nelson et al. 2016).

The 2017 wildfire season in British Columbia burned more than 1.2 million ha, which was a record in the province's recorded history until 2018, when an additional 1.3 million ha burned; together, the 2017 and 2018 fire years burned more area than the previous 31 years combined. A very large portion of these fires burned through areas that in the last 20 years had experienced the largest and most severe MPB outbreak ever documented. Observations made by fire behaviour analysts indicate that the fires that burned in the 2017 and 2018 seasons were larger, spread faster, and burned more intensely than they would have in the absence of the MPB-affected fuels. These recent observations have yet to be quantified, but we can make effective use of these recent fires to advance our knowledge with regard to understanding how MPB-killed trees affect the rate of spread of fire, and how this in turn affects the relative burn probability of the landscape. The current fire regime of the Alberta foothills and boreal forest is characterized by a fire regime fundamentally different from British Columbia and the northwestern United States. The fire regime in Alberta as well as in the boreal eastern forests is characterized by shorter fire return intervals, a broader range in fire size (including some very large areas), and more intense wildfires due to different vegetation types: all of these would increase the probability of fire occurring with beetle affected fuels. Therefore, it is of paramount importance to understand how an MPB epidemic will affect wildfire risk in this region.

### UNCERTAINTY

1. Low uncertainty that red attack (dead trees with needles) will increase wildfire rate of spread, intensity, and probability of ignition and crowning (surface fire transitioning to a crown fire).
2. Moderate uncertainty regarding the effects of grey attack (dead trees with no needles) on wildfire rate of spread, intensity, ignition, and crowning.
3. High uncertainty regarding the effects of attacked trees once they begin to fall to the ground on wildfire rate of spread, intensity, ignition, and crowning. It is likely to be highly variable due to high structural complexity at this stage.
4. High uncertainty regarding how wildfire risk is affected by a landscape mosaic consisting of all of these different stages occurring in unique proportions and patterns across the landscape.

#### Research Needs

1. Field-based controlled burns in various stages of MPB-attack to determine the precise nature of the effects of MPB kill on fire behavior variables.
2. Thorough examination of remotely sensed data on recent wildfires that have burned through MPB-affected fuels to deduce changes in fire behaviour caused by MPB.
3. Modelling-based studies to examine the landscape mosaic effects on wildfire risk.
4. The development of spatially accurate and temporally current forest inventories to document the current stage of MPB infestation across the landscape.

# References

Adams, A.S., Boone, C.K., Bohlmann, J., and Raffa, K.F. 2011. Responses of bark beetle-associated bacteria to host monoterpenes and their relationship to insect life histories. Journal of Chemical Ecology, 37(8): 808–817. doi:10.1007/s10886-011-9992-6

Adger, W.N. 2003. Social aspects of adaptive capacity. *In* Climate change, adaptive capacity and development. Edited by J.B. Smith, R. Klein, and S. Huq. Imperial College Press, London, United Kingdom. p. 29–49. doi:10.1142/9781860945816_0003

Ainslie, B., and Jackson, P.L. 2011. Investigation into mountain pine beetle above-canopy dispersion using weather radar and an atmospheric dispersion model. Aerobiologia, 27(1): 51–65.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., and Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1(1): 95–111.

Amman, G.D. 1972. Mountain pine beetle (Coleoptera: Scolytidae) brood production in relation to thickness of lodgepole pine phloem. Journal of Economic Entomology 65(1): 138–140. doi:10.1093/jee/65.1.138

Amman, G.D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology, 11(3): 590–593. doi:10.1093/ee/11.3.590

Amman, G.D., and Cole, W.E. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II. Population dynamics. United States Forest Service General Technical Report INT-145. Available from https://www.usu.edu/beetle/documents2/1983Amman%20Cole_MPB%20Dynamics%20in%20LPP%20Forests%20Part%20II.pdf

Amoroso, M.M., Coates, K.D., and Astrup, R. 2013. Stand recovery and self-organization following large-scale mountain pine beetle induced canopy mortality in northern forests. Forest Ecology and Management, 310: 300–311.

Arora, V.K., Peng, Y., Kurz, W.A., Fyfe, J.C., Hawkins, B., and Werner, A.T. 2016. Potential near-future carbon uptake overcomes losses from a large insect outbreak in British Columbia, Canada. Geophysical Research Letters, 43(6): 2590–2598. doi:10.1002/2015GL067532

Astrup, R., Coates, K. D., and Hall, E. 2008. Recruitment limitation in forests: lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management, 256(10): 1743–1750.

Aukema, B.H., Carroll, A.L., Zheng, Y., Zhu, J., Raffa, K.F., Moore, R.D., Stahl, K., and Taylor, S.W. 2008. Movement of outbreak populations of mountain pine beetle: influence of spatiotemporal patterns and climate. Ecography, 31(3): 348–358. doi:10.1111/j.0906-7590.2007.05453.x

Axelson, J.N., Hawkes, B.C., van Akker, L., and Alfaro, R.I. 2018. Stand dynamics and the mountain pine beetle—30 years of forest change in Waterton Lakes National Park, Alberta, Canada. Canadian Journal of Forest Research, 48(1): 1159–1170. doi:10.1139/cjfr-2018-0161

[BC FLNRO] British Columbia Ministry of Forests Lands and Natural Resource Operations. 2016. Provincial-Level Projection of the Current Mountain Pine Beetle Outbreak. Current Projection Results (Year 13). Government of British Columbia. Retrieved from https://www.for.gov.bc.ca/hre/bcmpb/Year13.htm

Beaudoin A., Bergeron, T., Bernier P.Y., Guindon L., Villemaire P,. Guo X.J., Stinson, G., Magnussen S., Hall R.J. 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Canadian Journal of Forest Research, 44(5): 521–532. doi:10.1139/cjfr-2013-0401

Bentz B.J., Boone C., and Raffa, K.F. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. Agricultural and Forest Entomology, 17(4): 421–432. doi:10.1111/afe.12124

Bentz, B.J., and Hansen, E.M. 2018. Evidence for a prepupal diapause in the mountain pine beetle (*Dendroctonus ponderosae*). Environmental Entomology, 47(1): 175–183. doi:10.1093/ee/nvx192

Bentz, B.J., Hood, S.M., Hansen, E.M., Vandygriff, J.C., and Mock, K.E. 2016. Defense traits in the long-lived Great Basin bristlecone pine and resistance to the native herbivore mountain pine beetle. New Phytologist, 213(1): 611–624. doi:10.1111/nph.14191

Bentz, B.J., Logan J.A., and Amman, G.D. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. The Canadian Entomologist, 123(5): 1083–1094.

Bentz, B.J., and Mullins, D.E. 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the Intermountain West. Environmental Entomology 28(4): 577–587. doi:10.1093/ee/28.4.577

Bentz, B.J., Régnière, J., C., Fetting, C.J. Matthew Hansen, E., Hayes, J.L., Hicke, J.A., Kelsey, R.G. Negrón, J.F., and Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience, 60(8): 602–613. doi: 10.1525/bio.2010.60.8.6

Bentz, B., Vandygriff, J., Jensen, C., Coleman, T., Maloney, P., Smith, S., Grady, A., and Schen-Langenheim, G. 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the Western United States. Forest Science, 60(3): 434–449. doi:10.5849/forsci.13-056

Berkes, F., and Ross, H. 2016. Panarchy and community resilience: sustainability science and policy implications. Environmental Science & Policy, 61: 185–193. doi:10.1016/j.envsci.2016.04.004

Bleiker, K.P., O'Brien, M.R., Smith, G.D., and Carroll, A.L. 2014. Characterization of attacks made by the mountain pine beetle (Coleoptera: Curculionidae) during its endemic population phase. The Canadian Entomologist, 146(3): 271–284. doi:10.4039/tce.2013.71

Bleiker K.P., and Smith G.D. 2016. Mountain pine beetle cold tolerance and seasonality: implications for population dynamics and range expansion in Canada. *In*. SERG-International Workshop Proceedings, 2–4 February 2016. Saskatoon, Saskatchewan. p. 52–64.

Bleiker K.P., and Smith G.D. 2017. Mountain pine beetle and climate: implications for continued range expansion in Canada *In* Proceedings of the Western Forest Insect Work Conference. 1–4 May 2017. Jackson, Wyoming. p. 16.

Bleiker, K.P., Smith, G.D., and Humble, L.M. 2017. Cold tolerance of mountain pine beetle (Coleoptera: Curculionidae) eggs from the historic and expanded ranges. Environmental Entomology, 46(5): 1165–1170. doi:10.1093/ee/nvx127

Bleiker, K.P., and Van Hezewijk, B.H. 2016. Flight period of mountain pine beetle (Coleoptera: Curculionidae) in its recently expanded range. Environmental Entomology, 45(6): 1561–1567. doi:10.1093/ee/nvw121

Boone, C.K., Aukema, B.H., Bohlmann, J., Carroll, A.L. and Raffa, K.F., 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research, 41: 1174–1188.

Borden, J.H. 1993. Uncertain fate of spot infestations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins. The Canadian Entomologist, 125(1): 167–169. doi:10.4039/Ent125167-1

Borden, J.H., Ryker, L.C., Chong, L.J., Pierce, H.D., Jr., Johnston, B.D., and Oehlschlager, A.C. 1987. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. Canadian Journal of Forest Research, 17(2): 118–128. doi:10.1139/x87-023

Bourbonnais, M.L., Nelson, T.A., and Wulder, M.A., 2014. Geographic analysis of the impacts of mountain pine beetle infestation on forest fire ignition. The Canadian Geographer / Le Géographe canadien, 58(2): 188–202. doi:10.1111/j.1541-0064.2013.12057.x

Brunelle, A., Rehfeldt, G., Bentz, B., and Munson, A.S. 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. Forest Ecology and Management, 255(3–4): 836–846. doi:10.1016/j.foreco.2007.10.008

Burch, S. 2010. Transforming barriers into enablers of action on climate change: insights from three municipal case studies in British Columbia, Canada. Global Environmental Change, 20(2): 287–297. doi:10.1016/j.gloenvcha.2009.11.009

Burke, J.L., Bohlmann, J., and Carroll, A.L. 2017. Consequences of distributional asymmetry in a warming environment: invasion of novel forests by the mountain pine beetle. Ecosphere, 8(4): e01778. doi:10.1002/ecs2.1778

Burke, J.L., and Carroll, A.L. 2016. The influence of variation in host tree monoterpene composition on secondary attraction by an invasive bark beetle: implications for range expansion and potential host shift by the mountain pine beetle. Forest Ecology and Management, 35: 59–64. doi:10.1016/j.foreco.2015.09.044

Burke, R., and Sankey, S. 2013. Canadian Forest Service Mountain Pine Beetle Strategy. Natural Resources Canada, Canadian Forest Service, May 2013.

Cale, J.A., Muskens, M., Najar, A., Ishangulyyeva, G., Hussain, A., Kanekar, S.S., Klutsch, J.G., Taft, S., and Erbilgin, N. 2017. Rapid monoterpene induction promotes the susceptibility of a novel host pine to mountain pine beetle colonization but not to beetle-vectored fungi. Tree Physiology, 37(2): 1597–1610. doi:10.1093/treephys/tpx089

Campbell, E., Saunders, S.C., Coates, D., Meidinger, D., MacKinnon, A., et al. 2009. Ecological resilience and complexity: a theoretical framework for understanding and managing British Columbia's forest ecosystems in a changing climate. Technical Report 055, Ministry of Forests and Range, Forest Science Program, Victoria, British Columbia.

Campbell, E.M., Alfaro, R.I., and Hawkes, B. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: a dendroecological analysis. Journal of Integrative Plant Biology, 49(2): 168–178.

Campbell, E.M. and Antos, J.A. 2015. Advance regeneration and trajectories of stand development following the mountain pine beetle outbreak in boreal forests of British Columbia. Canadian Journal of Forest Research, 45(10): 1327–1337. doi:/10.1139/cjfr-2015-0104

Carroll, A., Seely, S., Welham, C., and Nelson, H., 2017. Assessing the effectiveness of Alberta's forest management program against the mountain pine beetle: final report for the fRI Research project 246.18 parts 1 and 2 [online]. Available from https://friresearch.ca/sites/default/files/MPBEP_2017_07_%20Control%20Efficacy%20report_0.pdf

Carroll, A.L., Shore, T.L., and Safranyik, L. 2006. Direct control: theory and practice. *In* The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Edited by L. Safranyik and W.R. Wilson. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada. p. 155–172.

Carroll, A.L., Taylor, S.W., Régnière, J., and Safranyik, L. 2004. Effects of climate and climate change on the mountain pine beetle. *In* Proceedings of the mountain pine beetle symposium: challenges and solutions. 30–31 October, 2003. Kelowna, British Columbia, Canada. Edited by T.L. Shore, J.E. Brooks and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia. Information Report BC-X-399. p. 223–232.

Cerezke, H. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts. The Canadian Entomologist, 127(6): 955–965. doi:10.4039/Ent127955-6

Cerezke, H.F. 1989. Mountain pine beetle aggregation semiochemical use in Alberta and Saskatchewan, 1983–1987. *In* Proceedings—Symposium on management of lodgepole pine to minimize losses to the mountain pine beetle. 12–14 July, 1988. Edited by G.D. Amman. Kalispell, Montana. USDA, Forest Service, Ogden, Utah. General technical report INT-262. Available from http://cfs.nrcan.gc.ca/publications/download-pdf/11443

Chiu, C.C., Keeling, C.I., and Bohlmann, J. 2017. Toxicity of pine monoterpenes to mountain pine beetle. Scientific Reports, 7(1): 8858. doi:10.1038/s41598-017-08983-y

Clark, E.L., Carroll, A.L., and Huber, D.P. 2010. Differences in the constitutive terpene profile of lodgepole pine across a geographical range in British Columbia, and correlation with historical attack by mountain pine beetle. The Canadian Entomologist, 142(6): 557–573. doi:10.4039/n10-022

Clark, E.L., Pitt, C., Carroll, A.L., Lindgren, B.S., and Huber, D.P.W. 2014. Comparison of lodgepole and jack pine resin chemistry: implications for range expansion by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae). PeerJ, 2:e240. doi:10.7717/peerj.240

Cooke, B.J. 2009. Forecasting mountain pine beetle-overwintering mortality in a variable environment. Mountain Pine Beetle Working Paper 2009-03. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada. Available from https://cfs.nrcan.gc.ca/publications/download-pdf/29920

Cooke, B.J., and Carroll, A.L. 2017. Predicting the risk of mountain pine beetle spread to eastern pine forests: considering uncertainty in uncertain times. Forest Ecology and Management, 396: 11–25. doi:10.1016/j.foreco.2017.04.008

Creeden, E.P., Hicke, J.A., and Buotte, P.C. 2014. Climate, weather and recent mountain pine beetle outbreaks in the western United States. Forest Ecology and Management, 312: 239–251. doi:10.1016/j.foreco.2013.09.051

Cullingham, C.I., Cooke, J.E.K, Dang, S., Davis, C.S., Cooke, B.J., and Coltman, D.W. 2011. Mountain pine beetle and host-range expansion threatens the boreal forest. Molecular Ecology, 20(10): 2157–2171. doi:10.1111/j.1365-294X.2011.05086.x

Dhar, A., Parrott, L., and Hawkins, C.D.B. 2016a. Aftermath of mountain pine beetle outbreak in British Columbia: stand dynamics, management response and ecosystem resilience. Forests, 7(8): 171. doi:10.3390/f7080171

Dhar, A., Parrott, L., and Heckbert, S. 2016b. Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. Canadian Journal of Forest Research, 46(8): 987–999. doi:10.1139/cjfr-2016-0137

Dodds, K.J. 2010. Assessing the threat posed by indigenous exotics: a case study of two North American bark beetle species. Annals of the Entomological Society of America, 103(1): 39–49. doi:10.1603/008.103.0106

Dooley, E.M., Six, D.L., and Powell, J.A. 2015. A comparison of mountain pine beetle (Coleoptera: Curculionidae, Scolytinae) productivity and survival in lodgepole and whitebark pine after a region-wide cold weather event. Forest Science, 61(2): 235–246. doi:10.5849/forsci.14-014

D'Orangeville, L., Houle, D., Duchesne, L., Phillips, R.P., Bergeron, Y., and Kneeshaw, D.2018. Beneficial effects of climate warming on boreal tree growth may be transitory. Nature Communications, 9(1): 3213. doi:10.1038/s41467-018-05705-4

Edburg, S., Hick, J., Brooks, P., Pendall, E., Ewers, B., Norton, U., Gochis, D., Gutmann, E., and Meddens, A., 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes [online]. Frontiers in Ecology and the Environment, 10(8): 416–424. doi:10.1890/110173

Eidson, E.L., Mock, K.E., and Bentz, B.J. 2017. Mountain pine beetle host selection behavior confirms high resistance in Great Basin bristlecone pine. Forest Ecology and Management, 402: 12–20. doi:10.1016/j.foreco.2017.06.034

Eidson, E.L., Mock, K.E., and Bentz, B.J. 2018. Low offspring survival in mountain pine beetle infesting the resistant Great Basin bristlecone pine supports the preference-performance hypothesis [online]. PLOS One, 13(5): e0196732. doi:10.1371/journal.pone.0196732

Emerson, K., Nabatchi, T., and Balogh, S. 2012. An integrative framework for collaborative governance. Journal of Public Administration Research and Theory, 22(1): 1–29. doi:10.1093/jopart/mur011

Engle, N. L. 2011. Adaptive capacity and its assessment. Global Environmental Change, 21(2): 647–656. doi:10.1016/j.gloenvcha.2011.01.019

Erbilgin, N. 2019. Phytochemicals as mediators for host range expansion of a native invasive forest insect herbivore. New Phytologist, 221(3):1268–1278. doi:10.1111/nph.15467

Erbilgin, N., Cale, J.A., Hussain, A., Ishangulyyeva, G., Klutsch, J.G., Najar, A. and Zhao, S. 2017a. Weathering the storm: how lodgepole pine trees survive mountain pine beetle outbreaks. Oecologia 184(2): 469–478. doi:10.1007/s00442-017-3865-9

Erbilgin, N., Cale, J.A., Lusebrink, I., Najar, A., Klutsch, J., Sherwood, P., Bonello, P., and Evenden, M.L. 2017b. Water-deficit and fungal infection can differentially affect the production of different classes of defense compounds in two host pines of mountain pine beetle. Tree Physiology 37(3): 338–350. doi:10.1093/treephys/tpw105

Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najar, A., and Evenden, M. 2014. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naïve host ecosystem. New Phytologist, 201(3): 940–950. doi:10.1111/nph.12573

Evenden, M.L., Whitehouse, C.M., and Sykes, J. 2014. Factors influencing flight capacity of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). Environmental Entomology, 43(1): 187–196. doi:10.1603/EN13244

Fettig, C.J., Gibson, K.E., Munson, A.S., and Negrón, J.F., 2014. Cultural practices for prevention and mitigation of mountain pine beetle infestations. Forest Science, 60(3): 450–463. doi:10.5849/forsci.13-032

Fettig, C.J. and Hilszczański, J. 2015. Management strategies for bark beetles in conifer forests. *In* Vega, F.E., and Hofstetter, R.W. (Eds.), Bark beetles: biology and ecology of native and invasive species. (1st ed., p. 555–584). doi:10.1016/B978-0-12-417156-5.00014-9

Fielding, N.J., Evans, H.F., Williams, J.M., and Evans, B. 1991. Distribution and spread of the great European spruce bark beetle, *Dendroctonus micans*, in Britain–1982 to 1989. Forestry: An International Journal of Forest Research, 64(4): 345–358. doi:10.1093/forestry/64.4.345

Finney, M.A. 2005. The challenge of quantitative risk analysis for wildland fire. Forest Ecology and Management, 211(1–2): 97–108. doi:10.1016/j.foreco.2005.02.010

Forrest, G.I. 1980. Geographical variation in the monoterpenes of Pinus contorta oleoresin. Biochemical Systematics and Ecology, 8(4): 343–359. doi:10.1016/0305-1978(80)90037-x

Furniss, M., and Schenk, J. 1969. Sustained natural infestations by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. Journal of Economic Entomology, 62(2): 518–519.

Furniss, M.M., and Furniss, R.L. 1972. Scolytids (Coleoptera) on snowfields above timberline in Oregon and Washington. The Canadian Entomologist, 104(9): 1471–1478. doi:10.4039/Ent1041471-9

Gagné J., Zayat, M.A. and Nisbet, D. 2017. Firewood pathway analysis for Canada. Prepared for the Forest Pest Working Group–Canadian Council of Forest Ministers. Invasive Species Centre, Sault Ste. Marie, Ontario. Available from: https://www.ccfm.org/pdf/2017-FirewoodPathwayAnalysis.pdf

Garrett, W.M., Harold, S.J.Z., John, L.C., William, S.K., and Robert, E.K. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? [online]. Environmental Research Letters 11(4): 045008. doi:10.1088/1748-9326/11/4/045008

Geiszler, D.R. and Gara, R.I. 1978. Mountain pine beetle attack dynamics in lodgepole pine. *In* Symposium proceedings: theory and practice of mountain pine beetle management in lodgepole pine forests. April 25–27, 1978. Edited by A.A. Berryman, G.D. Amman and R.W.

Stark. Pullman WA. Moscow, Idaho. University of Idaho, Forest, Wildlife and Range Experiment Station. p. 182–187.

Gillette, N. E., Wood, D.L., Hines, S.H., Runyon, J.B., and Negrón, J.F. 2014. The once and future forest: consequences of mountain pine beetle treatment decisions. Forest Science, 60(3): 527–538. doi:10.5849/forsci.13-040

Gillis, M., Omule, A., and Brierley, T. 2005. Monitoring Canada's forests: The National Forest Inventory. Forestry Chronicle, 81(2): 214–221. doi: 10.5558/tfc81214-2

Girardin, M.P., Hogg, E.H., Bernier, P.Y., Kurz, W.A., Guo, X.J., and Cyr, G. 2016. Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Global Change Biology, 22(2): 627–643. doi:10.1111/gcb.13072

Goodsman, D.W., Grosklos, G., Aukema, B.H., Whitehouse, C., Bleiker, K.P., McDowell, R.S., and Xu, C. 2018. The effect of warmer winters on the demography of an outbreak insect is hidden by intraspecific competition. Global Change Biology, 24(8): 3620–3628. doi:10.1111/gcb.14284

Government of British Columbia, Forest Practices Branch (2016). Mountain Pine Beetle Projections [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/forest-pests/bark-beetles/mountain-pine-beetle/mpb-projections

Government of Saskatchewan. 2018. Forestry in Saskatchewan [online]. Saskatchewan Forestry Development Branch. Available from http://publications.gov.sk.ca/documents/310/104973-Forestry%20Information%20Factsheet.pdf

Graf, M., Reid, M.L., Aukema, B.H., and Lindgren, B.S. 2012. Association of tree diameter with body size and lipid content of mountain pine beetles. The Canadian Entomologist, 144(3): 467–477. doi:10.4039/tce.2012.38

Gupta, J., Termeer, C., Klostermann, J., Meijerink, S., van den Brink, M., Jong, P., Nooteboom, S., and Bergsma, E. 2010. The adaptive capacity wheel: a method to assess the inherent characteristics of institutions to enable the adaptive capacity of society. Environmental Science and Policy, 13(6): 459–471. doi:10.1016/j.envsci.2010.05.006

Hansen, E.M., 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science, 60(3): 476–488. doi:10.5849/forsci.13-039

Hall, D.E., Yuen, M.M.S., Jancsik, S., Lara Quesada, A., Dullat, H.K., Li, M., Henderson, H., Arango-Velez, A., Liao, N.Y., Docking, R.T., Chan, S.K., Cooke, J.EK., Breuil, C., Jones, S.JM., Keeling, C.I., and Bohlmann, J. 2013. Transcriptome resources and functional characterization of monoterpene synthases for two host species of the mountain pine beetle, lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*). BMC Plant Biology, 13(1): 80. doi:10.1186/1471-2229-13-80

Hart, S., Schoennagel, T., Veblen, T. and Chapman, T. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences, 112(14): 4375–4380. doi:10.1073/pnas.1424037112

Harvey, B.J., Donato, D.C. and Turner, M.G. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences, 111(42): 15120–15125. doi:10.1073/pnas.1411346111

Hawkins, C.D., Dhar, A., Balliet, N.A., and Runzer, K.D. 2012. Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia. Forest Ecology and Management, 277: 107–115.

Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., and Vogelmann, J., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biology, 18(1): 7–34. doi:10.1111/j.1365-2486.2011.02543.x

Hiratsuka, Y., Cerezke, H.F., Moody, B.H., Petty, J., and Still, G.N. 1982. Forest insect and disease conditions in Alberta, Saskatchewan, Manitoba, and the Northwest Territories in 1981 and Predictions for 1982. Environment Canada, Canadian Forest Service, Edmonton, Alberta. Information Report NOR-X-239. Available from http://cfs.nrcan.gc.ca/publications/download-pdf/11784

Hiratsuka, Y., Cerezke, H.F., Petty, J.A., and Still, G.N. 1981. Forest insect and disease conditions in Alberta, Saskatchewan, Manitoba, and the Northwest Territories in 1980 and predictions for 1981. Environment Canada, Canadian Forest Service, Edmonton, Alberta. Information Report NOR-X-231. Available from http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/11783.pdf

Hodge, J.C. 2012. Mountain pine beetle pest risk analysis for Yukon lodgepole pine forests. Contract report for Yukon Forest Management Branch, Whitehorse, Yukon, Canada.

Hodge, J.C. 2014. Mountain pine beetle pest risk analysis for Northwest Territories pine forests. Contract report for NWT Forest Management Division, Fort Smith, Northwest Territories, Canada.

Hodge, J.C., Cooke, B.J., and McIntosh, R. 2017. A strategic approach to slow the spread of mountain pine beetle across Canada. Draft report prepared for the Forest Pest Working Group of the Canadian Council of Forest Ministers. Available from https://www.ccfm.org/pdf/2017-MPBStrategicContainmentApproach.pdf

Huber, D.P.W., Aukema, B.H., Hodgkinson, R.S., and Lindgren, B.S. 2009. Successful colonization, reproduction, and new generation emergence in live interior hybrid spruce *Picea engelmannii* x *glauca* by mountain pine beetle *Dendroctonus ponderosae*. Agricultural and Forest Entomology, 11(1): 83–89. doi:10.1111/j.1461-9563.2008.00411.x

Jackson, P.L., Straussfogel, D., Lindgren, B.S., Mitchell, S., and Murphy, B. 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. Canadian Journal of Forest Research, 38(8): 2313–2327. doi:10.1139/X08-066

Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., and Bentz, B.J. 2014. Interactions among the mountain pine beetle, fires, and fuels. Forest Science, 60(3): 489–501. doi:10.5849/forsci.13-017

Keefover-Ring, K., Trowbridge, A., Mason, C.J., and Raffa, K.F. 2016. Rapid induction of multiple terpenoid groups by ponderosa pine in response to bark beetle-associated fungi. Journal of Chemical Ecology, 42(1): 1–12. doi:10.1007/s10886-015-0659-6

Keeling, C.I., and Bohlmann, J. 2006. Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens. New Phytologist 170(4): 657–75. doi:10.1111/j.1469-8137.2006.01716.x

Kerner, D.A., and Thomas, J. S. 2014. Resilience attributes of social-ecological systems: framing metrics for management. Resources, 3(4): 672–702. doi:10.3390/resources3040672

Klutsch, J.G., Battaglis, M.A., West, D.R., Costello, S.L., and J.F. Negrón. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. Western Journal of Applied Forestry, 26(3): 101–109.

Klutsch, J.G., Cale, J.A., Whitehouse, C., Kanekar, S.S., and Erbilgin, N. 2017. Trap tree: an effective method for monitoring mountain pine beetle activities in novel habitats. Canadian Journal of Forest Research, 47: 1432-1437.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., and Weed, A.S. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecology and Management, 380: 321–334. doi:10.1016/j.foreco.2016.04.051

Krishnaswamy, A., Simmons, E., and Joseph, L. 2012. Increasing the resilience of British Columbia's rural communities to natural disturbances and climate change. BC Journal of Ecosystems and Management, 13(1): 1–15. Available from http://jem-online.org/index.php/jem/article/view/168

Kulakowski, D. and Veblen, T. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology, 88(3): 759–769. doi:10.1890/06-0124

Kulig, J., and Botey, A. P. 2016. Facing a wildfire: what did we learn about individual and community resilience? Natural Hazards, 82(3): 1919–1929. doi:10.1007/s11069-016-2277-1

Kunegel-Lion, M., McIntosh, R.L., and Lewis, M.A. 2019. Management assessment of mountain pine beetle infestation in Cypress Hills, SK. Canadian Journal of Forest Research, 49: 154–163.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature, 452(7190): 987–990. doi:10.1038/nature06777

Kurz, W.A., Shaw, C.H., Boisvenue, C., Stinson, G., Metsaranta, J., Leckie, D., Dyk, A., Smyth, C., and Neilson, E.T., 2013. Carbon in Canada's boreal forest—a synthesis. Environmental Reviews, 21(4): 260–292. doi:10.1139/er-2013-0041

Lahr, E.C. and Sala, A. 2014. Species, elevation, and diameter affect whitebark pine and lodgepole pine stored resources in the sapwood and phloem: implications for bark beetle outbreaks. Canadian Journal of Forest Research, 44(11): 1312–1319. doi:10.1139/cjfr-2014-0063

Langor, D.W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). The Canadian Entomologist, 121(1): 149–157. doi:10.4039/Ent121149-2

Langor, D.W., Spence, J.R., and Pohl, G.R. 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Evolution, 44(3): 609–618. doi:10.2307/2409438

Lewis, K. and Thompson, D. 2011. Degradation of wood in standing lodgepole pine killed by mountain pine beetle. Wood and Fiber Science, 43(2): 130–142.

Lewis, K.J., Hrinkevich, K. 2013. Post mortality rate of wood degradation and tree fall in lodgepole pine trees killed by mountain pine beetle in the Foothills and Rocky Mountain Regions of Alberta. Final Report for Foothills Research Institute. 29 p. https://friresearch.ca/sites/default/files/MPBEP_2013_01_shelf%20life%20MPB%20killed%20pine.pdf

Logan, J., and Powell, J. 2001. Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist, 47(3): 160–172. doi:10.1093/ae/47.3.160

Logan, J. A., White, P., Bentz, B.J., and Powell, J.A. 1998. Model analysis of the temporal evolution of spatial patterns in mountain pine beetle outbreaks. Theoretical Population Biology 53(3): 236–255. doi:10.1006/tpbi.1997.1350

Lusebrink, I., Erbilgin, N., and Evenden, M.L. 2016. The effect of water limitation on volatile emission, tree defense response, and brood success of *Dendroctonus ponderosae* in two pine hosts, lodgepole, and jack pine [online]. Frontiers in Ecology and Evolution 4: 2. doi:10.3389/fevo.2016.00002

Lusebrink, I., Evenden, M. L., Blanchet, F. G., Cooke, J. E., and Erbilgin, N. 2011. Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. Journal of Chemical Ecology, 37(9): 1013–1026. doi:10.1007/s10886-011-0008-3

Magis, K. 2010. Community resilience: an indicator of social sustainability. Society & Natural Resources, 23(5): 401–416. doi:10.1080/08941920903305674

Maurer, G.E., Chan, A.M., Trahan, N.A., Moore, D.J.P., and Bowling, D.R. 2016. Carbon isotopic composition of forest soil respiration in the decade following bark beetle and stem girdling disturbances in the Rocky Mountains. Plant, Cell & Environment, 39(7): 1513–1523. doi:10.1111/pce.12716

McIntosh, A.C. and Macdonald, S.E. 2013. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. Forest Ecology and Management, 295: 11–19.

McKee, F.R., Huber, D.P.W., and Aukema, B.H. 2013. Comparisons of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) reproduction within a novel and traditional host: effects of insect natal history, colonized host species, and competitors. Agricultural and Forest Entomology, 15(3): 310–320. doi:10.1111/afe.12019

Meigs, G., Campbell, J., Zald, H., Bailey, J., Shaw, D., and Kennedy R. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere, 6(7): 1–24. doi:10.1890/ES15-00037.1

Moeck, H. A. and Simmons, C. S. 1991. Primary attraction of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae), to bolts of lodgepole pine. The Canadian Entomologist. 123: 299–304.

Moran, C. J., and Cochrane, M. A. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology, 93(4): 939–950. doi:10.1890/11-1035.1

Nealis, V.G. 2015. A risk analysis framework for forest pest management. The Forestry Chronicle, 91(1): 32–39. doi:10.5558/tfc2015-008

Nealis, V.G. and Cooke, B.J. 2014. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Natural Resources Canada, Canadian Forest Service, and the Canadian Council of Forest Ministers Forest Pest Working Group, Pacific Forestry Centre, Victoria, BC, Canada. Available from http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/28891.pdf

Nealis, V.G. and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Information Report BC-X-417. Victoria, British Columbia, Canada. Available from https://cfs.nrcan.gc.ca/publications/download-pdf/28891

Nelson, T., Boots, B., Wulder, M.A., Shore, T., Safrayik, L., and Ebata, T. 2006. Rating the susceptibility of forests to mountain pine beetle infestation: the impact of data. Canadian Journal of Forest Research, 36(11): 2815–2825. doi:10.1139/x06-163

Nelson, M., Ciochina, M., and Bone, C. 2016. Assessing spatiotemporal relationships between wildfire and mountain pine beetle disturbances across multiple time lags. Ecosphere, 7(10): 1–16. doi:10.1002/ecs2.1482

Nicholls, D. 2017. Quesnel timber supply area: rationale for Allowable Annual Cut (AAC) determination. Effective June 16, 2017. British Columbia Ministry of Forests, Lands, and Natural Resource Operations Report. Available from https://www2.gov.bc.ca/assets/gov/farming-natural-resources-and-industry/forestry/stewardship/forest-analysis-inventory/tsr-annual-allowable-cut/quesnel_tsa_rationale.pdf

Oboite, F.O. and Comeau, P.G. 2018. Release response of black spruce and white spruce following overstory lodgepole pine mortality due to mountain pine beetle attack. Forest Ecology and Management, 432: 446–454. doi: 10.1016/j.foreco.2018.09.029

O'Halloran, T.L., Law, B.E., Goulden, M.L., Wang, Z., Barr, J.G., Schaaf, C., Brown, M., Fuentes, J.D., Göckede, M., Black, A., and Engel, V. 2011. Radiative forcing of natural forest disturbances. Global Change Biology, 18(2): 555–565. doi:10.1111/j.1365-2486.2011.02577.x

Parkins, J.R. and MacKendrick, N. A. 2007. Assessing community vulnerability: a study of the mountain pine beetle outbreak in British Columbia, Canada. Global Environmental Change, 17(3–4): 460–471.

Perrakis, D., Lanoville, R., Taylor, S., and Hicks, D. 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia, Canada. Fire Ecology, 10(2): 10–35. doi:10.4996/fireecology.1002010

Pfeifer, E.M., Hicke, J.A., Meddens, A.J.H., 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. Global Change Biology, 17(1): 339–350. doi: 10.1111/j.1365-2486.2010.02226.x

Phillips, B., Beck, J., and Nickel, T. 2007. Managing the economic impacts of mountain pine beetle outbreaks in Alberta—foothills model forest case study. Information Bulletin No. 100. Western Centre for Economic Research, University of Alberta, Edmonton, Alberta, Canada.

Pokorny, S., and Carroll, A. 2018. Persistence or extinction? Quantifying the fate of an eruptive herbivore in novel habitats following climate change-induced range expansion. Abstract for a presentation at the Joint Meeting of the Entomological Societies of America, Canada, and British Columbia. 11–14November 2018, Vancouver, British Columbia, Canada. https://esa.confex.com/esa/2018/meetingapp.cgi/Paper/132842

Powell, J.A., and Bentz, B.J. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. Landscape Ecology, 24(2): 657–672. doi:10.1007/s10980-009-9340-1

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H., 2008. Cross-scale drivers of natural disturbances: the dynamics of bark beetle eruptions. Bioscience, 58(6): 501–517. doi:10.1641/B580607

Raffa, K.F., and Berryman, A.A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs 53(1): 27–50. doi:10.2307/1942586

Raffa K.F., Powell E.N., and Townsend P.A. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. Proceedings of the National Academy of Sciences, 110(6): 2193–2198. doi:10.1073/pnas.1216666110

Raffa, K.F., Mason, C.J., Bonello, P., Cook, S., Erbilgin, N., Keefover-Ring, K., Klutsch, J.G., Villan, C., and Townsend, P.A. 2017. Defence syndromes in lodgepole–whitebark pine ecosystems relate to degree of historical exposure to mountain pine beetles. Plant, Cell and Environment, 40(9): 1791–1806. doi:10.1111/pce.12985

Raymond, C.L., Healey, S., Peduzzi, A., and Patterson, P. 2015. Representative regional models of post-disturbance forest carbon accumulation: integrating inventory data and a growth and yield model. Forest Ecology and Management, 336: 21–34. doi:10.1016/j.foreco.2014.09.038

Reed, D.E.R., Ewers, B.E. and Pendall, E. 2014. Impact of mountain pine beetle induced mortality on forest carbon and water fluxes [online]. Environmental Research Letters 9(10): 105004. doi:10.1088/1748-9326/9/10/105004

Régnière, J., and Bentz., B.J. 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. Journal of Insect Physiology, 53(6): 559–572. doi:10.1016/j.jinsphys.2007.02.007

Régnière, J., Powell, J., Bentz, B., and Nealis, V. 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. Journal of Insect Physiology, 58(5): 634–647. doi:10.1016/j.jinsphys.2012.01.010

Reid, M.L., Sekhon, J.K., and LaFramboise, L. 2017. Toxicity of monoterpene structure, diversity and concentration to mountain pine beetles, *Dendroctonus ponderosae*: beetle traits matter more. Journal of Chemical Ecology, 43(4): 351–361. doi: 10.1007/s10886-017-0824-1

Reid, R.W., and Gates, H. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). The Canadian Entomologist, 102(5): 617–622. doi:10.4039/Ent102617-5

Robertson, C., Nelson, T.A., and Boots, B. 2007. Mountain pine beetle dispersal: the spatial-temporal interaction of infestations. Forest Science, 53(3): 395–405.

Rosenberger, D.W., Venette, R.C., and Aukema, B.H. 2018. Development of an aggressive bark beetle on novel hosts: implications for outbreaks in an invaded range [online]. Journal of Applied Ecology, 55(3): 1526–1535. doi:10.1111/1365-2664.13064

Rosenberger, D.W., Venette, R.C., Maddox, M.P., and Aukema, B.H. 2017. Colonization behaviors of mountain pine beetle on novel hosts: implications for range expansion into northeastern North America [online]. PlOS One, 12(5): e0176269. doi:10.1371/journal.pone.0176269

Roth, M., Hussain, A., Cale, J.A., and Erbilgin, N. 2018. Successful colonization of lodgepole pine trees by mountain pine beetle increased monoterpene production and exhausted carbohydrate reserves. Journal of Chemical Ecology, 44(2): 209–214. doi:10.1007/s10886-017-0922-0

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. *In* Symposium Proceedings: Theory and practice of mountain pine beetle management in lodgepole pine forests. April 25–27, 1978. Edited by D.L. Kibbee, A.A. Berryman, G.D. Amman and R.W. Stark. Washington State University, Pullman, Washington. College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho.

Safranyik, L., and Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In* The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Edited by L. Safranyik and W.R. Wilson. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada. p. 3–66.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist, 142(5): 415–442. doi:10.4039/n08-CPA01

Safranyik, L., and Linton, D. 1982. Survival and development of mountain pine beetle broods in jack pine bolts from Ontario. Canadian Forest Service Research Notes, 2: 17–18.

Safranyik, L. and Linton, D.A. 1983. Brood production by three spp. of *Dendroctonus* (Coleoptera: Scolytidae) in bolts from host and non-host trees. Journal of the Entomological Society of British Columbia, 80: 10–13.

Safranyik, L. and Linton, D.A. 1991. Unseasonably low fall and winter temperatures affecting mountain pine beetle and pine engraver beetle populations and damage in the British Columbia Chilcotin region. Journal of the Entomological Society of British Columbia, 88: 17–21.

Safranyik, L. and Linton, D.A. 1998. Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia, 95: 81–87.

Safranyik, L., Linton, D.A., Silversides, R., McMullen, L.H. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology, 113(1–5): 441–450.

Safranyik, L., Shrimpton, D., and Whitney, H. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. *In* Management of lodgepole pine ecosystems, Proceedings of a symposium held 9–11 October 1973. Edited by D.M. Baumgartner. Washington State University, Pullman, Washington, United States of America. p. 406–428.

Sambaraju, K.R., Carroll, A.L., Zhu, J., Stahl, K., Moore, R.D., and Aukema, B.H. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. Ecography, 35(3): 211–223. doi:10.1111/j.1600-0587.2011.06847.x

Seidl, R., Donato, D.C., Raffa, K.F., and Turner, M.G., 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proceedings of the National Academy of Sciences, 113(46): 13075–13080. doi:10.1073/pnas.1615263113

Shepherd, R.F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). The Canadian Entomologist, 98(5): 507–518. doi:10.4039/Ent98507-5

Shore, T., and Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada. Available from https://cfs.nrcan.gc.ca/publications/download-pdf/3155

Shore, T.L., Safranyik, L., and Lemieux J.P. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Canadian Journal of Forest Research, 30(1): 44–49. doi:10.1139/x99-182

Simard, M., Romme, W., Griffin, J. and Turner, M. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs, 81(1): 3–24. doi:10.1890/10-1176.1

Six, D.L., Biber, E., and Long. E. 2014. Management for mountain pine beetle outbreak suppression: does relevant science support current policy? Forests, 5(1):103–133 doi:10.3390/f5010103

Six, D.L., Vergobbi, C., and Cutter, M. 2018. Are survivors different? Genetic-based selection of trees by mountain pine beetle during a climate change-driven outbreak in a high-elevation pine forest. Frontiers in Plant Science, 9: 1–11. doi:10.3389/fpls.2018.00993

Smith, R.H. 1983. Monoterpenes of lodgepole pine xylem resin: a regional study in western United States. Forest Science, 29(2): 333–340.

Smith, R.H., Cramer, J.P., and Carpender, E.J. 1981. New record of introduced hosts for the mountain pine beetle in California. United States Forest Service Research Note PSW-354.

Stinson, G., Kurz, W.A., Smyth, C.E., Neilson, E.T., Dymond, C.C., Metsaranta, J.M., Boisvenue, C., Rampley, G.J., Li, Q., White, T.M., and Blain, D., 2011. An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. Global Change Biology, 17(6): 2227–2244. doi:10.1111/j.1365-2486.2010.02369.x

Stinson, G., Magnussen, S., Boudewyn, P., Eichel, F., Russo, G., Cranny, M., and Song, A. 2016. Canada. *In* National forest inventories: assessment of wood availability and use. Edited by C. Vidal, I Alberdi, L., Hernández Mateo., and J. Springer Redmond. Springer, Cham, Switzerland. p. 233–247. doi:10.1007/978-3-319-44015-6_12

Strohm, S., Reid M.L., and Tyson, R.C. 2016. Impacts of management on mountain pine beetle spread and damage: a process-rich model. Ecological Modelling, 337:241-252. doi: 10.1016/j.ecolmodel.2016.07.010

Sturgeon, K.B. 1979. Monoterpene variation in ponderosa pine xylem resin related to western pine beetle predation. Evolution, 33(3): 803–814. doi:10.1111/j.1558-5646.1979.tb04736.x

Taft, S., Najar, A., Godbout, J., Bousquet, J., and Erbilgin, N. 2015. Variations in foliar monoterpenes across the range of jack pine reveal three widespread chemotypes: implications to host expansion of invasive mountain pine beetle. Frontiers in Plant Science, 6: 342. doi:10.3389/fpls.2015.00342

Thornes, J.E. 2002. Climate change 2001: impacts, adaptation and vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Edited by McCarthy, J.J., Canziani, O.F., Leary N.A., Dokken, D.J., and White, K.S. International Journal of Climatology, 22(10), 1285–1286.

Troy, A. and Bagstad, K. 2009. Estimating ecosystem service values in southern Ontario. Prepared for the Ontario Ministry of Natural Resources. Spatial Informatics Group, Pleasanton, USA. Available from: http://longpointbiosphere.com/download/Environment/estimation-of-ecosystem.pdf

Trzcinski, M.K., and Reid, M.L., 2008. Effect of management on the spatial spread of mountain pine beetle (*Dendroctonus ponderosae*) in Banff National Park. Forest Ecology and Management, 256(6): 1418–1426. doi:10.1016/j.foreco.2008.07.003

Tyler, S., and Moench, M. 2012. A framework for urban climate resilience. Climate and Development, 4(4): 311–326. doi:10.1080/17565529.2012.745389

von Rudloff, E., and Lapp, M.S. 1987. Chemosystematic studies in the genus *Pinus*. VI. General survey of the leaf oil terpene composition of lodgepole pine. Canadian Journal of Forest Research, 17(9): 1013–1025. doi:10.1139/x87-157

Walker, B., Holling, C., Carpenter, S., and Kinzig, A. 2004. Resilience, adaptability and transformability in social-ecological systems [online]. Ecology and Society, 9(2): 5. Available from http://www.ecologyandsociety.org/vol9/iss2/art5/

West, D.R., Briggs, J.S., Jacobi, W.R., and Negrón, J.F. 2016. Mountain pine beetle host selection between lodgepole and ponderosa pines in the southern Rocky Mountains. Environmental Entomology, 45(1): 127–141. doi:10.1093/ee/nvv167

Williamson, T.B., Price, D.T., Beverly, J.L., Bothwell, P.M., Parkins, J.R., Patriquin, M.N., Pearce, C.V., Stedman, R.C., and Volney, W.J.A. 2007. A framework for assessing vulnerability of forest-based communities to climate change. Information Report NORX414. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.

Wood, D.L. 1982. The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, 27(1): 411–446. doi:10.1146/annurev.en.27.010182.002211

Wood, S.L. 1963. A revision of bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Naturalist, 23: 1–117. doi:10.5962/bhl.part.22188

Wulder, M.A.; Ortlepp, S.M.; White, J.C.; Coops, N.C.; Coggins, S.B. 2009a. Monitoring the impacts of mountain pine beetle mitigation. Forest Ecology and Management, 258(7): 1181–1187.

Wulder, M.A., White, J.C., Carroll, A.L., Coops, N.C., 2009b. Challenges for the operational detection of mountain pine beetle green attack with remote sensing. The Forestry Chronicle, 85(1): 32–38. doi: 0.5558/tfc85032-1

Yan, Z., Sun, J., Owen, D., and Zhang, Z. 2005. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodiversity and Conservation, 14: 1735-1760. doi: 10.1007/s10531-004-0697-9

Yemshanov, D., McKenney, D.W., and Pedlar, J.H. 2011. Mapping forest composition from the Canadian National Forest Inventory and land cover classification maps. Environmental Monitoring and Assessment, 184(8): 4655–4669. doi:10.1007/s10661-011-2293-2