Potential for range expansion of mountain pine beetle into the boreal forest of North America

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Abstract—The potential for mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), to expand its historical range in North America from west of the continental divide into the eastern boreal forest was assessed on the basis of analyses of the effects of climate and weather on brood development and survival, and key aspects of the interaction of mountain pine beetle with its hosts and associated organisms. Variation in climate suitability and high host susceptibility in the boreal forest create a finite risk of establishment and local persistence of low-level mountain pine beetle populations outside their historical range. Eventually, these populations could become widespread and cause epidemic infestations, creating an ecological pathway eastward through the boreal forest. Such infestations would reduce the commercial value of forests and impose an additional disturbance on native ecological systems.

Résumé—L'évaluation du potentiel d'expansion de l'aire historique de répartition du dendroctone du pin ponderosa, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), à partir de l'ouest de la ligne continentale de partage des eaux vers la forêt boréale de l'est est basée sur des analyses des effets du climat et des conditions météorologiques sur le développement et la survie du couvain et des aspects essentiels de l'interaction entre le dendroctone du pin ponderosa et ses hôtes et les organismes associés. La variabilité des conditions climatiques favorables et la forte vulnérabilité des hôtes dans la forêt boréale créent un risque fini d'un établissement éventuel et de la persistance de populations locales de faible densité du dendroctone du pin ponderosa hors de son aire historique de répartition. Ces

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populations pourraient éventuellement atteindre des répartitions étendues et causer des infestations épidémiques, en créant un passage écologique vers l'est à travers la forêt boréale. De telles infestations diminueraient la valeur commerciale des forêts et ajouteraient une perturbation supplémentaire aux systèmes écologiques indigènes.

[Traduit par la Rédaction]

Introduction

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is a native bark beetle of western North America. Populations are normally innocuous, infesting only a few damaged, decadent, or suppressed trees. However, populations occasionally erupt into large-scale outbreaks, making mountain pine beetle the most destructive biotic agent of mature pine (Pinaceae) forests in western North America (Safranyik and Carroll 2006). The historical range of mountain pine beetle (pre-2000) extends from northern Mexico (latitude 31°N) to central British Columbia in Canada (latitude 56°N), and from the Pacific Coast to the Black Hills of South Dakota in the United States of America. Although the distribution of the beetle is extensive, it includes only the southern portion of the current range of the main host, lodgepole pine (*Pinus contorta* Douglas *ex* Louden var. *latifolia* Engelm. *ex* S. Watson). Thus, the range of mountain pine beetle has not been limited in the north by the availability of lodgepole pine (Fig. 1).

Mountain pine beetle can successfully attack and reproduce in 22 species of *Pinus* L., including 4 species not native to North America (Furniss and Schenk 1969; Smith *et al.* 1981; Amman and Cole 1983). In western Canada the beetle infests principally lodgepole pine but also four other native pine species: western white pine, *P. monticola* Douglas *ex* D. Don; ponderosa pine, *P. ponderosa* C. Lawson; whitebark pine, *P. albicaulis* Engelm.; and limber pine, *P. flexilis* James. At least six eastern species of North American pine have also been attacked in arboreta in the western United States of America (Furniss and Schenk 1969), including eastern white pine, *P. strobus* L.; pitch pine, *P. rigida* Mill.; red pine, *P. resinosa* Aiton; and jack pine, *P. banksiana* Lamb. Only Jeffrey pine, *P. jeffreyi* Balf., appears to be unsuitable as a host. Mountain pine beetle has also been occasionally recorded attacking other conifers such as firs (*Abies* Mill.) and spruces (*Picea* A. Dietr.), but successful reproduction is not normally observed in non-pine hosts (Beal 1939; Evenden *et al.* 1943; Furniss and Schenk 1969). Nonetheless, during the extreme outbreaks that occurred in Canada in the last decade of the 20th century and the first decade of the 21st century, successful reproduction within interior hybrid spruce, *P. engelmannii* Parry *ex* Engelm. × *glauca* (Moench) Voss (Huber *et al.* 2009), and black spruce, *Picea mariana* (Mill.) Britton, Stearns and Poggenb., has been observed (D. Langor, unpublished data).

Large-scale outbreaks of mountain pine beetle cause mortality of hundreds of millions of trees over large areas (Safranyik and Carroll 2006). Extensive tree mortality has an impact on a variety of forest values, including timber supply and wildlife habitat, can force dramatic changes in the forest industry (Safranyik *et al.* 1974; McGregor 1985), and in extreme cases converts large forested landscapes from carbon sinks to carbon sources (Kurz *et al.* 2008). The most extensive recorded outbreaks have occurred in the southern interior of British Columbia (Unger 1993) and the Rocky Mountain states of the United States of America (Amman and Cole 1983). Occasionally, small satellite infestations (indicated by clusters of dead trees) have developed at distances of up to approximately 100 km from large infestations within the the beetle's historical range. These satellite populations typically do not persist for more than 1 or 2 years (*e.g.*, Powell 1966), although one such infestation in the Cypress Hills, an isolated remnant of lodgepole pine forest on the Alberta−Saskatchewan border (see Fig. 1), has persisted for nearly 30 years since its origin in the early 1980s (Cerezke and Edmond 1989).

In climatically marginal habitats, the distribution and abundance of mountain pine

Fig. 1. Historical distribution of mountain pine beetle (*Dendroctonus ponderosae*) and the distribution of lodgepole pine (*Pinus contorta*) and jack pine (*P. banksiana*); regions where lodgepole pine and jack pine hybridize are also indicated (adapted from Logan and Powell 2001).
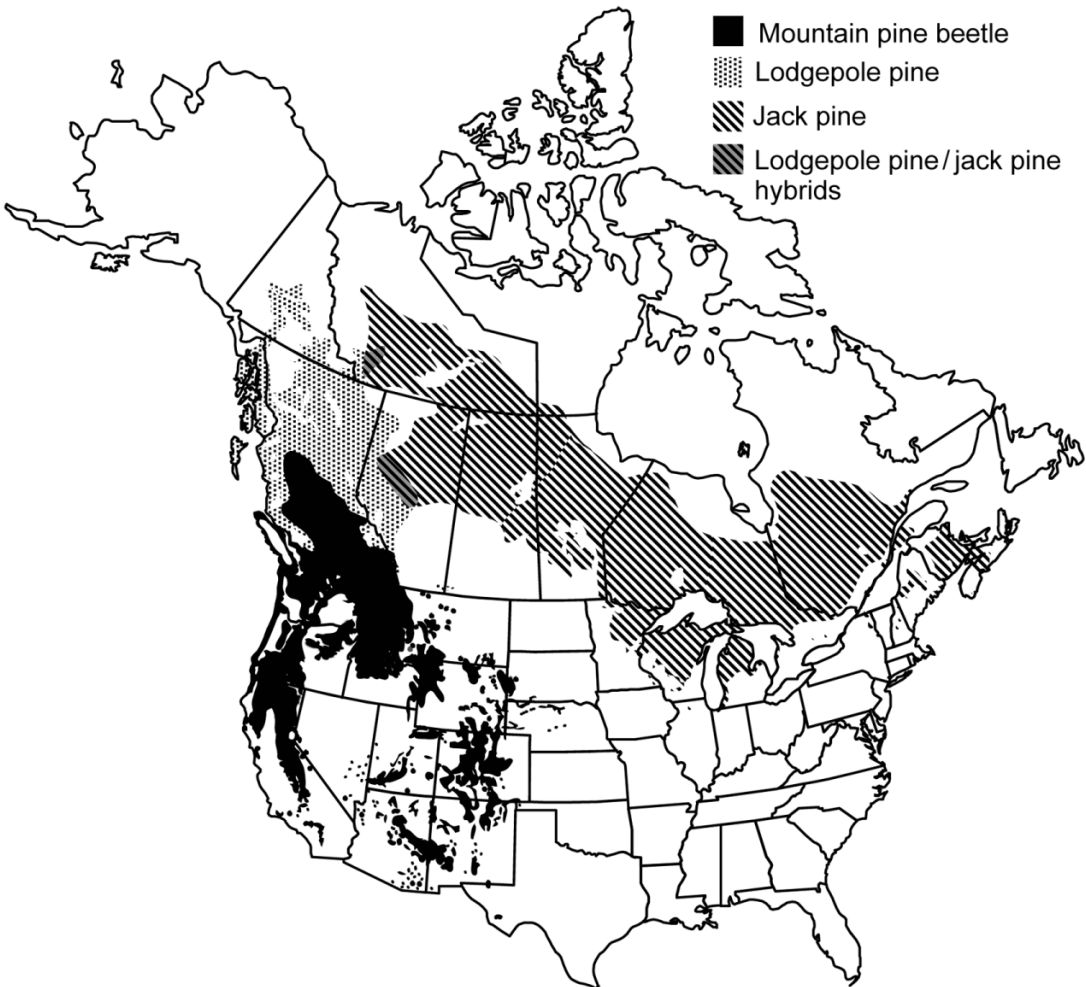

beetle populations are highly sensitive to variation in the mean annual temperature (Logan and Bentz 1999; Powell *et al.* 2000; Logan and Powell 2001). For example, Logan and Powell (2001) showed that occupation of high-elevation pine forests by epidemic beetle populations was contingent upon a relatively small increase in seasonal temperatures. These results led to speculation that the mountain pine beetle range could shift under global warming (Logan and Bentz 1999; Logan and Powell 2001). Subsequently, Carroll *et al.* (2004) found that even during non-outbreak

years, mountain pine beetle populations (as indicated by detectable infestations) have established and persisted in new areas that have become climatically suitable because of a warmer environment.

By 2008, the mountain pine beetle outbreak first noted in central British Columbia in the mid-1990s had affected a total of almost 14 million ha of pine forests (Fig. 2), an area more than $10\times$ larger than in any previously recorded outbreak. In 2004, scattered infestations were discovered along the northeastern slopes of the Rocky Mountains in the Peace River

Fig. 2. Spatial representation of the mountain pine beetle (*Dendroctonus ponderosae*) outbreak from 1999 to 2007 (*a*, *b*, *c*), and the annual area affected since 1928 (*d*) in western Canada (AB, Alberta; BC, British Columbia) (data from the Canadian Forest Service Forest Insect and Disease Survey and the British Columbia Ministry of Forests and Range).
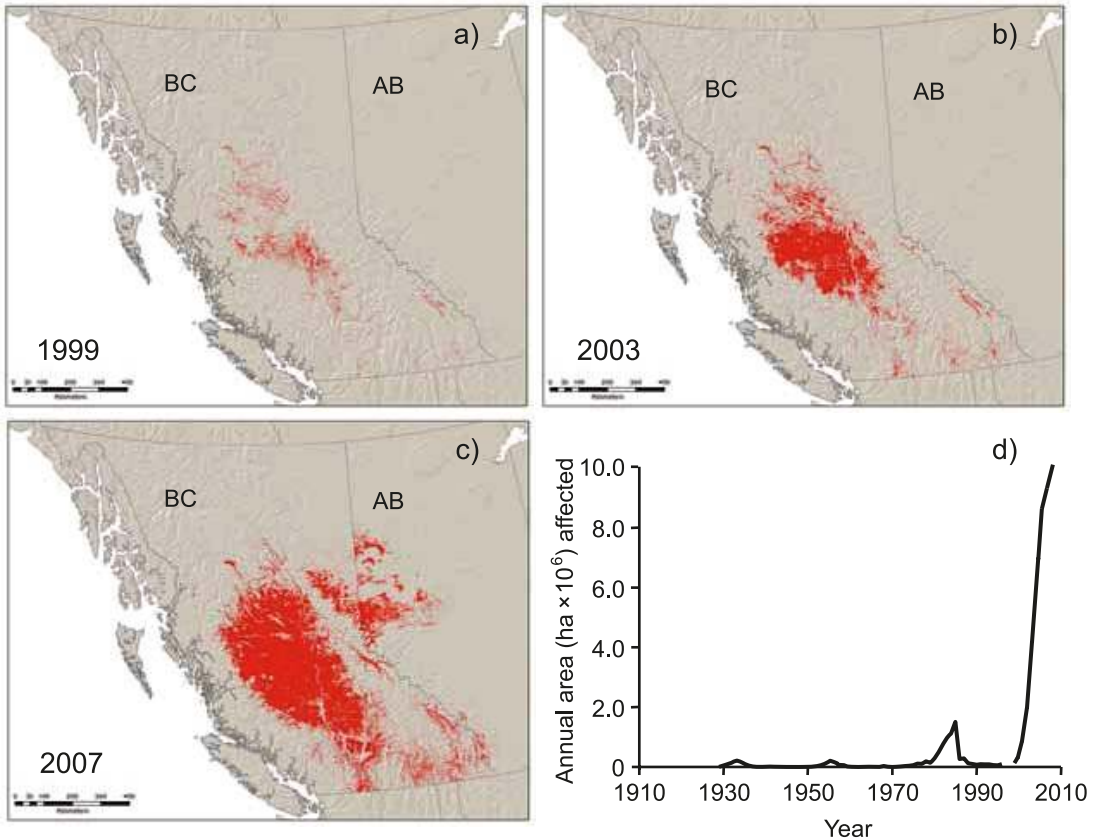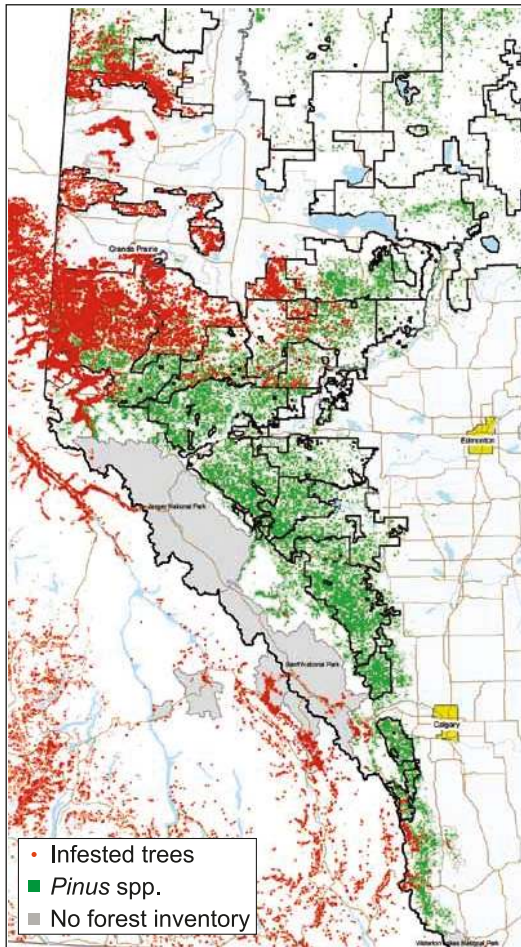

region of British Columbia, an area from which the beetle had not been previously recorded (Fig. 1). Close examination of these infestations indicated that without exception they originated in 2002, probably as a result of long-distance dispersal from outbreak populations to the west (A. Carroll, unpublished data). In 2006, dispersing beetles were detected over large areas of north-central Alberta (Alberta Sustainable Resources Development 2006), resulting in widespread infestations extending as far east as Slave Lake (Fig. 3). There seemed little doubt that these incursions by mountain pine beetle into northeastern British Columbia and adjacent Alberta resulted from long-range transport of beetles from the most intense region of the epidemic in central

British Columbia (Safranyik and Carroll 2006; Jackson *et al.* 2008). This was confirmed by genetic analysis (Bartell 2008). The rapid spread of mountain pine beetle into north-central Alberta, combined with its capacity to quickly colonize new habitats as they become climatically benign (Logan and Powell 2001; Carroll *et al.* 2004), raised concern that it may continue to spread eastward into the boreal pine forests that extend across the continent, and led to an emergency risk assessment sponsored by the Government of Canada (Nealis and Peter 2008).

The objective of this paper is to extend the risk assessment by Nealis and Peter (2008) by considering the potential of mountain pine beetle to establish and persist in the boreal

Fig. 3. Mountain pine beetle (*Dendroctonus ponderosae*) infestations in Alberta as of 2007 (data provided by Alberta Sustainable Resources).

- • Infested trees
- ■ *Pinus* spp.
- ■ No forest inventory

Methods of assessment

This assessment is based on published literature, unpublished reports, synthetic risk and susceptibility models, and expert judgement. Because much of the information on the biology and epidemiology of mountain pine beetle is related to studies conducted within its historical range, expert judgement was used to interpret the relevance of this information to the boreal forest and the relative uncertainty of conclusions regarding aspects of expected population behaviour. Our main focus is on the effects of a warming environment on the climate suitability of the boreal forest for mountain pine beetle. However, because the establishment and persistence of an invasive species are also contingent upon trophic interactions in the new habitat, we also focus on evaluating interactions of mountain pine beetle with its associated organisms at the tree, stand, and landscape scales. We consider primarily the capacity of mountain pine beetle to exploit jack pine, because it is the most abundant and widespread pine species in close proximity to the historical range of the beetle and is closely related both biologically and ecologically to lodgepole pine. The two species hybridize naturally in the area of greatest potential risk for range expansion (see Fig. 1). We employ a series of models to inform our assessment; details of these are provided in appendices.

Climate, weather, and range expansion

Climate and weather are critical determinants of the distribution and abundance of mountain pine beetle (Safranyik 1978). The ambient temperature determines the rates and limits of beetle development and, in combination with insolation and wind, is important in dispersal and host-seeking activities. Precipitation has an important effect on tree growth and vigour in terms of defensive-resin production (Franceschi *et al.* 2005; Raffa *et al.* 2005; Safranyik and Carroll 2006). Climatic conditions that most favour the persistence of mountain pine beetle infestations are (*i*) seasonal temperatures that allow synchronous

forest, based on a review and analysis of the key components of the interactions of the beetle with its biotic and abiotic environments. Specifically, we (*i*) examine the effects of weather and climate on mountain pine beetle populations and, using a moderate climate change scenario, project the distribution of suitable conditions into the near future, (*ii*) review the critical aspects of the life history and epidemiology the beetle that are expected to affect its potential to establish and persist in new habitats, (*iii*) assess the susceptibility and connectivity of potential host trees within the boreal forest, and (*iv*) examine some of the socioeconomic and ecological impacts that may result from range expansion.

Fig. 4. Historical climatic limits to the northern and eastern distribution of mountain pine beetle (*Dendroctonus ponderosae*). Data points represent the observed distribution of infestations up to and including 1970; shading indicates regions where, on average (1941–1970), there were fewer than 833 day-degrees above 5.6 °C within a growing season, and the heavy line denotes the isotherm where −40 °C occurred, on average (1941–1970), on at least 1 day each winter (data from the Canadian Forest Service Forest Insect and Disease Survey and Environment Canada's Meteorological Service).
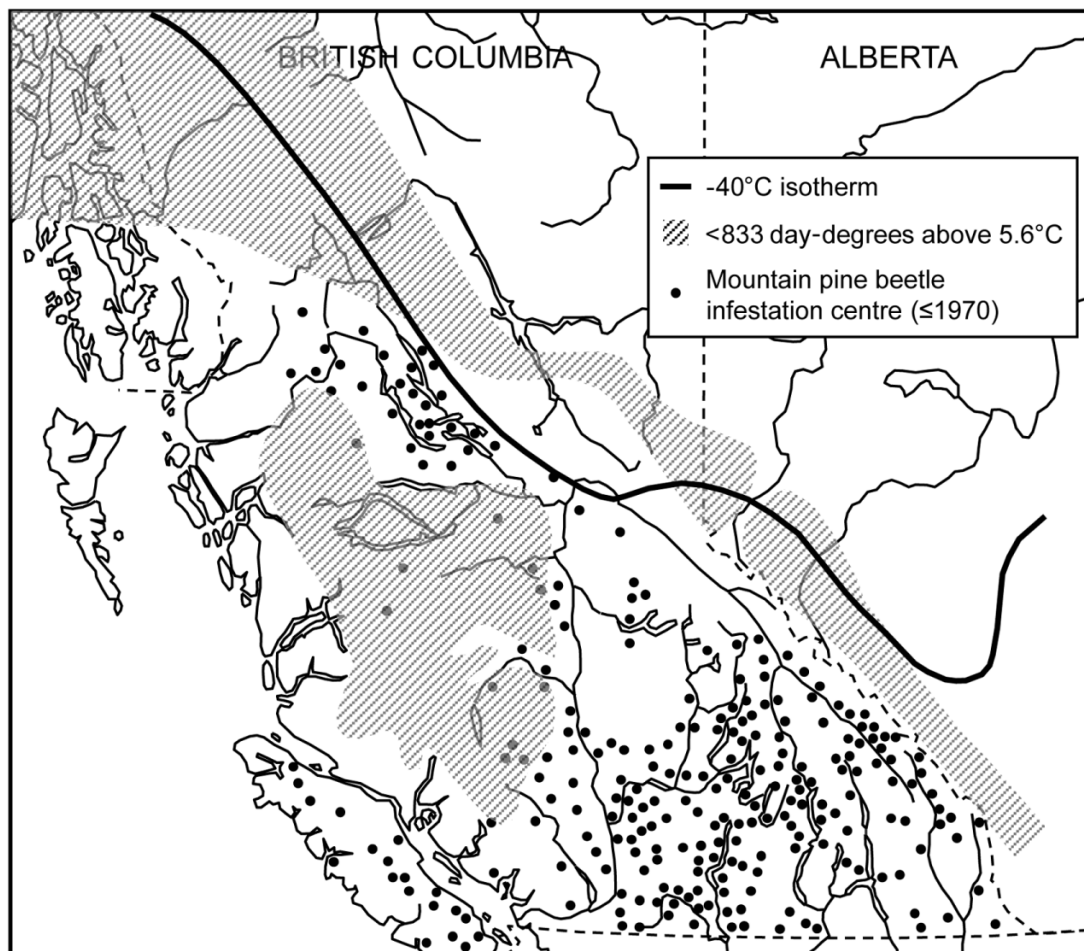
adult emergence and attack (Bentz *et al.* 1991), (*ii*) univoltine development, which allows the most cold-hardy brood stages (larvae) to enter winter (Logan and Bentz 1999), (*iii*) a mild winter, which promotes survival (Safranyik and Linton 1998; Bentz and Mullins 1999), and (*iv*) reduced moisture during the growing season, which has a negative impact on host resistance (Safranyik *et al.* 1975).

Historically, the range of mountain pine beetle has been limited by climate (Safranyik *et al.* 1975; Carroll *et al.* 2004; Aukema *et al.* 2008). Summer temperature regimes that

preclude a univoltine life cycle (Safranyik *et al.* 1975; Powell *et al.* 2000; Logan and Powell 2001) and (or) minimum winter temperatures of −40 °C or below explain much of the beetle's past distribution (Fig. 4; Safranyik *et al.* 1975; Mock *et al.* 2007). A comparison of annual surveys of mountain pine beetle infestations with maps of the historical distribution of climatically suitable habitats shows that climatic conditions have become more favourable to the mountain pine beetle over large portions of western Canada during the past 30 years (Carroll *et al.* 2004). This has

enabled populations to expand into formerly climatically unsuitable habitats, especially toward higher elevations and more northerly latitudes (Carroll *et al.* 2004). Determining the present and future climate suitability of forest landscapes is a critical aspect of quantifying the risk of continued range expansion.

Climate-suitability models

Three models were used to assess the present and future climate suitability of the North American boreal forest for the establishment and spread of mountain pine beetle populations. The Safranyik *et al.* model of climate suitability (Safranyik *et al.* 1975; Carroll *et al.* 2004) determines the joint likelihood of a univoltine life cycle, over-winter survival, optimal emergence/dispersal conditions, and the adequacy and variability of spring precipitation. The Logan *et al.* model of adaptive seasonality (Bentz *et al.* 1991; Logan and Powell 2001) estimates the likelihood of a synchronized univoltine life cycle (*i.e.*, adaptive seasonality) based on stage-specific development rates. The Régnière and Bentz model of winter mortality (Régnière and Bentz 2007) simulates cold-induced mortality of larvae based on the dynamics of the supercooling points of individuals.

The Safranyik et al. model

The Safranyik *et al.* model of climate suitability is based on six key climatic variables that jointly determine beetle attack success, development, and survival (see Appendix A, Table A1). Heat accumulation during the growing season determines areas where the beetle can complete its life cycle in one year or less. The minimum winter temperature determines the winter survival rate. The mean maximum August temperature determines the level of flight activity of attacking beetles. Three variables address the moisture balance that influences tree vigour and thus beetle attack success and brood survival. The model produces classes of climate suitability that were calibrated using historical-outbreak records from British Columbia. The basic biological assumption is that the climate-suitability classes (see Appendix A, Table A2) based on the relative frequency of joint occurrence of

these six climatic variables are close indirect measures of brood establishment and survival. Because this model was developed with reference to lodgepole pine, there is some uncertainty about whether the water-deficit conditions as expressed in the model represent a similar biological condition in jack pine in the boreal forest. Furthermore, it should be noted that the Safranyik *et al.* model does not consider completion of development in less than one year to have a negative impact on population growth.

The Logan et al. model

The main premise in the Logan *et al.* model is that predominantly univoltine seasonality is necessary for persistence of populations and development of epidemics. The model determines adaptive seasonality based on the criteria of univoltism and a stable and viable oviposition date (see Appendix B). Mountain pine beetle has no diapause to functionally synchronize populations with critical phenological events; its entire seasonal development is under direct temperature control (Logan and Bentz 1999; Logan and Powell 2001). Outside a relatively narrow optimal range, population synchrony may degrade over time. The high mortality associated with asynchrony has selected for thermal responses that increase the likelihood of synchronous adult emergence, maximize the chances of successful mass attacks, and enable broods to mature to the most cold-tolerant life stages before winter (Logan and Bentz 1999; Logan and Powell 2001).

It is generally accepted that mountain pine beetle populations that pose the greatest risk of developing into outbreak populations are characterized by a univoltine seasonality (one generation per year), with oviposition occurring in late summer (late July–August) and overwintering mostly in the larval stages (reviewed by Safranyik and Carroll 2006). Because of the absence of a diapausing life stage, slower development leads to fractional voltinism, or hemivoltinism, which means that the beetle is less well adapted (and less likely to cause outbreaks). For similar reasons, faster development is also maladaptive. Therefore, the main premise in the Logan *et al.* model is that predominantly univoltine

seasonality is necessary for the persistence of populations and development of epidemics (see Appendix B).

The Régnière and Bentz model

This model is based on the following biological assumptions: (*i*) cold-induced mortality is the largest single weather-caused factor driving the dynamics of mountain pine beetle populations (Cole 1975, 1981; Safranyik 1978; Safranyik and Carroll 2006); (*ii*) larval stages are most cold-tolerant; (*iii*) late larval instars are the most common overwintering stage in persistent populations (Amman 1973; Safranyik *et al.* 1974); and (*iv*) the supercooling point of mountain pine beetle larvae is representative of mortality induced by acute cold exposure. In response to declining temperatures during the autumn, cold-tolerance is acquired through the production of glycerol in the haemolymph (Somme 1964; Bentz and Mullins 1999). The larval stages are the most cold-tolerant, followed by adults, pupae, and eggs. The cold-tolerance of larvae increases as they develop (Amman 1973; Safranyik *et al.* 1974; Langor 1989). Lethal low temperatures for larvae range from $-23\ °C$ for first-instar larvae to $-40\ °C$ for third- and fourth-instar larvae (Logan *et al.* 1995). The supercooling point fluctuates throughout the year and by location (Bentz and Mullins 1999). A model of processes that leads to these fluctuations and determines the tolerance of a population of mountain pine beetle larvae to cold exposure was developed by Régnière and Bentz (2007) (see Appendix C).

The Régnière and Bentz model simulates mortality only of the larvae, the most cold-tolerant life stages. Thus, its predictions represent minimum mortality under the assumption of adaptive seasonality (where the larval stages represent the bulk of the overwintering population). Under climatic conditions that lead to less adaptive seasonality, actual mortality may be much higher.
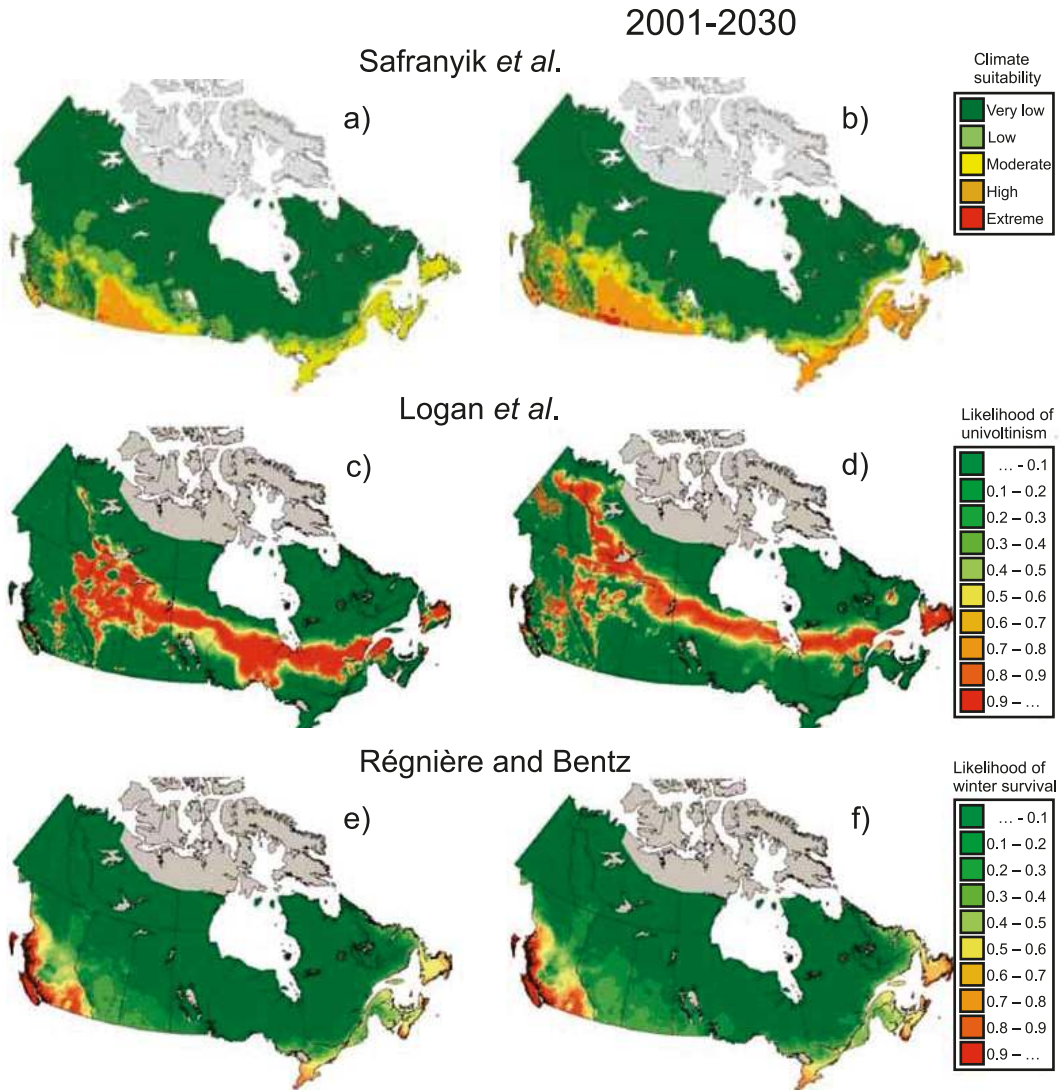
Climate data and projections

Climate-suitability projections were prepared by running the three models described above under BioSIM, a simulation environment that integrates biological models with climate and weather data to produce maps of model outputs across a landscape (Régnière 1996). BioSIM uses climate normals to generate stochastic time series of daily minimum and maximum temperatures and precipitation that closely mimic the statistical characteristics of natural weather time series (Régnière and St.-Amant 2007). Twenty thousand simulation points were distributed at random over Canada, using normals from the four weather stations nearest to each point after applying vertical, latitudinal, and longitudinal gradients by the gradient inverse distance squared method of Nalder and Wein (1998). Model runs were replicated 30 times for each point.

Two series of maps were produced by universal kriging with elevation as the external drift variable (Régnière and Sharov 1999). The first series was constructed by running the models using observed monthly climate normals for the most recent complete standard normal-generating period (1971–2000). The second series was produced from normals for the period 2001–2030 adjusted for expected climate change. To obtain these, the daily output of a global circulation model, CGCM-1 (Flato *et al.* 2000), with an annual 1% increase in CO_2 starting in 2000 (a moderate scenario) for the period 1961–2030, was used. Monthly normals for the period 1961–1990 were computed from this daily output. Deviations of these normals from the monthly mean minimum and maximum air temperatures and precipitation for each year between 2007 and 2030 were calculated (hereinafter "monthly anomalies"). The spatial resolution of these anomalies was increased by thin-plate splicing (Price *et al.* 2001). Climate-changed daily observations for the years 2007–2030 were obtained by adding monthly anomalies from the "node" nearest to each weather station in the BioSIM daily weather database from 2007 to 2030. Thus, monthly anomalies from 2007 were added to daily observations from 1967 to generate daily data for 2007, and so forth. From these climate-changed daily records, new normals were calculated for the period 2001–2030 (actual records for 2001–2007, generated records for 2007–2030).

Fig. 5. Distribution of relative climatic suitability for mountain pine beetle (*Dendroctonus ponderosae*) in the recent past (1971–2000) and the near future (2001–2030), as defined by the Safranyik *et al.*, Logan *et al.*, and Régnière and Bentz models (see the text for details).

Climate-change models predict not only gradually rising temperatures but also temperature and precipitation extremes. The simulations on which our projections are based include such extreme events.

The impact of current* versus *future climate

The spatial distribution of climatically suitable habitat produced by the Safranyik *et al.* model (Figs. 5a, 5b) is generally broad in the north–south direction in western Canada and the Maritime Provinces. Moderate to extreme climate-suitability classes occur in the hotter, drier places with mild winters, where conditions that favour beetle establishment and survival tend to occur more frequently. As expected, during the recent past (1971–2000), these conditions prevailed in southern and central British Columbia (Fig. 5a). In the remainder of Canada, however, climatically suitable areas occurred primarily to the south of the boreal pine forests, with the exception

of southern Ontario and the Maritime Provinces (see Fig. 7). In the near future (2001–2030), under a moderate climate change scenario, this pattern intensifies, with an increase in climatically suitable areas to the north (and at higher elevations), particularly in western Canada (Fig. 5b), such that the southern margins of the boreal forest become moderately suitable for increase by mountain pine beetle.

Predictions by the Logan *et al.* model for the recent past that climatic conditions conducive to adaptive seasonality will occur produced a distinctive band of climatically optimal habitat across the boreal forest (Fig. 5c). In mountainous areas (British Columbia and western Alberta) this band is intricately patterned because of the complex topography. Farther east, latitude and the influence of longitude on air-mass circulation create a long arch of suitability that coincides very well with the current distribution of pine species in the boreal forest (Fig. 7). In the near future, under climate change, the area of habitat with a high probability of adaptive seasonality is predicted to diminish and shift northward (Fig. 5d), beyond the regions with high-volume boreal pine.

The Régnière and Bentz winter-mortality model predicts that, except in south-central British Columbia and on the extreme west and east coasts, the likelihood of winter survival by mountain pine beetle is extremely low, in both the recent past (Fig. 5e) and the near future (Fig. 5f). It is important to note, however, that most mortality (see the review by Safranyik and Carroll 2006), even among epidemic populations, occurs during winter. Because of the spatial and temporal variation in mortality factors and the nature of their interactions with mountain pine beetle populations, it is not possible to provide a general winter-mortality level that would, in most situations, lead to the collapse of an infestation. But we can estimate "normal" levels of winter mortality for the beetle from its historical range, as follows. There are three main sources of variation in overall mortality, M, during a mountain pine beetle generation has three main sources: inadequate food quality and quantity (M_f), natural enemies

(M_p), and cold temperatures (M_c). To these mortality sources correspond the survival rates $S_f = 1 - M_f$, $S_p = 1 - M_p$, and $S_c = 1 - M_c$. Assuming that these are independent sources of mortality we have $S = S_f S_p S_c$. Based on Safranyik and Linton (1983) and Safranyik and Whitney (1985), mortality of a beetle generation in lodgepole pine bolts in the laboratory at constant 24 °C averaged 56%. It is presumed that this mortality rate was mainly due to the effects of food quality and abundance. Hence, $M_f = 0.56$, or $S_f = 0.44$. In southern British Columbia, total mortality to the adult stage over a 4-year period in the field averaged 93% (range 89%−97%) ($M_a = 0.93$, or $S_a = 0.07$) and the corresponding average mortality exclusive of that inflicted by woodpeckers and insect natural enemies was 86% (range 78%−94%) ($M_b = 0.86$, or $S_b = 0.14$) (Safranyik and Carroll 2006; L. Safranyik, unpublished data). Thus, an estimate of M_p can be based on the fact that $S_a = S_b S_p$. Therefore, $S_p = S_a/S_b = 0.07/0.14 = 0.5$. Assuming that zero population growth results from 97% mortality within a generation ($M = 0.97$, or $S = 0.03$; Safranyik and Carroll 2006), an estimate of mortality due to low temperatures (M_c) alone can be obtained from $S_c = S/(S_f S_p)$ and $M_c = 1 - S_c = 1 - 0.03/(0.5 \times 0.44)$, or 86.4%. Because losses of beetles during emergence and dispersal, or mortality from host resistance, were not considered (mortalities that could amount to 30%–40% of the beetles surviving to the adult stage; Cole *et al.* 1985), the threshold winter mortality from low temperatures that, on average, would prevent population growth would be near 80%. Reinterpretation of the Régnière and Bentz winter-mortality model in light of this calculation (*i.e.*, suitable regions are those where the likelihood of winter survival is >0.2) indicates that the pattern of its predictions is very similar to that of the Safranyik *et al.* model for both the recent past and the near future (see Figs. 5a, 5b, 5e, 5f).

The apparent contradictions between the predictions from the Safranyik *et al.* climate suitability model and the Logan *et al.* model of adaptive seasonality can be attributed to two main factors. First, the Logan *et al.* model does not take lethal winter temperatures into

account. Second, the Safranyik *et al.* model does not consider the fact that excessive heat can lead to partial multivoltinism, which should be deleterious to the beetle's fitness. The Logan *et al.* model is highly sensitive to any life-cycle duration that is not strictly equal to 1 year. Even though we applied a "relaxed" version of the Logan *et al.* model (see Appendix B), which allows maladaptive voltinism for up to 2 consecutive years, predictions of climate suitability were restricted to well-defined bands with little variability. Depending on the length and temporal distribution of runs of adaptive and maladaptive seasonality in a given habitat, it is likely that simulations based on the relaxed model still represent conservative estimates of the spatial extent of climatically benign habitat. Indeed, there is evidence that mountain pine beetle populations persist and outbreaks can develop in areas with local climates that periodically result in life cycles both shorter and longer than 1 year (Evenden *et al.* 1943; Safranyik 1978). Furthermore, past mountain pine beetle outbreaks have been highly synchronous over enormous areas (Aukema *et al.* 2006, 2008), which highlights the importance of the interactions of density-related factors such as host availability and condition, natural enemies, and climatic factors in the dynamics of beetle populations. The relative impact of these mortality factors, independently and in combination, on survival of a generation depends to a significant extent on the temporal distribution and abundance of the various brood stages. Consequently, depending on local environmental conditions, expected survival rate in a generation and annual population growth are not necessarily maximized by strictly adaptive seasonality.

Despite differences amongst the models in their predictions of climatic suitability, consideration of the amalgam of their outputs provides valuable insights into the distribution of optimal habitats for mountain pine beetle. Because outputs from the Safranyik *et al.* and Régnière and Bentz models together represent the relative favourability of conditions for winter survival and those factors that negatively affect host vigour, as well as an index of the likelihood of rapid, if not strictly univoltine, development it is

expected that climatically optimal habitats for mountain pine beetle will occur in those areas where high values for climate suitability and likelihood of winter survival overlap the band of adaptive seasonality produced by the Logan *et al.* model. In the recent past (1971–2000) these areas were predominantly in southern and central British Columbia, southern and west-central Alberta, and southern Saskatchewan (Fig. 5). In the near future (2001–2030), overall climate suitability is expected to intensify in southern and central British Columbia and shift north into the western boreal region, while the remainder of the boreal forest will remain unsuitable, even though a univoltine life cycle for the mountain pine beetle is possible (Fig. 5).

The implications of this analysis for the potential invasion of the boreal forest by mountain pine beetle are manifold. The areas of north-central Alberta where the beetle has recently established were formerly considered to be climatically marginal, a statement that is supported both by the amalgam of the model outputs (Figs. 5*a*, 5*c, 5e*) and by observations of over-winter survival (*e.g.*, Alberta Sustainable Resources Development 2008). However, by the 2001–2030 time step, large areas of northern Alberta will have moderate to high climate suitability (Fig. 5*b*), a high likelihood of adaptive seasonality (Fig. 5*d*), and a probability of winter survival that can facilitate the growth of mountain pine beetle populations (Fig. 5*f*). Therefore, it is improbable that mountain pine beetle will be limited as frequently by climate in northern Alberta in the near future, and so the risk of expansion toward the boreal forest has increased. It is predicted that east of Alberta, the southern margins of the boreal forest will have low to moderate climate suitability (Fig. 5*b*) and winter conditions that may allow mountain pine beetle to persist (Fig. 5*f*). By 2001–2030, however, these regions of greater suitability will not overlap areas of adaptive seasonality (Fig. 5*d*). Thus, in the near future, spread of the beetle through the central boreal forest is more likely to be limited by climate, although the strength of these limits is contingent upon the degree to which strict adaptive seasonality affects the establishment and persistence of mountain pine beetle. Despite the predicted increase in regions of adaptive seasonality in Yukon and Northwest Territories

in the near future (Fig. 5*d*), the limited distribution and abundance of pine (Fig. 7), together with the other limiting aspects of climate (Fig. 5*b*, 5*f*), significantly reduce the risk of northward expansion.

Mountain pine beetle bionomics in relation to range expansion

Mountain pine beetle is a typical scolytine bark beetle that feeds and reproduces within the phloem tissue of its host trees. Successful brood production is normally contingent upon the death of its host and, as a result, tree species historically exposed to mountain pine beetle have evolved an array of mechanisms to inhibit attacks and the beetle has coevolved a series of adaptations to overcome them (Safranyik and Carroll 2006; Raffa *et al.* 2008). Within climatically benign habitats, the potential for mountain pine beetle populations to establish and persist depends primarily upon the outcome of the complex interactions that occur at the level of individual trees. These interactions can be considered in three broad categories: host-tree selection, colonization, and brood development and emergence.

Host-tree selection

Within a stand of susceptible trees, the first mountain pine beetles to arrive/emerge (*i.e.*, pioneer beetles) employ a combination of random landings and visual orientation (Hynum and Berryman 1980), followed by direct gustatory assessment of host suitability based upon compounds present in the bark (Raffa and Berryman 1982). If a tree is acceptable, beetles begin to bore through the bark and construct galleries. Trees respond to attacks with physical and chemical defences consisting of resins released from constitutive resin ducts that are severed as the beetles bore through the bark, and secondary induced resinosis by tissues surrounding the wound (Franceschi *et al.* 2005; Raffa *et al.* 2005; Keeling and Bohlmann 2006). Mountain pine beetles have adapted to exploit the defensive response of their host trees. As beetles penetrate the bark they oxidize one of the monoterpene resin constituents, α-pinene, to produce the aggregation pheromone

trans-verbenol (Seybold *et al.* 2006). Production of aggregation pheromones instigates a mass attack during which large numbers of foraging beetles orient to the tree and attack within a short period (often less than 2 days), thereby overwhelming the capacity of trees to produce sufficient resin for adequate defence (Safranyik and Carroll 2006).

Several compelling studies suggest that the mechanisms of host selection employed by mountain pine beetle are relevant within jack pine forests. Furniss and Schenk (1969) reported mountain pine beetles attacking jack pine planted in Idaho, well outside the beetle's native range; Cerezke (1995) demonstrated that the beetles can naturally attack cut bolts of jack pine placed in infested lodgepole pine stands. Levels of α-pinene tend to be high in both the constitutive and induced resins of jack pine (Raffa and Smalley 1995; Wallin and Raffa 1999), and Clark (2008) showed that α-pinene concentrations induced by simulated mountain pine beetle attacks are several times greater in jack pine than in lodgepole pine. Thus, once pioneer beetles have initiated attacks on jack pine, high levels of α-pinene may facilitate production of aggregation pheromones and increase the probability of successful mass attack.

Colonization

Successful colonization following mass attack by mountain pine beetle is contingent upon circumventing the defensive response induced in trees. To that end, the beetle has evolved a mutualistic relationship with several species of ophiostomatoid blue-stain fungi and bacteria. Microorganisms are carried by dispersing beetles and inoculated into trees as they bore through the bark. Spores of blue-stain fungi, aided by several species of bacteria (Adams *et al.* 2009), germinate quickly and penetrate living cells in both phloem and sapwood xylem, terminating resin production by the tree (Ballard *et al.* 1982; Solheim 1995). Two species of blue-stain fungi, *Grosmannia clavigera* (Robinson-Jeffery and Davidson) Zipfel, de Beer and Wingfield and *Ophiostoma montium* (Rumbold) von Arx, are consistently and commonly associated with mountain pine beetle throughout its historical range (Lee *et al.* 2006*a*; Rice *et al.* 2007*a*). A third species,

Leptographium longiclavatum Lee, Kim and Breuil, occurs at low frequency (Lee *et al.* 2005). The virulence of these fungal species varies. *Grosmannia clavigera* is capable of killing trees in the absence of beetles, whereas *O. montium* is not (Yamaoka *et al.* 1990; Solheim 1995). *Leptographium longiclavatum* is also capable of killing lodgepole pine in the absence of beetles, although its virulence appears to be lower than that of *G. clavigera* (Lee *et al.* 2006*b*).

Evidence suggests that the form and function of the beetle–blue-stain fungi association east of the Rocky Mountains may differ in a way that could increase the risk of successful invasion of the boreal forest. In northern Alberta, in addition to the common association of mountain pine beetle with *G. clavigera* and *O. montium*, it is also regularly found with *L. longiclavatum* (Rice *et al.* 2007*b*). *Grosmannia clavigera* and *L. longiclavatum* are adapted to cold boreal winters, but *O. montium* is not (Rice *et al.* 2008). Thus, for expanding mountain pine beetle populations, association with the phytopathogenic mutualists *G. clavigera* and *L. longiclavatum* will be favoured by cold winters, at least in the near to medium term, before large changes to winter minimum temperatures are manifested through global warming.

Brood development and emergence
Host-tree effects

Epidemic mountain pine beetles preferentially attack mature trees, primarily because larger trees have a thicker bark (that protects offspring from natural enemies and weather extremes) and phloem (that provides superior nutrition to developing larvae) (Amman 1969; Shrimpton and Thomson 1985; Safranyik and Carroll 2006). Populations breeding in small trees have a much lower potential rate of increase, and trees ≤25 cm in diameter tend to be beetle sinks, with more beetles attacking than emerging (Safranyik *et al.* 1974). Although the comparative aspects of tree size and characteristics of the bark and phloem of eastern pines have not yet been systematically investigated, evidence from several independent sources indicates that jack pine is a highly suitable host for brood production. Several studies have shown that mountain pine beetles

inserted into jack pine logs in the laboratory are capable of successfully reproducing, and that egg-gallery length, number of offspring, and size and sex ratio of emerged brood adults do not differ from those of beetles associated with lodgepole pine (Safranyik and Linton 1982; Cerezke 1995). D.W. Langor (unpublished data) found that mountain pine beetles produced at least as many offspring in jack pine bolts as in lodgepole pine and hybrid pine bolts with similar phloem thickness, but brood adults were significantly smaller than parent adults. Smaller beetles may reproduce successfully in thinner phloem, thereby effectively reducing the threshold diameter at which jack pine trees become beetle sinks as opposed to sources.

Competitors

The presence of secondary bark beetle species can significantly affect the establishment, development, and survival of epidemic mountain pine beetles (Safranyik and Carroll 2006). For example, aggregation pheromones emitted by the pine engraver, *Ips pini* Say, reduce the number of mountain pine beetle attacks, and larvae of *Ips* De Geer species compete directly with mountain pine beetle larvae for food and space (Rankin and Borden 1991; Safranyik *et al.* 1996, 1999). Approximately 30 other species of bark beetles can be found associated with epidemic mountain pine beetle infestations in lodgepole pine in central British Columbia (Safranyik *et al.* 2000). Eighteen of these species do not occur in the boreal forest (Bright 1976). By contrast, approximately 13 species of bark beetles inhabit jack pine but not lodgepole pine (Bright 1976). Of these boreal species, only three, *Hylastes porculus* Erichson, *Ips calligraphus* (Germar), and *I. grandicollis* (Eichhoff), commonly attack boles of trees and would be competitors with mountain pine beetle. However, all of these are distributed from Manitoba eastward, and so would not be present to compete with mountain pine beetle in its initial invasion of jack pine forests in Alberta and Saskatchewan.

Interactions with other bole-infesting bark beetles are particularly important to mountain

pine beetle when populations are in the sub-outbreak or endemic phase, when there are too few individuals to successfully mass-attack vigorous trees. During that phase the beetle is restricted to colonizing weakened, damaged, or decadent trees, the resource also utilized by a diverse assemblage of secondary bark beetle species (Safranyik *et al.* 2004; Safranyik and Carroll 2006). The secondary bark beetle assemblage may facilitate the maintenance and persistence of endemic mountain pine beetles by enhancing the development and survival of beetles that exploit trees previously colonized by the secondary species (Smith 2008). The same species of bole-infesting secondary bark beetles are present in jack pine forests (Bright 1976). Thus, interactions with secondary bark beetle species critical to the persistence of endemic mountain pine beetle populations in the historical range may also occur in the boreal forest.

Natural enemies

The role of natural enemies in the population dynamics of mountain pine beetle is not well known. Comprehensive lists of natural enemies associated with the beetle are given in DeLeon (1934) and Amman and Cole (1983). In general, the abundance of natural enemies varies considerably among stands as well as within and among trees within stands. Parasitoids, arthropod predators, and woodpeckers are the most common natural enemies; diseases, nematodes, and other vertebrate predators are not normally a significant cause of mortality (Safranyik and Carroll 2006).

The most common parasitoid associated with late-instar larvae of mountain pine beetle throughout its historical range is *Coeloides rufovariegatus* (Provancher) (Hymenoptera: Braconidae) (DeLeon 1935*b*; Reid 1963; Langor 1989). Parasitism rates vary widely, but seldom exceed 5% or 6% (DeLeon 1935*b*; Reid 1963; Amman 1984; Langor 1989). This parasitoid would not be expected to be a factor in the establishment of new populations of mountain pine beetle (Moeck and Safranyik 1984). A similar conclusion was reached concerning the principal arthropod predator associated with mountain pine beetle populations, *Medetera aldrichii* Wheeler (Diptera:

Dolichopodidae), a generalist subcortical insect (DeLeon 1935*a*), which has been found associated with the expanding mountain pine beetle populations in north-central Alberta (A.L. Carroll, unpublished data). Woodpeckers are also common throughout the boreal forest. They may cause very high localized mortality in beetle populations (Otvos 1965; Amman and Cole 1983; Safranyik and Carroll 2006), but territoriality limits their numerical response to increases in mountain pine beetle populations (Berryman 1973; Korol 1985).

Host susceptibility and connectivity in the boreal forest

There is a high degree of uncertainty regarding the behaviour of mountain pine beetle populations once they are established in a new habitat. Outbreaks are the result of very small changes in mortality within generations determined by trophic interactions combined with several years of favourable weather conducive to beetle development and survival (as outlined above). Although the susceptibility of individual jack pine trees may be high, it is the distribution and abundance of susceptible host trees within a forest that determine the behaviour of mountain pine beetle populations and their capacity for spreading. Beetles undertake short- and long-range dispersal following emergence from trees colonized the previous year (Safranyik and Carroll 2006). Short-range host-seeking dispersal takes place under the forest canopy . It is a diffusive but highly predictable event that is determined by the relative proximity of brood trees within individual stands and by stand-level parameters that determine the availability of high-quality hosts (Aukema *et al.* 2006; Safranyik and Carroll 2006; Whitehead *et al.* 2006). Long-range dispersal takes place above the forest canopy, aided by wind currents carrying beetles to new habitats. Jackson *et al.* (2008) combined direct observations of mountain pine beetle emergence with weather radar imagery and aerial capture of beetles and estimated that there were approximately 18 600 beetles/ha above the canopy at peak emergence during an outbreak in central British Columbia. They calculated that beetles

could travel up to 110 km in a single day, perhaps farther with wind speeds greater than those that occurred during the study.

Following a long-distance dispersal event, host location and attack success within a new habitat depend mainly on the density, distribution, and susceptibility of host trees relative to the size of the arriving beetle population (Safranyik and Carroll 2006). Calculation of a susceptibility index for forests requires detailed data regarding inherent characteristics of stands and landscapes that affect their likelihood of attack by and damage due to mountain pine beetle populations (Shore and Safranyik 1992). The required level of detail for the entire boreal forest is unavailable, but susceptibility can be estimated directly for the western boreal region (Alberta and Saskatchewan), which is at the greatest immediate risk of attack by mountain pine beetle.

Stand-susceptibility rating: western Nearctic boreal zone

A modified version of the stand susceptibility rating system of Shore and Safranyik (1992) and Shore *et al.* (2006) was used to assess the susceptibility of pine stands in the western boreal forest of North America. This rating system is based primarily on stand structure and includes four variables: (1) the percentage of susceptible pine by basal area, (2) the age of dominant/codominant pine in a stand, (3) stand density, and (4) an index of climate suitability (see Appendix D). The index of climate suitability (Carroll *et al.* 2004) replaces the "location factor" in the original stand susceptibility rating system. Each stand is given a rating between 0 and 100. This system was applied to the provinces of Alberta and Saskatchewan, based on provincial vegetation-resource inventories, using routines developed in Alberta (Beverly Wilson, Alberta Sustainable Resource Development, unpublished data).

The susceptibility index for outbreaks was determined in two classes, 1–30 and 31–60, because epidemic mountain pine beetle populations are typically associated with stands having a susceptibility index >30, whereas outbreaks are rare in stands with values ≤30 (T.L. Shore, unpublished data). The results

indicate that a large proportion of the pine stands in Alberta must be considered susceptible to mountain pine beetle epidemics (Fig. 6). The majority of susceptible stands are distributed across the eastern slopes of the Rocky Mountains and the adjacent foothills, where trees are large and stands well stocked. However, susceptible pine stands also extend throughout the region in which lodgepole pine and jack pine hybridize (Fig. 1), and are common across the boreal zone in northeastern Alberta (Fig. 6). Stands with a susceptibility index > 30 are less frequent in Saskatchewan.

The decline in stand susceptibility eastward in the northern boreal zone suggests that the high rate of spread of mountain pine beetle seen in the recent past is less likely to persist east of Alberta. This interpretation assumes that the stand parameters that determine susceptibility of lodgepole pine would be similar for jack pine and lodgepole pine–jack pine hybrids. As discussed above, for mountain pine beetle, host selection and colonization success may be greater in jack pine as a result of differences in the interactions between the beetle, its mutualistic fungi, and jack pine trees. This could enable epidemic beetle populations to persist and spread in stands with a susceptibility index < 30. Also, the susceptibility rating includes an index of climate suitability derived from current conditions (Carroll *et al.* 2004), whereas the evident trend is for climate suitability in the boreal forest to increase as a consequence of climate change (see above).

A susceptibility surrogate: pine volume in the boreal zone

The volume of lodgepole pine and jack pine can be used as a surrogate measure to approximate the abundance and distribution of stand-level susceptibility. Stands in which pine is dominant (*i.e.*, > 50% of trees) occupy at least[4] 35 million ha of Canada's land base

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[4]The actual area and volumes are likely higher, owing to the presence of additional pine stands within the "unclassified" and "unspecified conifer" categories, as well as areas that are not classed as "stocked forest."

Fig. 6. Map showing stand susceptibility to mountain pine beetle (*Dendroctonus ponderosae*) in Alberta and Saskatchewan, modified from Shore and Safranyik (1992). Stands with values >30 can generally support epidemic populations, whereas outbreaks are uncommon in stands with values <30.
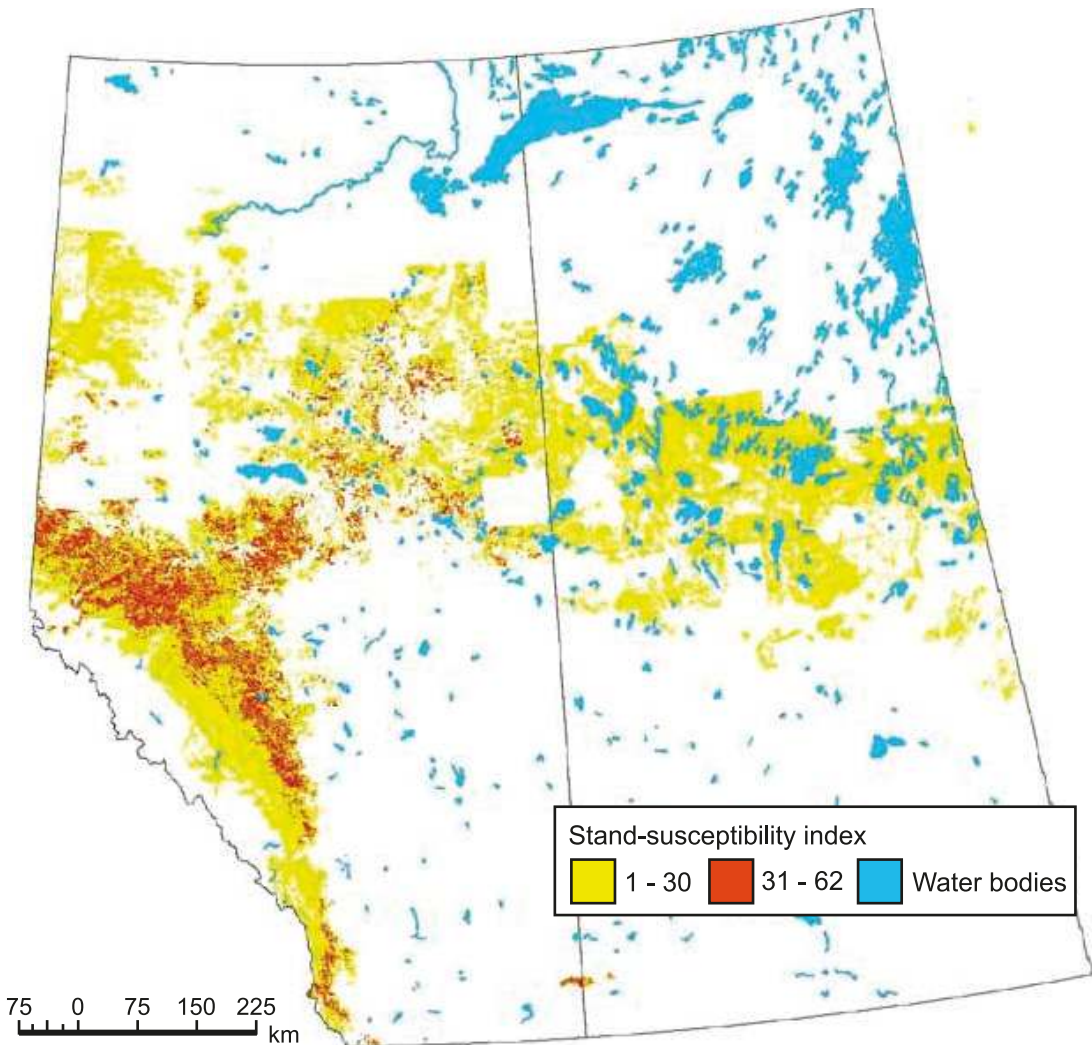
(Power and Gillis 2006), and much of the interior of British Columbia and western Alberta have fairly contiguous units of high-volume pine (*i.e.*, > 40 m³/ha (Fig. 7)). Forests characterized by these volumes are highly susceptible to outbreak populations of mountain pine beetle (A.L. Carroll, unpublished data). The volume of pine on the landscape, however, decreases eastward across the Prairie Provinces and then increases again in Ontario (Fig. 7). Contiguous areas of high-volume pine are relatively rare in the remainder of

eastern Canada. The greater fragmentation of areas with large volumes of pine east of the Alberta foothills is due to differences in abiotic factors as well as to patterns of anthropogenic activity in their disturbance history (*e.g.*, Taylor and Carroll 2004; Taylor *et al*. 2006). Together with the estimate of stand susceptibility presented above, the fragmented distribution of high-volume pine east of the Rocky Mountains suggests that rates of mountain pine beetle population growth and spread through the boreal forest

Fig. 7. Estimated volumes of pine species in Canada (data from the Canadian Forest Service forest inventory).
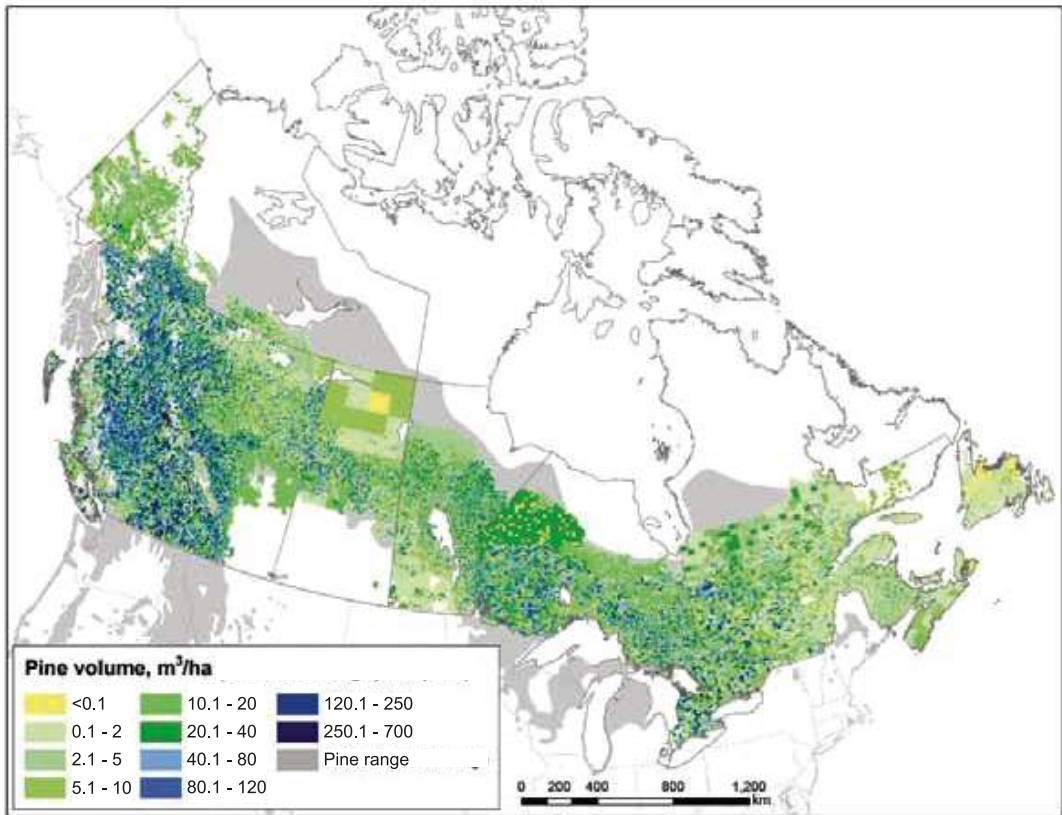

will be significantly lower than have been observed in the beetle's historical range. This suggestion is strengthened by a landscape-scale analysis of genetic variation in mountain pine beetle populations. According to Mock *et al.* (2007), genetic structuring among populations indicates a geographical pattern of historical gene flow that follows the core distribution of the beetle's host species. These authors also showed that variation in genetic structure among populations followed a pattern of isolation by distance. In combination, these two results suggest that beetle infestations will most likely spread from along leading edges of population sources to nearby areas containing the largest concentrations of susceptible host species. The following analysis of host connectivity is supported by this concept.

Host connectivity

Maps of susceptible pine stands illustrate the potential availability of suitable habitat for mountain pine beetle east of the Rocky Mountains, but to understand the rate of population spread, estimates of the degree of connectivity of these stands are also necessary. The likely spread of the beetle throughout the western boreal forest was quantified using the Mountain Pine Beetle Graph-based Landscape Connectivity Model (Shore *et al.* 2008). This model is based on the stand-susceptibility index and examines how high-susceptibility stands are connected across the landscape and the cost of beetle movement in terms of the distance between patches and intervening land types (see Appendix E). Connectivity is defined as the degree to which pattern impedes or facilitates movement (Taylor *et al.* 1993).

Fig. 8. Areas of connected susceptible stands, with distances from locations of known attacks by mountain pine beetle (*Dendroctonus ponderosae*) in Alberta in 2006 (see the text for details).
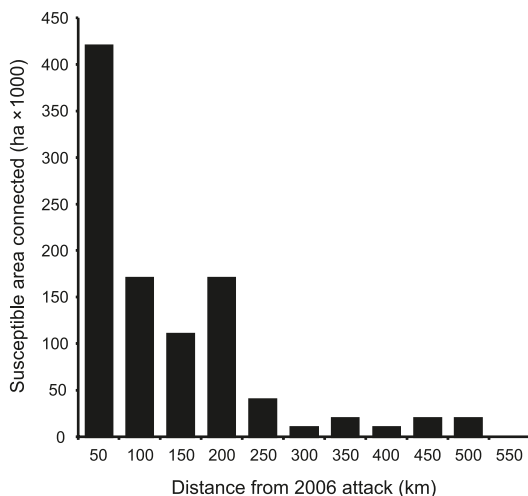
The underlying assumption is that mountain pine beetle will move eastward along least-cost pathways, following higher susceptibility stands via terrain that best permits movement. The model is based on "spatial graphs," an extension to graph theory (Harary 1972) that captures features relevant to geospatial ecological analysis (O'Brien *et al.* 2006; Fall *et al.* 2007).

It is evident that large areas (> 400 000 ha) of susceptible pine stands in the boreal forest are situated in close proximity (*i.e.*, within 50 km) and have high connectivity to mountain pine beetle populations that invaded north-central Alberta in 2006 (Fig. 8). Specifically, more than 450 000 ha of susceptible connected pine stands are within 200 km of the infestations established during that period, well within the range of long-distance dispersal by epidemic beetles (Jackson *et al.* 2008). Thus, both the susceptibility and the connectivity of the boreal forest within range of beetle dispersal from current outbreaks favour the continuing spread of mountain pine beetle eastward, at least throughout the remainder of Alberta. Beyond 200 km east, the amount of susceptible and connected pine declines dramatically, and spread from

Saskatchewan eastward would likely be less rapid (Fig. 8).

Potential impacts of mountain pine beetle range expansion

North American boreal and sub-boreal pine forests provide a wide range of social, ecological, and economic benefits. Possible impacts on these benefits by a novel disturbance such as mountain pine beetle attack are discussed in Nealis and Peter (2008).

Boreal forests contain a high proportion of low-volume stands that may already be close to the margins of operability for commercial timber harvesting; even moderate volume or quality losses could render some stands unusable. Additional uncertainty arises from the limitations of processing capacity, labour supply, and markets for products made from beetle-affected wood.

Boreal and eastern pine stands also provide revenue from tourism, commercial recreation, and trapping as well as social and ecological benefits including conservation and high quality of water, aesthetic values, windbreaks, carbon storage, wildlife habitat, and traditional uses. The values of these factors vary widely by location, but are significant in all provinces and territories. Mountain pine beetle infestation may have indirect impacts by causing changes to stand structure, fuel dynamics, and succession and thus altering fire behaviour (Lynch *et al.* 2006) and the amount of resources devoted to the development and implementation of strategies and tactics designed to reduce losses. The potential impact of mountain pine beetle on nontimber values is difficult to predict and depends on rates of spread and mortality.

The range expansion of mountain pine beetle in the 1990s and the first decade of the 21st century led to this native insect behaving like an invasive species. As a result, in newly infested regions, management tactics beyond those associated with the beetle's historical range may need to be considered. Environment Canada's (2004) strategy for controlling invasive species focuses on prevention, early detection, and rapid response and emphasizes actions that contain species or

block pathways for further spread. With this strategy, the conventional tactics used to control beetle populations (Carroll *et al.* 2006) remain relevant but other responses may have equal priority. For example, monitoring to ensure detection of very low populations along host range boundaries becomes more critical for containment and rapid response. Sanitation may be considered a greater priority than salvage in terms of slowing the natural spread of populations. But the characteristic long-range spread due to human activities is often the focus of management responses to invasive species. In the case of mountain pine beetle, we have shown that biological impediments to invading large portions of eastern Canadian pine forests are few and that the climate is, or will become, suitable. Therefore, to address the risk of further invasion, a logical recommendation is to pay greater attention to blocking the pathways that may result from moving infested logs across the country. With large amounts of forest resources at risk from a demonstrably destructive and mobile insect, a more diverse management response is merited.

Summary and conclusions

In the late 20th and early 21st centuries, there has been a significant expansion in the geographical range of mountain pine beetle in Canada. The beetle has invaded a susceptible portion of the Boreal Plains Ecoregion and is now breeding successfully in lodgepole pine stands adjacent to the boreal jack pine forests that extend across the continent. Our analysis indicates that mountain pine beetles can successfully attack and breed in a wide range of host pine species (including jack pine, the most abundant pine species in the boreal and eastern forests) and that they will be accompanied by their necessary mutualistic organisms. Because there are no major differences between the assemblages of competitors or natural enemies of mountain pine beetle in jack pine and lodgepole pine hosts, there appear to be no major biological impediments to the establishment, persistence, and spread of mountain pine beetle in the Nearctic boreal zone. The principal caveat concerns aspects of

host susceptibility that influence beetle population dynamics. Jack pine stands in the boreal zone are less susceptible to outbreaks than are lodgepole pine stands in western Canada because of relatively lower pine volume in these stands. Jack pine trees tend to be smaller and stands less contiguous in the boreal zone than in pine stands in which mountain pine beetle outbreaks have been observed. These differences will likely reduce the rates of growth and spread of mountain pine beetle populations.

The principal abiotic limits to range expansion by mountain pine beetle are the direct and indirect effects of weather and climate. Current climate suitability for the beetle is greatest in central British Columbia and the dry foothills of the Rocky Mountains in northeastern British Columbia and western Alberta. The suitability of these areas is evident in the rapid spread and population increases in the first decade of the 21st century. Climate suitability is moderate in central Alberta east to Saskatchewan and decreases steadily eastward to low in northern Ontario; there is a finite but decreasing likelihood that climate will continue to favour a rapid eastern expansion of populations. Although climate suitability decreases eastward across the boreal forest, susceptibility begins to increase again as volumes and contiguity of pine forests increase northwest of the Great Lakes.

Canada's boreal forests are an important source of timber and provide a range of other economic, social, and ecological values. The socioeconomic impacts of mountain pine beetle attack in the boreal forest will depend on the extent to which this added disturbance further reduces timber values in what are already low-volume stands, and on the consequences for maintaining forestry as a component of a diversified resource economy. Continued range expansion into the boreal forest could have a negative impact on these values, and fire risk adds another dimension to the potential impacts. Our analysis indicates that the greatest potential risk lies in the high likelihood of establishment of persistent, low-level populations of mountain pine beetle outside its historical range. Eventually, this

activity could become more widespread and, under favourable weather conditions, lead to development of epidemic infestations and an ecological pathway across the prairie region that would allow the continued spread of mountain pine beetle populations farther east into areas with more susceptible pine forests.

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Table A1. Description of climatic variables utilized to construct a model of climate suitability of habitats for mountain pine beetle populations (adapted from Safranyik *et al.* 1975).

Criterion	Description	Rationale
P_1	>305 day-degrees above 5.5 °C from 1 August to the end of the growing season (Boughner 1964) *and* >833 day-degrees from 1 August to 31 July	A univoltine life cycle synchronized with critical seasonal events is essential for beetle survival (Logan and Powell 2001); 305 day-degrees is the minimum heat requirement from peak flight to 50% egg hatch, and 833 day-degrees is the minimum required for a population to be univoltine (adapted from Reid 1962)
P_2	Minimum winter temperatures less than or equal to −40 °C	Under-bark temperatures at or below −40 °C causes 100% mortality within a population (Safranyik and Linton 1998)
P_3	Mean maximum August temperatures ≥18.3 °C	The lower threshold for flight is approximately 18.3 °C (McCambridge 1971); it is assumed that when the frequency of maximum daily temperatures ≥18.3 °C is ≤5% during August, the peak of emergence and flight will be protracted and mass-attack success reduced
P_4	Sum of precipitation from April to June less than long-term average	Significant increases in populations have been correlated with periods of 2 or more consecutive years of below-average precipitation over large areas of western Canada (Thomson and Shrimpton 1984)
Y_1	CV of growing-season precipitation	Because P_4 is defined in terms of deviation from the average, the CV of precipitation was included; its numerical values were converted to a relative scale from 0 to 1 (see the text)
Y_2	Index of water deficit*	Water deficit affects the resistance of lodgepole pine, as well as subsequent development and survival of beetle larvae and associated blue-stain fungi; the water deficit is the yearly sum of rainfall minus evapotranspiration in months with mean air temperature >0 °C

*Replaces the water-deficit approximation (Department of Energy, Mines, and Natural Resources 1970) in the original model of Safranyik *et al.* (1975).

Appendix A

The Safranyik *et al.* model

Originally developed by Safranyik *et al.* (1975) and later modified by Carroll *et al.* (2004), this model combines the effects of several critical aspects of climate on mountain pine beetle and its host trees (Table A1). It was developed from an analysis of climatic variables measured at 42 locations for the period 1950−1971 (Safranyik *et al.* 1975); the locations were chosen to represent the historical range of mountain pine beetle in British Columbia.

The criteria P_1, P_2, P_3, and P_4 are either true or false and combine to provide an estimate of the probability of outbreak, as follows:

$$[1] \qquad P_S = P_1 \wedge P_2 \wedge P_3 \wedge P_4$$

where $\wedge$ is the logical AND operator. P_S is TRUE (= 1) if, and only if, P_1, P_2, P_3, and P_4 are all TRUE, and is FALSE (= 0) otherwise.

Y_1 was derived from the coefficient of variation, $\mathrm{CV} = \sqrt{\mathrm{variance}}\big/\mathrm{mean}$, for April, May, and June precipitation. Y_2, the index of water deficit (WD), was calculated as the yearly sum of rainfall minus evapotranspiration in months with mean air temperature > 0 °C

(evapotranspiration was computed by the standard Thornthwaite method (see Dunne and Leopold 1978)). The quantitative criteria Y_1 and Y_2 were converted to relative scales as follows:

if $(CV < -0.3)$ $Y_1 = 0.2$ if $(WD = 0)$ $Y_2 = 0.2$
if $(CV > 0.30)$ $Y_1 = 0.4$ if $(WD > 0)$ $Y_2 = 0.4$
if $(CV > 0.35)$ $Y_1 = 0.7$ if $(WD = 4)$ $Y_2 = 0.7$
if $(CV > 0.40)$ $Y_1 = 0.9$ if $(WD = 8)$ $Y_2 = 0.9$
if $(CV > 0.45)$ $Y_1 = 1.0$ if $(WD = 12)$ $Y_2 = 1.0$

The index of outbreak risk, F_S, is determined as

$$[2] \qquad F_S = \frac{n_{\mathrm{run}}}{n_{\mathrm{max.}}} \sqrt{Y_1 + Y_2}$$

where n_{run} is the number of years belonging to "runs" of 2 or more consecutive years with P_S = TRUE, and $n_{\mathrm{max.}}$ is the number of years over which the calculation is performed (*i.e.*, 30 years). Thus, a single F_S value was obtained from a 30-year weather time series. The formal definition of n_{run} is

$$[3] \qquad \begin{aligned} n_{\mathrm{run}} &= \left[(P_S)_1 \wedge (P_S)_2 \right] \\ &+ \sum_{t=2}^{n_{\mathrm{max.}}-1} \left\{ \left[(P_S)_{t-1} \wedge (P_S)_t \right] \vee \left[(P_S)_t \wedge (P_S)_{t+1} \right] \right\} \\ &+ \left[(P_S)_{n_{\mathrm{max.}}-1} \wedge (P_S)_{n_{\mathrm{max.}}} \right] \end{aligned}$$

where $\vee$ is the logical OR operator.

F_S values range from 0 to 1. Climate-suitability classes (Table A2) were created by comparing index values with the frequency of infestations of mountain pine beetle across its historical range (Powell 1966).

Table A2. Climate-suitability classes for mountain pine beetle derived from an index of climate suitability, F_S (adapted from Safranyik *et al.* 1975).

Climate suitability	F_S range
Very low	0
Low	0.01–0.05
Moderate	0.06–0.15
High	0.16–0.35
Extreme	0.36+

Appendix B

Logan *et al.* model, relaxed

The Logan *et al.* model (for a detailed description see Logan and Powell 2001) determines whether or not a single year's weather time series (daily minimum and maximum air temperatures) is adaptive and could support an outbreak population of mountain pine beetle. The detailed, stage-specific median rate-summation (nonlinear) model is started at a user-specified initial oviposition date ($O_0 = O_{\mathrm{ini.}}$) and run for $n_{\mathrm{gen.}}$ (say, $n_{\mathrm{gen.}} = 15$), resetting O_0 for each successive generation to the date of the previous generation's peak adult female emergence. Once the model has run for $n_{\mathrm{gen.}}$, three criteria for adaptive seasonality are assessed (logical variables, TRUE or FALSE):

Q_1: univoltinism

Running the model repeatedly for $n_{\mathrm{gen.}}$ generations on a single 365-day weather time series (daily min.$-$max.), the number of years per generation in the last year of simulation ($n_{\mathrm{gen.}}$) must equal 1 (univoltinism).

Q_2: stable oviposition date

The value of the oviposition date must be constant by the end of $n_{\mathrm{gen.}}$. That is,

$$[4] \qquad O_{n_{gen}} = O_{n_{gen}-1}$$

Q_3: viable oviposition date

The last generation's peak oviposition date must be within user-defined viability limits: $O_{\min} < O_{n_{years}} < O_{\max}$. The model has been used with the values $O_{\min.} = 180$ (end of June) and $O_{\max.} = 243$ (end of August). Under all weather regimes tested, Q_3 is always satisfied when Q_1 and Q_2 are true.

The adaptive-seasonality flag for a given temperature time series is the logical

$$[5] \qquad P_L = Q_1 \wedge Q_2 \wedge Q_3$$

This process is repeated for $n_{\mathrm{max.}}$ years (each with a different 1-year daily temperature time series considered a replicate), and the resulting probability of adaptive seasonality is

$$[6] \quad F_L = \frac{\sum_{i=1}^{n_{\max.}} (P_L)_i}{n_{\max.}}$$

We then calculated $F_L{}'$, the proportion of years that are NOT part of a series of 3 or more consecutive $F_L = 0$ (misadaptive seasonality).

Appendix C

The Régnière and Bentz model

This model describes the supercooling-point distribution of a population of mountain pine beetle larvae (instars not distinguished) based on the changing proportion of individuals in one of three states: (1) a non-cold-hardened, feeding state, (2) an intermediate state in which insects have ceased feeding, voided their gut content, and eliminated as many ice-nucleating agents as possible from the body, and (3) a fully cold-hardened state where insects have accumulated a maximum concentration of cryoprotectants (*e.g.*, glycerol). Each state is characterized by a distribution (mean and variance) of supercooling points from warmest in state I to coldest in state III. The proportion of individuals in each state shifts in response to the daily fluctuations of minimum temperature and range of phloem temperatures influencing the opposite rates of gain and loss of cold-hardening. This highly dynamic model fits very closely the empirical supercooling-point data of Bentz and Mullins (1999) on which it is based, and its predictions are very close to observations reported by Safranyik and Linton (1998). A favourable formal comparison between predicted winter mortality and observations made in Alberta in 2006 and 2007 (validation) has yet to be published (B.J. Cooke, unpublished data).

Appendix D

Susceptibility-rating system

A stand is defined as an aggregation of trees or other vegetation occupying a specific site that is sufficiently uniform in age, species composition, and density as to be distinguishable within the forest or from other vegetation on adjoining areas (Hocker 1979). Stand susceptibility to mountain pine beetle is rated in terms of a susceptibility index based on factors calculated for each of the following four variables: percentage of susceptible pine basal area, age of dominant and codominant live pine, stand density, and stand climate suitability (see Shore and Safranyik 1992; Carroll *et al.* 2004).

*Percentage of susceptible pine basal area (**P**)*

The percentage of susceptible pine basal area is calculated as in equation 1:

$$[7] \quad P = \frac{(Average\ basal\ area/ha\ pine \geq 15\ cm\ dbh) \times 100}{Average\ basal\ area/ha\ of\ all\ species \geq 7.5\ cm\ dbh}$$

where DBH is diameter at breast height (1.3 m).

*Age of dominant and codominant live pine (**A**)*

The age factor is determined as given in Table D1. It is calculated using a series of equations that yield a continuous function that will prevent jumps in values at the class limits.

*Stand density (**D**)*

Like the age factor, the density factor is calculated using a continuous function that will prevent jumps in values at the class limits (Table D2).

*Stand climate suitability (**C**)*

An index of climate suitability for stands was determined using the Safranyik *et al.* model described in Appendix A.

Table D1. Determination of the age factor (A) using current continuous functions.

If the average age in years of dominant or codominant pine is:	Then A is:
40–80	$0.1 + 0.1[(\text{age} - 40)/10]^{1.585}$
81–120	1.0
121–510	$1.0 - 0.05\ [(\text{age} - 120)/20]$
<40 or >510	0.1

Table D2. Determination of the density factor (D) using current continuous functions.

If the density of the stand in stems per hectare (sph) for all species ≥ 7.5 cm DBH is:	Then D is:
<650	$0.0824 \,(sph/250)^{2.0}$
650–750	$1.0 - 0.7 \,(3 - sph/250)^{0.5}$
751–1500	1.0
>1500	$1.0/[0.9 + (0.1e^{[0.4796 \,(sph/250 \,- \,6)]})]$

The stand-susceptibility index (SSI)

Once P, A, and C are determined for a stand, the stand susceptibility index is calculated as the simple product

[8] $SSI = P \times A \times D \times C$

Stand-susceptibility indices will range from 0 to 100, the highest values indicating the most susceptible stands.

Appendix E

Connectivity analysis

The connectivity of susceptible pine stands (see Appendix D; Fig. 6) in Alberta and Saskatchewan, relative to the distribution of mountain pine beetle east of the Rocky Mountains in 2006, was determined by spatial graphing methods developed for assessing woodland caribou habitat (O'Brien *et al.* 2006; Fall *et al.* 2007). The primary assumption of the analysis is that population growth and spread occur principally in highly susceptible habitat patches. Therefore, the objective was to identify such patches, particularly those with current mountain pine beetle populations, and determine the degree to which they are connected in terms of the relative "cost" of population growth and dispersal to other susceptible patches.

Stand susceptibility was assessed for Alberta and Saskatchewan using Shore and Safranyik's (1992) susceptibility-rating system as described in Appendix D. High-susceptibility patches (*highSusc*) were defined as areas larger than 10 ha with a susceptibility rating >30 (see Fig. 6). From the map of high-susceptibility patches a minimum planar graph was extracted (Fall *et al.* 2007). Nodes of this graph are composed of high-susceptibility patches, while links represent connections between patches. Links track the Euclidian distance or cumulative cost between nodes. The minimum planar graph was "reoriented" from the perspective of the 2006 mountain pine beetle attack in Alberta to account for the connectivity of high-susceptibility patches to existing infestations. By starting in patches of existing attack and then spreading outward to the high-susceptibility patches, the shortest distance or cost to each node and link was identified (for details see Fall *et al.* 2007). A simple cost function for mountain pine beetle movement across the landscape (and between susceptible patches) was generated on the basis of the following rules:

A value representing the maximum cost of movement (max*Cost*), 10, was selected (the actual value of this parameter is not overly critical because it is used to determine relative cost pathways). The cost of moving through areas with a stand-susceptibility index of 0 will be equal to max*Cost* multiplied by the distance; the cost of moving through areas with susceptibility ratings equal to or greater than that of *highSusc* will be 1 multiplied by the distance (*i.e.*, Euclidian cost), with a linear declination in cost between the two. That is,

[9] $Cost = 1, \; susceptibility \geq highSusc$

[10] $Cost = \dfrac{\text{max}Cost - susceptibility(\text{max}Cost - 1)}{highSusc},$

          $susceptibility < highSusc$

At each threshold k, all links greater than k were removed from the minimum planar graph in order to determine the area of high-susceptibility habitat (see Keitt *et al.* 1997). The connectivity model was implemented as described in Fall *et al.* (2007).