Canada

Mountain Pine Beetle Initiative
Canadian Forest Service

Impacts of Climate Change on Range Expansion by the Mountain Pine Beetle

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Mountain Pine Beetle Initiative Working Paper 2006-14

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Mountain Pine Beetle Initiative P.O. # 1.02

Natural Resources Canada
Canadian Forest Service
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506 West Burnside Road
Victoria, British Columbia V8Z 1M5
Canada

2006

Printed in Canada

Library and Archives Canada Cataloguing in Publication

Impacts of climate change on range expansion by the mountain pine beetle
/ A.L. Carroll ... [et al.].

(Mountain Pine Beetle Initiative working paper 2006-14)
"Mountain Pine Beetle Initiative P.O. # 1.02".
Includes bibliographical references.
ISBN 0-662-44349-7
Cat. no.: Fo143-3/2006-14E

1. Mountain pine beetle--Geographical distribution--Climatic factors--British Columbia. 2. Mountain pine beetle--Habitat--British Columbia. 3. Pine--Diseases and pests--British Columbia. I. Carroll, A. L. II. Pacific Forestry Centre III. Series.

SB945.M78I46 2006 634.9'7516768 C2006-980256-4

Abstract

The current latitudinal and elevational range of mountain pine beetle (MPB) is not limited by available hosts. Instead, its potential to expand north and east has been restricted by climatic conditions unfavorable for brood development. We combined a model of the impact of climatic conditions on the establishment and persistence of MPB populations with a spatially explicit, climate-driven simulation tool. Historic weather records were used to produce maps of the distribution of past climatically suitable habitats for MPB in British Columbia. Overlays of annual MPB occurrence on these maps were used to determine if the beetle has expanded its range in recent years due to changing climate. An examination of the distribution of climatically suitable habitats in 10-year increments derived from climate normals (1921-1950 to 1971-2000) clearly shows an increase in the range of benign habitats. Furthermore, an increase (at an increasing rate) in the number of infestations since 1970 in formerly climatically unsuitable habitats indicates that MPB populations have expanded into these new areas.

The potential for additional range expansion by MPB under continued global warming was assessed from projections derived from the CGCM1 global circulation model and a conservative forcing scenario equivalent to a doubling of CO_2 (relative to the 1980s) by approximately 2050. Predicted weather conditions were combined with the climatic suitability model to examine the distribution of benign habitats from 1981-2010 to 1941-2070 for all of Canada. The area of climatically suitable habitats is anticipated to continue to increase within the historic range of MPB. Moreover, much of the boreal forest will become climatically available to the beetle in the near future. Since jack pine is a viable host for MPB and a major component of the boreal forest, continued eastward expansion by MPB is probable.

Keywords: Mountain pine beetle, climate change, global warming, range expansion

Résumé

L’aire de distribution du dendroctone du pin ponderosa (DDP) selon les latitudes et l'élévation n'est pas limitée par les hôtes disponibles. En fait, les possibilités de l’expansion de son aire de distribution vers le Nord et vers l’Est sont limitées par des conditions climatiques qui ne favorisent pas le développement des larves.Nous avons combiné un modèle des incidences des conditions climatiques sur l'établissement et la persistance des populations du DDP avec un outil de simulation spatialement explicite fondé sur les conditions climatiques. À partir d'annales météorologiques, on a établi des cartes de la répartition des habitats du DPP, en Colombie-Britannique dont les conditions climatiques s’étaient révélées propices à l’espèce. La superposition de la présence annuelle du DDP sur ces cartes a permis de préciser dans quelle mesure l’aire de distribution du dendroctone avait pris de l’expansion au cours des dernières années en raison du climat. L’examen de la répartition des habitats propices par tranches de dix ans à partir de conditions climatiques normales (de 1921-1950 à 1971-2000) révèle clairement une expansion des habitats propices au DPP.Qui plus est, depuis 1970, l’accroissement du nombre d’infestations dans les habitats naguère défavorables montre que les populations du DPP s’étalent désormais dans ces régions.

Le potentiel d’expansion de l’aire de distribution du DDP par suite du réchauffement de la planète a été déterminé à partir de projections obtenues au moyen du modèle de circulation générale CGCM1 et d’un scénario de forçage conservateur correspondant au doublage du CO_2 (par rapport aux années 1980) d’ici 2050 ou à peu près. Les prévisions météorologiques ont été combinées avec un modèle écoclimatique pour examiner la répartition des habitats propices, de 1981 à 2010 et de 1941 à 2070, pour l’ensemble du Canada. On prévoit que la superficei des habitats favorisés par le climat continuera de s’accroître dans l’aire de distribution historique du DDP. Qui plus est, une grande partie de la forêt boréale offrira un climat favorable au ravageur dans un proche avenir.Comme le pin gris est un hôte viable du DDP et que cette essence compte pour une importante proportion des essences de la forêt boréale, l'expansion du DPP vers l'Est relève du domaine de la probabilité.

Mots-clés : Dendroctone du pin ponderosa, changement climatique, réchauffement de la planète, expansion de l’aire de distribution

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1 Introduction

Every aspect of an insect's lifecycle is dependent upon temperature. Consequently, these organisms are expected to respond quickly to changing climate by shifting their geographical distribution and/or population behaviour to take advantage of new climatically benign environments. Rapid ecological and genetic adaptation by insects in response to global warming has already been documented in Europe (Thomas et al. 2001). However, for North America, despite the development of several models predicting climate change impacts (e.g., Logan and Powell 2001; Logan et al., 2003), there is little empirical evidence that global warming has affected insect populations.

The mountain pine beetle, *Dendroctonus ponderosae* (Hopkins) (MPB), is one of the most significant sources of mortality in mature pine forests in western North America (Safranyik et al. 1974; Taylor et al. 2006). Mountain pine beetle will successfully attack most western pines, but lodgepole pine is its primary host throughout most of its range (Safranyik and Carroll 2006). Although it is widespread in western North America, occurring from northern Mexico to central British Columbia (BC), extensive outbreaks have occurred mainly within the southern interior regions of British Columbia and the northern Rocky Mountains within the US (Safranyik and Carroll 2006). Despite its significant distribution, the current latitudinal and elevational range of MPB in western Canada is not restricted by the availability of suitable host trees. Indeed, lodgepole pine extends north into the Yukon and Northwest Territories, and east across much of Alberta. Instead, the potential for MPB to expand north and east has been limited by climate (e.g., Safranyik 1978). It is anticipated that under global warming, former climatically hostile environments will become climatically benign, allowing MPB to significantly expand its range (Logan and Powell 2001, 2004; Carroll et al. 2004).

Recent observations suggest that MPB infestations may be occurring in areas previously considered climatically unfavourable (Carroll et al. 2004). This study was initiated to address the following questions: i) has there been a shift in climatically benign habitats for MPB during the past three decades; ii) have MPB populations expanded into these new habitats; and iii) given a plausible climate change scenario, what will be the range of climatically benign habitats in the future?

2 Material and Methods

2.1 Climatically benign habitats

2.1.1 The Safranyik model

To quantify the climatic suitability of habitats for MPB, we adapted a model of the impact of climatic conditions on the establishment and persistence of MPB populations originally developed by Safranyik et al. (1975). The model combines the effects of several critical aspects of climate on the beetle and its host trees (Table 1). It was developed from the analysis of climatic variables measured at 42 locations for the period 1950 to 1971 (Safranyik et al. 1975). The locations were chosen to represent the historic range of MPB in BC.

Table 1. Description of climatic variables utilized to construct a model of climatic suitability of habitats to mountain pine beetle populations (adapted from Safranyik et al. 1975).

Criteria	Description	Rationale
P_1	> 305 degree-days above 5.5°C from Aug. 1 to end of growing season (Boughner 1964), *and* >833 degree-days from August 1 to July 31	A univoltine lifecycle synchronized with critical seasonal events is essential for MPB survival (Logan and Powell 2001). 305 degree-days is the minimum heat requirement from peak flight to 50% egg hatch, and 833 degree-days is the minimum required for a population to be univoltine (adapted from Reid 1962).
P_2	Minimum winter temperatures >-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 MPB flight is ≈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 MPB emergence and flight will be protracted and mass attack success reduced.
P_4	Sum of precipitation from April to June < long-term average	Significant increases in MPB populations have been correlated with periods of two or more consecutive years of below-average precipitation over large areas of western Canada (Thomson and Shrimpton 1984).
Y_1	Variability of growing season precipitation	Since P_4 is defined in terms of a deviation from average, the coefficient of variation of precipitation was included. Its numerical values were converted to a relative scale from 0 to 1 (see text).
Y_2	Index of water deficit[a]	Water deficit affects the resistance of lodgepole pine to MPB, as well as subsequent development and survival of larvae and associated blue-stain fungi. Water deficit is the yearly sum of (rainfall – evapotranspiration) in months with mean air temperature > 0 (see text).

[a] The index of water deficit replaces the water deficit approximation (National Atlas of Canada 1970) in the original model of Safranyik et al. (1975).

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

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

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, $CV = Variance^{1/2}/Mean$ of April, May and June precipitation. Y_2, the index of water deficit (WD), was calculated as the yearly sum of (rainfall – evapotranspiration) in months with mean air temperature > 0 [evapotranspiration was computed by the standard Thornthwaite method (see Dunne &

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 ($WD = 12$) $Y_2 = 1.0$

F_S, the index of outbreak risk, is determined as:

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

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

$$n_{run} = [(P_s)_1 \wedge (P_s)_2] + \sum_{t=2}^{n_{\max}-1} \{[(P_s)_{t-1} \wedge (P_s)_t] \vee [(P_s)_t \wedge (P_s)_{t+1}]\} + \left[(P_s)_{n_{\max}-1} \wedge (P_s)_{n_{\max}}\right] \qquad [3]$$

where $\vee$ is the logical OR operator.

The values of F_S range from 0 to 1. Climatic suitability classes (CSCs; Table 2) were created by comparing index values with the frequency of MPB infestations across its historic range (Powell 1966).

Table 2. Climatic suitability classes (CSCs) for mountain pine beetle derived from an index of climatic suitability F_S (adapted from Safranyik et al. 1975)

Climatic suitability	Range of index (F_S)
Very low	0
Low	0.01 – 0.05
Moderate	0.06 – 0.15
High	0.16 – 0.35
Extreme	0.36+

2.1.2 Historic climate data

Historic daily weather data (1920 – 2000) for BC were obtained from Environment Canada, Meteorological Services (2002). The number of stations reporting data over the period ranged from 703 in 1920 to 2924 in 1990. To generate a stochastic series of daily values that minimize the effect of short-term weather anomalies and focus on longer-term climatic trends, we first converted the data to monthly normals (30-year means and extreme minima and maxima). We then produced stochastic daily values from the normals using a daily weather generator developed by Régnière and Bolstad (1994).

2.1.3 Landscape-level simulations

We constructed landscape-wide projections of climatically suitable habitats for MPB, generated by the Safranyik climatic suitability model, using BioSIM© software (Régnière et al. 1995; Régnière 1996). BioSIM requires two inputs; digital representations of the terrain and suitable weather data. We extracted a digital elevation model of British Columbia from the US Geological Survey ≈1-km-resolution global coverage. Point sources of weather data (i.e., stations) are usually sparse relative to the spatial resolution required for mapping biological phenomena. Therefore, spatial interpolation methods must be used to obtain air temperature and precipitation information for unsampled points across a landscape from a limited source of geo-referenced weather stations. We used the 'gradient-plus-inverse distance squared' algorithm developed by Nalder and Wein (1998); an approach that combines multiple linear regression and distance-weighting.

We generated a series of maps depicting the distribution of CSCs for MPB as a function of climate normals derived from the historic daily weather data in 10-year intervals from 1931-1960 to 1971-2000. Universal kriging (e.g., Davis 1986) (with elevation as a drift variable) was used for interpolation between simulation points. The map outputs comprise grid coverage of CSC values for ≈1.2 million 64-ha cells.

2.2 Past range expansion

From 1959 to 1996, the Canadian Forest Service, Forest Insect and Disease Survey (FIDS), in cooperation with the BC Ministry of Forests, conducted annual aerial assessments of forest insect and disease conditions in BC and the Yukon. During these surveys, boundaries of MPB infestations were recorded on 1:250,000 NTS topographic maps (for details see Van Sickle et al. 2001). We digitized these maps (≈1000 in total) using ArcInfo® geographic information software (GIS), joined them into annual province-wide coverages (Albers projection, NAD87), and converted them to shape files.

To quantify whether range expansion by MPB has occurred during the past 30 years, we chose the map of climatic suitability classes based on the 1941-1970 climate normals to represent the historic distribution of climatically suitable habitats for MPB. The gridded map was reclassified to produce an Arc shape file. We overlayed annual MPB infestation maps using ArcInfo to create new MPB × CSC polygons. Because the climatic suitability grid cells generated by BioSIM are relatively small (64 ha), the intersection process divided many of the large MPB infestation polygons into several MPB × CSC polygons. We summarized the number of infestations in each CSC class by year such that only one intersection per MPB × CSC class was counted per infestation polygon.

Range expansion was assessed by regressing the number of MPB infestations *versus* year for each of the CSCs derived from the historic distribution of climatically suitable habitats (i.e., based on the 1941-1970 normals). We used polynomial regressions only when they explained significantly more of the variation in the data (P<0.05) than simple linear regressions. Since outbreak populations are often forced to briefly occupy sub-optimal habitats prior to their collapse due to the localized depletion of high-quality stands (e.g., Safranyik et al. 1999), data for the peak of the last (i.e., 1983 to 1985, inclusive) and current (i.e., 1997 to present) province-wide outbreaks were not included in the analysis.

2.3 Future range expansion

2.3.1 A plausible climate change scenario

The distribution of potential future climatically suitable habitats was projected from predicted conditions based on the CGCM1 general circulation model (Flato et al. 2000). The climate change "forcing scenario" was derived from a modified version of the IPCC IS92a scenario (Mitchell et al. 1995) and comprises a 1% per year increase in atmospheric CO_2 concentration and an associated change in the distribution and magnitude of sulphate aerosol loading (see Boer et al. 2000). The scenario is equivalent to a doubling of CO_2 (relative to the 1980s) by approximately 2050 and a tripling of CO_2 by the year 2100. These increases in greenhouse gases produce simulated increases in mean global temperatures of 1.7 °C by 2050 and 2.7 °C by 2100 (Boer et al. 2000).

2.3.2 The Safranyik-Logan hybrid model

For MPB, there is no winter diapause, which implies that seasonality is entirely determined by climatic conditions. Although the Safranyik climatic suitability model accounts for more than the direct effects of temperature on MPB populations (i.e., over-winter survival, emergence/dispersal conditions, and host resistance), it does not consider the potential negative impact of generational asynchrony (i.e., partial multivoltinism) that may result from excess summer heat accumulation. Logan and Powell (2001) developed a model that can be used to determine if a given weather regime will lead to an adaptive seasonality for MPB, as defined by voltinism and the stability of oviposition dates from one generation to the next. To assess the potential effects of excessive warming associated with continued climate change on MPB populations, and examine the distribution of climatically benign habitats into the future, we merged the models of Safranyik et al. (1975) and Logan and Powell (2001, 2004).

Logan and Powell (2001, 2004) assess adaptive seasonality for MPB through a detailed, stage-specific median rate-summation (non-linear) model that is started at a user-specified initial oviposition date (O_0=O_{ini}) and run for n_{gen} (e.g., n_{gen}=15), resetting O_0 for each successive generation to the previous generation's peak adult female emergence date. Once the model has run for n_{gen}, three criteria for an adaptive seasonality are assessed (logical variables TRUE or FALSE) as shown in Table 3.

Table 3. Criteria for adaptive seasonality for the mountain pine beetle (from Logan and Powell 2001).

Criteria	Description	Rationale
Q_1	Univoltinism	The number of years per generation in the last year of simulation (n_{gen}) must equal 1.
Q_2	Stable oviposition date	The oviposition date must be constant by the end of n_{gen}. That is, $O_{n_{gen}} = O_{n_{gen}-1}$.
Q_3	Viable oviposition date	The last generation's peak oviposition date must be within user-defined[a] viability limits: $O_{\min} < O_{n_{years}} < O_{\max}$.

[a] For the purposes of this investigation, viability limits were set at O_{min}=180 (end of June) and O_{max}=243 (end of August).

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

$$P_L = Q_1 \wedge Q_2 \wedge Q_3 \qquad [4]$$

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

$$F_L = \frac{\sum_{i=1}^{n_{\max}} (P_L)_i}{n_{\max}} \qquad [5]$$

The Safranyik-Logan hybrid model is formed by simply replacing the P_1 criterion from Table 1 and equation [1] with Logan's P_L. Thus, the logical P_S in Safranyik's model becomes P_H in the hybrid model:

$$P_H = P_L \wedge P_2 \wedge P_3 \wedge P_4 \qquad [6]$$

and the overall value of F_H is computed in the same manner as in equation [2], from P_H instead of P_S:

$$F_H = \frac{n_{run}}{n_{\max}} \sqrt{Y_1 + Y_2} \qquad [7]$$

where

$$n_{run} = \left[(P_H)_1 \wedge (P_H)_2\right] + \sum_{t=2}^{n_{\max}-1} \left\{\left[(P_H)_{t-1} \wedge (P_H)_t\right] \vee \left[(P_H)_t \wedge (P_H)_{t+1}\right]\right\} + \left[(P_H)_{n_{\max}-1} \wedge (P_H)_{n_{\max}}\right] \qquad [8]$$

Climatic suitability classes were defined for F_H as described in Table 2. Projections of future climatically suitable habitats for MPB based on the climate change scenario were constructed in 10-year intervals from 1981-2010 to 2041-2070 using BioSIM© software

(Régnière et al. 1995; Régnière 1996) as described above (section 2.1.3) for both the Safranyik and Safranyik-Logan hybrid models.

2.3.3 Latitudinal variation in development rate

The existing models of climatic suitability for MPB rely on established relationships between heat accumulation derived from a given weather regime, and beetle developmental thresholds and rates (see Logan and Powell 2001, 2004; Safranyik et al. 1975). Recently in the US, Bentz et al. (2001) found that the developmental rate of MPB from southern populations (i.e., warmer habitats) was slower than that of more northern populations (i.e., cooler habitats). They speculated that this was an evolutionary adaptation to ensure adaptive seasonality. If this is a phenomenon that is widespread throughout the range of MPB, then predictions of potential range expansion at the beetle's northern limits may significantly underestimate the rate of actual range expansion.

Table 4. Source data for a meta-analysis of MPB degree-day requirements in relation to effective latitude.

Population	Latitude	Longitude	Elevation (m)	Degree-days (eggs to teneral adult)	Reference
Wasatch National Forest, Utah[a]	40° 55' N	110° 40' W	1829	375	Amman & Cole 1983
Sawtooth National Recreation Area, Idaho	44° 07' N	114° 52' W	1999	502[b,c]	Bentz et al. 2001
Dixie National Forest, Utah	37° 30' N	112° 37' W	2463	812[b,c]	Bentz et al. 2001
Wasatch National Forest, Utah	40° 55' N	110° 40' W	1829	392[c]	Bentz et al. 1991
Horse Thief Creek, BC	50° 30' N	116° 00' W	835	278	Reid 1962
Riske Creek, BC	51° 58' N	122° 33' W	1006	392[c]	Safranyik & Whitney 1985
Riske Creek, BC	51° 58' N	122° 33' W	1006	408[c]	Safranyik & Whitney 1985
Riske Creek, BC	51° 58' N	122° 33' W	1006	434	Whitney & Spanier 1982

[a] Location information provided by B.J. Bentz (pers. comm.)

[b] Degree-days recalculated for the period from egg lay to emergence of teneral adults based on proportion of time spent in each life stage as determined by Safranyik and Whitney [1985 (see text for details)]

[c] Degree-days standardized for accumulation threshold T_{min}=10ºC (see text for details)

To determine if MPB populations exhibit a latitudinal gradient in development rates we conducted a meta-analysis of MPB degree-day requirements based on published data for beetle populations throughout western North America. Six studies with sufficient data for eight distinct beetle populations were identified (Table 4). In several cases, authors did not assess development over equivalent portions of the beetle lifecycle. However, Safranyik and Whitney (1985) reported stage-specific developmental parameters. Therefore, we chose to standardize degree-day requirements for the period beginning with egg lay and ending with emergence of teneral (i.e., new) adults, and then recalculated the degree-days reported by those studies that considered larger portions of the lifecycle (e.g., eggs to mature adults) by adjusting values based on the proportion of time spent in each life stage (see Safranyik and Whitney 1985). In addition, not all studies utilized the same minimum temperature threshold (T_{min}) to determine degree-day accumulation. Therefore, where required we recalculated degree-day values based on T_{min}=10°C (Table 4).

Location data for each population (i.e., latitude and elevation) were used to calculate effective latitude (Hopkins 1920). A simple linear regression was used to determine whether MPB populations exhibited a latitudinal gradient in the number of degree-days required to complete development.

3 Results and Discussion

3.1 Climatically benign habitats

During the latter half of the last century, there has been a substantial shift in climatically benign habitats for MPB northward, and toward higher elevations. Areas most suitable for MPB have expanded dramatically in south-central and south-eastern British Columbia (Fig. 1). Indeed, the amount of climatically optimal habitat for MPB (i.e., extreme CSCs) has increased by more than 75% since approximately 1970 (Fig. 2).

Increases in the amount of optimal habitat for MPB have occurred largely as a consequence of a reduction in the area of unsuitable habitat (i.e., very low and low CSCs) during the last several decades (Fig. 2). The relatively sudden increase in the amount of optimal habitat is most likely due to an increase of >1°C in the average annual temperature of central BC over the same period (BC Ministry of Water, Land & Air Protection 2004). Interestingly, the CSC coverage derived from the most recent weather normals (i.e., 1971 – 2000) very accurately delineates the regions affected during the early stages (up to 2000) of the current outbreak (see http://www.for.gov.bc.ca/hfp/health/ overview/overview.htm).

3.2 Past range expansion

Mountain pine beetle populations have followed the apparent shift in climatically suitable habitats during the past three decades. Prior to 1968, no infestations had ever been recorded in areas with very low and low CSCs (Safranyik et al. 1975). Since then, the increase (at an increasing rate) in the number of infestations over time in the historically very low and low CSCs (Fig. 3) indicates that there has been sufficient change in the climatic conditions in these habitats to have allowed the establishment and persistence of MPB populations.

It is important to note that the increase in the occurrence of MPB in these formerly climatically unsuitable areas can only be explained by changes in climate. Although temporal changes in the distribution of susceptible hosts (i.e., the amount of mature pine) will affect the distribution of MPB infestations, unless the climatic conditions outlined

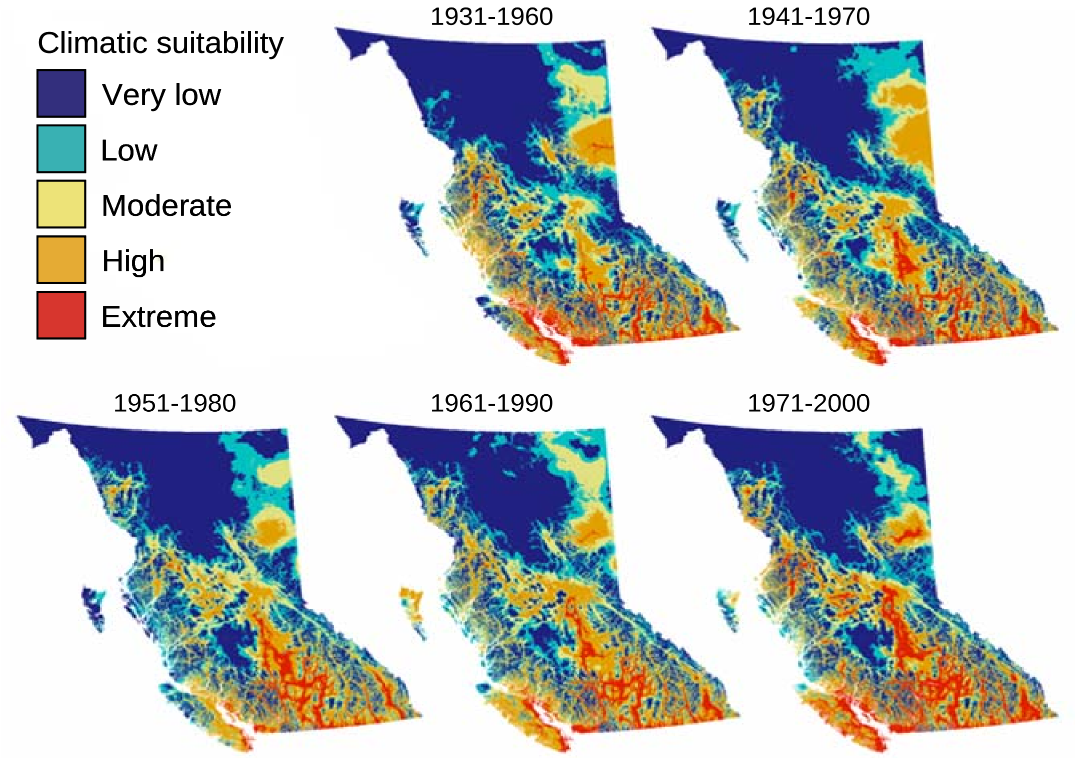

Figure 1. Historic distributions of climatically suitable habitats for the mountain pine beetle in BC derived from real weather data and an empirical model of the influence of climate on the establishment and persistence of beetle populations. Areas with “very low” suitability are unsuitable for mountain pine beetle whereas “extreme” areas are those considered climatically optimal.

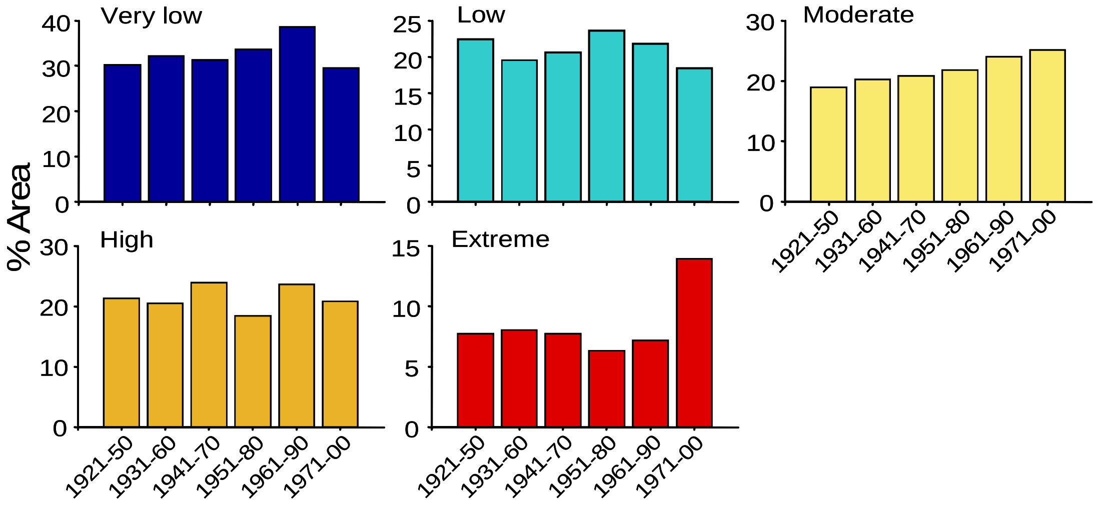

Figure 2. Changes through time in percentage area of climatically suitable habitats for the mountain pine beetle in BC. Areas with “very low” suitability are unsuitable for mountain pine beetle whereas “extreme” areas are those considered climatically optimal.

in the Safranyik model are met within a mature pine stand, successful establishment of a beetle population is precluded (Safranyik et al. 1975; Safranyik 1978).

As expected, if climatic conditions have improved in historically unsuitable areas, then conditions should ameliorate, and the number of infestations increase, in the more suitable habitats. This was the case in the historically moderate and high CSCs (Fig. 3). However, by the mid-1980s the number of infestations in the habitats that were previously most suitable to MPB (i.e., extreme CSC) declined dramatically (Fig. 3). There are two potential explanations for a decrease in the number of infestations in the formerly extreme CSC: it may be a consequence of (i) a reduction in the amount of mature pine in these habitat types due to disturbance (i.e., harvesting, fire, past MPB outbreaks), or (ii) adverse effects of warmer temperatures due to climate change. Recent modelling efforts (Taylor and Carroll 2004; Taylor et al. 2006) strongly suggest that the amount of mature lodgepole pine has increased dramatically in BC during the past century in all habitat types. Therefore, the decline in infestations is most likely due to the adverse effects of changing climate. Studies by Logan and Bentz (1999) and Logan and Powell (2001) have shown that if heat accumulation during summer is sufficiently high, MPB populations may be forced into partial multivoltinism which will cause cold-susceptible stages (eggs, pupae, adults) to overwinter and thus interrupt flight synchrony and mass attack success in the following year.

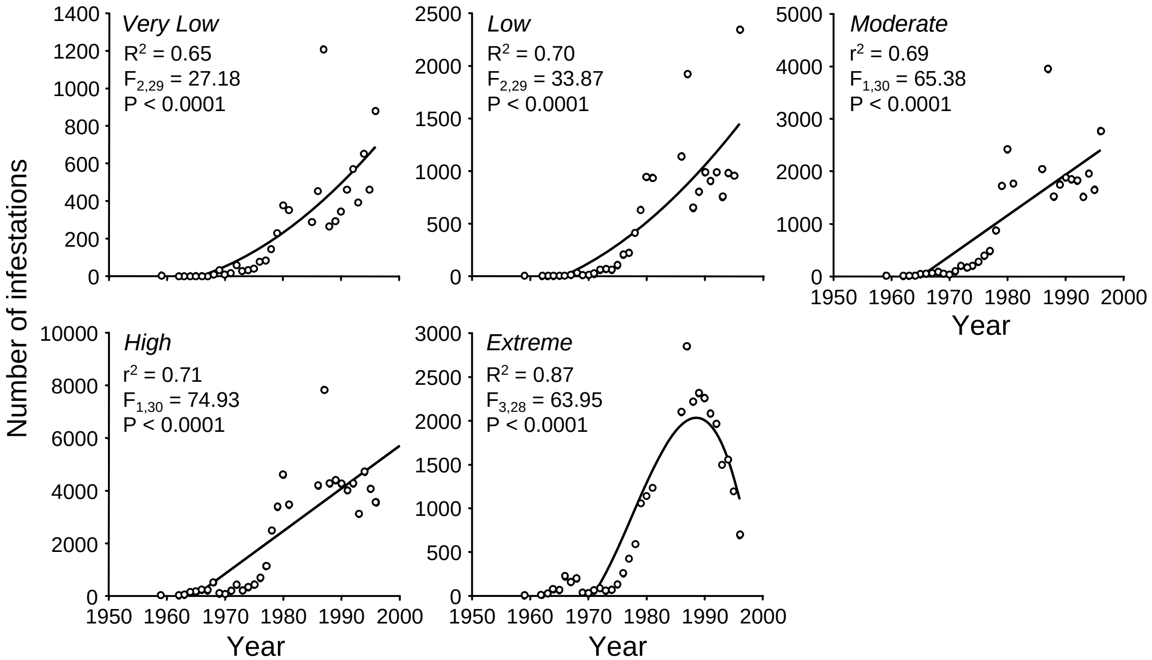

Figure 3. Number of infestations *versus* year and climatic suitability class (CSC) derived from 1941-1970 climate normals (30-year monthly means and extreme minima and maxima) for mountain pine beetle in BC. “Very low” CSCs are habitats with climatic conditions unsuitable for mountain pine beetle whereas “extreme” CSCs are those considered climatically optimal.

3.3 Future range expansion

Under the plausible climate change scenario, the Safranyik climatic suitability model predicts steadily improving conditions for MPB across Canada. By the 2011-2040 time step, large parts of the boreal forest are projected to be within moderate CSCs, and by 2041-2070 most of the western and central regions (north of the prairies) are predicted to be climatically optimal for MPB (Fig. 4).

By contrast, the Safranyik-Logan hybrid model is much more conservative. The inclusion of the tightly constrained requirement for an adaptive seasonality renders most of the boreal forest climatically unsuitable during the projected near future. However, as the climate change scenario progresses, a band of low to moderately suitable habitats spreads across Canada such that by the 2011-2040 time step there is a more-or-less contiguous corridor of climatically marginal habitat extending through the boreal forest (Fig. 5).

Conditions within the band of climatically marginal habitat, as predicted by the hybrid model, steadily improve with additional warming. However, the band itself shifts northward, and by 2041-2070 most of the climatically optimal habitats east of the Rocky Mountains are situated within the northernmost portions of the boreal forest (Fig. 5). The northward shift in climatically suitable habitats is a direct consequence of excessive warming of southern regions, and the resultant partial multivoltinism within MPB populations (Logan and Powell 2001, 2004).

The differences in the predictions of future climatically suitable habitats for MPB by the two models results from the narrow range of temperatures within which the adaptive seasonality flag, P_L from equation [4], is satisfied within the Safranyik-Logan hybrid model. An upper limit of temperature accumulation for the maintenance of adaptive seasonality for MPB is strongly suggested by the dramatic decline in the number of infestations in the historically optimal habitats in recent years in BC (see Fig. 3). Thus, the hybrid model should more accurately reflect the distribution of climatically benign habitats under the climate change scenario. However, upon closer examination of the predictions based on the earliest future time step (i.e., 1981-2010), the Safranyik-Logan hybrid model appears to significantly underestimate the availability of suitable habitats compared with the historic distribution of MPB (see Fig. 5).

Clearly, as suggested by Fig. 3 (and from basic physiological expectations), an upper threshold for temperature accumulation must exist. Since MPB seasonality is under direct temperature control (i.e., there is no diapause), regional populations will be adapted to regional climate (Logan and Bentz 1999). The under-estimation of climatic suitability by the Safranyik-Logan hybrid model through the inclusion of an upper thermal threshold required for adaptive seasonality, likely results from fine-scale adaptations to local climate by MPB. Although our meta-analysis did not detect a latitudinal gradient in development time for MPB, there was considerable variation among the subpopulations

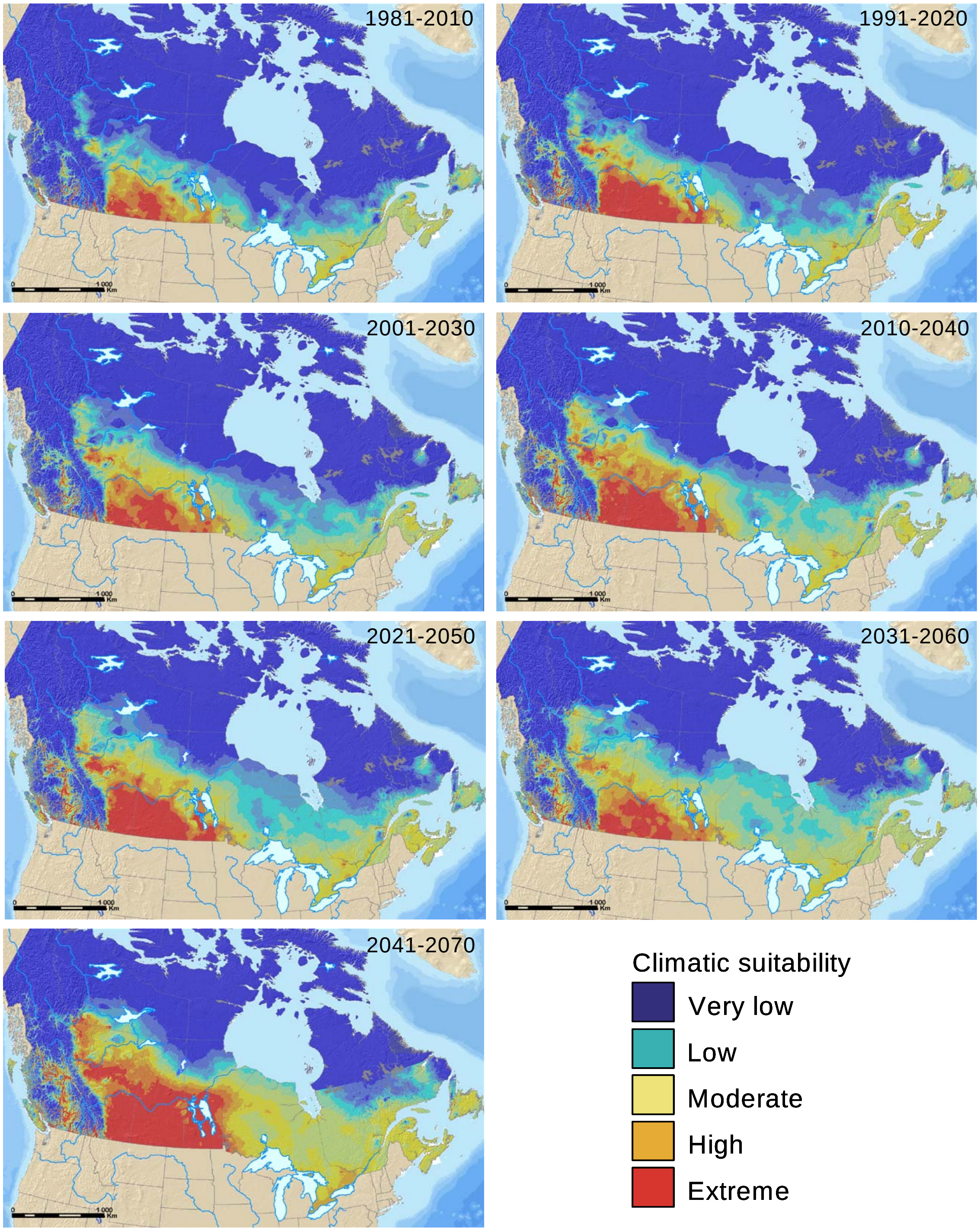

Figure 4. Future distributions of climatically suitable habitats for the mountain pine beetle in Canada derived from a plausible climate change scenario [i.e., a doubling of atmospheric CO_2 relative to the 1980s by approximately 2050 (see Boer et al. 2000)] and the Safranyik model of climatic suitability (Safranyik et al. 1975). Areas with "very low" suitability are unsuitable for mountain pine beetle whereas "extreme" areas are those considered climatically optimal.

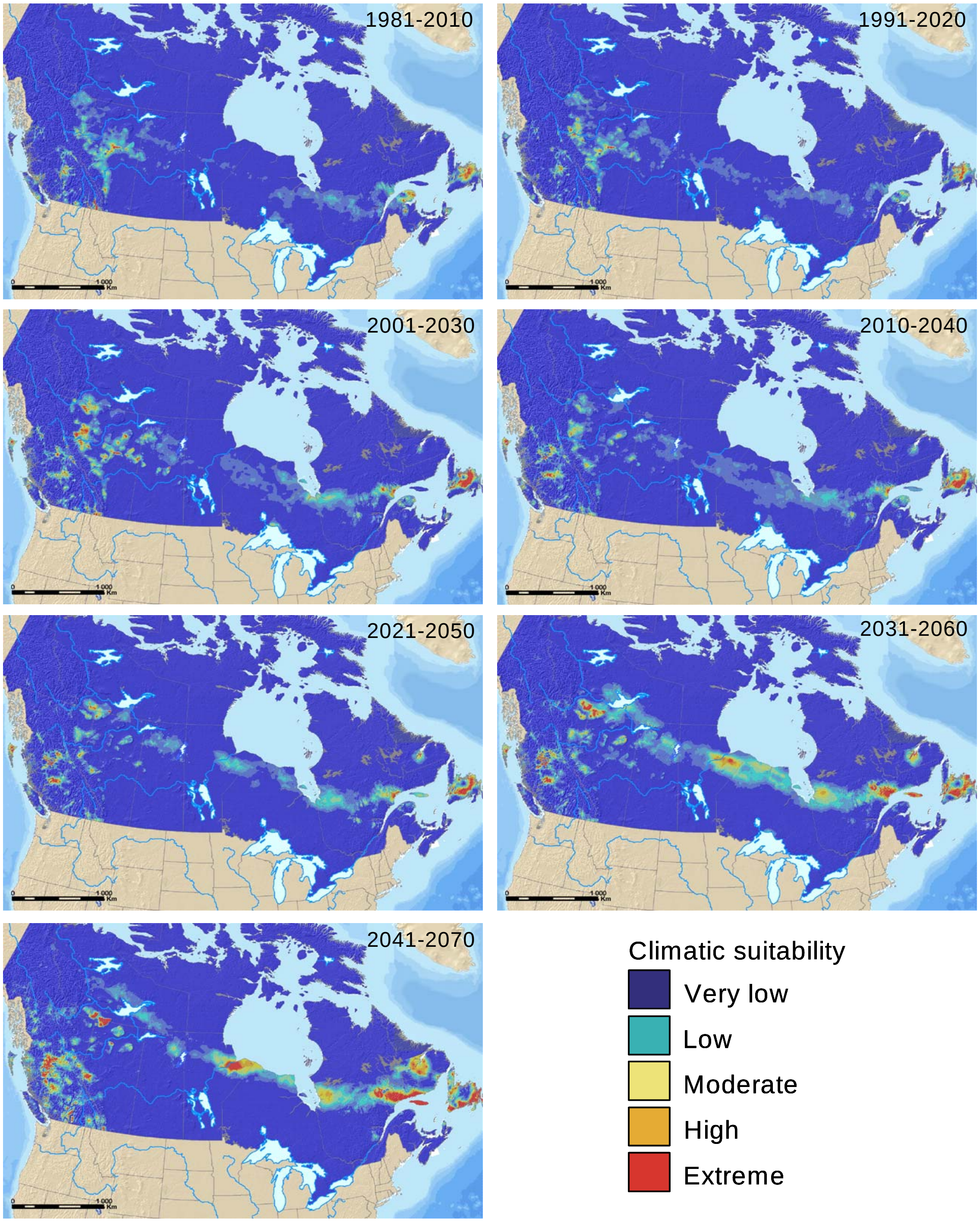

Figure 5. Future distributions of climatically suitable habitats for the mountain pine beetle in Canada derived from a plausible climate change scenario [i.e., a doubling of atmospheric CO_2 relative to the 1980s by approximately 2050 (see Boer et al. 2000)] and the Safranyik-Logan hybrid model of climatic suitability [Safranyik et al. 1975; Logan and Powell 2001 (see text for details)]. Areas with "very low" suitability are unsuitable for mountain pine beetle whereas "extreme" areas are those considered climatically optimal.

in their degree-day requirements to reach the teneral adult stage (Fig. 6). Given the significant dispersal capacity of MPB (see Safranyik and Carroll 2006) and the rapid colonization of new climatically benign habitats by MPB in recent years (see Fig. 3), it is possible that as thermal conditions of a habitat degrade due to excessive warming, beetles from subpopulations capable of maintaining adaptive seasonality under the new thermal regime will rapidly invade. Thus, MPB may persist for a time in environments considered unsuitable based upon predictions derived from static developmental parameters, and in doing so, cause the apparent under-estimation of climatically suitable habitats by the hybrid model.

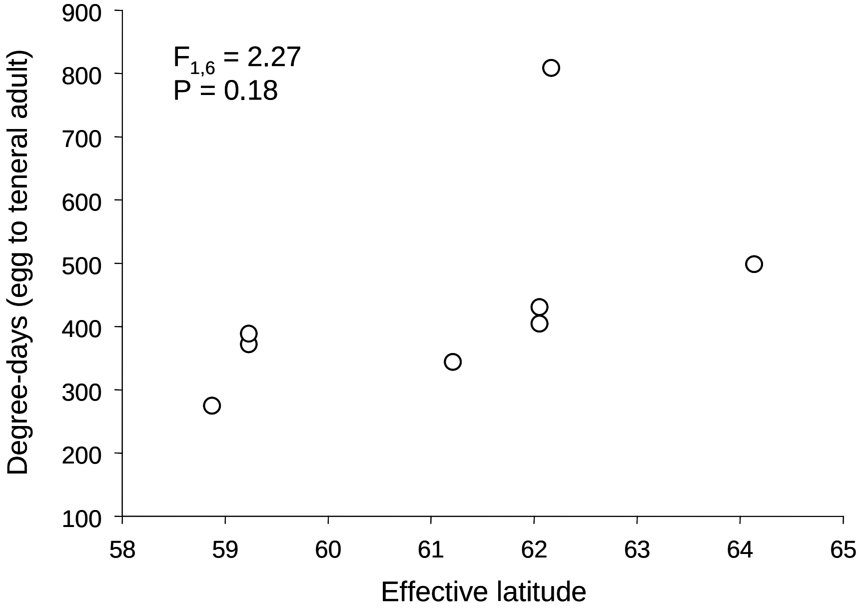

Figure 6. Degree-day requirements for development of mountain pine beetle from eggs to teneral adults in relation to effective latitude derived from Hopkins' Bioclimatic Law (Hopkins 1920). Data were obtained from a meta-analysis of data from six studies involving eight populations (see text for details).

Additional research is required to quantify the geographical variation in MPB developmental parameters and determine the relevant upper threshold(s) for temperature accumulation for adaptive seasonality. Until then, it will remain difficult to predict the point at which excessive warming may render a region unsuitable for MPB. However, for short-term predictions of MPB range expansion into formerly unsuitable (i.e., too cold) habitats, inclusion of an upper threshold is not critical unless the rate of climate change is much higher than expected. Thus predictions derived from the Safranyik model should comprise adequate projections of potential range expansion by MPB under climate change for the near future.

Predictions of the potential for continued range expansion in the near future have become critical with the recent establishment of infestations along the north-eastern slopes of the Rocky Mountains. Historically, invading beetles could not persist there due to adverse climate; however, climatic suitability has improved dramatically in recent decades (see Fig. 1). Assessments of the new infestations revealed that they arrived largely in 2002 as a consequence of long-distance dispersal from outbreak populations most probably located several hundred kilometers to the southwest, across the Rocky Mountains (Safranyik and Carroll 2006). Mountain pine beetle is now situated in close proximity to the boreal forest. Jack pine, a viable host for MPB (Furniss and Schenk 1969; Safranyik and Linton 1982; Cerezke 1995), forms a significant component of the boreal forest, extending all the way to the eastern seaboard (Fig. 7a). Moreover, jack and lodgepole pines hybridize across northern Alberta, potentially forming an effective corridor through which MPB may invade the boreal forest (Fig. 7b). The predictions of future climatic suitability through the "invasion" corridor by both models indicate that climate is unlikely to be a barrier to continued eastward expansion by MPB (see Figs.4 and 5).

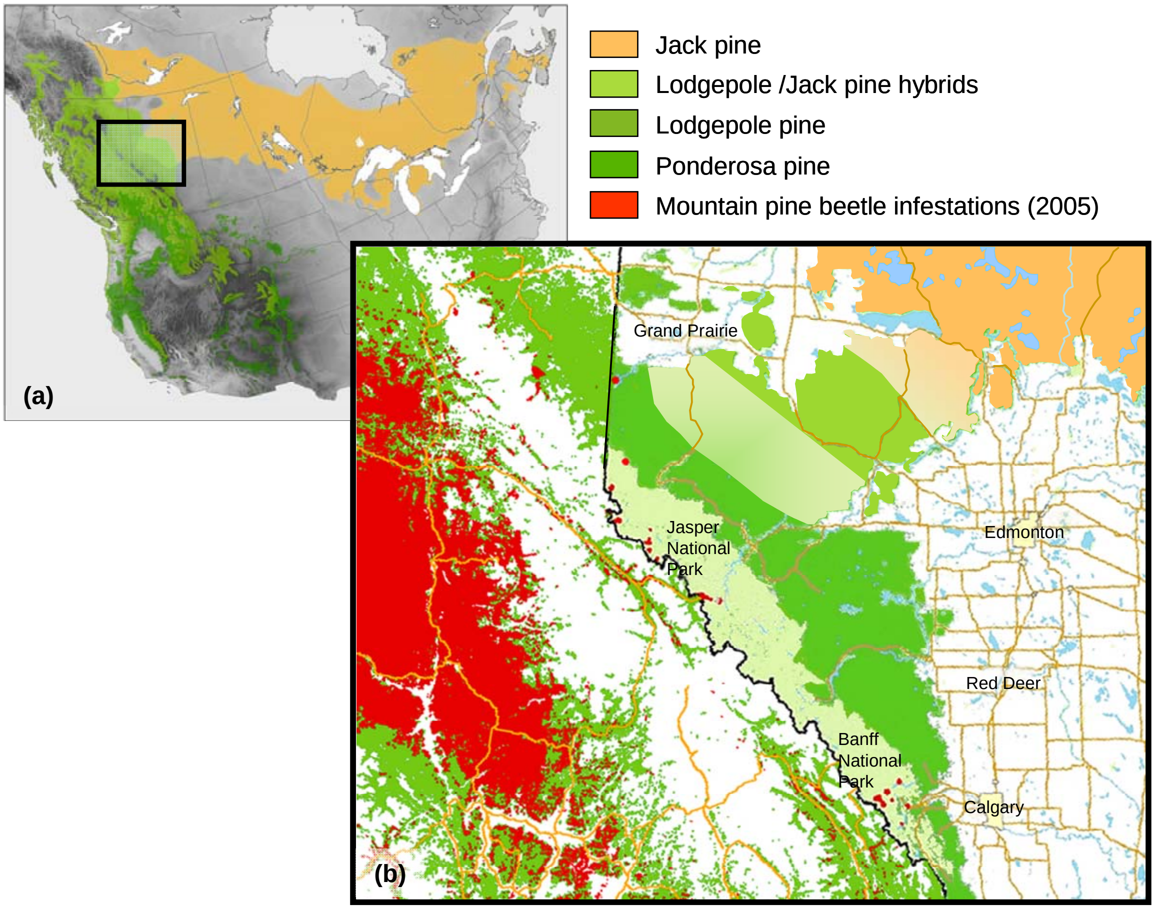

Figure 7. Distribution of the major hosts of mountain pine beetle in North America (lodgepole and ponderosa pines) in relation to the jack pine, a potential host within the boreal forest (a) [adapted from Little and Critchfield (1969)], and the north-eastern distribution of mountain pine beetle infestations as at 2005 (b). Note the proximity of mountain pine beetle to the areas of hybridization of jack and lodgepole pines.

4 Conclusions

Since the mid 1990s, MPB populations have erupted across interior BC to form the largest outbreak ever recorded. For an outbreak to occur, two main conditions must be satisfied. First, there must be an abundance of large, mature pine trees; the beetle's preferred resource. Second, there must be several years of favourable weather for beetle survival; specifically, hot summers that facilitate beetle reproduction, and mild winters that allow their offspring to survive (reviewed by Safranyik and Carroll 2006). Recently, it has been shown that largely as a consequence of effective fire suppression, there was >3 times the amount of mature pine in BC at the start of the current outbreak when compared with 100 years ago (Taylor and Carroll 2004; Taylor et al. 2006). Furthermore, climatic conditions during recent decades have been highly amenable for beetle survival (Carroll et al. 2004). Thus, both conditions for an outbreak have coincided with sufficient magnitude to cause the largest MPB outbreak in recorded history.

In the past, large-scale MPB outbreaks collapsed due to localized depletion of suitable host trees in combination with the adverse effects of climate (Safranyik 1978). The results of our investigation suggest that in the absence of an unusual weather event (i.e., an unseasonable cold period or an extreme winter), the current outbreak may not entirely collapse as in the past. Expansion by the beetle into new habitats as global warming continues will provide it a small, continual supply of mature pine, thereby maintaining populations at above-normal levels for some decades into the future.

Historically, MPB populations have been most common in south-central BC and the north-western US. Non-forested prairies and the high elevations of the Rocky Mountains have contributed to confining it to that distribution. Over the last several decades, the amount of climatically benign habitat for MPB has increased significantly, followed closely by rapid invasion of these new habitats by the beetle. More recently, the enormous ongoing epidemic in BC appears to have exacerbated the rate of range expansion. During emergence and dispersal, a small proportion of beetles will fly above the forest canopy and be carried aloft by winds (Jackson et al. 2005), often travelling tens or even hundreds of kilometres (Safranyik and Carroll 2006). The sheer size of the current outbreak has ensured that vast numbers of beetles have been available in recent years for long-distance dispersal, thereby increasing the probability that large populations will encounter new climatically suitable pine forests. By this mechanism, MPB has successfully breached the Rocky Mountain geo-climatic barrier and established in north-eastern BC and adjacent Alberta.

The climate change scenario utilized in this study comprises a relatively conservative rate of warming (Houghton et al. 1990). However, even our most restrictive predictions of the distribution of climatically suitable habitats suggest that much of the boreal forest will be available to MPB in the near future. Although both the potential rate of increase of MPB populations in jack pine, and the abundance and distribution of susceptible stands within the boreal forest is currently unknown, continued eastward expansion by MPB seems probable.

5 Acknowledgements

Invaluable technical assistance was provided by Gurp Thandi and Rémi St-Amant. This project was funded by the Government of Canada through the Mountain Pine Beetle Initiative, a six-year, $40 million Program administered by Natural Resources Canada, Canadian Forest Service. Publication does not necessarily signify that the contents of this report reflect the views or policies of Natural Resources Canada – Canadian Forest Service.

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