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**Mountain pine beetle range expansion:
Assessing the threat to Canada's
boreal forest by evaluating the endemic niche**
Final Report Ver. 1.1

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**Mountain Pine Beetle Working Paper 2010-02**

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# Abstract

Mountain Pine Beetle (MPB) recently breached the Continental Divide and invaded northern Alberta. While the region is only marginally climatically suitable for the MPB (see review in Nealis and Peter 2008), populations could increase in the short term, given successive years of favourable weather.  In addition, if the beetle is able to establish itself in the region and persist, even at very low (endemic) population levels, there is the potential for future eruptions with climate change (Safranyik et al. 2010). This study investigated the endemic niche for MPB in north-western Alberta at two sites.

Our results indicate that an endemic niche for the MPB likely exists at the two sites that we sampled in the region based on the availability of susceptible trees and the assemblage of secondary bark beetles, which may impact endemic MPB populations (Carroll et al. 2006a; Smith et al. 2011). Over one-third of pine trees greater than 10 cm in diameter at both sites had at least two putative vigour-impairing injuries. Endemic-type attacks were located on trees in both stands and the number of trees with endemic-type attacks remained relatively consistent between years at one site. Ten of the 12 trees we located with endemic-type MPB attacks were already colonized by secondary bark beetles. The number of trees attacked by secondary bark beetles ranged from three to eight trees per hectare. The assemblage of secondary bark beetles colonizing the lower boles of trees consisted of eight species in northern Alberta, with trees most frequently attacked by *Orthotomicus latidens, Dendroctonus murrayanae* and *Hylurgops* spp.

After the 2006 immigration event, beetle populations at our sites in northern Alberta declined in 2007 and 2008, with a reduction in the number of mass-attacked trees and an estimated population decrease of 44%. The explosive 420% population increase at one site in 2009 far exceeded our estimate of production by the *in situ* 2008 population and was likely the result of another major long-distance dispersal event that purportedly occurred in the region.

During our study we observed great variation in MPB attack behaviour (e.g., annual attack), phenology (e.g., early adult emergence, multiple cohorts), and overwintering survival within and among stands. There are apparent geographic differences in MPB attack dynamics and reproductive success that may result in unexpected local and regional population dynamics (Clark et al. 2010; Cudmore et al. 2010). Future research should focus on understanding MPB biology and population dynamics in its expanded range under changing environmental conditions because this knowledge is critical for assessing the threat to our boreal forest resources and for developing effective management strategies for the region.


**Keywords:** mountain pine beetle, *Dendroctonus ponderosae*, bark beetle, population dynamics, endemic populations, boreal forest, lodgepole pine, jack pine, hybrid pine

# Résumé

Le dendroctone du pin ponderosa a récemment franchi la ligne continentale de partage des eaux et envahi le nord de l'Alberta. Bien que l'espèce puisse tout juste vivre dans les conditions climatiques de cette région (voir Nealis et Peter, 2008), elle pourrait connaître un accroissement rapide de population si les conditions climatiques demeuraient favorables plusieurs années consécutives. De plus, si l'espèce parvient à s'établir dans la région de façon durable, même à des niveaux de population très faibles (endémiques), elle pourrait connaître une explosion démographique sous l'effet du réchauffement climatique. Nous avons étudié la possibilité de survie du dendroctone du pin ponderosa à un niveau endémique dans deux localités du nord-ouest de l'Alberta.

Nos recherches montrent que le dendroctone du pin ponderosa pourrait probablement survivre à un niveau de population endémique dans les deux localités, compte tenu des deux facteurs susceptibles d'avoir une incidence sur sa population, à savoir la présence d'arbres vulnérables et l'assemblage de scolytes secondaires (Carroll *et al*., 2006a; Smith, 2008). Dans les deux localités, plus du tiers des pins de diamètre supérieur à 10 cm présentaient au moins deux blessures susceptibles d'affaiblir l'arbre attribuées au dendroctone. Des attaques de niveau endémique ont été observées dans les deux peuplements, et dans l'un d'eux le nombre d'arbres attaqués demeurait sensiblement le même d'une année à l'autre. Dix des 12 arbres sur lesquels nous avons observé des attaques de niveau endémique étaient déjà colonisés par des scolytes secondaires. Le nombre d'arbres attaqués par des scolytes secondaires variait entre trois et huit arbres par hectare. Nous avons identifié huit espèces de scolytes secondaires attaquant la partie inférieure du tronc des arbres, les plus fréquentes étant l'*Orthotomicus latidens*, le *Dendroctonus murrayanae* et des *Hylurgops* spp.

Après l'épisode d'immigration de 2006, l'effectif du dendroctone a décliné en 2007 et en 2008 dans les deux localités du nord de l'Alberta où nous avons réalisé notre étude, et le nombre d'arbres subissant des attaques massives a diminué. Le déclin de la population de dendroctone a été estimé à 44 %. L'explosion de la population du ravageur (augmentation de 420 %) survenue dans une des localités en 2009 dépassait de loin notre estimation de la productivité de la population en place en 2008 et résultait probablement d'un autre épisode de dispersion massive à grande distance.

Au cours de l'étude, nous avons observé des variations importantes du comportement d'attaque (taux d'attaque annuel, etc.), de la phénologie (émergence précoce des adultes, cohortes multiples, etc.) et de la survie hiémale du ravageur, entre peuplements comme au sein d'un même peuplement. Le comportement d'attaque et le succès de reproduction du ravageur semblent différer d'une région à l'autre, et les différences peuvent avoir des effets inattendus sur la dynamique des populations à l'échelle locale et régionale (Clark, 2008; Cudmore, 2009). Il faudrait étudier la biologie et la dynamique des populations du dendroctone du pin ponderosa dans sa nouvelle aire de répartition et au vu des changements climatiques, car l'évaluation de la menace pour les forêts boréales et la mise au point de méthodes de lutte adaptées à la région reposent sur ces connaissances.


**Mots clés :** dendroctone du pin ponderosa, *Dendroctonus ponderosae*, scolyte, dynamique des populations, population endémique, forêt boréale, pin tordu latifolié, pin gris, pin hybride

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# 1. Introduction

Mountain pine beetle (MPB; *Dendroctonus ponderosae* [Hopkins]) populations cycle through four phases: endemic, incipient-epidemic, epidemic, and post-epidemic or collapse (Safranyik and Carroll 2006). The epidemic or outbreak phase is the most well-known because of the economic and ecological impacts caused by enormous populations of beetles as they kill large areas of trees across the landscape. During outbreaks, host tree resistance has little impact on the beetles' success as large populations are able to overcome the defences of healthy trees by attacking *en masse*. Landscape-level outbreaks, such as the 1990–2000s epidemic that has affected over 16 million ha as of 2010 in British Columbia, usually collapse and enter the post-epidemic phase once the insect runs out of suitable large-diameter host trees. Lethal low temperature events over multiple, successive years may also cause populations to collapse; however, very large populations of beetles are capable of rebounding quickly from single, high-mortality events.

Most of the time MPB populations exist in the endemic state, which is characterized by very low numbers of beetles per hectare. Endemic populations are restricted to attacking weakened or moribund trees because their numbers are insufficient to coordinate mass attacks on healthy, well-defended trees (Safranyik and Carroll 2006). The thin phloem and often relatively small diameter of such marginal hosts are not conducive to brood development (Amman 1972). In the endemic population phase, interactions with host trees and secondary species of bole-infesting bark beetles, which are non-aggressive and only attack severely stressed and dead trees, are likely major factors affecting beetle success. In southern British Columbia, endemic populations of MPB may compete with secondary bark beetles for habitat (Safranyik et al. 1999), or the presence of secondary species may actually benefit endemic MPB populations by promoting their establishment and long-term persistence (Carroll et al. 2006a). Through competition and facilitation, secondary bark beetles may in part define MPB's endemic niche.

Once MPB populations increase to a point where there are enough beetles in a stand to successfully coordinate mass attacks on trees, the incipient-epidemic phase begins (Safranyik and Carroll 2006). Initially, beetles may select old or stressed trees that have reduced defences; however, these trees still have the capacity to resist attacks by secondary bark beetles. As populations rise, MPB is able to kill more vigorous hosts with thicker phloem that support greater brood production. More vigorous hosts can be successfully attacked *en masse* as beetle density increases, thus host availability increases as populations increase. Such positive feedback may result in an outbreak that lasts until all susceptible large-diameter host trees in a stand are killed.

Large populations of MPBs from the recent epidemic in British Columbia managed to breach the Rocky Mountain Continental Divide and invade the Peace River Region in British Columbia and northern Alberta. The largest known incursion occurred in 2006, but there is also evidence of a smaller invasion in 2002. The fate of these invading populations, and the threat they present to Canada's boreal forest, which contains significant amounts of susceptible pine species, is difficult to determine (Nealis and Peter 2008; Safranyik et al. 2010). The region is only marginally climatically suitable for MPB development; however, climatic suitability is expected to increase in the future, based on climate change predictions (Carroll et al. 2006b; Safranyik et al. 2010). Thus, if an endemic niche exists for the MPB east of the Divide and the beetle is able to establish and persist even at very low, virtually undetectable levels, a potential threat looms over the future as climatic conditions become more favourable for population growth.

## 1.1 Project Overview and Objectives

We investigated whether an endemic niche exists for the MPB in north-western Alberta, a region east of the Rocky Mountains that was recently invaded by beetles. Our approach was to sample

endemic or endemic-incipient MPB populations in the region *in situ*, including the assemblage of secondary bark beetles with which the MPB may interact.

The objectives of this project were threefold: (i) determine the potential for MPB to persist at endemic levels east of the Rockies; (ii) if persistence is possible, determine the rate of population increase or decrease to assess the potential for eruptions and spread; and (iii) provide data to existing and emergent decision support tools to re-parameterize, where appropriate, to accommodate MPB dynamics in a new habitat.

# 2. Methods

## 2.1 Site Selection

In mid-June 2008, we established two sites to assess the potential endemic niche available to the MPB in the recently invaded lodgepole–jack pine hybrid zone east of the Rocky Mountain Continental Divide (Figure 1). The Musreau Lake site (baseline point of commencement [POC]: 54.5597 N, 118.6634 W; elevation 930 m) was approximately 70 km south of Grande Prairie, Alberta. The Two Lakes site (baseline POC: 54.6575 N, 119.8077 W; elevation 1130 m) was approximately 90 km southwest of Grande Prairie. We selected sites that were well within the region invaded by the MPB in 2006 according to provincial overview survey data (Alberta Sustainable Resource Development 2007). However, to assess the local dynamics of endemic populations, we selected sites that had few to no mass-attacked trees in the stand in recent years, based on a rapid ground survey. In addition, aerial overview survey data indicated little to no MPB activity in adjacent stands. We also targeted stands deemed suitable for endemic MPB populations and secondary bark beetle species: stands with a significant component of large-diameter pine stems older than 80 years of age as well as suppressed, moribund pine trees. Site identification was aided by consultations with staff from the Alberta Ministry of Sustainable Resource Development.

At each site, the extent of the stand was determined and drawn on an aerial photograph. Stand boundaries were delimited by features such as creeks or ravines, roads, and clearcuts, or by changes in forest species composition and age. The stand at the Musreau Lake site totalled 9.5 ha in size, and the stand at the Two Lakes site was 6.2 ha.

## 2.2 Stand Layout

A spatial referencing system with transect strips to facilitate surveys and stations for geo-referencing specific trees was established in each stand. A baseline was established along one edge of the stand and marked with flagging tape. Transect lines running perpendicular to the baseline were established at 25 m intervals (starting at 0 m on the baseline POC) and marked with flagging tape. Stations were flagged every 50 m along each transect line for its entire length, which varied with the shape of the stand. Stations were labelled as follows: line number, starting at line 0 for the first transect at 0 m on the baseline; distance of transect line along the baseline; and distance of station along the transect line. For example, the station at 150 m along the second transect line was labelled "line 1, 25 m – 150 m." Using this method, we were able to locate a station within 25 m of every tree in the stand.
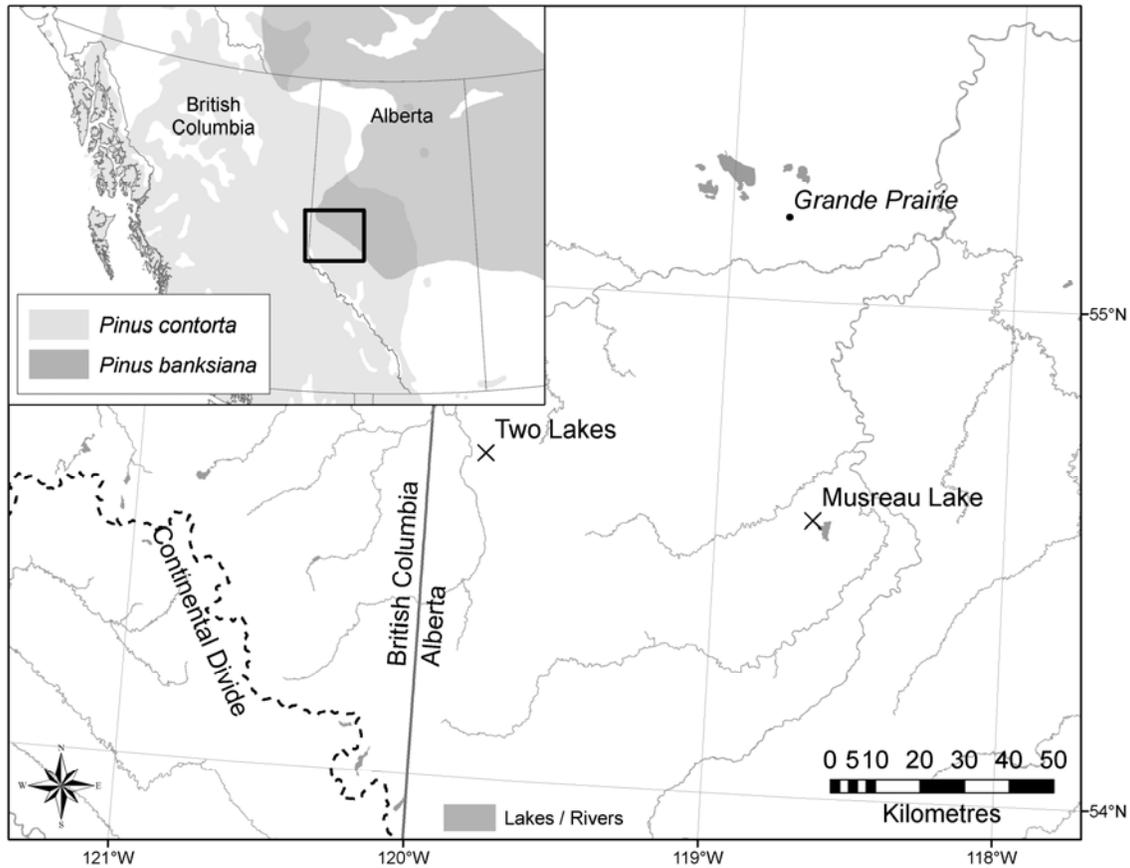
**Figure 1.** Location of two study sites in the region recently invaded by the mountain pine beetle east of the Rocky Mountains in north-western Alberta where the ranges of lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) overlap.

## 2.3 Stand Cruises

Once the transect strips were delineated, every pine tree was assessed for signs of bark beetle attack during a 100% cruise of the stand. MPB attacks on healthy trees are readily identified by the presence of pitch tubes on the outer bark, produced by the trees as a defence against attack. Highly stressed trees attacked by endemic populations of MPB or by secondary bark beetle species have compromised defences. Such trees are often difficult to locate because they do not produce visible pitch tubes on the outer bark. However, boring dust produced by attacking beetles remains visible in bark crevasses for a period of time following attack. The lower 2.5 m of the bole of each tree was examined for boring dust.

From previous work in the region, we knew that MPB flight could start by July in some locations and, based on temperature, we suspected that it could extend through August. Flight periods of secondary bark beetles vary by species, starting early in the spring and extending through the summer, with some species producing multiple generations per year (Bright 1976; Wood 1982). Therefore, to identify the timing of attacks by secondary species with respect to endemic-type attacks by the MPB, we conducted cruises in mid-June and again in mid-September. Cruising in June allowed us to identify trees attacked by secondaries prior to being attacked by MPB. The study was repeated in 2009 at each site; however, the September cruise was not conducted at the Two Lakes site as the stand was unexpectedly (to us) clearcut in early September 2009.

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Endemic-type MPB attacks are often located on trees already attacked by secondary species, but from our experience, MPB only attacks portions of the tree that still have living (pink) phloem. In contrast to some species of secondary bark beetles, MPB will not attack an area of the tree where the phloem has already started to discolour. Therefore, trees without any suitable habitat for MPB in the future, in the form of some pink phloem (e.g., a MPB mass-attacked tree, or a tree with red needles and all discoloured or sour phloem), were not re-assessed in subsequent cruises. As a result, attacks by secondary bark beetles on such trees were not assessed in this study.

## 2.4 Sampling Attacked Trees

For each pine tree located during the cruise with bark beetle attack (secondaries or MPB), we recorded the paced distance and azimuth to the nearest station, tree diameter at 1.3 m (DBH), the presence of any injuries, and the year of attack. Occasionally, we found trees mass attacked by MPB prior to 2007, and these were aged based upon bark, foliage, and fine branch condition, as well as the succession of other wood boring insects, using the methods of Carroll et al. (2006a).

We measured phloem thickness for attacked trees with living (pink) phloem still present; some trees required multiple sampling attempts to acquire a suitable pink sample. A 1.5 cm diameter arch punch was used to remove a sample from the north and south aspects at approximately 1.3 m. If bark samples (see below) were removed from trees, the phloem samples were taken adjacent to the bark samples. Samples were placed in small ziplock bags and transported in coolers to a hotel room or laboratory, where they were cut in half. The thickness of the phloem was measured to the nearest 0.1 mm using a dissecting microscope equipped with an ocular micrometer.

An increment hammer was used to remove two short increment cores at 90º to each other at 1.3 m on the bole. Cores were placed in short straws, transported in coolers to the laboratory, mounted in grooves on wooden boards, and sanded. The width of each annual ring for the last 12 years was measured using a Kutschenreiter Digital Positiometer (Measu-Chron, Bangor, ME, USA).

We identified most species of secondary bark beetles at the time of the cruise by carefully examining gallery morphology under the bark (Bright 1976; Wood 1982). In addition, some representative samples of adult insects were collected and identified using taxonomic keys in the laboratory (Bright 1976; Wood 1982). Because multiple species may attack one tree, the different textures of frass (boring dust) on the lower bole and the base of the tree were carefully examined to capture all species present. We limited the amount of disturbance to developing insects and the phloem, which may be potential bark beetle habitat in the future, by peeling back relatively small sections of bark and, where possible, pushing the bark flap back in place so that insects could continue gallery construction into adjacent, undisturbed phloem. Representative specimens of the different species were deposited in the Canadian Forest Service's (CFS) Reference Collection at the Pacific Forestry Centre (PFC) in Victoria, British Columbia (see Results).

For MPB-attacked trees with pitch tubes present (i.e., non-endemic type attack behaviour) we also estimated total attack height and classified each tree as follows:

1. Mass-attacked tree—attacks around the whole circumference of the lower bole and successful egg hatch likely;

2. Strip-attacked tree—attacks limited to a portion of the circumference of the lower bole resulting in localized necrosis; successful egg hatch likely somewhere in strip; and

3. Unsuccessfully attacked tree— tree that resisted attack by pitching-out parent beetles or by drowning the eggs in toxic resin.

For trees with strip attacks, we recorded the percentage of the bole circumference attacked. Trees

with frass produced by MPB (according to the size and texture), but with no pitch tubes on the outer bark, were classified as "endemic attacks." We checked under the bark to confirm that the frass was associated with a MPB gallery; however, this was often done during subsequent cruises to avoid disrupting attacking parents and potentially affecting brood production. Without pitch tubes present, it was not possible to determine total attack height.

In June 2008, when the plots were established, we counted the number of attack starts on 15 × 15 cm bark samples on the north and south aspects of the bole at 1.3 m of all mass-attacked trees. For strip-attacked trees, one bark sample was positioned in the centre of the attacked strip regardless of aspect. Clear plexiglass templates were used to determine the boundaries of the samples. For trees attacked in 2006 or earlier, we also recorded the number of emergence holes in the samples. For trees mass-attacked by MPB in 2007, we also carefully removed the bark samples using a hammer and chisel. The number of living insects in each life stage (larvae, pupae, and adults) in each bark sample was recorded, as well as the number of attack starts (ovipositional gallery starts), the total number of ovipositional galleries, and the cumulative length of all ovipositional galleries on the sample. Similarly, in June 2009 we assessed the number of attack starts and living insects in trees attacked in summer 2008. The number of emergence holes for trees attacked in 2007 or 2008 was sampled in September of the following year once emergence was complete. Emergence holes in the outer bark were counted in a 15 x 15 cm area located just above where the samples were removed in June. The bark sample method described above, used to assess potential brood production for mass and strip attacked trees, is not appropriate for endemic-type attacks because attack density is low on these trees.

## 2.5 Variable-radius Prism Plots

Variable-radius prism plots were established at each site to determine stand mensurational characteristics. Only trees with a DBH ≥ 10 cm were sampled. Nine plots were sampled at the Musreau Lake site and six plots were sampled at the Two Lakes site. Prism plots were located systematically along transects. Because we wanted to sample the characteristics of pine trees, we selected prisms with a basal area factor (BAF) between 2 and 5 based on their ability to capture at least seven pine trees per plot. Two prism plots at Two Lakes fell short of this target: one plot had no pine trees and another contained two pine trees.

For all trees in the prism plots, species and DBH was recorded. For all pine trees, height was determined using a sonic hypsometer. Samples of bark, phloem, and a small portion of sapwood were removed from each tree on the north and south sides with an arch punch 14 mm wide. Phloem samples were handled and measured as described above. Pine trees were examined for any damage or growth condition that could potentially result in loss of vigour, such as broken top, scarred bole, stem canker, thin crown, over-topping by neighbour trees and suppression, or leaning. Additionally, any insect activity, such as wood borer or Warren's root collar weevil (*Hylobius warreni* Wood.), was noted. Seven prism plots were randomly selected from the nine plots at Musreau Lake and two increment cores were taken from each pine tree in the seven plots to determine stand age as described above. In the five plots at the Two Lakes site that contained pine, every pine tree was sampled. Increment cores were prepared as described above, and the number of annual rings was counted using a dissecting microscope.

## 2.6 Data Analysis

To account for the basal area factor (BAF) used for each variable radius plot, a weighted stem density was calculated for each tree as follows (Avery and Burkhart 1994):

Weighted stems/ha = (BAF × 40 000) / ($\pi$ × DBH$^2$)

The weighted stems/ha were summed within prism plots, and the stand mean was calculated.

Weighted means were calculated for DBH, cumulative 5-year growth, height, age, and phloem thickness of pine. All variables were weighted by the ratio of the stem density for that particular tree to the stem density of the plot. Values were summed within plots and the mean was taken across plots.

Weighted mean percent pine density was calculated by dividing the weighted density of pine per plot by the weighted total density of all trees per plot and multiplying by 100. Weighted density of pine per plot was calculated by summing the individual weighted density values for each pine tree per plot. Total density was determined in the same manner. Similarly, the percentage of pine stems with at least one injury was determined by summing the weighted densities of pine trees with such injuries per plot and dividing by the total stem density for that plot and multiplying by 100.

Basal area per hectare was calculated by multiplying the number of trees in each prism plot by the prism factor. The basal areas for each prism plot in the stand were summed and divided by the total number of prism plots to calculate the average basal area.

For the Musreau lake stand, one-factor ANOVAs were used to test for differences among years in the diameter of attacked trees, attack density, and length of the attack zone. Significant $F$ tests were followed by Tukey-Kramer's Honestly Significant Difference test. Analyses were conducted using JMP® 8.0.2 (SAS Institute, Cary, NC), and significance was declared at $P \leq 0.05$.

# 3. Results

## 3.1 Stand Characteristics

Pine trees accounted for 84% of the basal area in the Musreau Lake stand and 48% of the basal area in the Two Lakes stand (Table 1). Both sites were within the lodgepole–jack pine hybrid zone in northern Alberta (Figure 1). Spruce (white spruce *Picea glauca* [Moench] Voss, Engelmann spruce *Picea engelmannii* Parry ex Engelm., or their hybrid) and trembling aspen (*Populus tremuloides* Michx.) accounted for the non-pine basal area component captured in the prism plots at both sites. There was also a small pocket of black spruce (*Picea mariana* [Mill.] BSP) the Two Lakes site.

Almost all of the pine trees in prism plots at the Musreau Lake site and over three-quarters of the pine trees at the Two Lakes site had at least one putative vigour-impairing injury (Table 1). The most common injury recorded at the Musreau Lake site was root feeding by Warren's root collar weevil (*Hylobius warreni* Wood.). It was found on 95% of the trees. The next most common injuries were stem crooks or sweeps (20 % of trees), stem scarring (16% of trees), and forked tops (12% of trees). Other types of injuries occurred on less than 8% of trees. The most common injuries recorded at the Two Lakes site were feeding by *H. warreni* (54% of trees), forked tops (27% of trees), stem scarring (15% of trees), stem crooks or sweeps (12% of trees) and broken tops (5% of trees). Approximately 45% of pine trees at the Musreau Lake site and 34% of pine trees at the Two Lakes site had two or more potentially vigour-impairing injuries.

**Table 1**. Mensurational characteristics of two forest stands used to assess the endemic niche available for the mountain pine beetle in the recently invaded lodgepole–jack pine hybrid zone east of the Rocky Mountain Continental Divide in northern Alberta. Only trees with diameters ≥ 10 cm at 1.3 m were sampled.

| Stand Attribute | Musreau Lake | Two Lakes |
|---|---|---|
| | Mean (SE) Weighted by Basal Area [a] | |
| Size of stand sampled (ha) | 9.5 | 6.2 |
| Basal area of all species ($m^2$/ha) | 38 (3) | 57 (5) |
| Basal area of pine ($m^2$/ha) | 32 (4) | 27 (7) |
| Percentage basal area pine (%) | 83 (6) | 48 (11) |
| Density of all species (stems/ha) | 584 (97) | 1561 (365) |
| Diameter of pine at 1.3 m (cm) | 30 (1) | 29 (1) |
| Cumulative 5-yr growth for pine (mm) | 1.7 (0.3) | 2.1 (0.4) |
| Height of pine (m) | 26 (0.3) | 21 (1) |
| Age of pine (yrs) | 105 (1) | 120 (1) |
| Phloem thickness of pine (mm) | 1.9 (0.1) | 2.2 (0.1) |
| Percentage of pine stems with 1 or more injuries (%) | 98 (2) | 76 (13) |

[a] To account for the slight bias of variable-radius prism plots towards larger trees, means were weighted by basal area. The mean for each prism plot was calculated from the number of stems per hectare that each sample tree in the prism plot represented, using the formula: (Prism basal area factor × 40,000)/(π × (Diameter at 1.3 m)$^2$) (Avery and Burkhart 1994).

## 3.2 Secondary Bark Beetle Assemblage

At each site a total of eight species of secondary bark beetles were found over two years infesting the lower 3 m of the boles of pine trees. Six species were common to both sites and one species was unique to each site (Table 2). The most commonly found species were the smaller western pine engraver *Orthotomicus latidens* (LeConte) and the lodgepole pine beetle *Dendroctonus murrayanae* (Hopkins) (Table 2). Also common at both sites were species of *Hylurgops* LeConte: *H. rugipennis rugipennis* (Mannerheim), *H. porosus* (LeConte), and *H. rugipennis pinifex* (Fitch). To differentiate between the species or subspecies, adult insects must be carefully examined under a dissecting microscope (Wood 1982). Although we cannot say what the relative abundance of each species was in the stands, the vast majority of the specimens collected (over 50 adults) at both sites were *H. rugipennis rugipennis*. Sample specimens of all species have been deposited in the CFS Reference Collection at the PFC with the following accession numbers: *O. latidens*, PFC 2010–0011 and PFC 2010–0012; *D. murrayanae*, PFC 2010–0016 and PFC 2010–0017; *H. rugipennis rugipennis*, PFC 2010–0004 and PFC 2010-0005; *H. porosus*, PFC 2010–0007 and PFC 2010–0008; and *H. rugipennis pinifex*, PFC 2010–0006.

Five species were found occasionally or rarely (Table 2). Certain species in the genus *Picea* are the main hosts for *Polygraphus rufipennis* (Kirby) and *Xylechinus montanus* Blackman, but both *Picea* and *Pinus* species are listed as hosts for *Dryocoetes autographus* (Ratzeburg) (Wood 1982). The Monterey pine beetle (*Pseudips mexicanus* [Hopkins]) and *Xylechinus montanus* Blackman are new records for the area according to Wood (1982) and Bright (1976). Specimens of all species except *D. autographus* were deposited in the reference collection at the PFC with the following accession numbers: *P. rufipennis*, PFC 2010–0009 and PFC 2010– 0010; *P. mexicanus*, PFC 2010–0002 and PFC 2010–0003; and *X. montanus*, PFC 2010–0001.

At the Musreau Lake site in June 2008 and 2009, there were a total of 80 and 71 pine trees, respectively, with current attacks by at least one secondary bark beetle species on the lower 3 m of the bole. That represents 8.4 and 7.5 trees/ha in 2008 and 2009 respectively. Similarly at the Two Lakes site in June 2008 and 2009, there were a total of 30 and 20 pine trees, respectively,

with current attacks by secondary species. That represents 4.8 and 3.2 trees/ha in 2008 and 2009 respectively. Many trees were attacked in multiple years with only a portion of the cambium being killed in a single year.

**Table 2.** Secondary bark beetle species (Coleoptera: Curculionidae, Scolytinae) found infesting the lower 3 m of the boles of living or moribund pine trees at two sites in the lodgepole-jack pine hybrid zone in northern Alberta. Individual trees may be attacked in more than one year and by more than one species.

| Species | | Number of Trees Attacked per Hectare (Total Number of Trees)[b] | | | |
| --- | --- | --- | --- | --- | --- |
| | | Musreau Lake (9.5 ha stand) | | Two Lakes (6.2 ha stand) | |
| Scientific Name [a] | Common Name | 2008 | 2009 | 2008 | 2009 |
| *Orthotomicus latidens* (LeConte) | Smaller western pine engraver | 6.8 (65) | 6.5 (62) | 2.4 (15) | 2.9 (18) |
| *Dendroctonus murrayanae* (Hopkins) | Lodgepole pine beetle | 6.2 (59) | 3.7 (35) | 3.2 (20) | 1.9 (12) |
| *Hylurgops* LeConte *spp.* | — | 3.5 (33) | 3.6 (34) | 1.9 (12) | 0.8 (5) |
| *Dryocoetes autographus* (Ratzeburg) | — | 0.8 (8) | - | - | - |
| *Ips pini* (Say) | Pine engraver | 0.2 (2) | 0.2 (2) | - | - |
| *Pseudips mexicanus* (Hopkins)[c] | Monterey pine beetle | 0.1 (1) | - | 0.2 (1) | 0.2 (1) |
| *Polygraphus rufipennis* (Kirby) | Four-eyed spruce beetle | - | 0.3 (3) | - | - |
| *Xylechinus montanus* Blackman[c] | — | - | - | - | 0.2 (1) |

[a] Sample specimens of all species have been deposited in the CFS Reference collection at the PFC, Victoria, British Columbia. For accession numbers see text.
[b] Excludes trees that were attacked by the mountain pine beetle before they were attacked by secondary bark beetles.
[c] New records for the area.

## 3.3 Mountain Pine Beetle

In the 9.5 ha stand sampled at the Musreau Lake site, we found a total of 16 trees that had evidence of endemic-type MPB attack: five trees were attacked in 2009, five trees in 2008, one tree in 2007, four trees in 2006, and one tree in 2005. Note that, as stated in Section 2.3 Methods, trees with endemic-type attacks prior to 2008 may be under-represented because evidence of attack becomes less apparent over time and using these trees to infer population trends before 2008 should be done with caution. All of the trees with endemic-type MPB attack had at least one putative vigour-impairing injury and over 90% had more than one injury. The most common injuries on these trees were root feeding by *H. warreni* (81% of trees), broken tops (56% of trees), stem scarring (44% of trees), and dead tops that were usually due to cankers on the upper stem (19% of trees). Additionally, 19% of the trees were suppressed by neighbouring trees. In the 6.5 ha stand sampled at the Two Lakes site, only two trees with endemic-type MPB attacks were located. Both were attacked in 2008 (note: it was not possible to locate 2009 attacks at this site

because it was clearcut logged in September 2009just prior to our field trip). One of the trees was suppressed and had a forked top, and the other was leaning and had multiple cracks through the lower stem.

Attack by secondary bark beetles preceded endemic-type MPB attack on most trees; however, given the small sample sizes, no statistical analysis was conducted. Eight of the 10 trees with endemic-type MPB attacks in 2008 or 2009 at the Musreau Lake site were already colonized by secondary bark beetle species (Figure 2). One of the trees with endemic-type MPB attacks in 2008 was attacked by secondary bark beetles in 2007 and was also unsuccessfully attacked by the MPB in 2007. Both trees with endemic-type MPB attacks in 2008 at the Two Lakes site were already colonized by secondary species. One of these trees was also unsuccessfully attacked by the MPB in 2006 and the other one was strip-attacked by the MPB around 60% of its circumference in 2007.

The only evidence of MPB activity that we found at the Musreau Lake site prior to 2006 was one tree that was mass attacked in 2002—presumably a product of the initial, limited invasion that same year—as well as one unsuccessfully attacked tree, and a tree with endemic-type attack from 2005. In 2006, a small population of beetles likely arrived at the Musreau Lake site as a result of a major immigration event into the region from west of the Rocky Mountains that same year. This resulted in 14 mass-attacked trees, nine strip-attacked trees and two unsuccessfully attacked trees in 2006 (Figure 3). We also found evidence of endemic-type MPB attack on four trees that year; but, as stated earlier, endemic-type attacks prior to 2008 may be under-estimated. With an average of only 1.5 mass-attacked trees per ha, the beetle population at the Musreau Lake site in 2006 was approaching the endemic–incipient transition threshold. The number of trees that may potentially produce broods (mass- and strip-attacked trees) and contribute to the MPB population
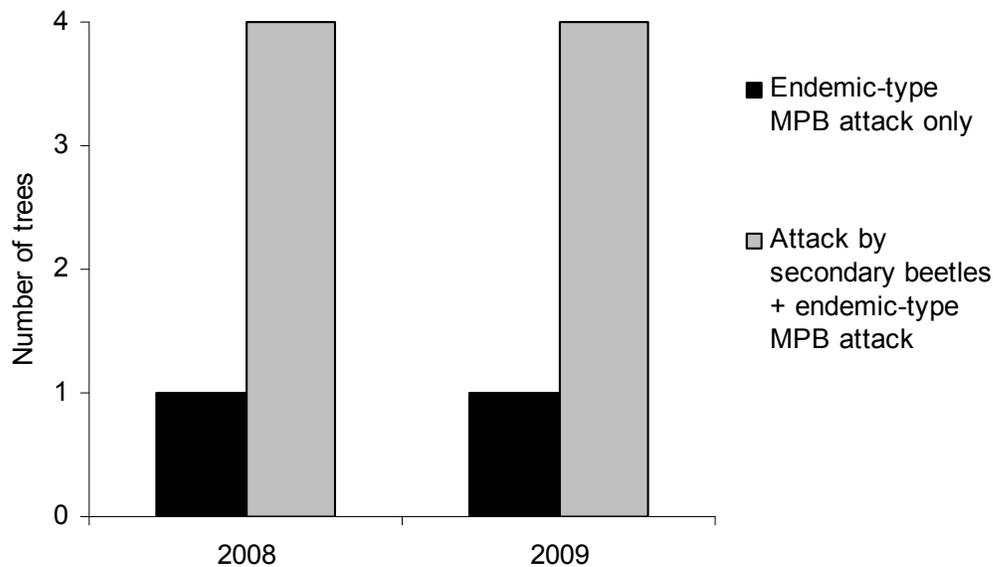


**Figure 2**. Number of trees with endemic-type mountain pine beetle (MPB) (*Dendroctonus ponderosae*) attacks in 2008 and 2009 in a 9.5 ha stand in the region recently invaded by the MPB east of the Rocky Mountain Continental Divide in northern Alberta. All trees were surveyed in June of each year (just prior to MPB flight) to identify trees that were colonized by species of secondary (non-aggressive) bark beetles prior to being attacked by the MPB.
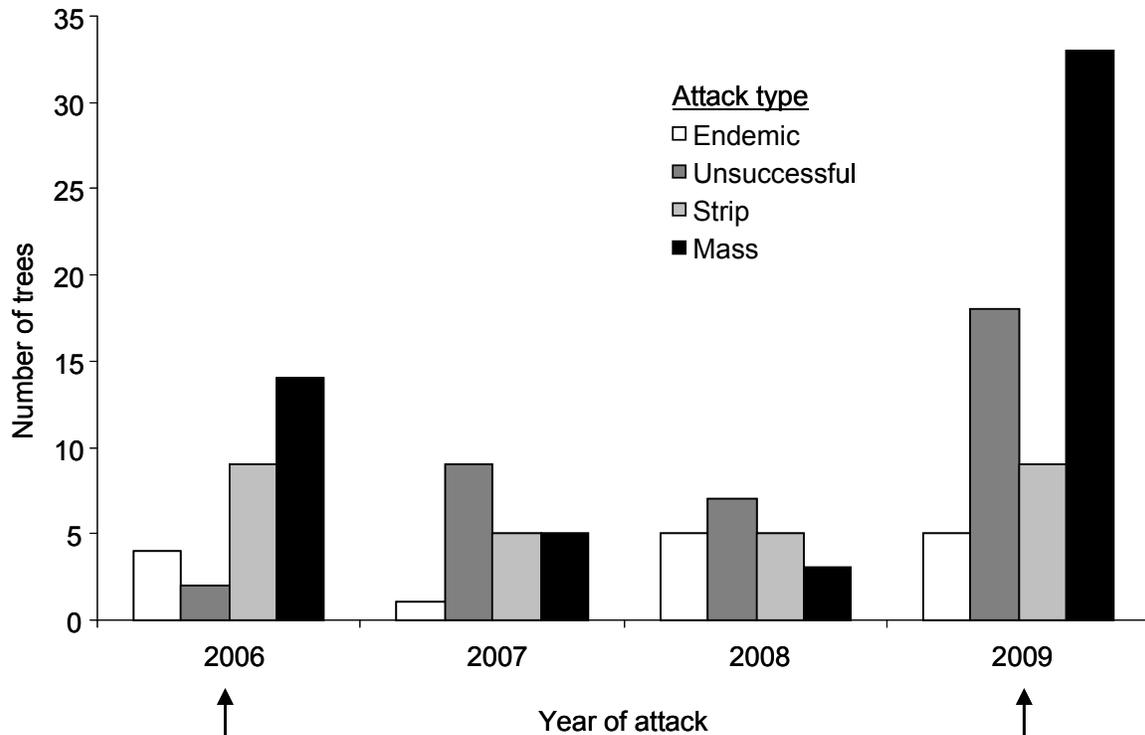
**Figure 3.** Number of trees attacked by the mountain pine beetle (MPB) in 2006 through 2009 in a 9.5 ha stand in the region recently invaded east of the Rocky Mountain Continental Divide in northern Alberta. Attacked trees were classified as follows: (1) endemic—trees with low-density MPB attack and severely reduced defenses (no visible constitutive pitch response); (2) unsuccessful—trees with resisted attacks where attacking beetles abandon the tree or perish; (3) strip—trees with successful mass-like attacks, but only a portion of the circumference of the bole is attacked resulting in partial necrosis; and (4) mass—trees with successful beetle attacks around the whole circumference of the bole. Arrows indicate years in which there was likely significant immigration of beetles into the region and stand. Prior to 2006, the only evidence of MPB activity in the stand was one tree that was mass attacked in 2002 and one tree with endemic-type attacks in 2005. Note that the number of endemic-type attacks in 2006 and 2007 may be undercounted due to the first survey being conducted in 2008 (see text).

decreased slightly in 2007, while the number of unsuccessfully attacked trees increased (Figure 3). The number of trees potentially producing broods remained low in 2008, but increased more than fivefold in 2009, likely a result of significant immigration into the stand (discussed below) (Figure 3) There was no evidence of MPB activity prior to 2006 at the Two Lakes site. A small population arrived in 2006, presumably a result of the long distance dispersal event that occurred in the region that summer. Three trees were unsuccessfully attacked. One tree had endemic-type attacks and was the only tree in the stand that would have produced a brood. However, it was an exceptional tree: it was relatively large (29 cm DBH) and apparently healthy up until the upper bole containing the entire crown broke off (presumably just prior to being attacked). Although some of the bark had sloughed off the tree, it appeared that no pitch tubes were produced. This was likely an ideal tree for an endemic population because it was likely healthy, with high quality phloem, until it suffered an acute stress that rendered it largely defenceless. Egg gallery length (up to 1.2 m long) and pupal chamber density far exceeded what are normally observed for endemic-type attacks on marginal host trees. In 2007, the population increased slightly with three strip-attacked trees and two unsuccessfully attacked trees. Beetles attacking in 2007 were either produced from the aforementioned exceptional tree or were

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immigrants into the stand (the nearest beetle population that we observed was at least 10 km away). In 2008, the only evidence of MPB activity was two marginal trees with endemic-type attacks. Unfortunately, this stand was clearcut in September 2009 just prior to our data collection trip.

## 3.4 An Exercise in MPB Population Dynamics

Potential brood production and population growth were estimated from bark samples taken in June of 2008 and 2009 and used to estimate the expected number of attacked trees in the summer of each year (described below). The projections were then compared to the actual number of attacked trees that were located during the September cruises each year. Only data from the Musreau Lake site was used for this exercise as few attacked trees were located at the Two Lakes site.

The number of live insect life stages, counted in bark samples in June of each year, was divided by the number of attack starts to obtain an estimate of the number of brood beetles produced by each female parent. Calculations were done at the tree level for mass- and strip-attacked trees and then averaged for the site. The number of emerging beetles was estimated by counting the number of live insects present in late spring just prior to pupation and emergence. Because attacks are initiated by female beetles on trees, the number of attack starts is equal to the number of female beetles in the population. The result of the calculation is known as an R value. It is used to infer population trends: an R value $\leq 2.5$ indicates that a population is decreasing; an R value between 2.6 and 4.0 indicates that a population is static; and an R value $> 4$ indicates that a population is increasing.

The number of brood adults produced per female parent, or R value calculated above, was multiplied by 2/3 to account for the female-biased sex ratio (Reid 1962) and to estimate the proportional change in the number of female beetles or attack starts. This is also the number of trees predicted to be attacked by emerging beetles, assuming similar attack and tree characteristics (e.g., attack density, length of bole attacked, tree DBH). For example, a tree attacked in the summer of 2008 with an R value of 5 (calculated from bark sample data obtained in June 2009) would be expected to produce enough beetles to attack 3.3 trees in the summer of 2009. Strip-attacked trees were converted into whole tree equivalents by adjusting the R values by the proportion of the circumference attacked (e.g., 0.6 for a 60% strip). Attack density, i.e., attack starts per $m^2$, was calculated from the number of attack starts on the $15 \times 15$ cm bark samples.

Assuming similar attack and tree characteristics, we projected that 8.6 trees would be attacked in the 2008 summer flight, based on June 2008 bark sample data. However, only 4.9 trees were actually attacked (Table 3). In 2009, only 9.4 trees were expected to be attacked, but 35.8 trees were actually attacked. Although the DBH of trees attacked in 2007, 2008, and 2009 were similar ($F_{2,52}$=1.06, $P$=0.35)(Table 3), some attack characteristics varied between years (Table 3). The length of the attack zone on the bole was significantly shorter in 2008 than in 2007 or 2009 ($F_{2,52}$=4.0, $P$=0.02) (Table 3). Attack density in 2008 was almost double the attack density in 2007; however, it was highly variable among trees and not significantly different among years ($F_{2,52}$=2.5, $P$=0.09) (Table 3). We adjusted the number of observed attacked trees by proportional changes in the average attack density, length of the bole attacked, and diameter of trees attacked (Table 3). Using 2008 as an example, the adjusted number of observed attacked trees was calculated as follows:

$$\text{Observed \# of attacked trees in Sept. 2008} \times \frac{\text{Attack density Sept. 2008}}{\text{Attack density June 2008}} \times \frac{\text{Attack length on bole Sept. 2008}}{\text{Attack length on bole June 2008}} \times \frac{\text{Diameter or attacked trees Sept. 2008}}{\text{Diameter of attacked trees June 2008}}$$

**Table 3.** The number of expected and observed trees attacked by the mountain pine beetle in a 9.5 ha stand at Musreau Lake in northern Alberta in 2008 and 2009.

| Year | Number of Attacked Trees[a] | | | Beetles | Mean (SE) Attack and Tree Characteristics | | |
|---|---|---|---|---|---|---|---|
| | Expected[b] | Observed[c] | Adjusted Observed[d] | % Change from Previous Year | Attack Density per $m^2$ | Length of Attack on Bole (m) | Tree Diameter (cm) |
| 2007 | n/a | 7.8 | n/a | n/a | 54.3 (12.2) | 9.2 (1.2) | 32.8 (2.0) |
| 2008 | 8.6 | 4.9 | 4.8 | - 44% | 95.2 (13.8) | 5.6 (1.3) | 32.4 (2.2) |
| 2009 | 9.4 | 35.8 | 48.8 | + 420% | 68.9 (5.9) | 9.7 (0.6) | 35.2 (1.0) |

[a] Strip-attacked trees were converted into whole tree equivalents by multiplying by the proportion of the circumference attacked (e.g., 0.6 for a 60% strip).
[b] Based on survival of overwintering brood sampled in June of the same year just prior to beetle dispersal in July/August.
[c] Actual (observed) number of trees attacked based on ground surveys.
[d] Adjusted for actual (observed) attack density, length of bole attacked, and tree diameter. See text.

Adjusting for differences in attack and tree characteristics had little effect on the observed number of trees attacked in 2008, because the increase in attack density was offset by the decrease in the length of the bole attacked (Table 3). However, in 2009, the 35.2 observed attacked trees was adjusted up to 48.8 trees (Table 3). Based on the adjusted number of observed attacked trees, there was a 44% decrease in the MPB population between 2007 and 2008 and a 420% increase in the MPB population between 2008 and 2009 (Table 3). The noteworthy population increase in 2009 was likely due to a significant immigration event in the region (discussed below).

# 4. Discussion and Conclusions

The endemic niche for MPB is characterized by the presence of susceptible host trees and secondary bark beetles (Carroll et al. 2006a; Safranyik and Carroll 2006). The two stands that we sampled differed greatly in their basal areas and stem densities, but both had a significant component of large-diameter, old pine trees with sufficient phloem. These trees would be susceptible to MPB attack and likely suitable for brood development. In addition, trees with putative vigour-impairing injuries, including multiple injuries, were common. These trees represent potential habitat for endemic and endemic-incipient MPB populations. Excluding damage from *H. warreni* (discussed below), scars on the bole, broken tops, and thin crowns were the most common injuries on trees attacked by MPB. Therefore, ecological processes (e.g., diseases, fires) or management activities (e.g., selective harvesting) that result in such injuries may facilitate the transition from the endemic to the incipient MPB population phase.

We considered the presence of *H. warreni* to be a putative vigour-impairing injury. There was high variation in the severity of *H. warreni* attacks on mature pine trees. In many cases the direct impact on large trees was likely diminutive. Occasionally though, we observed severe infestations on trees with larval tunnels etched through the phloem and into the sapwood, resulting in copious resin production and localized necrosis. We also isolated ophiostomatoid fungi from the galleries of *H. warreni* and from dark-stained sapwood adjacent to larval galleries. Because only the presence/absence of the insects was recorded, and it was abundant at both sites, we were unable to test for an association between *H. warreni* and MPB, or with secondary bark beetles. The potential impact of *H. warreni* on mature trees warrants further investigation, but the severity of the infestation and effect on the trees needs to be qualified (Cerezke 1970, 1994).

The diverse assemblage of secondary bark beetles found inhabiting the lower bole of pine trees in northern Alberta was similar to the community found in southern British Columbia (Carroll et al. 2006a). In southern British Columbia, *O. latidens* and *P. mexicanus* were the most common species. *O. latidens* was also common in northern Alberta, but *P. mexicanus*, the species posited to maintain endemic MPB populations in southern British Columbia, was rarely found (Table 2) (Carroll et al. 2006a; Smith et al. 2011). The two other common secondary species in northern Alberta, *D. murrayanae* and *Hylurgops* spp., were also found by Carroll et al. (2006a) in southern British Columbia. If endemic MPB populations in southern British Columbia benefit from the presence of *P. mexicanus*, it remains to be seen whether other secondary species could fill this role in northern Alberta. The number of trees attacked by secondary bark beetles per hectare in the seven stands sampled in southern British Columbia by Carroll et al. (2006a) was on average higher than in the two stands we sampled in northern Alberta. However, considering variation among years, our results were within the range reported by Carroll et al. (2006a).

Most of the endemic-type MPB attacks that we located occurred on trees that were already colonized by one or more species of secondary bark beetles that infest the lower bole (Figure 2). Carroll et al. (2006a) reported that MPB tends to attack trees already colonized by secondary beetles when populations are less than 1000 MPB females per hectare. However, we are unable to determine if this is due to a secondary bark beetle effect or a host tree effect—that is, does MPB preferentially select trees because they are attacked by secondary bark beetles or does MPB prefer the same type or quality of host trees as secondary bark beetles? There is evidence that MPB may both compete with, and benefit from, the presence of different secondary species (Safranyik et al. 1999; Carroll et al. 2006a; Smith et al. 2011). The next step needed is to conduct controlled experiments to elucidate the nature of interspecific interactions and identify any mechanisms involved.

The earliest evidence of MPB activity that we found was from 2002 at the Musreau Lake site. The fate of the small initial population is difficult to determine, but it apparently declined below the incipient threshold because no trees were mass attacked in the stand in 2003, 2004, or 2005. Such trees would have been readily identified during our surveys in 2008 by the presence of old, yellow pitch tubes on the outer bark. However, the beetles may have persisted in the endemic phase in the stand, as we found evidence of endemic-type attack from 2005, despite the challenges involved with locating endemic-type attacks from 2007 or earlier. After the 2006 immigration event, the population declined in 2007 and 2008 with fewer mass-attacked trees and an estimated population decrease of around 44% (Figure 3, Table 3). The population explosion in 2009 (Table 3) far exceeded production by the *in situ* population. Significant immigration of beetles into the stand likely occurred in the summer of 2009. The source of these beetles is unknown: they may have emigrated from active and growing populations in the vicinity or the region (e.g., within Alberta or north-east British Columbia), or they may have come from a very large active population around Mackenzie, BC west of the Continental Divide.

The number of trees per hectare with endemic-type MPB attacks for the two sites in northern Alberta was lower than that reported for southern British Columbia by Carroll et al. (2006a). There are a number of possible explanations, including differences in stand characteristics and the availability of susceptible hosts. However, it may also be due, at least in part, to higher beetle populations in the stands sampled in northern Alberta, resulting in more aggregative-type attacks (mass or strip attacks) and less endemic-type attacks. Regardless of absolute numbers, it is noteworthy that endemic-type attacks occurred at both sites, and rather consistently at the Musreau Lake site, among years (Figure 3). This suggests that MPB could likely persist in the region at endemic population levels; however, our data was limited to just a few years.

An endemic niche likely exists for the MPB in the two stands that were sampled in northern Alberta. Our sites were in the most favourable climatic area for MPB in the region, yet *in situ*

beetle populations were low and tended to decline in the absence of immigration events (Figure 3). However, we surveyed only two sites and our temporal frame was limited. Insect populations may respond rapidly to successive years of favourable weather if other population-regulating factors are favourable. Assuming the presence of an endemic niche and beetle persistence in the region, the MPB poses a potential threat to the boreal forest, especially in the future, if conditions become more favourable for both development and winter survival (Safranyik et al. 2010).

During our study we observed great variation in MPB attack behaviour (e.g., annual attack density, Table 3), phenology (e.g., early adult emergence, within-stand asynchronous development), and overwintering survival. There are apparent geographic differences in the development, behaviour, and reproductive success of MPB populations (Bentz et al. 2001; Clark et al. 2010; Cudmore et al. 2010). Future research should focus on understanding MPB biology and population dynamics in the beetle's expanded range under changing environmental conditions because such information is critical for assessing the threat to our boreal forest resources and for developing effective management strategies.

# 5. Acknowledgements

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