

Effects of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations on forest stand structure in the southern Canadian Rocky Mountains

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Abstract

Forests in the montane and lower subalpine ecoregions of the southern Canadian Rocky Mountains may have been more open and structurally diverse at the beginning of the 20th Century than today. Today, the area of mature *Pinus contorta* subsp. *latifolia* Dougl. forest that is conducive to mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) infestations, infrequent high severity fires, and herbivory appears to have increased in Banff and Kootenay National Parks. Based on a review of the literature, we hypothesised that MPB infestations increase forest stand structural diversity and tree species diversity. Stand structure parameters were investigated in mesic montane and lower subalpine stands approximately 15, 25, and 65 years after MPB outbreaks. Parameters measured were stand density (number of trees per ha), diameter at breast height, height class, species, age class distribution, and coarse woody debris mass. Influences of fire frequency, time since fire, and fire severity on these parameters were assessed to determine whether fire history had a confounding influence on stand structure. The Shannon–Wiener index indicated higher stand structural diversity 15 years but not 25 and 65 years after MPB infestations. MPB infestations led to general decreases within stands in the number of living trees, small diameter snags, and *Pinus* tree species and an increase within stands in the number of large diameter snags. Management that allows the occurrence of the natural fire regime of variable severity fires, in addition to some MPB infestations, would provide for more open and diverse stands. MPB infestations have some effects on stand structure that are similar to those of fire. Changes in stand structure resulting from recent declines in burning rates within Banff and Kootenay National Parks can be reversed to some extent by MPB infestations.

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1. Introduction

Fire and mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) have been two of the dominant disturbance agents in Banff (BNP) and Kootenay (KNP) National Parks in the southern Canadian Rocky Mountains. Although MPB is endemic, it has recently reached epidemic levels in this area. Several major MPB outbreaks in KNP can be dated back to the 1940s, with the most recent beginning in the 1990s. Banff National Park, on the other hand, has not been as affected by

MPB. There, MPB outbreaks have been much smaller and MPB was probably not a significant natural disturbance agent historically. Recently, however, MPB infestations have expanded in the park (McFarlane et al., 2006).

In western North American forests, mature *Pinus contorta* subsp. *latifolia* Dougl. is the most commonly killed species, followed by *Pinus ponderosa* subsp. *ponderosa* Douglas ex C. Lawson, and other pines such as *Pinus albicaulis* Dougl. ex Hook. The most susceptible trees appear to be between the ages of 80 and 100 years (Van Sickle, 1988; Shore et al., 2000; The Mountain Pine Beetle Initiative, 2004) and with breast height diameters >25 cm (Whitehead et al., 2001; The Mountain Pine Beetle Initiative, 2004). Turner et al. (1999) found that stands in Yellowstone National Park (YNP) with severe MPB infestations had extensive areas of dead *P. contorta*, creating gaps which stimulated understory growth, suggesting MPB infestations could lead to a more structurally diverse forest. This is

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supported by studies in southwestern Montana (Armour, 1982), and in KNP (Shrimpton, 1994), where proportions of *Picea* in a dominantly *Pinus* overstory have increased following MPB infestations.

Since MPB kill only *Pinus* in the *P. contorta* ecosystems of the southern Canadian Rockies (Shore et al., 2000), they may actually facilitate development of more floristically diverse tree canopies. In the absence of fire, consecutive MPB infestations may convert even-aged to uneven-aged forests (Roe and Amman, 1970). Thus, MPB may act as a disturbance agent that results in more structurally diverse forests.

The main factors responsible for the current outbreak are weather and the availability of the primary host, mature *P. contorta* (Carroll et al., 2004). Warm and dry summers stress trees, reducing their ability to pitch out attacking beetles. Also, periods of low temperatures (below $-25\text{ }^{\circ}\text{C}$ in the fall or $-40\text{ }^{\circ}\text{C}$ in late winter for prolonged periods) that can also kill the beetle (Carroll et al., 2004) have not occurred sufficiently in recent years. Finally, forest fire suppression has resulted in an abundance of susceptible host trees in the study area (Ono, 2004).

Ecological integrity is the first management priority in Canada's national parks. Ecological integrity is defined as "a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" (Parks Canada, 2000). According to this definition, insects and pathogens that are endemic, and at levels within their historical range, should be allowed to persist without interference (McFarlane et al., 2006). It has been proposed that the MPB represents a natural disturbance agent within the parks' *P. contorta* ecosystems, and that MPB may play an important role in rejuvenating those ecosystems by creating forest canopy gaps, which may facilitate increased growth of young trees and increased species diversity (Parks Canada, 2002). Any measures to control the beetle could be regarded as inconsistent with the principles of ecological integrity (McFarlane et al., 2006). However, the current outbreak of MPB may also be viewed as uncharacteristic, resulting from the historic fire suppression in the parks (McFarlane et al., 2006) and human induced changes in climate. Thus, MPB or its habitat could be managed if its abundance is not within the range of ecological integrity (Dalman, 2004).

Due to the increasing influence of MPB on the forests of the southern Canadian Rocky Mountains, and the previous lack of knowledge of the effects of MPB on these forests, we investigated MPB effects on forest stand structural diversity. We tested the hypothesis that MPB infestations increase the structural diversity of forest stands. We also sought to determine whether this effect is confounded by fire history. To test our hypothesis, we examined stand structure characteristics and fire history in mesic montane and lower subalpine stands in the southern Canadian Rocky Mountains that had been affected by MPB outbreaks 15, 25, and 65 years previously.

2. Study area

The study was conducted at lower elevations (1100–1800 m) in BNP and KNP. The area occurs within the Interior Douglas-fir (IDF) and Montane Spruce (MS) biogeoclimatic zones as used in British Columbia (Meidinger and Pojar, 1991). According to the land classification system used by Parks Canada, the lower elevation areas belong to the montane ecoregion (Holland and Coen, 1982). The lower part of the montane ecoregion corresponds to the IDF, while the upper part corresponds to the MS biogeoclimatic zone. Ecoregions are then subdivided into ecoregions, which are again subdivided into ecosites, based on soil, landform, and vegetation differences.

The climate of BNP is frequently influenced by warm west föhn winds (Chinooks) from the Pacific, which interrupt the more continental climatic conditions. Banff (1395 m) has a mean annual temperature of $2.5\text{ }^{\circ}\text{C}$, with mean daily maximum values of $22.3\text{ }^{\circ}\text{C}$ in July and mean daily minimum values of $-16.4\text{ }^{\circ}\text{C}$ in January, and a mean annual precipitation of 477 mm (Achuff et al., 1984). The climate of KNP is influenced by warm and moist Pacific air. Kootenay Crossing (1170 m) has a mean annual temperature of $1.7\text{ }^{\circ}\text{C}$, with a mean daily maximum of $24.1\text{ }^{\circ}\text{C}$ in July and a mean daily minimum of $-18.1\text{ }^{\circ}\text{C}$ in January and a mean annual precipitation of 505 mm (Achuff et al., 1984).

Forests are dominated by *P. contorta*, *Pseudotsuga menziesii* (Mirbel) Franco var. *glauca* (Beissn.) Franco, *Picea glauca* × *engelmannii*, *Populus balsamifera* L. ssp. *trichocarpa* (Torr. and Gray ex Hook.) Brayshaw, and *Populus tremuloides* Michx. *Larix occidentalis* Nutt. also occurs occasionally within KNP. At higher elevations, *Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa* and *Picea engelmannii* Parry ex Engelm. are more common, but *Betula* spp. are less common. The understory vegetation is generally classified as pine/buffaloberry associations dominated by *Shepherdia canadensis* L. Nutt., *Elymus innovatus* Beal, *Arctostaphylos uvaursi* (L.) Spreng, *Linnaea borealis* L., *Aster conspicuus* Lindl., and *Juniperus communis* L. (Holland and Coen, 1982; Achuff et al., 1984). The soil orders in BNP and KNP include Brunisols, Luvisols and Regosols.

3. Methods

Stands that had been subjected to MPB outbreaks in the 1940s and 1980s in BNP, and in the 1980s and 1990s in KNP, were located. Eleven study plots were placed in each of the stands infested in the 1940s and 1980s and fifty study plots in areas of the 1990s outbreak. Additionally, sixty-four plots were placed in the same or on a similar ecosite in stands of similar age that had not been influenced by MPB infestations since the most recent stand-initiating fire. The plots covered ten different ecosites according to the BNP classification (Table 1). Stand ages were stratified into 3 classes (50–99, 100–149, and >150 years).

Since we had mapped records of only a limited number of MPB infestations, the time frame captured was necessarily

Table 1
Sites that were sampled in Banff National Park (BNP) and Kootenay National Park (KNP)

Origin (year)	Stand type	N	BNP ecosites	KNP ecosites
1990	Control	28	PT3	DR2, DR3, DR8
1990	MPB	50	PT3	DR2, DR3, DR8
1980	Control	8	PT1	DR7
		9	PR1	Not sampled
1980	MPB	4	PT1	DR7
		1	AL1	Not sampled
		1	BK6	Not sampled
		1	GA1	Not sampled
		3	PR1	Not sampled
		1	PR2	Not sampled
1940	Control	1	NY1	DG6, WY1
		10	PR4	Not sampled
		8	PR6	Not sampled
1940	MPB	1	NY1	DG6, WY1
			PT1	DR7
		2	PT3	DR2, DR3, DR8
		2	AL1	Not sampled
			BK6	Not sampled
		1	GA1	Not sampled
			PR1	Not sampled
		2	PR2	Not sampled
		1	PR4	Not sampled
2	PR6	Not sampled		

The total sample size (*N*) includes plots in both BNP and KNP. Ecosites are described in detail by Holland and Coen (1982) for BNP and by Achuff et al. (1984) for KNP.

narrow. It was also not always possible to sample stands with and without MPB in close proximity that experienced the same fire history patterns. As a result, the present study should be viewed as a snap-shot restricted to certain points in time and to the ecosites investigated.

3.1. Plot selection

Study plots were located using ecosystem classification maps for KNP and BNP, a hand drawn map by Hopping and Mathers (1945), and archived documents of BNP. Records of MPB infestations were obtained from GIS data from Parks Canada and from the Canadian Forest Service. Plots in areas with past MPB infestations that had been sampled in previous years were relocated using given UTM coordinates and permanent markers; these were then resampled. These plots were all about 100 m apart and at least 2 tree lengths away from the nearest road. New plots established for the present study were at least 2 tree lengths away from the nearest road and at least 30 m apart.

For MPB plots, every indication of MPB activity (blue stain within tree disc/stumps, green-, red-, or grey attack, pitch tubes and galleries) was recorded for each tree within a study plot. Stands from the 1940 MPB infestations were subjected to an extensive fall-and-burn program in the 1940s (Hopping and Mathers, 1945), so coarse woody debris (CWD) levels were low. When establishing plots in areas without MPB infestations,

a visual assessment was first made of an area to ensure there was no evidence of such an infestation.

3.2. Field measurements

For each sample plot, measurements were taken to characterize horizontal and vertical stand structure, stand characteristics and fire history. A sample plot consisted of a circular plot of 15 m radius (707 m² area) within which all trees with DBH (diameter at breast height) ≥ 30 cm were measured. Within this plot was a circular subplot of 7.1 m radius (158 m² area) within which all trees with heights \geq breast height (1.3 m) were measured. Within this subplot was a smaller circular subplot of 3.99 m radius (50 m² area) within which the heights of all trees with heights $<$ breast height were measured. For horizontal structure, the following tree measurements or information were recorded for the 7.1 m and 15 m radius plots: tree species, condition (live or dead), and DBH (cm). Using these parameters, stand density (number of trees per ha), basal area (m²/ha), and tree canopy cover (%) were calculated. For characterizing vertical stand structure in each plot, individual tree heights were measured and the proportion of tree species in different height classes was estimated. Shrub and herb cover were also estimated by height class in the 3.99 m radius plots. The six vertical height classes into which the vegetation was stratified were: A1 (tree canopy, >10 m), A2 (tree upper subcanopy, 5–10 m), B1 (tree lower subcanopy, 2–5 m), B2 (tree saplings and shrubs, 0.5–2 m), C (shrubs, <0.5 m), and H (herbs) (Lastra, 2001). Stem counts were made individually for each tree species. Seedlings were counted in 3.99 m radius plots, saplings in 7.1 m radius plot, and mature trees in 7.1 m and 15 m radius plots. Herbivory on the vegetation was visually quantified as browsing intensity on a 5-point ordinal scale (1 = no browsing, to 5 = severe browsing).

Stands were also characterized according to age structure and CWD amounts. The range of tree ages in a stand was estimated by taking increment cores from early successional *P. contorta* and from other later successional species (*Abies* or *Picea*) if present. Cores were taken from a tree visually representative of the dominant large size class present, together with one representative of any dominant small size class present for each tree species sampled. For each tree species a minimum number of two trees were cored in each plot. Trees were cored as close to the ground and to the pith as possible to get the best estimate of the tree age by counting rings. Broadleaved trees could not be aged as they were often decayed in the centre, causing increment borers to jam. Coarse woody debris mass was visually estimated using a photo guide derived from similar forest types in Montana, USA (Fischer, 1981).

The age structure of the trees present in a stand, together with visual evidence of fires was used to estimate the disturbance history of a stand. This was done using the following assumptions:

1. A stand-initiating disturbance occurred 'X' years previously, where 'X' corresponded approximately to the age of the largest early successional *P. contorta* tree cored.

2. All similar sized, large *P. contorta* trees present were of a similar age to the large trees cored and all regenerated after the stand-initiating disturbance.
3. This stand-initiating disturbance was fire in all stands without a known history of MPB infestation, and where charcoal could be found in the forest floor.
4. Any trees substantially larger and older in appearance than the large trees cored had survived the stand-initiating disturbance.
5. Fire scars on the large *P. contorta* trees present in a stand indicated at least one relatively low severity fire had occurred in the stand since its initiation. Discs were cut from trees, through the fire scars, and the approximate dates of fire scars were determined by ring counting. Increment cores were used to determine the age distribution resulting from the number and intensity of previous fires.
6. The presence of smaller *P. contorta* trees of a similar age to those of any fire scars indicated post-fire regeneration. The presence of smaller *P. contorta* trees substantially (>20 years) younger than the large trees present, but with no fire scars indicated the stand was disturbed either by a lower severity fire which left no fire scars, or by insects or pathogens.

The relative severity of the last fire was assessed at each plot on the basis of the extent of fire-caused mortality of trees present at the time of the fire. This was determined by estimating the number of trees in the stand at the time of sampling which were likely present at the time of the last fire and which survived that fire. Thus, the relative severity of fires or extent of fire-caused mortality that occurred in a stand was determined using the age of early and later successional tree species present. Ages of the largest later successional trees present (*Abies* or *Picea*) indicated whether or not these trees had survived the most recent fire, dated using *P. contorta* ages as described above. We used a scale of 1–4 to indicated relative fire severity (1 for >95% tree mortality, 2 for 50–95% tree mortality, 3 for 5–49% tree mortality, 4 for <5% tree mortality).

3.3. Data analysis

Comparisons between MPB and non-MPB plots, and among different aged forests, were made using ANOVA. To make these comparisons, the datasets were stratified according to time since MPB infestation. Structural diversity measures (DBH class, height class and tree species distributions) were compared among disturbance and age classes using Shannon–Wiener indexes. Logarithmic transformations were necessary for some variables to meet the assumptions of ANOVA. In cases where the data could not be transformed to meet ANOVA assumptions, non-parametric Kruskal–Wallis or Mann–Whitney range tests were used. Where main effects were significant, means were separated using the Bonferroni adjustment. Differences were considered significant at $\alpha = 0.05$.

4. Results and discussion

4.1. Effects of MPB on stand structure

For each of the three MPB infestation times, mean stand ages did not differ significantly between the MPB and corresponding control plots (Table 2), so comparisons between MPB and control stand structures for a given MPB infestation time were not confounded by stand age differences. The number of larger diameter trees per hectare (DBH >7.5 cm) was significantly lower in plots with than without a previous MPB infestation, but this difference decreased with time since the infestation due to increasing densities of larger diameter trees in older MPB-infested stands (Table 2). The significantly lower tree density for the 1980 and 1940 infestations, but a similar total basal area compared to the corresponding control plots, suggests that trees remaining after the MPB disturbance might have experienced accelerated growth due to release from competition, thus increasing total basal area.

The basal area of larger *P. contorta* trees (DBH > 15 cm) was significantly lower on the MPB than on corresponding control plots. The low basal area of *P. contorta* in stands with previous MPB infestations suggests these stands will be less

Table 2

Mean values, with standard errors in parentheses, of stand age, tree structural characteristics, coarse woody debris quantities and browsing intensity in MPB and control plots

Origin (year)	Stand type	Plots (n)	Average stand age (years)	Stems/ha DBH > 7.5 cm	Basal area ^a (m ² /ha)	<i>Pinus</i> basal area ^b (m ² /ha)	Coarse woody debris (kg/m ²)	Regeneration density ^c (stems/ha)	Browsing intensity (1–5)
1990	Control	28	100 (5.9)	1335* (111)	34.8* (2.4)	23.7* (2.3)	2.8* (0.3)	1535 (347)	2.1 (0.2)
	MPB	50	109 (4.4)	496 (46)	24.3 (2.2)	8.1 (1.4)	4.2* (0.2)	824 (178)	3.4* (0.1)
1980	Control	17	130 (7.5)	1750* (148)	37.1 (2.8)	22.9* (3.0)	2.3 (0.3)	905 (205)	1.8 (0.3)
	MPB	11	129 (9.4)	689 (161)	32.5 (4.1)	6.5 (2.6)	3.0 (0.7)	3658* (1173)	2.7 (0.5)
1940	Control	19	112 (3)	1781 (285)	37.7* (2.8)	20.3* (2.7)	1.6 (0.2)	1705 (597)	1.3 (0.2)
	MPB	11	121 (9.4)	883 (139)	31.6 (7.5)	6.9 (3.8)	1.6 (0.3)	762 (241)	2.9* (0.4)

^a For total basal area, only trees with DBH > 7.5cm were included in order to exclude regeneration and suppressed trees.

^b For *Pinus* basal area, only trees with DBH > 15 cm were included in order to include only those trees most susceptible to MPB infestations (Shore and Safranyik, 1992).

^c Species most commonly found were (in decreasing order)—Control 1990: spruce, birch, Douglas fir; MPB 1990: aspen, spruce, Douglas fir; Control 1980: subalpine fir, spruce, lodgepole pine; MPB 1980: subalpine fir, spruce, birch; Control 1940: spruce, Douglas fir, aspen; MPB 1940: maple, spruce, lodgepole pine.

* For a given year of origin, the mean value in the MPB plots is significantly different from that in the control plots at $p < 0.05$.

susceptible to future MPB infestations. However, in the face of a massive outbreak, it is expected that these stands will also be subject to MPB mortality (Stockdale et al., 2004).

Coarse woody debris mass was higher in MPB plots than in control plots for the 1990 (statistically significant) and 1980 (not statistically significant) infestations, but not for the 1940 infestations. The lack of coarse woody debris in stands from infestations in 1940 may be explained by past fall-and-burn practices in the 1940s (Hopping and Mathers, 1945). Without this previous removal of CWD, higher CWD loads in the 1940 MPB infestation stands would also have been expected. In the 1990 MPB plots, collapse of MPB killed *P. contorta* snags has led to a relatively high mass of coarse woody debris on the forest floor. The smaller difference in CWD mass between 1980 MPB and corresponding control plots is likely due to relatively slower collapse of MPB-killed trees, as suggested by a greater number of standing dead trees in the 1980 than in the more exposed 1990 MPB plots where wind throw had occurred (Table 3).

Significantly more regeneration was found in MPB than in control plots from infestations in the 1980s, unlike the infestations of the 1940s and the 1990s. It is not completely clear why this occurred, but it might be due to heavy ungulate browsing in the 1940 and 1990 MPB infestation areas (Table 2), which was also supported by frequent observations of moose and elk droppings in those plots. Browsing was observed most commonly on trembling aspen and subalpine fir, followed by Douglas fir, spruce, lodgepole pine and birch.

Small snags (Table 3), which were most likely killed by inter-tree competition, were separated from larger diameter ones, which were potentially killed by MPB, using a DBH limit of 15 cm (Shore and Safranyik, 1992). Even larger diameter snags may have originated from trees that died due to old age or previous fires. Larger *P. contorta* with DBH > 30 cm, tended to be older, often about 120 years, and are less susceptible to MPB attack (Shore and Safranyik, 1992). Significantly fewer small diameter snags (DBH < 15 cm) were found in MPB plots compared to control plots, probably due to the lower tree density and hence less intense competition from larger trees. Small diameter trees in MPB plots may have had a higher chance of survival than those in the more dense control plots.

More open stands in the 1940s MPB-infested stands may have caused a trend to fewer 15–30 cm DBH snags than in the corresponding control plots (Table 3). Intermediate diameter

(15–30 cm DBH) snags were more abundant in the 1980 and 1990 MPB plots than in the corresponding control plots, possibly due to a higher density of MPB-killed *P. contorta* trees. The difference was statistically significant only for the 1980 plots, however. The relatively high proportion of MPB-killed trees that had fallen down in the 1990 MPB plots might explain why relatively fewer 15–30 cm DBH snags occurred there than in the 1980 MPB plots. The relatively small number of 15–30 cm snags in the 1940 MPB plots may be attributed to the felling and burning of MPB-killed trees in these plots.

The proportion of large diameter snags (>30 cm DBH) was highest in the 1990 plots and decreased with time since infestation. This was also found by Armour (1982), and is likely the result of collapsing MPB-killed *P. contorta*. These larger snags were significantly more abundant in 1990 MPB than in corresponding control plots, despite the observed windthrow in the MPB killed stands. This may have resulted from such trees becoming resistant to windthrow while they were living, as they rose above the canopy. Also, these snags may have belonged to tree species with root systems less susceptible to windthrow.

Relatively few differences were found between MPB and control plots in stand structural diversity (Table 4). This diversity, as measured by the Shannon Wiener Index, increased only in the MPB 1990 infestation plots, compared to control plots (Table 4). It was not significantly affected by either the 1940s or 1980s infestations. The Shannon Wiener Index for tree species diversity tended to decrease with time since the last MPB infestation (Table 4), but this occurred in both control and MPB plots, and was likely due to ecosystem differences.

The proportion of *Pinus* tended to increase with time since MPB infestation, and this corresponded with a decline in the proportion of *Picea* (Fig. 1 and Table 5). A trend towards increasing canopy dominance by *Picea* after disturbance, as observed by Armour (1982) and Antos and Parish (2002), was only found for the most recent 1990 MPB disturbance. This was mainly due to the low numbers of *Pinus* in the 1990 MPB plots, since densities of *Picea* were similar in MPB and control plots (Table 5). The proportion of *Pinus* was lower in all of the older MPB-infested stands, but the density of *Pinus* increased with time since the infestation. Relatively higher *Pinus* densities in the 1940 MPB plots than in the 1980 or 1990 MPB plots may be due to more open stands after the 1940 than after the 2 subsequent MPB infestations, thereby facilitating new regeneration of *Pinus*. This is suggested by lower densities of species

Table 3
Mean snag density (number of snags/ha), with standard errors in parentheses, in MPB and control plots

Origin (year)	Stand type	Plots (n)	Snag size class		
			DBH < 15 cm	DBH 15–30 cm	DBH > 30 cm
1990	Control	28	801 (188)	106 (23)	4 (1)
	MPB	50	126* (25)	143 (36)	29* (6)
1980	Control	17	1355 (240)	41 (13)	3 (1)
	MPB	11	350* (59)	247* (32)	38 (20)
1940	Control	19	1020 (270)	53 (16)	0
	MPB	11	237* (63)	21 (9)	1 (1)

* For a given year of origin, the mean value in the MPB plots is significantly different from that in the control plots at $p < 0.05$.

Table 4

Mean Shannon–Wiener index values for DBH and tree height class distributions, and tree species composition, in control and MPB plots for three different times of MPB infestations

Origin (year)	Stand type	Plots (<i>n</i>)	Stand structure (Shannon–Wiener index)			Species composition (Shannon–Wiener index)
			Height class	DBH class	DBH/height class	
1990	Control	28	0.54 (0.07)	0.72 (0.04)	1.07 (0.06)	1.63 (0.09)
	MPB	50	0.86* (0.05)	0.78 (0.04)	1.27* (0.05)	1.68 (0.06)
1980	Control	17	0.73 (0.1)	0.58 (0.05)	1.19 (0.09)	1.52 (0.11)
	MPB	11	0.69 (0.12)	0.47 (0.1)	1.20 (0.15)	1.51 (0.18)
1940	Control	19	0.89 (0.07)	0.72 (0.04)	1.25 (0.06)	1.43 (0.12)
	MPB	11	0.79 (0.09)	0.73 (0.07)	1.17 (0.11)	1.46 (0.17)

Standard errors are given in parentheses.

* For a given year of origin, the mean value in the MPB plots is significantly different from that in the control plots at $p < 0.05$.

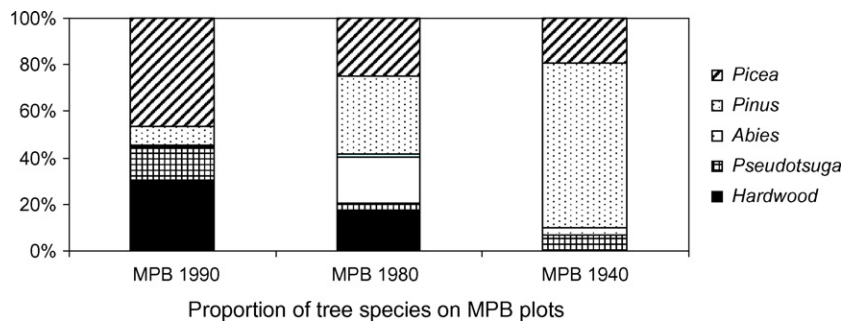


Fig. 1. Tree species distribution in stands with MPB infestations in different years. *Larix* is not represented since its proportion is $< 1\%$.

other than *Pinus* (Fig. 1). These low densities might have resulted from the cutting and burning operations after the 1940 infestation, or from post-stand initiation low severity fires which occurred on five out of eleven (45%) 1940 MPB plots, but on only 1 out of 10 (10%) and 11 out of 50 (22%) of the plots in the 1980 and 1990 MPB plots, respectively.

Although the differences between MPB infested and control plots were not significant, hardwoods appeared to have been promoted by MPB infestation and declined with time since the infestation (Table 5). This was expected since hardwoods in these ecosystems are early seral species (Braumandl and Curran, 1992).

4.2. Fire history as a potentially confounding factor

The fire history of a stand can have a profound influence on stand structure (Brown and Smith, 2000). To assess whether

variations between stands in fire history might be confounding our assessment of MPB impacts on stand structure, comparisons of stand structure characteristics were made between stands with different fire histories and without documented or visible MPB occurrence.

Stand age tended to increase with the number of fires a stand had experienced, as well as time since the last fire (Tables 6 and 7), but none of the stand structure variables measured in the present study appeared to be related to either number of fires or time since fire (Tables 6 and 7). There may have been a trend towards decreasing regeneration density with increasing number of fires and time since the last fire, but high within-stand variability, as seen by high standard errors, render this trend not statistically significant. Consequently, we assume that our observations of MPB effects were not due to differences in fire history between the plots.

Table 5

Mean tree density (stems/ha) for different tree genera in MPB and control plots

Origin (year)	Stand type	Plots (<i>n</i>)	Hardwood	<i>Pseudotsuga</i>	<i>Abies</i>	<i>Larix</i>	<i>Pinus</i>	<i>Picea</i>
1990	Control	28	201 (74)	157 (38)	2 (2)	17 (10)	750 (133)	506 (89)
	MPB	50	345 (93)	152 (35)	9 (4)	4 (3)	93* (17)	528 (75)
1980	Control	17	19 (13)	4 (4)	19 (12)	0 ^{id}	1298 (143)	1103 (273)
	MPB	11	202 (182)	34 (25)	230 (154)	12 ^{id} (12)	390* (145)	289* (123)
1940	Control	19	7 (5)	10 (8)	153 (65)	0 ^{id}	1301 (301)	1073 (315)
	MPB	11	0 ^{id}	80 (68)	33 (17)	0 ^{id}	820 (122)	220 (63)

Standard errors are given in parentheses. 'id': Insufficient data for comparing MPB and control means.

* For a given year of origin, the mean value in the MPB plots is significantly different from that in the control plots at $p < 0.05$.

Table 6
Mean values of percent cover by vegetation layer and stand structure parameters as related to the number of fires after the stand-initiating fire

Number of fires	Plots (n)	Percent cover ^a (%)						Mean age ^b (years)	Stems/ha	Basal area ^c (m ² /ha)	Pinus basal area ^d (m ² /ha)	Coarse woody debris (kg/m ²)
		A1	A2	B1	B2	C	CWD					
0	44	50 (3.0)	9 (1.8)	10 (1.4)	23 (3.5)	13 (2.0)	30 (3.9)	102 ^a (3)	1652 (135)	37.4 (1.8)	23.4 (1.8)	2.2 (0.2)
1	17	47 (3.9)	11 (2.1)	8 (1.4)	26 (6.1)	12 (2.4)	31 (6.7)	127 ^b (8)	1393 (153)	33.0 (3.2)	20.8 (2.7)	2.7 (0.5)
2–3	3	48 (10.9)	8 (3.3)	4 (3.0)	18 (7.3)	10 (2.9)	45 (20.2)	159 ^b (77)	1537 (849)	38 (2.9)	26 (5.7)	2.3 (0.5)

Standard errors are given in parentheses.

^a Percent covers do not add up to 100% due to overlapping layers.

^b Mean values followed by different superscripts are significantly different at $p < 0.05$.

^c For total basal area, only trees with DBH > 7.5 cm were included in order to exclude regeneration and suppressed trees.

^d For Pinus basal area, only trees with DBH > 15 cm were included in order to include only those trees most susceptible to MPB infestations (Shore and Safranyik, 1992).

Table 7
Mean values of percent cover by vegetation layer and stand structure parameters as related to the time since the last fire after the stand-initiating fire

Time since fire (years)	Plots (n)	Percent cover ^a (%)						Mean age ^b (years)	Stems/ha	Basal area ^c (m ² /ha)	Pinus basal area ^d (m ² /ha)	Coarse woody debris (kg/m ²)
		A1	A2	B1	B2	C	CWD					
0–50	3	38 (1.7)	12 (4.4)	10 (5.5)	43 (8.8)	8 (1.7)	50 (17.6)	84 ^{ab} (16)	1389 (386)	39.5 (8.3)	22.1 (6.4)	1.7 (0.5)
51–100	33	51 (3.2)	9 (1.2)	10 (1.7)	25 (4.1)	14 (2.5)	32 (4.9)	100 ^a (4)	1373 (112)	34.1 (2.2)	22.7 (2.2)	2.6 (0.3)
101–150	28	48 (3.8)	11 (2.8)	8 (1.2)	21 (4.3)	11 (1.9)	27 (4.4)	128 ^b (8)	1833 (194)	39 (2.2)	23 (2.1)	2.0 (0.2)

Standard errors are given in parentheses.

^a Percent covers do not add up to 100% due to overlapping layers.

^b Mean values followed by different superscripts are significantly different at $p < 0.05$.

^c For total basal area, only trees with DBH > 7.5 cm were included in order to exclude regeneration and suppressed trees.

^d For Pinus basal area, only trees with DBH > 15 cm were included in order to include only those trees most susceptible to MPB infestations (Shore and Safranyik, 1992).

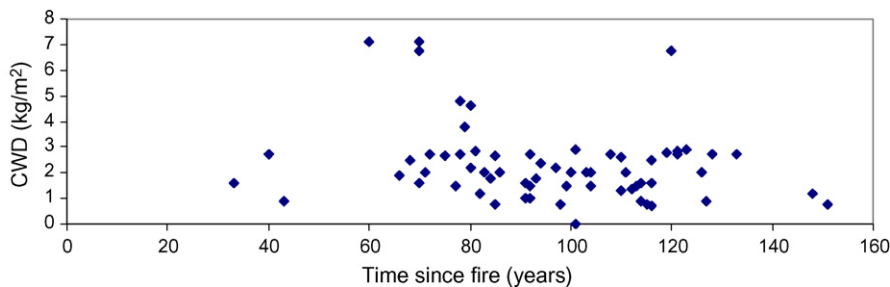


Fig. 2. Coarse woody debris (CWD) in the control plots as a function of time since fire. Only control plots ($n = 64$) were used in order to avoid confounding influences by MPB disturbances.

Coarse woody debris greatly increases following a disturbance, followed by a decrease due to decomposition, and then an increase again in older forests as trees collapse, generally following a U-shaped curve over time (Feller, 2003; Muraro, 1971). Departures from this trend occur, however, depending on individual stand dynamics and the nature of individual disturbances (Feller, 2003). Such a departure may have occurred in the forests studied because there was no trend in CWD with time since fire (Fig. 2). However, data were not collected for the first 30 years following fire.

Open forest conditions containing snags and early successional tree species have been characteristic of many forests in BNP and KNP. However, the burning rate from forest fires has declined since 1940 in BNP and 1840 in KNP due to fire suppression (Van Wagner et al., 2006), resulting in more closed forest conditions. To some extent, MPB has opened the forests

and increased structural diversity, reducing the need for prescribed fire, which is expensive and can threaten human facilities. In keeping with management priorities of Canada's national parks, MPB can be a more natural disturbance than prescribed fire. Consequently, in parks and protected areas where MPB populations and their habitats are within the range of ecological integrity, and do not threaten neighbouring lands, park managers can maintain the long-term pattern of MPB-caused forest tree mortality.

5. Conclusions

The study set out to test the hypothesis that MPB infestations increase the structural diversity of forest stands in the study area. We conclude that MPB infestations in the study area appear to have had a minor but lasting influence on stand

structure and tree species distribution in the forests studied. A management approach that tolerates a certain extent of MPB infestation, but also promotes low and high intensity fires, would foster more open and diverse stands in the ecosystems of the southern Canadian Rocky Mountains.

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