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Mountain Pine Beetle Dispersal through Managed and Unmanaged Landscapes

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Abstract

Dispersal of mountain pine beetles, *Dendroctonus ponderosae*, is expected to be influenced by the energetic costs of dispersal that in turn may be influenced by the species composition and tree density of forest stands. In Banff and Kootenay National Parks, three times as many mountain pine beetles were captured in pheromone-baited traps within lodgepole pine stands than within white spruce stands, with more beetles captured in Kootenay than in Banff National Parks. Clearcuts and thinned stands showed little reduction in mountain pine beetles 90 m from the edge, except in a clearcut at the sapling stage. Two other bark beetles, *Ips pini* and *Pityogenes knechteli*, showed significant reductions in clearcuts relative to adjacent intact stands, but not in thinned stands. These species tended to have highest abundances at the edge of intact stands, while this pattern was not clearly seen for mountain pine beetles. Overall, while bark beetles tend to occur in lower numbers in non-host stands, they are still commonly found in such stands.

The effects of dispersal costs may explain discrepancies in metrics used to evaluate the success of a management zone in Banff National Park, but these may be more related to reductions in population size than to stand characteristics. In the management zone east of Banff, where all detected green-attacked trees were removed since 2002, the area affected by mountain pine beetles (measured as area of red attack) changed little compared to the monitoring zones, but the number of 25 ha cells with some red attack was greatly reduced. Trap catches in the two zones revealed that there were fewer beetles captured and they were in poorer body condition in the management zone than in the monitoring zone. This could not be attributed to poorer production in the management zone, and instead is consistent with the idea that reduced population size limited the long-distance dispersal success of mountain pine beetles resulting in beetles in poorer condition. Thus, while the costs of dispersal may influence the spread of mountain pine beetles, these costs appear to depend more on population size than on stand attributes.

Keywords: landscape heterogeneity, non-host stands, edges, body condition, management

Résumé

On estime que la dispersion du dendroctone du pin ponderosa, *Dendroctonus ponderosae*, sera influencée par les coûts énergétiques de la dispersion, laquelle pourrait, à son tour, être influencée par la composition taxinomique et la densité des arbres des peuplements forestiers. Dans les parcs nationaux Banff et Kootenay, le nombre de dendroctones du pin ponderosa capturés dans les pièges appâtés aux phéromones était trois fois supérieur dans les peuplements de pins tordus que dans les peuplements d'épinettes blanches, et le nombre de dendroctones du pin ponderosa capturés dans le parc national Kootenay était supérieur à celui du parc national Banff. Dans les zones de coupe à blanc et les peuplements éclaircis, le nombre de dendroctones du pin ponderosa n'avait que peu diminué à 90 m de la limite, sauf dans une zone de coupe à blanc au stade de gaule. La présence de deux autres scolytes, le *scolyte du pin* et le *Pityogenes knechteli* a considérablement baissé dans les zones de coupe à blanc par rapport aux peuplements adjacents intacts, mais pas dans les peuplements éclaircis. D'ordinaire, ces espèces sont les plus présentes à la limite de peuplements intacts; cette caractéristique n'a pas été clairement observée chez le dendroctone du pin ponderosa. Dans l'ensemble, alors que les scolytes sont généralement présents en moins grand nombre dans les peuplements non hôtes, on les trouve encore principalement dans ce type de peuplement.

Les effets des coûts de dispersion pourraient expliquer les divergences dans les mesures utilisées pour évaluer le succès d'une zone de gestion dans le parc national de Banff; celles-ci pourraient toutefois être davantage liées aux diminutions de la taille de la population qu'aux caractéristiques du peuplement. Dans la zone de gestion à l'est de Banff, dans laquelle tous les arbres au stade vert sont abattus depuis 2002, la zone touchée par les dendroctones du pin ponderosa (mesurée comme étant une zone au stade rouge) a peu changé comparativement aux zones surveillées, mais le nombre de cellules de 25 ha dans lesquels des arbres au stade rouge étaient présents a considérablement diminué. Les prises relevées dans les pièges installés dans les deux zones ont révélé que le nombre de dendroctones capturés a diminué et que leur état corporel était moins bon dans la zone de gestion que dans la zone de surveillance. Il n'était pas possible de déterminer que la diminution résulte du fait que la production est moins bonne dans la zone de gestion, mais plutôt qu'elle est compatible avec l'idée que plus la population est petite, plus le rayon de dispersion du dendroctone du pin ponderosa est limité, ce qui se traduit par un état corporel moins bon des dendroctones. Par conséquent, même si le coût de la dispersion pouvait avoir une incidence sur la propagation des dendroctones du pin ponderosa, ces coûts dépendraient davantage de la taille de la population que des caractéristiques du peuplement.

Mots-clés : hétérogénéité du paysage, peuplements non hôtes, limites, état corporel, gestion

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1 Introduction

The logistical difficulties of directly controlling infestations of mountain pine beetles, *Dendroctonus ponderosae*, have prompted the idea that landscapes should be managed to minimize the probability that infestations will develop (Whitehead et al. 2006). Intuition suggests that landscape heterogeneity should reduce the impacts of pests. However, while this idea has been examined in agroecosystems, the evidence in forested ecosystems is scarce (Jactel et al. 2002, Gilbert et al. 2005, Yllioja et al. 2005).

Several processes may influence the propensity of mountain pine beetles to travel through areas that have few host trees. A starting assumption is that dispersal is energetically costly, and energy expended during travel reduces reproductive investment at the host tree (Elkin and Reid 2005) and reduces the ability to tolerate host defensive compounds (Gries et al. 1990, Reid and Purcell in prep). This may explain the short (less than 100 m) dispersal distances observed for most mountain pine beetles (Robertson et al. 2007, Trzcinski and Reid 2008a). Mountain pine beetles are also able to detect and avoid stands of deciduous trees (Huber and Borden 2001). Thinning stands of host trees is thought to deter bark beetles (Fettig et al. 2007), but there is limited evidence that this is because fewer beetles enter such stands (Schmitz et al. 1989). The lower proportion of attacked trees in thinned stands may arise because pheromone plumes are disrupted by higher temperatures and winds in thinned stands relative to unthinned stands (Thistle et al. 2004).

While all these processes suggest that mountain pine beetles may view non-host or thinned stands as barriers, the actual response to a boundary also depends on the natural likelihood of encountering such habitats and the benefits of long-range dispersal for at least some individuals (Fahrig 2007). If individuals are not particularly sensitive to boundaries, then increases in non-suitable ("matrix") habitat can actually enhance the spread of individuals (Cronin 2003) as they travel faster and more linearly through these habitats (Fahrig 2007). If individuals do avoid crossing into matrix habitat, they may accumulate at edges (Desrochers and Fortin 2000, Haynes and Cronin 2003). This is pertinent to mountain pine beetles because increased concentrations of beetles should enhance the probability of successful mass attacks. Thus, it is important to establish the extent to which mountain pine beetles respond negatively to non-host or thinned stands, and the consequences of that response for the distribution of beetles within stands and across the landscape.

In this report, I examine the distribution of mountain pine beetles with respect to stand composition at various scales in terms of both tree species and density. I further examine how the body condition of mountain pine beetles varies across the landscape, and suggest that these findings may explain some discrepancies in the evaluation of the success of management practices in Banff National Park.

2 Material and Methods

2.1 Distribution within and among host and non-host stands

To examine the effect of tree species composition on the occurrence of mountain pine beetles, we selected stands dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) or burned lodgepole pine in Kootenay and Banff National Parks (Fig. 1). Stands were selected to maximize the proximity of the different stand types across this landscape, resulting in the interspersion of stand types. In each stand, two 12-funnel Lindgren traps where placed 50 m apart and at least 100 m from the edge of the stand. Traps were baited with mountain pine beetle lures (Phero Tech Inc.; exo-brevicomin, myrcene and terpinolene). In each trap collection cap, a 1 cm^3 piece of solid insecticide (Vapona) was placed to kill beetles upon capture. Traps were installed in August 2006 and collected two weeks later. All captured mountain pine beetles were counted, while those from Banff National Park were also sexed, and measured for pronotum width and body length (using a dissecting scope fitted with an ocular micrometer) and dry weight.

We examined distribution of beetles across stand boundaries using managed stands (clearcuts and thinned stands) where the boundaries were distinct. Clearcuts and their adjacent intact mature pine stands were selected in Kananaskis, west of Calgary, Alberta (n = 3 sites) and in Tembec's TFL (tree farm licence) 14 near Parson, BC (n = 3 sites). An additional three thinned pine stands and their adjacent unthinned mature pine stands were studies in TFL 14. At all sites, traps were placed 20 and 90 m from the edge of the harvested stand into both the harvested and intact stands. In Kananaskis, funnel traps were baited with pheromones (Phero Tech Inc) of *Ips pini* because of the desired low numbers of mountain pine beetles there. These traps also captured *Pityogenes knechteli* (henceforth *Pityogenes*). Two replicate traps, spaced 50 m apart, were placed at each 20 and 90 m distance. In TFL 14, two funnel traps at each distance from the edge were baited with mountain pine beetle pheromones (as above), while one trap at each distance was baited with *Ips pini* pheromones; all traps at each distance were 50 m apart. Traps again had insecticide in the collection cups and captured beetles were collected after two weeks (August 2007) and identified.

The temperature and wind in stands differing in species composition and tree density were sampled in 2007 using Hobo Onset weather stations and data loggers. The two weather stations were placed in contrasting stands for one week and then moved to a new pair of stands through the summer. Within two stands in 2006, 10-12 funnel traps baited with mountain pine beetle pheromones (as above) were arranged at least 50 m apart, and captures of wild beetles and mark and released beetles were collected hourly on one day. The number of captures was related to the local density of trees within 5 m of each trap as well as the temperature and wind speed and direction.

2.2 Landscape Patterns

The effectiveness of mountain pine beetle management in Banff National Park was examined as a joint effort between Banff National Park and this project, both funded by the Mountain Pine Beetle Initiative (Trzcinski and Reid 2008b). In brief, in 2002 Banff

National Park established a management zone east of Banff townsite (Fig. 2) where trees were baited with mountain pine beetle pheromones and all detected attacked trees were felled and burned prior to beetle emergence. West of the Banff townsite was a monitoring zone where no baiting or removal of attacked trees occurred. Using Canadian Forest Service aerial data of red-attacked trees and the geo-referenced trees that were removed, the area of red-attacked trees was determined for the two zones from 1997 through 2004. Area affected (red-attacks) was examined in two ways, as the area of all red-attacked polygons, and as a proportion of all 500 x 500 m cells with mountain pine beetle habitat that had attacked trees.

To elucidate the pattern of red-attacked trees in the two zones, we investigated the source and quality of mountain pine beetles across the Banff landscape. We examined the productivity of trees from six locations in Banff by felling 2-11 infested trees at each site in fall 2005. A 1 m log was cut from near breast height of each tree and left *in situ* until June 2006. At that time, each log was enclosed within black geotechnical screening and an emergence tube leading to a collecting jar was placed at one end to collect all emerging beetles. In October 2006, all bark beetles were collected from the collection jar, within the screening, and on the bark, and the cages were dismantled. Bark beetles were identified to species, and a subset were measured for pronotal width and body length (body weight was not useful because beetles were not killed upon emergence). Tree traits of diameter at breast height (dbh), average growth rate over the last five years, and phloem thickness were recorded for each log, as well as attack density. To examine the quality of dispersing beetles across the Banff landscape, the size and dry weight of mountain pine beetles captured in survey traps (above) was determined. Stable isotopes of C and N were also determined from the elytra of beetles emerging from logs and from those caught in traps to assess beetle movement, but the final results were not available at the time of writing.

2.3 Analyses

All data were analyzed using JMP 5.1 statistical software (SAS 2001). The assumptions of normality and homogeneity of variance were checked for all models and data were transformed as required. Where appropriate, differences among treatments were tested using Tukey's Honestly Significant Difference. Least square means are reported from models with multiple variables.

3 Results and Discussion

3.1 Distribution within and among host and non-host stands

3.1.1 Among stands

The number of mountain pine beetles captured in funnel traps was greater in Kootenay National Park than in Banff National Park ($F_{1,13} = 17.35$, $p < 0.0001$). This was expected given the extent of the current outbreak that also corresponds to the historical range of mountain pine beetles: Kootenay is within the historic range of mountain pine beetles while Banff is at the periphery. Controlling statistically for park identity, more beetles tended to be captured in pine stands than spruce stands ($F_{1,13} = 4.00$, $p < 0.007$; two way ANOVA on ln-transformed data +1, $R^2 = 0.577$; Fig. 3). Using back-transformed values, the (least square) mean number of beetles captured in pine stands was 125.7 beetles (SE range: 93.6 – 170.7, n = 11 stands), while a mean of 40.4 beetles were caught in spruce stands (SE: 29.6-55.0 beetles, n = 6 stands). Burned stands were omitted from this analysis because they were few in number (n = 3 stands), but they were within the range of variation of the pine and spruce stands (Fig. 3). Thus, while these data suggest that fewer beetles are captured in non-host stands than in pine stands, mountain pine beetles commonly occur in non-host stands.

The propensity of bark beetles to occur in harvested stands was examined by comparing the numbers captured in traps on either side of a boundary between intact pine stands and either clearcut or thinned stands. *Ips pini* and *Pityogenes* were collected across clearcut boundaries in both Alberta and BC, but there was no detectable effect of province (main effect and interactions, all $p > 0.1$). In both provinces, both species were captured in higher numbers in the intact forest than in the clearcut ($F_{1,56} = 16.29$, $p < 0.0002$), though both species were common in clearcuts (Fig. 4a). *Ips pini* was more commonly caught than *Pityogenes* (Fig. 4a, $F_{1,56} = 31.69$, $p < 0.0001$), as might be expected given that the traps were baited with *Ips pini* pheromones. There were also some site effects ($F_{4,56} = 13.45$, $p < 0.0001$; whole model $R^2 = 0.669$).

The abundance of mountain pine beetles appeared less affected by clearcuts than the previous two species. In two of the three clearcuts, there were insignificant reductions in the number of mountain pine beetles captured, while there was a significant decline in the third clearcut (Fig. 4b; interaction between treatment and site: $F_{2,16} = 16.91$, $p < 0.0001$). This difference can be attributed to the age of the clearcuts. The two clearcuts where there were little effects on the abundance of mountain pine beetles were recent clearcuts with almost no trees. The third clearcut was at the sapling stage such that the traps were surrounded by small trees. The lower numbers caught in the sapling site may reflect absolutely lower numbers of mountain pine beetles, or the traps may simply have been less effective.

The abundance of all three bark beetles species in thinned stands did not detectably differ from their abundance in neighbouring intact stands (treatment effect and its interactions with species and site, all $p > 0.4$). This analysis pertains to only two of the three thinned stands studied because of loss of mountain pine beetle-baited traps in one stand. When only *Ips pini* and *Pityogenes* are examined for all three stands, there was again no effect of treatment or its interaction with species (all $p > 0.6$), in contrast to what was observed with clearcut sites (Fig. 4a).

The assessment of relative abundance across different stand densities or composition using pheromone traps should be viewed with caution because pheromone plume structure may affect the relative effectiveness of traps in different stands. As tree density declines, wind increases in speed and variability (Thistle et al. 2004, also this study, data not shown). Increased wind reduces pheromone concentration, while increased variability causes pheromone plumes to wander more widely (Thistle et al. 2004). We observed that trap catches within a stand increased when there were more trees (> 10 cm) within a 5 m radius of the trap (range 1 – 15 trees), which may be explained by more coherent local pheromone dynamics with more trees. Thus, the effectiveness of pheromone traps may be reduced in windier conditions. In that case, the reduction in the captures of bark beetles in harvested sites would be greater than the reduction of dispersing beetles. It is less clear how trap effectiveness might vary between intact pine and spruce sites, although burned sites are expected to be windier. Therefore, assuming that trap catches in harvested or burned sites are conservative, it appears that bark beetles, especially mountain pine beetles, commonly travel through harvested and non-host stands.

3.1.2 Within stands

If bark beetles are deterred by stands with few host trees (either due to species composition or density), then they may accumulate at the edges of intact stands of host trees (Desrochers and Fortin 2000). At the edges of clearcuts, there was some evidence that *Ips pini* and *Pityogenes* occurred at higher densities at the edge of the intact forest (Fig. 5a, -20 m dist; Distance effect $F_{3,48} = 4.92$, $p < 0.005$; no interactions with province or species; *Ips pini* was more common than *Pityogenes,* $p < 0.0001$, overall $R^2 = 0.683$). The response of mountain pine beetles to edges varied among clearcuts ($F_{6,10} = 6.01$, $p < 0.007$, overall $R^2 = 0.915$), corresponding to the site differences in overall abundance mentioned above. In the clearcut with saplings, there was a (non-significant) tendency for captures to be highest at the edge of the intact forest, while in the two other (recent) clearcuts, abundance did not vary greatly with distance from edge in either the intact forest or clearcut (Fig. 5b).

While there was no detectable difference in the overall abundance of *Ips pini* and *Pityogenes* between intact and thinned stands (see above), there was a detectable edge effect for these species (distance effect $F_{3,10} = 8.17$, $p < 0.005$, species effect $F_{1,10} = 65.98$, $p < 0.0001$, interaction $p > 0.7$, overall $\mathbf{R^2} = 0.920$). Within the intact forest, more beetles were captured at the edge than in the interior (Fig. 5c). While the greater abundance at the edge is consistent with an aversion to crossing a boundary, the pattern here and for the overall abundance does not suggest a strong aversion to entering thinned stands. Instead, the pattern may arise because there was actually or probabilistically more freshly fallen debris, the habitat of *Ips pini* and *Pityogenes*, at the edge of the thinned stand than in the interior of intact stands. The response of mountain pine beetles to the edges of thinned stands could not be examined because of limited data.

3.2 Landscape Patterns

The spread of mountain pine beetles in Banff National Park was examined coarsely in the context of the management experiment established in 2002 wherein infested trees were removed east of Banff townsite. The yearly change in the area affected by mountain pine beetles, as measured by red-attacks in the following year, did not differ greatly between the management zone and the monitoring zone (Fig. 6a,b; Trzcinski and Reid 2008b). However, when the spatial extent of mountain pine beetle activity was measured as the number of 500 x 500 m cells (with mountain pine beetle habitat) that were affected, the management zone had a greatly reduced spatial spread relative to the monitoring zone (Fig. 6c-f). The discrepancy in patterns between area affected and number of habitat cells affected suggests that there is a change in long distance dispersal by mountain pine beetles, such that beetles in the management zone were propagating spread closer to their natal trees.

Dispersal distances of mountain pine beetles are expected to be related to the energetic condition of beetles. Therefore, we examined how the abundance and condition of beetles captured in our survey traps (as in 3.1.1, above) varied spatially with Banff National Park, in particular relative to the management and monitoring zones. The number of beetles captured declined from west to east within Banff NP (Fig. 7a**,** easting: $F_{1,10} = 7.00$, $p < 0.03$), controlling for stand type (more in pine than spruce stands, $p < 0.02$). Considering the management (east) and monitoring (west) zones explicitly, approximately twice as many beetles were captured in the monitoring zone as in the management zone ($F_{1,9} = 5.16$, $p < 0.05$, controlling for stand type, $p < 0.03$). The least square mean number of beetles caught in the management zone was 16.3 (back-transformed from ln-transformation, SE spans 11.6 – 22.8) while in the monitoring zone a mean of 40.1 beetles were captured (SE spans 31.4 – 51.0). Thus, the general abundance of mountain pine beetles appeared to be reduced in the management zone.

Body condition was measured as the residual weight after accounting for beetle volume (Jakob et al. 1996). Condition of mountain pine beetles declined from west to east in Banff (Fig. 7b, ln-transformed condition $F_{1,22} = 26.48$, $p < 0.0001$), with no effects of either stand type or sex (both $p > 0.3$; overall $R^2 = 0.553$). This corresponded to a strong difference in condition between zones ($F_{1,22} = 22.90$, $p < 0.0001$, again with no effects of stand type or sex; overall $R^2 = 0.515$). In the monitoring zone, body condition was above average (LSM = 0.109 mg/mm^3 $\pm$ 0.064) while beetles were in below average body condition in the management zone (LSM = -0.208 mg/mm^3 $\pm$ 0.048).

The differences in abundance and condition between the two zones could arise because of intrinsic differences in the production of beetles, rather than to management. However, although there were site differences in the number of mountain pine beetles emerging from felled trees ($F_{5,35} = 4.61$, $p < 0.003$), they did not correspond well with the two zones (Fig. 8). Productivity was also positively affected by the tree's growth rate in the past five years ($F_{1,35} = 8.68$, $p < 0.006$) and negatively affected by attack density on the tree ($F_{1,35} = 7.25$, $p < 0.02$) and the ln-transformed number of *Ips pini* emerging from the log ($F_{1,35} = 10.06$, $p < 0.004$, overall $R^2 = 0.635$). These traits, as well as tree diameter and phloem thickness that did not affect the number of mountain pine beetles emerging from a log, did not vary consistently between zones (data not shown). If there was any difference among the zones in the number of mountain pine beetles produced, the trend was for the management zone to produce more beetles controlling for the other factors mentioned. Thus, when the Helena Ridge site was excluded, the number of beetles emerging increased with UTM easting ($F_{1,29} = 10.69$, $p < 0.003$; Fig. 7). This is in contrast to the observation that fewer beetles were caught in the monitoring zone. The body size of beetles emerging from the different sites did not differ detectably (data not shown; condition could not be examined because beetles were not promptly killed upon emergence).

Thus, the reduced abundance and quality of beetles captured in the management zone relative to the monitoring zone does not appear to be due to intrinsic differences in habitat quality between the two zones. Instead, it may be that the management actions significantly reduced the beetle population such that the density of dispersing beetles dropped too low to sustain mass-attacks beyond a few hundred meters from natal trees. Those beetles that did venture farther away would have to continue dispersing if unable to find an active mass-attack, resulting in their poorer condition when eventually captured in traps. Successful mass attacks could still happen near natal trees, resulting in increases in area attacked, but not far from natal trees, resulting in a reduced increase in the number of cells occupied (Fig. 6c-f).

4 Conclusions

Landscape heterogeneity affected the distribution of dispersing bark beetles, but stands with few host trees were still traversed, particularly by mountain pine beetles. Thus, mountain pine beetles were commonly found in spruce, burned, clearcut and thinned stands, and they did not appear to be very sensitive to pronounced stand boundaries such as at clearcuts edges. The abundance of two other bark beetles, *Ips pini* and *Pityogenes knechteli*, was lower (but still common) in clearcuts than intact forests, and tended to show highest abundances at the edge of intact mature pine stands. If the edge pattern occurred in mountain pine beetles, the edges of pine stands may concentrate beetles and increase the chance of mass attack (Schmid and Mata 2005). Further work on the distribution of mountain pine beetles across boundaries and in different stand types is warranted, and consideration of possible biases associated with using pheromone traps to determine the distribution of bark beetles is needed. Surprisingly, there has been relatively little work to date on the occurrence of mountain pine beetles across heterogeneous landscapes although it is commonly expected that non-host stands will limit the spread of bark beetles (Fettig et al. 2007). However, without strong boundary responses, non-host stands can increase rather than reduce the spread of insects (Cronin 2003). Our work suggests this is a reasonable possibility for mountain pine beetles.

Consideration of dispersal of mountain pine beetles may explain the consequences of their management in Banff National Park. Comparison of the management and monitoring zones using two different metrics produced different conclusions: the area affected by mountain pine beetles did not differ while there was a substantial decrease in the number of affected cells in the management zone relative to the monitoring zone (Fig. 6, Trzcinski and Reid 2008b). We found that the number and body condition of mountain pine beetles captured in the management zone was much lower than in the monitoring zone, and may explain the more contained occurrence in the management zone. Widely dispersing individuals may be too rare to establish mass-attacks, causing them to have to search longer, be in poorer condition, and in turn have a lower likelihood of successfully attacking trees. These results point to the value of reducing the population size of mountain pine beetles directly to reduce their successful establishment in new aggregations, rather than relying on landscape heterogeneity to limit their success. Future work is needed to link more explicitly the occurrence of mountain pine beetles in the two zones of Banff National Park with respect to spatially explicit distributions of habitat and management actions.

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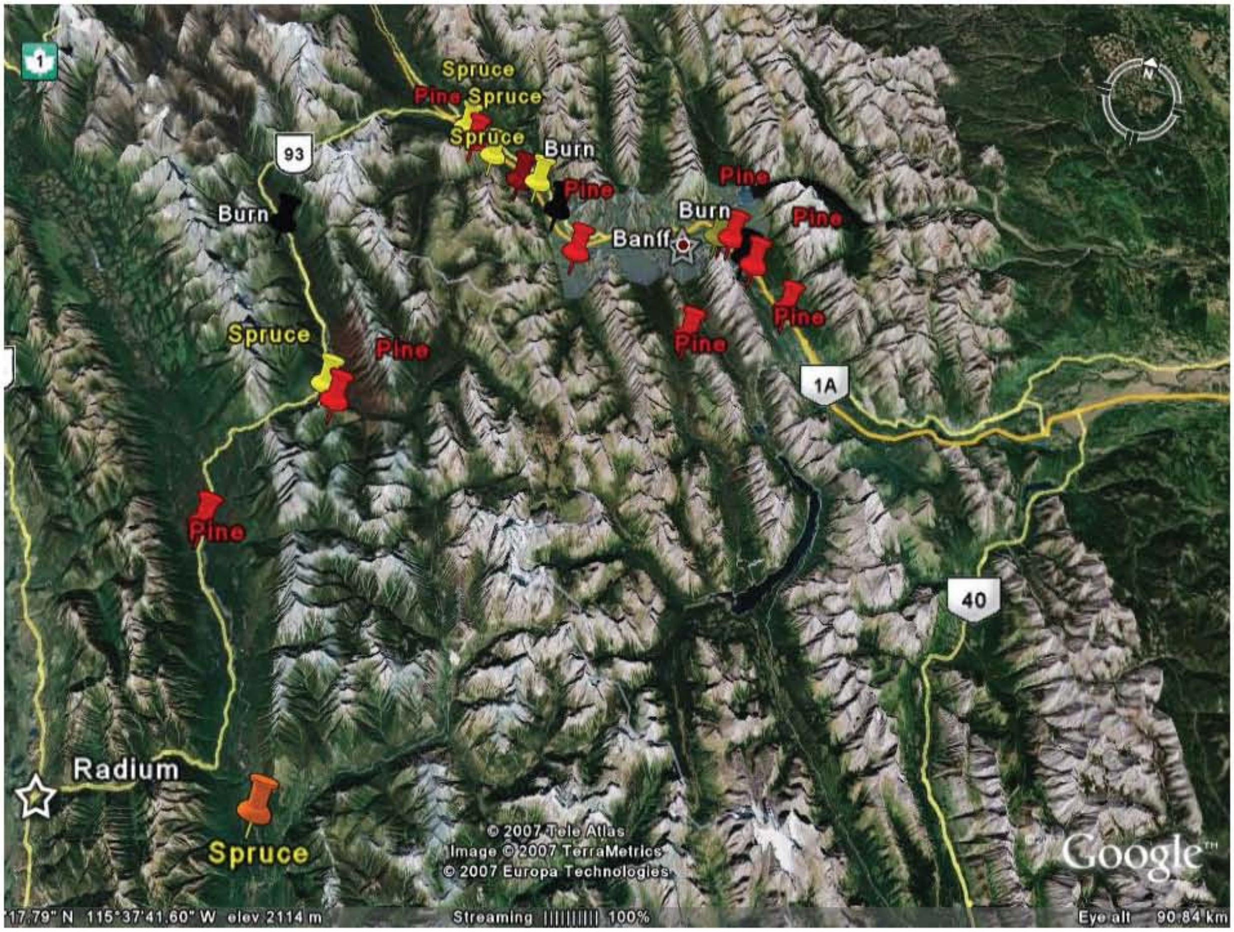

Figure 1. Location of stands in Kootenay and Banff National Parks that were surveyed for mountain pine beetle abundance using pheromone baited traps.

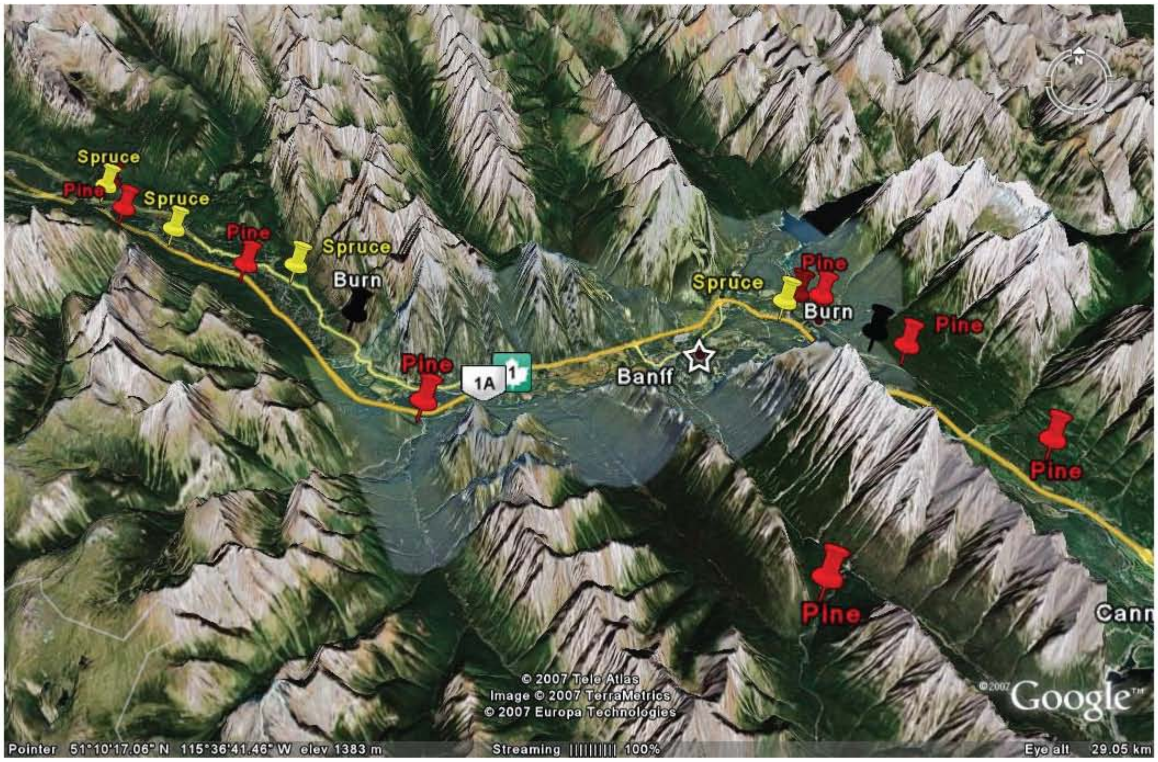

Figure 2. Stands sampled in Banff National Park in relationship to the management zone (east, or right, of area demarcated by solid black line) and the monitoring zone (west of black line).

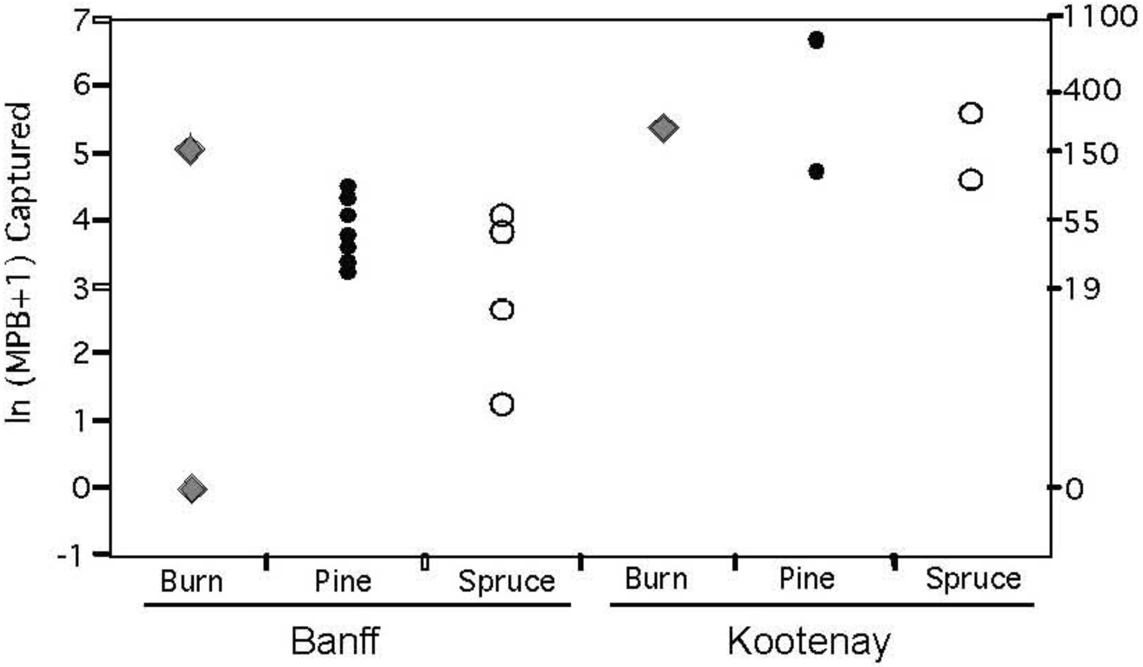

Figure 3. Number of mountain pine beetles captured per baited pheromone trap over two weeks in August 2006 in Banff and Kootenay National Parks. Left y-axis shows the ln-transformed values used in analyses; values on right axis indicate corresponding untransformed values.

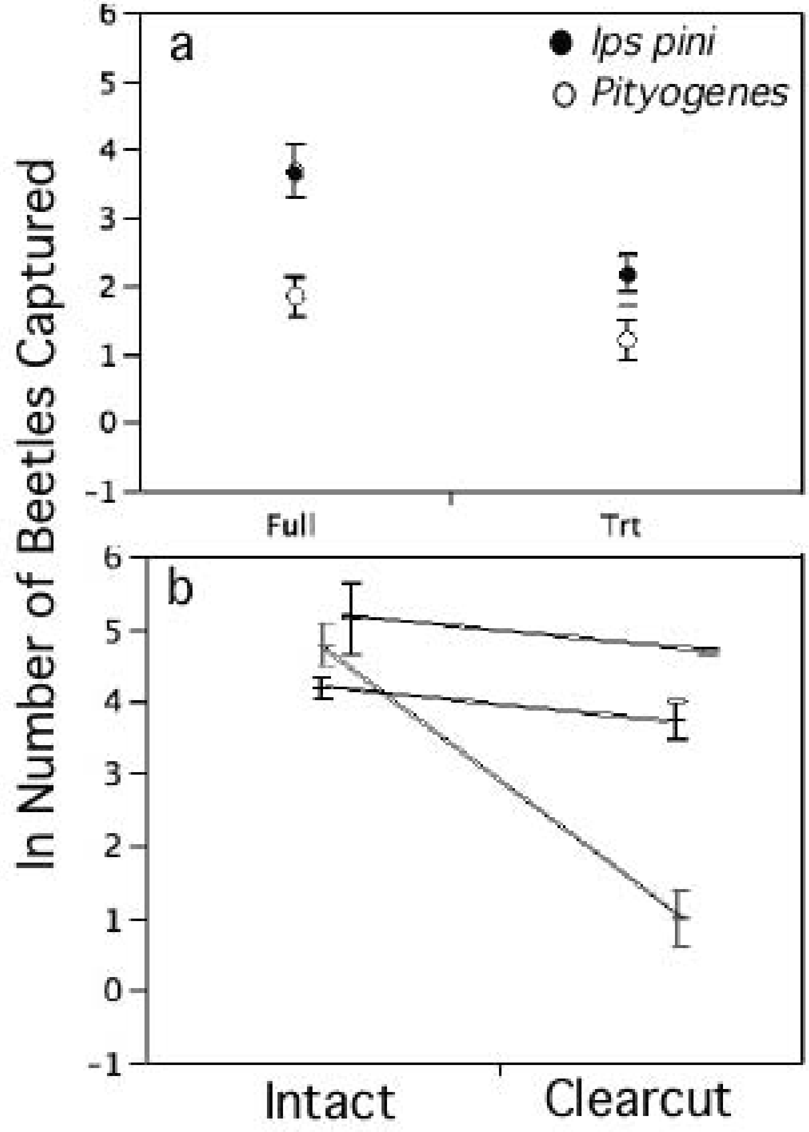

Figure 4. Number of beetles (ln-transformed least square means and SE) captured over two weeks in clearcut stands and their adjacent intact lodgepole pine stands. a) *Ips pini* and *Pityogenes* for 6 sites, combined, in Kananaskis and near Parson, BC. b) mountain pine beetles in three sites (each shown separately) near Parson, BC.

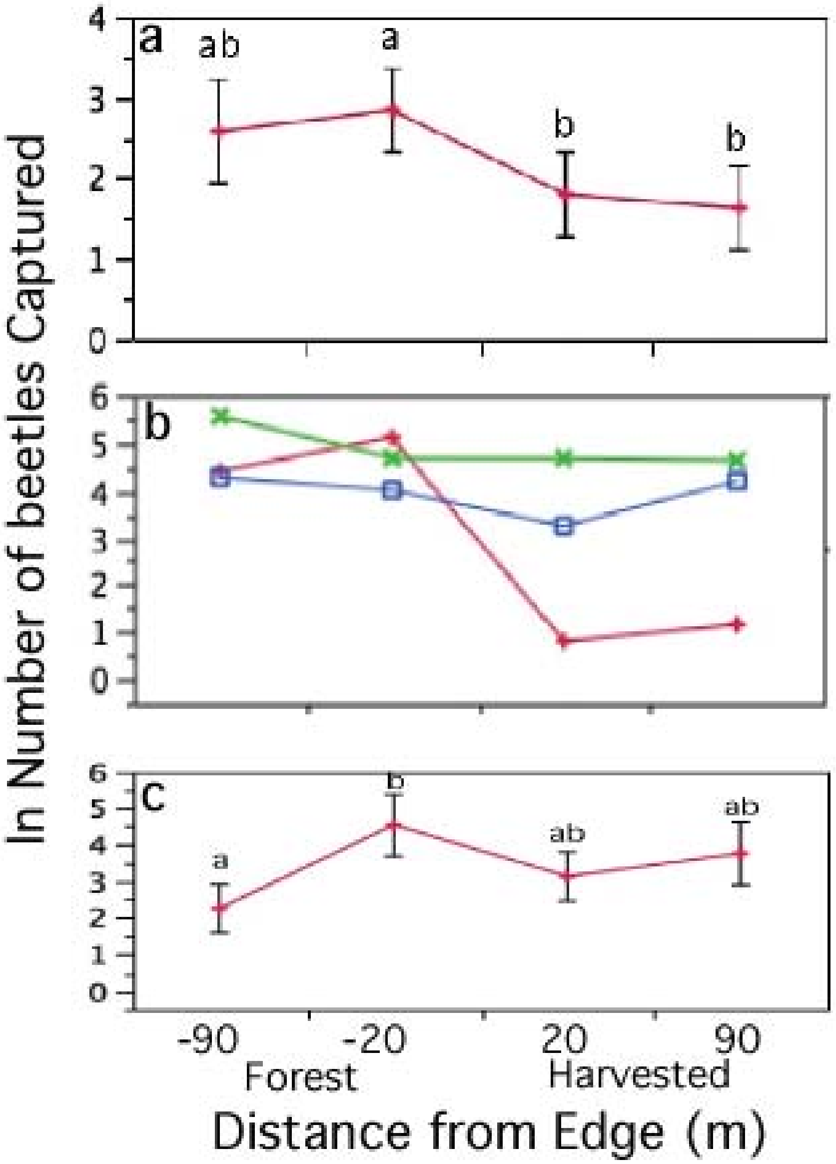

Figure 5. Abundance of bark beetles as a function of distance from the edge of harvested areas. a) Least square mean and SE response to clearcut edges for *Ips pini* and *Pityogenes* (no interaction between species and distance). b) Response of mountain pine beetles to clearcut edges for three sites shown separately. c) Least square mean and SE response to thinned edges for *Ips pini* and *Pityogenes* (no interaction between species and distance). Shared letters above bars indicate no significant difference between distances (Tukey's HSD).

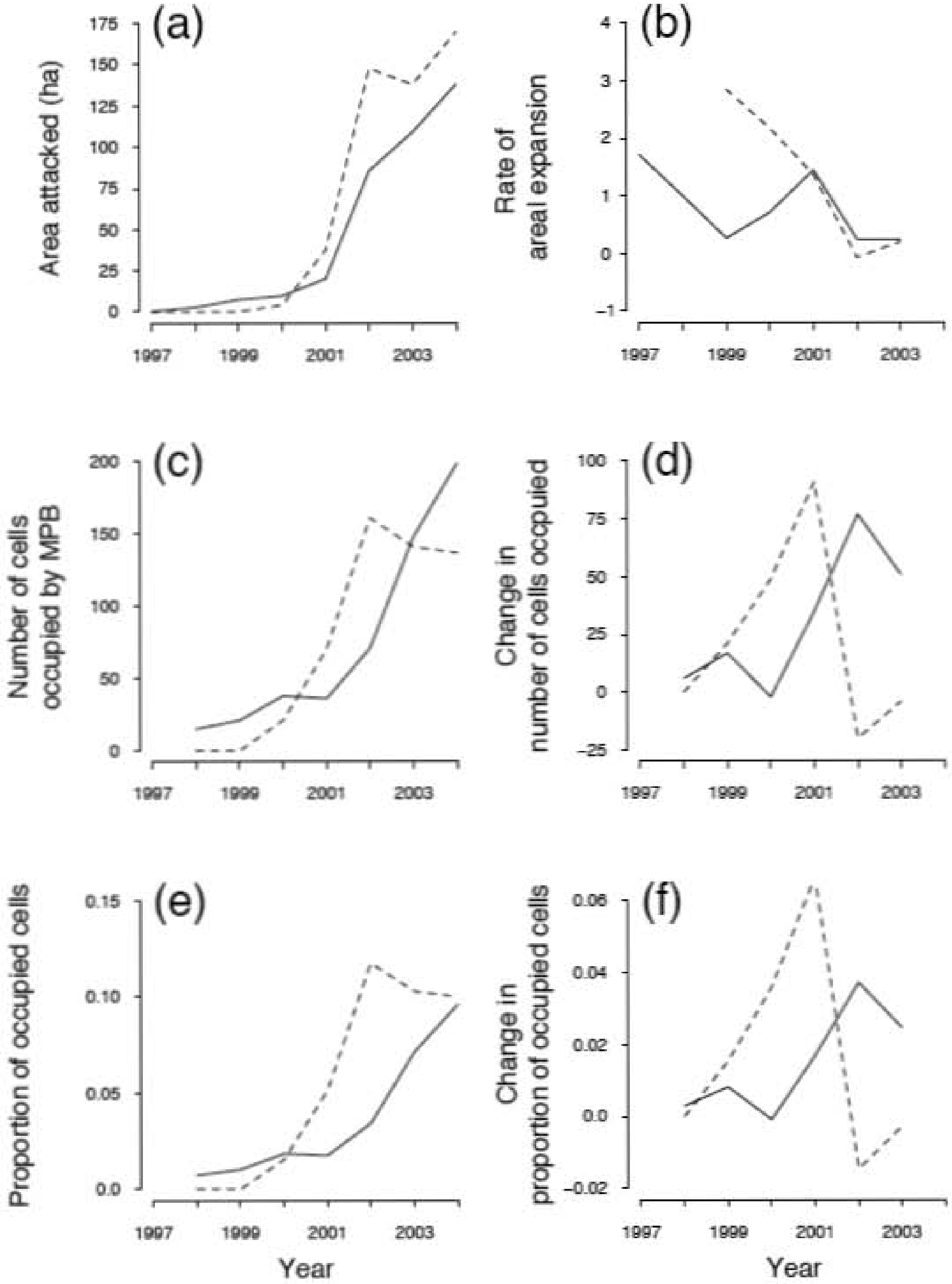

Figure 6. Mountain pine beetle (MPB) increase and spread in the monitoring (solid line) and management (dashed line) zones. (*a*) Area colonized by MPB, (*b*) the rate of areal increase ($\log_e$(area colonized next year / area colonized in current year)) by MPB, (*c*) Number of 25 ha cells with MPB colonized trees, (*d*) year-to-year change in the number of cells with MPB colonized trees, (*e*) proportion of available habitat cells occupied by MPB, (*f*) year-to-year change in the proportion of available habitat cells occupied by MPB. Number of cells with habitat: monitoring zone 2,077, management zone 1,371. Year indicates the year trees were colonized. (from Trzcinski and Reid 2008b).

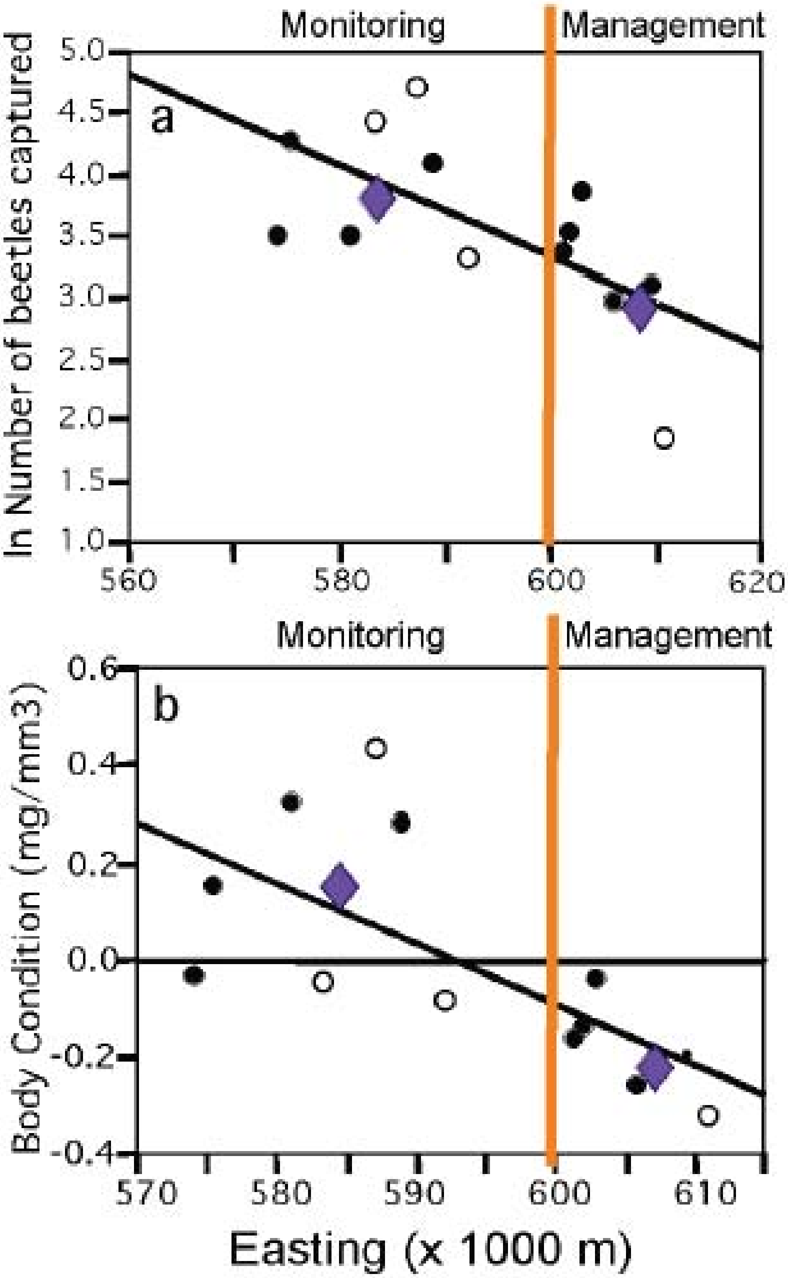

Figure 7. Spatial pattern of beetle abundance and condition in Banff National Park, measured as eastings (left to right is west to east). a) ln-transformed number of beetles captured in pheromone traps over two weeks, b) mean body condition (residual weight per volume) of captured beetles. Closed circles are pine stands, open circles are spruce stands, diamonds indicate means for monitoring and management zones (boundary indicated by vertical line). Points are from leverage plots controlling for stand type, and for condition, sex.

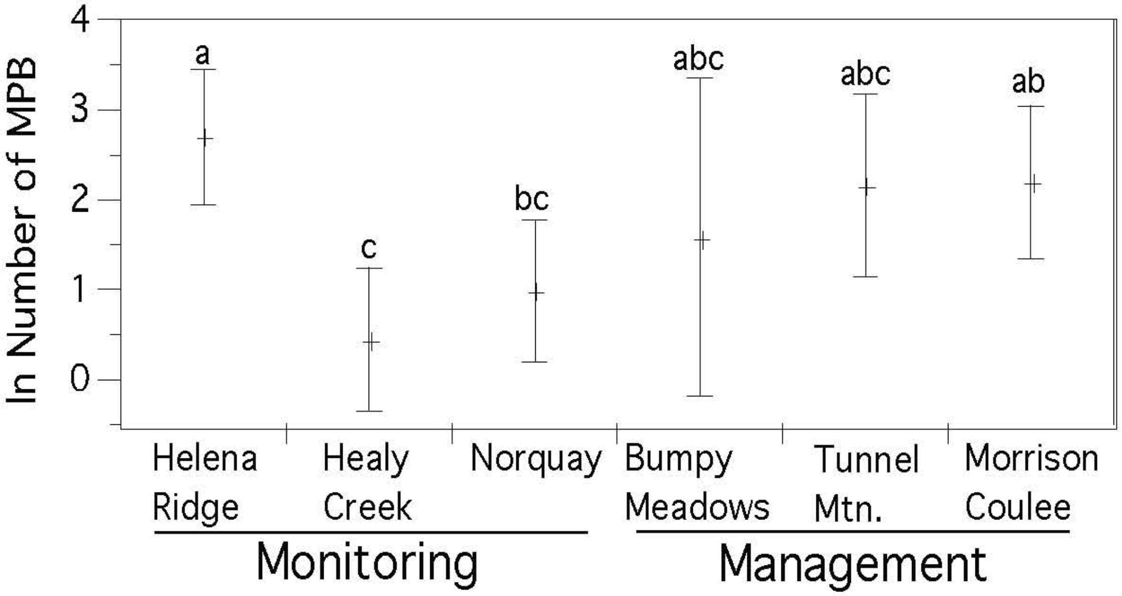

Figure 8. Mean (+ SE) ln-transformed number of mountain pine beetles (MPB) emerging from 1 m logs at six sites in Banff National Park. Sites are arranged from west to east, and within the monitoring or management zones. Sites sharing the same letter are not significantly different (Tukey's HSD).