

Article

Impact of Forest Fragmentation on Patterns of Mountain Pine Beetle-Caused Tree Mortality

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Abstract: The current outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, has led to extensive tree mortality in British Columbia and the western United States. While the greatest impacts of the outbreak have been in British Columbia, ongoing impacts are expected as the outbreak continues to spread eastward towards Canada's boreal and eastern pine forests. Successful mitigation of this outbreak is dependent on understanding how the beetle's host selection behaviour is influenced by the patchwork of tree mortality across the landscape. While several studies have shown that selective mechanisms operate at the individual tree level, less attention has been given to beetles' preference for variation in spatial forest patterns, namely forest fragmentation, and if such preference changes with changing population conditions. The objective of this study is to explore the influence of fragmentation on the location of mountain pine beetle caused mortality. Using a negative binomial regression model, we tested the significance of a fragmentation measure called the Aggregation Index for predicting beetle-caused tree mortality in the central interior of British Columbia, Canada in 2000 and 2005. The results explain that mountain pine beetle

exhibit a density-dependent dynamic behaviour related to forest patterns, with fragmented forests experiencing greater tree mortality when beetle populations are low (2000). Conversely, more contiguous forests are preferred when populations reach epidemic levels (2005). These results reinforce existing findings that bark beetles exhibit a strong host configuration preference at low population levels and that such pressures are relaxed when beetle densities are high.

Keywords: mountain pine beetle; forest fragmentation; density dependent; insect outbreak

1. Introduction

The recent epidemic of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in British Columbia, Canada has led to tree mortality spanning 18.3 million ha [1]. Since the current outbreak began in the late 1990s, the insect, which is native to the pine forests of western North America, has killed a significant component of forests dominated by lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann—its main host and the most commercially viable species in the region [2]. It has since spread beyond the continental divide into Canada's boreal forest beyond its historic range [3–5]. While past outbreaks have led to widespread tree mortality in British Columbia and other parts of Canada as well as in the United States [6], beetles are selective in their attack strategy, resulting in a patchwork of tree mortality across the landscape [7]. Such observations have important implications for management as beetles exhibit selective behaviour that, if understood, could guide mitigation efforts to minimize tree mortality. Following the more than decade-long outbreak, we are now entering a period of retrospection regarding this unprecedented situation. While mitigation in British Columbia is not currently emphasized, observing the outbreak from a number of perspectives will inform on the nature of the year-on-year outbreak development and identify those factors (mitigation or otherwise) that can be seen to have influenced infestation spread.

The mountain pine beetle typically has a one-year life cycle. During the summer months of July and August, adult beetles emerge from their host tree and immediately begin some period of flight in search of a suitable tree to attack. Beetles exhibit a preference for larger diameter trees that have thicker phloem and bark, both of which facilitate successful reproduction and brood development [8–10]. Furthermore, microclimate conditions, particularly at forest edges, create favourable conditions for successful attack [11]. Once a beetle begins boring through the bark of a tree, it releases plumes of aggregation pheromones that attract other beetles to the suitable host [12,13]. Thousands of beetles can accumulate on a tree, known as mass attack, through pheromone communication [14]. Tree mortality is a typical consequence of mass attack resulting from gallery development and inhibited translocation due to fungal inoculation [15], which eventually facilitates beetle reproduction. However, reproduction is a density-dependent process in which reproductive success diminishes when the density of beetles crosses some threshold. As a result, beetles will emit anti-aggregation pheromones that repel additional beetles from coming to the tree once the tree's resistance has been exhausted [12,16]. Following the below-bark boring and aggregation, beetles mate and oviposit under the bark of the tree. Adult beetles

die, the eggs hatch, and the larvae remain in the tree through the winter until they pupate and prepare to emerge during acceptable climatic conditions the following summer [17].

An individual tree that is under attack produces a toxic resin that pitches invading beetles from the tree. The likelihood of overcoming the tree's defensive mechanisms increases with high beetle densities [18]; however, weakened or diseased trees have reduced vigour and are more likely to succumb to attack [19] and can be killed by a relatively smaller number of beetles. Therefore, during the incipient stages of an outbreak, beetles are more likely to be selective with regard to which hosts they attack [20]. As beetle populations increase due to favourable climatic conditions and availability of lodgepole pine, selective pressure declines as higher densities facilitate successful attack on more vigorous trees [18,21]. The selective behaviour of mountain pine beetle has been observed in studies that demonstrate that older, less defensible hosts are attacked in years previous to the attack of nearby younger and more vigorous trees [22]. At the stand level, tree density influences beetle selective behaviour as the presence of more trees leads to a decline in available resources needed for thwarting beetle attack [23,24], which allows us to expect a preference for stands with higher densities of lodgepole pine at low beetle populations.

While observations of mountain pine beetle selective behaviour at the tree [25] and stand level are pertinent for understanding outbreaks, the size of the outbreak in British Columbia requires an examination of beetle interactions at a broader scale. Questions concerning potential locations of beetle attack at varying beetle population densities need to transcend from individual trees towards landscape units if the impacts of mitigation strategies are to be understood over the scale of the outbreak. Forest landscape patterns, specifically those resulting from anthropogenic and natural fragmentation processes, can alter insect infestations as demonstrated by the selective behaviours of defoliating insects [26], such as the western spruce budworm, *Choristoneura occidentalis* [27], jack pine budworm *Choristoneura pinus* [28], and forest tent caterpillar, *Malacosoma disstria* [29,30]. While fragmentation patterns have been found to influence how mountain pine beetle traverse across forested landscapes from one year to the next [31] and to influence predator-prey ratios [32], it is unclear how fragmentation influences the beetle's selective behaviour over time, thereby resulting in observed patterns of tree mortality across the landscape. This leads us to ask: how does the arrangement of forest patches in a landscape influence the location of mountain pine beetle attack during low *versus* high population levels?

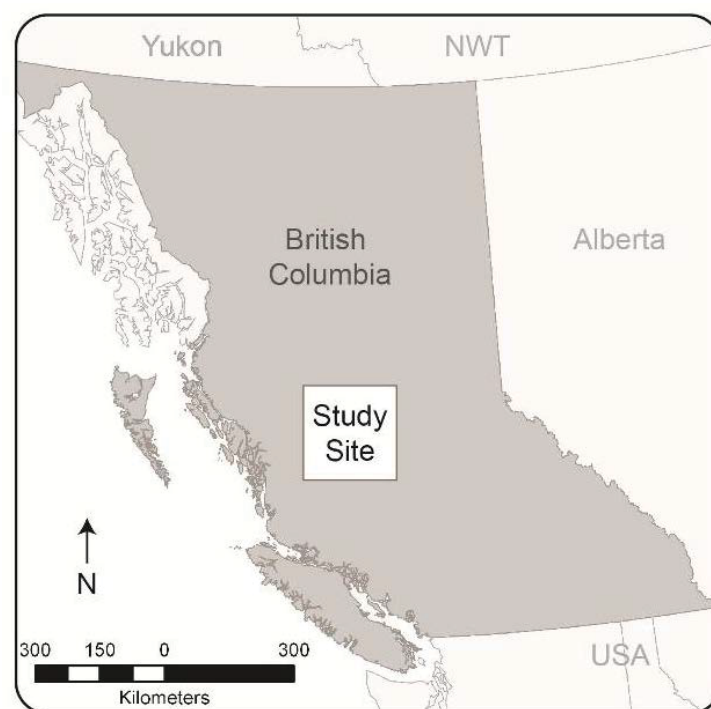
To address the proposed question, we seek in this study to estimate and compare mountain pine beetle caused mortality with a measure of forest fragmentation during the initial stage of an infestation when beetle population density is low *versus* during a later stage of an infestation when an epidemic population level is reached. We develop a negative binomial regression model for testing the significance of fragmentation (as estimated by a patch index) in explaining the variability of mortality caused by mountain pine beetle (estimated from aerial surveys during these two periods in time). The intent of this study is to provide more broad scale information to complement individual insect-host relationships that can aid managers in understanding the processes of mountain pine beetle infestation at specific infestation stages, as well as aid in building a retrospective understanding of how this unprecedented outbreak developed.

2. Experimental Section

2.1. Study Site and Data

Our analysis was carried out over a 200 km × 200 km study site in the central interior of British Columbia, Canada (Figure 1). The site was selected based on previous observations that the current mountain pine beetle outbreak primarily commenced in this area in the late 1990s and subsequently spread to other lodgepole pine dominated forests in the province [33]. While beetle-caused tree mortality in this area is currently estimated at 18.3 million ha [1], this number represents the overall area that is affected (at any level of severity) and not the total amount of tree mortality [34]. Some areas experience widespread tree mortality, while other areas experience low mortality for a single year and, in some cases, little to no mortality the next year.

Figure 1. 200 km by 200 km study site in central interior of British Columbia, Canada.



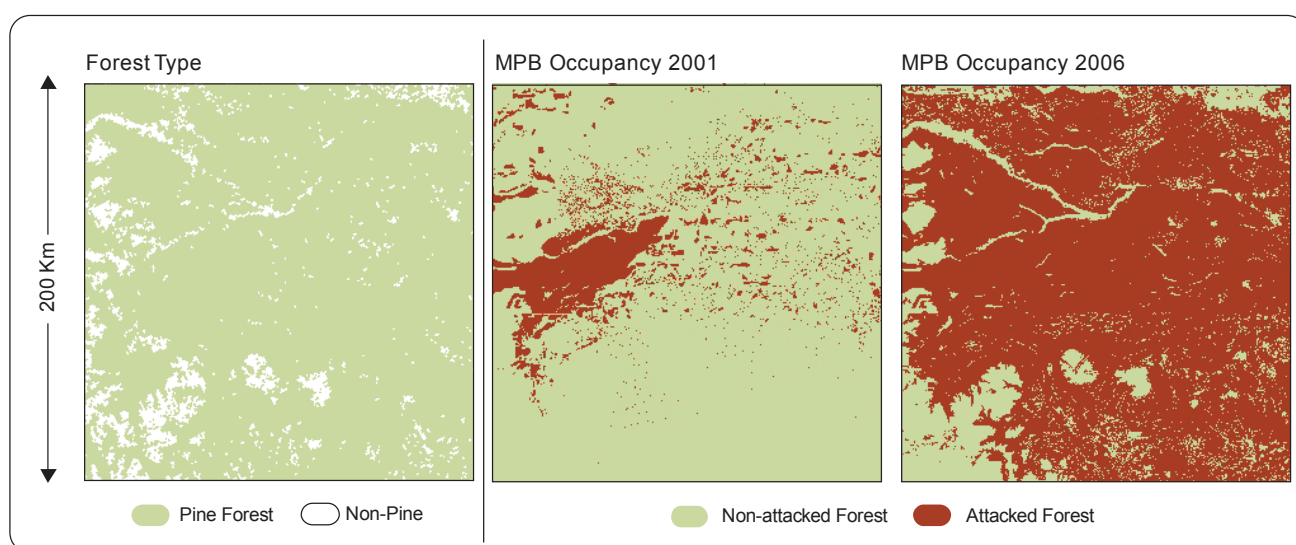
2.1.1. Mountain Pine Beetle Survey Data

Beetle induced pine mortality is surveyed annually as part of the Aerial Overview Survey (AOS) program administered by the British Columbia Ministry of Forests and Range [35]. Surveyors record locations of killed trees as polygons on 1:100,000 or 1:250,000 basemaps. Infestation locations are coded with a rating of severity that represents the percentage of beetle-induced tree mortality area in the polygon. All AOS data and detailed surveys were compiled and integrated for the province of British Columbia from 1999 to 2006 [34], from which the location and severity of infestations at a 1 ha resolution were derived. It is important to emphasize that the AOS data record locations where beetles have attacked and successfully killed host trees in the previous year, and that we use this information as a surrogate to identify where beetles have been (occupancy). Similarly, the severity rating provides

a surrogate for beetle population density, as large population densities are required to cause severe mortality.

For the purpose of this study, the AOS data were summarized into a binomial occupancy variable of presence/absence by assigning those areas to the “presence” class if beetle-induced tree mortality was greater than 0. The lack of current knowledge pertaining to how different levels of beetle populations respond to varying levels of forest fragmentation led to the selection of the binomial classification scheme. Furthermore, while beetle caused mortality in this area was first observed in the 1999 survey, we used the 2001 survey data to represent mountain pine beetle occupancy in 2000, as this year coincides with the land cover classification data that were used for obtaining measures of forest fragmentation. The 2006 AOS data were used to represent mountain pine beetle presence at the outbreak stage in 2005, as a notable proportion of the study site had been infested by this point in time. Figure 2 depicts the 2001 and 2006 AOS data that represent the presence of mountain pine beetle in the study site in 2000 and 2005, respectively. The number of hectares occupied by mountain pine beetle in the study site from 2000 to 2005 is presented in Figure 3.

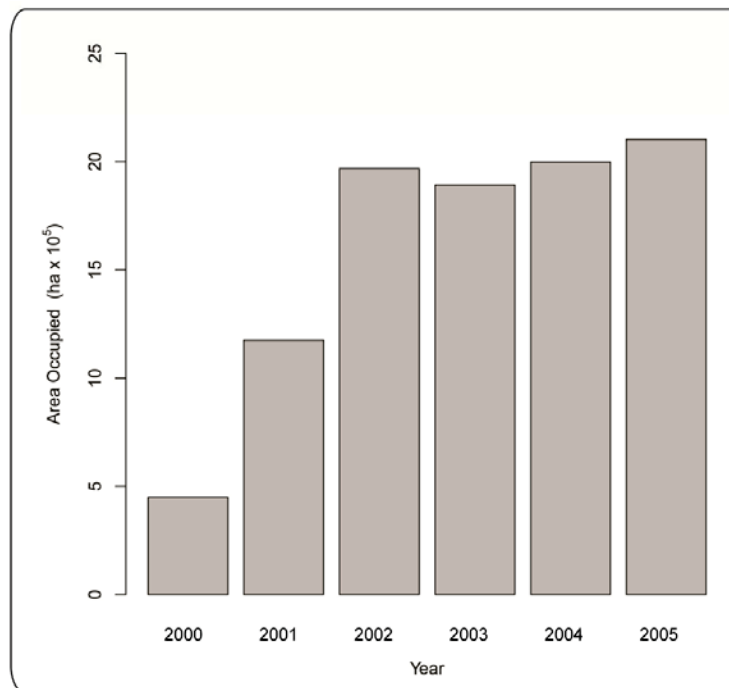
Figure 2. Mountain pine beetle (MPB) occupancy in study site in 2000 and 2005 based on aerial overview survey data acquired in 2001 and 2006.



2.1.2. Land Cover Classification

Land cover classification was derived from a Canada wide mapping project called Earth Observation for Sustainable Development of forests (EOSD) [36]. The EOSD project mapped land cover for the forested ecosystems of Canada. To cover the forested ecosystems of Canada, over 480 Landsat-7 Enhanced Thematic Mapper Plus (ETM+) images were classified. The classification resulted in a 23 category depiction of land cover for *circa* year 2000 with a spatial resolution of 25m, with all products available freely as mosaics or as 1:250,000 scale map tiles [36]. The resultant EOSD land cover classes were also subsequently reclassified into forest and non-forest binary maps to support the generation of landscape metrics [37].

Figure 3. Area occupied by mountain pine in study site during recent epidemic. Note that the Area Occupied (y-axis) reflects the number of 1 ha cells that contain at least some proportion of beetle-induced tree mortality. The total area of British Columbia covered by forest land is approximately 60 million ha.



2.2. Methods

2.2.1. Measure of Forest Fragmentation

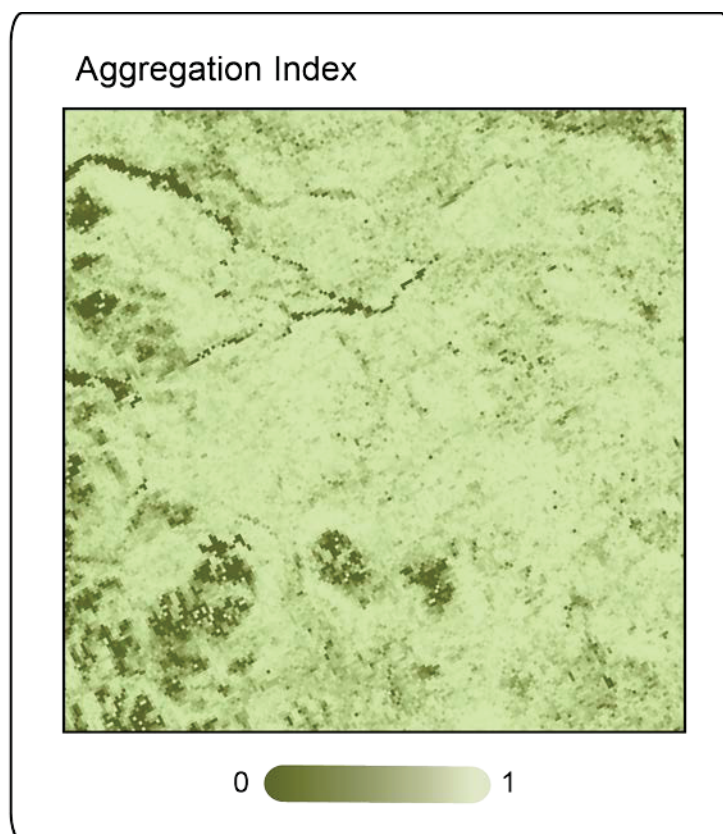
Landscape metrics, such as those estimated from the EOSD data, quantify some property of landscape pattern and have become widely used due to greater availability of software and growing quantities of spatial data available for large areas [37]. Understanding the role of landscape patterns in ecological processes is critical for proper management of natural resources as decision-makers can manipulate landscapes in order to achieve desired management outcomes [38,39]. While a large set of landscape metrics exist, recalling the need for appropriate selection of metrics [40], we chose the Aggregation Index (*AI*) [41] for measuring forest fragmentation in the study site. As appropriate for this study, the *AI* is used to measure the amount of forest patch edges that are adjacent with each other, which is calculated by:

$$AI = \frac{e_{f,f}}{\max[e_{f,f}]} \quad (1)$$

where the edge, *e*, of forest patch, *f*, adjacent with other forest patches is divided by the maximum potential shared edge between forest patches. Therefore, *AI* results in a value in the interval (0~1), where *AI* = 0 when no forest patches share an edge (*i.e.*, the area is non-forested), and *AI* = 1 when *e_{ff}* reaches the maximum (*i.e.*, there exists a single forest patch). That is, low values of *AI* represent fragmented forests while values close to 1 represent non-fragmented forests. While there are multiple

indices that estimate fragmentation, and the use of the *AI* (as well as all landscape metrics) has limitations [42], the *AI* was selected because it provides a linear measure of forest fragmentation that can be adequately utilized in a regression in order to explain the variability in mountain pine beetle populations. The *AI* values from the EOSD data at 1 km resolution are shown in Figure 4.

Figure 4. Values for the Aggregation Index in the study site as measured from the 2000 EOSD data [36].



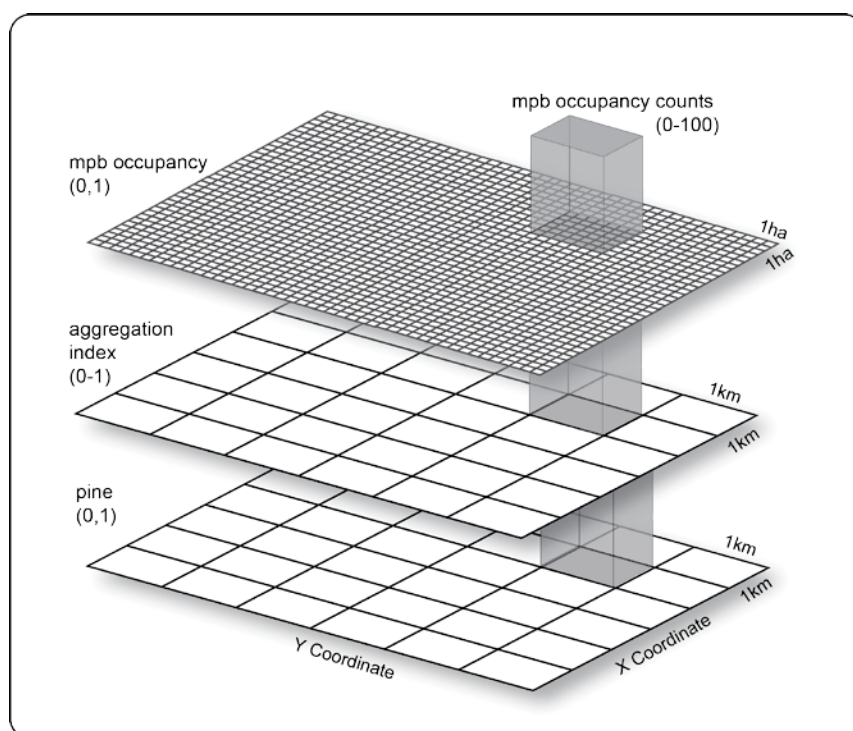
2.2.2. Regression Model

A negative binomial regression model was selected to estimate the degree to which forest fragmentation, as measured by the *AI*, explains the variation in presence of mountain pine beetle attack. This selection was based on the positively skewed (*i.e.*, over-dispersed) distribution of mountain pine beetle occupancy in the study site (discussed in detail in the results section).

Data from previous mountain pine beetle research [43] were classified for our study site into a binomial variable where pine = 0 represents an absence of any pine species, and pine = 1 indicates that at least some pine species are present. While other pine species are potentially present in all stands in the study site, lodgepole pine is by far the most dominant species. For providing a measure of fragmentation, each 1 km cell was also represented by an *AI* value between 0 and 1. Mountain pine beetle presence was calculated for each 1 km cell based on the count of 1 ha cells in which beetle-induced tree mortality was present, resulting in a value in the range 0–100. The presence-absence data set at the 1 ha scale thus provides density counts when aggregated to the 1 km scale. In summary, for each 1 km cell in which pine = 1, the *AI* value is measured against the count of

1 ha cells that are occupied by mountain pine beetle. Figure 5 provides a schematic of how the three variables are integrated.

Figure 5. Data integration for developing the regression model. For each 1 km cell in which pine is present, the significance of the Aggregation Index for predicting counts of mountain pine beetle occupancy was analysed.



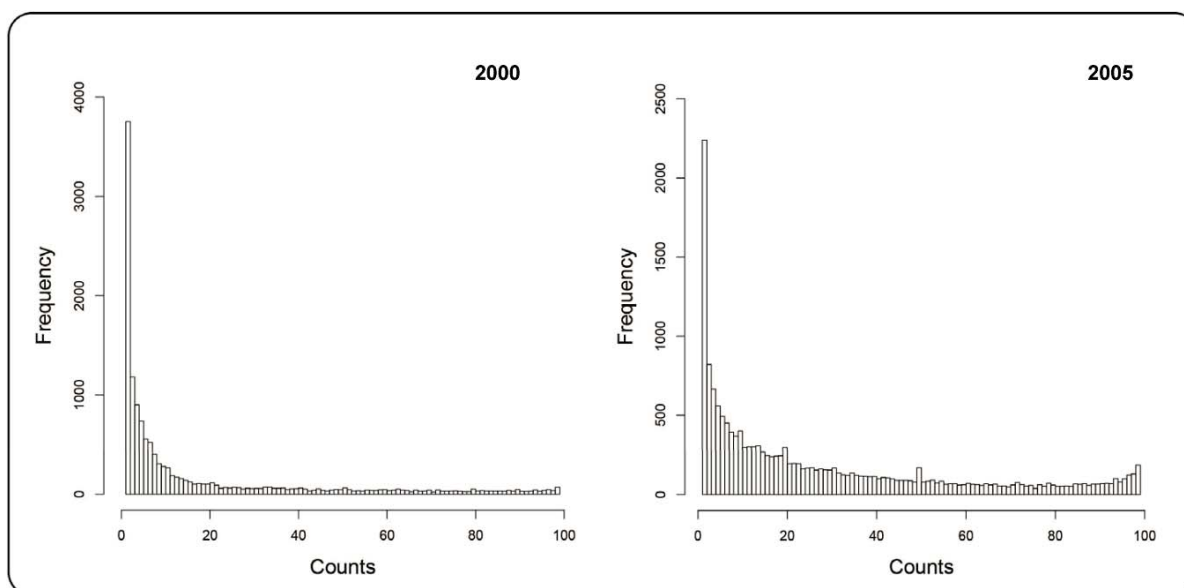
The occupancy counts for 2005 were adjusted in order for the data to correspond to a negative binomial distribution. In 2005, the majority of 1 km cells had high counts of beetle occupancy, while very few cells had low occupancy. Thus, we took the inverse counts (*i.e.*, 100—the number of 1 ha cells occupied by mountain pine beetle) to represent the counts for 2005. The adjustment to the 2005 data is accounted for in the evaluation of the regression results in the next section by reversing the relationship between fragmentation and occupancy counts in the analysis. That is, we interpret a positive relationship between occupancy counts and the *AI* in the regression results as a negative relationship. Furthermore, the spatially dependent nature of outbreaks led to the removal of 26,365 one ha cells that contained no beetle caused mortality, leaving 13,635 cells. The reason for this is because some cells may have an *AI* that is conducive to attack, but if that cell is far from all infested cells there is a very low likelihood that it will be attacked (similar to notions of risk, see [44]). The data were prepared using ArcMap 9.3 [45], and the negative binomial regression model was developed in the statistical software R 2.12.2 [46] using the *glm.nb* model in the MASS library.

3. Results and Discussion

The distribution of mountain pine beetle occupancy counts are displayed for 2000 and 2005 (adjusted) in Figure 6. The histograms depict a positively skewed distribution of beetle occupancy which represent patterns akin to the negative binomial distribution. In 2000, the majority of 1 km cells

have minimal beetle occupancy, and few cells are almost entirely occupied. Given the adjustment to the 2005 data, the majority of cells in the latter period of the infestation now have high beetle occupancy with few cells containing low beetle populations. The distribution in both years supports the use of a negative binomial regression model as occupancy counts are positively skewed.

Figure 6. Frequency of 1 km cells containing a specific number of 1 ha cells in which mountain pine beetle are present for the years 2000 (left) and 2005 (right). Note that for 2005, Counts = 100—the number of 1 ha cells occupied by mountain pine beetle.



The results from negative binomial regression for predicting the number of occupied 1 ha cells in 2000 from the *AI* are presented in Table 1. The model was statistically significant as indicated by Chi-square = 9.9733, $p < 0.001588$. Furthermore, the *AI* was found to be statistically significant with $p < 0.00378$. The negative binomial regression model is log linear, thus the coefficients can be translated into multiplicative effects. The expected log count increase for a one unit increase in the *AI* is -0.331 ; therefore, a one unit increase in the *AI* (which signifies less fragmentation) is associated with a decrease in mountain pine beetle occupancy count of $\exp(-0.3351) = 0.7153$. Thus, at the beginning of the outbreak in the study area, lower counts of mountain pine beetle-caused tree mortality are associated with less fragmented forest while higher counts are associated with more fragmented forests. It should be emphasized here that higher *AI* values are not a result of mountain pine beetle-induced mortality in 2000 because, while the data for both variables were collected in the same year, tree mortality resulting from attack occurs over several months.

Table 1. Results from negative binomial regression for predicting beetle occupancy based on the aggregation index in 2000.

	Estimate	Standard Error	<i>z</i> value	<i>p</i>
(Intercept)	3.2107	0.1094	29.352	<0.00001
<i>AI</i>	−0.3351	0.1157	−2.896	0.00378

The results from the negative binomial regression for predicting beetle occupancy in 2005 from the *AI* are presented in Table 2. Again, the model was found to be statistically significant with Chi-square = 1124.4 and $p < 0.0001$, and the *AI* is reportedly significant with $p < 0.001$. Since we measured 2005 counts as the inverse of beetle occupancy, the estimated coefficient for *AI* required adjustment from a negative to a positive value. The result is an expected log count increase for a one-unit increase in the *AI* of 2.21167. This result translates into a one unit increase in *AI* causing an increase in the expected mountain pine beetle occupancy by a factor of $\exp(2.21167) = 9.131$. Therefore, less fragmented forested areas experienced greater tree mortality during the latter stages of the outbreak in the study area. This finding is converse to the model predicting 2000 beetle occupancy, which indicated that the mountain pine beetle preferentially attacked and killed trees in fragmented forests during the initial portion of the outbreak when beetle populations densities were low. Conversely, the results from 2005 reveal that this behaviour switches during the later stages of the outbreak towards less fragmented or non-fragmented forests when beetle populations are much higher.

Table 2. Results from negative binomial regression for predicting beetle occupancy based on the aggregation index in 2006. * Coefficient estimate is adjusted to account for the use of inverse counts in the regression model. Adjustment was made by multiplying the coefficient estimate by -1 .

	Estimate	Standard Error	z value	p
(Intercept)	5.29606	0.05467	96.87	<0.0001
<i>AI</i>	2.21167 *	0.06006	−36.82	0.0001

The state of the current mountain pine beetle epidemic has raised several questions pertaining to the insect's biological traits and the consequential patterns of tree mortality. While previous outbreaks have been recorded throughout the twentieth century [47], favourable climatic conditions and availability of susceptible hosts has led to an outbreak in western North America that spans beyond the beetles' historic range, attacking trees in areas that have not evolved effective defensive mechanisms due to their 'naïve' experience with mountain pine beetle [48]. Furthermore, recent studies have revealed that the beetle has made the transition from its dominant host, lodgepole pine, to Jack pine, *Pinus banksiana* [4], a species that can be found across the longitudinal range of Canada's boreal forest, although broad areas of contiguous pine forest are increasingly rare as one moves east of the Rockies [5]. Challenges continue as damage caused by the mountain pine beetle is explicitly linked to other natural disturbances such as forest fires [49]. As the beetle infests new areas in the frontier of the outbreak, pioneer populations must seek out hosts that are susceptible to relatively lower beetle densities. Over time, beetle densities can grow in favourable host and climatic conditions to levels whereby such host selective pressures can be relaxed [14]. This study has exhibited that forest fragmentation may play a role in this process.

The coefficient estimates from the negative binomial regression models suggest that mountain pine beetle exhibit a density-dependent behavioural preference with regard to fragmented landscapes of host species. That is, at low population levels early in the outbreak, beetles preferentially attack fragmented forests. This preference is likely guided by ecological drivers such as beetle communication and the ability to locate susceptible hosts. While there is the possibility that harvesting activities can

influence our observations because both forest companies and mountain pine beetle display a preference for larger trees, the notable difference in host preference between 2000 and 2005 during which time beetle population levels rose considerably, indicates that landscape patterns are influencing beetle behaviour.

Beetles existing at lower population densities are more likely to attack fragmented forests where higher edge-to-area ratios may facilitate the nature of mountain pine beetle communication. Beetle communication takes place through the production and use of aggregation and anti-aggregation pheromones. When population levels are low, aggregation pheromones facilitate the aggregation of a limited number of beetles towards the most susceptible of hosts, and conversely anti-aggregation pheromones deter beetles in a timely manner so that reproductive success is not compromised. Although the same process takes place in non-fragmented forests and when population levels are high, the configuration of forest patches resulting from fragmentation is a likely contributor to the effectiveness of this communication mechanism when it is most needed (*i.e.*, as diminished forest areas serve to concentrate infestation). Higher edge-to-area ratios result from having a greater number of smaller forest patches from which the beetles should be able to more easily decipher pheromone source locations. This leads us to ask the following: how do the ambient micro-climates in fragmented forest patches affect production and dispersal of pheromones? Do pheromones on the edge spread easier and farther than in the centre of the patch due to increased wind speeds? Is pheromone communication more effective in smaller patches than in larger patches or in continuous forested areas, and how does this differ between short and long-range dispersal? Such questions are important for the focus of future research efforts that aim to understand how forest structure influences the success of mountain pine beetle infestations, particularly at low population densities. Models of the dispersion of bark beetle pheromones in forests have found that micrometeorological conditions (which are typically most unstable during the summer and in the middle of the day) and canopy structure played a large role in the efficacy of pheromone communication [50]. Open forests can disrupt the lateral movement of pheromone plumes, thereby reducing the efficacy of communication.

Another plausible reason why beetles existing at lower population densities prefer fragmented forests is because edge-to-area ratios provide more susceptible hosts or breeding success for the beetle as fragmentation results in temperature extremes and higher levels of solar radiation in smaller patches and in trees that are in close proximity to the patch edge [51]. The altered microclimate presented by fragmentation can assist the beetle during its flight period as well as in reducing overwinter mortality because the emergence of beetles from their hosts in the summer is mediated by the ambient environment as temperatures must reach a threshold before beetles depart and begin their search for a new host [52,53]. Patches in a fragmented landscape will be more exposed to warmer temperatures and direct solar radiation that can trigger an earlier-than-normal emergence, resulting in a longer flight period for the population and subsequently increasing their chances of finding a susceptible host. Increased tree exposure to solar radiation could also potentially assist beetle survival during the winter months when the larvae survival is directly related to the duration of cold lethal temperatures [54].

Trees that are relatively closer to fragmented edges are more susceptible to wind damage, which could compromise vigour and make a tree more susceptible to attack, not only by mountain pine beetle but also by secondary insects [25]. Damaged trees spend available resources on repairing tissues,

leaving less for use in defence against beetle attack. As edge effects persist some distance into the patch, small patches could potentially be composed of weakened susceptible hosts.

As population levels grow, previously non-susceptible trees can be successfully attacked and killed because higher beetle densities are able to overcome stronger mechanisms of defence [55]. This observation changes beetle behaviour from one that is focused on locating the most susceptible of hosts to finding trees in which beetle densities are below some threshold defined by reproductive success. Less patchy forests that contain a continuous spatial distribution of potential hosts become more beneficial at this stage as resource availability is higher and more easily accessed. When beetle populations reach the stage of an outbreak, beetles should prefer non-fragmented forests because of the cost of dispersal: beetles typically fly short distances to new hosts—approximately within 3–4 kilometres [56]—while only a small proportion of beetles engage in long distance dispersal. Short distance dispersal is thus facilitated in non-fragmented landscapes where resource availability is high.

Density-dependent dynamic behaviour in mountain pine beetle is not unique to the insect's relationship with forest fragmentation. The term “switching” [57] is used to explain the behaviour of beetles that make the switch from an under-attack-host to another nearby host due to the presence of a high density of beetles. Passing the threshold of densities in a given host will reduce reproductive success, thus switching increases the likelihood of brood survival. Similar to the findings of our study, [58] explains that mountain pine beetle exhibit dynamic behaviour in the choice of habitat quality based on population densities. The authors found that beetles were more selective at low densities with regard to breeding site availability. As population levels increased, beetles switch to a selection behaviour guided by intraspecific competition and the reliability of habitat quality cues. While we did not explicitly measure habitat quality, fragmented forests present a set of transformed biogeophysical and microclimatic conditions that can alter tree susceptibility and the probability of successful beetle attack. If these changes are conducive to beetle-induced mortality, such areas should be targeted for mitigation at low beetle densities.

The method implemented in this study provides useful information for considering how to manage forests in light of beetle disturbances. Yet, future decisions must acknowledge some of the issues that arise when integrating disparate data sets with varying resolutions and covering relatively large areas. First, creating a binomial variable of presence/absence to represent beetle populations does not consider the severity of beetle-induced tree mortality from one area to another. Thus, more focus needs to be paid to the severity-fragmentation relationship in order to better understand the degree to which fragmentation facilitates infestations. Second, integrating the EOSD data that provided the measures of *AI* with the AOS data, which provided mountain pine beetle counts, could potentially introduce sources of error. For instance, estimating forest fragmentation at the 1 km scale may overlook the presence of relatively small stands of trees. If such stands are infested with mountain pine beetle, the result is an *AI* value of 0 associated with beetle presence. Thus, integrating the two data sets may lead to scenarios where beetles are present but there is very little or no forests. However, the consequences of such scenarios are likely insignificant in this study as the number of 1 km cells where *AI* = 0 is less than 1.0% of the total number of cells.

4. Conclusions

In this study, we examined how the spatial arrangement of hosts influenced mountain pine beetle behaviour at two different stages of an outbreak in British Columbia. Building upon knowledge of individual insect-host relationships [59], we revealed that density-dependent dynamic behaviour may contribute to the observable patchwork of tree mortality across beetle-impacted landscapes. The results of this study suggest that beetles exhibit preferences at scales beyond the individual tree, which is in part related to forest fragmentation. While we have presented some of the reasons why this may be the case, further research is needed to fully understand the complex interactions of factors that may be driving this phenomenon. It would be overly simplistic for us to conclude that forest managers should seek to systematically alter the spatial arrangement of potential hosts in order to keep beetle populations at endemic levels; however, there are lessons to be learned from the most recent outbreak in British Columbia that could inform future forest managers. Moreover, as the current mountain pine beetle epidemic in western North America continues to spread beyond the beetle's historic range, our contemporary understanding of host susceptibility [56,60–62] will need to be revisited to incorporate new knowledge of the beetle in novel habitats. This study suggests that the dynamic relationship between beetles and the spatial pattern of potential hosts is one of the factors that need to be studied further.

Acknowledgments

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Conflict of Interest

The authors declare no conflict of interest.

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