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A Provincial and Regional Assessment of the Mountain Pine Beetle Epidemic in British Columbia: 1999-2008

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ABSTRACT. Western Canada is currently experiencing an epidemic infestation of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). In British Columbia, the infestation extends over more than 13 million ha and has resulted in a wide-range of social, economic, and ecological impacts. In this study, we compile the known environmental drivers of the infestation and assess these drivers against the actual outcomes of the infestation to date. To support our investigation, we defined the population at risk to mountain pine beetle attack as the spatial extent of pine in British Columbia (approximately 525,329 km^2) and used a range of driver variables known to influence the location and success of beetle infestations (i.e., proportion of pine, climatic factors, and latitude adjusted elevation) as inputs to a two-step clustering algorithm. We generated 15 clusters representing unique combinations of these driver variables. Variables that represent resulting conditions or infestation outcomes (i.e., cumulative amount of pine killed, proportion of pine remaining, distance to nearest infestation, or stand susceptibility) were then used to characterize these clusters and to identify areas of the province with similar drivers, but with different infestation conditions and outcomes. When the entire study area is considered, our findings indicate that the most susceptible areas of pine in British Columbia were attacked by the beetle first and that heretofore uninfested areas with similar conditions were likely spared from infestations initially due to their abundance of immature pine. However, infestations in less optimal areas increased markedly in 2007 and 2008, as the competition for hosts increased. A regional assessment of the clusters (for areas in the north, central, and southern regions of British Columbia) further indicated that the beetles may have opportunities to expand in northern and central areas-depending on short-term climatic conditions. By relating our current understanding of infestation drivers to the 2008 infestation, we were able to identify those areas of the province that are most vulnerable to continued infestation. Our results confirm that mountain pine beetle will likely continue to be the dominant forest health concern in British Columbia for many years to come.

Keywords: mountain pine beetle, infestation, spread, susceptibility, 2-step clustering

1. Introduction

The current epidemic of mountain pine beetle (*Dendroctonus ponderosae* Hopkin) began in the central interior of British Columbia, Canada, in 1995 (Ministry of Forests, 2003). The infestation had affected 164,000 ha of forests by 1999 and more than 13 million ha by 2008 (Raffa et al., 2008). In western North America, lodgepole pine (*Pinus contorta var. latifolia Engelm*) is the primary host; however, almost all pine species may be attacked and killed by the beetle (Wood, 1963; Furniss and Schenk, 1969). Although endemic to pine forests of British Columbia, the mountain pine beetle has spread to areas outside its historical range (Carroll et al., 2003) and may pose a risk to Canada's boreal forests and eastern pine stands (Nealis and Peter, 2008).

At endemic population levels, mountain pine beetle populations are typically constrained by predators, pathogens, and host availability and susceptibility (Amman and Cole, 1983; Aukema et al., 2008). Several environmental drivers are known to influence the location and success of mountain pine beetle infestations; however, once populations reach epidemic levels, there are few constraints on population growth, and climate and host availability become the dominant population drivers at the landscape scale (Safranyik, 1978; Amman and Cole, 1983).

Compilation statistics on the total area impacted by the mountain pine beetle are determined by annual systematic forest health surveys. Although these surveys provide timely information on a range of forest health parameters, they are conducted at a coarse spatial scale and the information they provide is strategic - not operational (Wulder et al., 2006a). In the context of mountain pine beetle, these surveys indicate the proportion of pine that has been killed in a given area (i.e. infestation severity). If the total area affected by mountain pine beetle is reported without accounting for variation in infestation severity (i.e. large areas are lightly infested by the beetle), the actual mortali-

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ty of pine may be overestimated (Wulder et al., 2009a). As a result, significant areas of pine may remain on the landscape (Robertson et al., 2009), supplying hosts that will enable the continuation of the current epidemic into the future. The goal of this study was to analyze the pine forest resource within British Columbia according to common environmental drivers for mountain pine beetle infestation, and then to characterize these areas by the level of infestation they have experienced to date.

2. Methods

2.1 Study area

The study area (Figure 1) is 525,329 km^2 of pine forest in the province of British Columbia. The western extent of the study area coincides with the 2008 provincial mountain pine beetle management units (Ministry of Forests and Range, 2008), the northern extent represents the northern limit of pine within the province (Hamman et al., 2005), and the southern and eastern extents correspond to the provincial boundary. The study area encompasses a broad range of ecosystem types, and has an elevation range of 100 to 3,937 metres.

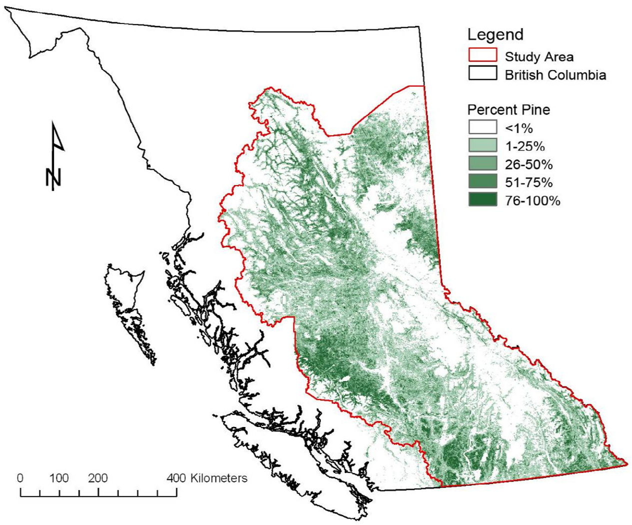

Figure 1. Study area boundary (red) shown around the combined ranges of six pine species found in BC (Hamman et al, 2005): *P. albicaulis, P. banksiana, P. contorta, P. flexilis, P. monticola, P. ponderosa*.

Three specific regions within the larger study area were selected for more detailed analysis (Figure 2). The boundaries of these focus areas correspond to provincial ecoregion boundaries defined according to major physiographic and minor macroclimatic variation (Demarchi, 1996). The northern region (composed of four ecoregions) represents an area that was historically considered climatically unsuitable for the mountain pine beetle (Carroll, 2007). The central region (Fraser Plateau) represents the area where the current epidemic started in 1999 and where infestation severity has been the greatest (Aukema et al., 2008; Westfall and Ebata, 2008). Finally, the southern region (Columbia Mountains and Highlands) is an area that has ongoing, relatively low severity mountain pine beetle infestation. These three regions represent 43% of the total study area. These three regions were selected because they have different patterns of current and historical infestation.

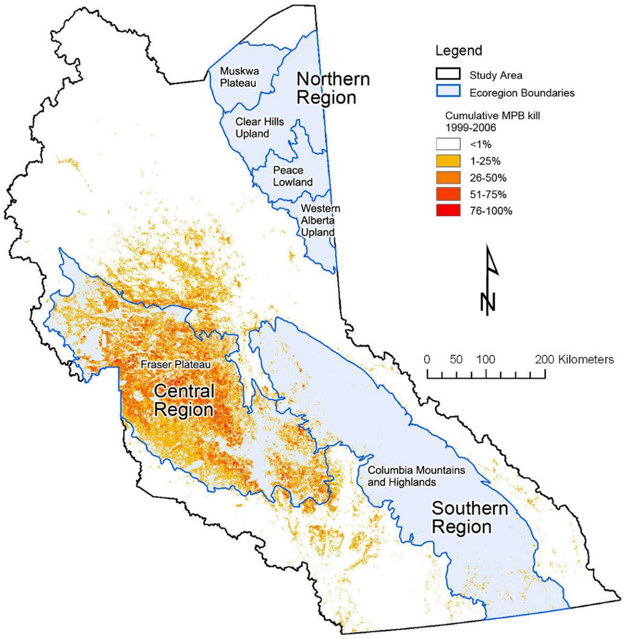

Figure 2. Northern, central, and southern focus-area regions in British Columbia with cumulative mountain pine beetle mortality data (1999 to 2006) from Robertson et al. (2009).

2.2 Data

Driver variables are those environmental factors that influence the location and success of beetle infestations including percentage pine, minimum mean winter temperature, mean August temperature, annual degree day (> 5°C) accumulation, latitude adjusted mountain pine beetle elevation, and annual solar radiation (Table 1). Explanatory variables are those factors that characterize the outcome of the current epidemic in British Columbia and include cumulative mountain pine beetle caused mortality (1999 ~ 2006), stand susceptibility, distance to nearest infestation, and percentage pine remaining on the landscape (Table 2). The proportion of pine and cumulative mountain pine beetle mortality data (1999 ~ 2006) were taken from Robertson et al. (2009). As Robertson et al. (2009) estimated cumulative mortality up to and including 2006, the location and extent of the infestation post-2006 was characterized by the cumulative severity calculated from the 2007 and 2008 aerial overview survey (AOS) data (Westfall and Ebata, 2008; 2009), using the midpoints of the severity class as per Wulder et al. (2009a). The other driver and infestation outcome data were rasterized to a standardized spatial representation (100 m by 100 m; 1 ha) as per Robertson et al. (2009), and reprojected to the British Columbia Albers Equal Area projection (North American Datum 1983). The stand susceptibility index is a product of stand age,

Table 1. Driver Variables

Description	Source	Rationale
Proportion of pine	Robertson et al., (2009)	Derived from pre-1999 forest inventory data. Represents the proportion of pine within a 1 ha unit. The mountain pine beetle has a broad range extending from northern Mexico to northwestern British Columbia, Canada (Carroll, 2007). Over this range, almost all species of native and introduced pine are susceptible to attack (Huber et al., 2009). The most susceptible pines are between the ages of 80 and 100 years, with a diameter greater than 25 cm (Shore and Safranyik, 1992; see also Björklund and Lindgren, 2009).
Minimum mean winter temperature (°C)*	Climate BC v.3.21	Depending on when in the winter season they occur, sustained periods of time with temperatures less than -40 °C can cause significant mortality to even the cold-tolerant larval stage (Safranyik, 1978; Safranyik and Carroll, 2006; Safranyik and Linton 1991, 1998). See also Régnière and Bentz (2009) for additional insights regarding the link between temperature changes and mountain pine beetle population growth rates.
Mean August temperature (°C)*	Climate BC v.3.21	Mean August temperatures influence emergence and flight period. Under cool conditions (< 18.3°C), timing of flight will be spread out and beetles' ability to mass attack potential hosts will decline (Safranyik, 1978; Carroll et al., 2003; Aukema et al, 2008; Bentz et al., 1991).
Annual degree day (> 5°C) accumulation (days)*	Climate BC v.3.21	In order to complete their lifecycle in one year (i.e., to be univoltine), mountain pine beetles require > 833 degree days (Reid, 1962; Safranyik et al. 1975; Carroll et al., 2003; Aukema et al., 2008).
Latitude adjusted mountain pine beetle elevation (m)	Generated using a digital elevation model with a 25 m spatial resolution	Latitude and elevation limit the mountain pine beetle range to those locations where heat accumulation sustains a univoltine life cycle, and winter temperatures do not cause significant mortality (Bentz et al., 2001; Safranyik, 1978; Amman, 1973). To the north, the beetle's range is limited by the -40 ºC isotherm for minimum mean annual temperature. The upper elevation for mountain pine beetle in southern British Columbia is approximately 1600 m and, as latitude increases, the maximum elevation at which mountain pine beetle can survive decreases (Safranyik, 1978). The relationship between latitude and elevation was used to generate a raster representing the maximum MPB elevation for a given latitude. The actual elevation (derived from a digital elevation model) was then subtracted from the latitude gradient to produce a latitude adjusted mountain pine beetle elevation. A negative value indicates that the actual elevation exceeds the maximum mountain pine beetle elevation; whereas a positive value indicates the actual elevation is less than the maximum for a given latitude. Thus, large positive values would indicate areas more likely to be attacked.
Annual solar radiation (WH/m^2)	Generated using a digital elevation model with a 25 m spatial resolution	Climate data is typically interpolated from point measurements; solar radiation may be modeled spatially from topographic information. Since air temperature is dependent on incident solar radiation (Kumar et al., 1997), modeling radiation accounts for the topographic effect on temperature, and this is particularly important in areas with complex topography such as British Columbia. Cumulative annual total incident solar radiation was calculated in ArcGIS v. 9.2 using the Spatial Analyst Area Solar Radiation algorithm. Solar radiation and related variables can aid in the prediction of vegetation type and growth (Franklin, 1995). Solar radiation has been used in models to predict locations of mountain pine beetle attack (Coops et al., 2006; Wulder et al., 2006b). The ArcGIS Area Solar Radiation tool calculates the direct and diffuse radiation based on the hemispherical view-shed algorithm developed by Fu and Rich (2002). The solar radiation values were scaled to 8-bit data prior to clustering.

* Climate variables were generated from 30 year normals for points at 400 metre spacing using the Climate BC v.3.21 (Wang et al., 2007).

stand density, the percentage of susceptible pine in the stand, and the location (latitude, longitude, elevation) of the stand (Shore and Safranyik, 1992).

2.3 Clustering with driver variables

The driver variables (Table 1) were input into a two-step clustering algorithm to identify areas with similar environmental drivers; this algorithm is particularly well suited to the clustering of large datasets (SPSS, 2001). On the first pass, the algorithm assigns cases to "preclusters" based on log-likelihood distance measure between cases, with the objective of reducing the size of the case distance matrix. On the second pass, the "preclusters" are further grouped using a standard hierarchical clustering algorithm (Norušis, 2009). In this approach, input variables are automatically standardized.

To determine the optimal number of clusters for this application, clustering was performed with 10, 15, and 20 output clusters, with each iteration having an outlier class to account for up to 5% of the cases. The clusters output from each of these iterations were assessed using a one-way ANOVA and posthoc Tukey-Kramer tests of the cluster mean value for each of the driver variables, with the objective of selecting the iteration that produced the maximum number of clusters while minimizing the withincluster variance and maximizing the between-cluster variance.

Table 2. Infestation Outcome Variables

Description	Source	Rationale
Cumulative mountain pine beetle caused mortality from 1999 to 2006 (%)	Robertson et al. (2009)	Stands which have been attacked by mountain pine beetle historically will have a reduced amount of pine, while still being a beetle source (Wulder et al., 2009a). Robertson et al. (2009) created a 1 ha tessellation of British Columbia. Using the best available survey data, they determined the proportion of each 1 ha cell that had experienced mountain pine beetle caused mortality.
Proportion of pine remaining (%)	Calculated in PCI Geomatica v.9.18	The percentage of pine remaining when the proportion of cumulative MPB mortality is subtracted from the percentage pine.
Stand susceptibility to mountain pine beetle (unitless; values range from 0 to 100)	Shore and Safranyik, 1992	Rates the susceptibility of a stand in the event that a beetle infestation should enter the stand. This index rates on the basis of stand characteristics and is a long term rating of potential loss to the stand as a whole (not just the pine component) (Shore and Safranyik, 1992). Susceptibility is unitless and values range from 0 to 100. A low susceptibility index value indicates that if the stand is attacked by mountain pine beetle, there will not be a significant loss to the stand (i.e., it does not indicate that the stand does not contain pine, or that the stand is not at risk of attack by mountain pine beetle). The susceptibility layer was generated from Vegetation Resources Inventory (VRI) data using the Shore and Safranyik susceptibility model (Shore and Safranyik, 1992). The resulting polygon layer was rasterized to 100 metre resolution.
Euclidean distance to nearest infestation (m)	Calculated in ArcMap 9.2	Proximity (Euclidean distance) in metres to nearest infestation influences the chance of infestation in a pixel (Aukema et al., 2008, Wulder et al., 2009a).

2.4 Assessment of clusters with infestation outcome variables

The output clusters were characterized using the infestation outcome variables (Table 2) for the study area as a whole. These outcome variables included cumulative pine mortality from 1999 to 2006, the proportion of pine remaining, the stand susceptibility rating, and the Euclidean distance to the nearest infestation. These particular variables were selected because they allow us to characterize the cumulative damage caused by the infestation, as well as the potential for the infestation to be sustained (based on available hosts). Furthermore, consideration of the stand susceptibility rating (Shore and Safranyik, 1992) allows us to conduct a large-area assessment of the correspondence between the susceptibility rating system and the actual damage caused by the mountain pine beetle.

Infested areas were identified as those areas within the study area that had cumulative mortality from 1999 to 2006 (Robertson et al., 2009) or those areas that were identified in the 2007 and 2008 AOS data; the corollary of this area was considered uninfested. ANOVA and post-hoc Tukey-Kramer tests were used to assess the mean cluster values of the infestation outcome variables. A two-tailed t-test was used to assess the differences between infested and uninfested areas within clusters dominated by pine.

We also characterized the pre- and post- 2006 attack conditions in pine-dominated clusters and generated regional summaries for three broad ecological areas in northern, central, and southern British Columbia that have distinctly different spatial patterns of present-day mountain pine beetle infestations, as well as different histories of infestation. Consideration of the resulting clusters according to these different contexts provided insights into the infestation that may not have been apparent when considering the full extent of the study area (Figure 1).

3. Results

3.1 Clustering with driver variables

To determine the most appropriate scenario of either the 10, 15, or 20 output clusters, differences between the mean values of the driver variables for the clusters were assessed using an ANOVA and post-hoc Tukey-Kramer tests. The results of these tests indicated that the mean values of the driver variables were significantly different for the 10- and 15-cluster iterations, but not for the 20-cluster iteration. Therefore, the 15-cluster iteration was selected as the output that maximized the number of clusters and maintained a statistically significant difference between clusters for each of the driver variables ($p < 0.05$ for proportion pine; $p < 0.001$ for all other variables) (Table 3). Note that although the sample sizes are large, the magnitudes of the differences are not minor.

The spatial distribution of the 15 clusters is shown in Figures 3a and 3b. While clusters 1 and 6 have a compact spatial distribution, most other clusters are spatially discontinuous and extend over a large area. Clusters 3 and 8 are the largest clusters and clusters 11 and 13 are the smallest. None of the clusters have a mean minimum winter temperature that is greater than -21 °C, or a mean August temperature that is greater than 17 °C. The influence of topography in British Columbia is indicated in the latitude adjusted elevations: most of the clusters have mean latitude adjusted elevations that exceed the maximum limit for a univoltine mountain pine beetle lifecycle.

Clusters 4, 5, and 9 were differentiated from all other clusters because they have a large proportion of pine (Table 3) and therefore represent the areas with the greatest number of hosts available to the mountain pine beetle. Furthermore, these three clusters account for more than 9 million ha, or 17% of the total study area and 56% of the total pine area. These three clusters

Table 3. Cluster Mean and Standard Deviation (in parentheses) for Driver Variables

Cluster	Sample size (pixels)*	Pine (%)^{***1}	Minimum mean winter temperature (°C)^{***2}	Mean August temperature (°C)^{***2}	Annual degree day (> 5°C) accumulation (days)^{***2}	Latitude adjusted elevation (m)$^{**, ***2}$	Annual solar radiation (WH/m^2)^{***2}
1	2445874	8.08	-10.23	16.90	1649.40	739.05	142.02
		(18.15)	(7.15)	(0.97)	(204.92)	(193.19)	(16.20)
2	2550235	6.75	-11.31	14.80	1212.07	275.03	162.43
		(11.67)	(1.01)	(0.71)	(128.28)	(171.01)	(12.51)
3	6683427	2.43	-13.98	13.95	1140.70	205.28	144.78
		(6.68)	(1.15)	(0.59)	(96.66)	(129.09)	(10.68)
4	4427395	65.32	-15.37	13.00	1002.63	-24.50	144.47
		(19.96)	(1.75)	(0.67)	(113.66)	(180.42)	(11.27)
5	1860080	79.35	-11.74	13.80	1042.75	61.19	167.46
		(18.44)	(1.21)	(1.10)	(199.88)	(251.38)	(13.47)
6	3522360	2.34	-20.98	13.54	1155.19	-55.59	132.63
		(8.53)	(1.75)	(0.35)	(70.38)	(116.16)	(6.20)
7	4793246	4.28	-15.58	12.85	986.42	-122.55	130.30
		(8.77)	(1.59)	(0.62)	(113.40)	(176.26)	(11.72)
8	6637996	3.79	-14.26	12.45	876.97	-102.64	155.56
		(8.37)	(1.45)	(0.60)	(90.39)	(160.33)	(11.23)
9	3014881	77.98	-16.31	10.94	673.87	-344.00	155.81
		(17.63)	(1.55)	(0.97)	(141.05)	(220.83)	(17.53)
10	3805119	2.89	-15.74	10.43	604.63	-635.98	130.79
		(8.23)	(1.31)	(0.82)	(112.51)	(188.90)	(9.00)
11	1559795	5.16	-14.98	11.18	705.67	-456.16	98.10
		(14.40)	(1.51)	(0.93)	(137.49)	(235.29)	(13.58)
12	2522746	0.18	-16.52	7.89	298.54	-1156.11	172.27
		(2.33)	(1.20)	(1.07)	(96.52)	(234.66)	(21.91)
13	1594808	0.19	-16.66	8.19	371.14	-1090.93	106.09
		(2.23)	(1.01)	(1.00)	(98.99)	(210.92)	(17.62)
14	4146480	3.11	-14.85	11.21	663.61	-452.55	169.27
		(8.37)	(1.42)	(0.64)	(94.37)	(185.54)	(15.17)
15	2968345	1.71	-15.83	9.60	476.72	-799.45	159.50
		(6.52)	(1.25)	(0.67)	(87.46)	(177.04)	(11.79)

* ha pixels;

** A negative elevation value indicates that the actual elevation exceeds the maximum mountain pine beetle elevation; whereas a positive value indicates the actual elevation is less than the maximum for a given latitude. Thus, large positive values would indicate areas more likely to be attacked;

***Results of ANOVA post-hoc Tukey-Kramer tests of difference between cluster mean values: ^{1} $p < 0.05$; ^{2} $p < 0.001$.

have experienced sustained infestation: 55.96% of cluster 4, 42.19% of cluster 5, and 52.57% of cluster 9, by area, has been infested since 1999 (Table 6).

3.2 Assessment of clusters with infestation outcome variables

This analysis allows us to identify those regions of the province that have substantial areas of pine remaining as well as environmental conditions that are favourable to beetle. In addition, this analysis enables identification of those areas that have had similar drivers, but different infestation outcomes from 1999 to 2008. Such areas may merit further investigation and/or management intervention to determine the potential causes of the variation in infestation levels.

Although clusters 4, 5, and 9 have similar average susceptibility ratings and a similar average proportion of pine remaining (Table 4), cluster 9 has less area that is considered favourable to the beetle (Figure 4); however, a substantial portion of the area represented by cluster 9 has experienced the most severe infestation and has the second largest mean cumulative mortality at 8.33% (Table 4). An ANOVA and post-hoc Tukey-Kramer tests of the infestation outcome variables indicated that there was a significant difference between clusters for all of the infestation outcome variables ($p < 0.05$ for pine remaining; $p < 0.001$ for all other outcome variables) (Table 4). The average proportion of pine remaining is 59.5% in cluster 4, 77.04% in cluster 5, and 72.37% in cluster 9. Cluster 4 had the greatest mean amount of cumulative pine kill (by area; 10.93%) and the highest mean susceptibility rating (38.12). Cluster 5 had the shortest average distance to the nearest infestation, and cluster 6 had the longest. Although cluster 5 had a similar mean susceptibility to clusters 4 and 9 (Table 4) it had a lower mean cumulative mortality. In contrast, cluster 9 had a mean degree day accumulation that was less than the 833 day threshold and a large negative latitude adjusted elevation.

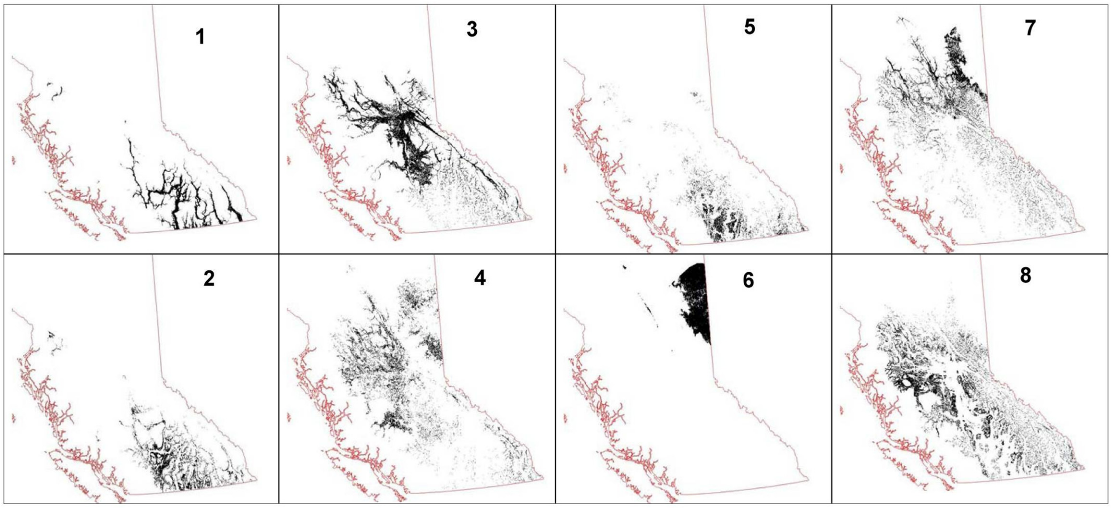

Figure 3a. BC-wide output clusters, 1 to 8.

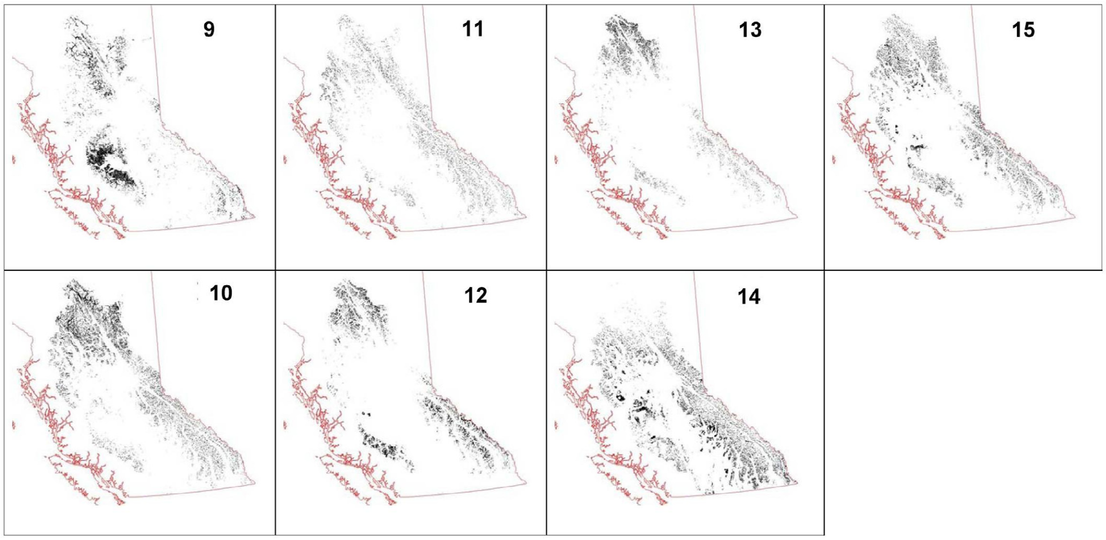

Figure 3b. BC-wide output clusters, 9 to15.

3.2.1 Comparison of infested and uninfested areas within clusters

Two-tailed t-tests indicated that the mean values for the uninfested and infested areas within clusters dominated by pine (4, 5, and 9), for each of the infestation outcome variables, were significantly different ($p < 0.001$) (Table 5). Although the sample sizes are very large, the magnitude of the differences are not minor, ranging from 15.52 to 25.85% for cumulative mortality, 18.54 to 22.69% for proportion of pine remaining, 18.16 to 25.79% for susceptibility, and 1,441.39 to 10,425.04 m. The average proportion of pine remaining in all three clusters is significantly greater in the uninfested areas than the infested areas, and the average stand susceptibility to mountain pine beetle attack is significantly lower for the uninfested areas. Since there will be no cumulative mortality in uninfested areas, it is not surprising that the amount of cumulative mortality in infested and uninfested areas is significantly different. Cluster 4 has the largest proportion of cumulative mortality in infested areas (25.85%), followed closely by cluster 9 (21.34%), and then by cluster 5 (15.52%). Of note are the differences in average cumulative mortality for the clusters as a whole (Table 4) and for the infested area of the clusters (Table 5). Finally, the average Euclidean distance to infestation is smallest for cluster 5 (1.4 km) and largest for cluster 9 (10.4 km).

The uninfested areas of cluster 5 have the shortest average Euclidean distance to the nearest infestation, while the uninfested areas of cluster 9 have the longest average Euclidean distance (Table 5). Theoretically, the closer proximity of cluster 5 to areas of existing infestation should result in increased beetle pressure on this area, leading to greater levels of infestation in the future. In reality, when infestation data for 2007 and 2008 were interrogated (Table 6), we found that cluster 5 did indeed

Table 4. Cluster Mean and Standard Deviation (in parentheses) for Infestation Outcome Variables

Cluster	Cumulative mortality (%)^{*1}	Pine remaining (%)^{*1}	Susceptibility rating^{*1}	Euclidean distance to nearest infestation (m)^{*2}
1	0.10 (1.45)	8.05 (18.10)	7.30 (16.78)	3891.76 (6224.83)
2	1.00 (6.65)	6.56 (11.41)	11.48 (20.09)	2988.79 (7920.53)
3	2.51 (12.19)	2.05 (5.92)	12.85 (25.05)	3415.58 (8995.89)
4	10.93 (17.57)	59.50 (23.93)	38.12 (33.32)	4488.85 (15209.22)
5	3.30 (8.76)	77.04 (20.54)	37.85 (32.37)	1134.53 (3506.99)
6	0.00 (0.09)	2.34 (8.53)	1.73 (7.99)	68797.92 (54412.19)
7	1.07 (7.82)	4.11 (8.54)	9.61 (19.98)	9503.46 (17947.25)
8	5.93 (19.49)	2.79 (6.83)	18.51 (27.74)	3643.79 (8368.76)
9	8.33 (14.76)	72.37 (22.46)	37.49 (27.78)	6355.43 (18634.35)
10	0.14 (2.91)	2.87 (8.18)	2.69 (8.91)	19299.11 (25917.73)
11	0.09 (1.75)	5.13 (14.35)	3.04 (9.85)	14101.46 (21035.93)
12	0.00 (0.42)	0.18 (2.32)	0.09 (1.42)	23649.82 (29504.52)
13	0.00 (0.08)	0.19 (2.23)	0.11 (1.27)	36507.77 (36025.23)
14	2.61 (13.31)	2.63 (7.52)	7.31 (17.87)	5963.46 (8621.03)
15	0.79 (7.29)	1.53 (6.01)	1.98 (8.23)	14631.55 (20179.73)

* Results of ANOVA post-hoc Tukey-Kramer tests of difference between cluster mean values: $^1p < 0.05$; $^2p < 0.001$.

have more attack post-2006 (20.9%) than either cluster 4 or cluster 9 (approximately 14%).

3.2.2. Pre- and post-2006 attack conditions

Post-2006 data on the extent and severity of the infestation indicates that between 44.04 and 57.81% of the pine-dominated clusters (4, 5, and 9) remained unaffected by mountain pine beetle as of 2008 (Table 6). These unaffected areas also had the lowest mean susceptibility rating and a greater mean Euclidean distance from existing infestation than attacked areas within the same clusters. Similarly, areas with sustained infestation (i.e. areas that were attacked both before and after 2006) had the greatest mean susceptibility ratings, often much greater than the areas that were attacked prior to 2006 only. An example of these trends can be found by examining results for cluster 4: approximately 44.04% of cluster 4 had never been attacked by mountain pine beetle as of 2008; however, approximately the same proportion of cluster 4 was attacked both pre- (14.11%) and post-2006 (13.68%), and furthermore, 28.17% of the cluster's area was attacked both before and after 2006. Both cluster 4 and 9 had more area attacked both before and after 2006 than were attacked only before or after 2006, indicating that beetle attack persisted in previously infested areas (and it was these areas that also had the highest average susceptibility (Table 6)). Cluster 5 and 9 both experienced an increase in the total area affected by beetle post-2006, as well as an increase in the severity of attack (Table 6). In contrast to conditions in clusters 4 and 9, less area was attacked both before and after 2006 (13.5%), with more area attacked after 2006 (20.9%) in cluster 5 than was attacked before 2006 (7.79%).

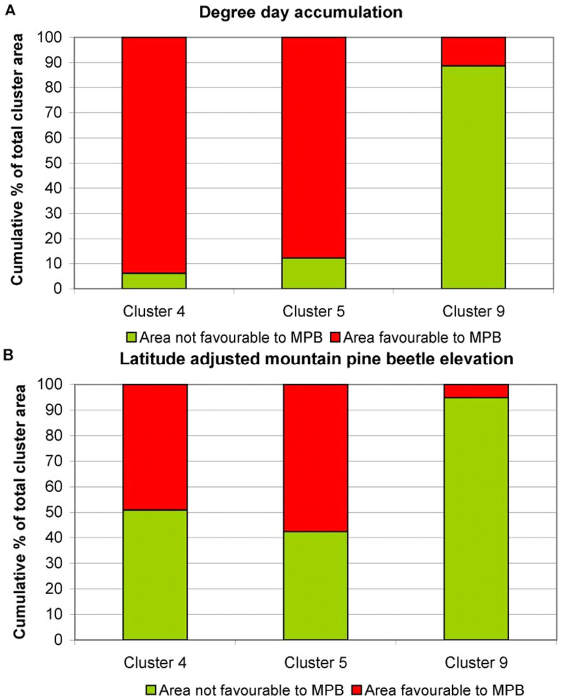

Figure 4. Areas of the three pine dominated clusters (4, 5, and 9) that are favorable to mountain pine beetle attack based on (A) degree day accumulation and (B) latitude adjusted mountain pine beetle elevation.

3.2.3 Regional assessment of clusters

The regional characterization of the clusters is summarized in Table 7. The northern region (Figure 2) is dominated by three clusters (4, 6, and 7) representing 95% of the region's area (Table 7). Clusters 6 and 7, which account for approximately 81% of the northern region's area, are characterized by a small average proportion of pine (Table 3) and a low average susceptibility rating (Table 4). Cluster 4 accounts for 14.5% of the region's area and has an average of 70.3% pine remaining, which is 5% higher than the overall average for this region.

In the central region, clusters 3 and 8 represent 52% of the area and have less than 5% pine; clusters 4 and 9 represent another 30% of the region's area and have an average of 61% and 77% pine, respectively**.** Within the area of cluster 4 located in

Table 5. Comparison of Infested and Uninfested Areas Using a Two-tailed t-test ($p < 0.001$)

	Infestation outcome variable	Uninfested Mean	Infested Mean	Absolute Difference	t	df
Cluster 4	Cumulative mortality (%)	0.00	25.85	25.85	-1905.7	1871897.0
	Pine Remaining (%)	69.10	46.41	22.69	1103.5	3867477.4
	Susceptibility Rating (%)	27.21	53.00	25.79	-852.2	3687723.2
	Euclidean Distance (m)	7776.93	0.00	7776.93	641.8	2555496.0
Cluster 5	Cumulative mortality (%)	0.00	15.52	15.52	-746.7	395997.0
	Pine Remaining (%)	80.99	62.45	18.54	513.5	585198.4
	Susceptibility Rating (%)	33.86	52.60	18.73	-332.5	626640.0
	Euclidean Distance (m)	1441.39	0.00	1441.39	447.6	1464081.0
Cluster 9	Cumulative mortality (%)	0.00	21.34	21.34	-1382.2	1176915.0
	Pine Remaining (%)	80.37	59.88	20.49	809.6	1993842.3
	Susceptibility Rating (%)	30.40	48.55	18.16	-575.1	2378633.4
	Euclidean Distance (m)	10425.04	0.00	10425.04	615.6	1837964.0

Table 6. Pre- and post-2006 Attack Conditions

		Area km^2	% of cluster area	Mean cumulative mortality 1999-2006 (%)	Mean cumulative mortality 2007-2008 (AOS) (%)	Pine remaining (%)	Susceptibility rating	Euclidean distance to nearest infestation (m)
Cluster 4	No MPB attack	19496	44.04	0.00	0.00	68.55	25.00	9644.8
	Attack pre 2006	6247	14.11	23.97	0.00	47.00	42.74	0.00
	Attack post 2006	6058	13.68	0.00	19.39	70.88	34.34	1766.4
	Attack both pre and post 2006	12472	28.17	26.79	29.46	46.11	58.14	0.00
Cluster 5	No MPB attack	10754	57.81	0.00	0.00	80.55	31.49	1618.6
	Attack pre 2006	1448	7.79	14.73	0.00	62.49	46.79	0.00
	Attack post 2006	3887	20.9	0.00	19.43	82.21	40.42	951.2
	Attack both pre and post 2006	2512	13.5	15.98	34.57	62.43	55.95	0.00
Cluster 9	No MPB attack	14302	47.44	0.00	0.00	78.80	27.30	13155.2
	Attack pre 2006	1840	6.1	16.52	0.00	63.26	29.38	0.00
	Attack post 2006	4078	13.53	0.00	19.15	85.88	41.28	849.5
	Attack both pre and post 2006	9930	32.94	22.23	32.5	59.25	52.11	0.00

the central region, 38% of the area has seen a high infestation severity with an average cumulative mortality of nearly 50% (results not shown). Cluster 9 shows a similar distribution, with high severity areas covering 25% of the total area and a cumulative loss of 47%. In both clusters 4 and 9, the areas without infestation account for approximately 20% of the total area and are, on average, within several hundred metres of an infestation (results not shown). While the percentage pine in the uninfested regions of cluster 4 is on average 72%, cluster 9 has a percentage pine of almost 90%. Up to 2006, cluster 4 was the cluster with the highest cumulative loss to mountain pine beetle at 25%, followed closely by cluster 9 (19%) (Table 7). The cumulative mortality from 2007 and 2008 shows a reversal in this trend, with cluster 9 having cumulative mortality of 26% and cluster 4 having a cumulative mortality of 15%**.** Even though the percentages of pine are very low (less than 6%) for clusters other than 4, 5, and 9 in this central region, with the exception of clusters 1, 12, and 13, infestation continued post-2006, with cumulative mortality ranging from 3.4 to 15.5% (Table 7). Three clusters that have had no attack (1, 12, and 13) have a mean percent pine of 1% or less, and susceptibility ratings less than 1. Over this region, these three clusters account for only 1.6% of the area.

The southern region is characterized by an even more dispersed distribution of clusters and comparatively lower levels of cumulative mortality compared to the central region. Only three clusters (3, 8, and 14) represent more than 10% of the area, and the largest one (cluster 14) represents 17% of the region's total area. Clusters 3, 8, and 14 have low levels of pine and a correspondingly low susceptibility rating. Conversely, the three clusters with the greatest proportion of pine remaining (4, 5, and 9) cover 6.8% of the area and are distributed throughout the region. The highest level of cumulative mortality is found in cluster 4, which has had a 3% loss of pine due to mountain pine beetle since 1999. Within this southern region, the areas of clusters 4, 5, and 9 which have not been infested as of 2006 account for 83, 85, and 92% of the cluster areas, respectively (results not shown). The mean percent pine remaining within these uninfested areas in this southern region is approximately 64% for cluster 4 and 78% for clusters 5 and 9.

Table 7. Region-based Summaries of Cluster Mean Values

Cluster	Area (km)	% of Region	Mean cumulative mortality 1999-2006 (%)	Pine Remaining (%)	Susceptibility rating	Euclidean distance to nearest infestation (m)
Northern						
3	728	1.5	0.0	3.3	8.1	1558
4	7144	14.5	0.1	70.3	25.5	22708
5	26	0.1	0.1	95.8	43.9	749.8
6	28818	58.4	0.0	2.7	2.0	52839
7	10886	22.1	0.0	6.2	7.6	20446
8	543	1.1	0.0	7.9	13.9	4252
9	792	1.6	0.0	81.3	26.0	37101
10	284	0.6	0.0	10.5	14.8	43960
11	63	0.1	0.0	12.5	6.7	56476
14	42	0.1	0.0	11.0	13.4	31961
Central						
1	960	1.1	0	1.1	0.6	3282
2	1698	1.9	3.4	4.3	11.5	1020
3	22202	25.3	5.1	1.8	20.4	498.1
4	13647	15.5	25	48.2	46.1	66.6
5	1584	1.8	8.6	72.3	33.2	129.1
7	2673	3	11.4	2.4	35.2	323.4
8	23121	26.3	14.4	2.1	35.3	321.5
9	12265	14	19.2	63.7	44.7	74.8
10	699	0.8	6.2	1.6	13.8	1797
11	145	0.2	2.6	3.9	10.5	1836
12	358	0.4	0.3	0.4	0.6	2458
13	71	0.1	0	0.1	0.1	3876
14	6496	7.4	15.5	2.2	29.5	594.3
15	1898	2.2	12.2	2.5	17	1277
Southern						
1	6776	7.6	0.1	4.5	4.2	5310
2	5280	6.0	0.5	6.4	7.9	3940
3	10236	11.5	0.4	2.2	5.2	5629
4	2146	2.4	3.1	61.8	23.7	882.2
5	2350	2.7	1.9	76.3	30.5	752.6
7	5865	6.6	0.2	1.7	2.2	7629
8	13560	15.3	0.5	2.0	4.7	5724
9	1529	1.7	1.0	77.1	22.0	1339
10	6688	7.5	0.0	0.8	0.5	9391
11	4682	5.3	0.0	1.7	0.8	9948
12	6014	6.8	0.0	0.2	0.1	11115
13	1790	2.0	0.0	0.1	0.0	10850
14	15326	17.3	0.2	1.7	1.9	7470
15	6405	7.2	0.0	0.6	0.2	10757

The empirical approach presented herein is intended to characterize the status of the current infestation as a complementary approach to more process-based modelling efforts. The problem with this approach, as indicated by Raffa et al. (2008) is that "similar patterns of damage can arise from different dynamics and mixtures of causalities". Thus, while the drivers we have selected may be biologically meaningful and readily characterized over large areas, they are likely not the only factors that have contributed to the current infestation. Furthermore, our approach does not account for the complex interactions amongst these drivers, nor does it imply a direct cause and effect relationship.

4. Discussion

4.1 Assessment of clusters with infestation outcome variables

When considered provincially, all of the pine dominated clusters (4, 5, and 9) had similar susceptibility to mountain pine beetle attack; however, cluster 5 has had a lower level of attack to date. The closer proximity of cluster 5 to existing infestation increases beetle pressure on pine stands in this cluster, even on areas of less suitable hosts. This, coupled with the larger proportion of pine remaining in cluster 5, suggests that increasing levels of attack may be expected in cluster 5 in the future, compared to clusters 4 and 9.

4.1.1 Comparison of infested and uninfested areas

The average proportion of pine remaining in all three pine-dominated clusters is greater in the uninfested areas than the infested areas and furthermore, the average susceptibility is significantly lower for the uninfested areas than for the infested areas, suggesting that the most susceptible areas of pine in clusters 4, 5, and 9 have already been attacked as of 2008. The remaining uninfested areas will likely contain pine that is less susceptible to mountain pine beetle; however, research has demonstrated that the mountain pine beetle has successfully colonized in areas of suboptimal hosts (Maclauchlan, 2006).

4.1.2 Pre- and post-2006 attack conditions

Areas that remained unattacked by mountain pine beetle as of 2008 had a low severity and a larger distance to infestation than areas that had been attacked. Although these unattacked areas had a large average proportion of pine remaining, the pine available may not have been as susceptible to infestation, due principally to host age. After 2006, all three pine-dominated clusters showed an increase in the areas attacked by mountain pine beetle, as well as an increase in the severity of attack. The trends from the 2007 and 2008 AOS data indicate that most of the infestation persisted in areas that were already infested prior to 2006, rather than spreading into new locations. Although caution should be used when interpreting the AOS data (Wulder et al., 2009a), the trends in infestation extent and severity are captured by this data and, therefore, are considered indicative of changes in the infestation in these areas. As indicated earlier in the discussion, the potential for future attack was expected to be greater in cluster 5, and the 2007 and 2008 data indicate that this was the case, with cluster 5 having the largest mean cumulative mortality in 2007 and 2008.

In terms of areas attacked by mountain pine beetle, clusters 4 and 9 each had approximately 30% of their total area attacked both pre- and post-2006, while cluster 5 had only 13% of its area attacked in both time periods. This could indicate that in cluster 5, the beetles were primarily spreading into new areas (which makes sense since there was less attack in this cluster pre-2006), while in clusters 4 and 9, the beetles were primarily concentrated in areas that were previously infested, while also expanding into new areas. This trend is in keeping with other results that indicate that opportunities for the continuation and expansion of the infestation were likely greatest in cluster 5.

The areas in all three pine-dominated clusters that had not been attacked by mountain pine beetle prior to 2006 have the largest average proportion of pine remaining. Interestingly, the areas that were attacked only after 2006 had a slightly larger average proportion of pine remaining and higher susceptibility ratings than the areas that have not been attacked. This indicates that the areas with the highest susceptibility and that were in closest proximity to the existing pre-2006 infestation were attacked first in 2007 and 2008. Once again, the mountain pine beetle demonstrated its propensity to preferentially seek out the most desirable hosts in a given area first (Nelson et al., 2007).

4.1.3 Regional assessment of clusters

Prior to 2003, there had been no recorded incidence of mountain pine beetle in the northern region; however, due to long range dispersal (Jackson et al., 2008) and warmer winter temperatures (Carroll et al., 2003), the susceptibility of pine in the area has increased—as has the beetle population in the area (Wulder et al., 2009b) (Figure 5). In this region, the average Euclidean distance to the nearest infestation is 23 km for cluster 4 and as of 2006, there was only a small proportion (less than 1% of the region area) of cumulative mortality.

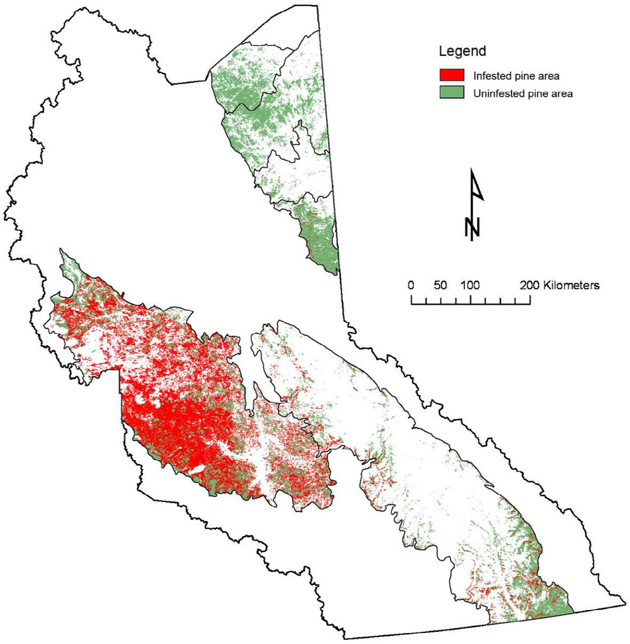

Figure 5. Infested and uninfested areas of pine in the northern, central, and southern focus regions.

The average susceptibility for the area of cluster 4 within this region is lower than the overall cluster 4 average susceptibility rating. This is expected since the susceptibility rating has a location factor that adjusts for latitude, and this region is at the northern extent of the study area. However, as climate change has already been implicated in the expansion of mountain pine beetle into new habitats (Carroll et al., 2003), both the susceptibility rating and the latitude adjusted mountain pine beetle elevation will likely underestimate the suitability of this northern region, since both of these variables are based on research that was conducted at more southern latitudes. Furthermore, the current and ongoing large-scale outbreak in British Columbia may change forests from carbon sinks to carbon sources (Kurz et al., 2008)—potentially exacerbating climate change effects. As indicated by Raffa et al. (2008), climate changes and forest management activities can have synergistic effects, making it difficult to separate their individual contributions to the mountain pine beetle's range expansion.

The central region encompasses the area where the current epidemic is believed to have started in 1999 (Raffa et al., 2008) and therefore, the amount of cumulative mortality in the region is substantially greater than the amount of cumulative mortality in the northern and southern regions. Cluster 4 has more favourable conditions than cluster 9 for mountain pine beetle, as well as a higher susceptibility rating and closer proximity to current infestations, therefore, it is expected that, in the future, cluster 4 will continue to experience a greater level of attack than cluster 9. Furthermore, the amount of uninfested pine in those areas of cluster 4 and 9 that are within this central region indicate that these areas have a high risk of continuing infestation. As would be expected in an area of heavy infestation such as the central region, sub-optimal hosts are becoming increasingly susceptible to attack. When competition is high, the mountain pine beetle will seek out and attack any remaining host trees (Maclauchlan, 2006). As host selection will initially favour large host trees with thick phloem, these trees will be attacked and killed first. However, as these trees are killed, and beetles have to fly longer and farther to find new hosts, less suitable host trees will be accepted and attacked (Chubaty et al., 2009).

Even though the environmental and climatic conditions would indicate that the southern region should be highly susceptible to mountain pine beetle, the low cumulative mortality that has been experienced in this area to date may result from the heterogeneity of the host distribution in this area. This heterogeneous spatial distribution of pine may help to slow the infestation spread; however, the uninfested areas of clusters 4, 5, and 9 in this region are, on average, only 1 km away from the nearest infestation, increasing pressure on the areas of remaining pine. Overall, this southern region had had low cumulative mortality up to 2006. Post-2006, the average cumulative mortality increased five-fold in the area of cluster 9 in this southern region, and doubled in the area of cluster 5 in this region. All of these results indicate that areas of this southern region have the capacity to support ongoing epidemic-level population of mountain pine beetle.

5. Conclusions

The goal of this study was to group areas of pine forest in British Columbia according to common environmental drivers for mountain pine beetle infestation and then to characterize these areas by the level of infestation they have experienced to date. Using a robust two-step clustering approach, we were able to group areas of pine in British Columbia according to selected infestation drivers, and then further characterize the resulting clusters by several infestation outcome variables. Our result indicate that mountain pine beetle attack has persisted for several years in areas where abundant hosts are available, and gradually expanded into heretofore previously uninfested areas. Our results confirm the management utility of the susceptibility model over large spatial extents: those areas with greater average susceptibility ratings were attacked first (i.e., before 2006), and had greater average cumulative mortality when compared to areas with lower average susceptibility ratings.

The large average proportion of pine remaining, coupled with the moderate susceptibility rating for some of the clusters in the regions of interest (i.e., cluster 5 in the northern region, clusters 4 and 9 in the central region, and cluster 5 in the southern region) indicate that opportunities remain for the mountain pine beetle to expand in these areas in the future, provided environmental conditions remain favourable. Since only a small proportion of areas have a cumulative pine loss that exceeds 50%, even in the hardest hit central region (Figure 5), and given the likelihood of continued warming, the current infestation is likely to persist for some time. As suitable host trees continue to be depleted within infested areas, mountain pine beetles will seek new hosts further afield, and as this study demonstrates, there are substantial areas of British Columbia that remain vulnerable to attack.

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