Research Report

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Environmental characteristics of mountain pine beetle infestation hot spots

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Abstract

A combination of favourable temperatures and abundant host trees has resulted in a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic over the majority of the lodgepole pine forests of British Columbia, Canada. Understanding temporal trends in the interactions between mountain pine beetle infestations and landscape characteristics can improve our understanding of beetle biology, inform modelling of future impacts, and support management. In this paper, we demonstrate a practical technique for characterizing spatial interactions between beetles and the environment. The locations with the highest-intensity infestations (hot spots) were identified using point data derived from annual helicopter-based surveys of beetle-infested pine, and a kernel density estimator. By examining the environmental characteristics associated with hot spots through time, an increased understanding of how the mountain pine beetle utilizes resources over large areas is generated. The effect of treatment on the persistence of hot spots is also explored. Results indicate that beetles intensely infest mature trees with a shift to younger trees over time. Hot-spot locations are most commonly associated with stands composed of 30–80% pine and almost always occur at elevations between 800 m and 1000 m. In the early years of an infestation, hot spots are typically found on warmer (south and west) aspects. As well, relative to non-treatment, any type of treatment reduces the persistence of hot spots the following year.

KEYWORDS: *hot spot, landscape, mountain pine beetle, spatial pattern, spatial-temporal, treatment.*

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Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is native to pine (*Pinus*) forests throughout western North America. Periodic population eruptions occur when an abundance of susceptible host trees coincides with climatic conditions amenable for beetle survival (e.g., Taylor and Carroll 2004). Although epidemic populations are a natural component of forest disturbance, large infestations have substantial impacts and provide unique challenges to forest managers (Safranyik *et al.* 1974; Safranyik and Carroll 2006). At present, Western Canada is experiencing the largest mountain pine beetle epidemic on record. By 2006, over 9 million ha of lodgepole pine forest had been infested (Westfall 2007).

To date, stand-scale mountain pine beetle relationships have been used to develop landscape-scale management models (see Nelson *et al.* 2006c for a discussion). However, using relationships observed at a stand scale for landscape-scale management may be problematic as the general principle of ecological fallacy indicates that relationships do not necessarily hold across spatial scales (Wiens 1989; Levin 1992). By locating and exploring high-intensity infestations (termed "hot spots" in this paper), it is possible to characterize landscape conditions favourable for hosting large beetle populations. Such analysis is important in improving our knowledge of mountain pine beetle dynamics over large areas.

Our goal is to present an exploratory spatial data analysis approach that characterizes the nature of the environment associated with the most intensely infested locations. Following a growing trend in geographic data analysis (e.g., Fotheringham *et al.* 2000; Le Gallo and Ertur 2003), we explore and describe trends in the associations between hot spots and the environment as a first step towards developing hypotheses for further testing. To begin, we demonstrate a practical method for identifying hot spots over the landscape. This method is designed for use with point data collected from a helicopter where visual estimates on insect species and number of affected trees are recorded (Wulder *et al.* 2004; Nelson *et al.* 2006a). We also examine hot spots using data on management activity. Our methods are demonstrated for a Timber Supply Area (TSA) in British Columbia. Analysis carried out on a data set spanning 8 years of insect activity highlights how these methods can be used to investigate the changing interaction between beetles and the environment over the course of an infestation. The methods we outline can be applied in any forest management area; however, by demonstrating our approach on a specific TSA, we generate new information on the spatial and temporal trends associated with intense infestations over large areas.

By locating and exploring high-intensity infestations, or "hot spots," it is possible to characterize landscape conditions favourable for hosting large beetle populations.

Study Area and Data

The Morice TSA is located in north-central British Columbia, Canada (Figure 1). Covering an area of approximately 1.5 million ha, it is dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) and spruce (*Picea*) species. This TSA marks the traditional northern spatial extent of the mountain pine beetle range, with epidemic populations present since 1995. The onset of infestation was not contemporaneous throughout the TSA. In the north and central regions, the infestation was established by the mid-1990s, whereas the infestation in the southern region became established in 1999 and expanded more rapidly. For our analysis, the Morice TSA was divided into North, Middle, and South sub-areas (Figure 1) on the basis of initial date of infestation. These sub-areas are also unique in forest conditions and management. Management, which typically consists of single-tree treatments and small patch harvesting, has been most aggressive in the North sub-area. The Middle sub-area has more young trees than the other sub-areas, and the South sub-area is the most mountainous (Nelson *et al.* 2006b).

The infestation has been monitored since 1995 using point-based, global positioning system helicopter ("heli-GPS") surveys (Nelson *et al.* 2006a). Aerial surveys of infestations use indicators of pine mortality, such as changes in crown foliage colour, to monitor beetle activity. During helicopter surveys, the cluster centre of visually infested trees, typically those with yellow (fading) and red crowns, are located with a GPS. For each cluster, the number of infested trees is estimated and the infesting insect species recorded. The maximum area represented by a point is 0.031 km^2, equivalent to a circle with a radius of 100 m (Nelson *et al.* 2006a).

FIGURE 1. Location of the Morice Timber Supply Area in British Columbia (54°24'N, 126°38'W).

A total of 43 751 heli-GPS points, representing 268 112 trees, were identified during aerial surveys conducted from 1995 to 2002.

British Columbia Ministry of Forests and Range inventory data were used to characterize forest age and percentage of pine cover. Forest inventory data are primarily generated via aerial photo (1:15 000) interpretation (Leckie and Gillis 1995). Stand age is the age, in 20-year increments, of the forest stand on the date of stand classification, and is based either on ring counts from a bored core or on estimates from aerial photographs. The dominant tree species occupies the largest percentage of the stand by volume. Forest age and percentage of pine cover data are representative of mid-1990s conditions, when the forest inventory was last updated.

Data on elevation and aspect were obtained from 1:20 000 Terrain Resource Information Management data (Province of British Columbia 1996). Elevation data were interpolated using a linear process and the resulting digital elevation model (DEM) is accurate to within 10 m. Aspect data were also derived from the DEM.

Treatment data available for 2001 enabled an exploration of the effect of treatment on hot spots in 2001 and 2002. Each infestation cluster was assigned a treatment code and given a date that reflected treatment timing. Five different treatments were applied in 2001 (see Nelson *et al*. 2006b for detailed descriptions):

- Monosodium menthanearsonate (MSMA) applications killed both the tree and beetles under the bark.
- Pheromone-baited traps attracted beetles to tree hosts that were later removed.
- Fell and burn treatments removed trees by burning the tree and stump on the spot.
- Small patch harvesting removed single trees or small patches of trees.
- Block harvesting created harvested patches larger than 1 ha.

Methods

Identifying Hot Spots

As a precursor to identifying hot spots in heli-GPS data, point data were converted to surfaces of infestation intensity using kernel density estimators (Nelson *et al*. 2006a). Kernel density estimators improve the visualization of large sets of point data, allow continuous representation of the infestation, and enable data to be presented as infestation intensity rather than counts. (See Nelson *et al*. 2006a for a more detailed discussion of the benefits of using kernel density estimators.) The continuous raster representation produced by kernel density estimation enables all locations within a study region to be mapped as either hot spots or non-hot spots.

Conceptually, the intensity $\hat{\lambda}(z)$ at a particular location z in a study area A can be estimated as:

$$\hat{\lambda}(z) = \frac{\text{the number of events in a disk centred on } z}{\text{area of the disk}} \qquad [1]$$

A more precise estimate, $\hat{\lambda}_\tau(z)$ is defined by:

$$\hat{\lambda}_\tau(z) = \left\{ \sum_{i=1}^{n} \frac{1}{\tau^2} k\left(\frac{(z - z_i)}{\tau} \right) y_i \right\} \quad z \in A \qquad [2]$$

where: z and A are defined as above;
τ is the radius of a disk centred on z;
$k(\ )$ is the kernel or a probability density function which is symmetric around the origin;
z_i (i = 1, …, n) are locations of n observed events; and
y_i is the attribute value at z_i.

The type of kernel $k(\ )$ determines how events within the disk will be weighted. Although different kernel forms may be defined, they have little effect on the intensity estimate (Silverman 1986; Scott 1992; Simonoff 1996). The standard kernel shape is Gaussian. For this study, a quartic kernel was used, as it provides a good approximation of the Gaussian kernel yet is computationally less burdensome (Silverman 1986; Waller and Gotway 2004). For large data sets, such as the mountain pine beetle data used in this study, computational speed is a consideration. The implementation of kernel density estimation in the Spatial Analyst extension of ArcMap, a commonly used GIS software, makes the approaches outlined here accessible and practical.

The amount of smoothing is controlled by τ (Kelsall and Diggle 1995). Small values of τ will reveal small-scale features of the data, while larger values will reveal more general features. We defined τ using the nature of spatial dependence in the data as characterized using variograms. The variogram range, or the maximum distance at which the data exhibit spatial dependence, provides a range of appropriate τ values. From 1995 to 2002, variogram distances varied from 280 m to 1996 m; the median range distance was 1599 m. Arguably, any distance within this scope of values is an appropriate distance for τ. As we are interested in landscape-level (i.e., spatially general) trends, we chose to use the upper limit and set τ at 2000 m.

Edge effects may also affect kernel estimators. As the study area is large relative to τ, edge effects are minimal, negating the need for a correction term. An additional issue, which arises in software that stores intensity estimates in a raster format, is the definition of surface cell size. As the data points represented circular areas with a maximum diameter of 200 m, we used a 200 × 200 m grid cell.

Within each sub-area in this study, hot spots were defined as locations (grid cells) in the estimated intensity surface with values in the upper 10% of the frequency distribution of all sub-area cell values. The use of the 10% threshold is supported by practical management needs; that is, it represents a realistic target for the amount of forest area that can be actively managed when beetle populations are epidemic. Also, exploratory analysis indicated that the 10% threshold identified locations with landscape conditions that differed from those in the study area. For other studies, this threshold may be set to a different value depending on the nature of the research or management questions.

For 2001, the year when treatment data are available, the impact of the five treatment categories on the persistence of hot spots was also explored. We determined the number of infestation cluster points that intersected polygon-represented hot spots in 2001, and both 2001 and 2002. If the majority of infestation clusters that were associated with hot spots in 2001 were still associated with hot spots in 2002, then the treatment had little effect on the persistence of hot spots.

Comparing Hot Spots and the Environment

To better understand causes of both spatial and spatial-temporal variations in infestation magnitude, we explored landscape characteristics associated with hot spots through time. The nature of hot spots was explored in each year and also over many years. For each location (cell), hot spots were represented as the number of hot-spot years, the maximum number of consecutive hot-spots years, the first hot-spot year, and the proportion of active years that were hot. This last category is the number of hot-spot years divided by the total number of years that beetles were active at a location. This normalizes variability caused by the different onset times of beetle infestations within sub-areas. The normalized representation of multiple time periods was used for comparisons with environmental characteristics.

Relationships between hot-spot locations and the environment provide the information necessary to:

- determine the likelihood that a particular location will be attacked,
- estimate the duration of an attack at a particular location, or
- forecast temporal changes in infestation magnitude.

Environmental conditions investigated include forest age, percentage of pine cover, elevation, and aspect. Forest age is an important factor that affects host susceptibility (Safranyik and Carroll 2006). While we recognize that forest density is also important, density data were not available for the Morice TSA. Associations between hot spots and percentage of pine cover are often used for landscape-level modelling of the susceptibility of forests to mountain pine beetle (Nelson *et al*. 2006c). Elevation and aspect data help to investigate associations between high-magnitude infestations and temperature. For example, evidence shows that warmer slopes are important for outbreak initialization (Safranyik *et al.* 1974; Safranyik *et al*. 1989) and elevation is a critical factor in host selection (Safranyik and Carroll 2006). Temperature trends are particularly important in studies at the margins of the mountain pine beetle's spatial range.

To investigate relationships between hot spots and the physical environment, the relative frequency distributions of landscape characteristics for all pine cells were visually compared to the relative frequency distributions of hot-spot locations. If hot spots were randomly located on the landscape, we would expect the two relative frequency distributions to have a similar form. Disparities in the shape of these distributions were the basis for exploratory investigations into landscape conditions associated with hot spots. Similar comparisons were made between landscape characteristics and categories of hot-spot persistence.

Results and Discussion

Hot Spots

The method used to generate hot spots ensures that the number of hot cells is always proportional to the number of cells with some mountain pine beetle activity. Figure 2, which shows hot spots from 1995 to 2002, clearly illustrates which sub-areas have the most mountain pine beetle activity, and within a sub-area, which locations are heavily infested. Initially, beetle activity was greatest in the North and Middle sub-areas; however, by 2002 the South sub-area had the majority of large infestations. This pattern reflects general trends observed in British Columbia (Aukema *et al.* 2006). Initially, the provincial infestation was dominated by processes that were spatially localized, but in the late 1990s populations increased and the infestation spread quickly. In the Morice TSA, starting in 1999, beetles emigrated from Tweedsmuir Provincial Park, which borders the study area to the south. The Tweedsmuir infestation did not cause the outbreak, as the infestation was well established in the early 1990s in more northerly regions of the TSA; however, the park's abundance of susceptible hosts sustained a large beetle population that eventually affected the southern portion of the TSA.

Figure 3 shows categories of hot-spot persistence and Tables 1–3 present the numbers of locations (cells) in each category. Using multi-temporal representations, we visualized locations that were hot for many years, when areas were initially hot, and the proportion of active years that were hot. Although cells with a large number of hot years occurred mostly in the North and Middle sub-areas where beetle activity has been present the longest, locations in the South were hot for a large portion of active years. The most common number of hot years and the maximum number of hot-spot years was one or two, and the proportion of active years having hot spots was typically 25% or less. This suggests that hot spots are not very persistent. Although hot spots may not persist for many years, 94% of hot spots were located where beetle activity occurred in the previous

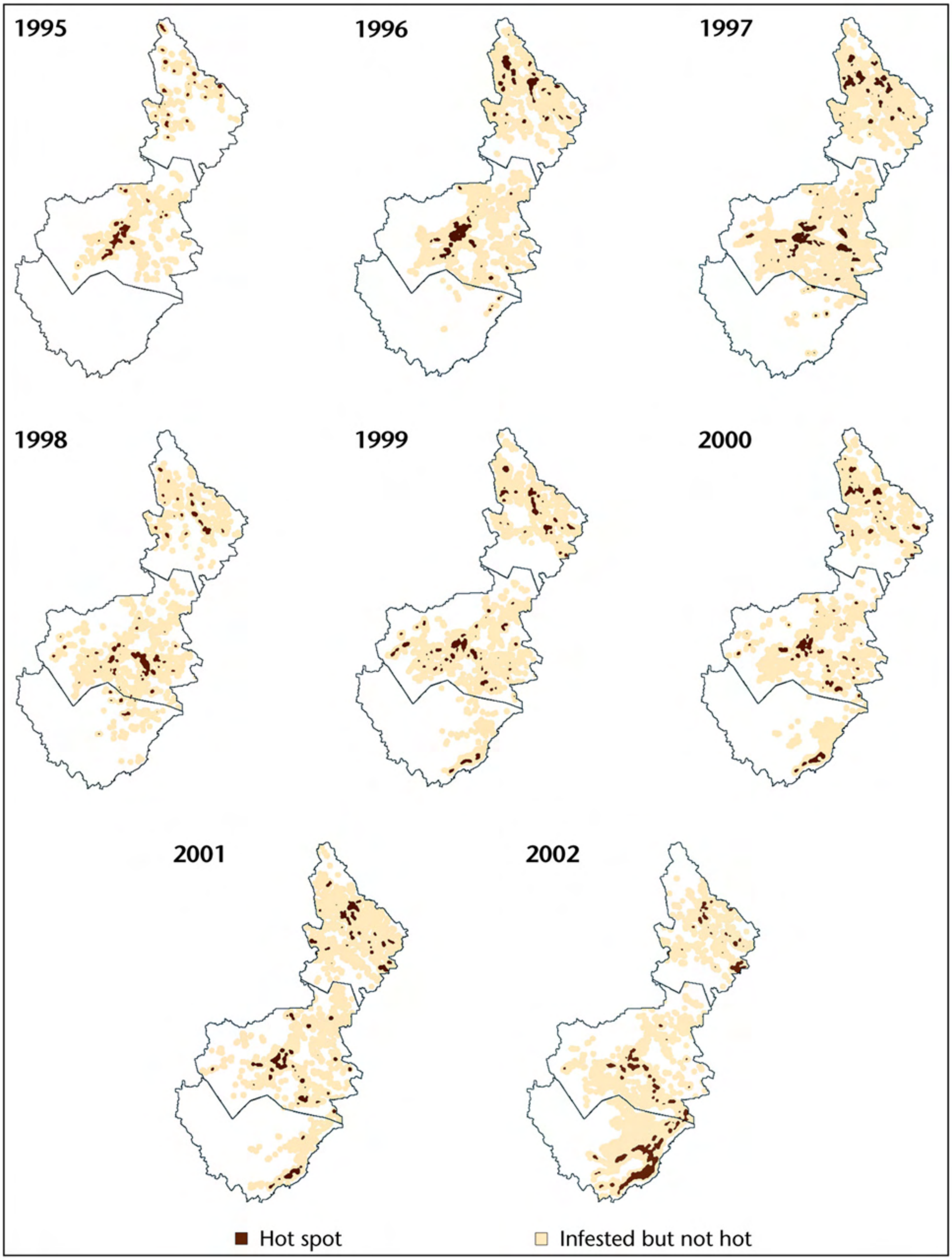

FIGURE 2. The spatial location of mountain pine beetle infestation hot spots from 1995 to 2002.

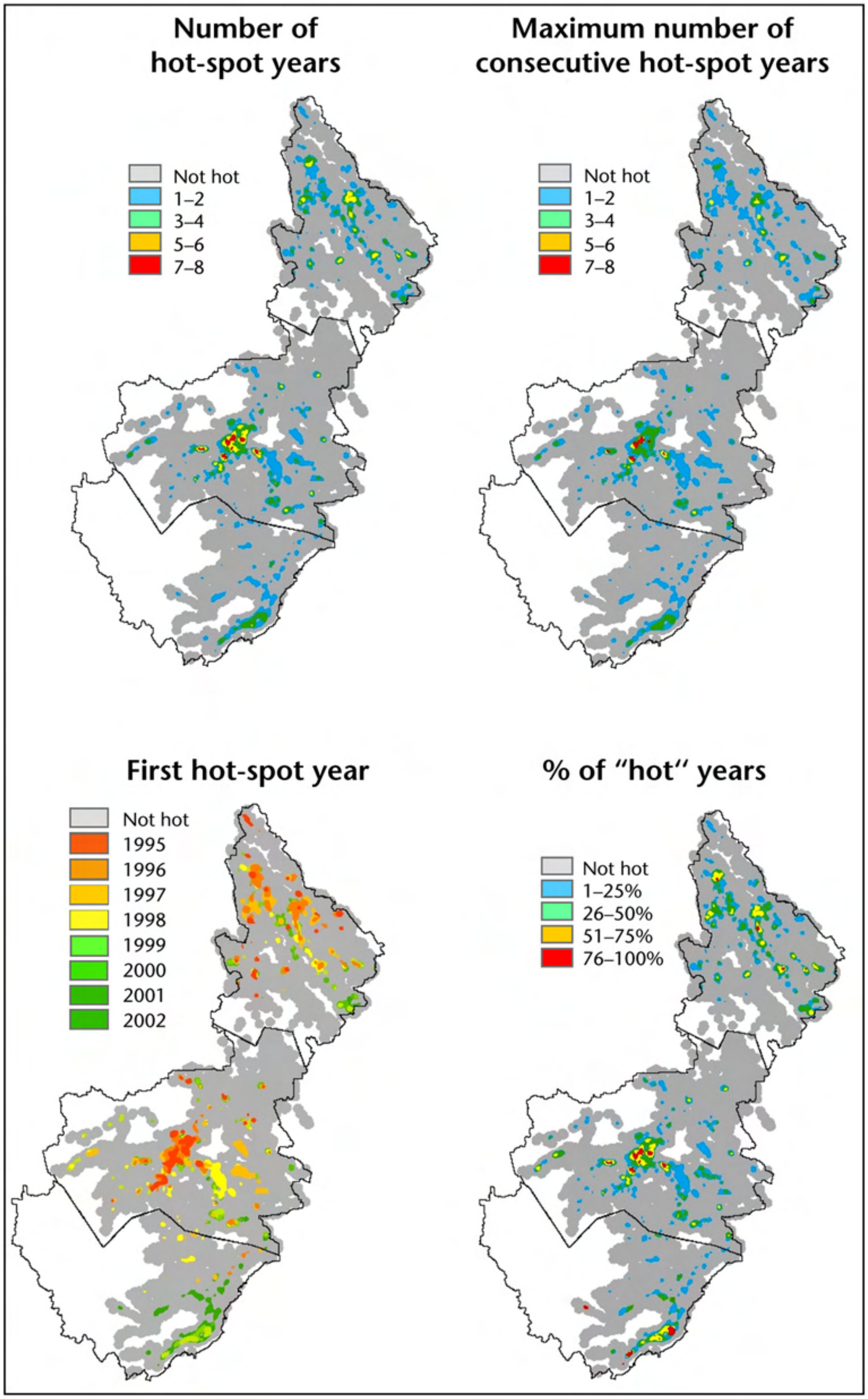

FIGURE 3. Classifications of infestation hot-spot persistence over 8 years. "Not hot" areas (grey) had mountain pine beetle infestations, but were not considered hot spots in any time period. White locations are free of mountain pine beetle during the study duration.

TABLE 1. Locations categorized by the number of hot-spot years or the maximum number of hot-spot years

No. years	No. hot-spot years	Max. no. hot-spot years
1	17890	21392
2	6927	7223
3	4695	3841
4	2840	1803
5	1444	473
6	968	241
7	518	309
8	121	121

TABLE 2. Locations categorized by the first hot-spot year

Year	First hot-spot year
1995	5449
1996	7027
1997	6035
1998	4359
1999	3315
2000	2596
2001	2869
2002	3753

TABLE 3. Locations categorized by the proportion of years with mountain pine beetle infestation

Years (%)	Proportion of active years
1–25	20778
26–50	9771
51–75	3670
76–100	1184

year. The lack of persistence in hot spots may be partially explained by previous observations of beetle emergence and movement to new areas despite the presence of acceptable hosts (Borden 1993; Robertson *et al.* [2007]). In the absence of forest density data, we cannot explore the influence of beetle damage on future hot spots. Within 1 year, however, beetles can kill a large proportion of available host trees. Although hosts and beetles remain in the area, the levels of either (or both) are not sufficient to retain a hot spot as defined through this work.

Another explanation for temporal trends in hot spots is the effect of management. Table 4 presents the

TABLE 4. Percentage of infestation clusters that intersect hot spots in 2001, and in both 2001 and 2002 (based on treatment categories applied in 2001)

Treatment	2001 (%)	2001 and 2002 (%)
MSMA	22.40	9.90
Pheremone-baited traps	61.10	33.20
Fell and burn	24.20	14.30
Small patch harvesting	20.20	4.50
Block harvesting	92.80	0.00
Non-treated	39.70	33.80

percentages of infestation clusters that were treated in 2001 and that intersect hot spots in 2001 and in both 2001 and 2002. Forty percent of non-treated infestation cluster points were associated with polygon-represented hot spots in 2001. While almost all block harvesting (92.9%) occurred within 2001 hot spots and over half of pheromone-baited trap treatments (61.1%) occurred in hot spots, other treatments were focussed in non-hot spot locations. This may indicate a preference to treat areas where the infestation magnitude is still small enough for treatments to be effective.

When the percentage of infestation clusters associated with hot spots in 2001 is similar to the percentage associated with hot spots in both 2001 and 2002, these clusters were associated with persistent hot spots. For non-treated sites this difference was 5.9%. For treated sites, the difference was always higher and ranged from 9.9–92.8%. Block harvesting removed large patches of trees (> 1 ha) and none of these sites were found in 2002 hot spots. For small patch harvesting, only 25% of locations associated with hot spots in 2001 persisted into 2002. About half of the pheromone-bait trapping, MSMA, and fell and burn treatments located in 2001 hot spots were still associated with hot spots in 2002. Because of data availability, treatment analysis was only possible for one year in this study. However, results indicate that block harvesting leads to non-persistent hot spots. All other forms of treatment reduce the likelihood that hot spots will persist by a greater amount than if no treatment was performed.

Hot Spots and Forest Age

A comparison of the relative frequency distributions of pine age associated with single-year hot-spot locations to the background distributions of all pine age shows that distributions vary with each sub-area and time period; however, common trends emerge. Figure 4 illustrates

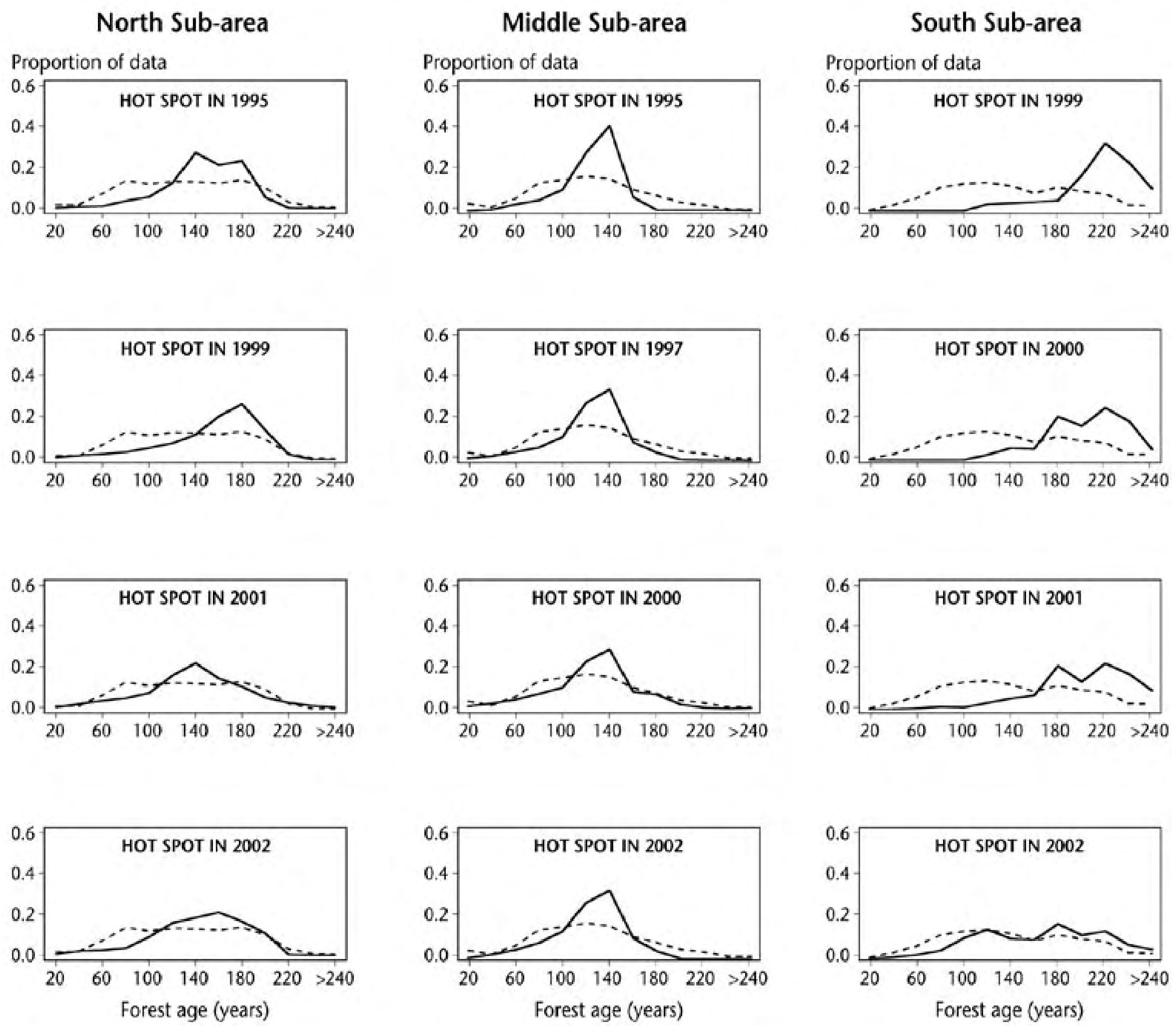

FIGURE 4. Relative frequency distributions of forest age for hot-spot locations (solid line) and all pine locations (dotted line).

a representative subset of over 600 comparisons between hot spots and landscape characteristics (forest age, percentage of pine cover, elevation, and aspect) to demonstrate these general temporal trends. In all sub-areas, few hot-spot locations were associated with forests younger than 100 years. Once the infestation was well established, hot spots were located in the oldest age class, which accounted for 5% or more of the forest by area (North 140–180 years; Middle 140 years; South > 180 years). In the North and South sub-areas, younger trees were infested through time and eventually the frequency distribution of forest age associated with hot spots became similar to the background frequency distribution. One difference between the North and South sub-areas is the temporal scale with which the relative frequency distributions become similar. In the North, the hot spot frequency distribution of forest age changed over several years (i.e., $\geq$ 7 years) and was likely the result of smaller, localized mountain pine beetle infestations and intensive management through harvesting. In contrast, infestations in the South were more intense and forest age associated with hot spots changed over a shorter time period relative to the other sub-areas (i.e., ~4 years). In the Middle sub-area, the relative frequency distributions of forest age associated with hot spots did not change through time.

For comparison with environmental characteristics, the proportion of active years that were hot was calculated and classified as zero, 1–25%, 26–50%, 51–75%, and greater than 75%. The lower the proportions

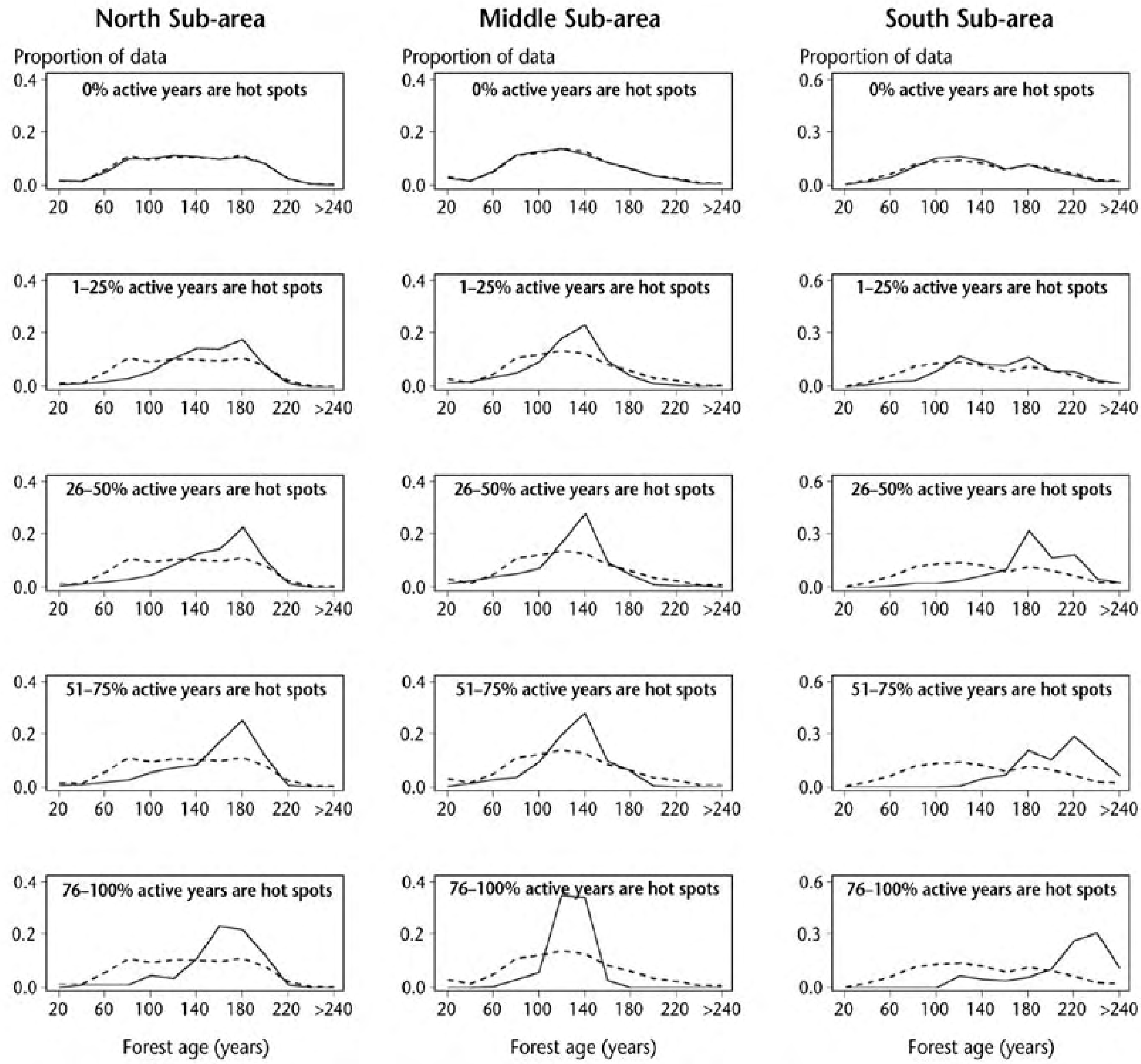

FIGURE 5. Relative frequency distributions of forest age for hot-spot locations (solid line) partitioned by the proportion of years a location is a hot spot. For comparison, relative frequency distributions of forest age for all pine locations are also provided (dotted line).

of years that are hot, the greater the similarity between the hot spot and background relative frequency distributions (Figure 5). Locations that were never hot have a frequency distribution similar to the background distribution of forest age; this trend is the same through time and between sub-areas. Higher proportions of years that are hot are associated with larger percentages of locations with trees older than 120 years.

Over large areas, the interaction between mountain pine beetle infestations and forest age seems consistent with published findings on stand-scale relationships (Safranyik *et al.* 1974; Safranyik *et al.* 1989). Hot spots occurred in forests older than 100 years, and the intensity and duration of mountain pine beetle infestations were greatest in areas with mature trees.

Temporal changes in the frequency distribution of forest age associated with hot spots were related to initial forest conditions and the intensity of the infestations. In all sub-areas, the mountain pine beetle infested younger trees and the frequency distribution of forest age associated with hot spots became more similar to the background frequency distribution; in other words, over time, the locations of high-intensity infestations became more random. Research suggests that mountain pine beetle epidemics initiate in mature trees, but once the infestation is established the beetles will attack younger trees (Safranyik *et al* 1974; Mitchell and Preisler 1991). Forest depletion occurs in a predictable manner, in part, because a direct relationship exists between tree mortality and tree size (Safranyik and Carroll 2006). More beetles are produced in large trees and as the size of tree, which correlates with age, decreases, the number of beetles produced declines so that very small trees are considered beetle sinks. Therefore, it is likely preferable for beetles to infest the largest trees first.

Hot Spots and Percentage of Pine Cover

In the Morice TSA, where the percentage of pine cover was less than 30% or greater than 80%, high-intensity infestations did not occur. In the North, 36–47% of single-year hot spots were associated with 30–40% pine and only 9–23% of hot spots occurred where the percentage of pine was greater than 60% (Figure 6). The Middle sub-area also showed little change over time; areas with 60–80% pine were associated with 43–57% of hot spots depending on the year. In the South, once the infestation established, hot spots occurred at locations that had 40–70% pine, but by 2002 the relative frequency distribution of percentage pine associated with hot spots was nearly the same as the background frequency distribution.

Although trends vary between sub-areas, the relationship between the proportion of hot-spot years and the percentage of pine demonstrates that locations hot for the longest time periods are often associated with higher percentages of pine (Figure 7). In the North sub-area, the dominant percentage of pine associated with locations where hot spots persisted for less than 75% of years was 30–40%; however, this increased to between 40% and 50% when a location was hot in more than 75% of active years. In the Middle sub-area, the dominant percentage of pine was consistently between 60% and 80%. Yet, when locations were hot spots for more than 75% of active years, a larger portion of locations occurred in high percentage pine areas and only a small portion in lower percentage pine areas. This trend was also noted in the South sub-area. Although 47–56% of hot spots occurred where the percentage of pine fell between 40% and 70%, locations hot for more than 75% of active years most often (47% of hot spots) had 70–80% pine. As with age, locations that were never hot spots had a similar frequency distribution to the background distribution of percentage pine.

In the Morice TSA, mountain pine beetles seem to initially infest locations with a low to moderate percentage of pine. This is counter to stand-scale observations that mountain pine beetles typically infest pure stands (Safranyik *et al.* 1974). In part, the preference for stands with a medium percentage of pine may be explained by the inverse relationship between forest age

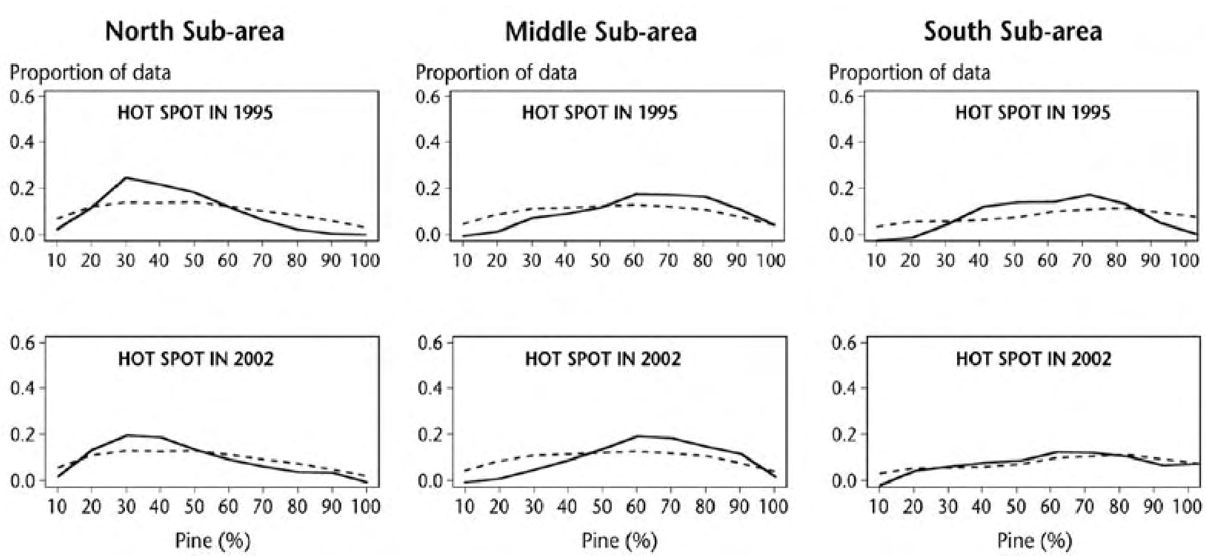

FIGURE 6. Relative frequency distributions of percentage pine cover for hot-spot locations (solid line) and all pine locations (dotted line).

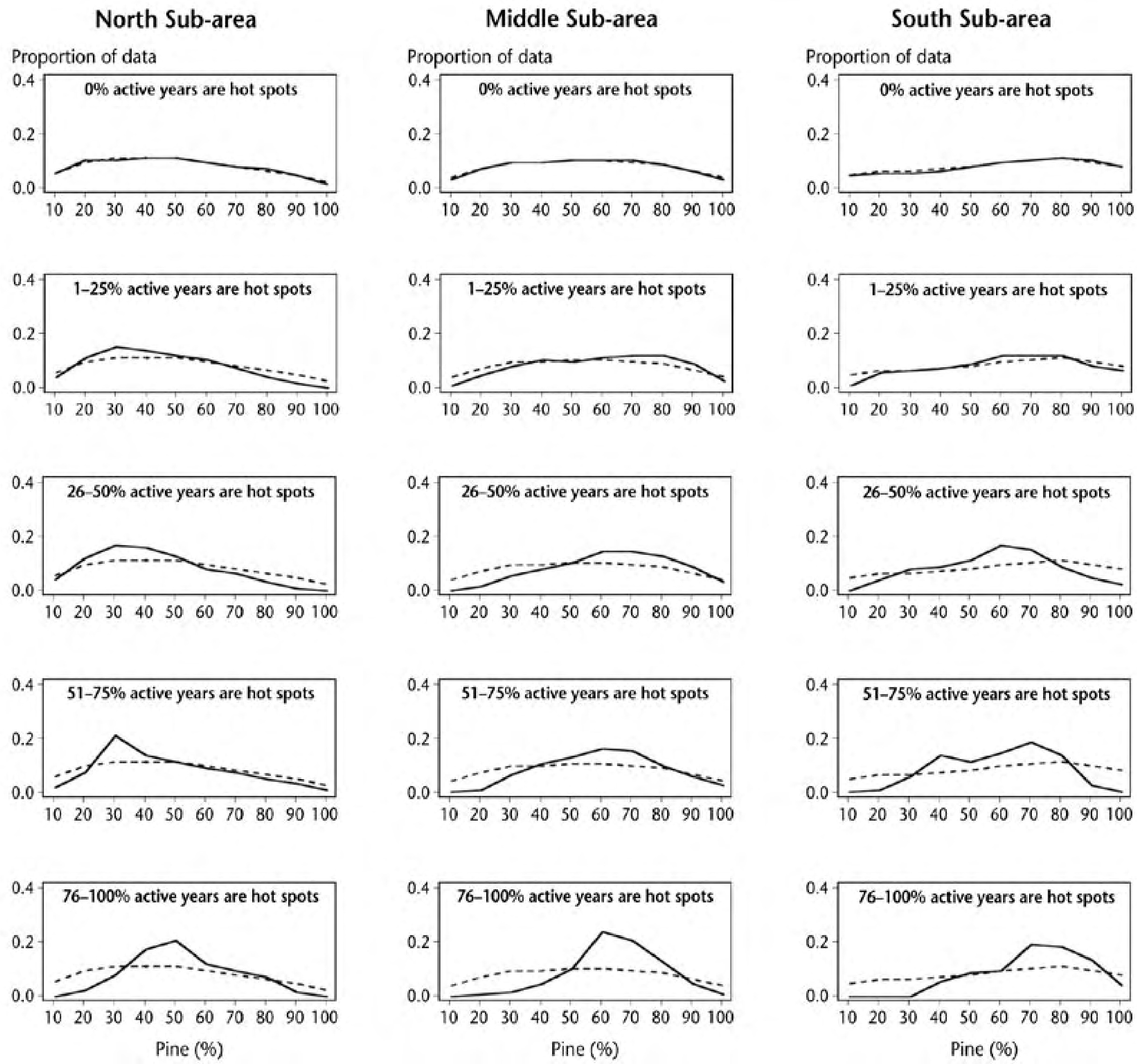

FIGURE 7. Relative frequency distributions of percentage pine cover for hot-spot locations (solid line) partitioned by the proportion of years a location is a hot spot. For comparison, relative frequency distributions of percentage pine cover for all pine locations are also provided (dotted line).

and the percentage of pine in this region. Mature trees are found where pine cover is low to moderate (40–80%). After fire, pine also regenerates in very dense even-aged stands (Lotan and Perry 1983; Turner *et al.* 2004). The high stem density of these stands results in small-diameter trees that are less suitable hosts for beetles. If stands of all pine are unmanaged after fire, they are likely unsuitable for beetles.

The temporal variability in the relationship between high-magnitude infestations and percentage of pine cover is an important finding of this study. Locations with moderate pine cover (40–70%) had high-magnitude infestations when beetles were infesting a new area; however, large beetle populations persisted the longest when pine cover was at the higher end of this range (i.e., 70–80%). Within a stand, if more, large pine hosts are available for infestation, then the capacity is greater to produce more beetles that will, in turn, enable persistence of infestation hot spots (Safranyik *et al.* 1974; Safranyik and Carroll 2006). Therefore, stands with a higher percentage of pine have a greater potential to host large beetle populations for a longer time.

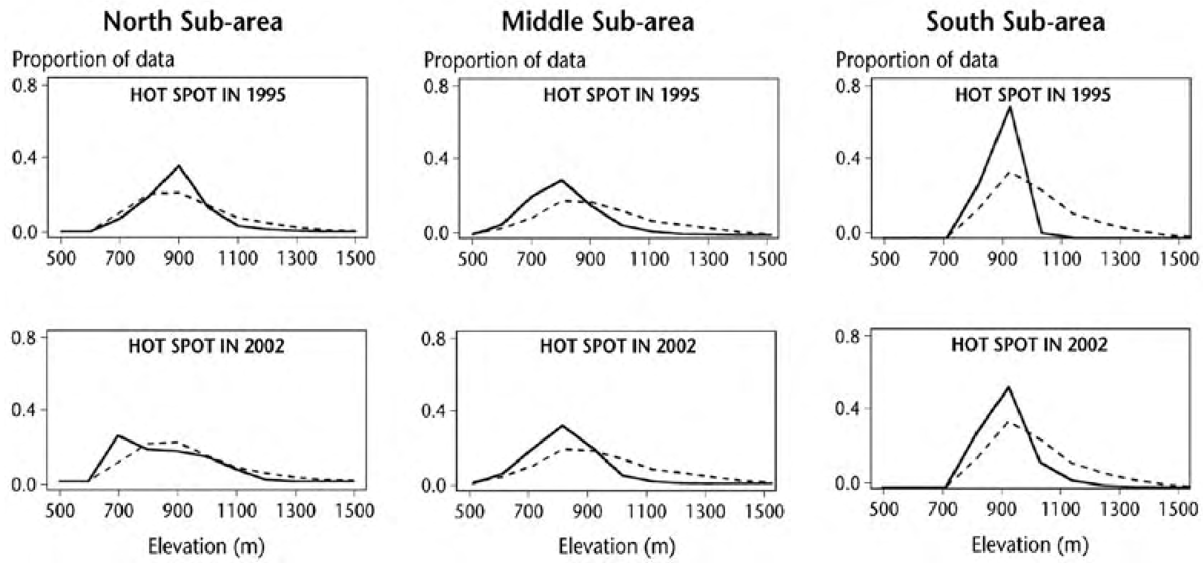

FIGURE 8. Relative frequency distributions of elevation for hot-spot locations (solid line) and all pine locations (dotted line).

Hot Spots and Elevation

Because the Morice TSA borders the northern extent of the mountain pine beetle's spatial range, trends relating to elevation are particularly important. Temperature is known to affect beetle success and mortality (Amman 1973), and at the northern periphery of the beetles' range, temperature variations caused by terrain will determine which locations are suitable for the beetle. The most prevalent elevations associated with hot spots were 800 m in the Middle sub-area, 900 m in the North sub-area, and 1000 m in the South sub-area. In the North sub-area, the relative frequency distributions of elevations associated with single-year hot spots tended to deviate from the background frequency distribution at a single-elevation class (Figure 8). In 1995 and 1996, 900-m elevations were most frequently associated with hot spots (44.7% and 36.1%, respectively). In 1999 and 2000, the dominant elevation was 1000 m (29.6% and 32.6%, respectively), and in 2001 this changed to 700 m (31.3%). For other years, strong preferences were not clear. In the Middle sub-area, hot spots occurred most frequently at elevations of 800 m (ranging from 28.6% to 40%), and this did not change with time. Similarly, in the South sub-area 900 m was the preferred elevation for hot spots (ranging from 24.9 to 29.1%; elevations greater than 1000 m make up between < 1% and 24.9% of all pine forests). Over time, the frequency distribution of elevations associated with hot spots became more similar to the background frequency distribution.

Comparisons between the proportion of hot-spot years and elevation demonstrate that as the proportion of hot-spot years increase in the North, the percentage of locations with elevations between 900 m and 1000 m also rises (Figure 9). In the Middle and South sub-areas, when the proportion of hot-spot years was greater than 26%, relative frequency distributions of elevation associated with hot spots had a consistent shape.

Elevations associated with hot spots are constrained by the range of elevations suitable for pine growth, which in the Morice TSA is 600–1400 m. Further limitations are associated with elevation and climate (Amman 1973; Safranyik *et al.* 1974). Beetle populations are most successful where temperatures are warm enough to allow the production of a beetle population within 1 year. If the life cycle is longer than 1 year, beetle mortality rises. For example, cool temperatures related to elevations greater than 1900 m near the Grand Teton National Park delayed mountain pine beetle development and increased mortality (Amman 1973). Mortality also increases if mountain pine beetles emerge when climate conditions are less than optimal. Although it is difficult to make direct comparisons with different geographical locations, the climatic limitations for a 1-year life cycle can be a determined linearly using elevation and latitude (Amman 1973; Safranyik and Carroll 2006). For the Morice TSA, at approximately 54°N, 1-year life cycles are generally limited to elevations of less than 900 m (Amman 1973; Safranyik and Carroll

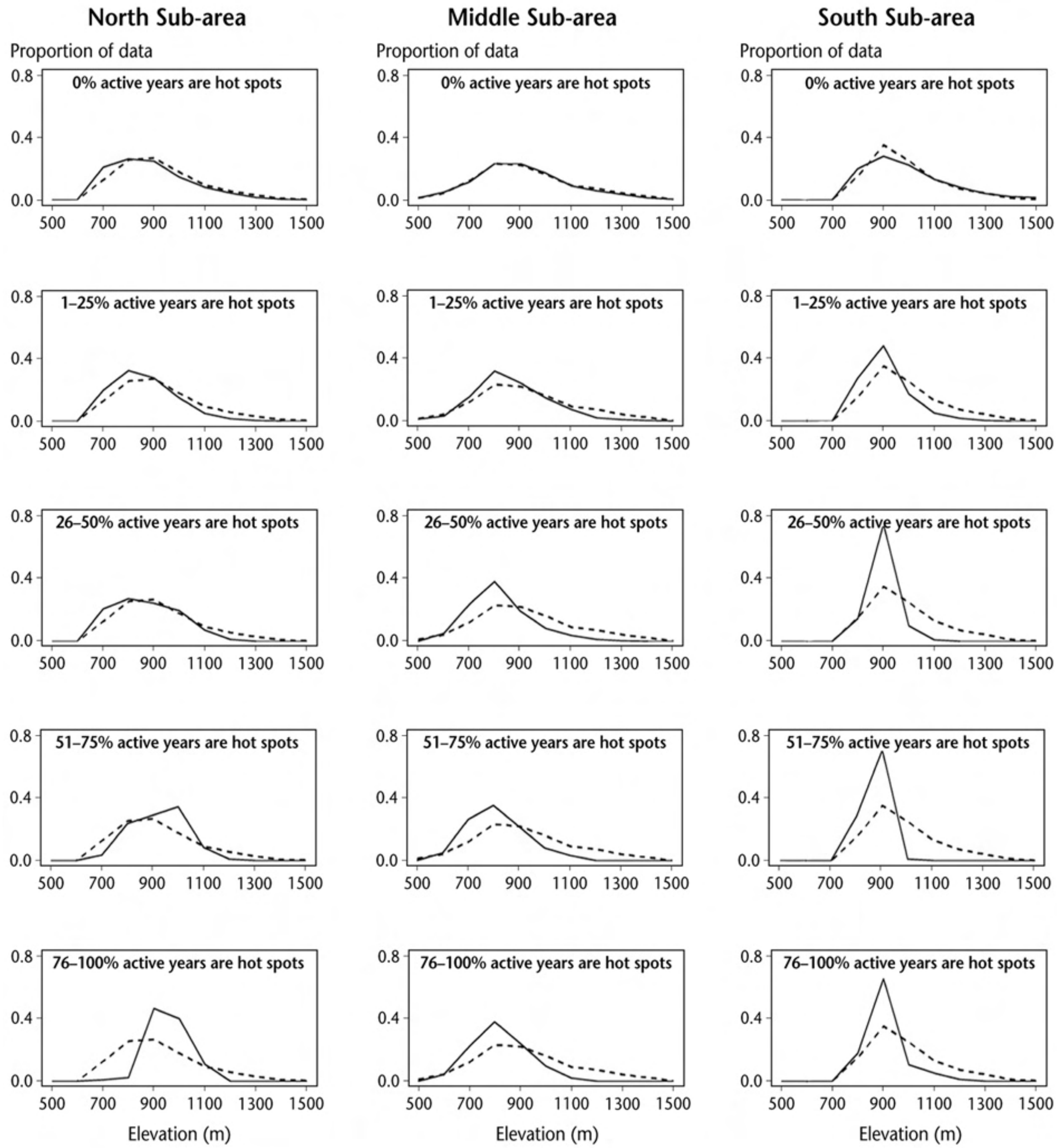

FIGURE 9. Relative frequency distributions of elevation for hot-spot locations (solid line) partitioned by the proportion of years a location is a hot spot. For comparison, relative frequency distributions of elevation for all pine locations are also provided (dotted line).

2006). The South sub-area may be able to sustain populations at higher elevations because of temperature inversions. During the winter, temperatures may invert, causing the coolest temperatures to occur in valleys, which improves the success of beetle populations at higher elevations.

Hot Spots and Aspect

As with elevation, trends relating to aspect are linked to temperature. For single-year comparisons between hot spots and aspect, the North and Middle sub-area aspect distributions were always similar to the background distributions. In the South sub-area, 33–54% of hot spots were located on warmer south-facing slopes (Table 5). The dominance of south-facing slopes decreased through time, and by 2002 the frequency distribution of aspects associated with hot spots approximated the background proportion of 31%.

The relationship between the proportion of hot-spot years and aspect is inconsistent between sub-areas, yet temporal trends emerge within sub-areas (Table 6). In the North sub-area, 57% of hot spots were located on western slopes when hot spots occurred in more than 75% of active years. In the Middle sub-area, south and eastern slopes were most commonly (71%) associated with locations hot for more than 75% of active years. In the South sub-area, the largest deviation from the background trend occurred when cells were hot for 51–75% of years. In this case, 51% of hot spots were located on warmer, south-facing slopes.

The relationship between aspect and beetle infestations was clearest during the initiation of a widespread infestation in the South sub-area, when southern slopes appeared to be preferred. Mountain pine beetles first infested the most suitable habitat and through time attacked more marginal hosts. Suitable habitats were those that maximized beetle survival and allowed a 1-year life cycle. At the northern extent of the mountain pine beetle's range, host trees on warm locations were preferred. In more southerly locations, precipitation rather than temperature limited beetle success.

TABLE 5. Percentage of aspects for hot-spot locations and all pine locations, for the South sub-area

Aspect	All	1999	2000	2001	2002
North	26.3	5.4	9.2	10.1	22.9
East	25.1	23.8	23.6	25.3	30.7
South	30.5	53.8	48.6	45.9	32.6
West	18.1	17.0	18.5	18.8	13.7

Populations will be limited by temperature, particularly at the northern margins of the mountain pine beetle range. Aspect is important, as south- and west-facing aspects are warmer. These warmer aspects seem important for outbreak initialization (Safranyik *et al.* 1974). As well, newly emergent beetles prefer direct sources of light, which are likely warmer locations in a microclimate (Safranyik *et al.* 1989). As beetles expand into new territories, due to climate variability, understanding the significance of terrain is increasingly important (Carroll *et al.* 2004).

TABLE 6. Percentage of aspects for hot-spot locations and all pine locations based on the proportion of hot-spot years

	All	1–25%	26–50%	51–75%	> 75%
NORTH SUB-AREA					
North	24.6	26.4	18.0	22.3	10.6
East	23.9	22.8	33.1	25.2	19.1
South	23.7	23.6	23.3	20.9	12.8
West	27.7	27.2	25.6	31.5	57.4
MIDDLE SUB-AREA					
North	24.9	26.0	25.2	23.1	14.5
East	23.9	23.8	23.1	26.8	36.6
South	27.6	27.1	26.1	29.6	34.2
West	23.6	23.1	25.6	20.5	14.6
SOUTH SUB-AREA					
North	26.3	29.3	26.1	12.2	11.2
East	25.1	23.8	27.4	18.6	26.3
South	30.5	29.8	33.2	50.9	40.2
West	18.1	17.1	13.3	18.3	22.2

Conclusions

Detecting and mapping infestation hot spots in data collected to monitor mountain pine beetle populations adds value to existing forest health management programs. By identifying where infestations are most intense, it is possible to better understand interactions between the mountain pine beetle and its underlying environment. These relationships have rarely been described with data for large areas. The methods outlined here provide an important approach to exploratory investigation of the spatial and spatial-temporal variability in mountain pine beetle population dynamics over large areas.

Kernel density estimation enables the generation of intensity surfaces from survey points. Using these surfaces, each location within a study area can be classified as a hot spot or non-hot spot. When hot spots are defined as the top 10% of estimated intensity values, hot-spot locations are variable through time. Locations are rarely categorized as hot spots in more than 1 or 2 years and typically less than 25% of years have hot-spot infestations. Epidemic beetle populations will deplete the suitable hosts within a stand in 1 year. Hot spots do not persist because there is not enough mature pine at a particular location to sustain a large population for multiple life cycles.

The lack of persistence in hot spots is partially a response to treatment. We determined that, in 2001, infestation clusters associated with hot spots which underwent any type of treatment were less likely to be associated with hot spots in 2002. Not surprisingly, infestation clusters treated with block harvest in 2001 were never associated with hot spots in 2002. This indicates that at least some of the lack of persistence in hot spots is associated with management. Regardless of the type of treatment, management reduced the persistence of hot spots. Because 51% of hot spots were only hot in 1 year, and in 2001 22% of locations received treatment, it is reasonable to assume that the observed trends are capturing processes in addition to treatment.

Our research results indicate that forest models which use environmental conditions to determine a particular location's susceptibility to infestation will need to vary relationships between environmental factors and infestation levels depending on the stage of the infestation. When a beetle outbreak occurs in a historically infested area, the environmental variables will differ from those associated with a beetle outbreak in a previously non-infested region. As such, when landscape-scale modelling is conducted to predict future beetle infestations and impacts, the significance of a specific forest age class will change depending on the infestation phase.

Our research results indicate that forest models which use environmental conditions to determine a particular location's susceptibility to infestation will need to vary relationships between environmental factors and infestation levels depending on the stage of the infestation.

For some environmental conditions, stand-scale research can help explain large-area processes; for other conditions, scaling up stand-scale models is more problematic. For instance, relationships between infestation hot spots and forest age are similar to observations made at the stand scale; that is, mature trees are preferred by the mountain pine beetle and over time younger trees are infested. However, the mountain pine beetle's preferential selection of moderate pine forest cover at the landscape level is unexpected, although this is likely linked, in part, to relationships between forest age and percentage of pine cover in the Morice TSA.

The methods outlined in this study are applicable to all forest districts where insect infestations are occurring. The Morice TSA sits at the northern extent of the mountain pine beetle's range, and therefore some of the relationships between hot spots and the environment we have described are likely specific to this area. In particular, we anticipate that variables related to climate, such as elevation and aspect, may exhibit location-specific relationships with hot spots, whereas the relationships with forest age and percentage of pine are likely transferable to a wider spatial scale. The exact associations between hot spots and environmental characteristics or treatment will vary depending on the nature of the underlying landscape, the climatic regime, the beetle population, and management activities. Although the relationships described in this study may not be directly transferable to other areas, the analysis approaches and general trends can inform research and management conducted elsewhere.

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Test Your Knowledge . . .

Environmental characteristics of mountan pine beetle infestation hot spots

How well can you recall some of the main messages in the preceding Research Report? Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. The relationship between hot spots and forest age does not:
   - A) Vary with the age of the infestation
   - B) Vary with the landscape distribution of pine age
   - C) Favour forest ages greater than 160 years
   - D) Differ depending on the temporal persistence of hot spots

2. In the Morice TSA, the temporal persistence of hot spots increases when . . .
   - A) Forests are mature
   - B) Percentage of pine cover is low
   - C) Aspects are south-facing
   - D) Percentage of pine cover is high

3. Kernel density estimation is a helpful first step in locating hot spots because:
   - A) It is useful for determining a hot-spot threshold
   - B) It converts points to a continuous surface
   - C) It aids in the delineation of boundaries

ANSWERS

1. C 2. D 3. B