



# Spatial–temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*

Colin Robertson<sup>1\*</sup>, Trisalyn A. Nelson<sup>1</sup>, Dennis E. Jelinski<sup>2</sup>, Michael A. Wulder<sup>3</sup> and Barry Boots<sup>4</sup>

<sup>1</sup>Spatial Pattern Analysis & Research (SPAR)

Laboratory, Department of Geography,  
University of Victoria, Victoria, BC,

<sup>2</sup>Laboratory for Ecosystem and Landscape  
Ecology, Department of Geography, University  
of Victoria, Victoria, BC, <sup>3</sup>Canadian Forest  
Service (Pacific Forestry Centre), Natural  
Resources Canada, Victoria, BC and

<sup>4</sup>Department of Geography and Environmental  
Studies, Wilfrid Laurier University, Waterloo,  
ON, Canada

## ABSTRACT

**Aim** The spatial extent of western Canada's current epidemic of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is increasing. The roles of the various dispersal processes acting as drivers of range expansion are poorly understood for most species. The aim of this paper is to characterize the movement patterns of the mountain pine beetle in areas where range expansion is occurring, in order to describe the fine-scale spatial dynamics of processes associated with mountain pine beetle range expansion.

**Location** Three regions of Canada's Rocky Mountains: Kicking Horse Pass, Yellowhead Pass and Pine Pass.

**Methods** Data on locations of mountain pine beetle-attacked trees of predominantly lodgepole pine (*Pinus contorta* var. *latifolia*) were obtained from annual fixed-wing aircraft surveys of forest health and helicopter-based GPS surveys of mountain pine beetle-damaged areas in British Columbia and Alberta. The annual (1999–2005) spatial extents of outbreak ranges were delineated from these data. Spatial analysis was conducted using the spatial–temporal analysis of moving polygons (STAMP), a recently developed pattern-based approach.

**Results** We found that distant dispersal patterns (spot infestations) were most often associated with marginal increases in the areal size of mountain pine beetle range polygons. When the mountain pine beetle range size increased rapidly relative to the years examined, local dispersal patterns (adjacent infestation) were more common. In Pine Pass, long-range dispersal (> 2 km) markedly extended the north-east border of the mountain pine beetle range. In Yellowhead Pass and Kicking Horse Pass, the extension of the range occurred incrementally via ground-based spread.

**Main conclusions** Dispersal of mountain pine beetle varies with geography as well as with host and beetle population dynamics. Although colonization is mediated by habitat connectivity, during periods of low overall habitat expansion, dispersal to new distant locations is common, whereas during periods of rapid invasion, locally connected spread is the dominant mode of dispersal. The propensity for long-range transport to establish new beetle populations, and thus to be considered a driver of range expansion, is likely to be determined by regional weather patterns, and influenced by local topography. We conclude that STAMP appears to be a useful approach for examining changes in biogeographical ranges, with the potential to reveal both fine- and large-scale patterns.

## Keywords

Canada, climate change, Coleoptera, *Dendroctonus ponderosae*, infestation, insect outbreak, mountain pine beetle, *Pinus*, range expansion, spatial–temporal patterns.

\*Correspondence: Colin Robertson, Spatial Pattern Analysis & Research (SPAR) Laboratory, Department of Geography, University of Victoria, PO Box 3060, Victoria, BC, V8W 3R4, Canada. E-mail: colinr23@gmail.com

## INTRODUCTION

The world's climate warmed by  $0.6 \pm 0.2^\circ\text{C}$  during the last century, with the mean global temperature projected to increase by  $1.4\text{--}5.8^\circ\text{C}$  by 2100 (IPCC, 2007). The response of an ecosystem to warming is often difficult to predict, but many recent studies have highlighted the impact of global climate change on animal and plant species (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Robinet *et al.*, 2007). One common trend is the shifting of species ranges. Many studies have demonstrated the expansion of species distributions towards the poles and higher elevations (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006).

Climate and weather can limit the geographical distribution of animal populations directly, by influencing survival and fecundity, or indirectly, through their effects on interacting species, that is, on food sources, predators and competitors (Bale *et al.*, 2002; Gaston, 2003). The interaction between species (host/predator, etc.) is typically believed to determine the warm limits of a species' distribution, whereas direct climatic factors impose the cool boundaries (MacArthur, 1972; Brown *et al.*, 1996; Parmesan, 2005). Many insects are ideally suited for analyses exploring the effects of a warming climate owing to their physiological dependence on climate (Karban and Strauss, 2004) and, consequently, their rapid response to climate change (Thomas *et al.*, 2001; Bale *et al.*, 2002). Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), currently responsible for an unprecedented epidemic in the pine forests of western Canada, has a geographical distribution that is tightly linked to its bioclimatic envelope and is well within the range of its host (Safranyik, 1978). As such, the mountain pine beetle is poised to continue its range expansion as these cool boundaries are extended further.

The biogeographical range of the mountain pine beetle extends from northern Mexico, throughout the western United States and into northern British Columbia (BC), Canada, with small disjunct populations in Alberta and south-east Saskatchewan. Within western Canada, the vast majority of mountain pine beetles are confined to the Canadian Cordillera, west of the Rockies and south of  $56^\circ\text{N}$  latitude (Safranyik, 1978). Mountain pine beetle populations routinely undergo outbreaks and cause widespread disturbances in pine forests in North America (Raffa, 1988; Carroll, 2007). However, the mountain pine beetle populations in this region are currently at epidemic levels, having reached the largest population sizes on record in BC (Westfall, 2007).

In order to overcome the defences of its hosts, the mountain pine beetle has evolved synchronous, pheromone-mediated mass-attacks, with symbiotic relationships with several species of fungi (Ophiostomatales: Ophiostomataceae, *Ophiostoma*) (Safranyik & Carroll, 2006). Tree death typically occurs 1–2 years after a successful attack, and, for a given location, outbreaks generally last 6–10 years (Safranyik *et al.*, 1974). The mountain pine beetle remains active during the winter and its cold tolerance is dependent on life stage. In BC, extreme cold

events normally regulate its populations (Safranyik, 1978). However, over the last two decades, favourable winter temperatures, attributed to the positive and neutral phases of the Pacific Decadal Oscillation, have occurred (Moore *et al.*, 2005). This shift in climate, resulting in reduced cold-mortality (Logan and Powell, 2001), along with the abundance of connected habitat resulting from decades of fire suppression (Taylor *et al.*, 2006), has created an ecological opportunity for the current outbreak and for the expansion of the geographical range of the mountain pine beetle eastwards and northwards.

The eastern slopes of the Rocky Mountains have large forested areas of lodgepole pine (*Pinus contorta* var. *latifolia*), the primary host of mountain pine beetles. The corridors, through which eastward spread is likely to occur, are the three mountain passes: Kicking Horse Pass, Yellowhead Pass and Pine Pass (Moore *et al.*, 2005). These lower-elevation routes cross the continental divide and provide conduits to the pine forests on the eastern slopes of the Rockies. In the northern extreme of this region, lodgepole pine forests transition into jack pine (*Pinus banksiana*) forests. The latter is a potential host for the mountain pine beetle (Carroll *et al.*, 2006).

There are three principal modes of mountain pine beetle dispersal: beetles emerge to attack the nearest suitable host trees; beetles emerge to attack suitable hosts after a period of flight exercise (Safranyik *et al.*, 1992); and beetles become caught in convective upward drafts, in which they are transported long distances by wind (Furniss & Furniss, 1972). Range expansion and movement patterns of the mountain pine beetle can be investigated through the analysis of changes in the spatial patterns of infestation.

The aim of this paper is to use spatial analysis to explore the frequency of these dispersal processes occurring in the Kicking Horse Pass, Yellowhead Pass and Pine Pass of the Rocky Mountains of Canada. It is hypothesized that expansion beyond the recent biogeographical limits would be such that mountain passes would be the conduits of spread to the eastern side of the Rockies via short-range dispersal. We also demonstrate how a new method of spatial-temporal analysis, namely spatial-temporal analysis of moving polygons (STAMP), may be used to quantify the nature and variability of this spread. STAMP characterizes changes in patch-scale dynamics via a series of events that describe spatial changes in patch formation and function.

## MATERIALS AND METHODS

### Study area

Three mountain passes through the Canadian Rockies – Kicking Horse Pass, Yellowhead Pass and Pine Pass – are likely to be the principal conduits for beetle movement from BC to Alberta (Moore *et al.*, 2005). Centred on each pass, a  $300 \times 150\text{ km}$  rectangular study area was created. A rectangular study area was chosen to enable the detection of west to east migration over the Rockies. A study area width of 300 km

was used to approximate the distance of regional spatial synchrony in pine mortality during mountain pine beetle epidemics (Aukema *et al.*, 2006). Therefore, populations within each mountain pass should be relatively synchronous. The rectangular study area boundaries were aligned with the boundary of the encompassing forest district, as these are the primary delineator of fine-scale aerial survey programmes in BC. For Yellowhead Pass and Kicking Horse Pass, each rectangle approximately straddles the BC/Alberta provincial border, whereas Pine Pass is completely within BC (Fig. 1). Within each of the study areas, beetles were present in 1999, providing evidence that the range intersects each of the study areas at time  $T_1$  (1999). Given that historically much of the area in these mountain passes has been climatically unsuitable for the mountain pine beetle (Carroll *et al.*, 2006), we assume that the range boundary lies within each of the study areas in the first year of our study.

## Data

### Coarse-scale aerial surveys

The mortality of lodgepole pine (*Pinus contorta* var. *latifolia*) was estimated from annual overview surveys (AOS) carried out by the British Columbia Ministry of Forests (1999–2005) and the Alberta Land and Forest Division (1998–2005) using fixed-wing aircraft. Surveyors identified the locations of dead trees based on crown discoloration, a visible indicator typically used to locate trees attacked by the beetle in the previous year (Wulder *et al.*, 2006). During aerial surveys, areas of infestation were delineated on base maps (1 : 250,000 NTS topographic maps) and later digitized into geo-referenced vector datasets. Clusters of attacked trees were mapped as point data,

and more geographically dispersed infestations were mapped as polygonal data. Infestations mapped as points consisted of no more than 50 trees (British Columbia Ministry of Forests, 2000).

### Fine-scale aerial surveys

In addition to the spatially exhaustive coarse-scale aerial surveys, fine-scale surveys were also employed. Fine-scale surveys were conducted at a lower altitude than fixed-wing aerial surveys and were able to capture small patches and individual trees infested by mountain pine beetle and to provide data for tactical forest planning. Helicopter-based global positioning system (GPS) surveys were conducted at the forest district level. Surveyors recorded the locations of infested trees as a GPS point and estimated the number of infested trees in each cluster. The area represented by each point varied, but typically ranged from 0.25 to 0.50 ha. Previous research has found that the fine-scale survey data are accurate to  $\pm 10$  trees in 93% of cases, and within a spatial error of  $\pm 25$  m (Nelson *et al.*, 2006).

### Data representation

We used both coarse-scale and fine-scale datasets to represent mountain pine beetle presence or absence for the delineation of what we call range polygons. Because our data represent incipient-epidemic and epidemic populations (i.e. capable of mass-attacking healthy trees), ranges can be considered as outbreak ranges (Williams & Liebhold, 2002). Ranges were delineated by overlaying the coarse-scale and fine-scale aerial survey data on a 1-ha hexagon grid and aggregating hexagons intersecting the beetle survey data.



**Figure 1** Map showing the study areas in the three mountain passes of the Canadian Rocky Mountains (Kicking Horse Pass, Yellowhead Pass and Pine Pass) (grey shade, parks; grey lines, BC forest district boundaries) where data were obtained on the locations of mountain pine beetle (*Dendroctonus ponderosae*) infestations in 1999–2005.

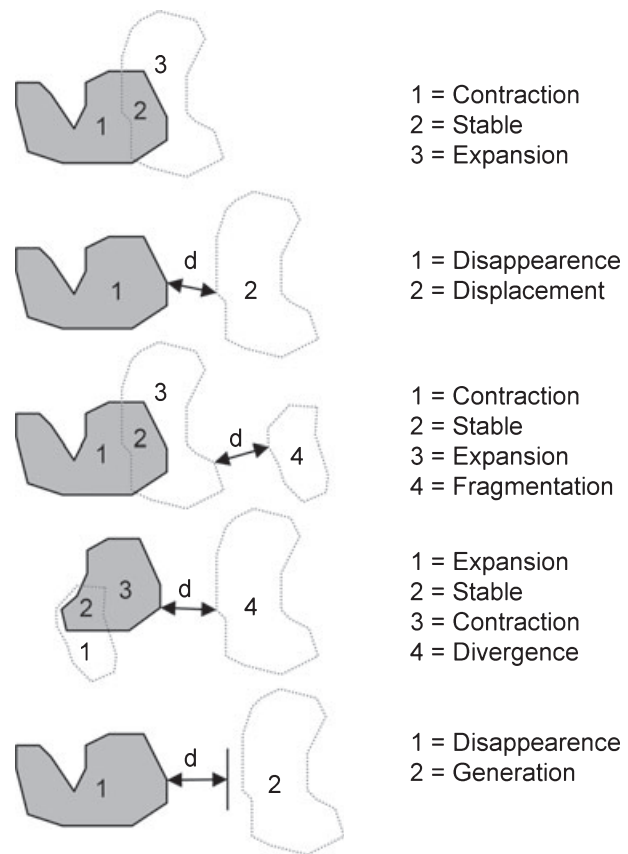
A hexagon grid was used for several reasons. First, compared with the typical square, a hexagon more closely approximates the shape of spot infestations, the characteristic pattern associated with beetle-attacked tree clusters (Gieszler *et al.*, 1980). Second, hexagons are often used in mapping species' occupancy because of attractive statistical properties, such as equal area and perimeter across a study area (Polasky *et al.*, 2000; White *et al.*, 1992). Finally, hexagons ensure that grouped occurrences of species' presence form cohesive polygons, avoiding the ambiguous relationship of diagonal grid cells (i.e. bishop's case neighbours). For each year, from 1999 to 2005, hexagons were grouped according to beetle presence, and internal hexagon boundaries were dissolved, yielding range polygon datasets for each year representing the mountain pine beetle range. These range polygons were then used for all subsequent processing and analysis.

### Spatial-temporal pattern analysis

To extract spatial-temporal patterns of movement from the mountain pine beetle range polygons, we used a new method for spatial-temporal analysis of moving polygons – STAMP (Robertson *et al.*, 2007) – a refinement of an event-based approach to polygon change developed by Sadahiro & Umemura (2001). To detect event-based change in polygons, the union of polygons from time periods  $T_1$  and  $T_2$  creates a change layer ( $T_1 \cup T_2$ ). Spatial-temporal relationships based on the intersections and proximity of polygons in  $T_1$  and  $T_2$  are characterized by different change events in each change layer (Fig. 2).

Intersection-based events include contraction, expansion and stability. For intersecting polygons, the portions common to both  $T_1$  and  $T_2$  are called stable portions, those present only in  $T_1$  are contraction portions, and portions only in  $T_2$  are expansion. If polygons in  $T_2$  have no intersections with polygons in  $T_1$  and the distance between them is beyond a movement threshold distance, they are categorized as generation events.

For proximity-based events a movement threshold distance is specified prior to running STAMP and is the maximum edge-to-edge distance at which polygons from neighbouring time periods will be related. If polygons in  $T_2$  have no intersections with polygons in  $T_1$  and the distance between them is within the threshold distance, they are classified as a movement event. Movement events that relate to the mountain pine beetle study include displacement, divergence and fragmentation. Displacement occurs when a  $T_2$  polygon occurs within the distance threshold of a  $T_1$  polygon. Divergence is represented by a polygon in  $T_2$  that appears within the threshold distance of a contraction polygon. Fragmentation is defined as a  $T_2$  polygon within the threshold distance of an expansion polygon. A 2-km threshold was used to distinguish between short-range and long-range dispersal. For detailed information about the relationships between STAMP events and dispersal processes, see Appendix S1 in Supporting Information.



**Figure 2** STAMP (spatial-temporal analysis of moving polygons) events generated from spatial-temporal relationships of mountain pine beetle (*Dendroctonus ponderosae*) range polygons in three mountain passes of the Canadian Rocky Mountains (Kicking Horse Pass, Yellowhead Pass and Pine Pass) in 1999–2005. Shaded polygons are from time period one ( $T_1$ ) and grey-border polygons are from time period two ( $T_2$ ). Overlapping polygons are decomposed into individual events. The events of interest for this analysis include expansion ( $T_2$  overlaps  $T_1$ ), divergence ( $T_2$  closest to contraction), displacement ( $T_2$  closest to disappearance), fragmentation ( $T_2$  closest to expansion), generation ( $T_2$  not within distance threshold) and stability (areas of  $T_1$ ,  $T_2$  overlap).

Event-based changes were summarized in a number of ways. First, we examined the frequency distribution of observed movement distances using boxplots for information about the sensitivity of the spatial patterns to the threshold distance, as well as additional information about mountain pine beetle movement processes. Next, for each polygon change layer ( $T_1 \cup T_2$ ), we calculated three spatially global (single-value) change metrics: the number ratio (NR), the area ratio (AR), and the average area ratio (AAR) (Table 1a–c). The NR measures the change in the number of polygons over two time periods. The AR measures the change in the area of polygons over two time periods. The AAR normalizes the AR by the NR. The AAR will be below 1.00 when area decreases relative to the NR, and greater than 1.00 when area increases relative to the NR. When the NR is not different from AR, the AAR will be 1.00. Finally, local

**Table 1** Measures of global spatial change in the number and area of mountain pine beetle (*Dendroctonus ponderosae*) range polygons in three mountain Passes of the Canadian Rocky Mountains (Kicking Horse Pass, Yellowhead Pass and Pine Pass) in 1999–2005.

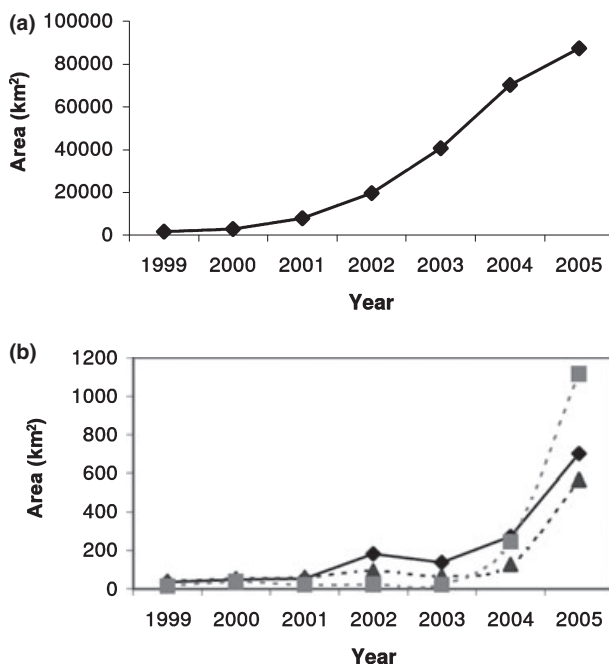
(a) Number ratio	Years					
Location	99/00	00/01	01/02	02/03	03/04	04/05
Kicking Horse Pass	0.74	0.95	0.78	0.43	1.30	4.60
Yellowhead Pass	1.60	1.23	0.67	19.89	0.07	8.78
Pine Pass	5.38	0.13	0.17	43.44	2.75	1.61
(b) Area ratio	Years					
Location	99/00	00/01	01/02	02/03	03/04	04/05
Kicking Horse Pass	1.34	1.11	1.56	0.70	1.91	4.47
Yellowhead Pass	1.38	1.11	3.38	0.75	2.00	2.56
Pine Pass	2.43	0.57	1.09	0.94	11.65	4.53
(c) Average area ratio	Years					
Location	99/00	00/01	01/02	02/03	03/04	04/05
Kicking Horse Pass	1.79	1.16	1.99	1.64	1.47	0.97
Yellowhead Pass	0.86	0.90	5.01	0.04	28.25	0.29
Pine Pass	0.45	4.53	6.42	0.02	4.23	2.81

The number ratio is calculated as the number of  $T_{n+1}$  polygons/number of  $T_n$  polygons, where  $T_n$  represents time period  $n$ , or one year of range polygons. The area ratio is calculated as the area of  $T_{n+1}$  polygons/area of  $T_n$  polygons. The average area ratio is calculated as the area ratio/number ratio.

directional analysis (see Robertson *et al.*, 2007) was performed for all years; however, the results are not reported because large-scale directional trends could not be detected using the 2-km threshold for local movement.

## RESULTS

The area affected by mountain pine beetle infestation in BC increased rapidly between 2001 and 2005 (Fig. 3a). In the three



**Figure 3** Area (km<sup>2</sup>) affected by mountain pine beetle (*Dendroctonus ponderosae*) in 1999–2005: (a) British Columbia; and (b) Kicking Horse Pass (triangles), Yellowhead Pass (diamonds) and Pine Pass (squares).

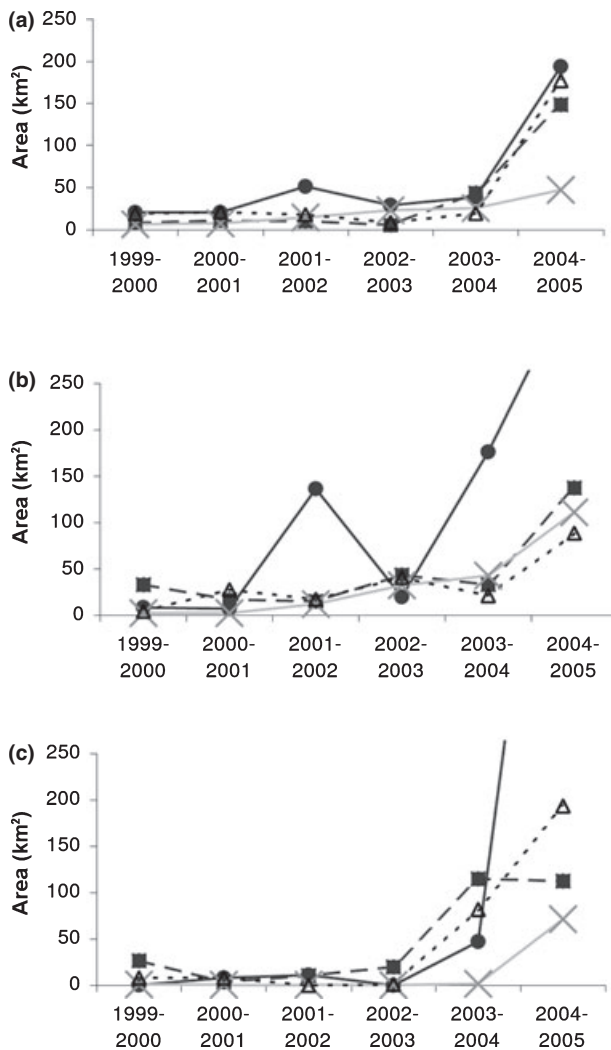
study areas, the areal extent of mountain pine beetle range polygons increased in most years from 1999 to 2005; however, all three areas experienced decreases from 2002 to 2003. This decline occurred as the larger province-wide trend was starting to increase rapidly (Fig. 3a). After 2003, range size increased rapidly in all study areas (Fig. 3b). This temporal lag between the province-wide trend and the study-area trends in the size of infested areas, shown by the slopes of Fig. 3a,b, suggests that our study areas were centred on the range boundary of mountain pine beetles. Reduced spatial synchrony at these locations peripheral to where the epidemic began supports the idea of an epicentral pattern to the current epidemic (e.g. Aukema *et al.*, 2006).

### Kicking Horse Pass

Changes in mountain pine beetle range size can be determined by examining the AR of range polygons in consecutive years. The AR in Table 1b indicates that positive changes in area occurred in all years except 2002–2003 and that a large increase occurred in 2004–2005. All AARs are greater than 1.00, signifying that range areas increased locally, as existing infestations grew in size (Table 1c). The largest AAR (1.99) occurred during 2001–2002, when expansion events made up the largest proportion of possible range changes (Fig. 4a).

In the early years of this study (1999–2002), Kicking Horse Pass was characterized by even amounts of different event types (Fig. 4a). Displacement was the dominant movement event most years, accounting for the greatest proportion of movement until 2004–2005 (Fig. 5a). Expansion events were abundant in all years, with a marked spike in 2001–2002 and an exponential increase after 2003. Generation events were relatively uncommon in Kicking Horse Pass until 2003–2004, when the number of infested hectares increased from 6,603 to





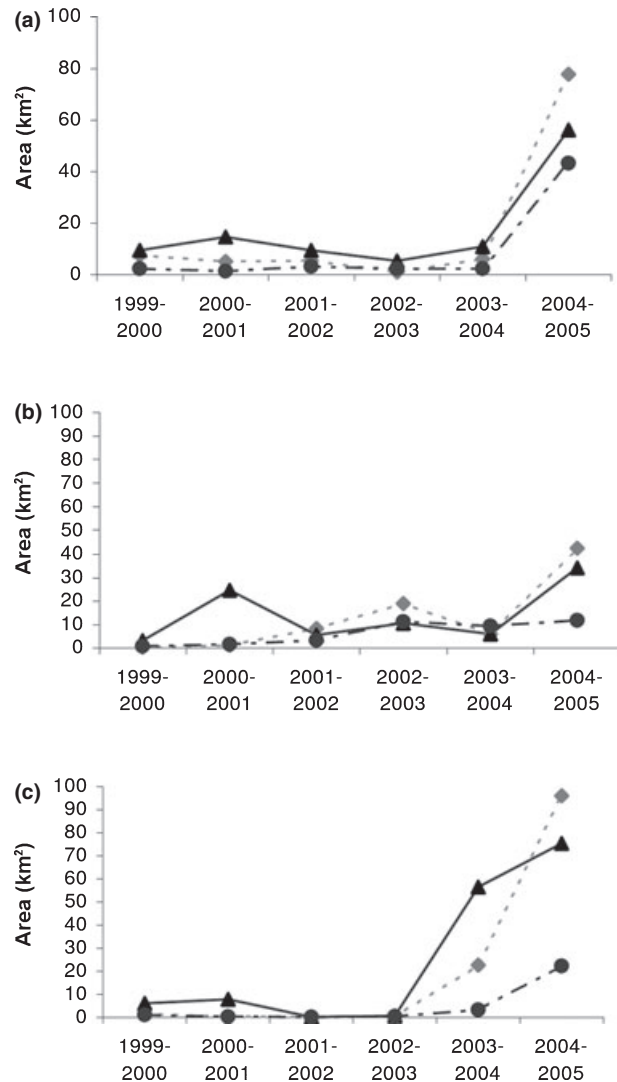
**Figure 4** Distribution of events derived from spatial-temporal analysis of mountain pine beetle (*Dendroctonus ponderosae*) range polygons, in three mountain passes of the Canadian Rocky Mountains in 1999–2005: (a) Kicking Horse Pass, (b) Yellowhead Pass, (c) Pine Pass study areas (circles, expansion events; squares, generation events; crosses, stable events; triangles, movement events).

12,667 and infestations occurred in previously uninhabited areas (Figs 4a & 6c). The spatial distribution of generation events (Fig. 6c) indicates that spatially isolated beetle populations were confined to BC until the first patch of new infestation appeared in 2002 in Alberta.

Median displacement distances ranged from 434 m (2000–2001) to 885 m (2003–2004). Over time, greater displacement distances were observed (Fig. 7a). Median divergence distances ranged from 296 m (1999–2000) to 668 m (2002–2003). Median fragmentation distances tended to be shortest, ranging from 275 m (1999–2000) to 585 m (2003–2004).

### Yellowhead Pass

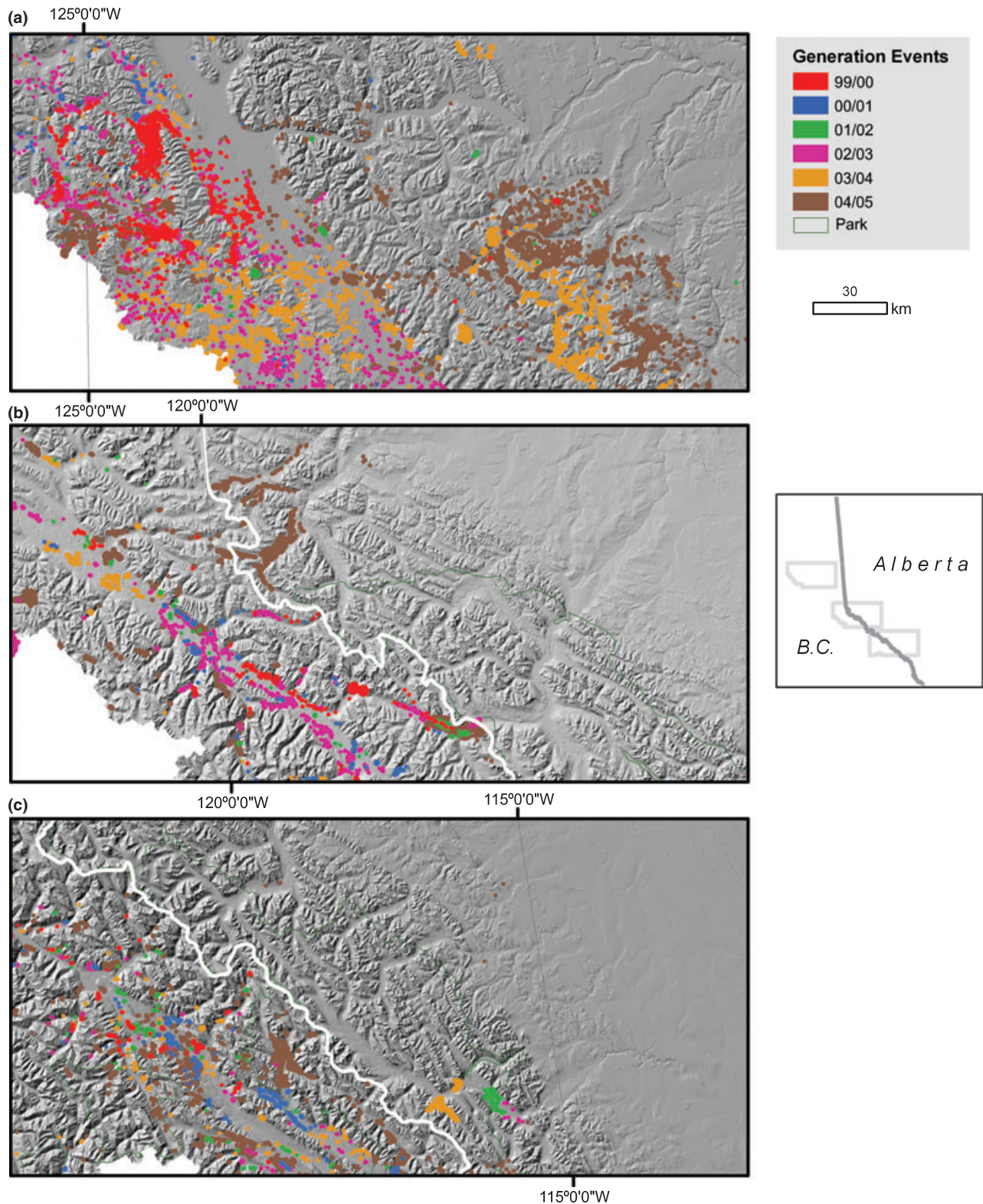
In Yellowhead Pass, the size and number of mountain pine beetle range polygons were highly variable (Table 2a,b). The



**Figure 5** Distribution of movement events derived from spatial-temporal analysis of mountain pine beetle (*Dendroctonus ponderosae*) range polygons in three mountain passes of the Canadian Rocky Mountains in 1999–2005: (a) Kicking Horse Pass, (b) Yellowhead Pass, (c) Pine Pass study areas (triangles, displacement events; circles, fragmentation events; diamonds, divergence events).

overall area of infestation increased every year, except for 2003. The AAR increased in this region in 2001–2002 and 2003–2004, indicating greater range area in fewer polygons compared with other years. This suggests that in this area the appearance of large and compact mountain pine beetle populations may be followed by an increase in dispersed spot infestations.

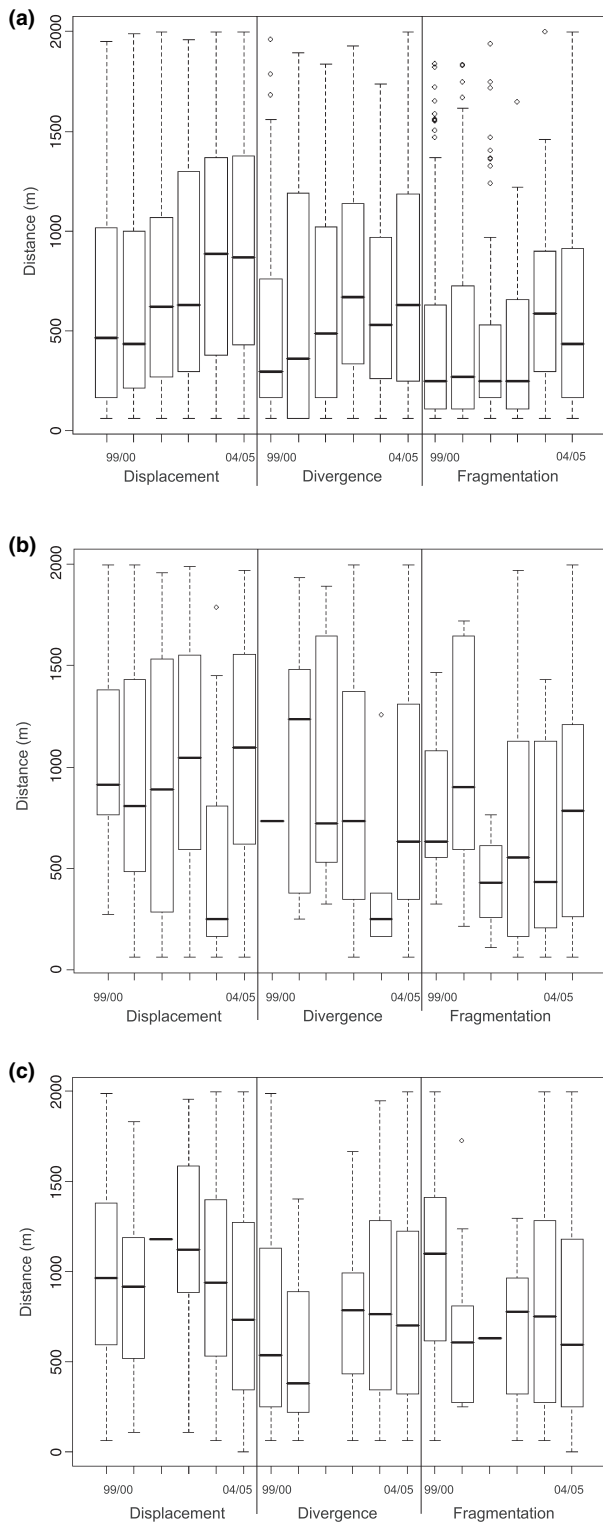
Movement and generation events occurred over similar sized areas in Yellowhead Pass during 1999–2001 (Fig. 4b), followed by a large increase in expansion in 2001–2002. For movement events, displacement and fragmentation were the prevailing patterns (Fig. 5b). Initially, displacement was common, but after the expansion spike in 2001–2002 fragmenta-



**Figure 6** Spatial distribution of generation events derived from spatial–temporal analysis of mountain pine beetle (*Dendroctonus ponderosae*) range polygons in three mountain passes of the Canadian Rocky Mountains in 1999–2005. Study areas are in geographical order from north to south: (a) Pine Pass, (b) Yellowhead Pass, (c) Kicking Horse Pass.

tion dominated, although not by a large margin. Greater infestation levels, occurring as a result of expansion, especially in 2001–2002, led to a greater likelihood of infestation

fragmentation. Fragmentation events suggest the establishment of transition areas between patches and spots of mountain pine beetle-infested trees.



**Figure 7** Boxplots of movement distances (m) associated with various event types derived from spatial-temporal analysis of mountain pine beetle (*Dendroctonus ponderosae*) range polygons, 1999–2005, in three mountain passes of the Canadian Rocky Mountains: (a) Kicking Horse Pass, (b) Yellowhead Pass and (c) Pine Pass study areas. Boxplot whiskers are calculated as the product of 1.5 and the interquartile range.

Initially, most generation events were located in the valley between Valemount and McBride ( $53^{\circ}4' N$ ,  $119^{\circ}39' W$ ; Fig. 6b). As the infestation progressed, generation events occurred further east towards Alberta, and increased on the Alberta side of the border, particularly in the northern portion of this pass. Additional generation events were found north of McBride. The most spatially isolated generation events were those north-east of McBride. It is possible that these areas were being influenced by beetles from north-eastern BC, moving long distances southwards along the eastern slopes of the Rockies. Movement distances were more variable in Yellowhead Pass than in Kicking Horse Pass (Fig. 7b). Displacement median distances ranged from 248 m (2003–2004) to 1098 m (2004–2005); median divergence distances ranged from 248 m (2003–2004) to 1236 m (2000–2001); and fragmentation median distances ranged from 432 m (2001–2002) to 901 m (2000–2001).

### Pine Pass

In Pine Pass, the overall trend was markedly different from trends in Yellowhead Pass and Kicking Horse Pass. The size of the mountain pine beetle range was comparatively small until 2004. By 2005, however, Pine Pass had the largest mountain pine beetle range of all three areas (Table 2b).

In Pine Pass, there was little variation in events during the early years (Fig. 4c). In 2004–2005, however, the amount of expansion increased to over 70,000 ha. During this time period there was also a greater amount of overlapping range polygons (stable), suggesting a major spatial coalescence of infested areas. Given that the NR was also large, while there was more area covered by the range, there were also greater numbers of range polygons. Displacement was the dominant movement pattern in Pine Pass (Fig. 5c); however, as more expansion occurred in 2003–2004 and 2004–2005, greater amounts of fragmentation movement were identified.

Three spatial-temporal trends can be identified in the spatial distribution of generation events in Pine Pass (Fig. 6a). First, the majority of generation events occurring in 1999–2000 were clustered in valleys on the eastern side of a major lake (Williston Lake), which lies in the centre of the study area. Second, in 2002–2003, generation events were dispersed uniformly across lower elevations on the eastern side of the Rockies. Third, beginning in 2003–2004, generation events occurred over large areas east of the Rocky Mountains, indicating an important eastward range shift.

Median displacement distances were large in the Pine Pass, ranging from 731 m to 1123 m (Fig. 7c). Median divergence distances ranged from 377 m to 784 m, and median fragmentation distances ranged from 591 m to 1097 m. In all three study areas, the distributions of movement distances tended to be centred close to 1 km. Very few events had movement distances approaching 2 km, justifying our selection of 2 km as a reasonable maximum dispersal distance. Since movement distance distributions tend to be leptokurtic,



**Table 2** Summaries of mountain pine beetle (*Dendroctonus ponderosae*) range polygons in three mountain Passes of the Canadian Rocky Mountains (Kicking Horse Pass, Yellowhead Pass and Pine Pass) in 1999–2005.

(a) Number of polygons	Year						
Location	1999	2000	2001	2002	2003	2004	2005
Kicking Horse Pass	1286	958	911	716	308	401	1846
Yellowhead Pass	70	112	138	93	1850	131	1150
Pine Pass	279	1500	188	32	1390	3825	6144
(b) Total area of polygons (ha)	Year						
Location	1999	2000	2001	2002	2003	2004	2005
Kicking Horse Pass	3999	5360	5962	9352	6603	12667	56594
Yellowhead Pass	3510	4833	5336	18094	13651	27307	69984
Pine Pass	1493	3621	2055	2246	2109	24571	111379

a small number of 2-km movement events conform to biological reality.

## DISCUSSION

The conditions that allow a species to disperse are commonly cited as potential determinants of a species' range (Brown *et al.*, 1996; Gaston, 1994, 2003; Lester *et al.*, 2007). In an abstract sense, a species' range is a geographical manifestation of a species' response to spatial and temporal variation in a range of environmental influences (Lubina & Levin, 1988; Gaston, 2003; Holt *et al.*, 2005). Expansion rates are likely to increase with habitat availability (Thomas *et al.*, 2001). Furthermore, habitat availability may increase as a function of ameliorating environmental conditions, catalyzing range extension as a function of ecological, physiological and population dynamic processes (Thomas *et al.*, 2001). In the case of this study, regional warming at the previously cooler margins facilitated expansion into previously climatically unsuitable habitat.

### Observed spatial patterns

We found evidence for two time periods with unique patterns of mountain pine beetle spread in Kicking Horse Pass. The period from 1999 to 2003 was characterized by low rates of mountain pine beetle population increases (Fig. 4a), with expansion as a common movement pattern. This, combined with the relative lack of generation events, suggests that spread occurred over short distances. Additional evidence for this is that, in general, there were fewer polygons covering a greater area as time progressed. The dominant movement event during this period was displacement. Existing infestations grew incrementally, while new spot infestations were established at the range edge.

We found that the initial period of low-increase movement and expansion was followed by a period of rapid mountain pine beetle expansion from 2003 to 2005. In the second phase, movement events remained dominant, but generation events increased in frequency up to 2005, thus resulting in newly established populations. The occurrence of increased generation events imply that range expansion was accelerating. One

possibility is that significant numbers of beetles were transported eastwards by wind, which is known to be a vector for long-distance dispersal for this and other insects (Furniss & Furniss, 1972).

In Yellowhead Pass, prior to 2001–2002 the spatial–temporal patterns of mountain pine beetle infestation were similar to the early patterns observed in Kicking Horse Pass. However, in contrast, the Yellowhead Pass beetle range polygons increased in size in proportion to their number during this period (AAR values near 1.0). Thus, mountain pine beetles appeared to be moving to new habitat, but at the same time did not expand rapidly. Where expansion did occur, the mountain pine beetle spread northwards, up the trench, and eastwards, through the valleys. There did not appear to be significant long-distance dispersal occurring.

The trend towards a greater number of stable events, or overlapping range polygons, indicates that persistent infestations were increasingly common in Yellowhead Pass. The increase in generation events in 2004–2005 occurred in the northern areas of Yellowhead Pass, which may indicate the spread of beetles south-eastwards from mountain pine beetle populations that invaded Alberta from the Peace River area of north-east BC.

The early patterns of mountain pine beetle range polygons in Pine Pass were also similar to those of the two other study areas, with low to moderate rates of increase, especially prior to 2003, when Pine Pass had the smallest range. This pattern shifted in 2003–2004, when the range area increased exponentially. The majority of this increase may be the result of long-distance dispersal, as generation events make up the majority of events during this time. Although mark–recapture research has estimated that a small percentage of dispersing beetles will attempt long-distance dispersal (2.5% in Safranyik *et al.*, 1992), it is generally thought that the establishment of new populations as a result of wind-driven transport is caused by synoptic weather patterns (Jackson & Murphy, 2004). Although conditions for mountain pine beetles have been improving east of the Rocky Mountains, it is unlikely that the amount of new infestation in Pine Pass is the result of build-up from local populations, especially given the rapid expansion of mountain pine beetles when barriers have been breached in other parts of the province (see Nelson *et al.*, 2007). The

spatial pattern of generation events in 2004–2005 further suggests that beetles are spreading through Pine Pass.

Another area of increased mountain pine beetle infestation in Pine Pass is the eastern arm of Williston Lake towards Hudson's Hope. A large number of range polygons appear on the western edge of the lake in valley areas. Much of this area was covered by generation events in the first year of our analysis (Fig. 6a). The establishment of new populations in the eastern arm in 2004–2005 suggests that the lake has ceased to act as a barrier to eastward spread. Depending on host suitability, and thermal conditions along the eastern-arm slopes of Williston Lake, this area may be the site of new population centres in the future.

### Potential climate effects

It is difficult to predict the impacts of climate change on forest insect pests because of the complexity of the interactions between insects and trees. Ungerer *et al.* (1999) predicted that warmer winter temperatures, and less variance in temperature, would be more important than warmer summers for the northward expansion of the southern bark beetle (*Dendroctonus frontalis*) in the United States.

More pertinent to our study, Logan & Powell (2001) evaluated potential mountain pine beetle invasion in relation to climate change, particularly with respect to the species' seasonal life cycle. They considered the life-history traits of timing and synchrony in relation to thermal environmental cues, recognizing that adult emergence has to occur early enough to maximize time for oviposition, but late enough to avoid lethal spring temperatures. In addition, synchrony is critical given the mountain pine beetle's mass-attack strategy of invasion. Logan & Bentz (1999) reported that the thermal ecology of mountain pine beetle remained resilient to a range of about 2.5°C in mean annual temperature. Climate modelling of CO<sub>2</sub>-doubling scenarios have predicted intense summer warming at high elevation (greater than 3,000 m) and at latitudes between 35°N and 55°N (Bradley *et al.*, 2004). As noted by Logan & Powell (2005), this corresponds to the northern US Rocky Mountains, and the predicted warming occurs at the most biologically critical time of year. Logan & Powell (2001) concluded that insects such as mountain pine beetle, with direct temperature control of life-stage development, are pre-adapted to take advantage of a warming climate.

Our findings are in agreement with previous predictions and processes related to the thermal ecology of beetles (i.e. Logan & Powell, 2005). Our analysis does not directly measure changes in climate in the region, partly because of the complex topography with its attendant macro and microclimates, but also because of the paucity of meteorological stations. Notwithstanding the absence of data in this study on beetle expansion in relation to climate events, we can look to Moore *et al.* (2005) for some insight. Moore *et al.* (2005) examined whether changes in climatic favourability for mountain pine beetle spread could be related to larger-scale phenomena, such as the Pacific Decadal Oscillation (PDO) and El Niño–

Southern Oscillation. They also considered whether stand-scale responses to climate may influence susceptibility to infestation. Coincident with this study, they focused on the same three Rocky Mountain passes. They concluded that the dominance of neutral and positive phases of PDO since 1977 is associated with less frequent and less severe cold-weather events, thus catalyzing range expansion. Their caveat was, however, that the PDO shift is only one possible large-scale phenomenon responsible for mountain pine beetle spread. However, with respect to this study, their study provides context and cause for the results we find in terms of exhibited mountain pine beetle expansion.

### Influence of beetle ecology

Three modes of dispersal were detected based on different spatial patterns of infestation; these spatial patterns of infestations were described by events. Expansion events indicate spot growth or dispersal to adjacent areas; movement events indicate spot proliferation, or dispersal to areas within 2 km but not adjacent to existing infestation; and generation events indicate evidence of long-distance dispersal. The distinction between growth and proliferation may be strongly related to landscape characteristics. Beetle dispersal as represented by spatial patterns of mass-attacked trees is largely governed by the pheromone conditions present, or, in the sense of Tischendorf & Fahrig (2000), by the 'functional connectivity' of the landscape. Spatial variation in factors that influence the pheromone connectivity of a landscape may therefore determine the patterns of infestation. For example, stand density and composition can impact on the ambient mixing environment, and thus pheromone concentrations (Thistle *et al.*, 2004). Another possibility is that physiological characteristics, such as dispersal behaviour, may vary geographically. The genotypes for other physiological traits in mountain pine beetle, namely development rate and size, have been found to vary according to local thermal regimes (Bentz *et al.*, 2001). Indeed, even local-scale microclimate may play a critical role in synchrony for invasion (Logan & Powell, 2001). Examination of other climate-driven range expansions found dispersive types to be favoured at the expanding range edge (Thomas *et al.*, 2001).

### Relation to the ongoing epidemic in western Canada

In the context of the current mountain pine beetle epidemic, it is not surprising that Pine Pass had the largest beetle range in 2005, given its proximity to the central interior of the province, where the first major epidemics occurred. Recent research has demonstrated a high degree of spatial synchrony during the epidemic (1999–2003) (Aukema *et al.*, 2006). However, it is interesting that Pine Pass had the lowest level of infestation until 2003. Aukema *et al.* (2006) point out that increases in mountain pine beetle populations in southern areas of the province were less spatially synchronous and were probably the result of localized build-ups. Thus, it would seem that similar

trajectories of growth at range margins, as displayed in Fig. 3b, are likely to be the result of an independent environmental effect. As indicated earlier, Moore *et al.* (2005) computed climate suitability indices for transects in each of the study regions and found that climate was generally moderating for mountain pine beetle survival in these areas from 1998 to 2003. Thus, increases across study areas are likely to be the result of increasing climate suitability at range margins, and the exponential growth in Pine Pass may be the result of an insect influx from central BC.

There are few methods available for characterizing change in multi-temporal polygonal data. The approach used in this research (STAMP) provided two important analytical outputs. First, through calculation of spatially global change metrics (NR, AR, AAR), trends in the number and size of polygons in each year were determined. These are straightforward operations in GIS, yet can be highly informative of large-scale change in biogeographical ranges over time. Second, spatially local patterns in polygon change based on proximity and overlap were determined and described by change events. By associating change events with particular mountain pine beetle movement processes, we were able to examine the relative frequency of these processes in each of the study areas. This analysis provided insights into the possible mechanisms generating variation in infestation patterns in different parts of the mountain pine beetle range edge, and could guide the design of more in-depth field experiments. Furthermore, generating a better understanding of how these patterns manifest at larger scales could aid in forest disturbance management and planning.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Relationship between STAMP events and mountain pine beetle dispersal.

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## BIOSKETCH

**Colin Robertson** completed an MSc degree in geography at the University of Victoria, where he is currently a PhD candidate. His research focuses on the development and application of novel approaches to the spatial analysis of large-area spatial processes in ecology and epidemiology.

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