



Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle

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ABSTRACT

Aim Our aim is to examine the historical breach of the geoclimatic barrier of the Rocky Mountains by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). This recent range expansion from west of the North American continental divide into the eastern boreal forest threatens to provide a conduit to naïve pine hosts in eastern North America. We examine the initial expansion events and determine potential mechanism(s) of spread by comparing spread patterns in consecutive years to various dispersal hypotheses such as: (1) meso-scale atmospheric dispersal of insects from source populations south-west of the Rocky Mountains in British Columbia (i.e. their historical range), (2) anthropogenic transport of infested plant material, and (3) spread of insect populations across adjacent stands via corridors of suitable habitat.

Location British Columbia, Canada.

Methods We explore potential mechanism(s) of invasion of the mountain pine beetle using spatial point process models for the initial 3 years of landscape-level data collection, 2004–2006. Specifically, we examine observed patterns of infestation relative to covariates reflecting various dispersal hypotheses. We select the most parsimonious models for each of the initial 3 years of invasion using information criteria statistics.

Results The initial range expansion and invasion of the beetle was characterized by aerial deposition along a strong north-west to south-east gradient, with additional aerial deposition and localized dispersal from persisting populations in following years.

Main conclusions Following deposition of a wave front of mountain pine beetles parallel to the Rocky Mountains via meso-scale atmospheric dispersal, the areas of highest intensity of infestations advanced up to 25 km north-east towards jack pine (*Pinus banksiana*) habitat in a single year. There appeared to be no association between putative anthropogenic movement of infested materials and initial range expansion of the mountain pine beetle across the continental divide.

Keywords

British Columbia, Coleoptera, Curculionidae, *Dendroctonus ponderosae*, dispersal patterns, forest insects, landscape ecology, long-distance dispersal, mountain pine beetle, range expansion.

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INTRODUCTION

Examining the spatio-temporal attributes of populations of invasive organisms can provide insights into their rates and

patterns of spread, which in turn can suggest mechanisms driving their establishment and persistence (Peterson & Vieglais, 2001). Climate plays a central role in many invasion events, by impacting host distribution (Iverson & Prasad,

1998), creating directional gradients in critical temperature thresholds that restrict reproduction, or introducing organisms via weather fronts or other disturbances such as hurricanes (Tackenberg, 2003). Humans also can play a major role in introduction of organisms, through inadvertent transportation of potentially invasive species (Brockerhoff *et al.*, 2006; Skarpaas & Økland, 2009). Investigation of resulting patterns of spread allows researchers to determine which processes may have contributed to the establishment of an organism, and can provide helpful clues for mitigation in the event of an organism's persistence.

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an insect native to western North America that intermittently undergoes dramatic population fluctuations (Safranyik *et al.*, 1974; Amman & Cole, 1983; Aukema *et al.*, 2008). A phloeophagus insect with a short-lived adult phase, mountain pine beetles survive outside of host trees for only a few days. Numerous species of conifers in the genus *Pinus* are susceptible to colonization by the mountain pine beetle, although lodgepole (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and ponderosa pine (*P. ponderosa* Dougl.) are considered the insect's primary hosts. Adult female beetles bore into the phloem of mature trees, producing aggregation pheromones (Renwick & Vite, 1970; Libbey *et al.*, 1985). Trees respond with copious amounts of toxic resin that impede access to the cambium tissues. However, at epidemic population phases, the mass attack, in concert with fungi that beetles vector (Safranyik *et al.*, 1975), may collectively exhaust host defences. Mated females lay eggs in small niches along ovipositional galleries under the bark. Larval development is temperature dependent (Bentz *et al.*, 1991), progressing through four larval instars through the winter before pupation in the spring. In July or early August, new adults take flight *en masse* to seek new hosts (Reid, 1962; Bright, 1976).

Exposure to cold winter temperatures (Reid, 1963; Reid & Gates, 1970) and limited mosaics of suitable hosts in space and time (Shore & Safranyik, 1992) typically restrict the mountain pine beetle to endemic levels where tree-killing activity is not observed. However, in the late 1990s, a large outbreak irrupted in the central interior of British Columbia, Canada (Aukema *et al.*, 2006), currently encompassing a total area of 16.3 million hectares of pine forests (British Columbia Ministry of Forests and Range, 2009). The outbreak has been exacerbated by anthropogenic activities, such as fire suppression, as well as by increasingly warmer summer and winter temperatures reflective of a changing climate (Safranyik & Carroll, 2006; Kurz *et al.*, 2008; Raffa *et al.*, 2008).

Outbreking populations of the mountain pine beetle breached the historical geoclimatic barrier of the northern Rocky Mountains in approximately 2002 as entomologists discovered that the beetle had become established in the Peace River region of British Columbia. This area has not been considered part of the insect's historical distribution (Nealis & Peter, 2008; Robertson *et al.*, 2009; Cudmore *et al.*, 2010). This invasion event immediately commanded critical attention due to the proximity of a potentially suitable new host, jack pine

(*Pinus banksiana* Lamb.), in north-eastern Alberta (Safranyik & Linton, 1983; Cerezke, 1995; Cullingham *et al.*, 2011), which could provide a potential conduit for the mountain pine beetle to spread towards eastern North America (Wood, 2006; Nealis & Peter, 2008; Safranyik *et al.*, 2010). In many ways, the mountain pine beetle demonstrates the ideal properties of an invasive insect (Holway & Suarez, 1999) due to its relatively high fecundity (Cudmore *et al.*, 2010), its ability to attract mates necessary for host procurement via aggregation pheromone signals (Conn, 1981), and its ability to take advantage of seemingly 'novel' hosts (Safranyik & Linton, 1983; Cerezke, 1995; Huber *et al.*, 2009; Cullingham *et al.*, 2011).

Not surprisingly, given the potential for range expansion to the east coast of North America, a flurry of research has recently been conducted on risk analysis and climatic suitability (Safranyik *et al.*, 2010), reproductive potential and host distribution (Cudmore *et al.*, 2010; Cullingham *et al.*, 2011), and dispersal and landscape dynamics (Robertson *et al.*, 2009; Ainslie & Jackson, 2011; de la Giroday *et al.*, 2011). In this paper we examine the initial range expansion event as the mountain pine beetle breached the continental divide. Studying the location of infestations of forest insects within the landscape can help elucidate the insects' dominant mechanism(s) of dispersal. For example, the spread of organisms via short-distance or within-stand movements (e.g. Jactel, 1991) may result in diffuse patterns (cf. Hengeveld, 1988; Gamarra & He, 2008), while long-distance movements can result in wave-like or leptokurtic (i.e. stratified) dispersal patterns dependent on the coordination of dispersing individuals (Baltensweiler & Fischlin, 1979; Bjørnstad *et al.*, 2002; Johnson *et al.*, 2006a; Tobin & Blackburn, 2008; Robertson *et al.*, 2009). Although mountain pine beetles primarily disperse within a stand (Safranyik *et al.*, 1992) and are generally not considered strong dispersers at landscape scales (Furniss & Carolin, 1977; Raffa & Berryman, 1979), at outbreak levels the insect may be transported great distances via meso-scale atmospheric currents (Furniss & Furniss, 1972; Safranyik *et al.*, 1992; Jackson *et al.*, 2008; Ainslie & Jackson, 2011).

In addition, human activities may also facilitate range expansions or new invasions, often unintentionally (Brockerhoff *et al.*, 2006). Notable examples in North America involving forest insect systems include the spread of emerald ash borer, *Agrilus planipennis* Fairmaire, in the Great Lakes region via the transport of infested firewood (BenDor *et al.*, 2006), the spread of Asian long-horned beetle (*Anoplophora glabripennis* Motschulsky) via wood pallets from international trade (Haack, 2006), and the spread of gypsy moth (*Lymantria dispar* L.) via the transport of egg masses on automobiles and nursery stock (Johnson *et al.*, 2006b). Within the forest industry of the United Kingdom in the 1970s, harvesting and transport of infested logs facilitated the spread of a related *Dendroctonus* species, *D. micans* (Kugelann) (Gilbert *et al.*, 2003). In the mountain pine beetle system, there are frequent points of contact between humans and infested host materials throughout the newly invaded areas of British Columbia and Alberta. For example, control and treatment tactics used

throughout the region include on-site falling and burning as well as harvesting of insect-colonized trees. Although harvesting companies are careful with infested host material and prioritize its processing at mill locations, storage of infested host material during periods of insect emergence and flight could potentially result in increased occurrence of infestations in areas surrounding storage and processing sites.

Using annual survey maps of infestation locations based on aerial detections of beetle-killed trees, we use inferential statistics to test hypotheses reflecting various modes of movement in relation to observed patterns of establishment within the initial zone of range expansion. We focus on two broad hypotheses. First, we examine evidence of transport above the ‘insect boundary layer.’ Although the term ‘boundary layer’ is typically restricted to the field of fluid dynamics (representing a viscous layer between two mediums), here we define ‘insect boundary layer’ as the altitude below which an insect will determine its own spread and direction of movement *sensu* Taylor (1974). At altitudes above the insect boundary layer, the passive transport of insects, dependent on wind speed and direction, is termed ‘aeolian dispersal’ (Szymkowiak *et al.*, 2007; Jackson *et al.*, 2008; Zhang *et al.*, 2008). In examining evidence for above-boundary layer transport, we compare establishment patterns to landscape feature-independent patterns, such as a large east–west gradient, suggesting progressive movement of mountain pine beetle populations from sources parallel to the western edge of the Rocky Mountains in British Columbia, or inbound patterns, suggesting long-distance aeolian dispersal and ‘rainout’ as the primary mechanisms of invasion, respectively. Second, we examine evidence for transport based on movement within the insect boundary layer. Mechanisms of dispersal occurring within the insect boundary layer include insect flight through suitable habitats located primarily along low-elevation corridors such as river valleys (Robertson *et al.*, 2009), and human-assisted dispersal due to transport of infested material along roads and storage of infested material at milling sites.

MATERIALS AND METHODS

Study area and spatial datasets

The northern and southern extent of the research area, delineated between 54° and 56.5° N, spanned from the Great Continental Divide within the North Rockies Mountains to the British Columbia–Alberta border, covering a total area of approximately 3 million ha (Fig. 1a). The topography in this region ranges from the sharp relief of the Rocky Mountains at the western edge, the undulating topography of the foothills in the centre, and plateaus deeply incised by various rivers in the east. Most rivers in the Peace region flow into the Arctic Ocean, as the area is east of the Great Divide but south of the Northern Continental Divide. These rivers include the Kiskatinaw, Moberly, Murray, Narraway, Peace, Pine, Pouce Coupé, Sukunka and Wapiti rivers as well as a large creek in the southern portion of the area called Red Deer Creek. Primary

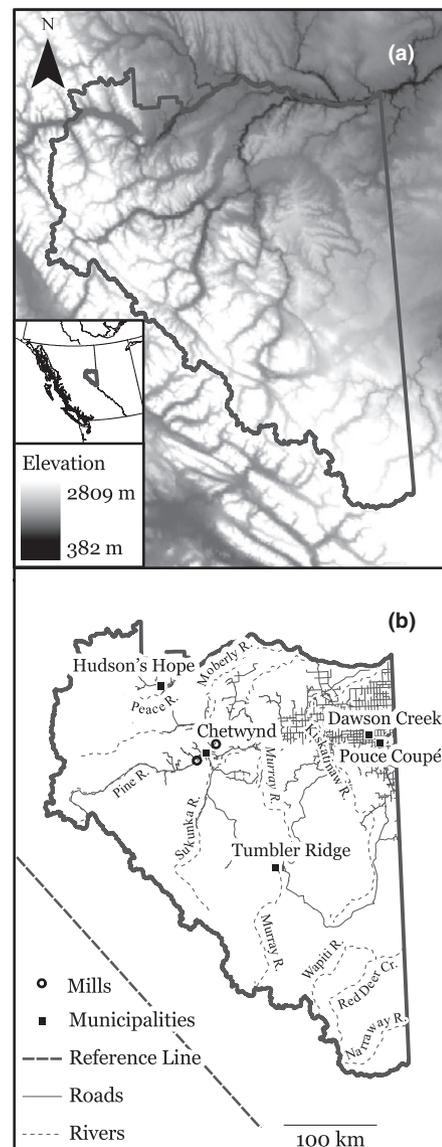


Figure 1 Map of the Peace River region of British Columbia: (a) elevation, (b) municipalities, mill locations, primary rivers, and highways. The straight dashed line represents the line of reference parallel to the Rocky Mountains and perpendicular to the direction of spread of the mountain pine beetle (*Dendroctonus ponderosae*) in 2004, the initial year of detection (see Materials and Methods).

industries in the region include oil and gas extraction, mining, and forestry operations that include harvesting of softwood conifers for lumber. Forestry companies operate over a majority of this Peace River region, as the provincial government of British Columbia is the predominant landowner and leases tree harvesting rights to forest management companies. There are two mills in the Peace River region that process lodgepole pine, both in Chetwynd, British Columbia (Fig. 1b).

During the initial spread of the mountain pine beetle into the region, forestry companies coordinated with federal and provincial governments to respond swiftly to the building outbreak. We obtained annual inventories of discrete,

tree-killing populations of the mountain pine beetle (referred to hereafter as infestations), initially collected to facilitate management planning, from these forest licensees. The infestations surveyed in a single year were considered to have been attacked in the previous year, as they were characterized by dead trees with chlorotic or red foliage (i.e. 'red attack'). Patches were at least 0.01 ha in size.

Locations of red-attack trees had been inventoried from helicopter using GPS with further ground reconnaissance work in some areas. Because epidemic populations of the mountain pine beetle must kill their hosts to reproduce, fading foliage can be used to identify trees attacked 1 year ago (Safranyik *et al.*, 1974) and serve as a useful proxy for insect abundance and distribution (Wulder *et al.*, 2006; Aukema *et al.*, 2008; Nelson & Boots, 2008). Surveys were conducted in 2004, 2005 and 2006 from May to September. Unique surveys were conducted each year, as infestation growth would shift the centre points. Centre point locations for each infestation were recorded in Universal Transverse Mercator (UTM) coordinates. Additional data collected for each infestation included its size, the approximate number of trees affected, ecological land classification scheme, land tenure, and any control strategy implemented.

To consider the potential influence of anthropogenic factors or the effect of rivers on spread of the mountain pine beetle, three datasets representing mill locations, primary and secondary roads, and rivers were secured from Global Forest Watch (2009). From these vector (i.e. point and line) datasets, the Euclidean distances for all locations in the research area to features of interest (i.e. infestations in the previous year, mills, roads and/or rivers) were calculated. This resulted in four raster datasets with a 73×73 m pixel size (i.e. just over one-half hectare in size).

Statistical analysis

We used regression models to examine the spatial association of the density of mountain pine beetle infestations with different covariates reflective of different hypothesized mechanisms of dispersal. These covariates are described in further detail below. The regression framework uses an analogue of Poisson regression for an inhomogeneous Poisson point process (Baddeley & Turner, 2000, 2005), where the point process reflects, in this case, the locations of infestation events across the landscape. The regression equation models the intensity of this process, λ , conditional on covariates that must be spatially explicit:

$$\lambda(x_1, \dots, x_p) = \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_p x_p)$$

where λ is the conditional density at a given map pixel, β are regression coefficients, and $x_1 \dots x_p$ are covariates. Substituting covariate values into the resulting regression equation yields an estimated intensity at a given point on the pixel map of the study area (an example is provided in Results). This regression technique represents a useful way to analyse maps and images that can be interpolated or converted to high definition raster

images for use as the spatially explicit covariates. Moreover, the method has an advantage of being able to contend with spatial autocorrelation that can affect experimental inference, as the spatial dependence is inherent within the point process. As in Poisson regression, model coefficients are estimated using maximum likelihood methods, significance of coefficients can be evaluated using Wald tests, and nested models can be compared by examining the change in deviance relative to a χ^2 reference distribution. Non-nested models can be compared by examining information criteria, such as the Akaike information criterion (AIC), with the lowest AIC value identifying the models of best fit for a given data set (Arnold, 2010).

As these point process regression models require spatially explicit covariates, we used the individual raster map(s) unique to each different hypothesized mode of dispersal for each covariate(s). Specifically, we tested whether there was evidence for anthropogenic activities contributing to spread via distances from insect locations to roads and mills, evidence for natural low-elevation corridors via associations of infestations with river pathways, and evidence for aeolian dispersal via diffusion processes (e.g. a linear distance gradient from the Rocky Mountains, and distances from point-source infestation locations in the previous year, and/or wave propagation via polynomial distance terms). In our system, due to the uniform directional spread of infestations in a north-east direction (see Results), there was a high degree of correlation between the x and y data. Evaluating the effects of highly collinear variables in regression models can create computational challenges, especially in estimating standard errors (Graham, 2003). Hence, x and y location data for models testing evidence consistent with gradient or wave-propagation aeolian dispersal were collapsed into a single variable measuring distance from a line of reference (d) just outside of the research area. The line of reference, with a 138° bearing, was positioned parallel to the Rocky Mountains and perpendicular to the dominant direction of spread for 2004 infestations, reflecting the initial invasion event from the interior of British Columbia (48° ; de la Giroday *et al.*, 2011; also see Results). As all of the spatial point process regression models require raster image datasets with spatially explicit covariates, we used a raster map with each pixel representing the distance from the reference line for tests reflecting dispersal consistent with a gradient or wave-propagation.

Each year was analysed separately. In addition to examining AIC values, the suitability of model fits were judged by examination of plots of the smoothed residuals. All data were handled in ARCVIEW v.9.2 (ESRI, 2008). Analyses were completed using the SPATSTAT package v.1.14-9 (Baddeley & Turner, 2005) within R v.2.8.1 (Ihaka & Gentleman, 1996; R Development Core Team, 2009).

RESULTS

The occurrence of infestations of the mountain pine beetle within the research area increased annually between 2004 and 2006. In 2004 and 2005, 10,536 and 12,275 infestations were mapped, respectively. These numbers tripled in 2006 to 35,084

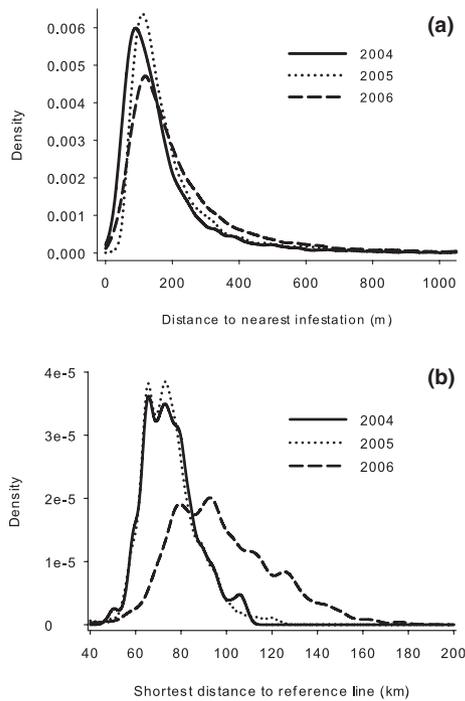


Figure 2 Distribution of (a) nearest neighbour distances and (b) shortest distances to the line of reference parallel to the Rocky Mountains and perpendicular to the direction of spread in 2004 of the mountain pine beetle (*Dendroctonus ponderosae*), the initial year of detection, in the Peace River region of British Columbia, Canada, in 2004, 2005 and 2006.

recorded infestations. Median nearest neighbour distances increased from 129 m in 2004 to 172 m in 2006 as the invasion front expanded (Fig. 2a). The invasion front was relatively stationary in 2004 and 2005, as the median of the distributions

of shortest distances from each infestation to the reference line south-east of the Rocky Mountains (Fig. 2b) was 73.6 km. The invasion front advanced rapidly in the summer of 2005, as the median distance to the reference line increased to 94.4 km when the dead trees were mapped in 2006 (Fig. 2b).

The mean area of patches of red-attack trees killed by the mountain pine beetle was quite small in 2004, covering approximately one-third of a hectare on average. The mean size increased to approximately 1 ha by 2006. Sizes of patches of dead trees became more variable due to expanding areas that were colonized, as the largest areas measured in 2006 were 2440 ha, vs. 6 ha and 133 ha in 2004 and 2005, respectively. By 2006, the total area of trees killed by the mountain pine beetle had expanded to 35,084 ha.

Summaries of model fits reflecting different modes of dispersal are represented by the AIC values in Table 1, with the lowest AIC value for a given year indicating the model most parsimonious with the inventory data. The spread pattern of mountain pine beetles into the region closely resembled that of a propagating wave in 2004. Areas closest and furthest from the initiation source had fewer infestations than those in the middle of the research area (Fig. 3a). This ‘wave-propagation’ model, consistent with a hypothesis of aeolian dispersal, was improved for 2005 and 2006 by adding a term for distance to the nearest infestations in the previous year (Table 1). Hence, the initial invasion appeared to be due to aerial deposition along a strong north-west to south-east gradient, with additional aerial deposition and localized dispersal from persisting populations in following years (Fig. 3b,c). There appeared to be no association between putative anthropogenic movement of infested materials and initial range expansion of the mountain pine beetle across the continental divide.

The full equations for all models are provided in Table 2. For example, the density of infestations at any point 75 km to

Table 1 Akaike information criterion (AIC) values for the spatial point process models reflecting various hypotheses of the dispersal of the mountain pine beetle (*Dendroctonus ponderosae*) for 2004, 2005, and 2006 in the Peace River region of British Columbia, Canada. Each model uses the spatially explicit intensities of beetle-killed trees for the respective year as a function of an intercept term and a similarly spatially explicit covariate(s), as listed (see Materials and Methods). Models with the lowest AIC values, in bold, are judged to fit the best.

Hypothesis	Covariate(s)	2004	2005	2006
Dispersal primarily occurs above insect boundary layer (i.e. aeolian dispersal)	Distance* (linear gradient from source)	324,186	373,781	1,024,656
	Distance* + distance ² (wave propagation)	315,602	364,567	1,009,046
Dispersal primarily occurs within insect boundary layer (i.e. human-assisted transport/natural corridors/adjacent stands)	Roads (anthropogenic activities)	333,332	383,898	1,027,245
	Mill locations (anthropogenic activities)	333,532	385,471	1,024,913
	River systems (natural corridors)	332,196	384,841	1,027,961
	Roads and mill locations	328,444	381,863	1,024,729
	Roads and rivers	331,337	383,182	1,027,197
	Rivers and mill locations	331,703	384,835	1,024,851
	Rivers, roads and mill locations	325,575	380,761	1,024,621
	Beetle locations _(t-1) (dispersal from previous year's establishment)	-†	370,646	1,023,605
Combination (above and within insect boundary layer)	Distance* + beetle locations _(t-1) insect bound	-†	369,445	1,023,607
	Distance* + distance ² + beetle locations _(t-1)	-†	361,856	1,004,025

*Distance from line of reference (parallel to the Rocky Mountains); see Materials and Methods and Fig. 2.

†No inventory data exist for 2003.

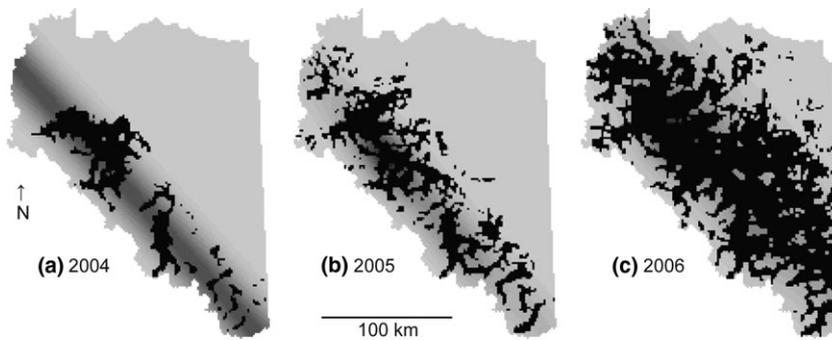


Figure 3 Location of infestations of the mountain pine beetle (*Dendroctonus ponderosae*) (in black) in the Peace River region of British Columbia, Canada, in (a) 2004, (b) 2005, and (c) 2006. Darker shaded areas within the maps indicate the highest densities of patches of trees killed by mountain pine beetles estimated from best models (i.e. the lowest AIC values in Table 1). Such areas may be partially obscured by overlaid mountain pine beetle data.

the north-east of the line of reference parallel to the Rocky Mountains (Fig. 1b) in 2006 can be estimated from the quadratic equation $\log(\lambda) = (-17 + 1.03 \times 10^{-4}(75 \times 10^3) - 7.23 \times 10^{-10}(75 \times 10^3)^2)$, yielding a density of 9.4×10^{-5} infestations m^{-2} , or approximately one spot infestation per hectare. A simple quadratic equation reflected the best model in 2004, and the second best model in 2005 and 2006. By solving these quadratic spatial regression equations for their maxima, we calculate the advance of the zone of greatest infestation density as a complement to the nearest-neighbour distance metrics provided in Fig. 2. The mountain pine beetle exhibited high densities of infestation 46 km from the edge of the research area in 2004 and 2005. This 'belt' progressed approximately 25 km to the north-east in 2006, as the maximum density of infestations occurred further from the south-western edge of the research area at 71 km.

DISCUSSION

Our findings of a north-east to south-west belt of a high density of infestations of mountain pine beetles within a habitat where they had not previously been detected is consistent with spread by aeolian dispersal above the insect boundary layer from sources west of the Rocky Mountains (Bartell, 2008). Such long-distance transport is not unknown in the mountain pine beetle system (Jackson *et al.*, 2008), occurring in more southern and eastern portions of its range (e.g. in Washington, Furniss & Furniss, 1972; and from Alberta to the Cypress Hills of Saskatchewan, Cerezke, 1981). The present occurrence is the first successful invasion of new habitat across the historical geoclimatic barrier of the Rocky Mountains in northern Canada (Kurz *et al.*, 2008; Robertson *et al.*, 2009; Safranyik *et al.*, 2010). Our study offers one of the first insights of the spatial extent of aeolian dispersal events by studying establishment at a landscape scale in the absence of populations with landscape signatures of dead trees confounded by localized endemic-incipient irruptions. The wave signature is consistent with deposition from weather fronts (Drake & Farrow, 1988).

Aeolian dispersal is not the norm for mountain pine beetles, as their pheromone-mediated host-seeking behaviour predisposes them to diffuse dispersal (Hengeveld, 1988) within the insect boundary layer. Upon emergence from a host tree, mountain pine beetles, although phototactic, will generally move within the stand a maximum of approximately 250 m from their natal host towards attractive stimuli such as an adjacent pine (Safranyik *et al.*, 1992). This movement may occur against wind speeds to a maximum of approximately 11 km h^{-1} if the stimulus is upwind of its natal host (Schmid *et al.*, 1992). However, mountain pine beetles, like some *Ips* species, generally require a short period of flight before engaging in host-seeking behaviour (Gray *et al.*, 1972; Jactel, 1991; Duelli *et al.*, 1997). Once attracted by host volatiles, the insect uses a combination of visual and gustatory cues for final host selection (Pureswaran & Borden, 2003). At optimum attack densities, the beetles release verbenone (Hunt & Borden, 1990), which, in combination with other semiochemicals, repels conspecifics and redirects them towards neighbouring trees, producing a 'spillover' attack. At late outbreak stages, a depletion of suitable hosts over a large area may predispose insects to move further from natal hosts, increasing above-canopy flight (Salle & Raffa, 2007). Above the forest canopy, insects may become entrained in advective currents above the insect boundary layer, facilitating long-distance transport occasionally observed among other scolytids such as *Dryocetes autographus* Ratz. (Nilssen, 1984) and *Ips typographus* L. (Byers, 2000).

Following 2004, the highest intensity of infestations in the wave front moved a further 25 km to the north-east from 2005 to 2006, even though the leading edge moved approximately 80 km (Fig. 2). This form of spread is not unlike that exhibited by other guilds of forest insects with strong dispersal capabilities, such as defoliators like larch budmoth (*Zeiraphera diniana* Gn.) that can move upwards of 200 km per year (Bjørnstad *et al.*, 2002; Johnson *et al.*, 2004). The spatial lag between the most intense central area and the margin of the invasion front in this system is typical of a stratified process (i.e. a combination of long-distance wind spread and local

Table 2 Coefficients (with SE) for equations of the spatial point process models reflecting spatially explicit densities of spots of trees killed by the mountain pine beetle (*Dendroctonus ponderosae*) as a function of various covariates reflecting different modes of dispersal for the years 2004, 2005 and 2006 in the Peace River region of British Columbia. A Wald test can be constructed by dividing the coefficient estimate by the standard error where available*; all estimates provided are statistically significant ($Z > 1.96, P < 0.0001$). Response variable for each year, λ , the number of patches of beetle-killed trees m^{-2} , is estimated on the log scale; an example equation is provided in the text.

Year	Intercept	Distance†	Distance to nearest				Rivers	Beetle locations _{s(t-1)}	AIC
			Distance ²	Roads	Mills	Rivers			
2004	-1.29 × 10 ¹ (2.02 × 10 ⁻²)	-3.12 × 10 ⁻⁵ (3.72 × 10 ⁻⁷)						324,186	
	-2.0 × 10 ¹	2.82 × 10 ⁻⁴	-3.05 × 10 ⁻⁹					315,602	
	-*	-	-						
	-1.51 × 10 ¹ (1.31 × 10 ⁻²)			1.42 × 10 ⁻⁵ (4.844 × 10 ⁻⁷)				333,332	
	-1.44 × 10 ¹ (2.06 × 10 ⁻²)				-6.01 × 10 ⁻⁶ (2.64 × 10 ⁻⁷)			333,532	
	1.43 × 10 ¹ (1.52 × 10 ⁻²)			6.91 × 10 ⁻⁵ (1.02 × 10 ⁻⁶)	-2.83 × 10 ⁻⁵ (4.42 × 10 ⁻⁷)		-7.92 × 10 ⁻⁵ (2.00 × 10 ⁻⁶)	332,196	
	-1.39 × 10 ¹ (1.96 × 10 ⁻²)			1.45 × 10 ⁻⁵ (4.62 × 10 ⁻⁷)				328,444	
	-1.45 × 10 ¹ (1.72 × 10 ⁻²)				-5.37 × 10 ⁻⁶ (2.49 × 10 ⁻⁷)		-8.07 × 10 ⁻⁵ (1.99 × 10 ⁻⁶)	331,337	
	-1.39 × 10 ¹ (2.24 × 10 ⁻²)			7.96 × 10 ⁻⁵ (1.11 × 10 ⁻⁶)	-3.19 × 10 ⁻⁵ (4.73 × 10 ⁻⁷)		-7.80 × 10 ⁻⁵ (2.00 × 10 ⁻⁶)	331,703	
	-1.31 × 10 ¹ (2.28 × 10 ⁻²)						-9.34 × 10 ⁻⁵ (1.96 × 10 ⁻⁶)	325,575	
2005	-1.27 × 10 ¹ (1.88 × 10 ⁻²)	-3.15 × 10 ⁻⁵ (3.46 × 10 ⁻⁷)						373,781	
	-1.93 × 10 ¹	2.56 × 10 ⁻⁴	-2.79 × 10 ⁻⁹					364,567	
	-	-	-						
	-1.50 × 10 ¹ (1.23 × 10 ⁻²)			1.83 × 10 ⁻⁵ (4.25 × 10 ⁻⁷)				383,898	
	-1.48 × 10 ¹ (1.96 × 10 ⁻²)				6.54 × 10 ⁻⁷ (2.2 × 10 ⁻⁷)			385,471	
	-1.44 × 10 ¹ (1.43 × 10 ⁻²)			4.89 × 10 ⁻⁵ (8.45 × 10 ⁻⁷)	-1.60 × 10 ⁻⁵ (3.69 × 10 ⁻⁷)		-3.89 × 10 ⁻⁵ (1.62 × 10 ⁻⁶)	384,841	
	-1.43 × 10 ¹ (1.93 × 10 ⁻²)			1.82 × 10 ⁻⁵ (4.13 × 10 ⁻⁷)				381,863	
	-1.47 × 10 ¹ (1.65 × 10 ⁻²)				6.16 × 10 ⁻⁷ (2.14 × 10 ⁻⁷)		-4.08 × 10 ⁻⁵ (1.61 × 10 ⁻⁵)	383,182	
	-1.45 × 10 ¹ (2.21 × 10 ⁻²)			5.31 × 10 ⁻⁵ (8.76 × 10 ⁻⁷)	-1.78 × 10 ⁻⁵ (3.79 × 10 ⁻⁷)		-3.89 × 10 ⁻⁵ (1.62 × 10 ⁻⁶)	384,835	
	-1.38 × 10 ¹ (2.26 × 10 ⁻²)						-4.95 × 10 ⁻⁵ (1.59 × 10 ⁻⁶)	380,761	
-1.62 × 10 ¹ (2.00 × 10 ⁻²)							2.45 × 10 ⁶ (2.11 × 10 ⁴)		
-1.48 × 10 ¹	-1.55 × 10 ⁻⁵						1.78 × 10 ⁶		
-	-						-		
-2.05 × 10 ¹	2.54 × 10 ⁻⁴	-2.64 × 10 ⁻⁹					1.30 × 10 ⁶		
-	-	-					-		

Table 2 Continued

Year	Intercept	Distance†	Distance to nearest					Beetle locations _(t-1)	AIC
			Distance ²	Roads	Mills	Rivers			
2006	-1.30×10^1 (1.15×10^{-2})	-8.20×10^{-6} (1.45×10^{-7})						1,024,656	
	-1.67×10^1	1.03×10^{-4}	-7.23×10^{-10}					1,009,046	
	—	—	—						
	-1.35×10^{-1} (6.78×10^{-3})			-1.03×10^{-5} (3.80×10^{-7})				1,024,245	
	-1.31×10^1 (1.12×10^{-2})				-8.00×10^{-6} (1.49×10^{-7})			1,024,913	
	-1.36×10^1 (8.66×10^{-3})						-8.79×10^{-6} (8.59×10^{-7})	1,027,961	
	-1.30×10^1 (1.15×10^{-2})			7.29×10^{-6} (5.32×10^{-7})	-9.80×10^{-6} (2.00×10^{-7})			1,024,729	
	-1.35×10^1 (9.29×10^{-3})			-9.98×10^{-6} (3.80×10^{-7})				1,027,197	
	-1.30×10^{-1} (1.26×10^{-2})						-6.10×10^{-6} (8.71×10^{-7})	1,024,851	
	-1.30×10^1 (1.32×10^{-2})						-6.81×10^{-6} (8.59×10^{-7})	1,024,621	
	-1.41×10^1 (9.35×10^{-3})			8.25×10^{-6} (5.39×10^{-7})	-9.92×10^{-6} (2.00×10^{-7})			1,023,605	
	-1.41×10^1	8.22×10^{-8}						1,023,607	
	—	—							
	-2.05×10^1	1.45×10^{-4}	-8.07×10^{-10}					1,004,025	
	—	—	—						

*Standard errors are not provided in instances where the variance-covariance matrix contains an exceedingly small number whose calculation surpasses computational capability.

†Distance from line of reference (parallel to Rocky Mountains; see Materials and Methods and Fig. 3).

AIC, Akaike information criterion.

dispersal) as populations build and then surge when a threshold is surpassed (Hengeveld, 1988). Recent work by Cudmore *et al.* (2010) has demonstrated higher reproductive capacity in novel host trees not historically exposed to beetle pressure, which would speed such processes. In addition, advective transport events facilitated by weather may have been less frequent in 2004–2005 after the initial invasion, and increased harvesting activity could have slowed the eastward progression of the zone of highest intensity in those years. We view the latter reason as unlikely, however, as harvesting was focused on the leading, eastern edge.

Our study found no evidence that the spread of the mountain pine beetle into the Peace River region was primarily influenced by anthropogenic activities such as road transport or mill storage of potentially infested logs within the region. Although invasive species can be readily transported along road corridors (Christen & Matlack, 2009) and bark beetles such as *Tomicus piniperda* (L.) have been noted to spread from infested material in mill yards surrounding forests (Poland *et al.*, 2000), our findings are not unexpected. Schaupp *et al.* (1993) found that emergence of mountain pine beetles from infested logs in transport is generally quite small during periods of peak emergence (0.03 insects m⁻² bark surface in July and August). This is considerably lower than the optimal attack density of the mountain pine beetle on standing living trees, of 62 insects m⁻² bark surface (Raffa & Berryman, 1983). In addition, the use of various storage methods, such as increasing sun exposure by avoiding piling during storage and covering logs in plastic to increase the air temperatures to a level that causes high mortality in broods infesting the logs, can minimize emergence from stored logs (Negrón *et al.*, 2001) (although we do not know if such methods were utilized). It appears as though mitigation strategies used by forestry companies in this situation, namely prioritization of processing of infested logs at the mill locations, effectively minimized the spread of the insect through emergence from host materials.

Documenting range expansion and long-distance dispersal events are particularly important for allowing the estimation of rate of spread and species' modes of dispersal (Brouwers & Newton, 2009). This quantification can be especially critical in ecosystems where patterns of land use are altered from historical norms (Meentemeyer *et al.*, 2008) and climate change adds further perturbations (Raffa *et al.*, 2008; Bentz *et al.*, 2010; Sambaraju *et al.*, 2011). In this system, while the mountain pine beetle is a natural disturbance agent, decades of fire suppression inadvertently created vast tracts of pine forest in age classes of the highest susceptibility to the insect (Taylor *et al.*, 2006). A 'perfect storm' was created when this landscape intersected with a trend of increasing winter temperatures that permitted increased overwinter survival of larval life stages (Taylor *et al.*, 2006; Safranyik *et al.*, 2010). Given the apparent elevated reproductive rates in evolutionarily naïve hosts (Cudmore *et al.*, 2010), coupled with the propensity for punctuated aeolian dispersal events as shown in this study, further rapid eastward expansion by the mountain pine beetle remains likely as long as susceptible host trees are available.

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BIOSKETCHES

Honey-Marie de la Giroday is pleased to share her MSc thesis work from the Natural Resources and Environmental Science program at the University of Northern British Columbia with you. Like the beetles, she has breached the continental divide, and is now at the University of Alberta.

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