

**Spatial Associations Between Infestations of Mountain Pine Beetle and Landscape  
Features in the Peace River Region of British Columbia**

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## ABSTRACT

An immense outbreak of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, currently covers a cumulative area of 14.5 million hectares of mature pine forests across the provinces of British Columbia and Alberta, Canada. In 2004, the first outbreaking populations of mountain pine beetle were observed in northeastern British Columbia, an area not considered part of the insect's native range. My thesis examines how landscape features and their orientation influence establishment patterns of the insect. Mountain pine beetle spread between 2004 and 2006 in patterns similar to a propagating wave, likely due to long-distance dispersal into the region. Large glacially-eroded valleys, canyons, deeply incised streams, local and midslope ridges or small hills in valleys and plains, and open slopes were often positively associated with infestations, providing evidence that the interaction of meso-scale convective currents and topography can mediate patterns of establishment. The orientation of landscape features also influenced establishment, as southwest-facing areas and linear features aligned in northeast-southwest directions were associated with increased densities of infestations in 2006. Management activities were typically associated with a decline in the density of mountain pine beetle infestations in the following year, indicating that such activities were effective in preventing short-distance dispersal of the insect. I found no evidence that anthropogenic activities such as transport and storage of infested material increased establishment of mountain pine beetle across the research area. These results may be used to prioritize preemptive treatments in mountainous regions in the absence of long-distance inputs of mountain pine beetle into expanding ranges.

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$7.82+5000 \times -5.03E-05 + -0.0296 + 1500 \times -3.85E-03 + 1.55$ ) or  $3.4E-06$  infestations per square meter (i.e., 0.034 infestations per hectare or one patch of tree-killing beetles every 30ha). 83

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## 1: INTRODUCTION

Range expansion of native species creates important challenges to the management of organisms and ecosystems. For example, the establishment of parks and protected areas is based on the assumption of temporal continuity of those regions as havens for rare or sensitive ecosystems and habitats of sensitive species and communities (Lemieux and Scott 2005). However, human alteration of climate has and will influence the distributions of animal and plant species. For example, the silver-spotted skipper butterfly (*Hesperia comma* L. [Lepidoptera: HesperIIDae]), an insect native to southern England, is increasingly expanding into new habitat types due to climate change (Thomas et al. 2001). Particularly interesting is the release of species from the northern confines of their distributions, such as the case of the sagem skipper (*Atalopedes campestris* Boisduval [Lepidoptera: HesperIIDae]) in northern California expanding into new habitats previously considered inhospitable (Crozier and Dwyer 2006).

The recent range expansion of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins [Coleoptera: Scolytidae]) into regions thought to be beyond its historical distribution (Carroll et al. 2004; Robertson et al. 2009) is a striking example of the potential impact of anthropogenic changes on ecosystem dynamics (Raffa et al. 2008). Although old mountain pine beetle strip attacks have been observed in northeastern British Columbia (i.e., the Peace River region; Allan Carroll pers. comm.<sup>1</sup>), the region was thought to have a climate too cold for the successful univoltine reproduction of mountain pine beetle. As a result, small populations dispersing into the region prior to a change in climatic regime of the region would not have established successfully due to high levels of mortality during the winter. However, in 2004, the first incipient-epidemic infestations of mountain pine beetle were

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found in the Peace River region (B. Staffan Lindgren, pers. comm.<sup>2</sup>). Since then, mountain pine beetle has spread throughout the region, with large outbreaks coalescing across the landscape. The forests of the Peace River region contain lodgepole pine (*Pinus contorta* var. *latifolia*), a primary host species of *D. ponderosae*, and jack pine (*P. banksiana*), a “novel host” in which the mountain pine beetle has been demonstrated in laboratory experiments to successfully reproduce (Safranyik and Linton 1983; Cerezke 1995). Of critical concern is the potential ability of mountain pine beetle to use jack pine as a conduit for movement further east (Nealis and Peter 2008).

The life cycle of mountain pine beetle is completed largely in a host tree of the genus *Pinus*, such as *P. monticola* and *P. ponderosae* (Amman 1982). Upon landing on a suitable host, a female will bore through the bark into the phloem and begin constructing a gallery by tunneling upward (Reid 1962). Attacks generally occur at mid-bole, although this can vary with attack density. The male will enter the gallery and mate with the female, who then lays eggs in niches along the gallery (Wood 1963). The eggs develop through four larval instars from the fall through the winter and into spring, although development is arrested during the coldest periods of the winter. Mountain pine beetle populations can experience large mortality in the early winter, late fall, or early spring due to unseasonal cold temperatures (e.g., -25 to 30°C in October or April) or prolonged cold winter temperatures of -40 °C or colder (Wygant 1940). However, the insect is more cold-tolerant during winter due to progressive removal of water from their tissues, resulting in high levels of glycerol, between late fall and the middle of winter (Safranyik and Linton 1998; Bentz and Mullins 1999). In the spring, development continues through the final instars until mountain pine beetle pupates and develops into an adult. In June, July or August (depending on the latitude,

elevation, and general climate in the region) new adults will emerge from the gallery by boring through the bark (Safranyik and Carroll 2006).

Upon emergence, mountain pine beetles take flight and seek out a new host tree to attack. A combination of visual and olfactory cues is used during host-seeking by mountain pine beetle. Typically, the insect is attracted to pheromones produced by conspecifics and host volatiles indicating host vigour (Hughes 1973). Attack *en masse*, with high numbers of conspecifics in concert with vectored blue-stain fungi, may be effective in overwhelming tree defenses. Attack densities of 62 attacks/m<sup>2</sup> typically characterize maximum per capita reproduction, with higher mortality due to tree defenses and interspecific competition above and below these densities, respectively (Raffa and Berryman 1983).

A majority of mountain pine beetles dispersing from a natal host travel short distances, staying within the stand (Safranyik et al. 1992). While moving short distances, under the canopy, they can actively fly against the wind at velocities to a maximum of 7.5 km/h if an attractive pheromone stimulus is located upwind (Gray et al. 1972). However, in the absence of attractants upwind, the insect will often fly downwind. The insect is also phototactic just after emergence, allowing for an upward trajectory (Reid 1962). Above the canopy, it may become incorporated into strong wind currents, where its dispersal can be determined largely by wind velocity and direction (Lewis 1966; Lewis and Stephenson 1966; Lewis 1970; Ashmole et al. 1983; Jackson et al. 2008). This “passive” insect dispersal will most likely result in dispersal patterns that differ from those of “active” dispersal due to the dominance of host seeking behavior in the latter. During “active” dispersal, biological mechanisms such as pheromone response, host selection, and micro-site conditions influence patterns of dispersal. Conversely, patterns of establishment resulting from “passive”

dispersal will be influenced by the interaction between weather processes, landscape patterns and particles (i.e., mountain pine beetles) (Robertson et al. 2009), including down-drafts in zones of convergence, changes in wind direction, and/or deposition or impaction of particles (Lewis 1966; Lewis and Stephenson 1966; Lewis 1970; Lewis and Dibley 1970; Spalding 1979; Pedgley 1982; Pasek 1988; Jasperson et al. 1990; Jackson et al. 2008). Examining the role of topography in the spread and establishment of wind-transported insects can provide information about the impact of mountainous terrain on long-distance dispersal (Fig. 1.1).

The founding populations of mountain pine beetle in the Peace River region are thought to be from regions southwest to the northern Rocky Mountains (Bartell 2008). Beginning in the mid-1990s, a large outbreak of *D. ponderosae* established and continued to spread at epidemic levels until the present time in the central and southern interior of British Columbia (Aukema et al. 2006). With a cumulative area of 14.5 million ha of forest affected (British Columbia Ministry of Forests and Range 2009), the insect has exerted landscape-level impacts on *P. contorta*, a tree that comprises ~47% of the harvestable timber supply in British Columbia (Westfall and Ebata 2008). Prior to the present outbreak, mountain pine beetle in the central interior of British Columbia predominantly existed at endemic levels, usually taking older, less vigorous trees, and occasionally flaring up into larger outbreaks such as those in the 1970s and early 1980s (Safranyik and Carroll 2006; Campbell et al. 2007; Aukema et al. 2008). However, fire suppression by humans post-World Wars I and II permitted an increase in the proportion of large tracts of even-aged stands of suitable hosts on the landscape (Carroll et al. 2004). Warmer summers and winters have also allowed mountain pine to successfully reproduce at higher rates with larger populations facilitating successful mass-attack on vigorous, large diameter trees (Carroll et al. 2004). Numerous

factors influencing population dynamics could have contributed to the increased long-distance dispersal as well. For example, large populations of insects attacking trees will eventually produce pheromones that repel additional insects (Hunt and Borden 1990), potentially causing increased levels of dispersal through indirect competition for available resources. Depletion of available hosts adjacent to a natal tree will also facilitate increased time aloft for mountain pine beetle searching for a host, possibly providing increased opportunity for the insect to become incorporated into meso-scale convective currents. These pheromones, coupled with meso-scale atmospheric transport, may have caused mountain pine beetle to increasingly disperse long-distances over the Rocky Mountains.

Patterns of infestation resulting from long-distance dispersal of mountain pine beetle have not been studied in the Peace River region of British Columbia. Due to the speed at which mountain pine beetle spread into this region, it has been speculated that mountain pine beetle was dispersed into this region primarily by meso-scale atmospheric currents rather than “active” local dispersal. This thesis examines the spatial patterns of the invasion event in the Peace River region to gain inference on the primary mechanism(s) of establishment and the influence of various landscape patterns on occurrences of infestations. The findings of this research will contribute an understanding of meso-scale atmospheric dispersal of insects within mountainous terrain, the potential distances that mountain pine beetles can travel, and may aid forest managers in making decisions for control and prevention tactics as the beetle potentially continues to spread in the region. In Chapter 2, the patterns of spread in the Peace River region of British Columbia are examined to gain inference on primary mechanisms of spread for mountain pine beetles into the Peace River region. These mechanisms include atmospheric transport, localized stand-level transport, and human-



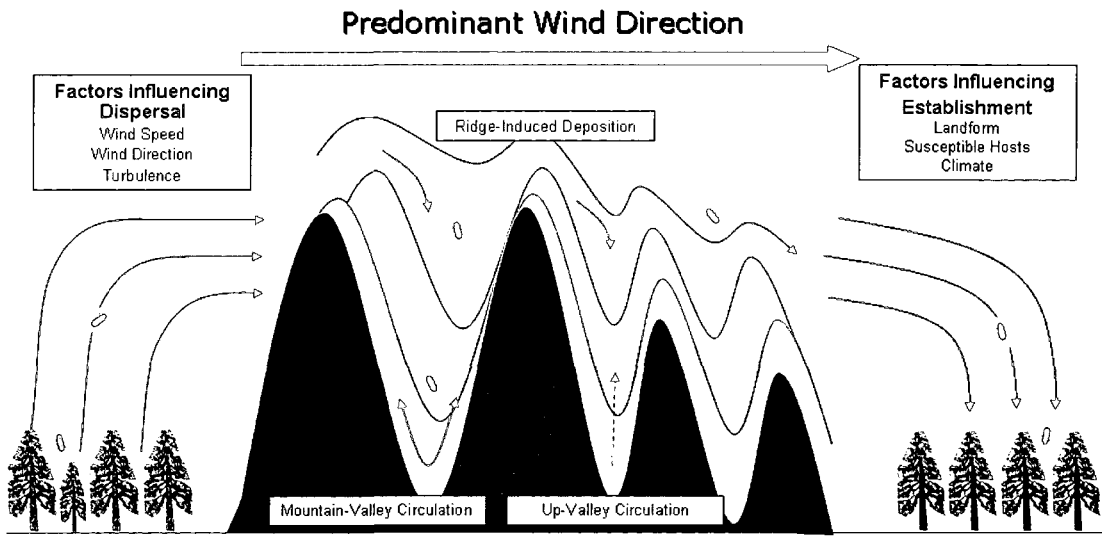
assisted transport along roadways. Annual inventory data for the first three years of infestation are compared to various dispersal patterns using spatial point process modeling. Using similar techniques, Chapter 3 examines the influence of topography and orientation of landforms on occurrence of mountain pine beetle infestations using a landscape feature classification index and annual inventory data for 2004 to 2006. Chapter 4 provides a synthesis of findings and recommendations to assist with mitigation of mountain pine beetle spread.

To facilitate publication of the following work in peer-reviewed journals, this thesis is written in manuscript format. As a result, there may be redundancy between chapters to allow each chapter be a stand-alone manuscript. These chapters were produced in cooperation with a number of authors hence sections will be presented in plural voice. I anticipate submitting Chapter 2 to *Biological Invasions* with Allan Carroll and Brian Aukema as coauthors. I anticipate submitting Chapter 3 to the *Journal of Animal Ecology* with Allan Carroll, Staffan Lindgren, and Brian Aukema as coauthors.

## **1.1: Figure Captions**

Figure 1.1 A schematic diagram of elucidating processes that could influence the long-distance dispersal of mountain pine beetle upon emergence, while dispersing long-distances and during settlement. Wind and topographic interactions are simplified for mountainous terrain to explore wind patterns that could impact deposition of mountain pine beetle while aloft.

Fig. 1.1



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**2: FIRST STEPS OF A RANGE-EXPANSION EVENT FACILITATED BY  
CLIMATE CHANGE: BREACH OF THE ROCKY MOUNTAIN  
GEOCLIMATIC BARRIER BY MOUNTAIN PINE BEETLE IN CENTRAL  
BRITISH COLUMBIA**

**2.1: Abstract**

In 2004, mortality of pine trees due to colonization by mountain pine beetle was observed northeast of the Northern Rocky Mountains in British Columbia. The insect was thought to have originally arrived in 2002. This was the first recorded incident of this insect in the Peace River region. The mountain pine beetle is native to central and southern British Columbia. Its speed and rate of spread into and within the Peace River region suggests that long-distance, above-canopy dispersal was the predominant dispersal mechanism rather than stand-level flight. We explore potential dominant mechanism(s) of dispersal using spatial point process modeling. Specifically, we examine observed patterns of infestation relative to covariates reflecting various hypotheses including meso-scale atmospheric dispersal above the insect boundary layer (an altitude below which insects would determine their own speed and direction of movement), anthropogenic transport of infested material, and the spread of insect populations into adjacent stands via corridors of suitable habitat. We select the most parsimonious models for each of the initial three years of invasion using information criteria statistics. We found that landscape patterns of trees killed by mountain pine beetle predominantly suggested a wave front of insects deposited parallel to the Rocky Mountains following meso-scale atmospheric dispersal above the “insect boundary layer”. The area of highest intensity of infestations advanced up to 25 km to the northeast in a single year.



## 2.2: Introduction

Examining the spatiotemporal patterns of invasive organisms can provide insight into organisms' rates and typical patterns of spread, which in turn can suggest mechanisms driving their establishment and persistence (Peterson and Vieglais 2001). Climate plays a central role in many invasion events, such as by impacting host distribution (Iverson and Prasad 1998), creating directional gradients in critical temperature thresholds that can restrict reproduction, or introducing organisms on strong weather fronts or through major disturbances such as hurricanes (Tackenberg 2003). Humans can play a major role in introductions of organisms as well, albeit inadvertently (Brockerhoff et al. 2006; Skarpaas and Økland 2009). Investigation of resulting patterns of spread allows researchers to determine which processes contribute to establishment of an organism in a region 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 and Cole 1983; Aukema et al. 2008). A phloeophagus insect with a short-lived adult phase relative to other insects, mountain pine beetles survive outside of host trees for only a few days. Numerous species of conifers in the *Pinus* genus are susceptible to colonization by mountain pine beetle, including, but not limited to, lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), and ponderosa pine (*P. ponderosa* Dougl.). Adult female beetles bore through the bark into the phloem, anywhere on the bole between the root-collar and crown, depending on the size of the tree. The tree responds with copious amounts of resin that is both toxic to the beetle and physically impedes access to the cambium tissues. However, at epidemic population phases, additional conspecifics may be

attracted to the host by host volatiles as well as aggregation pheromones released by pioneering mountain pine beetles (Renwick and Vite 1970; Libbey et al. 1985). Moreover, mountain pine beetles vector fungi that serve to impede host defenses (Safranyik et al. 1975). If access is successfully gained, females mate with males under the bark and lay eggs in small niches along ovipositional galleries. Once hatched, mountain pine beetles progress through four larval instars from the early fall into the winter. With onset of winter, development slows, usually by the third or fourth instar (Reid 1962). In the spring, after amassing enough heat units, the larvae pupate prior to developing into adults in early summer. In July or early August, new adults take flight *en masse* after a period of dry and warm weather (Reid 1962; Bright 1976).

Exposure to cold winter temperatures (Reid 1963; Reid and Gates 1970) and limited mosaics of suitable hosts in space and time (Shore and Safranyik 1992) generally limits mountain pine beetle to endemic levels. However, in the late 1990s, a large outbreak erupted in the central interior of British Columbia, Canada (Aukema et al. 2006), currently encompassing a total area of 14.5 million hectares of pine forests in that province (British Columbia Ministry of Forests and Range 2009). The outbreak has been exacerbated by anthropogenic activities such as fire suppression as well as increasingly warm summer and winter temperatures reflective of a changing climate (Safranyik and Carroll 2006; Kurz et al. 2008; Raffa et al. 2008).

Outbreking populations of the insect breached the historic geoclimatic barrier of the northern Rocky Mountains in approximately 2002 as entomologists discovered that the mountain pine beetle had become established in the Peace River region of British Columbia, an area not considered part of the insect's historical distribution (Robertson et al. 2009). This

invasion event immediately commanded critical attention due to the proximity of a potentially suitable new host, jack pine (*Pinus banksiana* Lamb.) in northeastern Alberta (Safranyik and Linton 1983; Cerezke 1995) which could provide a potential conduit for mountain pine beetle to spread toward eastern North America (Wood 2006; Nealis and Peter 2008). In many ways, the mountain pine beetle demonstrates ideal properties of an invasive scolytid (Holway and Suarez 1999) due to its relatively high fecundity in northern areas (Cudmore 2009), 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 and Linton 1983; Cerezke 1995; Huber et al. 2009).

Studying the positioning of tree-killing infestations of forest insects on the landscape can elucidate the insects’ dominant dispersal mechanism(s). 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), while long-distance movements can result in wave-like dispersal patterns dependent on the coordination of dispersing individuals (Suarez et al. 2001). Larch budmoth, *Zeiraphera diniana* Gn., may exhibit wave-propagation patterns, where large numbers of mated females are blown long-distances (Baltensweiler and Fischlin 1979; Bjørnstad et al. 2002; Johnson et al. 2006). Diffuse configurations, occasionally characterizing mountain pine beetle infestations, are indicative of short-distance dispersal as insects radiate from natal hosts into adjacent stands (Gamarra and He 2008). Although mountain pine beetles primarily disperse within a stand (Safranyik et al. 1992) and are generally not considered strong dispersers at landscape scales (Furniss and Carolin 1977; Raffa and Berryman 1979; Peltonen et al. 2002), at outbreak levels, the insect may be transported great distances via meso-scale atmospheric currents (i.e., aeolian dispersal; see

Chapter 3; Furniss and Furniss 1972; Safranyik et al. 1992; Jackson et al. 2008). Such long-distance transport can result in a variety of patterns of establishment including leptokurtic (i.e., stratified) patterns (Tobin and Blackburn 2008; Robertson et al. 2009) and/or wave-like patterns of distribution across the landscape (Bjørnstad et al. 2002).

Despite the importance of wind currents and insect flight to dispersal at either small or large scales, human activities may also facilitate the spread of invasives, often unintentionally (Brockerhoff et al. 2006). Notable examples from 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. 2006). 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. Moreover, unregulated transportation of infested logs for firewood

during periods of emergence could allow mountain pine beetle to spread along transportation corridors.

The initial movement of mountain pine beetle into the Peace River region was monitored closely between 2004 and 2006. As a result of this vigilance, the initial years of invasion are well documented. Using annual inventory maps of insect locations, the present study aims to examine patterns of establishment within the Peace River region for evidence suggestive of invasion mechanisms. We focus on two broad hypotheses. First, we examine evidence of transport within the “insect boundary layer”. Although the use of the term “boundary layer” is typically restricted to the field of fluid dynamics and represents a viscous layer between two mediums, the term “insect boundary layer” is defined as the altitude below which an insect will determine its own spread and direction of movement (Taylor 1974). Above this layer, the insect’s movement will be influenced largely by wind speed and direction. Mechanisms of dispersal occurring primarily within the insect boundary layer include flights 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. Second, we examine evidence for transport above the insect boundary layer, which we characterize as the spread of mountain pine beetles at altitudes in which they are blown passively, otherwise known as 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 gradient, suggesting progressive movement of mountain pine beetle populations from sources parallel to the western edge of the Rocky Mountains in BC, or a linear zone containing a high intensity of

infestations, suggesting long-distance aeolian dispersal and “rainout” as the primary mechanisms of invasion respectively.

## **2.3: Material and Methods**

### **2.3.1: *Study Area and Spatial Datasets***

The northern and southern extent of the research area, delineated between 54° and 56.5°, 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. 2.1). 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. During the initial spread of 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 mountain pine beetle (referred to hereafter as infestations), initially collected to facilitate management planning, from these forest licensees. The infestations inventoried in a single year were considered to have been attacked in the previous year as they had dead trees with chlorotic or red foliage and 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 insect must kill their hosts to reproduce, fading foliage can be used to identify trees attacked one year ago (Safranyik et al. 1974) and serve as a useful proxy for insect abundance (Wulder et al. 2006; Aukema et al. 2008; Nelson and Boots 2008). Surveys were conducted in 2004, 2005, and 2006 from approximately May to September. 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.

In order to consider the potential influence of anthropogenic factors or the effect of rivers on spread of mountain pine beetle, three datasets representing mill locations, primary and secondary roads, and rivers were secured from Natural Resources Canada and Global Forest Watch (2009). From these vector (i.e., point and line) datasets, the Euclidian 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 x 73 metre pixel size (i.e., just over one-half hectare in size).

### ***2.3.2: Statistical Analysis***

Spatial point process regression models were fit to each annual inventory dataset with covariates reflective of different hypothesized mechanisms of dispersal. This class of models evaluates the intensity of event occurrences,  $\lambda$  (infestations per  $m^2$ ), relative to spatial location (i.e.  $x$  and/or  $y$  positions) as well as other covariates (Baddeley and Turner 2008). Specifically, we tested whether there was evidence for anthropogenic activities contributing to spread via distances to roads and mills, evidence for natural low-elevation corridors via associations with rivers, and evidence for aeolian dispersal via diffusion processes (linear distance gradient from the Rocky Mountains and distances from point-source infestations in the previous year), and/or wave propagation (polynomial distance terms) (see Appendix A for R code). In our system, due to the uniform directional spread of infestations in a northwest direction (see Results), there was a high degree of correlation between  $x$  and  $y$  data. Evaluating the effects of highly collinear variables in regression models can create

computational challenges (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  $138^\circ$  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 ( $48^\circ$ ; see Chapter 3). A raster dataset was then produced with each pixel representing the distance from the reference line. Models were compared using Akaike's information criterion (AIC), with the lowest AIC values identifying the models of best fit (Akaike 1973). All data were handled in ArcView v.9.2. Analyses were completed using R v.2.8.1 and the spatstat package v.1.14-9 (Ihaka and Gentleman 1996; R Development Core Team 2009).

## **2.4: Results**

The occurrence of infestations of 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 recorded infestations (Fig. 2.2). The average nearest neighbor distance between infestations was greatest in 2006 (0.24 km) while in 2005 it was 0.23 km. Infestations in 2004 had the closest average nearest neighbors at 0.18 km. Mean area of patches of red trees killed by mountain pine beetle was quite small in 2004, 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 2,440 ha, versus 6 and 133 ha in 2004 and 2005 respectively. By 2006, the total area of trees killed by mountain pine beetle had expanded to 35,084 ha (Fig. 2.2).



The topography in the region ranges from the sharp relief of the Rocky Mountains at the western edge, undulate topography of the Foothills in the centre, and plateaus deeply incised by various rivers in the east (Fig. 2.1). 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 industries in the region include oil and gas extraction, mining and forestry such harvesting of soft wood conifers for lumber. There are two mills in the Peace River region that process lodgepole pine, both in Chetwynd, British Columbia.

The spread pattern of mountain pine beetles into the region closely resembled that of a propagating wave in all three years (Table 2.1). Areas closest and furthest from the initiation source had less infestation than those in the middle of the research area (Fig. 2.2). These “wave-propagation” models had the lowest AIC values, fitting the data better than models reflecting alternate modes or mechanisms of dispersal, including anthropogenic movement of infested material and simple within-boundary layer dispersal between adjacent stands. Anthropogenic movement of infested materials did not appear to impact the spread of mountain pine beetle.

By solving the best-fitting spatial regression equations (Table 2.1) for their maximums, we calculated the locations of greatest infestation densities in the study area (Table 2.2). Mountain pine beetle exhibited highest density of infestation 46 km from the edge of the research area in 2004 and 2005. This ‘belt’ progressed approximately 25 km to

the east in 2006, as the maximum density of infestations occurred further from the western edge of the research area at 71 km (Table 2.2; Fig. 2.3).

## **2.5: Discussion**

Our findings of a northeast-southwest belt of a high density of infestations of mountain pine beetle 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. 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 and 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 historic geoclimatic barrier of the Rocky Mountains in northern Canada (Kurz et al. 2008; Robertson et al. 2009). 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 eruptions. The wave front pattern is consistent with deposition from weather fronts (Drake and Farrow 1988).

Aeolian dispersal is not the norm for mountain pine beetle, as their pheromone-mediated host-seeking behaviour predisposes them to diffuse dispersal (Hengeveld 1988) within the insect boundary layer. Upon emergence, mountain pine beetle, although phototactic, will generally move within the stand a maximum of 250m from natal host towards attractive stimuli such as adjacent pine (Safranyik et al. 1992). This movement may occur against wind speeds to a maximum of approximately 11 km/h if the stimulus is upwind of its natal host (Schmid et al. 1992). However, mountain pine beetle, 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 and Borden 2003). Once mountain pine beetles have commenced attack on the new host, at the optimum attack density, the insects release verbenone produced by microbial symbionts in the gut (Hunt and Borden 1990). Verbenone, in combination with other semiochemicals, repel other mountain pine beetles. The repelled beetles tend to attack suitable hosts in the surrounding area, 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 and Raffa 2007). Above the forest canopy, insects may have become entrained in advective currents above the insect boundary layer, facilitating long-distance transport occasionally observed among other scolytids such as *D. autographus* Ratz. (Nilssen 1984) and *I. typographus* L. (Byers 2000).

Although landscape-scale wave-front patterns are not typically noted in mountain pine beetle outbreaks (Aukema et al. 2006; Gamarra and He 2008), it is a typical pattern characterizing other bark beetles in the genus *Dendroctonus*, such as the southern pine beetle (*Dendroctonus frontalis* Zimm.), as well as defoliators such as larch budmoth (*Zeiraphera diniana* Gn.). Approximately 95% of southern pine beetles disperse within 2.3 km of their natal host (Cronin et al. 2000), causing edges of wave-fronts to be separated by a maximum of 8 km (Schowalter et al. 1981) as insects progressively move into adjacent stands (Turchin and Thoeny 1993). Southern pine beetle is initially attracted to host volatiles, including  $\alpha$ -pinene (Payne 1980). Attacking females release frontalin, attracting conspecifics. Once an optimal attack density is reached, additional attacking individuals are repulsed by *endo-*

brevicommin and verbenone. Southern pine beetles dispersing from their natal hosts are highly repulsed by already infested trees and attracted to suitable hosts on infestation edges (Payne 1980). As a result, at the edges of infestations of the previous year, new infestations will establish, causing a wave-like pattern between years (Coulson et al. 1999). The stereotypic dispersal and attack sequence results in delineated wave-fronts that provide avenues for successful control in some areas of the southern United States.

Infestations of larch budmoth also progress in wave-like patterns that propagate in time and space (Bjørnstad et al. 2002; Johnson et al. 2004). However, the cause of these patterns is unclear, with explanations ranging from habitat permeability (Johnson et al. 2004) to aeolian dispersal to trophic interactions between the moth and its parasitoids (Bjørnstad et al. 2002). Making inference from landscape-level signatures can be challenging because similar signatures can be caused by different processes. The association of landscape features with insect establishment is the focus of Chapt. 3, while predators and parasitoids do not generally play a major role in incipient-epidemic population dynamics of mountain pine beetle (Cole 1981).

Following 2004, the highest intensity of infestations in the wave front moved a further 25 km to the northeast from 2005 to 2006, even though the leading edge moved approximately 80 km (Fig. 2.2). These distances are similar to dispersal exhibited by other guilds of forest insects with strong dispersal capabilities, such as defoliators like larch budmoth that can move upwards of 200 km per year (Bjørnstad et al. 2002). The slow progression of the zone of highest intensity of infestations from 2004 to 2005 suggests that there were fewer weather events facilitating long-distance transport of mountain pine beetle into the region after the initial invasion. Alternatively, the eastward progression of the zone

of highest intensity could reflect harvesting activities changing the densities of patches of dead trees between years, although this is unlikely as harvesting was focused on the leading, eastern edge. Eastward progression of the zone of highest intensity may have also reflected short-distance dispersal after the initial invasion events, or higher reproductive capacity in novel host trees not previously exposed to historic beetle pressure (Cudmore 2009).

Our study found no evidence that the spread of mountain pine beetle into the Peace River region was primarily influenced by anthropogenic activities such as storage of potentially infested logs within the region. Roads, along which infested logs harvested for firewood could have been transported, and mill locations, at which infested logs were stored, did not cause an increased occurrence of mountain pine beetle in the surrounding area. Although invasives can be readily transported along road corridors (Christen and Matlack 2009) and scolytids 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<sup>2</sup> July and August). This is considerably lower than the optimal attack density of mountain pine beetle on standing living trees, 62 insects per m<sup>2</sup> (Raffa and 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.

In conclusion, examination of establishment patterns across years supports the hypothesis that mountain pine beetles moved into the region via long-distance transportation by meso-scale atmospheric transport (Robertson et al. 2009). 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 and Newton 2009). Examining expansion at the northern margins of ranges, as in this case, also provides an accounting of impacts due to climate change. With mountain pine beetle first moving over a geoclimatic barrier and then successfully establishing outbreaking populations in a novel habitat, the patterns of continued spread can provide valuable information for predicting the potential extent of further range expansion.

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Wesche, and Doug Linton.

## **2.7: Figure Captions**

Figure 2.1 Map of the Peace River region of British Columbia including mill locations, primary rivers, and highways.

Figure 2.2 Location of infestations of mountain pine beetle in the Peace River region of British Columbia, Canada in 2004, 2005, and 2006. Dashed line represents the line of initiation which is parallel to the Rocky Mountains and perpendicular to the direction of spread in 2004, the initial year of detection.

Figure 2.3 Location of highest intensity of infestations of mountain pine beetle in 2004 and 2005 (line A) and 2006 (line B) within the research area.



Fig. 2.1

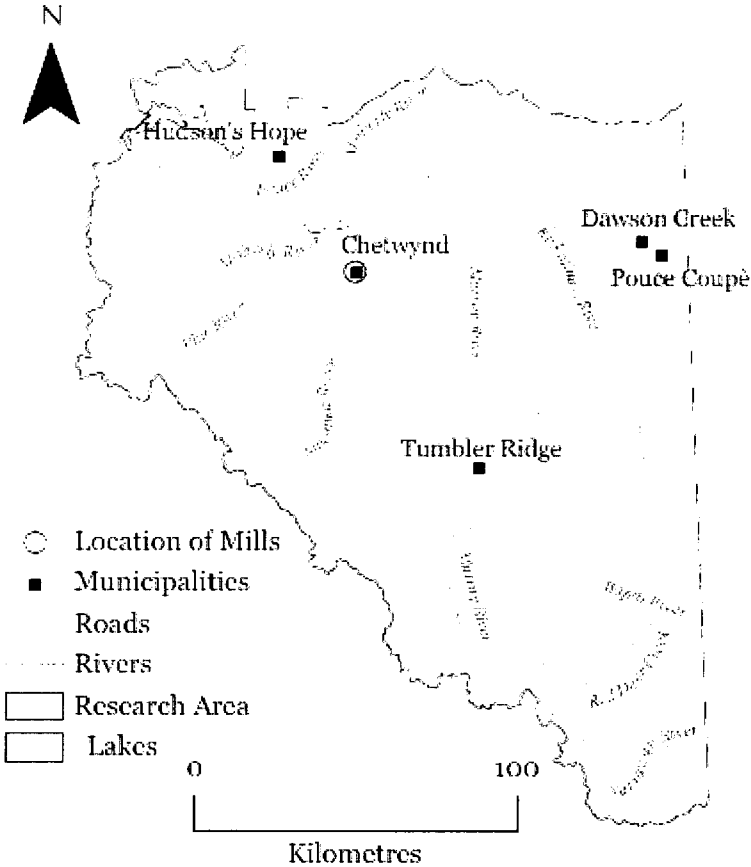


Fig. 2.2

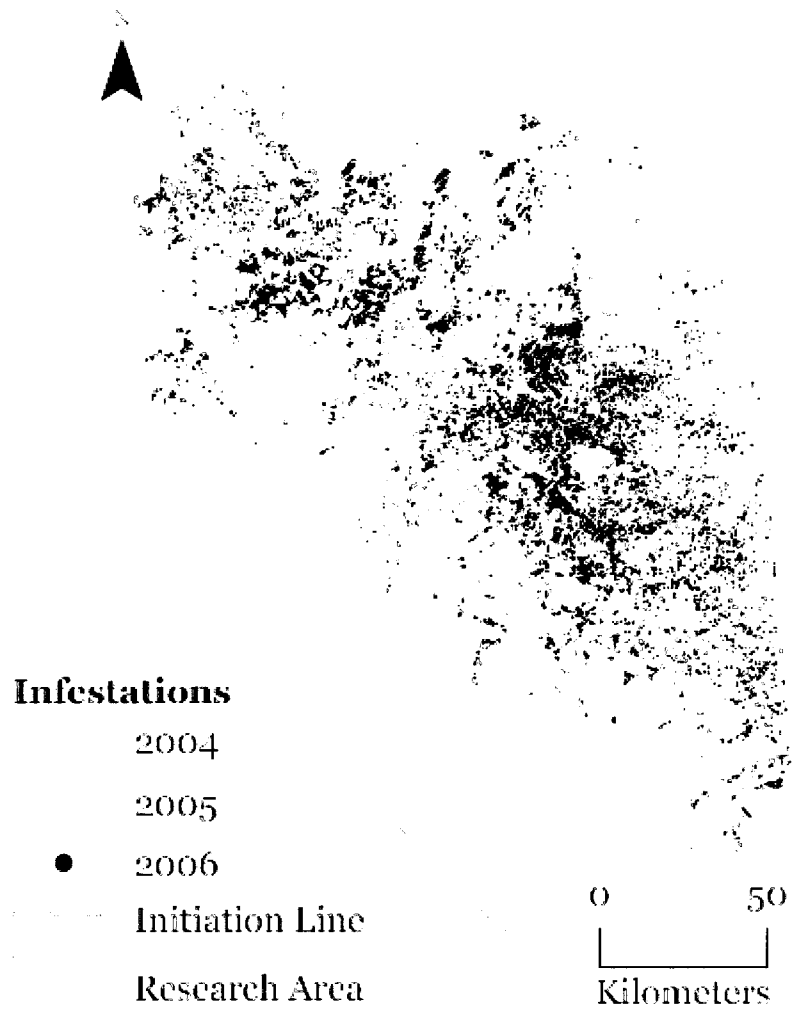


Fig. 2.3

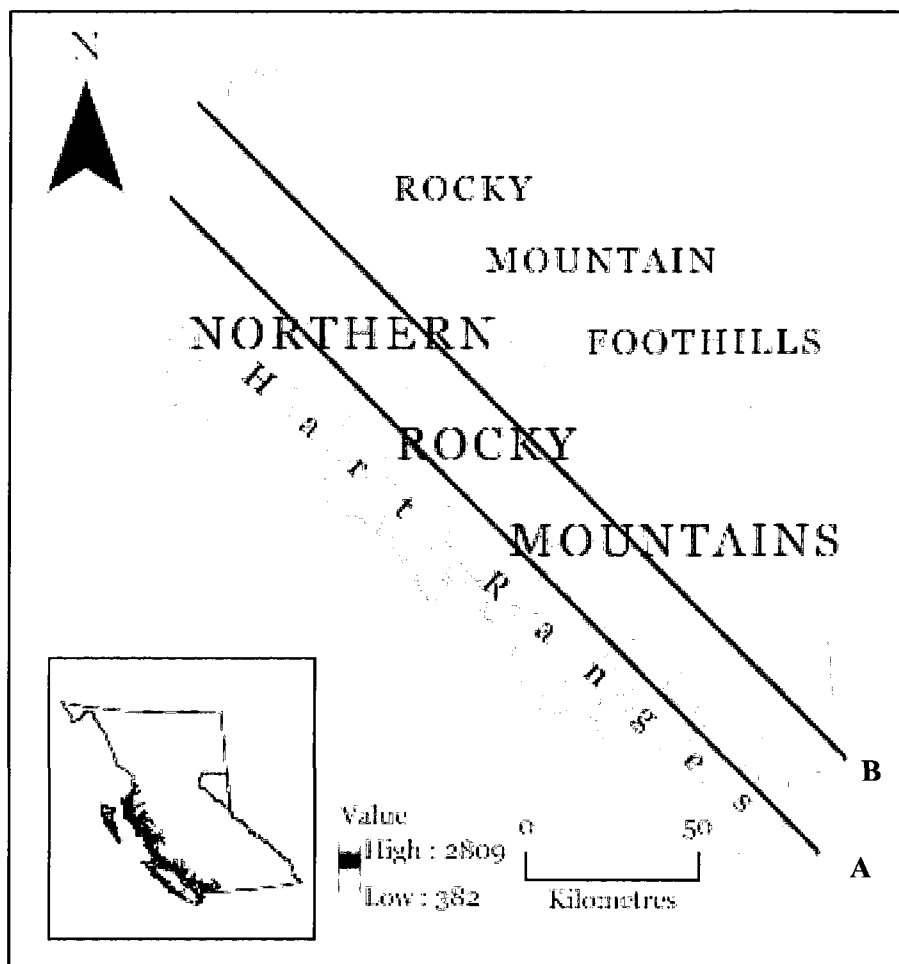


Table 2.1 AIC values for the spatial point process models reflecting various hypotheses of insect dispersal for 2004, 2005, and 2006 in the Peace River region of British Columbia. Each model uses the spatially explicit intensities of beetle-killed trees for the respective year as a function of an intercept term and a similarly spatially-explicit covariate(s), as listed (see Methods). Models with lowest AIC values are judged to fit the best.

Hypothesis	Covariate(s)	2004	2005	2006
Dispersal primarily occurs within insect boundary layer (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 <sub>(t-1)</sub> (dispersal from previous year's establishment) <sup>-a</sup>		370,646	1,023,605
Dispersal primarily occurs above insect boundary layer (aeolian dispersal)	Distance <sup>b</sup> (linear gradient from source)	324,186	373,781	1,024,656
	Distance + distance <sup>2</sup> (wave propagation)	<b>315,602</b>	<b>364,567</b>	<b>1,009,046</b>
Combination (above and within insect boundary layer)	Distance + beetle locations <sub>(t-1)</sub>	-	369,445	1,023,607
	Distance + distance <sup>2</sup> + beetle locations <sub>(t-1)</sub>	-	367,848	1,021,350

<sup>a</sup>No inventory exists for 2003

<sup>b</sup>Distance from line of initiation (parallel to the Rocky Mountains), see Methods  
Models of best fit are indicated in bold.

Table 2.2 The parameter estimates for spatial point process models judged to best fit infestation locations for 2004, 2005, and 2006 in the Peace River region of British Columbia (see Table 2.1). Distance from initiation line is represented by ' $d$ ' while the response variable for the models is  $\log(\lambda)$ , number of infestations of mountain pine beetle per  $m^2$ . The location of greatest density of infestations, i.e. distance from the initiation line, was estimated from the point of inflection for each polynomial regression equation.

Year	Model Parameters			Distance to maximum infestation intensity (from initiation line; see Methods) (km)
	Intercept	$d$	$d^2$	
2004	-20	2.82E-04	-3.05E-09	46.3
2005	-19	2.56E-04	-2.79E-09	45.8
2006	-17	1.03E-04	-7.23E-10	71.1

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### **3: THE ASSOCIATION BETWEEN ESTABLISHMENT AND SPREAD OF INFESTATIONS OF MOUNTAIN PINE BEETLE AND LANDSCAPE FEATURES IN THE PEACE RIVER REGION OF BRITISH COLUMBIA**

#### **3.1: Abstract**

The spread of mountain pine beetle since 2002 across the Rocky Mountains into northeastern British Columbia, an area not previously exposed to epidemic beetle pressure, has been facilitated largely by above-canopy dispersal of the insect by meso-scale atmospheric currents. Terrain-induced thermals likely influence population dispersal and establishment as insects may behave like inert particles at these scales. Spatial point process modelling was used to examine the impact of landscape-scale variables, including landscape features and their orientations, habitat suitability, and elevation, on occurrence of mountain pine beetle infestations in 2004, 2005, and 2006. The efficacy of treatment and control efforts in those years is also examined. The terrain within the research area was categorized according to a landscape feature classification scheme identifying landscape features that could potentially influence meso-scale convective currents and dispersal patterns of mountain pine beetle. Although plains, open slopes and U-shaped valleys occupied the largest areas in the landscape, mountain pine beetle infestations primarily established in U-shaped valleys. Other landscape features that had a positive association with infestations of mountain pine beetle differed between years. These features included canyons and deeply incised streams in 2004, local ridges and hills in valleys in 2005, midslope ridges and small hills in plains in 2004 and 2006, and open slopes in 2006. The orientation of landscape features was found to only influence the occurrence of mountain pine beetle infestations in 2006, with southwestern slopes of midslope ridges or small hills in plains, southwest facing open slopes,

and U-shaped valleys that run in a northeast-southwest cardinal direction positively influencing intensity. These findings may be used to prioritize treatment areas prior to infestation by mountain pine beetle based on the landscape features within a target area.

### 3.2: Introduction

Landscape pattern and structure play important roles governing the spread and impact of insect herbivores in forest ecosystems, both directly by influencing the dispersal capabilities of insect populations and indirectly by influencing the health and distribution of host trees (Bjørnstad et al. 2002; Ims and Coulson 2004). For example, *Adelges tsugae* Annand (Homoptera: Adelgidae) (hemlock woolly adelgid) feeds on native hemlock species in the eastern United States and disperses via wind (Orwig et al. 2002), severely impacting stands on xeric ridges and slopes. Similarly, frontal zones of outbreaks of *Operophtera brumata* L. (Lepidoptera: Geometridae) (winter moth), tend to vary in size according to topographic characteristics such as distance from the coast, altitude, and slope (Hagen et al. 2007). Specific landform characteristics can also greatly influence patterns of infestation, usually due to alteration of host vigour and levels of resistance. For example, infestations of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) (southern pine beetle) have been found to be closely associated with landforms including upland plateaus while showing lower-than-expected infestations on side slopes and steep side slopes (Hicks 1980). In western North America, recent range expansion events across presumed geoclimatic barriers by outbreaking populations of *D. ponderosae* Hopkins (mountain pine beetle) provide a new opportunity to study the effects of landforms and feature orientation in an invasion process.

The mountain pine beetle is a cryptic herbivore that spends all but a few days of its life cycle under the bark of mature pine trees. Typically, the insect exists for long periods at endemic levels, but may intermittently undergo drastic population eruptions (Safranyik et al. 1974; Amman and Cole 1983; Zhang and Alfaro 2003; Gamarra and He 2008). At epidemic population phases (Raffa and Berryman 1983), the insect must kill its host in order to

reproduce, exerting positive feedback in a system with landscape-scale consequences (Raffa et al. 2008). Outbreaks typically decline when the host supply is exhausted or large-scale, lethal climatological events result in mortality of a large proportion of the population (Stahl et al. 2006; Safranyik and Carroll 2006).

Currently, there is a massive outbreak of mountain pine beetle covering approximately 14.5 million ha of mature forests of *Pinus contorta* var. *latifolia* (Engelmann) Critchfield (lodgepole pine) in the provinces of British Columbia and Alberta in western Canada (British Columbia Ministry of Forests and Range 2009), exerting carbon-budget impacts in the order of megatonnes (Kurz et al. 2008). The occurrence of an outbreak is not unusual *per se* given the presence of a favourable climate for the insect and a high proportion of stands with suitable hosts available on the landscape (Thomson and Shrimpton 1984; Safranyik and Carroll 2006; Campbell et al. 2007; Aukema et al. 2008; Nelson and Boots 2008). However, the magnitude, extent, and severity have been unprecedented as the outbreak has been exacerbated in large part by anthropogenic impacts such as altered forest management regimes (i.e., fire suppression) and a changing climate (Carroll et al. 2004; Taylor et al. 2006; Raffa et al. 2008). The outbreak originated in the central interior of the province of British Columbia, Canada in the late 1990s (Aukema et al. 2006). However, the first inventory of incipient-epidemic infestations in northeastern British Columbia on the eastern slopes of the Rocky Mountains occurred in 2004, from an invasion presumed to have occurred in 2002 (Allan Carroll, pers. comm.<sup>1</sup>). Mountain pine beetle was previously thought not to be endemic to this area, as the Rocky Mountains in the central part of the province have historically been considered a geoclimatic barrier (Safranyik and Linton 1982). However, over the next few years, outbreaking populations of mountain pine beetle

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quickly spread from the eastern slopes of the Rocky Mountains in British Columbia into western Alberta. Currently, there is great concern that establishment in hybrid *P. contorta* × *P. banksiana* Lamb. (jack × lodgepole pine), and subsequently *P. banksiana* further to the east, may provide a conduit through the boreal forests of Canada to areas and hosts not previously exposed, such as *P. resinosa* Aiton (red pine) or *P. strobus* L. (eastern white pine) in eastern Canada and United States (Safranyik and Linton 1982; Cerezke 1995; Nealis and Peter 2008).

Host-seeking behaviour of mountain pine beetle is characterized primarily by short-distance dispersal in which adult progeny orient toward aggregation pheromones produced by conspecifics, attacking neighbouring hosts *en masse* (Safranyik et al. 1989). Dispersal flight is typically restricted to host-seeking behaviour within the stand (Safranyik et al. 1992), although newly emerged beetles do require a period of flight before becoming receptive to host volatiles (Shepherd 1966). Newly emerged beetles are attracted to dark objects on a light background (Shepherd 1966), and as a result may orient themselves towards spot sources and the canopy resulting in downwind and upward dispersal of individuals. This may allow beetles to move above the canopy and become incorporated into convective currents during warm, fair-weather periods (Chapman 1962; Safranyik et al. 1989). Once entrapped by meso-scale atmospheric currents the movement of insects is similar to the drift of inert particles (Taylor 1974), although insects may maintain a degree of flight control (Lewis and Dibley 1970). It is likely that population pressure, exacerbated by high levels of competition and lack of suitable hosts in the central interior of British Columbia, contributed to increased above-canopy movement, incorporation into advective currents, and subsequent long-distance dispersal of mountain pine beetle over the Rocky



Mountains (Jackson et al. 2005; Jackson et al. 2008; Robertson et al. 2009). Similar long-distance transport events of bark beetles have been noted previously. For example, infestations of mountain pine beetle in the Cypress Hills on the southern border of Alberta and Saskatchewan occurred approximately 200 km from outbreaking source populations in western Alberta in 1980 (Cerezke 1981; Safranyik and Linton 1982) and in the early 1970's Furniss and Furniss (1972) catalogued scolytids deposited on mountain glaciers in Oregon and Washington.

In situations where long-distance dispersal dominates, alterations of wind velocity, turbulence, and direction determine the transport, deposition, and, where there is susceptible host and suitable climate, the establishment of insect populations. The descent of mountain pine beetle from convective currents occurs via gravitational settling, active flight, rainout, and/or impaction (i.e. the contact of biota with objects). In particular, landscape features provide impactive surfaces for interception of insects (Defant 1951; Bullard et al. 2000), as demonstrated by arthropods in arctic ecosystems as well as gypsy moth in mountain-valley systems (Mason and McManus 1981; Ashmole et al. 1983; Antor 1994). The greater the mass of an airborne object, the more likely it will impact the ground or surface rather than be swept around the obstacle into lee-ward eddies (Westbrook and Isard 1999). Wind speed may decrease when the direction of motion is perpendicular to emergent landscape features, causing increased settlement in areas with reduced wind speeds (Ruel et al. 2001). Alternatively, wind speed may increase, depending on fetch, within open areas, which may increase the transportation of insects longer distances within valleys, as the insects become entrained within air currents in these regions.

Despite the importance of topography on settlement patterns of insects exhibiting aeolian dispersal, the influence of topography on the deposition patterns of mountain pine beetle in these recent range expansion events has not been studied. The Peace River region exhibits a diversity of topographical features. At the western edge of the region, the terrain is dominated by the Northern Rocky Mountains with strongly linear terrain features formed by erosion of folded and faulted sedimentary rocks (Harcombe 1978). These linear features include large U-shaped valleys, eroded by glaciers, separated by distinct ridges (British Columbia Ministry of Environment 1994). The Hart Range, the primary mountain range in the region containing the Solitude and Murray Ranges, dissects the region at a central belt of lower elevation in the Rocky Mountains. This range encompasses two low-lying passes, including the Pine Pass (874m), the lowest of six highway passes through the northern Rocky Mountains, and the Monkman Pass (1092m). The eastern portion of the research area is composed of flat-lying or gently dipping sedimentary rocks producing plateau topography (Harcombe 1978). Due to the relatively consistent directions of meso-scale winds in the region, it is likely that the interaction between landscape features and convective currents predictably influences deposition and the establishment patterns of *D. ponderosae* relative to feature orientation.

The primary objectives of the present study were fourfold: (1) to examine the association of landscape features on the establishment and persistence of insect populations of sufficient size to kill mature trees in a newly-invaded area, (2) to determine whether the specific orientations of those features provided additional inference on locations of insect establishment, (3) to examine the relative contributions of other landscape characteristics, including elevation and susceptible habitat, on the establishment patterns of mountain pine

beetle during the initial stages of invasion, and finally, (4) to assess the efficacy of treatment and control efforts on spread of infestations within the region to better understand the impact of long-distance dispersal on control efforts. Investigation of factors driving establishment of mountain pine beetle infestations within this region allows retrospective examination of the invasion event(s) and may provide critical information to formulate strategies to mitigate further invasion and range expansion events of this eruptive forest herbivore.

### **3.3: Materials and Methods**

#### ***3.3.1: Preparation of Insect Datasets***

A study area was delineated that encompassed the invasion process of outbreaking populations of mountain pine beetle over the northeastern slopes of the Rocky Mountains from 2004 to 2006. This area encompassed the Peace River region from the Rocky Mountains to the border of the province of Alberta, an area approximately 3 million hectares in size (Fig. 3.1).

Detailed annual survey maps of discrete outbreaking populations of mountain pine beetle were obtained from forest licensees. The provincial government is the predominant landowner in the province of British Columbia, particularly within the Peace River region, which in turn leases tree-harvesting rights to forest management companies. As such, we are confident in the spatial coverage of the data. The surveys were conducted by identifying and recording locations of “red-attack” trees from helicopter using GPS, in concert with further ground reconnaissance work in some areas. Because mountain pine beetles in epidemic population phases must kill their host in order to reproduce, and foliage fades from green to red within one year after colonization (Safranyik et al. 1974), mapping “red-attack” is a reliable proxy for estimates of insect abundance (Aukema et al. 2006; Wulder et al. 2006).

The surveys had been conducted in 2004, 2005, and 2006 from approximately May to September. 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 (Table 3.1).

Detailed error checking revealed that only 113 of 58,008 data points were of questionable quality (duplicates in year 2004; 1% of the data for that year). Duplicate sites were defined where the distance between sites were recorded as 0 metres. In such instances, the point with the largest infested area (ha) was retained for that location while the other point was deleted. Where attribute data were the same, the overlying point was deleted.

A separate dataset of infestation treatment data, including single tree treatments and harvesting of infested blocks, for 2005 and 2006 was procured from licensees. Polygonal and point treatment data were combined into a single point dataset using methods similar to those used for infestation data, such that all points had an affected area associated with them. Polygons were converted to points based on the centroid of the polygon. A pixel surface of distance from treatment location within the research area was produced using the Spatial Analysis distance tool in Arcview 9.2 (ESRI). Each pixel measured 73×73 metres, or approximately 0.53 ha in size.

### ***3.3.2: Preparation of Landscape Feature Datasets***

A stand susceptibility index (SSI) dataset, produced by the Canadian Forest Service, was used as a surrogate for habitat considered suitable for outbreaking populations of mountain pine beetle in our analyses. The index is typically calculated using four variables, including the relative abundance of pine, the ages of dominant and codominant pine, stand

density, and location (Shore and Safranyik 1992; Shore et al. 2000). We used an updated SSI dataset that substituted a climatic factor for the location factor in calculation of the index, which provided an assessment of habitat suitable for insect colonization and reproduction (Safranyik et al. 1975; Carroll et al. 2004). This climatic factor predicts the influence of realized climatic regimes on the susceptibility of forest stands by integrating daily weather data from meteorological stations in British Columbia with historic temperature regimes into a mechanistic model of mountain pine beetle population dynamics (Shore and Safranyik 1992; Carroll et al. 2004). Resulting stand susceptibility indices range between 0 and 100, and are categorized into five stand susceptibility classes with class 0 being the lowest susceptibility to infestation by mountain pine beetle and class 5 being the highest respectively. The highest stand susceptibility classes identify areas where there are suitable hosts (i.e., ages  $\geq$  60 yr, species composition, diameter, etc.) and the climate is typically amenable to the establishment and reproduction of mountain pine beetle populations (Safranyik et al. 1975; Carroll et al. 2004).

The research area was classified into ten classes of landscape features that potentially influence wind and circulation patterns within the region (Table 3.2).

Each 73 $\times$ 73m pixel within the research area was classified into a feature type based on its relative elevation using a Topographic Position Index (TPI) tool v.1.3a (Weiss 2001; Jenness 2006) as an extension within Arcview v.3.2 (ESRI). In brief, pixels are considered relative to the mean of a predefined neighbourhood of a user-specified size and shape (Fig. 3.2 A). The combination of TPI at small and large scales allows for predefined landscape features to be delineated in a digital elevation model (Fig. 3.2 B). The digital elevation model used for the TPI classification process was composed of 1:250,000 mapfiles identical to raster sizes in our

other datasets (i.e. 73×73m). The recommended circular neighbourhood was used during classification (Jenness 2006). Three combinations of small and large neighbourhood sizes were examined, including 1000 and 2000 metres, 1000 and 3000 metres, and 1000 and 6000 metres, respectively. Resulting TPI rasters were visually inspected and compared to the source digital elevation model. The first two TPI rasters resulted in a classification with a pixel resolution too coarse to accurately reflect the topography of the research area. The third classification scheme satisfactorily represented terrain within the region, as judged by visual inspection, and was selected for use in statistical analyses.

Using this map of landscape features classified across the study area, the orientation of certain landscape features was calculated to allow further investigation of the effects of feature orientation on the occurrence of mountain pine beetle infestations.

The orientation of landscape features was determined according to the type of feature (Table 3.2). Azimuth is defined as the cardinal direction in which a linear feature lies. For example, within the research area, canyons or deeply incised streambeds and U-shaped valleys may be characterized by their azimuths (Fig. 3.3 A). Similarly, aspect is defined as the direction in which non-linear features, such as open slopes or midslope ridges, face (Fig. 3.3 B). The linear azimuth for linear landscape features with predominantly linear orientations such as canyons or deeply incised streams, U-shaped valleys, and mountain tops or high ridges was determined by “breaking” features at changes in direction greater than 45 degrees. The orientation of the broken feature was then determined using an azimuth measurement tool (v. 1.6) in Arcview v.3.2 (Jenness 2005). The azimuths were then converted from compass bearing measurements (i.e., angular readings) to one of the following four categories: north-south, northeast-southwest, west-east, or southeast-northwest orientation. For non-linear

features, including open slopes, local ridges or hills in valleys, or midslope ridges or small hills in plains, aspects of the features were extracted by querying features based on one of eight directions (i.e., northwest, west, southwest, etc.). All datasets were then converted to binomial rasters (73×73m pixel size) where locations of a particular landscape feature with a specific orientation were noted by ones (i.e., presence) while the rest of the landscape was recorded as zeros (i.e., absence).

### ***3.3.3: Statistical Analyses***

As an initial step in data exploration, we tested whether the distribution of susceptible habitat, as well as the types of landscape features, affected the occurrence and distribution of infestations of mountain pine beetle using contingency tests for the 2004, 2005, and 2006 datasets. For each year, the spatial extent under analysis was restricted to the extent of area infested in that year plus a 25 kilometre buffer. As a result, the areas considered within each analysis increased in size from 2004 to 2006 as mountain pine beetle spread across the region (see Results). For contingency tests, observed values were calculated by summing the area infested per stand susceptibility class or landscape feature while expected values were calculated by multiplying proportion of total area occupied by a susceptibility class or landform type by the total area infested by mountain pine beetle in the research area (see Appendix B and Appendix C for R code). Boot-strapping procedures with 1000 repetitions were then used to develop a test statistic distribution, as simple  $\chi^2$  tests fail to contend with spatial autocorrelation within the dataset. This process involved randomizing the spatial points within the area of analysis, with the sample size equal to that of the dataset under consideration. The susceptibility class or feature for the location of each point was then sampled. The area of infestation for each point was also randomly permuted and the

contingency test statistic was then calculated for each randomization. The calculated test statistic for the initial test was then ranked relative to the generated test statistic distribution to determine if it was significant using  $\alpha = 0.05$  (see Appendix D for R code).

Spatial point process regression models were used to examine the potential influences of landscape features, their orientation, habitat suitability, elevation, distance from source infestations, and, for 2005 and 2006, the distances from locations of treatment in the previous year on the density of outbreaking populations of mountain pine beetle in the study area for each year (see Appendix E). Candidate landscape feature covariates for inclusion in these models were restricted to those with an area infested greater than expected (from exploratory data analysis above). Rather than considering all habitat suitability classes, only those with the highest susceptibility (i.e. class 5) were included. For our spatial regressions, a spatial point process (i.e., a spatially-explicit dataset of  $x$  and  $y$  locations of infestations of mountain pine beetle) was examined as a function of other spatially-explicit covariates (such as presence/absence of management activity, landscape features, orientation, etc.), yielding regression coefficient estimates and standard errors for all covariates. Substituting covariate values into the resulting spatial point process regression equation yields an estimated density  $\lambda$ , a spatially-explicit density of infestations per unit area (i.e., pixel of  $73 \times 73$  m in size, just over one half a hectare resolution). In this class of models, the likelihood is well-defined, allowing examination of the significance of individual regression coefficients via likelihood ratio tests among nested models using  $\chi^2$  test statistic distributions (Baddeley and Turner 2008). Moreover, each model yields AIC values useful for model selection, with lower values judged to be the best (Akaike 1973).



Spatial point process regression models share similar challenges in evaluating the effects of multiple variables as classic linear regression models in that the marginal effects of highly correlated variables may be difficult to estimate (e.g. inflated standard errors) (Graham 2003). In our system, due to the settlement patterns of mountain pine beetle in a general northwest-southeast pattern across the entire research area, there was an extremely high degree of correlation between  $x$  and  $y$  variables when examining the effects of distance from source populations on final establishment densities (see Results). To contend with this challenge, we reduced spatial location to one dimension by defining a new variable, the distance from a line of reference along the Rocky Mountains, perpendicular to the direction of spread. The direction of spread was determined by examining slope of a linear regression of northing versus easting values (i.e.  $y$  versus  $x$ ) for the first year infestation. The direction of spread in 2004 was estimated to be northeast or along a  $48^\circ$  bearing. Therefore, the line of reference had a  $138^\circ$  bearing. Hence, insect locations were measured as a distance from this line along the western edge of the research area (presumed source of the insects) and their established locations in the Peace River region of British Columbia.

Our spatial regressions yielded a multiple regression equation for each year (i.e., 2004, 2005, and 2006) providing inference on the influences of a variety of variables (e.g., landscape features, elevation, distance from line of initiation, etc.) on the locations of mountain pine beetle populations. We then returned to the initial inventory datasets and, for each year, fit simple linear regressions using one of the eight (for aspect) or four (for azimuth) landscape feature orientations for each type of landscape feature that was significant in the previous models. The best-fitting feature orientation was selected for each feature type in each year by examining AIC values, and then substituted into the previous

spatial regression models in place of the overall feature class (see Results). This allowed a comparison between models with landscape features, and those with features restricted to a specific best-fitting direction. The model with the lowest AIC value was judged to fit the best.

To determine if elevations of infestations within the study area each year were similar to the average elevation of infestations within the central interior (i.e. 1000 m; Safranyik and Carroll 2006), we used one thousand (1,000) single sample *t*-tests of randomly thinned subsets of the annual datasets ( $n = 50$ ). Resampled subsets were used to contend with spatial autocorrelation in the original dataset. All data was handled in Arcview v.9.2, ArcInfo Workstation, and Arcview v.3.2 while the spatstat package v.1.14-9 within R v.2.8.1 was used for statistical analyses (Ihaka and Gentleman 1996; R Development Core Team 2009).

### **3.4: Results**

#### ***3.4.1: Spatial Extent and Landscape of Invaded Area***

The number of incipient-epidemic infestations increased annually within the Peace River region of British Columbia between 2004 and 2006. There were 10,536 infestations mapped in 2004 and 12,275 in 2005. These numbers approximately tripled to 35,084 infestations in 2006 (Fig. 3.4). In 2004, the mean area of patches of red trees killed by mountain pine beetle was quite small; approximately one third of a hectare. However, the mean sizes of individual infestations increased to approximately 1 ha in 2006 (Table 3.3). Sizes of patches of dead trees became more variable due to expanding areas that were colonized, as the largest areas measured in 2006 were 2,440 ha, versus 6 and 133 ha in 2004 and 2005 respectively. By 2006, the total area of trees killed by mountain pine beetle had expanded to 35,084 ha (Fig. 3.4).

Patches of mortality were found in lodgepole pine forests between elevations of approximately 500-1700 m. After the initial invasion event, most successful attacks were at 1,000 m in elevation each year (Table 3.3). In 2005 and 2006, patches of dead trees were found at significantly higher elevations than those previously noted in outbreaks in the insect's conventional range. Infestations stretched from the western slopes of the Rocky Mountains in 2004 to the town of Tumbler Ridge, British Columbia (Fig. 3.5). By 2006, this extent had expanded two-fold in a northeasterly direction to encompass almost the entire Peace River region.

Dominant landscape features in the invaded region included plains, open slopes, and U-shaped valleys (Fig. 3.6). A numerical summary of their areas and elevations are provided in Table 3.4. Together, plains and open slopes comprised more than 50% of the landscape in the Peace River region. Other landscape features such as canyons and deeply incised streams, upper slopes and mesas, and midslope ridges or small hills in plains each comprised no more than 6% of the area proportionally, but absolute area was always more than 100,00 ha in size. The smallest landscape features in size were local ridges or hills in valley bottoms, comprising 1,122 ha across the region (0.04% of the total area). Plains exhibited the lowest mean elevation (877 m) while mountaintops/high ridges were found to have the highest (1,619 m; Table 3.4).

A map of habitat susceptibility classes is provided in Fig. 3.7, with a numerical summary of their relative abundances across the landscape in Table 3.5. Most of the Peace River region across northeastern BC was considered highly unsuitable for outbreaking populations of mountain pine beetle, as two thirds of the landscape was classified as suitability class 0. The most susceptible habitat, i.e. class 5, occupied only 3% of the

landscape (74,894 ha; Table 3.5). This habitat is stratified across nine different landscape features (Table 3.6). Of these, plains, open slopes, and U-shaped valleys comprised the largest proportion of highly susceptible habitat (49, 27, and 14% respectively). Upland drainages or headwaters, local ridges or hills in valleys, and upper slopes or mesas collectively comprised less than 1% of habitat classified as highly susceptible to outbreaking populations of mountain pine beetle (Table 3.6).

#### ***3.4.2: Which Landscape Features are Associated with Mountain Pine Beetle Infestations?***

Infestations of mountain pine beetle were not distributed uniformly across all types of landscape features, as demonstrated by goodness-of-fit tests (Appendix F). Exploratory analyses identified that certain landscape feature had more (or less) infestation than would be expected if infestations were distributed uniformly across the landscape. In 2004, canyons or deeply incised streams, local ridges or hills in valleys, midslope ridges or small hills in plains and U-shaped valleys had more area infested than expected. This pattern persisted into 2005, as midslope ridges or small hills in plains, and U-shaped valleys had greater areas infested than expected, along with canyons or deeply incised streams. In 2006, canyons or deeply incised streams, local ridges or hills in valleys, midslope ridges or small hills among plains, open slopes and U-shaped valleys exhibited a greater total area infested by mountain pine beetle than expected. Although open slopes and plains occupied a large proportion of the landscape, they had proportionally less area infested than would be expected from uniform settlement in 2004-2005. Landscape features including mountain tops or high ridges, midslope ridges or small hills in plains, upland drainages or headwaters, and upper slopes or

mesas each contained fewer infestations than would be expected by a uniform distribution across the landscape in all three years (Appendix F).

Given the differences in relative distribution of infestations of mountain pine beetle across landscape features, we fit spatial point process regression models to determine which landscape features might provide the best inference on locations of detected infestations (Table 3.7). These models, which measure intensity,  $\lambda$ , as a spatially-explicit number of infestation per unit area ( $\text{m}^2$ ), also included as covariates elevation, distance from source location, presence or absence of the most highly suitable habitat (i.e. class 5; see Fig. 3.7), and, in the latter two years, distance from the nearest sites where insect control tactics, such as fall and burn or single-tree removal, had been implemented the previous year. Landscape features associated with increased intensities of infestation included canyons or deeply incised streams in 2004, local ridges or hills in valleys in 2005, midslope ridges or small hills in plains in 2004 and 2006, open slopes in 2006, and U-shaped valleys in all three years (Table 3.7). In all three years, the presence of highly susceptible habitat was also positively correlated with infestation intensity. In 2004, canyons or deeply incised streams were associated with lower densities of mountain pine beetle

After accounting for the effects of landscape features, we found, not surprisingly, that the intensity of infestations decreased with distance from a line of initiation along the Rocky Mountains (see Methods). Furthermore, there were fewer patches of beetle killed trees at higher elevations after taking the effects of landscape features and distance from the Rocky Mountains into account. Beetle control tactics appeared to be efficacious. The density of infestations decreased with increasing distance from treatment sites in the previous year for both 2005 and 2006 (Table 3.7).

### ***3.4.3: Does Feature Orientation Influence Invasion Success?***

To determine which azimuths and aspects of landscape features had the greatest influence on intensity of patches of trees killed by mountain pine beetle infestations, spatial point process models were fit to annual inventory data with each of eight cardinal orientations per landscape feature as single covariates (Table 3.8). In the initial year of infestation, of the U-shaped valleys, those with a northeast-southwest azimuth best fit the pattern of infestation. Models of best fit for that year also included west-facing local ridges or hills in valleys, or midslope ridges or small hills in plains with southwestern aspects. Canyons or deeply incised streams with a north south azimuth and U-shaped valleys with a northeast southwest azimuth best fit patterns of infestation in years following initial establishment, 2005 and 2006. For 2005, a model incorporating southern aspects of local ridges or hills in valleys best fit patterns of infestation, while midslope ridges or small hills in plains with southwestern aspects and open slopes with southwestern aspects explained the most variation in insect establishment on the landscape in 2006.

Once the most-significant azimuth or aspect of each landscape feature was identified (Table 3.8), we substituted these best terms into the models of Table 3.7; i.e., replacing each significant global landscape feature with a more targeted subset of that feature class, to see if the orientation of the landscape feature provided better inference on the establishment patterns of mountain pine beetle throughout the Peace River region than simply the locations of features themselves. In 2004 and 2005, incorporating the best orientation of the landscape feature did not improve models that previously incorporated all orientations, as indicated by higher AIC values (2004: 311,275 vs. 311,338; 2005: 355,544 vs. 355,774; Table 3.7 and Table 3.9). However, persistence of tree killing populations of *D. ponderosae* in the Peace

River region in 2006 was readily influenced by orientation of landscape features as indicated by a lower AIC value (1,011,283 vs. 1,011,290) when feature orientations replaced landscape features as covariates (Table 3.9). Interestingly, a southwest orientation was common for all three landscape features included in the 2006 model (Table 3.9). For 2006, southwestern slopes of midslope ridges or small hills in plains, southwest facing open slopes, and U-shaped valleys that run in a northeast-southwest cardinal direction positively influenced intensity. As previously established by initial models lacking feature orientation, elevation and distance from the western edge of research area were inversely correlated to intensity of *D. ponderosae* infestations while distance from highly susceptible habitat was positively correlated. The intensity of infestations decreased with increasing distance from treatment in the previous year.

### **3.5: Discussion**

Our results demonstrate not only that specific landscape features are associated with establishment of an invading organism, but orientation of those landscape features is associated with the organisms potential persistence and spread. Initially, as mountain pine beetle crossed the Rocky Mountains into new areas of the province of British Columbia in western Canada, the majority of pockets of invaders were found in valleys in the central Peace region - which could have been acting as conduits for further dispersal - in the first two years of detection. This is consistent with the hypothesis that initial invasion of this territory occurred via aeolian dispersal (Chapter 2; Safranyik and Carroll 2006; Robertson et al. 2009). By 2006, increased densities of infestations of mountain pine beetle were associated with mid-slope ridges, small hills, and open slopes that were primarily facing in a southwest direction.

There are at least three reasons for the emergence of the importance of southwest feature orientation in the persistence of these invading herbivores. First, hosts may be more susceptible on drier, sun-exposed south-west facing slopes (Powers et al. 1999). Exudation of oleoresin, important in tree defense, is lowered when conifers are water-stressed (Waring and Pitman 1985). Second, insects established on southwest-facing sites may enjoy higher reproductive rates due to higher ambient temperatures, than insects on shaded slopes (Mattson and Haack 1987). Development of mountain pine beetle is strongly temperature-dependent, with progression between life stages critically dependent on accruing a sufficient number of heat units (Reid 1962; Amman 1973; Safranyik 1978; Bentz et al. 1991; Shore et al. 2000; Safranyik and Carroll 2006; Powell and Bentz 2009). Moreover, insect populations on landscape features oriented to receive less sun exposure would be more affected by cold temperatures during the winter. The cold tolerance of the over-wintering larval stage of mountain pine beetle increases incrementally over the winter as temperatures get progressively colder (Bentz and Mullins 1999). However, lethal temperatures, below  $-40^{\circ}\text{C}$ , can cause widespread brood mortality if they occur in October or mid-March, or for extended periods during the winter (Wygant 1940). Increased mortality and asynchronicity of development and emergence within populations associated with feature orientations receiving less sun would exhibit decreased local dispersal and likely lower infestation levels on those landscape features in successive years.

A third explanation for increased associations of mountain pine beetle with southwestern slopes, not mutually exclusive to the first two, is that additional episodes of aeolian dispersal may have deposited higher numbers in the Peace River region on southwestern slopes, as wind is strongly unidirectional and blows from the west and



southwest (Fig. 3.8). Mountain pine beetle tend to accumulate on windward sides of barriers, as large insects (i.e. those with bodies greater than a 4 or 5 mm<sup>2</sup> surface area, like mountain pine beetle) are less likely to be carried over top of a barrier to enter circulating leeward eddies because of their great inertia (Lewis and Dibley 1970). Hills that are relatively close to each other will also increase the amount of deposition on the windward slope of consecutive hills (Goossens 1996). The topography in the western portion of the Peace River region is characterized by consecutive ridges and valleys, causing ridgelines downwind to sustain more insect deposition on windward, southwestern slopes.

Thermal development thresholds linked to differing brood successes on southern versus northern aspects may be similarly associated with declining population densities at higher elevations, where temperatures are cooler (Amman 1973; Tishmack et al. 2005; Brunelle et al. 2008). High elevation sites within British Columbia and the Peace River region generally have lower mean winter and summer temperatures and a shorter growing season than low elevation sites. At higher elevations, populations may be particularly vulnerable to colder temperatures during August and September, forcing them into bivoltine developmental stages (Amman 1973). For example, Amman (1973) examined the life history of mountain pine beetle in lodgepole pine between 1923 and 2750 metres elevation in northwestern Wyoming. Between 1923 and 2130 metres the insects were univoltine, while at 2450 metres, part of the population was bivoltine. At elevations between 2573 and 2750 metres, two years were required to complete one entire life cycle. Asynchronous or mixed voltinism at high elevations also affects emergence synchronicity critical to the mountain pine beetles' ability to mass attack and successfully colonize hosts adjacent to their natal hosts (Amman 1969).

Our research area was between approximately 54 and 56° N. Despite the well-known negative correlation between insect success and elevation, we note that the mean elevation of outbreaking populations was significantly higher than 1000 metres in 2005 and 2006. In the insect's historic range within British Columbia, the majority of mountain pine beetle outbreaks have occurred historically at mean elevations of 1000 metres at 55° N, the same latitude as our study area (Taylor et al. 2006). The occurrence of more infestations at elevations higher than those typically exhibited in the insect's native range suggests three possibilities. First, it could signify that the climate in this newly invaded territory is suitable for establishment and brood production. Insects are particularly limited by temperatures that influence survival and reproduction at the northern edges of their habitat (Crozier 2004). Although dispersal is exceptionally lethal to bark beetles (Schmid 1969; Raffa 2001), warming of winter temperatures at the northeastern edge of mountain pine beetle's range may have facilitated increased survival of pioneer dispersers, allowing the insect to thrive in this new habitat (Carroll et al. 2004). Similar phenomena have been noted in other systems, such as *Atalopedes campestris* Boisduval (skipper butterfly) (Crozier 2004) and *Thaumetopoea pityocampa* Schiff. (pine processionary moth) (Battisti et al. 2005). Second, increased persistence at higher elevations could signify that host resistance is low in these areas, since, to our knowledge, populations of lodgepole pine in these areas have not been previously exposed to outbreaking populations of bark beetles. Of special concern is the threat of expansion into jack pine, which could provide this eruptive herbivore a conduit to the east coast of North America (Cerezke 1995). A third explanation, also not mutually exclusive to the first two, is simply that the persistence of outbreaking populations at higher elevation sites may reflect prior management activities at easy-to-access areas at lower

elevation. However, such activities was accounted for by its own covariate in the models, so any such signal is in addition to those already noted (Table 3.9).

In our study, as in others (e.g., Preisler and Mitchell 1993; Bentz and Munson 2000; Fettig et al. 2006; Nelson et al. 2006; Fettig et al. 2007; Trzcinski and Reid 2008) anthropogenic interventions against tree-killing eruptive herbivores decreased occurrences of infestations in the year following treatment. Management activities included single tree treatments using fall and burn, and harvesting of stands infested with mountain pine beetle. These control tactics decrease the potential for short-distance dispersal to adjacent stands (Trzcinski and Reid 2008). Treatments may have been efficacious in this region due to relatively low rates of increase among populations as a whole, either due to temperature or high levels of competition. Attacked hosts within the research area were noted to have greater than optimal levels of attack (i.e., 62 attacks/m<sup>2</sup>; Raffa and Berryman 1983; Allan Carroll pers. comm.<sup>1</sup>) resulting in lower per capita reproductive rates due to intraspecific competition (Safranyik and Carroll 2006). The persistence of a statistical signal for management activities for 2005 and 2006 also indicates that there were fewer, if any, long distance inputs of additional beetles into the study region, as the statistical signal for management activities associated with short-distance dispersal would likely have been obscured. Aeolian dispersal and rapid range expansion associated with insect outbreaks may be sporadic, but important events.

In summary, our results indicate that, following the initial invasion event, the continuing spread of the mountain pine beetle may potentially be facilitated by large, low-elevation valleys orientated along the dominant wind direction, acting as conduits of suitable habitat for the insect (e.g. Robertson et al. 2009). The orientation of landscape features also

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affects the establishment of mountain pine beetle, either by influencing the susceptibility of hosts or by allowing populations on warmer and drier sites to have greater reproductive rates facilitating spread into adjacent stands. These results may be of particular value in formulating management strategies as the insect progress eastward through the boreal forest of Canada, or in other areas where the insect is at epidemic population phases, such as regions of the southern Rocky Mountains of Colorado.

A result of this study of particular concern is the successful establishment of infestations at higher elevations than within their native range in the central interior of British Columbia. The elevation shift of mountain pine beetle indicates that the host within the region may be highly susceptible to attacks, or that the climate of such areas may be conducive to the establishment of infestations at those elevations (Carroll et al. 2004). Finally, while control measures such as single-tree fall and burn and harvesting of infested blocks are effective in minimizing dispersal between adjacent stands, it is not likely to be effective in preventing continuing spread where inputs of insects dispersing long-distances are present. In these situations, alternate control tactics will need to be used to effectively deal with long-distance inputs. In particular, predicting the potential spread of new infestations based on landscape features and their orientation, in concert with new landscape-scale spread modeling approaches (e.g., Gamarra and He 2008; Zheng et al. 2009) may provide newer coarse-scale tools for directing control activities.

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### 3.7: Figure Captions

Figure 3.1 Location of research area in the northeastern British Columbia. The research area includes a portion of the Northern Rocky Mountains, including the Hart Ranges, and the Rocky Mountain Foothills, an area of undulate topography that eventually becomes a plateau at the eastern edge of the research area. The inset map shows the location of the research area relative to the rest of British Columbia.

Figure 3.2 A) Determination of slope position using Topographic Position Index (adapted from Weiss 2001). B) Determination of general landform using Topographic Position Index (adapted from Jenness 2006).

Figure 3.3 Examples of (A) landscape features of linear canyons or deeply incised streambeds which are generally linear in nature and whose cardinal direction (i.e., feature orientation) is measured using azimuth. (B) Landscape features, such as midslope ridges or small hills in plains which are generally circular or complex in shape and whose orientation is measured compartmentally using azimuth.

Figure 3.4 Area and number of infestations of mountain pine beetle in the Peace River region of British Columbia in 2004, 2005, and 2006 as determined by aerial surveys of patches of red trees.

Figure 3.5 Location of infestations of mountain pine beetle in the Peace River region of British Columbia in 2004, 2005, and 2006. Dashed line in the three figures represents the line of initiation which is parallel to the Rocky Mountains and perpendicular to the direction of spread in 2004.

Figure 3.6 Map of landscape features within the Peace River region of British Columbia.

Figure 3.7 Distribution of habitat susceptibility classes in the Peace River region of British Columbia.

Figure 3.8 A general wind rose of the Peace River region of British Columbia (produced by Matthew Lynn of Garrad Hassan Canada Inc. with data from the Canadian Wind Energy Atlas)

Fig. 3.1

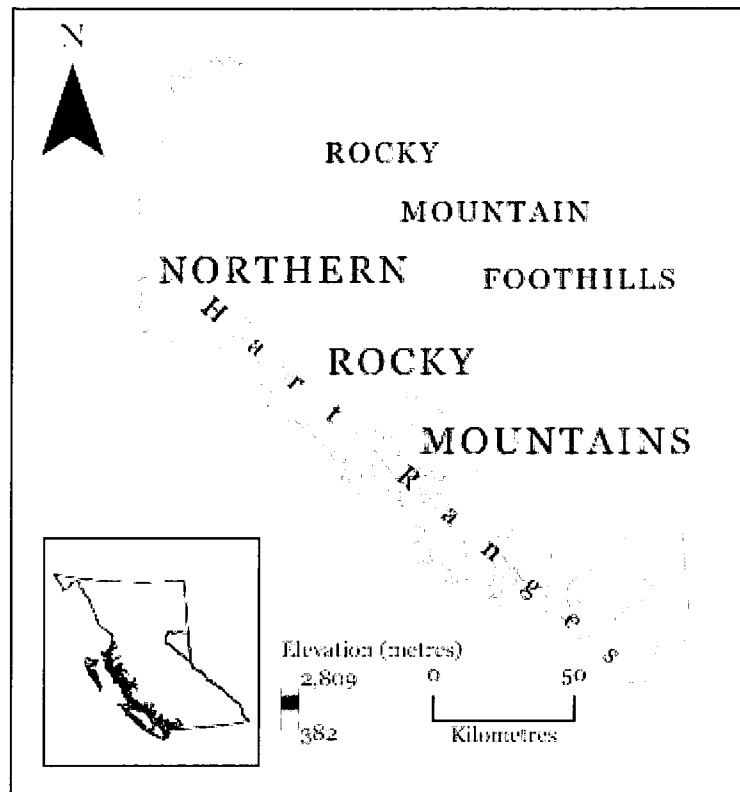




Fig. 3.2

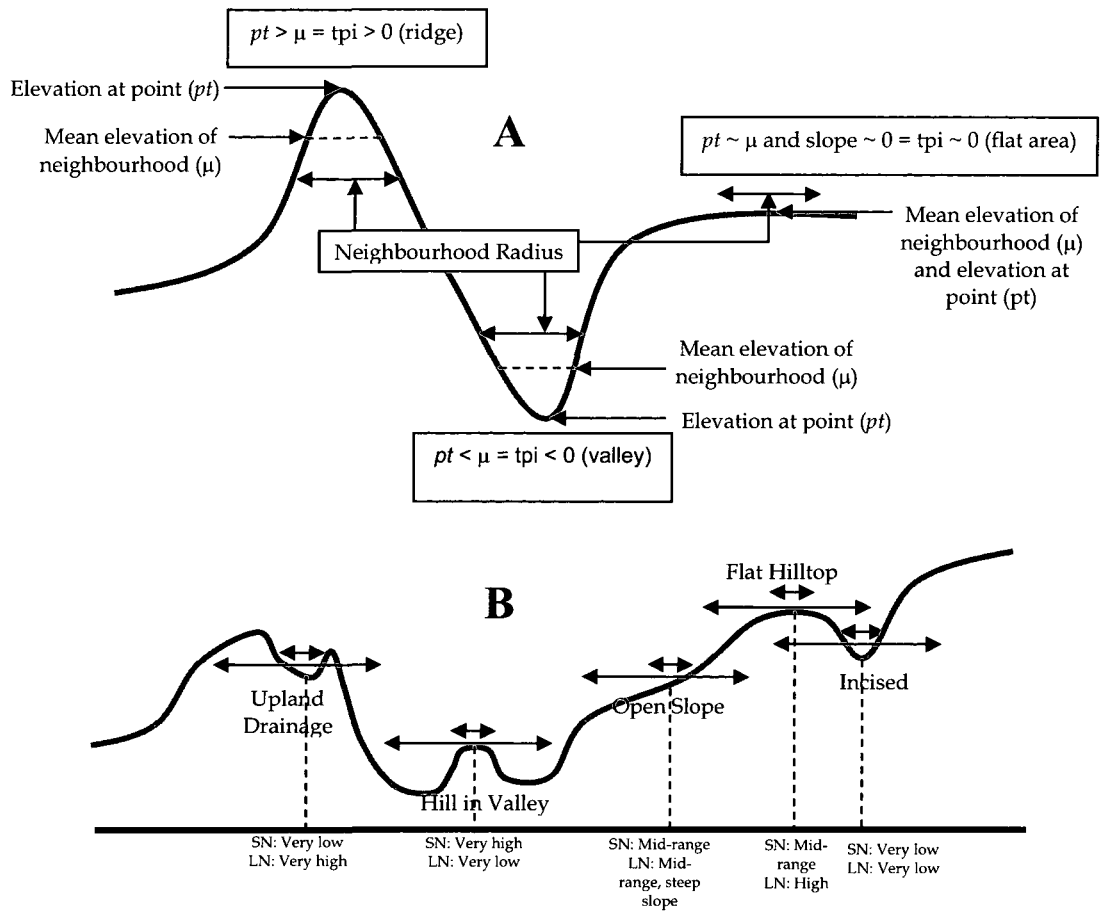


Fig. 3.3

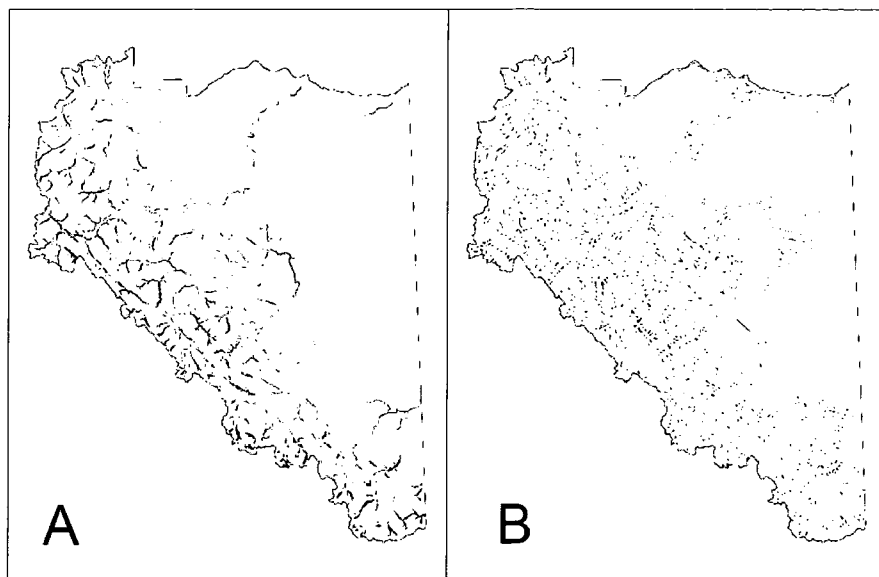


Fig. 3.4

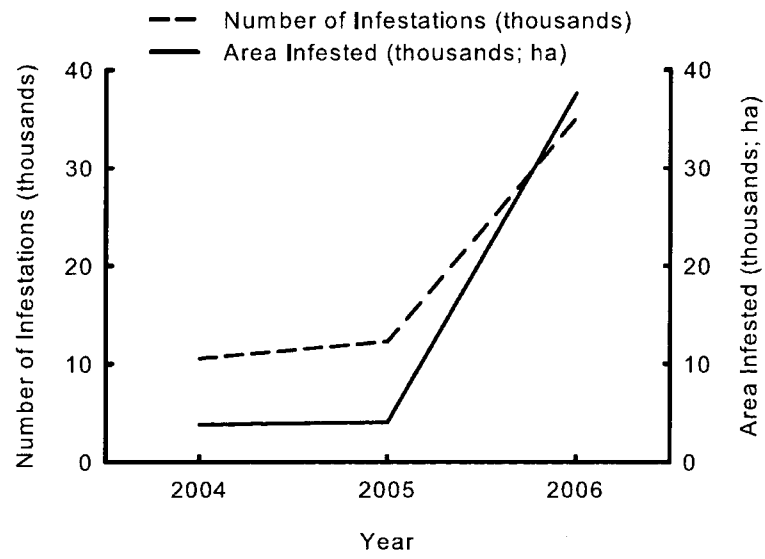


Fig. 3.5

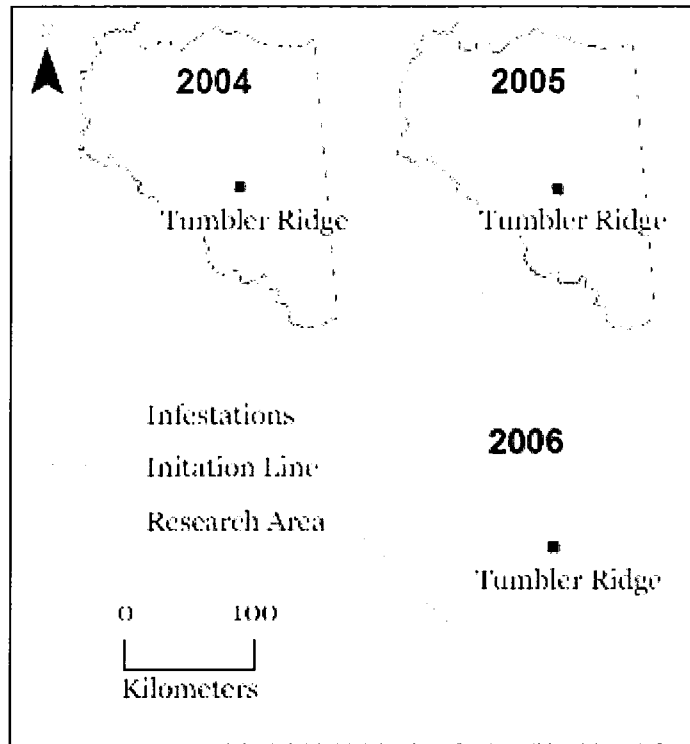


Fig. 3.6

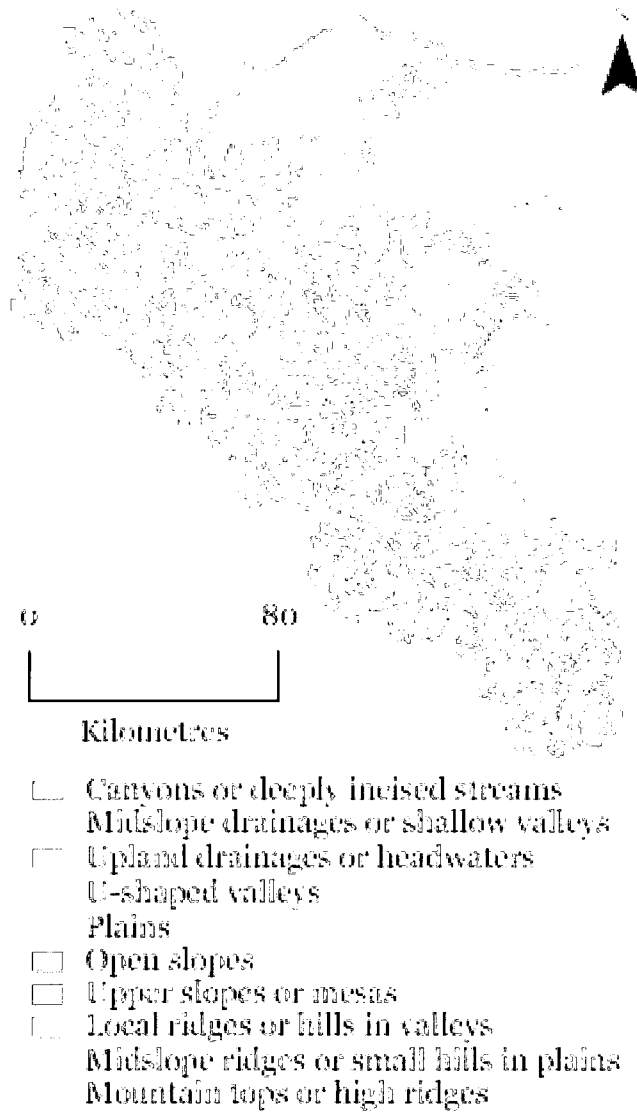


Fig. 3.7



Susceptibility Class

0            3

1            4

2            5



Fig 3.8

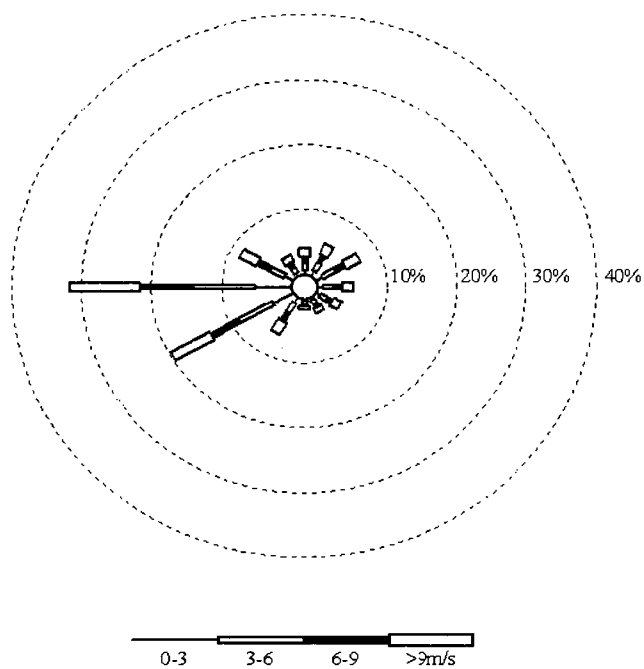


Table 3.1 Data fields of annual datasets inventorying patches of dead trees killed by mountain pine beetle within the Peace River region of British Columbia, 2004-2006.

Field Name	Description
Map_num	British Columbia Geographic System Mapsheet Number
Num_trees	Number of trees attacked
Spot_area	Area of attack in hectares
Comments	If there was green, red or grey attack in the site
Source	Source of original data
BEC_ndu	BEC zone, subzone, and variant
Easting	UTM easting
Northing	UTM northing
Park	Is the site within a park? 1 = yes, 0 = no
Ground	Was a ground survey completed? 1 = yes, 0 = no
BMU	Beetle Management Unit
Surveyed	Number of trees surveyed for mountain pine beetle attack within the site
Burned	Number of infested trees removed using fell and burn control treatment
GR_ratio	Ratio of red attacked trees to unattacked green trees



Table 3.2 Classes of landscape features in the Peace River region of British Columbia.

Landscape Features	Determination of Orientation
Canyons or deeply incised streams	Azimuth
Midslope drainages or shallow valleys	Aspect
Upland drainages or headwaters	Not applicable
U-shaped valleys	Azimuth
Plains	Not applicable
Open slopes	Azimuth
Upper slopes or mesas	Not applicable
Local ridges or hills in valleys	Aspect
Midslope ridges or small hills in plains	Aspect
Mountain tops or high ridges	Not applicable

Table 3.3 Summary statistics for infestation sizes and their characteristics of their elevations from annual inventories of mountain pine beetle infestations for 2004, 2005, and 2006 in the Peace River region of British Columbia. Results for *t*-tests examining the difference between average elevation for central British Columbia (1000m; Safranyik and Carroll 2006) conducted by 50 randomly sampled points in each annual dataset within the research area are reported as the percentage of 100 reiterations that were significant.

	Infestation Sizes (ha)				Elevation Summary Stats (m)				Different than historical average	
	Min	Mean	SD.	Max	Min	Mean	SD.	Max	<i>t</i> <sub>49</sub>	Significant T-tests (% of 100)
2004	0.001	0.36	0.34	6	621	1,002	162	1,652	9.2	100
2005	0.23	0.33	1.43	133	566	1,045	171	1,705	233.9	100
2006	0.001	1.07	17.33	2,440	462	1,049	175	1,686	34.3	100
Mean	0.001	0.78	13.51	860	462	1,040	173	1,705	-	-

Table 3.4 Average size and elevation of landscape features in Peace River region of British Columbia (see Fig. 3.6 for map).

Landform	Area (ha)	Percentage of Landscape	Elevation (m)				
			Mean	SD	Min.	Max.	Range
Plains	1,161,849	39.02	877	192	396	1,988	1,592
Open slopes	836,946	28.11	1,091	282	395	2,142	1,747
U-shaped valleys	237,761	7.98	964	255	382	1,806	1,424
Mountain tops/High ridges	168,347	5.65	1,619	277	764	2,808	2,044
Upper slopes/Mesas	159,454	5.36	1,468	257	726	2,491	1,765
Midslope drainages/Shallow valleys	158,742	5.33	1,238	309	396	2,138	1,742
Canyons/Deeply incised streams	122,853	4.13	1,007	256	384	1,817	1,433
Midslope ridges/Small hills in plains	116,685	3.92	1,219	280	477	2,121	1,644
Upland drainages/Headwaters	13,852	0.47	1,608	212	860	2,332	1,472
Local ridges/Hills in valleys	1,122	0.04	1,119	202	662	1,759	1,097
<b>Total</b>	<b>2,977,611</b>	<b>100</b>	<b>1,059</b>	<b>325</b>	<b>382</b>	<b>2,808</b>	<b>2,426</b>

Table 3.5 Numerical summary of “habitat susceptibility classes” across the Peace River region of British Columbia. See Methods for details of classification scheme.

Habitat Susceptibility Class <sup>a</sup>	Percent of Landscape	Area (ha)
0	66	1,958,090
1	15	437,895
2	5	163,763
3	5	163,292
4	6	179,675
5	3	74,894

<sup>a</sup> Class 0 is considered least susceptible to outbreaks of *D. ponderosae*

Table 3.6 Percentages of landscape features and total landscape with habitat considered highly susceptible to outbreaking populations of mountain pine beetle in the Peace River region of British Columbia (habitat susceptibility class 5).

Landscape Feature	Relative Distribution (%)	Percent of Landform Type	Percent of Landscape	Area (ha)
Plains	48.7488	3.142	1.22616	36,510.1
Open slopes	27.3921	2.451	0.68898	20,515.2
U-shaped valleys	14.3966	4.535	0.36211	10,782.3
Midslope ridges, small hills in plains	3.4471	2.213	0.08670	2,581.7
Canyons, deeply incised streams	2.7594	1.682	0.06941	2,066.6
Midslope drainages, shallow valleys	1.9672	0.928	0.04948	1,473.3
Upper slopes, mesas	0.6283	0.295	0.01580	470.6
Mountain tops, high ridges	0.6061	0.270	0.01525	454.0
Local ridges, hills in valleys	0.0537	3.582	0.00135	40.2
Upland drainages, headwaters	0.0007	0.004	0.00002	0.5
Total	100.0000	19.000	3.00000	74,895.0

Table 3.7 Spatial point process regression estimating the intensity of discrete beetle infestations as a function of landscape features, topography, distance from a source line, habitat susceptibility, and distance from control tactics in the previous year, 2004-2006, in the Peace River region of British Columbia.  $\text{Log}(\lambda)$  is the response variable for each model, where  $\lambda$  is the density of sites successfully attacked by mountain pine beetle populations per square meter. For example, in 2004, the estimated density of beetle patches at sites 5,000 kilometres from the source location in a canyon at 1,500 metres elevation and in highly susceptible habitat would be  $\exp^{(-7.82+5000 \times -5.03\text{E-}05 + -0.0296 + 1500 \times -3.85\text{E-}03 + 1.55)}$  or  $3.4\text{E-}06$  infestations per square meter (i.e., 0.034 infestations per hectare or one patch of tree-killing beetles every 30ha).

Year	Model Parameters	Estimate	Standard Error	Z	P-value
2004	Intercept	-7.82E+00	7.92E-02	-98.7	<0.0001
	Distance from source location	-5.03E-05	4.95E-07	-101.6	<0.0001
	Canyons, deeply incised streams	-2.96E-01	3.68E-02	-8.1	<0.0001
	Midslope ridges, small hills in plains	5.91E-01	4.11E-02	14.4	<0.0001
	U-shaped valleys	2.24E-01	2.69E-02	8.3	<0.0001
	Elevation	-3.85E-03	5.36E-05	-71.8	<0.0001
	Highly susceptible habitat	1.55E+00	2.86E-02	54.1	<0.0001
2005	Intercept	-8.76E+00	7.44E-02	-117.7	<0.0001
	Distance from source location	-3.96E-05	5.85E-07	-67.7	<0.0001
	Canyons, deeply incised streams	1.38E-01	3.23E-02	4.3	<0.0001
	Local ridges, hills in valleys	8.22E-01	2.01E-01	4.1	<0.0001
	U-shaped valleys	3.87E-01	2.42E-02	16	<0.0001
	Elevation	-2.39E-03	4.58E-05	-52.1	<0.0001
	Highly susceptible habitat	8.87E-01	2.96E-02	30	<0.0001
Distance from 2004 control tactics	-9.91E-05	1.46E-06	-67.9	<0.0001	
2006	Intercept	-1.16E+01	4.22E-02	-275.4	<0.0001
	Distance from source location	-5.44E-06	2.67E-07	-20.4	<0.0001
	Midslope ridges, small hills in plains	4.49E-01	2.42E-02	18.6	<0.0001
	Open slopes	2.82E-01	1.23E-02	22.9	<0.0001
	U-shaped valleys	2.04E-01	1.83E-02	11.2	<0.0001
	Elevation	-1.18E-03	2.49E-05	-47.2	<0.0001
	Highly Susceptible Habitat	9.77E-01	1.90E-02	51.3	<0.0001
Distance from 2005 control tactics	-5.31E-05	7.79E-07	-68.2	<0.0001	

AIC values for final models: 2004, 311,275.3; 2005, 355,543.6; 2006, 1,011,290

Table 3.8 Spatial point process regression models that identify which orientations of landscape features best fit the distribution of *D. ponderosae* infestations in three initial years of incipient-epidemic outbreaks (2004-2006) in the Peace River region of British Columbia.

Landscape Feature	Azimuth/Aspect <sup>a</sup>	2004		2005		2006	
		<i>P</i> -value	AIC	<i>P</i> -value	AIC	<i>P</i> -value	AIC
Canyons, deeply incised streams	Flat	0.0034	334,079.70	<0.0001	385,438.70	-	-
	North south	<0.0001	<i>333,771.80</i>	<0.0001	<i>385,036.8</i>	-	-
	Northeast southwest	<0.0001	333,967.30	<0.0001	385,251.40	-	-
	West east	<0.0001	333,977.30	<0.0001	385,377.20	-	-
	Northwest southeast	<0.0001	333,792.20	<0.0001	385,111.40	-	-
U-shaped valleys	Flat	<0.0001	334,058.10	<0.0001	385,427.90	0.0050	1,028,061
	North south	<0.0001	333,450.30	<0.0001	384,065.30	<0.0001	1,027,880
	Northeast southwest	0	<i>331,373.80</i>	<0.0001	<i>382,746.6</i>	<0.0001	<i>1,026,668</i>
	West east	<0.0001	333,617.20	<0.0001	384,223.50	<0.0001	1,027,645
	Northwest southeast	0	331,696.60	<0.0001	382,934.20	<0.0001	1,027,950
Local ridges, hills in valleys	East	0.0087	334,081.40	0.012	385,473.20	-	-
	North	0.0097	334,081.60	0.0013	385,469.30	-	-
	Northeast	1.00	334,088.30	1.00	385,479.50	-	-
	Northwest	0.00033	334,075.40	0.00012	385,464.70	-	-
	South	0.0047	334,080.30	<0.0001	385,458.2	-	-
	Southeast	1.00	334,088.20	1.00	385,479.30	-	-
	Southwest	0.41	334,087.60	0.47	385,479.00	-	-
	West	<0.0001	<i>334,069.40</i>	0.036	385,475.20	-	-
	East	0.0066	334,081.00	-	-	0.059	1,028,065
Midslope ridges, small hills in plains	North	0.064	334,084.90	-	-	0.38	1,028,068
	Northeast	0.19	334,086.60	-	-	1.00	1,028,068
	Northwest	1.00	334,088.20	-	-	<0.0001	1,028,043
	South	<0.0001	334,025.60	-	-	<0.0001	1,027,990
	Southeast	<0.0001	334,049.60	-	-	<0.0001	1,028,034
	Southwest	<0.0001	<i>333,973.30</i>	-	-	<0.0001	<i>1,027,893</i>
	West	<0.0001	334,058.00	-	-	<0.0001	1,028,039
	East	-	-	-	-	<0.0001	1,028,040
	North	-	-	-	-	0.00024	1,028,055
Open slopes	Northeast	-	-	-	-	0.0011	1,028,058
	Northwest	-	-	-	-	0.011	1,028,062
	South	-	-	-	-	<0.0001	1,027,683
	Southeast	-	-	-	-	<0.0001	1,027,967
	Southwest	-	-	-	-	<0.0001	<i>1,027,523</i>
	West	-	-	-	-	<0.0001	1,027,833

*P*-value reflects test for homogeneity of the point pattern (significance indicates heterogeneous intensity of infestations across the region). Best model (i.e., lowest AIC value) for a given landscape feature in a given is indicated by *italics*.

<sup>a</sup> Canyons/deeply incised streambeds and U-shaped valleys area reported as azimuths, while remainder of landscape feature directions reflect the aspect (see Table 3.2).

Table 3.9 Spatial point process regression models estimating intensity of *D. ponderosae* infestations replacing landscape feature with direction of landscape feature as a covariate. Data is for the years 2004-2006 in the Peace River region of British Columbia. Other variables are the same as in Table 3.7.

Year	Model Parameters	Estimate	Standard Error	Z	P-value
2004	Intercept	-7.97E+00	5.80E-02	-137.4	<0.0001
	Distance from source location	-4.99E-05	4.23E-07	-117.9	<0.0001
	Local ridges - West	1.06E+00	4.47E-01	2.4	0.0087
	Midslope ridges - Southwest	1.11E+00	8.66E-02	12.8	8.20E-38
	Valleys - Northeast-southwest	5.02E-01	2.92E-02	17.2	1.33E-66
	Elevation	-3.72E-03	4.44E-05	-84.0	<0.0001
	Highly susceptible habitat	1.58E+00	2.84E-02	55.6	<0.0001
2005	Intercept	-8.17E+00	5.79E-02	-141.1	<0.0001
	Distance from source location	-4.24E-05	5.31E-07	-79.8	<0.0001
	Canyons/Deeply incised streams: North south	1.35E-01	4.97E-02	2.7	6.53E-03
	Local ridges/Hills in valleys: South	9.94E-01	3.78E-01	2.6	8.60E-03
	U-shaped Valleys: Northeast southwest	1.68E-01	2.84E-02	5.9	3.31E-09
	Elevation	-2.70E-03	3.97E-05	-67.9	<0.0001
	Highly susceptible habitat	9.09E-01	2.96E-02	30.7	2.55E-207
	Distance from 2004 treatment	-1.01E-04	1.46E-06	-69	<0.0001
2006	Intercept	-1.15E+01	3.67E-02	-312.2	<0.0001
	Distance from source location	-6.04E-06	2.48E-07	-24.4	4.47E-131
	Midslope ridges/Small hills in plains: Southwest	7.58E-01	5.28E-02	14.4	8.81E-47
	Open slopes: Southwest	5.21E-01	2.33E-02	22.4	5.10E-111
	U-shaped Valleys: Northeast southwest	2.91E-01	2.31E-02	12.6	3.47E-36
	Elevation	-1.19E-03	2.31E-05	-51.6	<0.0001
	Highly Susceptible Habitat	9.67E-01	1.90E-02	50.9	<0.0001
	Distance from 2005 treatment	-5.40E-05	7.80E-07	-69.3	<0.0001

AIC values for final models: 2004, 311,337.8; 2005, 355,773.9; 2006, 1,011,283



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## 4: CONCLUSIONS AND AREAS FOR FURTHER RESEARCH

### 4.1: Conclusions

#### 4.1.1. *Influence of Atmospheric Processes on Aeolian Dispersal*

The colonization process of trees by bark beetles is often viewed as an active, behaviourally-driven process in which the insects take flight and orient towards suitable hosts, often attracted by a stimulus such as a host kairomone (Borden 1989). However, the ability of an insect to guide itself toward a stimulus requires the ability to counter forces that oppose it such as wind. This may occur within a stand, but insect dispersal within advective currents may be more passive (Jackson et al. 2008). Meso-scale (~100 km) convective processes within the planetary boundary layer, the zone in which the earth's surface affects the atmosphere (~1-2 km above the earth's surface) (Drake and Farrow 1988; Westbrook and Isard 1999), may have largely influenced the dispersal of mountain pine beetle into the Peace River region. These processes or weather events that may have affected mountain pine beetle dispersal could have included low-level jets (LLJ), a layer of maximum wind speed in the planetary boundary layer often at a few hundred meters altitude, and convergent zones, locations at which two frontal systems cause the descent of wind in a single area (Drake and Farrow 1988). LLJ tend to occur in areas of deflected large-scale airflows by mountain ranges, such as the Northern Rocky Mountains. Insects transported by wind are often uniformly distributed horizontally, lacking convergent circulation cells, but may be vertically concentrated in a single layer such as a LLJ. Alternatively, convergent zones can cause horizontal and vertical concentration of insects at high densities within the air column. Where convergent zones are stationary or form consistently, insects will be deposited (Drake and Farrow 1988).



Rain can also cause the deposition of insects due to “wash out”, which is defined as the removal of particles or insects from the air column due to their collision with water droplets. However, washout would likely have decreased the amount of successful attack by the insects after deposition. Rain events are often associated with decreases in temperature due to cloud cover, and gusty conditions. Mountain pine beetle will generally not emerge and fly in these conditions, waiting instead for prolonged periods of warm weather (Gray et al. 1972; Tishmack et al. 2005). Mechanisms of insect convergence in the air column are critical factors determining the success of insects establishing in a new host after dispersing long-distances and could result in populations persisting in an epidemic state in locations where convergence occurs.

The long-distance transport of mountain pine beetle in the Peace River region is most likely a result of convergent frontal zones (Drake and Farrow 1988). The relatively stationary location of infestation waves between 2004 and 2005 indicates that some kind of atmospheric event occurred at that location to allow for the descent of mountain pine beetle into the area. Alternatively, this pattern could also be indicative of the suitability and distribution of hosts in the region although such a band (Chapter 2) is more reflective of a weather front than landscape features *per se* (Chapter 3).

#### ***4.1.2. Lack of Evidence for Anthropogenic Transport***

I did not find evidence that anthropogenic spread of mountain pine beetle played a major role in the establishment and spread of infestations within the Peace River region between 2004 and 2006. In particular, I found no evidence that direct anthropogenic manipulation of beetle distribution via movement and/or storage of infested host material facilitated spread of incipient-epidemic populations. This contrasts, however, with the

influence of anthropogenic activities that indirectly influenced the mountain pine beetle system (Raffa et al. 2008). For example, human alteration of fire regimes in British Columbia has facilitated large tracts of suitable hosts for mountain pine beetle to establish (Taylor and Carroll 2004). Taylor and Carroll (2004) found that in the early 1900s approximately 17% of pine stands were in age classes susceptible to mountain pine beetle, which rose markedly by 2006 to 55% of pine stands on the landscape, well outside the range of natural variability. Changes in fire suppression have altered species composition as well as age class structure, causing a three-way interaction between mountain pine beetle, its host species, and humans that has allowed mountain pine beetle to take advantage of increased availability of suitable hosts. Another human-caused process that has indirectly facilitated spread and establishment of populations of mountain pine beetle in the Peace River region of British Columbia is climate change (Carroll et al. 2004; Kurz et al. 2008; Raffa et al. 2008). The ability of mountain pine beetle to successfully establish and spread in the Peace River region has been due to an increase in summer and winter temperatures that has facilitated univoltine development as well as high over-wintering survival within populations. The contrast between direct and indirect impacts of human activities exemplifies the importance of understanding the complexity of ecosystems when applying management and control techniques of pests.

#### ***4.1.3. Establishment of Infestations at Higher Elevations***

A result of this study of particular concern is the successful establishment of infestations at higher elevations than within their native range. The elevational shift of mountain pine beetle could indicate that the host within the region is highly susceptible to attacks, the climate of such areas is conducive to the establishment of infestations (Carroll et

al. 2004), and/or that insects dispersing long-distances had a greater relative likelihood of being dispersed to higher elevation sites by convective currents in this region than in other areas. It is likely that human mitigated climate change has provided opportunity for this eruptive herbivore to move into higher elevation sites, allowing them to successfully attack and kill host trees in this novel habitat.

#### ***4.1.4. Effect of Management on Spread of Beetle Infestations***

Control tactics, including fall and burn and single tree removal, successfully diminished the short-distance dispersal potential of mountain pine beetle. However, management for long-distance dispersal is much more difficult and may require the use of alternate methods such as use of baited traps outside of host stands (e.g. in large clearings or stands of non-host species). This would allow for capture of insects dispersing long-distances while limiting “spill-over” attack that could result from luring in mountain pine beetle populations.

#### ***4.1.5. Potential for Continued Spread of Mountain Pine Beetle***

The continuing spread of mountain pine beetle is still a large concern for forest managers across Canada but particularly in northern Alberta and Saskatchewan. Although mountain pine beetle broods in northern Alberta had an 80% rate of mortality in the winter in 2008 (Alberta Sustainable Resource Development 2008), the beetle has gained a foothold in northwestern British Columbia and northern Alberta and will probably continue to exist at endemic levels for a prolonged period (Alberta Sustainable Resource Development 2008). The continued spread of the insects, either in the Peace River region or in other mountainous regions such as the southern Rocky Mountains in Colorado, will potentially be facilitated by large, low-elevation valleys orientated along the dominant wind direction, acting as conduits

of suitable habitat for the insect. The orientation of landscape features will also influence the reproduction of mountain pine beetle and susceptibility of hosts, allowing populations on warmer and drier sites to have greater rates of increase and spread into adjacent stands. In order to minimize local spread of outbreaking populations, stake holders including forestry companies and government organizations should focus control efforts and inventory on such landscape features. As demonstrated within this study, control measures are effective in decreasing localized spread of populations; however, where long-distance dispersal is present alternate control tactics may have to be employed in order to effectively deal with long-distance inputs.

#### **4.2: Areas of Further Research**

Examining the influence of pattern of landscape-scale variables on occurrence of infestations within the Peace River region provides valuable baseline information about the ability of native insects to spread beyond geoclimatic barriers (Ranta et al. 2002) such as the Rocky Mountains (Carroll et al. 2004). In particular, movement of mountain pine beetle into higher elevation sites provides another example of the alteration of fauna to the changing climate regime. Predicting the spread potential of new infestations based on landscape features and their orientation, in concert with new spread modeling approaches (e.g., Gamarra and He 2008; Zhu et al. 2008; Zheng et al. 2009), may also provide coarse-scale tools for directing control activities. However, the underlying mechanisms of spread of mountain pine beetle infestations relative to landscape features and their orientation should be further examined in the field. For example, windward-facing slopes of various landscape features should be inventoried for infestations and compared with inventory of leeward sites to examine differences in establishment rates relative to wind vectors (both within stands and

at the meso-scale) and site conditions, such as soil moisture. Deposition patterns of mountain pine beetle could also be examined relative to multiple hill topography in small-scale simulated or computer modeling experiments.

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## Appendix A: R code for fitting spatial point pattern regression models to annual inventory datasets.

---

```
#Pattern of spread by mountain pine beetle infestations in Peace River
#region of British Columbia, Canada between 2004 and 2006.
#Description: Selection of covariates for 2004, 2005, and 2006 that
#provide the most inference about intensity of mountain pine beetle
#infestations.
#####

#Load packages
library(spatstat)
library(shapefiles)
library(maptools)

#Read in shapefile data (2004, 2005, and 2006)
mpb04 <- readShapePoints("2004mpb_licensees")
mpb05 <- readShapePoints("2005mpb_licensees")
mpb06 <- readShapePoints("2006mpb_licensees")

#Extract X and Y coordinates from ShapePoints
X04 <- mpb04$Easting
Y04 <- mpb04$Northing

X05 <- mpb05$Easting
Y05 <- mpb05$Northing

X06 <- mpb06$Easting
Y06 <- mpb06$Northing

#Create object window from research area boundary
landform1 <- readAsciiGrid("tpi_utm_sus1.txt", as.image=TRUE)#Canyons
tpil <- as.im(landform1)

#Create object window for analysis from one of the susceptibility datasets
(these have been clipped by tpi raster in Arcview but are slightly smaller
that tpi boundary in some areas)
tpil.win <- as.owin(tpil)

#Convert ShapePoints to point pattern manually
xxx04 <- ppp(x=mpb04$Easting, y=mpb04$Northing, window=tpil.win)
xxx05 <- ppp(x=mpb05$Easting, y=mpb05$Northing, window=tpil.win)
xxx06 <- ppp(x=mpb06$Easting, y=mpb06$Northing, window=tpil.win)

#Read in distance dataset! Use as covariate to represent location instead
of X and Y coordinates!
distance <- readAsciiGrid("dist_source.txt", as.image=TRUE)

#Distance from roads
roads <- readAsciiGrid("roads_utm.txt", as.image=TRUE)

#Distance from rivers
rivers <- readAsciiGrid("rivers.txt", as.image=TRUE)

#Distance from mills
mills <- readAsciiGrid("mills_utm.txt", as.image=TRUE)
```



```

#Create density plot of datasets
dens2004 <- density(xxx04)
dens2005 <- density(xxx05)

#Convert covariates to images
distance <- as.im(distance)
rivers <- as.im(rivers)
mills <- as.im(mills)
roads <- as.im(roads)

###Fit models to see which best fits the dataset

#2004

##Linear gradient
fm.linear <- ppm(xxx04, ~distance, Poisson(),
covariates=list(distance=distance))
fm.homo <- ppm(xxx04, ~1, Poisson())
AIC(fm.linear)
anova(fm.linear, fm.homo, test="Chisq")

##Wave propagation
fm.wave <- ppm(xxx04, ~ I(distance^2), Poisson(),
covariates=list(distance=distance))
AIC(fm.wave)
summary(fm.wave)
sqrt(diag(vcov(fm.wave)))
anova(fm.homo, fm.wave, test="Chisq")

##Distance from roads
fm.roads <- ppm(xxx04, ~roads, Poisson(), covariates=list(roads=roads))
AIC(fm.roads)

##Distance from mills
fm.mills <- ppm(xxx04, ~mills, Poisson(), covariates=list(mills=mills))
AIC(fm.mills)

##Distance from rivers
fm.rivers <- ppm(xxx04, ~rivers, Poisson(),
covariates=list(rivers=rivers))
AIC(fm.rivers)

#2005

##Linear gradient
fm.linear <- ppm(xxx05, ~distance, Poisson(),
covariates=list(distance=distance))
fm.homo <- ppm(xxx05, ~1, Poisson())
AIC(fm.linear)

##Wave propagation
fm.wave <- ppm(xxx05, ~ I(distance^2), Poisson(),
covariates=list(distance=distance))
AIC(fm.wave)

##Stratified dispersal (distance from infestations of the previous year)

```

```

fm.strat <- ppm(xxx05, ~ dens2004, Poisson(),
covariates=list(dens2004=dens2004))
AIC(fm.strat)
summary(fm.strat)
sqrt(diag(vcov(fm.strat)))
anova(fm.homo, fm.strat, test="Chisq")

##Distance from roads
fm.roads <- ppm(xxx05, ~roads, Poisson(), covariates=list(roads=roads))
AIC(fm.roads)

##Distance from mills
fm.mills <- ppm(xxx05, ~mills, Poisson(), covariates=list(mills=mills))
AIC(fm.mills)

##Distance from rivers
fm.rivers <- ppm(xxx05, ~rivers, Poisson(),
covariates=list(rivers=rivers))
AIC(fm.rivers)

#2006

##Distance from roads
fm.roads <- ppm(xxx06, ~roads, Poisson(), covariates=list(roads=roads))
AIC(fm.roads)

##Distance from mills
fm.mills <- ppm(xxx06, ~mills, Poisson(), covariates=list(mills=mills))
AIC(fm.mills)

##Distance from rivers
fm.rivers <- ppm(xxx06, ~rivers, Poisson(),
covariates=list(rivers=rivers))
AIC(fm.rivers)

##Linear gradient
fm.linear <- ppm(xxx06, ~distance, Poisson(),
covariates=list(distance=distance))
fm.homo <- ppm(xxx06, ~ 1, Poisson())
AIC(fm.linear)

##Wave propagation
fm.wave <- ppm(xxx06, ~ I(distance^2), Poisson(),
covariates=list(distance=distance))
AIC(fm.wave)
summary(fm.wave)
sqrt(diag(vcov(fm.wave)))
vcov(fm.wave)

##Stratified dispersal (distance from infestations of the previous year)
fm.strat <- ppm(xxx06, ~ dens2005, Poisson(),
covariates=list(dens2005=dens2005))
AIC(fm.strat)# 1023605

```

---

## Appendix B: R code for contingency tests (infestations relative to landscape features)

---

```
#Contingency test - Distribution of infestations relative to landform
#Description: Compare observed distribution of infestations, by area
#infested (ha), per landform class to expected area infested per #landform
class (i.e. area infested per landform class based on a #uniform
distribution of infestations within those classes)
#####
```

### ###Observed Area Infested per Landform Class

```
#Load foreign to be able to read dbf files
library(foreign)

#Read in infestation data
data<-read.dbf("mpb_licensees.dbf")

#Examine fields in dataset
summary(data)

#Subset dataset: "Year", "Area", "HAZ_CLASS", "SPOT"
frame <- data[,c("YEAR", "Area", "SPOT")]

#Subset dataset for records by years (2004, 2005, 2006)
yr2004 <- frame[frame$YEAR=='2004',]
yr2005 <- frame[frame$YEAR=='2005',]
yr2006 <- frame[frame$YEAR=='2006',]

#Calculate area infested in each landform class (ha)
summary2004 <- aggregate(yr2004[, "Area"], by=list(Landform=yr2004$SPOT),
function(x) sum (x))
summary2005 <- aggregate(yr2005[, "Area"], by=list(Landform=yr2005$SPOT),
function(x) sum (x))
summary2006 <- aggregate(yr2006[, "Area"], by=list(Landform=yr2006$SPOT),
function(x) sum (x))
summary2004

#Rename area columns
colnames(summary2004)[2] <- "Area2004"
colnames(summary2005)[2] <- "Area2005"
colnames(summary2006)[2] <- "Area2006"

#Combine area fields into one matrix
area <- cbind(Landform=summary2004$Landform,
Area2004.Obs=summary2004$Area2004, Area2005.Obs=summary2005$Area2005,
Area2006.Obs=summary2006$Area2006)
area <- as.data.frame(area)

#Change from Number to Name of landform
area[area$Landform==1, "Landform"] <- "Canyons, deeply inci"
area[area$Landform==2, "Landform"] <- "Local ridges/hills i"
area[area$Landform==3, "Landform"] <- "Midslope drainages,"
area[area$Landform==4, "Landform"] <- "Midslope ridges, sma"
area[area$Landform==5, "Landform"] <- "Mountain tops, high"
area[area$Landform==6, "Landform"] <- "Open slopes"
area[area$Landform==7, "Landform"] <- "Plains"
```

```

area[area$Landform==8, "Landform"] <- "U-shaped valleys"
area[area$Landform==9, "Landform"] <- "Upland drainages, he"
area[area$Landform==10, "Landform"] <- "Upper slopes, mesas"
area

#Total area infested per year (2004, 2005, and 2006 in hectares)
total.04 <- sum(area[,2])
total.05 <- sum(area[,3])
total.06 <- sum(area[,4])

###2004: Expected area infested (hectares per landform class)

#Read in landform dataset that is cut to extent of mountain pine beetle
infestations in 2004
L04<-read.dbf("2004tpihull.dbf")

#Examine fields in dataset
summary(L04)

#Convert GRIDCODE to factor
L04$GRIDCODE <- as.factor(L04$GRIDCODE)

#Sum area (m2) in each landform class
sum.L04 <- aggregate(L04[,c("F_AREA")], by=list(Gridcode=L04$GRIDCODE),
function(x) sum (x))
sum.L04
colnames(sum.L04)[2] <- "Area"
L04.total <- sum(sum.L04$Area)
L04.total#(m2)

#Calculate the proportion of area occupied by each landscape feature
sum.L04$Proportion <- sum.L04$Area/L04.total
sum.L04

#Calculate expected area infested for each landform class in hectares
sum.L04$Area2004.Exp <- (total.04*sum.L04$Proportion)
sum(sum.L04$Area2004.Exp)
total.04
sum.L04

#Convert Gridcode to numeric
sum.L04$Gridcode<-as.numeric(as.character(sum.L04$Gridcode))
class(sum.L04)
summary(sum.L04)

#Replace Gridcode values with equivalent landform class
sum.L04[sum.L04$Gridcode==1, "Gridcode"] <- "Canyons, deeply inci"
sum.L04[sum.L04$Gridcode==2, "Gridcode"] <- "Midslope drainages,"
sum.L04[sum.L04$Gridcode==3, "Gridcode"] <- "Upland drainages, he"
sum.L04[sum.L04$Gridcode==4, "Gridcode"] <- "U-shaped valleys"
sum.L04[sum.L04$Gridcode==5, "Gridcode"] <- "Plains"
sum.L04[sum.L04$Gridcode==6, "Gridcode"] <- "Open slopes"
sum.L04[sum.L04$Gridcode==7, "Gridcode"] <- "Upper slopes, mesas"
sum.L04[sum.L04$Gridcode==8, "Gridcode"] <- "Local ridges/hills i"
sum.L04[sum.L04$Gridcode==9, "Gridcode"] <- "Midslope ridges, sma"
sum.L04[sum.L04$Gridcode==10, "Gridcode"] <- "Mountain tops, high"
sum.L04

```

### ###2005: Expected area infested (hectares per landform class)

```
#Read in landform dataset that is cut to extent of mountain pine beetle
infestations in 2005
L05<-read.dbf("2005tpihull.dbf")

#Sum area (m2) in each landform class
sum.L05 <- aggregate(L05[,c("F_AREA")], by=list(Gridcode=L05$GRIDCODE),
function(x) sum (x))
colnames(sum.L05)[2] <- "Area"
L05.total <- sum(sum.L05$Area)
sum.L05

#Calculate the proportion of area occupied by each landscape feature
sum.L05$Proportion <- sum.L05$Area/L05.total
sum.L05

#Calculate expected area infested for each class in hectares
sum.L05$Area2005.Exp <- total.05*sum.L05$Proportion
sum.L05

#Convert Gridcode to numeric
sum.L05$Gridcode<-as.numeric(as.character(sum.L05$Gridcode))
class(sum.L05)
summary(sum.L05)

#Replace Gridcode values with equivalent landform class
sum.L05[sum.L05$Gridcode==1, "Gridcode"] <- "Canyons, deeply inci"
sum.L05[sum.L05$Gridcode==2, "Gridcode"] <- "Midslope drainages,"
sum.L05[sum.L05$Gridcode==3, "Gridcode"] <- "Upland drainages, he"
sum.L05[sum.L05$Gridcode==4, "Gridcode"] <- "U-shaped valleys"
sum.L05[sum.L05$Gridcode==5, "Gridcode"] <- "Plains"
sum.L05[sum.L05$Gridcode==6, "Gridcode"] <- "Open slopes"
sum.L05[sum.L05$Gridcode==7, "Gridcode"] <- "Upper slopes, mesas"
sum.L05[sum.L05$Gridcode==8, "Gridcode"] <- "Local ridges/hills i"
sum.L05[sum.L05$Gridcode==9, "Gridcode"] <- "Midslope ridges, sma"
sum.L05[sum.L05$Gridcode==10, "Gridcode"] <- "Mountain tops, high"
sum.L05
```

### ###2006: Expected area infested (hectares per landform class)

```
#Read in landform dataset that is cut to extent of mountain pine beetle
infestations in 2006
L06<-read.dbf("2006tpihull.dbf")

#Sum area (m2) in each landform class
sum.L06 <- aggregate(L06[,c("F_AREA")], by=list(Gridcode=L06$GRIDCODE),
function(x) sum (x))
colnames(sum.L06)[2] <- "Area"
L06.total <- sum(sum.L06$Area)
sum.L06

#Calculate the proportion of area occupied by each landscape feature
sum.L06$Proportion <- sum.L06$Area/L06.total
sum.L06
```

```

#Calculate expected area of infestations in each class in hectares
sum.L06$Area2006.Exp <- total.06*sum.L05$Proportion
sum.L06

#Convert Gridcode to numeric
sum.L06$Gridcode<-as.numeric(as.character(sum.L06$Gridcode))

#Replace Gridcode values with equivalent landform class
sum.L06[sum.L06$Gridcode==1, "Gridcode"] <- "Canyons, deeply inci"
sum.L06[sum.L06$Gridcode==2, "Gridcode"] <- "Midslope drainages,"
sum.L06[sum.L06$Gridcode==3, "Gridcode"] <- "Upland drainages, he"
sum.L06[sum.L06$Gridcode==4, "Gridcode"] <- "U-shaped valleys"
sum.L06[sum.L06$Gridcode==5, "Gridcode"] <- "Plains"
sum.L06[sum.L06$Gridcode==6, "Gridcode"] <- "Open slopes"
sum.L06[sum.L06$Gridcode==7, "Gridcode"] <- "Upper slopes, mesas"
sum.L06[sum.L06$Gridcode==8, "Gridcode"] <- "Local ridges/hills i"
sum.L06[sum.L06$Gridcode==9, "Gridcode"] <- "Midslope ridges, sma"
sum.L06[sum.L06$Gridcode==10, "Gridcode"] <- "Mountain tops, high"
sum.L06

###Contingency test

#Combine expected and observed values in a single dataframe
chi_area <- cbind(Landform=area$Landform, Area2004.Obs=area$Area2004.Obs,
Area2005.Obs=area$Area2005.Obs, Area2006.Obs=area$Area2006.Obs,
Area2004.Exp=sum.L04$Area2004.Exp, Area2005.Exp=sum.L05$Area2005.Exp,
Area2006.Exp=sum.L06$Area2006.Exp)

#Convert from matrix to a dataframe
chi_area <- as.data.frame(chi_area)

#Convert factors to numerical data
chi_area$Area2004.Obs <- as.numeric(as.character(chi_area$Area2004.Obs))
chi_area$Area2005.Obs <- as.numeric(as.character(chi_area$Area2005.Obs))
chi_area$Area2006.Obs <- as.numeric(as.character(chi_area$Area2006.Obs))

chi_area$Area2004.Exp <- as.numeric(as.character(chi_area$Area2004.Exp))
chi_area$Area2005.Exp <- as.numeric(as.character(chi_area$Area2005.Exp))
chi_area$Area2006.Exp <- as.numeric(as.character(chi_area$Area2006.Exp))

#Double check: Do total area infested in observed equal expected total
area infested per year? Yes!
sum(chi_area$Area2006.Obs)
sum(chi_area$Area2006.Exp)

#Subset expected and observed values for each year
chi2004 <- chi_area[1:10,c("Area2004.Exp", "Area2004.Obs")]
chi2005 <- chi_area[1:10,c("Area2005.Exp", "Area2005.Obs")]
chi2006 <- chi_area[1:10,c("Area2006.Exp", "Area2006.Obs")]

#Chi-squared test (Is the distribution of mountain pine beetle
infestations greater in some landforms relative to an expected uniform
distribution?)
chisq.test(chi2004)
chisq.test(chi2005)
chisq.test(chi2006)

```

---

## Appendix C: R code for contingency tests (infestations relative to susceptible habitat)

---

```
#Contingency test - Distribution of infestations relative to #susceptible
habitat
#Description: Compares observed distribution of infestations, by area
#infested (ha) per susceptibility class relative to expected (i.e. area
#infested per susceptibility class based on a uniform distribution of
#infestations within those classes).
#####

###Observed Area Infested per Susceptibility Class

#Load foreign to be able to read dbf files
library(foreign)

#Read in data for infested stands
data<-read.dbf("mpb_licensees.dbf")

#Subset dataset: "YEAR","AREA", "HAZ", "HAZ_CLASS"
frame <- data[,c("YEAR","Area", "HAZ", "HAZ_CLASS")]

#Subset dataset: three years (2004, 2005, 2006)
yr2004 <- frame[frame$YEAR=='2004',]
yr2005 <- frame[frame$YEAR=='2005',]
yr2006 <- frame[frame$YEAR=='2006',]

#Calculate area infested per class
area04 <- aggregate(yr2004[,c("Area")],
by=list(HazardCl=yr2004$HAZ_CLASS), function(x) sum (x))
area05 <- aggregate(yr2005[,c("Area")],
by=list(HazardCl=yr2005$HAZ_CLASS), function(x) sum (x))
area06 <- aggregate(yr2006[,c("Area")],
by=list(HazardCl=yr2006$HAZ_CLASS), function(x) sum (x))
area04

#Rename area columns
colnames(area04)[2] <- "Area2004"
colnames(area05)[2] <- "Area2005"
colnames(area06)[2] <- "Area2006"
summary(area04)

#Convert "HazardCl" (i.e susceptibility class) to numeric
area04$HazardCl <- as.numeric(as.character(area04$HazardCl))
summary(area04)

#Combine area fields into one matrix
area <- cbind(HazardCl=area04$Hazard,Area2004.Obs=area04$Area2004,
Area2005.Obs=area05$Area2005, Area2006.Obs=area06$Area2006)
area
total.04 <- sum(area[,2])
total.05 <- sum(area[,3])
total.06 <- sum(area[,4])
total.04
total.05
total.06
###2004: Expected area infested (hectares per susceptibility class)
```

```

landscape04<-read.dbf("2004hazhull.dbf")

#Subset "HAZ_CLASS" and "area_clip" columns
L04 <- landscape04[,c("HAZ_CLASS","Area_calc")]

#Sum area (meters squared) in each hazard class
sum.L04 <- aggregate(L04[,c("Area_calc")],
by=list(HazardCl=L04$HAZ_CLASS), function(x) sum (x))
colnames(sum.L04)[2] <- "Area"
sum <- sum(sum.L04$Area)
sum

#Simplify (find proportion)
sum.L04$Proportion <- sum.L04$Area/sum
sum.L04

#Create a column with total.04 as the only number in all rows
sum.L04$Total <- total.04
sum.L04

#Calculate expected area (ha) infested per class based on proportion of
that class on landscape
sum.L04$Area2004.Exp <- (sum.L04$Total*sum.L04$Proportion)
sum.L04

    ###2005: Expected area infested (hectares per susceptibility class)

landscape05<-read.dbf("2005hazhull.dbf")
landscape05[1:5,]

#Subset "HAZ_CLASS" and "area_clip" columns
L05 <- landscape05[,c("HAZ_CLASS","Area_calc")]

#Were all data imported?
dim(L05)

#Sum area (meters squared) in each hazard class
sum.L05 <- aggregate(L05[,c("Area_calc")],
by=list(HazardCl=L05$HAZ_CLASS), function(x) sum (x))
colnames(sum.L05)[2] <- "Area"
sum05 <- sum(sum.L05$Area)
sum05

#Simplify (find proportion)
sum.L05$Proportion <- sum.L05$Area/sum05
sum.L05

#Calculate expected area of infested in each class based on proportion
area in each class on landscape
sum.L05$Area2005.Exp <- total.05*sum.L05$Proportion
sum.L05

    ###2006: Expected area infested (hectares per landform class)

landscape06<-read.dbf("2006hazhull.dbf")
landscape06[1:5,]

```



```

#Subset "HAZ_CLASS" and "area_clip" columns
L06 <- landscape06[,c("HAZ_CLASS", "Area_calc")]

#Were all data imported?
dim(L06)

#Sum area (meters squared) in each hazard class
sum.L06 <- aggregate(L06[,c("Area_calc")],
by=list(HazardCl=L06$HAZ_CLASS), function(x) sum (x))
colnames(sum.L06)[2] <- "Area"
sum06 <- sum(sum.L06$Area)

#Simplify (find proportion)
sum.L06$Proportion <- sum.L06$Area/sum06
sum.L06

#Calc. expected area of infestations in each hazard class based on
proportion area per hazard class on landscape
sum.L06$Area2006.Exp <- total.06*sum.L05$Proportion
sum.L06

###Contingency test

#Combine exp and observed area columns fields into a single matrix
overall <- cbind(HazardCl=area04$Hazard, Area2004.Obs=area04$Area2004,
Area2004.Exp=sum.L04$Area2004.Exp, Area2005.Obs=area05$Area2005,
Area2005.Exp=sum.L05$Area2005.Exp, Area2006.Obs=area06$Area2006,
Area2006.Exp=sum.L06$Area2006.Exp)

#View result
overall

#Convert to data frame
overall <- as.data.frame(overall)

#Subset expected and observed values for each year
chi2004 <- overall[,c("Area2004.Exp", "Area2004.Obs")]
chi2005 <- overall[,c("Area2005.Exp", "Area2005.Obs")]
chi2006 <- overall[,c("Area2006.Exp", "Area2006.Obs")]
chi2004

#Double check: Do total area infested in observed equal expected total
area infested per year? Yes!
sum(overall$Area2006.Obs)
sum(overall$Area2006.Exp)

#Chi-squared test (Is the distribution of mountain pine beetle
infestations greater in some hazard classes relative to an expected
uniform distribution?)
chisq.test(chi2004)
chisq.test(chi2005)
chisq.test(chi2006)

```

---

## Appendix D: Example R code for bootstrapping

---

```
#Bootstrapping of contingency tests for stand susceptibility classes
#H0. The distribution of infestations is random relative to #susceptibility
classes
#Description: Compare distribution of infestations to a random
#distribution 1000 times for 2004 dataset
#####

#Start of program
for(i in 1:1000)
{
  cat(c("Test", i))

#Load foreign package (have to read .dbf first otherwise other packages
mask read.dbf function
library(foreign)

#Read in observed infestation data
data<-read.dbf("mpb_licensees.dbf")
data <- as.data.frame(data)

#Change column names: "dbf.YEAR", "dbf.Area", "dbf.HAZ", and
"dbf.HAZ_CLASS"
colnames(data)[6] <- "YEAR"
colnames(data)[3] <- "Area"
colnames(data)[4] <- "HAZ"
colnames(data)[5] <- "HAZ_CLASS"

#Subset dataset: "YEAR","AREA", "HAZ", "HAZ_CLASS"
frame <- data[,c("YEAR", "Area", "HAZ", "HAZ_CLASS")]

#Remove "data"
rm(data)

#Subset 2004 dataset
yr2004 <- frame[frame$YEAR=='2004',]

#Remove "frame"
rm(frame)

#Calculate area infested in each susceptibility class (i.e. HAZ_CLASS)
in hectares actual2004 <- aggregate(yr2004[, "Area"],
by=list(HazardClass=yr2004$HAZ_CLASS), function(x) sum (x))
actual2004

#Subset 2004 area column
area.yr2004 <- yr2004[,c("YEAR", "Area")]

#Randomize areas
random <- area.yr2004[sample(nrow(area.yr2004)), ]

#Remove "data"
rm(area.yr2004)

#Load spatial data packages
library(shapefiles)
```

```

library(maptools)
library(maps)

#Read in shapefile with extent of infested area
bndy2004 <- read.shape("2004hull_buf25clip")

#Convert shapefile to polygon
bndy2004.poly <- Map2poly(bndy2004)

#Read in susceptibility polygon data (creates a SpatialPolygonDataFrame)
susceptibility2004 <- readShapePoly("2004hazhull")

#Generate a shapefile of random points in infested area (bndy2004)
random.pnts04 <- dotsInPolys(bndy2004.poly, nrow(yr2004), f="random",
compatible=FALSE)

#Query hazard class for each point
query.haz <- overlay(susceptibility2004, random.pnts04)
summary(query.haz)

#Remove "landforms2004" and "random.pnts04"
rm(susceptibility2004, random.pnts04)

#Join randomized area column to query.landforms
final <-cbind(HazardClass=query.haz$HAZ_CLASS, Area=random$Area)
final <- as.data.frame(final)
summary(final)

#Calculate area infested in each hazard class (ha; RANDOM).
random2004 <- aggregate(final[, "Area"],
by=list(HazardClass=yr2004$HAZ_CLASS), function(x) sum (x))

#Join RANDOM and ACTUAL areas in a single dataframe
final2004 <- cbind(HazardClass=random2004$HazardClass,
ExpectedArea=random2004$x, ObservedArea=actual2004$x)
final2004 <- as.data.frame(final2004)

#Prepare chi-squared dataframe
chi2004 <- final2004[,c("ExpectedArea", "ObservedArea")]

#Chi-squared test (expected = random infestations, observed = actual
infestations) and write results of consecutive analyses to a single file
without over writing other previous (APPEND)
chi <- chisq.test(chi2004)
chi.clean <- c(chi$statistic, chi$parameter, chi$p.value)
write(chi.clean, "//home/honey/Transfer_linux/Output/2004SR_suscept.txt",
append=TRUE, sep="\t")

#Trigger garbage collection
cat(c("End", i, "Memory",gc()))

#Delete All Objects
rm(list=ls())

#Detach 'shapefiles' package so this it doesn't mask foreign package
detach(3)

```

```
#End loop  
}
```

---

## Appendix E: Example R code for selection of spatial point process models

---

```
#Influence of covariates on occurrences of mountain pine beetle
#infestations in the Peace River region of British Columbia
#Description: Backwards selection of covariates for 2004 point process
#models
#####

#Load packages
library(spatstat)
library(shapefiles)
library(maptools)

#Read in shapefile data (2004, 2005, and 2006)
mpb04 <- readShapePoints("2004mpb_licensees")

#Extract X and Y coordinates from ShapePoints
X04 <- mpb04$Easting
Y04 <- mpb04$Northing

#Creat object window from research area boundary
landform1 <- readAsciiGrid("tpi_utm_sus1.txt", as.image=TRUE)#Canyons #or
deeply incised streams
tpil <- as.im(landform1)

#Create object window for analysis from one of the susceptibility datasets
(these have been clipped by tpi and susceptibility rasters in Arcview)
tpil.win <- as.owin(tpil)

#Convert ShapePoints to point pattern manually
xxx04 <- ppp(x=mpb04$Easting, y=mpb04$Northing, window=tpil.win)

#Read in elevation data (ASCII)
elevation <- readAsciiGrid("ddcutm_sus.txt", as.image=TRUE)

##Read in landform covariates (ASCII)
#Canyons or deeply incised streams (north-south orientation)
lflns <- readAsciiGrid("lflns.txt", as.image=TRUE)
#U-shaped Valleys (northeast-southwest orientation)
lf4nesw <- readAsciiGrid("lf4nesw.txt", as.image=TRUE)
#Local ridges or hills in valleys (western aspect)
lf8w <- readAsciiGrid("lf8w.txt", as.image=TRUE)
#Midslope ridges or small hills in plains (southwest aspect)
lf9sw <- readAsciiGrid("lf9sw.txt", as.image=TRUE)

#Read in susceptibility covariate (ASCII)
sus5 <- readAsciiGrid("sus5.txt", as.image=TRUE)

#Read in distance dataset. Use as covariate to represent location instead
of X and Y coordinates.
distance <- readAsciiGrid("dist.txt", as.image=TRUE)

#Convert covariates from list class to image class
elevation.im <- as.im(elevation)
lflns <- as.im(lflns)
lf4nesw <- as.im(lf4nesw)
lf8w <- as.im(lf8w)
```

```

lf9sw <- as.im(lf9sw)
sus5 <- as.im(sus5)
distance <- as.im(distance)

#Extract sus0's object window
sus5.win <- as.owin(sus5)

#Use cut command to make landform and susceptibility a factor!
sus5 <- cut(sus5, 2)
lflns <- cut(lflns, 2)
lf4nesw <- cut(lf4nesw, 2)
lf8w <- cut(lf8w, 2)
lf9sw <- cut(lf9sw, 2)

###Model with all covariates
final2004 <- ppm(xxx04, ~ distance + NS.Canyons + NESW.Ushapedvalleys +
W.Localridges + SW.Midsloperidges + Elevation + High.Susceptibility,
Poisson(), covariates = list(distance=distance, NS.Canyons=lflns,
NESW.Ushapedvalleys=lf4nesw, W.Localridges=lf8w, SW.Midsloperidges=lf9sw,
Elevation=elevation.im, High.Susceptibility=sus5))

summary(final2004)
AIC(final2004)
vcovmatrix <- vcov(final2004, what="vcov")
sqrt(diag(vcovmatrix))

## fm2004.1 <- ppm(xxx04, ~ distance + NS.Canyons + NESW.Ushapedvalleys +
W.Localridges + SW.Midsloperidges + Elevation, Poisson(), covariates =
list(distance=distance, NS.Canyons=lflns, NESW.Ushapedvalleys=lf4nesw,
W.Localridges=lf8w, SW.Midsloperidges=lf9sw, Elevation=elevation.im))

AIC(fm2004.1)
anova(fm2004.1, final2004, test="Chisq")

## fm2004.2 <- ppm(xxx04, ~ distance + NS.Canyons + NESW.Ushapedvalleys +
W.Localridges + SW.Midsloperidges, Poisson(), covariates =
list(distance=distance, NS.Canyons=lflns, NESW.Ushapedvalleys=lf4nesw,
W.Localridges=lf8w, SW.Midsloperidges=lf9sw))

AIC(fm2004.2)
anova(fm2004.2, fm2004.1, test="Chisq")

fm2004.3 <- ppm(xxx04, ~ distance + NS.Canyons + NESW.Ushapedvalleys +
W.Localridges, Poisson(), covariates = list(distance=distance,
NS.Canyons=lflns, NESW.Ushapedvalleys=lf4nesw, W.Localridges=lf8w))

AIC(fm2004.3)
anova(fm2004.3, fm2004.2, test="Chisq")

fm2004.4 <- ppm(xxx04, ~ distance + NS.Canyons + NESW.Ushapedvalleys,
Poisson(), covariates = list(distance=distance, NS.Canyons=lflns,
NESW.Ushapedvalleys=lf4nesw))

AIC(fm2004.4)
anova(fm2004.4, fm2004.3, test="Chisq")

```

```
fm2004.5 <- ppm(xxx04, ~ distance + NS.Canyons, Poisson(), covariates =  
list(distance=distance, NS.Canyons=lflns))  
  
AIC(fm2004.5)  
anova(fm2004.5, fm2004.4, test="Chisq")  
  
fm2004.6 <- ppm(xxx04, ~ distance, Poisson(), covariates =  
list(distance=distance))  
  
AIC(fm2004.6)# 324185.7  
anova(fm2004.6, fm2004.5, test="Chisq")  
  
fm2004.7 <- ppm(xxx04, ~ 1, Poisson(), covariates=list(distance=distance))  
  
AIC(fm2004.7)#  
anova(fm2004.7, fm2004.6, test="Chisq")
```

---

Appendix F: Contingency tests examining the pattern of infestation relative to landscape features and susceptible habitat.

---

Results of contingency tests results indicate a significant difference between observed area infested per landscape feature and susceptibility classes, assuming uniform distribution of infested area per class. The expected area per classes was calculated based on the proportion of that class available within the research area. Results indicate that in 2004 U-shaped valleys, canyons or deeply incised streams, local ridges or hills in valleys, and midslope ridges or small hills in plains had more area infested than expected (Table F1 and Fig. F1). In 2005, U-shaped valleys, canyons or deeply incised streams, and midslope ridges or small hills in plains exhibited more area infested than expected. This pattern persisted for U-shaped valleys, canyons or deeply incised streams, local ridges or hills in valleys, midslope ridges or small hills in plains, as well as open slopes, in 2006.



## **Figure Captions**

Figure F1 Differences between expected and observed area (in hectares) infested by mountain pine beetle per (A) type of landscape feature and (B) stand susceptibility class within the Peace River region of British Columbia for initial year of recorded incipient-epidemic populations.

Fig. F1

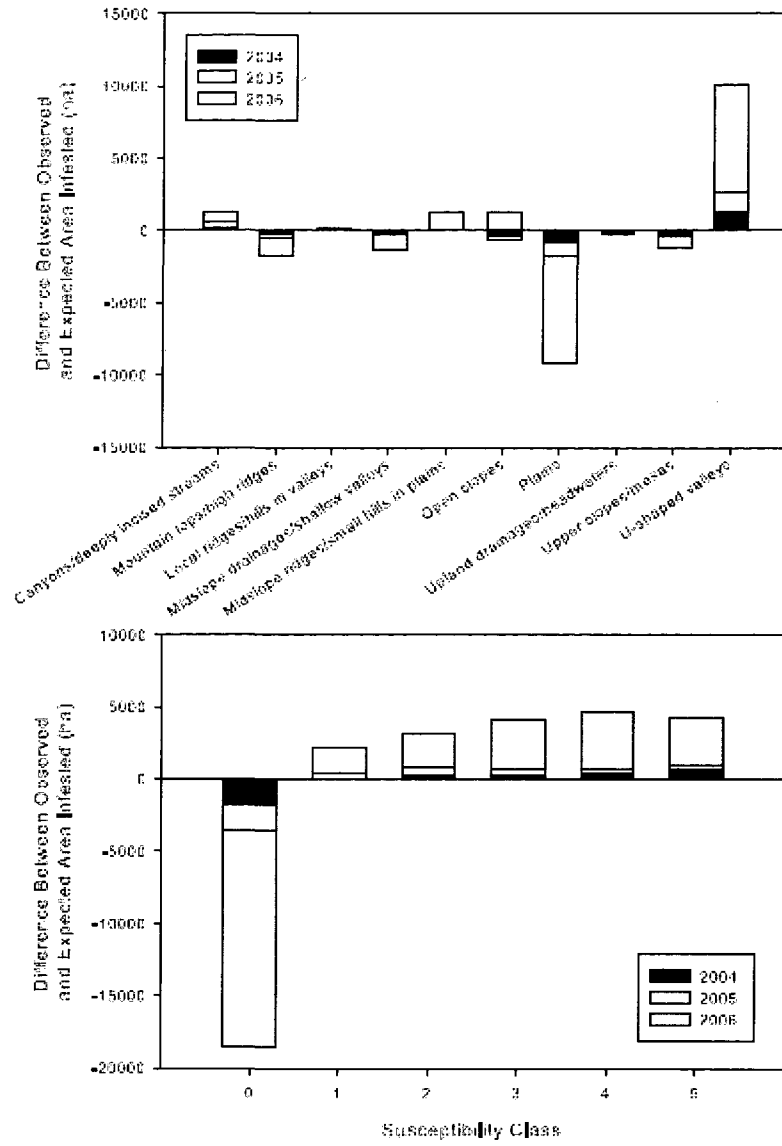


Table F1 Test statistics and *p*-values for contingency tests examining the effect of landscape features and distribution of highly susceptible habitat on the occurrence of mountain pine beetle infestations, assuming a uniform distribution across classes. Data is for the years 2004-2006 in the Peace River region of British Columbia.

Year	df	Influence of Type of Landscape Feature		Influence of Habitat Susceptibility	
		$\chi^2$	<i>P</i> -value	$\chi^2$	<i>P</i> -value
2004	9	1937.81	0.001	1,930.21	0.001
2005	9	2068.00	0.001	1,870.20	0.001
2006	9	9022.51	0.004	13,605.73	0.001