# SPATIAL AND TEMPORAL ANALYSES OF BARK BEETLE POPULATION DYNAMICS IN SOUTHERN BRITISH COLUMBIA: STAND-LEVEL STUDIES OF THE BOLE-INFESTING ASSEMBLAGE DURING ERUPTIVE TRANSITIONS OF MOUNTAIN PINE BEETLE, *DENDROCTONUS PONDEROSAE* HOPKINS

by

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B.Sc., University of Northern British Columbia, 2008

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#### ABSTRACT

Factors that trigger population transitions of mountain pine beetle from endemic to incipient-epidemic levels are poorly understood. The population dynamics of this insect may be influenced by associations with trees colonized by other bark beetles. This study explores the spatial and temporal relationships between mountain pine beetle and non-eruptive bark beetle species in lodgepole pine stands of southern British Columbia. Increasing populations of non-eruptive bark beetles were positively correlated with each other, and with endemic mountain pine beetle. Endemic and incipient-epidemic levels of mountain pine beetle were often positively spatially associated with the bark beetles *Pseudips mexicanus, Orthotomicus latidens, Ips pini*, and *Hylurgops* species, which themselves frequently colonized the same host trees. As populations grew, mountain pine beetle shifted from attacking injured/previously colonized hosts to uncolonized hosts. Identifying these potential triggers of population phase transitions may help prevent future epidemics in areas of economic importance.

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#### CHAPTER 1

#### General Introduction

The weevils (Coleoptera: Curculionidae) comprise the largest of the beetle families. With more than 50,000 species worldwide, they are easily the largest family of all animals (Ohsawa 2005). Nearly all curculionids feed on living or dead plants, with many specializing on woody material. The diverse group of curculionids known as bark beetles (Curculionidae, Scolytinae) primarily feed within the subcortical region of their host trees (Coulson 1979, Wood 1982a). Excluding a brief period of host-seeking dispersal, these insects complete their entire life cycle in or under the bark or within the cones of their host (Rudinsky 1962).

Bark beetles are vital components of forest ecosystems as they contribute to the breakdown and turnover of senescent, weakened, dying, and dead trees (Wood 1982a). Turnover activity is a key component of forest succession and is essential for the perpetuation of forests with vigorously growing trees (Mattson and Addy 1975, Lundquist 1995, Jones et al. 1997). However, many bark beetles, as agents of ecological disturbance (Raffa and Berryman 1987), may increasingly pose a threat to previously unsuitable habitats in concert with a changing climate (Carroll et al. 2004, Hicke et al. 2006).

Bark beetles have been informally classified as "primary" or "secondary" species, depending on the characterization of their colonization behaviour (Rudinsky 1962, Wood 1982a). "Primary" bark beetles are generally more aggressive species that are capable of overcoming the defenses of healthy trees. Typically, under outbreak conditions, primary bark beetles rely on the death of their host in order to successfully complete their life cycle (Berryman 1972). Large population fluctuations of primary bark beetles tend to be intermittent. In outbreak situations, these eruptive herbivores can cause landscape-level mortality to mature trees (Amman 1977, Wood 1982b, Safranyik and Carroll 2006).

"Secondary" species typically reproduce in material from weakened or dying host trees, including those damaged by fire, lightning, windthrow, drought, disease, and defoliation, as well as those suppressed by competition (Rudinsky 1962, Wood 1982a). Subsistence in weakened trees is not universally true, however. For example pine engraver beetle, *Ips pini* (Say) may kill healthy trees on occasion when populations reach sufficient numbers (Paine et al. 1997, Steed and Wagner 2004).

Even though records of outbreaks date back only to the early 1900's, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is believed to have been inhabiting pine ecosystems in western North America for millennia (Amman 1977, Seybold et al. 2000, Taylor and Carroll 2004). The insect is capable of colonizing both native and exotic species of pine within its range (Furniss and Schenk 1969, Cerezke 1995). In outbreak stages, adult beetles are able to overwhelm the defenses of vigorous host trees through mass attacks mediated by pheromones (Vité and Pitman 1968, Raffa and Berryman 1983) and by innoculating hosts with mutualistic fungi (Francke-Grossman 1967, Berryman 1972, Safranyik et al. 1974). These fungi are transported in specialized cuticular structures called mycangia (Paine et al. 1997). Fungi exhaust the defensive capacity of host trees, and may also provide nutritional benefits for phloem-feeding larvae (Ayres et al. 2000, Bleiker and Six 2007).

Development of mountain pine beetle is temperature-dependent. Adults typically emerge in late July through August, disperse via flight, and seek new hosts (Rasmussen 1974, Bentz et al. 1991). Female beetles construct straight vertical galleries and lay individual eggs within niches along the sides of these galleries (Furniss and Carolin 1977). Mountain pine beetles typically require one year to complete their life cycle, overwintering as larvae or adults (Furniss and Carolin 1977). Semivoltine populations may be found in areas of higher elevations or cool summer temperatures. Bivoltinism is also possible in some areas (Bentz et al. 2001), as low-elevation sugar pine, *Pinus lambertiana*, of California, may produce two generations per year (Furniss and Carolin 1977, Amman et al. 1990).

The current outbreak of mountain pine beetle within the Canadian provinces of British Columbia and Alberta as well as the northwestern United States has overwhelmed an unprecedented number of pine hosts. The British Columbia Ministry of Forests has reported that the cumulative area of attacked trees within British Columbia alone extends over 16.3 million hectares, comprising the vast majority of the mature lodgepole pine, *Pinus contorta* Douglas ex Louden, in the province (Westfall and Ebata 2009). Most disconcerting are the facts that the beetle has breached the historic Rocky Mountain geoclimatic barrier (Robertson et al. 2009, de la Giroday et al. 2010), is capable of reproducing in jack pine, *Pinus banksiana* Lamb. (Furniss and Schenk 1969, Cerezke 1995), and, with increased climatic suitability, poses a threat to Canada's boreal forest (Nealis and Peter 2008, Safranyik et al. 2010).

The economic impact of outbreaks by mountain pine beetle has fostered extensive

research focusing on the epidemic phase of the insect (Amman 1972, Safranyik et al. 1974, Berryman 1976, Thomson and Shrimpton 1984, Logan et al. 1998). A great deal is known about the biology of mountain pine beetle (Lyon 1958, Lanier and Wood 1968, Furniss and Carolin 1977, Safranyik 1988, Bentz et al. 1991, Pureswaran and Borden 2003, Safranyik and Carroll 2006, Safranyik et al. 2010) and its host selection behaviour at epidemic levels (Cole and Amman 1969, Geiszler et al. 1980, Hynum and Berryman 1980, Moeck et al. 1981, Raffa and Berryman 1982, Moeck and Simmons 1991, Pureswaran and Borden 2005). However, beetle populations are typically found at very low levels in endemic phases. Endemic populations are found in isolated pockets across the landscape and have been defined to consist of approximately forty beetles per hectare (Carroll et al. 2006). Consequently, the amount of research pertaining to the endemic phase is severely limited, as finding endemic beetles often poses a significant challenge (Tkacz and Schmitz 1986, Bartos and Schmitz 1998, Carroll et al. 2006).

Drawing on the knowledge of the behaviour of epidemic mountain pine beetle, it seems unlikely that endemic level beetles would be capable of successfully attacking vigorous hosts since their population densities do not reach the numbers required for mass attack (Raffa and Berryman 1983). Endemic populations must, therefore, be restricted to weakened and dying host trees that are unable to mount a sustained defensive response against colonization. Consequently, we might expect endemic levels of mountain pine beetle to behave much like secondary bark beetles. Secondary bark beetles may interact competitively with endemic mountain pine beetle and inhibit its reproductive success, or,

alternatively, may facilitate the persistence of endemic populations (Carroll et al. 2006).

A great deal is known about secondary bark beetles, their pheromones, and their interactions with other bark beetles and/or predators, particularly species from the *Ips* genus (e.g., Miller and Borden 1985, Miller et al. 1991, Miller and Borden 1992, Seybold et al. 1995, Poland and Borden 1998, Savoie et al. 1998, Aukema and Raffa 2000, Pureswaran et al. 2000, Erbilgin et al. 2002, Aukema et al. 2004). Secondary bark beetles may limit the reproductive success of mountain pine beetle at epidemic levels through interspecific competition (Bergvinson and Borden 1991, Rankin and Borden 1991, Safranyik et al. 1999, Boone et al. 2008) or they may partition host resources to limit competition as has been proposed in other bark beetle systems (Paine et al. 1981, Wagner et al. 1985, Byers 1989, Raffa 1991, Schlyter and Anderbrant 1993, Ayres et al. 2001). In either case, the interactions between endemic populations of mountain pine beetle and other bark beetles have not been well studied (Carroll et al. 2006, Smith et al. 2009). Thus, I examined the population dynamics and spatial interactions of the primary bark beetle mountain pine beetle with a number of secondary bark beetles including *Pseudips mexicanus* (Hopkins), *Orthotomicus* latidens (LeConte), Hylurgops porosus (LeConte), H. rugipennis (Mannerheim), I. pini, and D. murrayanae (Hopkins) in lodgepole pine stands undergoing population eruptions of mountain pine beetle from the endemic to the incipient-epidemic phase.

Ecological interactions can be assessed on a series of spatial and temporal scales, depending on the system. In forest systems, ecological interactions may occur at the tree, stand, and landscape levels, over a broad spectrum of time scales from days to decades. Coulson (1979) and White and Powell (1997) identified some challenges of studying bark beetles, such as defining a framework for studies of population dynamics. This research focused primarily on stand-level interactions over the course of several years.

In my thesis, I primarily used data collected from a study pioneered by Allan Carroll, formerly with the Canadian Forest Service of Natural Resources Canada. In this study, endemic to incipient-epidemic level phase transitions of populations of mountain pine beetle were monitored in seven lodgepole pine stands over the course of five years. In the first data chapter (Chapter 2), I examined the temporal interactions between secondary bark beetle species and mountain pine beetle. In the second data chapter (Chapter 3), I explored the interactions of secondary bark beetles with mountain pine beetle and looked at the growth of incipient populations of mountain pine beetle. The third data chapter (Chapter 4), examined the spatial relationships between secondary bark beetles and their associations with vigourimpaired trees during the endemic to incipient-epidemic phase transition of mountain pine beetle. General conclusions explore the significance of the results with respect to implications for prospective management. The appendices contain a summary of stand characteristics and colonization by bark beetles of the bole-infesting assemblage, as well as supplementary data for each chapter. The final appendix contains a laboratory bioassay that explored whether endemic populations of mountain pine beetle preferentially select trees colonized by *P. mexicanus*. Starved beetles were used as surrogates for endemic insects.

This thesis was written in a format where each chapter, though interrelated, is meant to be a stand-alone entity that will be disseminated to a peer reviewed journal upon successful thesis defense. As such, a small degree of ovlerlap may occur across chapters, especially in providing research context, in order to maintain chapter integrity.

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#### **CHAPTER 2**

Temporal associations between Dendroctonus ponderosae and non-eruptive species of bark

beetles in stands of lodgepole pine in southern British Columbia

### ABSTRACT

The majority of our knowledge of the ecology of mountain pine beetle, *Dendroctonus* ponderosae Hopkins, originates from studies of epidemic-level populations. Less is known about what factors might trigger population transitions from endemic to incipient-epidemic levels. The population dynamics of mountain pine beetle may be influenced by associations with trees colonized by secondary bark beetles, particularly when the former is at endemic levels and existing in habitat colonized by the latter. Temporal relationships between mountain pine beetle and species of secondary bark beetles comprising part of the boleinfesting bark beetle assemblage were examined over five years in seven lodgepole pine stands of southern British Columbia where mountain pine beetle was erupting from endemic to epidemic levels. Prior to the transition of populations of mountain pine beetle from endemic to incipient-epidemic levels, the number of trees attacked by secondary bark beetles increased. Increasing populations of secondaries were positively correlated with each other, and with increasing populations of endemic mountain pine beetle in all stands. Identifying potential triggers of population phase transitions may enable the minimization of mountain pine beetle epidemics in areas of economic, cultural, aesthetic, and/or recreational importance.

#### Key words: population dynamics; temporal dependence; interspecific competition

#### INTRODUCTION

Populations of phytophagous insects rise and fall under the influence of endogenous and exogenous pressures, and may exhibit points of stable equilibrium, cyclic oscillations, or a lack of periodicity (May 1974). Periodic oscillations, for example, are often seen in lepidopteran defoliator systems such as gypsy moth, *Lymantria dispar* (L.) (Williams and Liebhold 1995, Johnson et al. 2005), larch budmoth, *Zeiraphera diniana* (Guenée) (Baltensweiler and Fischlin 1988), spruce budworm, *Choristoneura fumiferana* (Clemens) (Blais 1965), and forest tent caterpillar, *Malacosoma disstria* (Hübner) (Cooke and Lorenzetti 2006). Aperiodical population fluctuations are often found in tree-killing bark beetle systems, and generally occur in an eruptive manner. Primary examples include southern pine beetle, *Dendroctonus frontalis* (Zimmerman), spruce bark beetle, *Ips typographus* (L.) (Økland and Bjørnstad 2006), and mountain pine beetle, *D. ponderosae* Hopkins (Raffa et al. 2008), a species of particular relevance to this study.

Mountain pine beetle is an eruptive species of bark beetle with a broad geographic range stretching across much of western North America (Safranyik and Carroll 2006). It is capable of colonizing nearly every species of native and introduced pine within this range (Furniss and Schenk 1969, Smith et al. 1981, Cerezke 1995, Carroll et al. 2004). British Columbia is currently experiencing the largest outbreak of mountain pine beetle in recorded history (Westfall and Ebata 2009). At outbreak levels, mass attacks coordinated by pheromones, in concert with vectored fungi, enable the beetles to overwhelm the defenses of healthy, large-diameter trees (Wood 1982a, Raffa and Berryman 1983). Mass attacks are promoted by synchronous emergence of adults between late July and early August, achieved through temperature-dependent development (Rasmussen 1974, Bentz et al. 1991, Safranyik et al. 2010). Outbreaks generally begin to decline with the depletion of mature hosts capable of sustaining an epidemic, sometimes in concert with mortality of brood caused by cold winter temperatures and larval desiccation (Reid 1963, Cole and Amman 1969, Safranyik et al. 1974, Amman 1984, Safranyik and Linton 1998, Régnière and Bentz 2007, Sambaraju et al. 2011). As mountain pine beetle populations begin to decline, they may also be outcompeted by other species such as *I. pini* (Say) whose populations build up in the tops of hosts killed by mountain pine beetle (Furniss and Carolin 1977, Rankin and Borden 1991).

Although the decline of outbreaks of mountain pine beetle is fairly well understood, there are still questions surrounding the growth of endemic populations. Mountain pine beetle populations typically exist for long periods at endemic phases. Researchers have long puzzled over what triggers an outbreak and why populations may persist at endemic levels in one area, but erupt in another (Logan et al. 1998), or erupt simultaneously over large areas (Aukema et al. 2006). Despite best efforts, hazard rating systems frequently fail to predict the risk of tree mortality by mountain pine beetle (Bentz 1993, Nelson et al. 2008). Favourable conditions for beetle reproduction include successive warm summers, mild winters, and stress events such as drought (Reid 1963, Safranyik et al. 1974). It is believed that when such conditions coincide with an adequate number of mature hosts, mountain pine beetle may enter the incipient-epidemic phase (Carroll et al. 2006). Because endemic mountain pine

theory of facilitation between "secondary" bark beetles and this primary bark beetle is beginning to emerge (Carroll et al. 2006).

"Secondary" species of bark beetles reproduce in the phloem of weakened, dead, and dying trees (Wood 1982a). Most species of secondary bark beetles remain at relatively low population levels, and contribute to the break-down and turnover of senescent and dead trees (Wood 1982a). Secondary species of bark beetles that may share hosts with mountain pine beetle in British Columbia include *D. murrayanae* (Hopkins), *Hylurgops porosus* (LeConte), *H. rugipennis* (Mannerheim), *I. pini* (Say), *Orthotomicus latidens* (LeConte), and *Pseudips mexicanus* (Hopkins). Many of these species are multivoltine, and, although their emergence and flight periods vary considerably, generally precede mountain pine beetle's flight in late summer (Schenk and Benjamin 1969, Miller and Borden 1985, Safranyik et al. 2000, Safranyik et al. 2004, Safranyik and Carroll 2006, Furniss and Kegley 2008, Smith et al. 2009).

This study examined the temporal interactions between endemic level mountain pine beetle and several species of secondary bark beetles as populations begin to build toward an epidemic. The current study explored five years of bark beetle colonization within seven lodgepole pine stands in two sites in southern British Columbia immediately prior to a population eruption of mountain pine beetle. The population dynamics of endemic mountain pine beetle within each stand were examined to identify any temporal associations with secondary bark beetle species during the transition from the endemic to the incipientepidemic phase. Temporal associations between mountain pine beetle and other boleinfesting bark beetles may provide inference regarding the mechanism of this phase transition and establish context for further spatial analyses in which these insects persist through time by partitioning host resources within and between trees.

#### **METHODS**

#### **Study Sites**

Two sites were established within southern British Columbia per Carroll et al. (2006). In brief, the site selection criteria included a historically suitable climate for mountain pine beetle, and a lack of tree-killing activity by the insect within 10 km of the sites. The first site, located at Angstad Creek, 25 km south of Merritt, was established in 2002. The second site, located on the Aberdeen Plateau, 35 km northeast of Kelowna, was established in 2003.

At Angstad Creek, three lodgepole pine stands were initially identified for study (stands A, B, and C). On the Aberdeen Plateau, two stands were chosen (stands D and E). An additional stand at Angstad Creek, and Aberdeen Plateau (stands F and G, respectively), were later added to the study to replace those stands in which mountain pine beetle populations transitioned from the endemic to the incipient-epidemic phase.

Stands were chosen to represent optimal mountain pine beetle habitat, i.e., lodgepole pine-leading, greater than 80 years old, and moderately dense (800 – 1500 stems/ha) (Safranyik and Carroll 2006). Furthermore, only stands with distinct boundaries formed by topographical features (e.g., water bodies, roads, clear cuts) or ecological conditions (e.g., forest age or species changes) were selected. These criteria were established to minimize the potential effects of immigration and emigration associated with immediately adjacent habitats, and thereby ensure assessments of local population dynamics. Stands chosen for study at each site were at least 1 km apart.

Following stand selection, variable radius prism plots were established within each stand at a density of one plot per hectare to ascertain average stand mensurational characteristics using the methods of Avery and Burkhart (2002). Tree diameter was measured at breast height (1.3 m). Tree height was determined using a laser hypsometer, and tree age was ascertained from cores collected at breast height.

The states of all trees in each variable radius plot were also assessed for conditions that could potentially impair tree vigour. These conditions included mechanical damage to the main stem or roots, competitive status (suppressed versus dominant), root or foliar infections, and previous non-lethal infestations by herbivorous insects.

#### The bole-infesting bark beetle assemblage

For purposes of spatial and temporal characterization of the bole-infesting bark beetle assemblage, a 25 x 50 m reference grid system was generated within each stand. An initial census was conducted to establish a baseline of all previous activity by bark beetles. The stems of all trees in each stand were carefully assessed for evidence of attack by bark beetles. Assessments were restricted to the lower 3 m of the boles where mountain pine beetle is most prevalent (Safranyik and Carroll 2006). The presence of boring dust in bark crevices, defensive resin exudate, and discoloured foliage was used to ascertain potential infestations. Portions of the bark were carefully removed in the vicinity of beetle activity (as evidenced by entrance holes and boring dust) and species were identified either directly when individuals were present or indirectly based upon diagnostic gallery patterns (Bright 1976, Wood 1982b). When beetles were present, only sufficient bark was removed ( $<225 \text{ cm}^2$ /tree, ca. 15 x 15 cm patch) to confirm the identity of the attacking species and thereby minimize impacts to their broods.

For attacked trees in which some or all beetles had completed development and dispersed, the year of attack was estimated based on the condition of remaining bark and phloem, the presence of wood boring beetles and saproxylic insects that follow bark beetle attacks, and the condition of foliage remaining on trees (Table 2.1). The accuracy of these estimations was later confirmed through comparison to the detailed sampling described below. Estimations of the year of attack were considered reliable for trees infested up to a maximum of two years in the past. The height, diameter and injury condition of attacked trees was determined as described above, and each tree was spatially referenced by recording its distance and azimuth to the nearest grid point.

Following the initial baseline censuses, detailed assessments were conducted to quantify variation in the abundance and distribution of the resident bole-infesting bark beetle assemblage within and among seasons. All trees in each stand were carefully inspected at 4-week intervals from early June to early September of each year (2002 – 2005 for Angstad Creek, 2003 – 2005 for Aberdeen Plateau). Trees were assessed, marked, spatially referenced, and their characteristics and condition recorded as described above. Due to the demanding effort required to carefully inspect all trees in each stand at 4-week intervals, the detailed assessments were restricted to 2 stands per site each year (initially stands A and B at

Angstad, D and E at Aberdeen). Thus, stand C at Angstad Creek was limited to a single inspection in mid-September of each year to provide a summary of total bark beetle abundance for the season.

Stands in which mountain pine beetle populations erupted in the course of the investigation were omitted from the detailed 4-week assessments in the year following eruption (stand B at Angstad, stand E at Aberdeen) and replaced with additional stands at each site. New stands (stands F and G at Angstad and Aberdeen, respectively) were chosen, established, censused and sampled in the same manner as described above.

#### **Temporal Analyses**

Graphical inspection revealed that the flight of mountain pine beetle was generally later than other bark beetles (Fig. 2.1), so data were first grouped into "early" (June - mid-July) and "late" (mid-July – September) time periods. Linear mixed effects models were used to examine associations between the numbers of trees colonized by each secondary species and by mountain pine beetle. The numbers of trees colonized by each species were incorporated as fixed effects. The variations between sites and stands within sites were incorporated as random effects. To examine whether the number of attacks on pines by mountain pine beetle across all stands was associated with secondary bark beetle activity in an earlier period, the number of trees attacked by mountain pine beetle was regressed against the number of trees colonized by secondaries lagged t-1. When assessing the associations solely between secondaries, original time periods and colonizations from all years were used. When assessing the associations between secondaries and mountain pine beetle, only the years where mountain pine beetle was believed to be at endemic or early incipient-epidemic population levels were used. These levels were defined to be less than five attacked trees per hectare. Analyses between species were compared using Akaike's Information Criterion (AIC) where the lowest AIC value indicated the best fitting regression model (Akaike 1973). Response variables were transformed as necessary to satisfy assumptions of each model including normal distribution, homogeneity of variances, and appropriate fit. Assumptions of homogenous variance and normal distribution of errors were assessed using residual plots. Only equations for the best models for each species are reported. Table 2.1: Criteria used to estimate the number of years since (A) partial, or (B) completeattacks by bole-infesting bark beetles on lodgepole pine trees within seven stands at two sitesin southern British Columbia between 1999 and 2002 (from Carroll et al. 2006).Item EvaluatedYears since initial bark beetle attack

	One	Тwo	Three (or morc)
A. Partial attack <sup>a</sup>			
Bark and phloem	Bark beetle galleries with emergence holes confined to portion of bole circumference	No remaining moist phloem, no visible decay fungi within region of partial attack	Loose bark, decay fungi visible within region of partial attack
Bark beetles	Current attacks by <i>Pseudips mexicanus</i> , <i>Orthotomicus latidens</i> and/or <i>Ips pini</i> in green phloem at margins of strip attack	Current attacks by <i>Hylastes</i> spp. of large roots directly beneath region of partial attack	Ongoing attacks by <i>Hylastes</i> spp. of large roots directly beneath region of partial attack
Wood borers and saproxylic insects <sup>b</sup>	Current attacks by <i>Trypodendron lineatum</i> within region of partial attack	N/A	Saproxylic insects beneath bark within region of partial attack
<b>B.</b> Complete attack <sup>e</sup>			
Bark and phloem	Remnants of moist phloem interspersed among bark beetle galleries with emergence holes	No remaining moist phloem, no visible decay fungi	Loose bark, decay fungi visible
Bark beetles	Current attacks in remnant phloem by <i>Pseudips mexicanus</i> . <i>Ips pini</i> , and/or <i>Orthotomicus latidens</i>	Current attacks by <i>Hylastes</i> spp. of root collar and large roots	Ongoing attacks by <i>Hylastes</i> spp. of root collar and large roots
Wood borers and	Current attacks by	Current attacks by	Emergence holes by
saproxylic insects	Irypodendron lineatum	wood-boring beetles ( <i>Cerambycidae</i> , <i>Buprestidae</i> )	wood-boring beetles ( <i>Cerambycidae</i> , <i>Buprestidae</i> ), saproxylic insects beneath bark
Foliage <sup>d</sup>	Fading or red foliage, 100% needle retention	Red foliage, 60% needle retention	Red foliage, 20% needle retention

<sup>a</sup>One or more years of infestation confined to "strips" of the circumference of the bole, trees remain alive.

<sup>b</sup>After Grove (2002)

<sup>c</sup>Attacks around the entire circumference of the bole, trees dead.

<sup>d</sup>Adapted from Wulder et al. (2006)
### RESULTS

The populations of mountain pine beetle in five of the seven stands (A, B, C, E, and F) underwent a transition from endemic to incipient-epidemic levels, judged by the number of trees colonized as a proxy for population density (a fair assumption in operational settings). The number of trees attacked by mountain pine beetle increased in these five stands each year (for mensurational characteristics see Appendix A, for colonization patterns see Appendix B: Tables B.1-B.3, B.5 and B.6). In two of the stands (D and G) the number of trees attacked by mountain pine beetle reached a small peak in 2004, but dropped substantially the following year (Appendix B: Tables B.4, and B.7). These two stands did not appear to enter the incipient-epidemic phase in the years under investigation.

*Pseudips mexicanus* colonized the most trees in all of the stands, followed by *O*. *latidens*, and *Hylurgops* spp. (Appendix B: Tables B.1-B.7). Colonization on the lower bole of trees by *I. pini* was found in all seven stands, but in much lower numbers than the aforementioned species. Trees colonized by *D. murrayanae* were also found in all stands, generally in smaller numbers than boles colonized by *I. pini*, with the exception of one stand (stand D; Appendix B: Table B.4).

The timing of attack for each bark beetle species was examined by determining the average number of trees colonized in each time period, each year, across all stands (Fig. 2.1). *Dendroctonus murrayanae*, *Hylurgops* spp., *O. latidens*, and *P. mexicanus* colonized the most trees earlier in the season (Fig. 2.1A, B, C, and E). The number of trees colonized by *O. latidens* and *D. murrayanae* in each month declined quite steadily from June peaks (Fig. 2.1B

and E), while a more dramatic decrease could be seen for *P. mexicanus* and *Hylurgops* spp. (Fig. 2.1A and C). Although *I. pini* appeared to attack trees primarily in May or June, a second peak in trees infested with *I. pini* was noted in the August censuses (Fig. 2.1D) indicative of colonization occurring between July and August. Trees colonized by mountain pine beetle were generally found later in the season, in the months of August and September (Fig. 2.1F).

#### **Temporal interactions between secondary bark beetles**

Populations of many bole-infesting bark beetles appeared to be positively correlated. In general, a greater number of trees colonized by any one secondary bark beetle species in a given time period was highly correlated with a greater number of trees colonized by other secondary species (see Fig. 2.2). For example, the number of trees colonized by *P. mexicanus* was significantly positively correlated with the number of trees colonized by *O. latidens* from the same year and time period (Fig. 2.2A). Likewise, the number of trees colonized with the abundance of *P. mexicanus*. However, AIC values were higher for these regression models indicating that the number of trees colonized by *O. latidens* was the best predictor for trees colonized by *P. mexicanus* (AIC<sub>0. Latidens</sub> = 776.49 < AIC<sub>0. murrayanae</sub> = 900.87 < AIC<sub>H.spp.</sub> = 918.06 < AIC<sub>1 pmn</sub> = 953.60). Similarly, the number of *O. latidens* attacks, although positively correlated with all species (some results not shown), was most significantly positively correlated with the number of trees attacked by *P. mexicanus* in the same year (Fig. 2.2B).

Colonization by Hylurgops spp., D. murrayanae, and I. pini were also strongly

correlated with all secondary species (some results not shown). However their abundance was best explained by the number of trees colonized by *P. mexicanus* (Fig. 2.2C, D, and E).

### Temporal interactions between secondary bark beetles and mountain pine beetle

The number of trees attacked by mountain pine beetle was correlated with the number of trees colonized by all species of secondary bark beetles (Fig. 2.3). As the number of trees attacked by secondaries in a season increased, an increase in all types of attack (resisted-attack, strip-attack, and mass-attack) by mountain pine beetle was also evident (Fig. 2.3). The best predictor of the number of trees colonized by mountain pine beetle was the number of trees colonized by *O. latidens*, (AIC = 199.75), followed by *Hylurgops* spp. (AIC = 200.46), *P. mexicanus* (AIC = 200.85), *D. murrayanae* (AIC = 204.51), and *I. pini* (AIC = 207.72). The positive trend between the numbers of trees colonized by mountain pine beetle was only evident when populations of mountain pine beetle were at either endemic or early incipient-epidemic levels. Once colonization by mountain pine beetle reached later stage incipient-epidemic levels, as judged by strip and mass attacks within the stands, their populations were no longer correlated with the number of trees colonized by other bark beetles in the bole-infesting assemblage (P>0.05 for all cases).



Figure 2.1: Mean number of trees colonized by various species of bark beetles per year as a function of cruise timing. Data reflect surveys of seven stands of lodgepole pine in southern British Columbia between 2000 and 2005.



Figure 2.2: Association of the number of trees colonized by one species of bark beetle with another for the same year and census period. Data reflect surveys of seven stands of lodgepole pine in southern British Columbia between 2000 and 2005.



Figure 2.3: Association of the number of trees colonized by mountain pine beetle with other bark beetle species lagged one census period. Data reflect surveys of seven stands of lodgepole pine in southern British Columbia between 2000 and 2005.

### DISCUSSION

The increases in populations of species of secondary bark beetles one to two years prior to the eruption of populations of mountain pine beetle in four of the five stands where a population phase transition took place, in conjunction with the positive temporal correlations between the number of trees colonized by secondary bark beetles early in the season and montain pine beetle later in each season, suggest two mechanisms by which mountain pine beetle may erupt. First, the increase in mountain pine beetle populations may be independent of the numbers of trees colonized by secondary bark beetles. The increase may simply reflect a delayed response to abiotic stresses that create increasingly favourable conditions for reproduction for all insects. Berryman (1976), for example, suggested that a rapid decline in stand resistance may trigger outbreaks of mountain pine beetle. Drought is one of many stress events that can promote scolytid reproduction by increasing the susceptibility, and perhaps nutritional quality, of host trees (Hopping and Mathers 1945, Rudinsky 1962, Berryman 1972, Mattson and Haack 1987, Allen and Breshears 1998, Kelsey and Joseph 2001, Berg et al. 2006, Raffa et al. 2008). The increase in the number of trees colonized by secondary bark beetles in this study is believed to be associated with an extended period of low spring precipitation (Carroll et al. 2006). However, as in the southern pine beetle system (Turchin 1991), there is conflicting evidence for drought as the solitary trigger of outbreaks of mountain pine beetle, as populations have erupted in periods of below normal, normal, and abundant precipitation (Blackman 1931, Beal 1943).

Second, the strong temporal relationships between secondary bark beetles and

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mountain pine beetle, particularly the most populous bole-infesting species in this study, O. *latidens* and *P. mexicanus*, lends support to a theory of facilitation in which a densitydependent facilitative relationship occurs exclusively at endemic levels of the population. Amman and Schmitz (1988), for example, proposed that scattered populations of mountain pine beetle must build up before an outbreak occurs. Species such as D. murrayanae, O. latidens, P. mexicanus, Hylurgops spp., and I. pini emerge and establish in hosts prior to flight of mountain pine beetle. In turn, endemic populations of mountain pine beetle emerging in late July, August, and early September have the opportunity to either seek out or reject trees inhabited by these insects. A study by Moeck et al. (1981) suggested mountain pine beetle does not reject trees that contain other species, such as D. valens (LeConte), D. brevicomis, H. subcostulatus (Mannerheim), O. latidens, and Pityophthorus serratus (Swaine). Small-scale population buildups of species such as P. mexicanus, O. latidens, I. *pini*, *Hylurgops* spp., and *D. murrayanae* may enable the accumulation of endemic mountain pine beetle by providing access to otherwise unsuitable hosts (see Smith et al. 2011). Once populations of mountain pine beetle gain sufficient numbers to initiate mass attack of a healthy host tree (i.e., approximately 300 to 500 beetles per hectare), they may no longer be dependent on other bark beetles or weakened hosts, and begin to shift their colonization behaviour accordingly (Carroll et al. 2006).

Strong interspecific competition could preclude facilitative relationships in this system, however. For example, secondary species frequently outcompete more aggressive primary bark beetles by rapid larval development (Rankin and Borden 1991). In weakened

and dying trees, secondary bark beetles are better suited to exploit available resources than their primary bark beetle counterparts such as *D. ponderosae* or *D. rufipennis* (McCambridge and Knight 1972, Poland and Borden 1998). While studies have provided compelling evidence to suggest mountain pine beetle at epidemic levels would be better off minimizing interspecific competition with secondary bark beetles such as *I. pini* (Rankin and Borden 1991, Safranyik et al. 1999), very little has been observed regarding endemic levels of the insect. Endemic populations of mountain pine beetle are found in surprisingly low numbers, estimated at less than forty beetles per hectare (Carroll et al. 2006). At such low numbers, their density in a host would not reach levels reflective of outbreaks tested by Rankin and Borden (1991) (i.e., 50 beetles/m<sup>2</sup>). Furthermore, Safranyik et al. (1999) suggested that high levels of *I. pini* may, in some instances, enhance survival of mountain pine beetle by accelerating the death of tissues in the upper part of the host.

Delayed density-dependent effects of predators and parisitoids, not uncommon in defoliating systems (Myers 1988, Roland and Taylor 1997, Rothman and Roland 1998, Roland 2005, Dwyer et al. 2004, Cooke and Lorenzetti 2006), that become diluted by increasing populations of secondary bark beetles, could also facilitate increasing survivorship of endemic populations of mountain pine beetle. Aggregation of the secondary bark beetle, *I. pini*, for example, may dilute the effect of predation by generalist clerids and other bark beetle predators (Aukema and Raffa 2004). Amman (1984) found that predation by clerids was significantly higher in endemic populations of mountain pine beetle than in epidemic or postepidemic populations. While the largest contributors to brood mortality of mountain pine beetle were cold over-wintering temperatures and desiccation, these factors did not differ between infestation levels (Amman 1984), possibly placing greater significance on predation as a mortality factor governing endemic populations. Although Boone et al. (2008) found heterospecifics add to competition and predator load, the densities of infestation in their experiments exceed levels found in endemic populations of mountain pine beetle (Carroll et al. 2006).

Although Amman and Schmitz (1988) have outlined several predisposing factors for an outbreak by mountain pine beetle, assessing the risk of outbreaks using hazard rating systems that include these factors has not met with much success (Katovich and Lavigne 1985, Bentz et al. 1993, Nelson et al. 2008). Bentz et al. (1993) partially attributed the inadequacy of hazard rating systems to a lack of knowledge concerning the endemic phase of the insect, and Logan et al. (1998) suggested that spatial inference is necessary. Although lacking evidence, for example, Amman and Schmitz (1988) believed there may be a close relationship between secondary bark beetles and endemic levels of mountain pine beetle. Likewise, Hamel and McGregor (1976) and Gohcen and Cobb (1980) suggested potential associations between low level populations of mountain pine bectle and secondary bark beetles, and Furniss and Carolin (1977) noted an association between endemic levels of mountain pine beetle and D. brevicomis. The annual emergence patterns of secondaries and mountain pine beetle in this study indicate that the latter were the last to enter host trees in a season and would have had the opportunity to reject trees containing secondary species. The next chapter examines spatial interactions between endemic levels of mountain pine beetle

and secondary bark beetles. Greater understanding of such interactions could provide new management tools, such as the use of beetle monitoring to identify endemic populations of mountain pine beetle on the verge of a population phase transition.

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### **CHAPTER 3**

Spatial associations of mountain pine beetle, *Dendroctonus ponderosae*, with secondary bark

beetles in the endemic to incipient-epidemic phase transition

## ABSTRACT

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is native to western North America and attacks most species of pine in its range. Its population dynamics are characterized by four phases: endemic, incipient-epidemic, epidemic, and post-epidemic. Beetles typically subsist at endemic levels for many years between outbreaks, reproducing in the tissues of weakened or dying trees. Very little attention has been paid to populations at endemic stages, because they do not kill large numbers of healthy trees. This study explored the stand-level spatial interactions of endemic beetles with other bark beetles frequently found in weakened pine hosts. Endemic and incipient-epidemic levels of mountain pine beetle were often positively spatially associated with secondary bark beetles such as *Pseudips* mexicanus (Hopkins), Orthotomicus latidens (LeConte), Ips pini (Say), Hylurgops porosus (LeConte), and H. rugipennis (Mannerheim). As populations grew, mountain pine beetle shifted from attacking injured and previously colonized hosts to more vigorous hosts in a clustered pattern. The positive spatial associations may indicate a facilitative relationship between endemic mountain pine beetle and other phloem-infesting bark beetles, and provide insight into mechanisms potentially facilitating the transition of the organism from the endemic to incipient-epidemic phase.

## Key words: phase transition; facilitation; competition; niche partitioning

### INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a bark beetle that exhibits a broad geographic range extending from the upper limits of Mexico northward to northwestern British Columbia, and from the Pacific coast eastward to South Dakota in the United States, and eastern Alberta in Canada (Safranyik and Carroll 2006). A generalist, mountain pine beetle is capable of colonizing nearly every species of native and introduced pine within its range, although lodgepole pine, *Pinus contorta* (Douglas ex Louden), is considered its principal host (Furniss and Schenk 1969, Smith et al. 1981, Cerezke 1995, Carroll et al. 2004, Safranyik and Carroll 2006). The population dynamics of this insect consists of four phases; endemic, incipient-epidemic, epidemic, and post-epidemic or collapse (Safranyik and Carroll 2006).

Mountain pine beetles are typically found at endemic levels, where populations experience significant mortality due to cold winter temperatures and larval desiccation (Amman 1984). Favourable conditions for beetle reproduction include successive warm summers, mild winters, and stress events such as drought (Reid 1963, Safranyik et al. 1974, Thomson and Shrimpton 1983). When such conditions coincide with an adequate number of mature hosts, the beetle may enter the incipient-epidemic phase (Carroll et al. 2006). From the incipient-epidemic phase, beetle populations may progress to outbreak status, where mass attacks coordinated by aggregation pheromones enable the beetles to overwhelm the defenses of healthy, large diameter trees (Wood 1982, Raffa and Berryman 1983). Mountain pine beetles are aided in overcoming the defenses of host trees by innoculating host tissue with mutualistic phytopathogenic fungi (Francke-Grossman 1967, Berryman 1972) transported in specialized cuticular structures called mycangia (Batra 1963, Paine et al. 1997). Fungal growth not only disrupts the defensive capacity of host trees, but may also provide nutritional benefits for phloem-feeding larvae (Bleiker and Six 2007).

At outbreak levels, the insects can kill trees over vast regions, exhibiting biome-level consequences (Aukema et al. 2006, Raffa et al. 2008, Kurz et al. 2008). Outbreaks typically collapse when the beetles exhaust the available large-diameter host resources, and/or cold winter temperatures induce sufficient brood mortality to reduce reproduction below the replacement numbers required to sustain an epidemic (Reid 1963, Cole and Amman 1969, Safranyik et al. 1974, Amman 1984). Mountain pine beetle populations thereby return to an endemic level where they will remain, often for decades, until favourable conditions arise again.

Our understanding of epidemic populations of mountain pine beetle is considerable, yet little is known about endemic populations or the transition of populations from endemic to incipient-epidemic levels. Even quantification of such populations remains challenging. It was previously thought, for example, that endemic beetles may be found infesting less than one tree in 40.5 hectares of forest (Amman 1984). However, Amman and Schmitz (1988) later referred to endemic populations as those comprising less than one mass-attacked tree per ten hectares. More recently, Carroll et al. (2006) estimated the number of endemic beetles to be less than forty individuals per hectare, and incapable of mass-attacking even a single tree.

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If endemic beetles are unable to overcome the defences of healthy trees (Raffa and Berryman 1983), they may rely on the presence of other bark beetles as well as other insects and diseases in marginal hosts to facilitate reproduction until the establishment of sufficiently viable populations enables them to overcome healthy trees (Carroll et al. 2006). This hypothesis is not without anecdotal evidence in the literature. For example, endemic levels of mountain pine beetle may utilise a broad spectrum of weakened hosts, and association with other bark beetles has been suggested by DeLeon (1934), Hamel and McGregor (1976), and Goheen and Cobb (1980). Moreover, previous studies have implied positive associations between mountain pine beetle and other host-stressing agents such as the root disease *Armillaria mellea* (Hinds et al. 1984, Lessard et al. 1985, Tkacz and Schmitz 1986), and dwarf mistletoe *Arceuthobium* spp. (McCambridge et al. 1982, Rasmussen 1987)

In this study I examined the stand-level spatial associations between endemic-level mountain pine beetle and other bark beetles including *Pseudips mexicanus* (Hopkins), *Orthotomicus latidens* (LeConte), *Ips pini* (Say), *Hylurgops porosus* (LeConte), *H. rugipennis* (Mannerheim) and *D. murrayanae* (Hopkins) over five years in seven lodgepole pine stands near Merritt and Kelowna, British Columbia. In five of these stands, mountain pine beetle transitioned from endemic to outbreak levels over the course of the study. I tested whether mountain pine beetle exhibits spatial dependencies with associated beetles through time, which would suggest that a suite of bole-infesting bark beetles may be key contributors to the development of incipient-epidemic populations of mountain pine beetle.

### METHODS

Refer to Chapter 2, Methods: Study Sites, for source of data. Maps for the locations of all trees inhabited by mountain pine beetle and secondary bark beetles were created using the 'spatstat' package v.1.13-3 in R v.2.6.2 (Ihaka and Gentleman 1996, Baddeley and Turner 2005, R Development Core Team 2008). Colonized trees were categorized by their respective year and species. Trees that were colonized by mountain pine beetle were further categorized as: resisted attack (where the beetles were pitched out by the tree), strip attack (where only a portion or strip of the bole was attacked), and mass attack (where the majority of the bole was attacked). Logistic regression was used to test Rasmussen's hypothesis (1974) that early emerging mountain pine beetle are more likely to attack trees with prior injury by analysing attacked/unattacked trees as a function of injury status.

Spatial point process models were used to evaluate the spatial relationships between trees colonized by mountain pine beetle and those colonized by other bark beetles. The other bark beetles were chosen if they exhibited temporal relationships with mountain pine beetle (Chapter 2). Analyses were conducted when there were two or more instances of colonization by both mountain pine beetle and the secondary species in the stand in that year.

New techniques in spatial point process modeling are powerful for discerning potential relationships between species or other biotic and abiotic factors that may otherwise go undetected (Stoyan and Penttinen 2000). Spatial point process models were used to examine the influence of previous years of colonization by other bark beetles on the varying types of mountain pine beetle attack. Furthermore, point process models also examined the effects of these insects colonizing trees the same year as mountain pine beetle, since they flew and were recorded prior to peak mountain pine beetle flight in July and August. Finally, the number of trees mass-attacked by mountain pine beetle were examined with respect to strip attacks in years t and t-1.

The response variable for each model, a spatially-explicit estimated density of trees colonized by mountain pine beetle ( $\lambda$ ), was measured as the number of trees bearing attacks by mountain pine beetle (either resisted attack, strip attack, mass attack, or a combination) per square meter of stand area. Covariates (here, the location of attacks by other bark beetles) were converted from point locations to density surfaces prior to fitting. This process incorporates a Gaussian kernel density smoother as a representation of the point process defined within the boundary of each stand (Cressie 1991, Baddeley and Turner 2000). A periodic border correction was tested for a subset of models, but not utilised, as results proved robust to methods with a default edge border correction.

Parameters in these spatial point process regression models were estimated using maximum pseudolikelihood methods. Significance of individual variables was judged by statistical comparison to a homogenous model, i.e., one estimating only an intercept or a constant intensity of resisted, strip, or mass attack by mountain pine beetle across the site, by examining the change in deviance relative to a  $\chi^2$  reference distribution. Where I sought to examine additive effects of multiple variables, a comparison of nested models was performed by examining the change in deviance relative to a  $\chi^2$  reference distribution. Models were compared using Akaike's Information Criterion (AIC), and models with the lowest AIC

values were judged to fit best (Akaike 1973).

Spatial analyses to determine the extent of clustering of strip and mass attack by mountain pine beetle were performed using Ripley's K functions. Simulation envelopes were used to construct a 95% confidence interval (n = 999 simulations). Trees were judged to be "clustered" if falling above the upper limits of this interval about the empirical function, but spatially "inhibited" if below the interval (Ripley 1981).

#### RESULTS

The populations of mountain pine beetle in five of stands (denoted A, B, C, F and E) underwent a transition from endemic to incipient-epidemic levels over the course of the study, as the number of trees strip- and mass-attacked by mountain pine beetle increased each year in these four stands (Tables 3.1 and 3.2). In stands in which populations of mountain pine beetle did not erupt (D and G), the number of trees strip- and mass-attacked by mountain pine beetle reached a small peak in 2004 and dropped substantially the following year (Tables 3.1 and 3.2). The number of trees strip- and mass-attacked by mountain pine beetle in stand E increased from 2002 to 2003 (Tables 3.1 and 3.2). Due to the large increase in populations between these years (likely due to immigration and not endogenous stand dynamics), this stand was dropped from censusing after 2003.

Many of the trees strip-attacked by mountain pine beetle prior to the population phase transition showed evidence of colonization by other species of bark beetle and/or some form of injury such as a broken or forked top, a scarred trunk, a thin crown, an infection of dwarf mistletoe (*Arceuthobium* spp.), an attack by mountain pine beetle greater than ten years prior,

or some other form of injury (Table 3.1; see Carroll et al. (2006) for a more detailed list of injuries). For the stands in which a phase transition from endemic to incipient-epidemic levels was occurring (i.e., stands A, B, C, and F), the number of trees strip-attacked by mountain pine beetle with injuries and/or secondary colonization began to decline in the final year of the study. During the transition from endemic to incipient-epidemic levels, many mass-attacked trees were also previously colonized by secondaries and/or possessed some form of injury (Table 3.2). Once populations of mountain pine beetle were established at the incipient-epidemic level however, the insects rarely mass-attacked trees that had been previously colonized by other species of bark beetles.

Table 3.1: Number of lodgepole pine trees strip-attacked by mountain pine beetle in seven stands in southern British Columbia, 1999-2005. Within the subset of these trees, the numbers bearing injuries and/or any one or multiple colonizations of other bark beetles (*Dendroctonus murrayanae*, *Hylurgops* spp., *Ips pini*, *Orthotomicus latidens*, *Pseudips mexicanus*) are listed.

Stand	No. Trees	Year							
		1999	2000	2001	2002	2003	2004	2005	
A	Strip attacks	4	9	17	25	37	32	70	
	Injured	4	9	17	22	18	14	9	
	Other bark beetles	0	3	10	18	11	10	10	
В	Strip attacks	3	11	27	37	52	-	-	
	Injured	2	8	24	30	36	-	-	
	Other bark beetles	0	3	16	19	9	-	-	
С	Strip attacks	-	2	5	5	9	21	65	
	Injured	-	2	4	5	4	5	6	
	Other bark beetles	-	1	4	3	3	1	1	
D	Strip attacks	_	-	-	1	14	17	3	
	Injured	-	-	-	1	9	7	1	
	Other bark beetles	-	-	-	1	10	12	3	
Е	Strip attacks	-	-	13	16	61	-	-	
	Injured	_	-	9	13	21	_	-	
	Other bark beetles	-	-	0	5	5	-	-	
F	Strip attacks	-	-	1	2	18	25	41	
	Injured	-	-	0	1	6	12	8	
	Other bark beetles	-	-	0	0	7	12	7	
G	Strip attacks	_	-	-	4	12	21	2	
	Injured	-	-	-	3	3	7	0	
	Other bark beetles		-	-	2	8	18	1	

Table 3.2: Number of lodgepole pine trees mass-attacked by mountain pine beetle in seven stands in southern British Columbia, 1999-2005. Within the subset of these trees, the numbers bearing injuries and/or any one or multiple colonizations of other bark beetles (*Dendroctonus murrayanae*, *Hylurgops* spp., *Ips pini*, *Orthotomicus latidens*, *Pseudips mexicanus*) are listed.

Stand	No. Trees	Year							
		1999	2000	2001	2002	2003	2004	2005	
A	Mass attacks	0	1	6	6	65	99	296	
	Injured	0	1	4	5	33	33	28	
	Other bark beetles	0	1	3	4	11	4	0	
В	Mass attacks	1	0	3	38	129	-	-	
	Injured	1	0	3	25	83	-	-	
	Other bark beetles	0	0	2	8	11	-	-	
С	Mass attacks	-	2	2	2	23	45	205	
	Injured	-	2	2	1	6	6	14	
	Other bark beetles	-	2	2	1	4	1	0	
D	Mass attacks	-	0	0	5	11	11	6	
	Injured	-	0	0	4	9	4	0	
	Other bark beetles	-	0	0	3	7	6	4	
Е	Mass attacks	-	0	5	36	322	-	-	
	Injured	-	0	3	18	68	-	-	
	Other bark beetles	-	0	2	9	9	-	-	
F	Mass attacks	-	-	0	5	24	47	191	
	Injured	-	-	0	3	13	19	44	
	Other bark beetles	-	-	0	2	11	9	1	
G	Mass attacks	-	0	0	3	11	14	4	
	Injured	-	0	0	0	6	3	1	
	Other bark beetles	_	0	0	1	6	6	2	

Emergence by mountain pine beetle in this study prior to late-July flight periods was rare; less than 2% of all trees colonized by mountain pine beetle were attacked between June and mid-July. The likelihood that beetles attacked an injured host was higher with beetles that flew earlier vs. later (71.4% vs. 34.2%, P(attack injured host) =  $\exp^{0.92 - 1.57x}/1 + \exp^{0.92 - 1.57x}$ , where x = 1 if late and 0 otherwise;  $Z_{2576} = -4.57$  for estimate of time coefficient; P < 0.0001).

# **Spatial Analyses**

Mountain pine beetle and other bark beetles in the bole-infesting assemblage were found occupying the same, or nearby, host trees in all stands. Significant spatial associations between trees bearing strip-attack by mountain pine beetle and secondary bark beetle colonization were generally uniform throughout stands undergoing a population eruption and are summarized using stand B as a representative case (Table 3.3). Due to the extensive nature of this study, the remaining stands have been placed in Appendix C (see Appendix C: Tables C.1-C.6). In the two stands where mountain pine beetle did not erupt to epidemic population levels, other bark beetles such as *P. mexicanus*, and *O. latidens* were often found in close proximity with mountain pine beetle, sometimes even sharing the same host tree (Appendix C: Tables C.3, C.6). These spatial associations, however, were not as numerous as those found in stands undergoing a population phase transition (Appendix C: Tables C.1, C.2, C.4, and C.5).

Table 3.3: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2000 to 2003 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. For example, the estimated density of strip attack by mountain pine beetle in 2001 in locations where all secondaries colonized trees at a rate of  $0.0005/m^2$ or 5 trees/ha is  $exp^{(-11.46 + 3870 \times 0.0005)} = 0.0001$  or 1 tree/ha. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		Slop	<u>se</u>	$\chi^2$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
Strip attack	2000	-10.05	0.30					245.11
P. mexicanus	2000	-11.46	0.88	31786	16262	4.49	0.03	242.58
Strip attack	2001	-9.15	0.19					550.22
All secondaries	2001	-11.14	1.01	3870	1849	4.40	0.04	547.73
<i>H</i> . spp.	2001	-10.51	0.74	7177	3568	4.29	0.04	547.84
Strip attack	2002	-8.84	0.16					729.95
All secondaries	2002	-10.08	0.63	1506	696	5.21	0.02	726.62
P. mexicanus	2002	-9.98	0.60	2699	1274	5.15	0.02	726.68
O. latidens	2002	-9.99	0.61	4530	2196	4.63	0.03	727.20
P. mexicanus	2001	-10.22	0.71	5461	2605	4.48	0.03	727.34
All secondaries	2001	-10.47	0.85	3201	1579	4.11	0.04	727.71
Strip attack	2003	-8.50	0.14					989.68
H. spp.	2003	-11.46	0.61	28745	5016	44.11	< 0.0001	947.38
H. spp.	2002	-10.57	0.42	17534	2869	38.89	< 0.0001	952.61
P. mexicanus	2003	-11.17	0.62	8839	1770	34.13	< 0.0001	957.37
I. pini	2003	-10.70	0.49	32277	6007	32.69	< 0.0001	958.80
All secondaries	2003	-10.95	0.57	3865	772	32.63	< 0.0001	958.86
All secondaries	2002	-10.96	0.66	2846	685	21.63	< 0.0001	969.86
P. mexicanus	2002	-10.51	0.61	4585	1251	17.35	< 0.0001	974.14
O. latidens	2003	-9.49	0.34	6264	1709	13.88	0.0002	977.61

In all stands, the locations of trees strip-attacked by mountain pine beetle were associated with all trees colonized by other bark beetles considered as a whole. Cohabitation or host sharing between endemic levels of mountain pine beetle and all secondary bark beetles is exemplified by stand A in 2002 (Fig. 3.1).

Often, however, the locations of trees strip-attacked by mountain pine beetle could be predicted by knowing the locations of trees colonized by only one species of bark beetle, rather than the entire complex. For example, the locations of strip-attacked trees were associated most frequently with colonization by *P. mexicanus* (e.g., similar AIC values for models with all secondaries vs. *P. mexicanus*; Table 3.3: 2000, 2002, 2003). However, trees strip attacked by mountain pine beetle also appeared to be positively associated with colonization by *Hylurgops* spp., primarily in the earliest years of study (Table 3.3: 2001; Appendix C: Tables C.1, C.2, C.4 and C.5), and with the locations of *O. latidens* (Table 3.3: 2002 and 2003; Appendix C: Tables C.1, C.2, C.5 and C.6). Fewer significant spatial associations between trees colonized by *I. pini*, and *D. murrayanae* and those strip-attacked by mountain pine beetle were apparent, however.



Figure 3.1: Locations of trees strip attacked by mountain pine beetle, and colonizations by *Dendroctonus murrayanae*, *Hylurgops* spp., *Ips pini*, *Orthotomicus latidens*, and *Pseudips mexicanus* in southern British Columbia, stand A, 2002. Colonizations by mountain pine beetle and other bark beetles comprise approximately 0.12 and 1.3% of the 19,500 pine trees in stand A respectively.

Although most associations between mountain pine beetle and other bark beetles were positive, strip attacks by mountain pine beetle following the endemic to incipient-epidemic transition in stand A were negatively associated with *I. pini*, *P. mexicanus* and *Hylurgops* spp. (Appendix C: Table C.1) in the final years of study. In stand E, there was also a weak negative association between *P. mexicanus* and trees that were strip-attacked by mountain pine beetle in 2002 (Appendix C: Table C.4).

Trees that were strip-attacked in one year were frequently mass-attacked by mountain pine beetle the following year, as there were significant positive associations between stripattacked and mass-attacked trees (Table 3.4). In stands where no population phase transition of mountain pine beetle was apparent (stands D and G), there were no significant associations between strip attack and mass attack by mountain pine beetle.

In 2001, when populations of mountain pine beetle were still at endemic or early incipient-epidemic levels, trees that exhibited strip attacks, although closely associated with other bark beetles, were scattered in a random pattern throughout the stand (empirical line of Ripley's K function is within simulation envelope. Fig. 3.3). However, as populations of mountain pine beetle began to transition from endemic to incipient-epidemic levels, trees that were strip- or mass-attacked began to be found in clusters (visual representation in Fig. 3.2, Ripley's K function above simulation envelope in 3.4, and see Appendix C: Figs. C.1-C.4). Clustering, of strip- and mass-attacked trees as the outbreak progressed was very pronounced in all stands except two (results not shown; stands D and G).

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Table 3.4: Association of trees strip-attacked by mountain pine beetle on the location of mass attacks from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Mass attack	2002	-8.81	0.16					747.60
Strip attack	2002	-11.24	0.68	13798	3385	20.35	< 0.0001	729.12
Strip attack	2001	-10.74	0.63	15449	4494	13.55	0.0002	735.92
Mass attack	2003	-7.59	0.09					2217.79
Strip attack	2003	-8.85	0.20	4557	530	71.95	< 0.0001	2147.39
Strip attack	2002	-9.88	0.36	13067	1801	63.62	< 0.0001	2155.71
Mass attack	2004	-6.17	0.04					7620.12
Strip attack	2003	-6.78	0.09	2418	266	79.08	< 0.0001	7541.18
Strip attack	2004	-6.57	0.07	8407	1123	52.22	< 0.0001	7568.04
Mass attack	2005	-4.93	0.02					21915.37
Strip attack	2005	-6.62	0.07	949	32	959.50	< 0.0001	20953.26
Strip attack	2004	-5.23	0.04	6479	615	104.5	< 0.0001	21808.26



Figure 3.2: Location of trees strip attacked by mountain pine beetle in 2002, and mass attacked in 2003 in southern British Columbia, stand A. Strip and mass attacks comprise approximately 0.12 and 0.33% of the 19,500 lodgepole pine trees in stand A respectively.



Figure 3.3: Ripley's K function for trees strip-attacked by mountain pine beetle in 2001 for stand A. Observed estimate is shown by the black solid line, the upper and lower limits of the 95% confidence interval are shown by the green and blue dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the red dashes. The focal distance (r) on the x-axis is represented in metres.


Figure 3.4: Ripley's K function for trees strip-attacked by mountain pine beetle in 2004 for stand A. Observed estimate is shown by the black solid line, the upper and lower limits of the 95% confidence interval are shown by the green and blue dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the smooth red dashes. The focal distance (r) on the x-axis is represented in metres.

## DISCUSSION

Colonization of hosts by bark beetles, particularly endemic-level mountain pine beetle, poses an ecological paradox (Light et al. 1983). At epidemic levels, mountain pine beetle reproduce in the tissues of vigorous hosts; however, such hosts are unavailable to the insects at endemic levels (Raffa and Berryman 1983). Therefore, endemic mountain pine beetle appear to rely on hosts unable to mount defensive responses capable of displacing the insects. Such hosts may include trees with root disease (e.g., *Armillaria* spp.), or dwarf mistletoe (e.g., *Arceuthobium* spp.) (McCambridge et al. 1982, Hinds et al. 1984, Lessard et al. 1985, Tkacz and Schmitz 1986, Rasmussen 1987). Although the level of root rot in our stands was low, the level of dwarf mistletoe was quite high. Many trees colonized by endemic mountain pine beetle possessed some form of injury or disease, with the most common being a broken top or dwarf mistletoe.

Colonizing trees with injury or disease poses a challenge, however. Weakened trees are often infested by secondary bark beetles (Amman and Schmitz 1988), such that endemic populations of mountain pine beetle and secondary bark beetles frequently inhabit the same types of hosts (Bartos and Schmitz 1998). In this study, not only did mountain pine beetle and secondary bark beetles inhabit the same types of hosts, but they frequently inhabited hosts together (Fig. 3.1). Selecting hosts that offer the best opportunity for survival may involve a degree of compromise where the probability of survival in a poorly defended host is higher, but the mortality cost due to interspecific competition is potentially higher as well.

The presence of such a diverse and abundant assemblage of bark beetle species in all

stands may be an indicator of relaxed levels of competition, however (Ratchke 1976). Competition can be reduced through strategies such as niche partitioning, for example (Byers 1989, Raffa 1991, Schlyter and Anderbrant 1993, Amezaga and Rodriguez 1998, Ayres et al. 2001). Amman and Schmitz (1988) suggest that the lower 30 to 60 cm of the bole may be freely available to mountain pine beetle when associated with other bole-infesting bark beetles. Moreover, Ayres et al. (2001) suggest that high numbers of interspecific associations may benefit the rarest species, such as endemic levels of mountain pine beetle in the present example.

This study provides evidence that the effects of competition as a mortality factor may be most pronounced as populations of mountain pine beetle transition to epidemic levels versus remaining at the endemic level. For example, there were only a few significantly positive spatial associations found between mountain pine beetle and *I. pini*, and the two insects colonized different hosts once mountain pine beetle entered the incipient-epidemic phase (Appendix C: Table C.1). This is consistent with observations that mountain pine beetles at epidemic levels may be outcompeted by *I. pini* (Bergvinson and Borden 1991, Rankin and Borden 1991, Safranyik et al. 1999, Boone et al. 2008).

In contrast, endemic populations of mountain pine beetle may benefit from close associations with bole-infesting heterospecifics. The majority of trees co-colonized by mountain pine beetle and other bark beetles contained *P. mexicanus*, *Hylurgops* spp., and/or *O. latidens* species. Seasonal phenologies of these bark beetle species (Chapter 2; Schenk and Benjamin 1969, Miller and Borden 1985, Safranyik et al. 2004, Furniss and Kegley 2008, Smith et al. 2009) indicate that mountain pine beetle colonized these trees following colonization by heterospecifics. The benefits of colonizing trees with established heterospecifics may include increased nutritional quality of the host (Hodges et al. 1968, Ayres et al. 2000, Bleiker and Six 2007), favourable moisture regulation due to extensive fungal innoculation (Reid 1963, Whitney 1971, Amman 1977), reduced likelihood of predation (Abrams et al. 1998, Ayres et al 2001, Aukema and Raffa 2004), and/or decreased probability of mortality due to exhaustion of host defenses (Christiansen et al. 1987, Carroll et al. 2006). For example, *Ips* spp. may colonize diseased trees prior to mountain pine beetle, further weakening the host and/or altering host physiology, potentially resulting in the production of chemicals attractive to *Dendroctonus* species (Hodges et al. 1968, Goheen and Cobb 1980). Moreover, Smith (2008) found that endemic level populations of mountain pine beetles reared with *P. mexicanus* in naturally infested host tissues developed more quickly, produced more offspring, and were not significantly different in size, than those reared on their own. Carroll et al. (2006) also found that phloem consumption by endemic mountain pine beetle was positively influenced by phloem consumption of secondary bark beetle species belonging to the bole-infesting assemblage.

In summary, these results are consistent with a model in which the colonization dynamics of mountain pine beetle change as populations increase. Early emerging beetles attack hosts with injury or attack from a previous year (Rasmussen 1974), particularly in endemic populations where very few conspecifics are present (Reid et al. 1967). Colonization of such trees, co-colonized by other bole-infesting bark beetles (Hamel and

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McGregor 1976, Furniss and Carolin 1977, Goheen and Cobb 1980, Amman and Schmitz 1988, Carroll et al. 2006, Safranyik and Carroll 2006) may enable the insect to evade a strong defensive response by the host. Such associations permit access to hosts, and, if these weakened trees are in close spatial proximity, mountain pine beetle may then produce enough offspring to strip-attack trees that are injured and/or colonized by other species of bark beetles, or even mass-attack healthy neighboring trees (Eckberg et al. 1994, Logan et al. 1998). Clustering of trees strip-attacked by mountain pine beetle, evident in stands undergoing a transition from endemic to incipient-epidemic levels, appeared to precipitate mass attacks in neighbouring trees, as trees adjacent to successfully attacked hosts are likely to become the foci of aggregation (Geiszler et al. 1980, Raffa and Berryman 1987, Eckberg et al. 1994).

We note, however, that although the switch from trees with secondary colonization or injury to healthy hosts is believed to be density-dependent (Carroll et al. 2006), spatial analyses suggest that the behavioural shift in host colonization by mountain pine beetle is not immediate, as the clustering process begins before epidemic levels have been reached. Before mountain pine beetle reached the incipient-epidemic level, many trees harboring other species of bark beetles and/or some form of injury were mass attacked. Prolonged endemic behaviour may suggest genetic differences between beetles attacking weakened trees and those attacking more vigourous hosts, as has been proposed in the spruce beetle *D. rufipennis* (Kirby) system (Wallin and Raffa 2004). Persistent endemic behaviour may also be the product of varying phenotypes within the population whose tolerance for population densities

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differ (Chitty 1958, Chitty and Phipps 1966). As the numbers of endemic beetles grow, beetles phenotypically less tolerant of increasing densities may be prone to dispersal and seek an alternative habitat such as healthy trees, leading to epidemic behaviour.

Spatial analyses within this study, in conjunction with the studies by Carroll et al. (2006) and Smith (2008), lend additional support to an emerging theory of facilitation. It is unknown how widespread such mechanisms of phase transitions may be in bark beetle systems. In the southern pine beetle system, for example, the southern pine beetle *D*. *frontalis* (Zimmerman) may benefit from associations with the secondaries *I. avulsus* (Eichhoff) and *I. calligraphus* (Germar) that potentially help overcome tree resistance (Wagner et al. 1985, Flamm et al. 1987).

This theoretical framework of shifting patterns of colonization by mountain pine beetle from trees previously colonized by secondaries to fewer and fewer hosts with secondaries and/or putative vigour impairing injuries, marked by the formation of clusters of strip and mass attacks, suggests points of intervention that could be exploited for beetle management. For example, the positive associations apparent between mountain pine beetle and secondary bark beetles within weakened host trees suggest one reason why thinning operations may be effective in preventing outbreaks (Mitchell et al. 1983, Larsson et al. 1983, Raffa and Berryman 1986, Powell et al. 1998, Negron and Popp 2004). However, the benefits of thinning are only realized if the risk of migration into the stand is low, as healthy trees may still be overcome by large populations of mountain pine beetle migrating into a stand. This phenomenon likely occurred in 2003 in stand E, for example. Furthermore, thinning operations must remove material suitable for secondary bark beetle reproduction, as population levels of secondaries may increase post-thinning (Kegley et al. 1997, Hindmarch and Reid 2001), which may lead to further associations with endemic level mountain pine beetle.

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## **CHAPTER 4**

Spatial associations of the bark beetles *Dendroctonus murrayanae*, *Hylurgops* spp., *Ips pini*, *Orthotomicus latidens* and *Pseudips mexicanus* in lodgepole pine stands of southern British Columbia

# ABSTRACT

Non-eruptive bark beetles can be important agents of tree mortality that serve to thin aging stands. Thinning of forests of lodgepole pine, Pinus contorta (Douglas ex Louden) is of particular interest, because outbreaks of mountain pine beetle, Dendroctonus ponderosae Hopkins, may be minimized in such stands. This study examines the spatial associations between the non-eruptive bark beetles D. murrayanae (Hopkins), Hylurgops porosus (LeConte), H. rugipennis (Mannerheim), Ips pini (Say), Orthotomicus latidens (LeConte), and *Pseudips mexicanus* (Hopkins) in seven lodgepole pine stands in British Columbia from 2002 to 2005 while D. ponderosae was transitioning from endemic to incipient-epidemic population phases. Trees colonized by O. latidens and P. mexicanus were located in close proximity in all stands; in fact, these species were frequently colonizing the same host trees. Trees colonized by *Hylurgops* spp. and *P. mexicanus* displayed similar spatial patterns, but not as frequently as the former. The majority of trees colonized by these insects exhibited some form of injury. Identifying the nature of interactions between bark beetles within the bole-infesting assemblage may further our understanding of the propensity for stands to harbour low density populations of mountain pine beetle and ultimately undergo an outbreak. Key words: competition; niche partitioning; pine engravers; forest management

# **INTRODUCTION**

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are important disturbance agents in forest ecosystems. Eruptive species may undergo intermittent population explosions resulting in landscape-level mortality (Raffa et al. 2008). The vast majority of bark beetle species, however, do not undergo such dramatic population changes, but instead subsist in weakened, dying, and dead trees (Rudinsky 1962, Wood 1982a). Although the number of vigour impaired or unthrifty trees containing phloem suitable for reproduction within a stand is often limited (Berryman 1973, Anderbrant et al. 1985), increased resource availability due to stress events, such as drought, may facilitate rapid growth in these non-eruptive bark beetle populations (Hopping and Mathers 1945, Rudinsky 1962, Mattson and Haack 1987, Kelsey and Joseph 2001, Berg et al. 2006). These "secondary" bark beetles are vital components of forest ecosystems, beneficial to forest succession, and essential to the perpetuation of vigorous trees (Lundquist 1995, Jones et al. 1997).

A diverse number of bark beetles have been identified inhabiting lodgepole pine, *Pinus contorta* (Douglas ex Louden), forests within western North America (Bright 1976, Safranyik et al. 2004, Carroll et al. 2006). Bark beetle species that may be found in British Columbia, Canada, include *Dendroctonus murrayanae* (Hopkins), *Hylurgops porosus* (LeConte), *H. rugipennis* (Mannerheim), *Ips pini* (Say), *Orthotomicus latidens* (LeConte), and *Pseudips mexicanus* (Hopkins). Each of these insects, like mountain pine beetle, *Dendroctonus ponderosae* Hopkins, during its endemic population phases, is often associated with the boles of weakened pine hosts. Collectively, they are termed the bole-infesting bark beetle assemblage (Safranyik and Carroll 2006).

Thinning is considered to be one of the few effective management options to reduce the growth rate and outbreak potential of eruptive species of bark beetles (e.g., see review by Fettig et al. 2007). There is a wide body of empirical evidence in support of thinning to reduce outbreak extent in the mountain pine beetle system in both stands of lodgepole and ponderosa pine, *Pinus ponderosa* (Douglas ex Lawson) (Sartwell and Stevens 1975, Mitchell et al. 1983, Larsson et al. 1983, Raffa and Berryman 1986, McGregor et al. 1987, Negron and Popp 2004, Whitehead and Russo 2005). The mechanisms by which thinning reduces bark beetle populations are multi-causal, and may include changes in microclimate within a stand (Amman et al. 1988, Hindmarch and Reid 2001), as well as increases in host vigour within the remaining trees released from competition (Mitchell et al. 1983, Raffa and Berryman 1986). It thus stands to reason that growing populations of bole-infesting bark beetles may influence the development of endemic and incipient-epidemic levels of mountain pine beetle not only through within-tree competition for resources, but also through natural stand attenuation or thinning.

In this chapter, I examined the spatiotemporal dynamics of the non-eruptive assemblage of bark beetles in the years preceding an outbreak of mountain pine beetle in several stands of lodgepole pine in British Columbia, Canada. Many of these species reproduce in phloem not utilized by the eruptive species of bark beetles during an outbreak (Safranyik et al. 1974, Furniss and Carolin 1977, Wood 1982b), such that subsequent postoutbreak numbers of these insects may kill small-diameter trees (Furniss and Carolin 1977,

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Paine et al. 1997, Steed and Wagner 2008). Less is known however, about population dynamics of these insects in years preceding a large outbreak of mountain pine beetle. The relationship between secondary bark beetles and mountain pine beetle is complex, as activity by non-eruptive bark beetles may facilitate populations of endemic mountain pine beetle rather than putatively increase stand resistance (Carroll et al. 2006, Smith et al. 2009; Chapter 3). To gain an understanding of how these insects potentially mediate dynamics of outbreaking species, we first need to understand the behaviour within their assemblage. To that end, this chapter examined the spatial interactions of the bole-infesting non-eruptive bark beetle assemblage prior to the eruption of populations of mountain pine beetle at a withinstand level. I examined whether the guild shares a comon resource, and, if so, exhibits a consistent sequence of activity. I also examined whether there is an association between putative vigour-impairing injuries and colonization. Answers to these questions of predisposing factors and colonization sequences may shed light on the mechanisms by which bark beetles erupt (Aukema et al. 2010, Boone et al. 2010 in press), and, by extension, may suggest new tactics for their management.

#### **METHODS**

Seven field sites were established in southern British Columbia and monitored for bark beetle activity by exhaustively censusing each tree. Trees colonized by bark beetles were then visually evaluated for injury such as a broken or forked top, a scarred trunk, a thin crown, an infection of dwarf mistletoe (*Arceuthobium* spp.), an attack by mountain pine beetle greater than ten years prior, or some other form of injury/suppression. For a detailed description, see the Methods section of Chapter 2. Maps of all trees colonized by secondary bark beetles were created using the 'spatstat' package v.1.13-3 in R v.2.6.2 (Ihaka and Gentleman 1996, Baddeley and Turner 2005, R Development Core Team 2008). Colonization of trees by secondary bark beetles was analysed by year and species. For all stands, with the exception of stand D, the secondaries included *O. latidens*, *P. mexicanus*, *I. pini*, *H. porosus*, and *H. rugipennis*. *Hylurgops porosus* and *H. rugipennis* are collectively termed *Hylurgops* spp. *Ips pini* were not analyzed in stand D due to low numbers. *Dendroctonus murrayanae* was analyzed in stands D and G, where sufficient numbers existed. Analyses were conducted only when there were at least two trees colonized by each species of secondary bark beetle in a given year.

Spatial point process models were used to evaluate the spatial relationships between secondary colonization events within each stand. New techniques in spatial point process modeling are quite powerful for discerning potential relationships between species or other biotic and abiotic factors that may otherwise go undetected (Stoyan and Penttinen 2000). Each spatial point process model incorporated previous years of colonization as well as colonization occurring in the same year. The response variable for each model, a density ( $\lambda$ ), was measured as the number of trees bearing colonization of a given species per square meter in a given year. For example, a spatially-explicit estimated density of *O. latidens* colonization was measured as the number of trees bearing *O. latidens* attack per square meter in any given year. In a model with *O. latidens* as a response, covariates could include the locations of colonization by *O. latidens* and all other secondaries in the preceding year, as well as all other secondaries in that same year. All covariates were converted to spatially-explicit density surfaces (i.e., the average number of trees colonized in a given area in a given stand) prior to fitting using a Gaussian kernel density smoother (Cressie 1991, Baddeley and Turner 2000). Parameters in these spatial point process regression models were estimated using maximum pseudolikelihood methods. The significance of individual variables were judged by statistical comparison to a homogenous model, i.e., one estimating only an intercept or a constant intensity of secondary bark beetle colonization across the stand, by examining the change in deviance relative to a  $\chi^{-2}$  reference distribution. Models were compared using Akaike's Information Criterion (AIC), and models with the lowest AIC values were judged to fit best (Akaike 1973).

# RESULTS

The colonization of lodgpepole pine trees by secondary bark beetles within study stands was generally quite low. Between 0.2% (stand C), and 3% (stand D) of the available host trees were colonized by secondary bark beetles over the seven year study (see Appendix A Table A.1). These estimates were calculated based on the number of secondary bark beetle attacks, the size of each stand in hectares, the average density of trees per hectare, and the percent of lodgepole pine within each stand. The number of injured trees was much higher, however. The mean injury rate of trees across all stands was 48%. Seventy-four percent of colonization by secondary bark beetles across all stands occurred in trees possessing at least one putative vigour-impairing injury (Table 4.1), such as a broken or forked top, a scarred trunk, a thin crown, an infection of dwarf mistletoe (*Arceuthobium* spp.), an attack by

mountain pine beetle greater than ten years prior, or some other form of injury or suppression.

Patterns and sequences of colonization between secondary bark beetle species were generally consistent among all seven stands. To simplify data presentation, results of analyses are presented primarily from stand A (1999-2005). Other than some information on *D. murrayanae* in stand D, which is also reported, analyses of the remaining stands for all species are found in Appendix D.

*Pseudips mexicanus* and *O. latidens* frequently colonized the same host trees in the same year (Tables 4.2 and 4.3). A visual representation of this cluster pattern is provided in Fig. 4.1, where approximately 0.6% and 0.4% of the trees in the stand were colonized by *P. mexicanus* and *O. latidens*, respectively, in 2002 (Fig. 4.1A). *Orthotomicus latidens* also colonized trees inhabited by *P. mexicanus* in previous years, estimated to be approximately 78 trees throughout the stand in 2002 (Fig. 4.1B). *Pseudips mexicanus* also re-attacked trees quite frequently (Fig. 4.2).

The locations of trees colonized by *O. latidens* in a previous year were a good predictor of the presence of *O. latidens* colonization in a subsequent year, indicative of reattack or colonization of neighbouring pine hosts (Table 4.2, and see Appendix D: Tables D.3-D.5). However, the best inference on the locations of trees colonized by *O. latidens* in a given year were the locations of trees previously attacked by *P. mexicanus* as judged by lower AIC values for these models (Table 4.2).

Pseudips mexicanus had a tendency to inhabit hosts colonized either previously or

concurrently by *Hylurgops* spp. particularly in the earlier years of study in each stand (Tables 4.3 and 4.4, Fig. 4.3A, and see Appendix D: Tables D.6-D.18). Trees colonized by *Hylurgops* spp. were near trees colonized by *O. latidens* in the same year and/or in future years (Tables 4.2 and 4.4, Fig 4.3B). However, *Hylurgops* spp. were generally not found in trees that had been colonized by *O. latidens* previously. Rather, *O. latidens* appeared to colonize hosts already inhabited by *Hylurgops*.

Positive associations between trees colonized by *I. pini* and those colonized by any other secondary species under investigation were apparent, and are detailed in Appendix D (Tables D.18-D.22). The locations of trees colonized by *I. pini* were often proximate to those colonized by *P. mexicanus*, such that the two were frequently found utilizing the same host trees (Table 4.5, Fig. 4.4). There were, however, solitary instances when the location of *I. pini* colonization was negatively associated with colonization by each of *P. mexicanus*, *O. latidens*, and *Hylurgops* spp. (Appendix D: Tables D.10, D.18, D.20). However, spatial analyses at the stand-level across years provided little evidence of inhibition between *I. pini* and other secondary bark beetles.

*D. murrayanae* colonization was present in low numbers in most stands, and was incorporated into spatial analyses in stands D and G only. Spatial analyses indicated that the locations of *D. murrayanae* could not be consistently explained by knowing the locations of other species of bark beetles, although *D. murrayanae* would occasionally colonize trees containing *P. mexicanus* (Appendix D: Table D.9), *Hylurgops* spp. (Appendix D: Table D.18) and *I. pini* (Appendix D: Table D.22). Once *D. murrayanae* had colonized a tree, it appeared

to re-attack the same tree or neighbouring trees (Table 4.6).

Stand	No. Trees	-	Year								
		1999	2000	2001	2002	2003	2004	2005			
A	Secondaries	9	20	157	263	193	130	96			
	Injured	9	18	155	256	138	88	64			
В	Secondaries	_	27	123	196	136	-	-			
	Injured	-	25	116	187	107	-	-			
С	Secondaries	-	11	43	36	13	14	11			
	Injured	-	10	40	34	8	5	0			
D	Secondaries	-	-	-	4	14	17	3			
	Injured	_	-	-	4	9	7	1			
Е	Secondaries	-	2	25	91	235	-	-			
	Injured	-	0	23	71	168	-	-			
F	Secondaries	_	-	-	26	59	171	94			
	Injured	-	-	-	18	38	95	59			
G	Secondaries	-	-	1	19	137	314	160			
	Injured	-	-	1	9	75	158	73			

Table 4.1: Number of lodgepole pine (*Pinus contorta*) trees colonized by one or more species of secondary bark beetle (*Dendroctonus murrayanae*, *Hylurgops* spp., *Ips pini*, *Orthotomicus latidens*, and/or *Pseudips mexicanus*) and, within those same trees, the number bearing injuries within seven stands in southern British Columbia.

Table 4.2: Best explanatory models for the location of *Orthotomicus latidens* colonization from 2001 to 2005 in lodgepole pine of stand A in southern British Columbia. The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the density estimate of trees colonized by a given species per square meter. For example, the estimated density of *O. latidens* colonization in 2002 in locations where *Pseudips mexicanus* colonized trees at a rate of  $0.0005/m^2$  or 5 trees/ha. is  $exp^{(971+2324 \times 0.0005)}$ = 0.0002 or 2 trees/ha. For each, year significant models are listed in order of best fit.

Insect	Year	'ear <u>Intercept</u>		<u>Slo</u>	pe	$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
O. latidens	2001	-9.14	0.22					427.85
O. latidens	2000	-9.42	0.26	13531	3943	8.43	0.004	421.43
O. latidens	2002	-7.85	0.11					1347.67
P. mexicanus	2002	-9.71	0.34	2324	351	44.45	< 0.0001	1305.23
H. spp.	2002	-8.70	0.21	4784	797	29.88	< 0.0001	1319.80
P. mexicanus	2001	-9.22	0.32	2916	555	26.26	< 0.0001	1323.43
<i>H</i> . spp.	2001	-8.50	0.24	2548	737	11.57	0.0007	1338.11
O. latidens	2003	-8.12	0.13					1060.31
P. mexicanus	2003	-9.78	0.53	3027	881	13.38	< 0.001	1048.94
P. mexicanus	2002	-9.07	0.35	1286	399	10.20	< 0.001	1052.13
<i>H</i> . spp.	2003	-8.54	0.21	3357	1091	8.09	0.004	1054.23
O. latidens	2004	-8.72	0.18					623.96
P. mexicanus	2004	-10.52	0.48	3495	714	23.09	< 0.0001	602.87
<i>H</i> . spp.	2003	-9.54	0.30	11489	2440	19.44	< 0.0001	606.52
H. spp.	2004	-9.36	0.28	8346	2268	11.14	0.001	614.83
O. latidens	2005	-8.55	0.16					727.51
P. mexicanus	2005	-10.00	0.37	4509	800	23.09	< 0.0001	699.84
P. mexicanus	2004	-9.57	0.39	2152	663	9.77	0.002	719.75

Table 4.3: Best explanatory models for the location of *Pseudips mexicanus* colonization from 2000 to 2005 in lodgepole pine of stand A in southern British Columbia. The line in bold represents the null model for each year; i.e., no explanatory variable (reflected by the absence of an estimated slope) thus modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the density estimate of trees colonized by a given species per square meter. For each year significant models are listed in order of best fit.

Insect	Year	Year <u>Intercept</u>		Slo	pe	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2000	-9.79	0.30					239.29
<i>H</i> . spp.	2000	-10.43	0.44	12882	4193	7.30	0.01	233.99
P. mexicanus	2001	-7.81	0.11					1394.67
H. spp.	2001	-8.59	0.24	3019	720	17.04	< 0.0001	1379.65
P. mexicanus	2000	-8.03	0.14	3180	1087	7.06	0.01	1389.62
P. mexicanus	2001	-8.07	0.17	3587	1539	5.04	0.02	1391.64
P. mexicanus	2002	-7.33	0.09					2134.93
O. latidens	2002	-8.40	0.20	2242	341	45.38	< 0.0001	2091.58
H. spp.	2002	-8.13	0.18	6736	1152	33.13	< 0.0001	2103.83
P. mexicanus	2001	-8.43	0.24	2365	434	28.29	< 0.0001	2108.67
H. spp.	2001	-7.90	0.18	2270	571	15.30	< 0.0001	2121.66
I. pini	2002	-7.64	0.14	2418	769	8.93	0.003	2128.03
P. mexicanus	2003	-7.63	0.10					1641.69
O. latidens	2003	-8.33	0.25	2110	648	10.33	0.001	1633.38
H. spp.	2003	-7.90	0.16	2247	923	5.31	0.02	1638.40
P. mexicanus	2004	-7.81	0.11					1394.67
O. latidens	2004	-8.45	0.19	3027	595	21.25	< 0.0001	1375.43
H. spp.	2003	-8.29	0.17	7521	1662	18.23	< 0.0001	1378.45
H. spp.	2004	-8.18	0.17	9602	2994	9.43	0.002	1387.26
O. latidens	2003	-8.45	0.27	1915	711	7.06	0.01	1389.63
P. mexicanus	2005	-8.31	0.14					896.01
O. latidens	2005	-9.70	0.33	5429	908	34.92	< 0.0001	863.10
P. mexicanus	2004	-9.25	0.34	1975	594	10.29	0.001	887.73
H. spp.	2005	-8.53	0.17	13711	4420	7.82	0.01	890.20

Table 4.4: Best explanatory models for the location of *Hylurgops* spp. colonization from 2001 to 2004 in lodgepole pine of stand A in southern British Columbia. The line in bold represents the null model for each year; i.e., no explanatory variable (reflected by the absence of an estimated slope) thus modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the density estimate of trees colonized by a given species per square meter. For each year significant models are listed in order of best fit.

Insect	Year	<b>Intercept</b>		<u>Slo</u>	<u>Slope</u>		<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
H. spp.	2001	-8.72	0.18					623.96
O. latidens	2001	-10.64	0.48	9137	1727	27.57	< 0.0001	598.39
P. mexicanus	2001	-10.09	0.49	2923	857	11.06	0.001	614.90
P. mexicanus	2000	-9.01	0.23	4095	1567	5.38	0.02	620.59
Н. ѕрр.	2002	-9.24	0.23					391.10
P. mexicanus	2002	-11.23	0.70	2479	710	12.46	0.0004	380.64
O. latidens	2002	-10.67	0.55	2873	819	11.53	0.001	381.57
<i>H</i> . spp.	2001	-10.42	0.55	6058	2231	7.05	0.01	386.05
P. mexicanus	2001	-10.66	0.64	3020	1111	7.03	0.01	386.07
O. latidens	2001	-9.75	0.35	3582	1461	4.98	0.03	388.12
H. spp.	2003	-9.99	0.33					199.76
P. mexicanus	2002	-13.37	1.25	3857	1126	13.56	0.0002	188.20
O. latidens	2003	-12.22	1.02	5886	2135	7.84	0.01	193.92
O. latidens	2002	-11.58	0.81	3142	1186	6.61	0.01	195.15
P. mexicanus	2003	-12.38	1.52	4263	2430	3.73	0.05	198.03
<i>Н</i> . spp.	2004	-10.39	0.41					138.70
O. latidens	2003	-12.96	1.32	6610	2667	6.52	0.01	134.19
H. spp.	2003	-11.47	0.74	13870	5534	5.58	0.02	135.13

Table 4.5: Best explanatory models for the location of *Ips pini* colonization from 2001 to 2003 in lodgepole pine of stand A in southern British Columbia. The line in bold represents the null model for each year; i.e., no explanatory variable (reflected by the absence of an estimated slope) thus modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the density estimate of trees colonized by a given species per square meter. For each year significant models are listed in order of best fit.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
I. pini	2001	-9.70	0.29			-		258.77
P. mexicanus	2001	-10.99	0.79	2763	1399	3.70	0.05	257.07
I. pini	2002	-9.14	0.22					427.85
O. latidens	2002	-10.55	0.52	2829	777	12.39	0.0004	417.46
P. mexicanus	2002	-10.31	0.60	1554	661	5.43	0.02	424.42
I. pini	2001	-9.60	0.34	5964	2795	4.09	0.04	425.77
I. pini	2003	-9.54	0.27					297.25
P. mexicanus	2003	-11.65	1.17	3790	1890	4.75	0.03	294.51
O. latidens	2003	-10.78	0.71	3525	1672	4.35	0.04	294.91

Table 4.6: Best explanatory models for the location of *Dendroctonus murrayanae* attack from 2003 and 2005 in lodgepole pine of stand D in southern British Columbia. The line in bold represents the null model for each year; i.e., no explanatory variable (reflected by the absence of an estimated slope) thus modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the density estimate of trees colonized by a given species per square meter. For each year significant models are listed in order of best fit.

Insect	Year	Intercept		<u>Slope</u>		$\chi^2$	P-value	AIC
		Est.	SE	Est.	SE			
D. murrayanae	2003	-8.69	0.23					370.12
D. murrayanae	2002	-9.65	0.54	8976	3484	4.56	0.03	367.33
D. murrayanae	2005	-8.45	0.20					455.78
D. murrayanae	2004	-9.26	0.46	3232	1479	4.03	0.05	453.46



Figure 4.1: Locations of secondary bark beetle colonization in lodgepole pine of stand A in southern British Columbia. A) Trees colonized by *Pseudips mexicanus* and *Orthotomicus latidens* in 2002 B) Trees colonized by *P. mexicanus* in 2001 and *O. latidens* in 2002 comprise approximately 0.4% of the 19,500 lodgepole pine trees in the stand respectively.



Figure 4.2: Locations of trees colonized by *Pseudips mexicanus* in lodgepole pine of stand A in southern British Columbia. Colonizations by *P. mexicanus* in 2001 and 2002 comprise approximately 0.4% and 0.6% of the 19,500 lodgepole pine trees in the stand respectively.



Figure 4.3: Locations of secondary bark beetle colonization in lodgepole pine of stand A in southern British Columbia. A) Trees colonized by *Hylurgops* spp. and *Pseudips mexicanus* in 2001 comprise approximately 0.2% and 0.4% of the 19,500 logepole pine trees in the stand respectively. B) Trees colonized by *H*. spp. and *Orthotomicus latidens* in 2002 comprise approximately 0.1% and 0.4% of the 19,500 lodgepole pine trees in the stand respectively.



Figure 4.4: Location of trees colonized by *Pseudips mexicanus* and *Ips pini* in lodgepole pine of stand A in southern British Columbia. Colonizations by *P. mexicanus* and *I. pini* in 2003 comprise approximately 0.45% and 0.07% of the 19,500 lodgepole pine trees in the stand respectively.

## DISCUSSION

This study suggests that colonization dynamics of secondary bark beetles in stands of lodgepole pine are not entirely random, but rather follow a stereotypic sequence of events and associations. The frequent within or between-tree associations between *Hylurgops* spp. and *P. mexicanus*, *Hylurgops* spp. and *O. latidens*, and *I. pini* and *P. mexicanus* from the endemic to the incipient-epidemic stages of population development of mountain pine beetle suggests that sufficient resource partitioning must occur to minimize interspecific competition and promote a robust assemblage of bark beetles (Birch et al. 1980, Byers 1989).

Temporal partitioning by secondary bark beetles is one effective means of limiting interspecific competition (Paine et al. 1981, Amezaga and Rodriguez 1998, Safranyik et al. 2004). However, temporal analyses (Chapter 2) suggested emergence, flight, and host colonization by these species of bark beetles overlap substantially. *Hylurgops* spp. emerge and colonize hosts prior to, or in quick succession with, *P. mexicanus*. The tendency for *O. latidens* to infest trees already occupied by *P. mexicanus* or *Hylurgops* spp. may be at least partially explained by its prolonged emergence through the time of study in each year, as well as its ubiquitous occurence in tissues in more advanced stages of deterioration (Miller and Borden 1985). For example, while *O. latidens* often reproduced in a host in the same year or in the year following colonization by *Hylurgops* spp. or *P. mexicanus*, *O. latidens* galleries do not overlap those of *P. mexicanus*, as colonization by *P. mexicanus* often occurs below *O. latidens* and *I. pini* galleries (A. Carroll, pers. comm., Smith et al. 2009). Although *P. mexicanus* may be found at greater heights and into the branches of trees in areas of

California (Fox et al. 1990) and Mexico (Schwerdtfeger 1956), attacks in lodgepole pine trees within British Columbia generally do not occur above one metre (Smith et al. 2009). *Hylurgops porosus* and *H. rugipennis* utilize the lower bole of various pine hosts at or below the root collar (Wood 1982b).

Avoidance of occupied hosts is a simple way to reduce interspecific competition. *Ips pini* ordinarily avoids trees inhabited by *O. latidens* (Poland 1997) or *P. mexicanus* (Poland 1997, Savoie 1998). We found, for example, that *I. pini* colonization was located on the westernmost side of stand E, while *O. latidens* and *P. mexicanus* inhabited trees on the eastern half. However, the new finding of positive spatial associations between *I. pini* and *P. mexicanus* colonization in our study may be attributed to the extensive number of trees surveyed. It is possible that *I. pini*, with the development of multiple generations within a year (Furniss and Carolin 1977), may have attacked hosts after *P. mexicanus* colonization had occurred. *Ips pini* often predominates phloem resources in the hosts it colonizes. Any remaining phloem lower down on the bole near the root collar, however, may be utilized by *P. mexicanus* (E. Teen, pers. comm.).

The majority of colonization occurred in trees with putative vigour-impairing injuries. The declining rate of trees with injuries colonized by non-eruptive bark beetles from 2003 to 2005 might be explained by mountain pine beetle activity. In this study, growing populations of mountain pine beetle shifted from injured and/or weakened trees to uninjured, vigorous hosts (Chapter 3; Carroll et al. 2006), and, after completing their life-cycle, left behind a source of previously uninjured hosts available for colonization (Safranyik et al. 1974, Furniss
and Carolin 1977, Wood 1982b, Paine et al. 1997, Steed and Wagner 2008). For stands D and G, where populations of mountain pine beetle did not exit an endemic phase, the large number of uninjured trees colonized by non-eruptive species could likely be attributed to *P*. *mexicanus* and *O. latidens* attack on small diameter, yet otherwise healthy, trees (Furniss and Carolin 1977, Paine et al. 1997). Stand D also contained the oldest trees, with an average age of nearly 150 years (Carroll et al. 2006). An infestation of *D. murrayanae* in uninjured, senescent hosts within this stand also likely contributed to a large number of the trees lacking injuries that were colonized by non-eruptive species of bark beetles.

The colonization behaviour of robust assemblages of bark beetles may naturally thin stands as weaker trees are killed. Trees not suffering mortality by bark beetles benefit from reduced competition for light, water, and nutrients (Oliver and Larson 1996). Lodgepole pine stands may outgrow their susceptibility to localized eruptions of mountain pine beetle if the majority of weakened hosts have been naturally thinned by the activity of secondary bark beetles. In this study, 74% of trees attacked by secondary bark beetles displayed an injury or some form of disease. Thinning activity may extinguish or severely limit reservoirs of endemic mountain pine beetle by eliminating their hosts. This could explain why some stands upwards of 160 to 170 years of age have never suffered serious depletion from more aggressive species of bark beetles (Hopping and Mathers 1945).

Resource sharing between bark beetles within the bole-infesting assemblage may enable or prolong localized eruptions of typically non-eruptive species following an epidemic of mountain pine beetle and contribute to the mortality of smaller, but otherwise healthy trees. Future work should focus on the nature of interactions between these species. Competition experiments, for example, between varying densities of bark beetles in the complete bole-infesting assemblage may lend valuable information concerning the positive spatial associations found here. A greater understanding of the extent of resource partitioning or competition at a within-tree level may enhance the projection of mortality to small trees following outbreaks of mountain pine beetle. Further research is also required to fully understand the interactions of non-eruptive species before they may be utilized as natural agents useful in stand management. However, the existence of stands in which bark beetles have thinned trees to a level such that they are essentially immune to localized eruptions suggests that natural approaches to future management have promise.

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### **CHAPTER 5**

#### General Conclusions

This study was undertaken to examine the temporal and spatial relationships between a bole-infesting asemblage of bark beetles, including the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, as the latter was transitioning from the endemic to the incipientepidemic phase. The extent of research pertaining to the endemic phase of this organism is severely limited, and finding endemic beetles often poses a significant challenge (Tkacz and Schmitz 1986, Bartos and Schmitz 1998, Carroll et al. 2006). Only recently were endemic populations defined to be approximately forty beetles per hectare (Carroll et al. 2006), thus contextualizing much existing research on low populations of mountain pine beetle as more relevant to the incipient phase. In the endemic phase mountain pine beetle is believed to inhabit weakened, diseased, and suppressed hosts (Blackman 1931, Furniss and Carolin 1977). Associations between low levels of mountain pine beetle and other bark beetles have been noted anecdotally by DeLeon (1934), Hamel and McGregor (1976), Goheen and Cobb (1980), Tkacz and Schmitz (1986), and Amman and Scnitz (1988).

Temporal relationships between non-eruptive species of bark beetles and mountain pine beetle in the first data chapter suggest facilitation between species. The number of trees colonized by mountain pine beetle increased in relation to the number of trees colonized by other species of bark beetles, trailing populations of other bark beetles by at least a year. Spatial analyses from the second data chapter determined that endemic mountain pine beetle frequently colonize hosts containing other bark beetle species and/or bearing some sort of injury. The greatest number of positive spatial associations was with *Pseudips mexicanus* (Hopkins), however, mountain pine beetle were found with a variety of bark beetle species including *Orthotomicus latidens* (LeConte), *Hylurgops* spp., and less frequently *Ips pini* (Wood). The colonization of trees utilised previously by other bole-infesting bark beetles (Hamel and McGregor 1976, Furniss and Carolin 1977, Goheen and Cobb 1980, Amman and Schmitz 1988, Carroll et al. 2006, Safranyik and Carroll 2006) may enable the insect to evade a strong defensive response by the host. As the number of colonizations by mountain pine beetle increased towards incipient-epidemic levels, the associations with other bark beetles and injured trees became less evident. These results are consistent with a model in which the colonization dynamics of mountain pine beetle change as populations increase, such that mountain pine beetle subsist in these "nurse trees" until suitable conditions occur to strip- or mass-attack healthy hosts.

Spatial analyses of the colonizations by secondary bark beetles in the final data chapter suggest that the bole-infesting community likely partitions host resources effectively to reduce interspecific competition. Furthermore, resource sharing between secondary bark beetles within the bole-infesting assemblage may enable or prolong localized eruptions following an epidemic of mountain pine beetle and contribute to the mortality of smaller, but otherwise healthy trees. It is likely that competition between mountain pine beetle and other bark beetles such as *I. pini* increases with the increasing density of mountain pine beetle in later population phases (Rankin and Borden 1991).

#### **Management Implications**

In summary, the interaction between mountain pine beetle and other bark beetles may be an important element to incorporate into future models predicting the risk of outbreaks of mountain pine beetle. Futhermore, the populations of other bark beetles may potentially be used to monitor for the development of growing populations of mountain pine beetle. Pheromone traps could be used to monitor the populations of bark beetles that appear to be very closely associated with endemic levels of mountain pine beetle such as *P. mexicanus* and *O. latidens*, within stands of particular importance. However, potential challenges arise, as the pheromone of *P. mexicanus* needs to be elucidated further (Smith et al. 2009).

Alternatively, the interaction between mountain pine beetle and other bark beetles may be manipulated in such a way as to reduce the ability for stands to harbour endemic levels of mountain pine beetle, possibly through thinning operations that reduce the number of weakened and injured trees within a stand. However, these operations must take into consideration the potential for immigration of populations of mountain pine beetle from neighbouring areas, as the insect is capable of aeolian dispersal over vast distances (de la Giroday et al. 2010). It is suspected that high levels of immigrating beetles can overwhelm local dynamics within a stand, as likely occurred in stand E.

## **Future Research**

Future work exploring the density-dependent relationship between secondary bark beetles and endemic level mountain pine beetle may shed considerable light on the question of facilitation. A further look at the nutritional changes of phloem tissue as well as the moisture content of host trees innoculated by secondary bark beetle fungi may also provide significant understanding of facilitative relationships. Future work should also focus on the nature of interactions between species of non-eruptive bark beetles. Competition experiments between varying densities of secondary bark beetles may lend valuable inference concerning their relationships. A greater understanding of the extent of resource partitioning or competition at a tree level may enhance the projection of mortality to small trees following outbreaks of mountain pine beetle. The existence of stands in which bark beetles have thinned trees to a level such that they are essentially immune to localized eruptions suggests that incorporating natural processes in approaches to future management has promise. Finally, the potential interactions of mountain pine beetle with bark beetle species found in the boreal forest may be of interest as the threat of populations spreading into new habitats is explored.

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### **APPENDICES**

### APPENDIX A

Table A.1: Mensurational characteristics of seven lodgepole pine stands at two sites in southern British Columbia used to assess the dynamics of mountain pine beetle and secondary bark beetle populations.

Site	Stand	Area	Density	Lodgepole pine <sup>a</sup>	Secondary	Trees Attacked
		(Ha)	(Stems/Ha)	(Percent)	Attacks	(Percent) <sup>b</sup>
Angstad	А	16.7	1263	92.5	922	1.2 - 4.7
	В	17.6	1273	94.2	490	0.6 - 2.3
	С	9.9	1554	96.8	129	0.2 - 0.9
	F	13.0	1325	90.4	393	0.6 - 2.5
Aberdeen	D	11.9	807	80.1	945	3.1 - 12.3
	Е	17.9	1257	90.6	434	0.5 - 2.1
	G	14.9	1424	94.2	669	0.8 - 3.3

<sup>a</sup> Remaining species included Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), interior spruce (*Picea* spp.) and subalpine fir (*Abies lasiocarpa*)

<sup>b</sup> First number represents a conservative estimate, second number a high estimate that does not take into account multiple attacks on a single tree. Number represents only trees attacked by species other than mountain pine beetle.

# APPENDIX B

assemblage in a lodgepole pine stand of southern British Columbia (Stand A).										
Species	1999	2000	2001	2002	2003	2004	2005	Total		
Dendroctonus ponderosae	5	16	29	37	117	184	383	771		
Ips pini	4	1	12	21	14	1	3	56		
Hylurgops spp.	0	6	43	27	20	11	4	101		
Orthotomicus latidens	1	2	21	76	58	32	38	228		
Pseudips mexicanus	4	11	79	128	95	79	47	444		

Table B.1: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand A).

Table B.2: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand B).

Species	1999	2000	2001	2002	2003	2004	2005	Total	
Dendroctonus ponderosae	5	19	41	85	201	546	2203	3100	
Ips pini	0	1	3	11	14	0	0	29	
Hylurgops spp.	0	17	43	23	20	0	0	103	
Orthotomicus latidens	0	0	15	58	33	0	0	106	
Pseudips mexicanus	0	9	59	96	62	0	1	227	

Table B.3: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand C).

Species	2000	2001	2002	2003	2004	2005	Total
Dendroctonus ponderosae	8	10	9	36	86	270	419
Ips pini	0	1	2	0	0	0	3
Hylurgops spp.	6	12	0	0	0	1	19
Orthtomicus latidens	0	3	13	2	4	2	24
Pseudips mexicanus	5	24	20	10	10	7	76

Species	2000	2001	2002	2003	2004	2005	Total
Dendroctonus ponderosae	0	5	12	28	37	11	93
Dendroctonus murrayanae	0	10	11	19	26	24	90
Ips pini	0	0	1	6	1	2	10
Hylurgops spp.	0	6	24	22	8	4	64
Orthomicus latidens	1	6	38	126	60	52	283
Pseudips mexicanus	3	21	82	180	11	82	479

Table B.4: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand D).

Table B.5: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand E).

Species	2000	2001	2002	2003	Total
Dendroctonus ponderosae	0	19	59	404	482
Ips pini	0	2	3	13	18
Hylurgops spp.	0	11	32	61	104
Orthotomicus latidens	1	5	26	71	103
Pseudips mexicanus	1	11	36	96	144

Table B.6: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand F).

Species	2001	2002	2003	2004	2005	Total
Dendroctonus ponderosae	2	7	46	84	232	371
Ips pini	0	0	1	4	8	13
Hylurgops spp.	0	2	4	12	2	20
Orthotomicus latidens	0	11	19	45	38	113
Pseudips mexicanus	0	15	37	111	46	209

					<u> </u>		
Species	2000	2001	2002	2003	2004	2005	Total
Dendroctonus ponderosae	0	0	8	27	50	7	92
Dendroctonus murrayanae	0	0	0	2	9	12	23
Ips pini	0	0	0	1	6	4	11
Hylurgops spp.	1	1	2	14	20	12	50
Orthomicus latidens	0	0	4	53	127	58	242
Pseudips mexicanus	1	2	15	75	158	76	327

Table B.7: Number of trees colonized by year for species of the bole-infesting bark beetle assemblage in a lodgepole pine stand of southern British Columbia (Stand G).

## APPENDIX C

Table C.1: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2001 to 2005 in a lodgepole pine stand of southern British Columbia (Stand A). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inter	cept	Slo	pe	$\chi^2$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
Strip attack	2000	-9.99	0.33					199.76
All secondaries	2000	-10.81	0.54	5228	1906	6.47	0.01	195.29
H. spp.	2000	-10.57	0.48	12121	4749	5.10	0.02	196.67
O. latidens	2000	-10.31	0.40	14927	5747	4.77	0.03	197.00
Strip attack	2001	-9.35	0.24					353.90
O. latidens	2000	-9.64	0.29	13831	4344	7.22	0.01	348.70
I. pini	2001	-8.82	0.27	-2583	3386	0.62	0.05	352.03
Strip attack	2002	-8.96	0.02					500.25
P. mexicanus	2002	-10.88	0.61	2401	616	15.44	< 0.0001	486.82
All secondaries	2002	-10.44	0.54	952	282	10.99	0.001	491.26
O. latidens	2002	-9.84	0.44	1885	735	6.19	0.01	496.06
<i>H</i> . spp.	2002	-9.70	0.41	6258	2606	5.59	0.02	496.66
Strip attack	2003	-8.57	0.16					710.39
P. mexicanus	2003	-9.66	0.61	2038	1038	4.16	0.04	708.24
I. pini	2003	-8.93	0.25	4340	1997	4.13	0.04	708.27
Strip attack	2004	-8.72	0.18					623.96
P. mexicanus	2003	-7.64	0.45	-2296	957	5.64	0.02	620.33
P. mexicanus	2004	-9.41	0.41	1508	745	3.83	0.05	622.14
Strip attack	2005	-7.94	0.12					1252.94
I. pini	2005	-7.79	0.13	-12255	6297	5.03	0.02	1249.93
H. spp.	2004	-7.64	0.17	-5651	2593	5.45	0.02	1249.51

Table C.2: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2001 to 2005 in a lodgepole pine stand of southern British Columbia (Stand C). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inte	rcept	<u>Slo</u>	<u>pe</u>	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Strip attack	2001	-9.77	0.45					109.67
H. spp.	2001	-12.85	1.44	15059	5035	10.19	0.001	101.44
H. spp.	2000	-10.80	0.75	12171	4595	5.44	0.02	106.19
Strip attack	2002	-9.77	0.45					109.67
H. spp.	2001	-12.19	1.30	12562	4838	7.37	0.01	104.26
All secondaries	2001	-12.20	1.29	12562	4838	7.36	0.01	104.26
P. mexicanus	2001	-10.74	0.75	2642	1171	3.94	0.05	107.69
Strip attack	2003	-9.18	0.33					185.23
All secondaries	2003	-11.18	0.83	6847	1695	19.38	< 0.0001	167.78
P. mexicanus	2003	-11.12	0.82	8022	2020	18.82	< 0.0001	168.33
P. mexicanus	2002	-10.34	0.57	2979	731	13.24	0.0003	173.91
All secondaries	2002	-10.52	0.61	2190	539	13.22	0.0003	173.94
O. latidens	2003	-10.23	0.58	21915	6201	11.48	0.001	175.67
O. latidens	2002	-10.55	0.70	7055	2396	7.99	0.005	179.16
Strip attack	2004	-8.33	0.22					393.95
P. mexicanus	2004	-8.76	0.30	2663	873	7.59	0.006	388.18
All secondaries	2004	-8.69	0.29	1632	584	6.29	0.01	389.48
All secondaries	2003	-8.75	0.32	2267	1022	4.45	0.04	391.32
P. mexicanus	2003	-8.73	0.32	2612	1218	4.15	0.04	391.62
O. latidens	2004	-8.55	0.26	3722	1714	3.72	0.05	392.05
Strip attack	2005	-7.20	0.12					1068.30
O. latidens	2005	-8.02	0.20	16618	1973	64.19	< 0.0001	1005.53
All secondaries	2005	-7.76	0.18	3102	469	37.31	< 0.0001	1032.41
P. mexicanus	2004	-7.71	0.17	2974	485	30.64	< 0.0001	1039.08
All secondaries	2004	-7.66	0.17	1923	318	29.16	< 0.0001	1040.56
P. mexicanus	2005	-7.65	0.17	3456	591	28.30	< 0.0001	1041.42
O. latidens	2004	-7.54	0.16	4953	873	24.16	< 0.0001	1045.56

Table C.3: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2003 and 2005 in a lodgepole pine stand of southern British Columbia (Stand D). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		Slo	pe	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Strip attack	2003	-8.99	0.27					281.80
P. mexicanus	2003	-12.42	1.45	1818	693	8.61	0.003	275.02
All secondaries	2003	-12.30	1.45	933	372	7.28	0.01	276.34
O. latidens	2003	-12.16	1.41	2459	1002	6.70	0.01	276.92
Strip attack	2005	-10.53	0.58					71.20
D. murrayanae	2005	-14.20	2.23	13428	6374	5.19	0.02	67.97

Table C.4: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2002 and 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inter	<u>cept</u>	<u>Slo</u>	<u>be</u>	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Strip attack	2002	-9.23	0.25					329.30
<i>H</i> . spp.	2002	-11.27	0.77	18801	5723	10.95	0.001	320.37
P. mexicanus	2002	-8.49	0.41	-4032	2201	4.52	0.03	326.81
Strip attack	2003	-7.89	0.13					1086.55
H. spp.	2002	-11.28	0.70	13677	2521	44.94	< 0.0001	1043.70
All secondaries	2003	-12.28	0.90	2515	470	44.05	< 0.0001	1044.59
P. mexicanus	2003	-10.24	0.54	3495	714	25.90	< 0.0001	1062.74
H. spp.	2003	-9.12	0.37	2728	703	16.50	< 0.0001	1072.14
I. pini	2002	-8.65	0.26	32913	8385	15.24	< 0.0001	1073.40
O. latidens	2003	-9.04	0.36	2292	610	14.23	0.0001	1074.41
All secondaries	2002	-8.79	0.33	1324	406	10.08	0.002	1078.57
O. latidens	2002	-8.44	0.25	2949	1010	8.01	0.005	1080.63
I. pini	2003	-8.39	0.25	5217	1929	7.67	0.006	1080.97

Table C.5: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2003 to 2005 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	r <u>Intercept</u>		<u>Slo</u>	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
Strip Attack	2002	-11.25	0.71					50.99
H. spp.	2002	-14.29	2.67	97282	57658	5.26	0.02	47.74
Strip attack	2003	-9.05	0.24					363.78
All secondaries	2003	-11.66	0.90	4883	1379	16.78	< 0.0001	349.11
P. mexicanus	2003	-11.41	0.91	7175	2270	14.83	0.0001	351.07
P. mexicanus	2002	-10.75	0.64	13064	3815	12.87	0.0003	353.03
O. latidens	2003	-10.43	0.55	8301	2442	11.11	0.001	354.78
All secondaries	2002	-10.43	0.60	5809	1960	9.74	0.002	356.16
O. latidens	2002	-9.74	0.44	7845	3570	4.67	0.03	361.23
Strip attack	2005	-8.23	0.16					758.55
O. latidens	2005	-9.14	0.39	3158	1128	8.06	0.01	752.76
P. mexicanus	2004	-9.20	0.46	1207	499	6.08	0.01	754.74
All secondaries	2005	-8.90	0.37	967	437	4.87	0.03	755.95
P. mexicanus	2005	-8.90	0.37	1992	931	4.59	0.03	756.23
I. pini	2004	-8.50	0.21	9251	4116	4.14	0.04	756.68
All secondaries	2004	-9.02	0.45	637	321	4.08	0.04	756.74

Table C.6: Association of trees colonized by other bark beetles on the locations of trees stripattacked by mountain pine beetle from 2003 and 2004 in a lodgepole pine stand of southern British Columbia (Stand G). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Intercept		<u>Slope</u>		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Strip attack	2003	-9.21	0.29					247.09
O. latidens	2002	-10.19	0.52	17229	5342	9.83	0.002	239.30
All secondaries	2002	-10.95	0.79	7419	2609	8.62	0.003	240.50
P. mexicanus	2003	-11.52	1.07	3138	1252	6.70	0.01	242.42
Strip attack	2004	-8.61	0.21					424.67
All secondaries	2004	-10.44	1.00	654	330	4.15	0.04	422.58

Table C.7: Association of trees strip-attacked by mountain pine beetle on the location of mass attacks from 2001 to 2005 in a lodgepole pine stand of southern British Columbia (Stand A). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	r <u>Intercept</u>		<u>Slo</u>	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
Mass attack	2001	-10.39	0.41					138.70
Strip attack	2001	-11.36	0.68	7581	3065	4.69	0.03	136.01
Mass attack	2003	-8.01	0.12					1173.22
Strip attack	2003	-10.31	0.36	8880	1050	70.51	< 0.0001	1104.73
Mass attack	2004	-7.59	0.10					1702.56
Strip attack	2004	-9.84	0.27	7160	551	201.86	< 0.0001	1502.72
Strip attack	2003	-9.35	0.27	7109	861	67.75	< 0.0001	1636.83
Mass attack	2005	-6.49	0.06					4438.12
Strip attack	2005	-8.05	0.13	3221	179	280.07	< 0.0001	4160.11
Strip attack	2004	-6.81	0.09	1585	301	25.80	< 0.0001	4414.38

Table C.8: Association of trees strip-attacked by mountain pine beetle on the location of mass attacks from 2003 to 2005 in a lodgepole pine stand of southern British Columbia (Stand C). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<b>Slope</b>		$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
Mass attack	2003	-8.24	0.21					427.09
Strip attack	2003	-9.54	0.39	5831	832	44.74	< 0.0001	384.15
Strip attack	2002	-8.68	0.26	5734	1405	10.41	0.001	418.48
Mass attack	2004	-7.57	0.15					773.30
Strip attack	2004	-8.33	0.25	2417	492	20.22	< 0.0001	754.68
Strip attack	2003	-7.93	0.20	2541	685	11.09	0.001	763.82
Mass attack	2005	-6.05	0.07					2894.01
Strip attack	2005	-7.78	0.16	962	50	447.28	< 0.0001	2446.90
Strip attack	2004	-6.60	0.11	1892	247	50.05	< 0.0001	2844.13

Table C.9: Association of trees strip-attacked by mountain pine beetle on the location of mass attacks from 20023 and 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inter	<u>cept</u>	<u>Slo</u> j	<u>pe</u>	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Mass attack	2002	-8.42	0.17					680.03
Strip attack	2001	-9.98	0.52	14668	3962	18.09	< 0.0001	664.00
Strip attack	2002	-9.52	0.42	9115	2736	12.41	0.0004	669.68
Mass attack	2003	-6.23	0.06					4655.57
Strip attack	2003	-8.56	0.23	4765	397	208.90	< 0.0001	4449.17
Strip attack	2002	-7.20	0.13	8317	903	93.27	< 0.0001	4564.80

Table C.10: Association of trees strip-attacked by mountain pine beetle on the location of mass attacks from 2004 and 2005 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		Slope		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
Mass attack	2004	-8.09	0.15					856.43
Strip attack	2004	-9.61	0.46	8337	2179	13.99	0.0002	844.75
Mass attack	2005	-6.69	0.07					2938.65
Strip attack	2004	-8.50	0.18	5202	381	189.28	<0.0001	2752.61



Figure C.1: Ripley's K function for trees strip-attacked by mountain pine beetle in 2002 for stand A. Observed estimate is shown by the solid black line, the upper and lower limits of the 95% confidence interval are shown by the green and blue ragged dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the smooth red dashes. The focal distance (r) on the x-axis is represented in metres.



Figure C.2: Ripley's K function for trees strip-attacked by mountain pine beetle in 2003 for stand A. Observed estimate is shown by the solid black line, the upper and lower limits of the 95% confidence interval are shown by the green and blue ragged dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the smooth red dashes. The focal distance (r) on the x-axis is represented in metres.



Figure C.3: Ripley's K function for trees mass-attacked by mountain pine beetle in 2003 for stand A. Observed estimate is shown by the solid black line, the upper and lower limits of the 95% confidence interval are shown by the green and blue ragged dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the smooth red dashes. The focal distance (r) on the x-axis is represented in metres.



Figure C.4: Ripley's K function for trees mass-attacked by mountain pine beetle in 2004 for stand A. Observed estimate is shown by the solid black line, the upper and lower limits of the 95% confidence interval are shown by the green and blue ragged dashes respectively. The theoretical estimate for a point process displaying complete spatial randomness is shown by the smooth red dashes. The focal distance (r) on the x-axis is represented in metres.

# APPENDIX D

Table D.1: Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2002 and 2003 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year <u>Intercept</u>		<u>cept</u>	<u>Slo</u>	<u>ope</u>	$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
O. latidens	2002	-8.39	0.13	· · · · · · · · · · · · · · · · · · ·				1090.97
P. mexicanus	2001	-11.08	0.63	10217	2177	23.64	< 0.0001	1069.13
P. mexicanus	2002	-10.49	0.59	4773	1200	20.70	< 0.0001	1072.07
Ips pini	2001	-8.88	0.23	33026	10742	8.65	0.003	1084.12
H. spp.	2002	-9.12	0.33	6987	2652	6.67	0.01	1086.10
H. spp.	2001	-9.42	0.23	33026	10742	5.64	0.02	1087.12
O. latidens	2003	-8.95	0.17					658.81
P. mexicanus	2003	-11.88	0.81	9576	2309	24.34	< 0.0001	636.35
<i>H</i> . spp.	2003	-11.04	0.65	21130	5591	17.23	< 0.001	643.47
Ips pini	2003	-10.48	0.55	23430	7110	11.58	0.001	649.11
H. spp.	2002	-9.87	0.45	8560	3488	5.78	0.02	654.91

Table D.2:, Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2001 to 2005 in a lodgepole pine stand of southern British Columbia (Stand C). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	ear <u>Intercept</u>		<u>Sla</u>	<u>ppe</u>	$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
O. latidens	2001	-10.28	0.58					69.67
P. mexicanus	2001	-12.48	1.35	4491	1508	8.64	0.003	63.01
H. spp.	2001	-12.53	1.63	11842	6171	3.97	0.05	67.67
O. latidens	2002	-8.81	0.28					257.11
H. spp.	2001	-10.65	0.72	10134	2892	12.78	0.0003	246.21
P. mexicanus	2001	-9.70	0.46	2485	744	8.64	0.003	250.35
O. latidens	2003	-10.68	0.71					48.73
P. mexicanus	2003	-12.78	1.84	8456	4435	4.52	0.03	46.20
O. latidens	2004	-9.99	0.50					89.92
P. mexicanus	2004	-12.23	1.34	7327	2332	13.33	0.0003	78.55
P. mexicanus	2003	-11.83	1.19	7767	2984	7.83	0.005	84.06
O. latidens	2005	-10.68	0.71					48.73
P. mexicanus	2005	-12.27	1.52	7446	3566	4.85	0.03	45.87
P. mexicanus	2004	-12.03	1.35	5472	2707	3.93	0.05	46.79

Table D.3: Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand D). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	'ear <u>Intercept</u>		<u>Sla</u>	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
O. latidens	2002	-7.99	0.16					685.56
H. spp.	2002	-9.94	0.72	8118	2871	8.52	0.004	678.58
P. mexicanus	2002	-9.52	0.63	1847	690	7.75	0.01	679.35
P. mexicanus	2001	-8.57	0.34	2592	1190	4.72	0.03	682.38
O. latidens	2003	-6.80	0.09					1966.48
P. mexicanus	2003	-8.60	0.39	1006	197	28.54	< 0.0001	1938.40
H. spp.	2003	-7.74	0.26	4144	996	17.02	<0.0001	1949.93
P. mexicanus	2002	-7.94	0.32	1410	365	15.69	< 0.0001	1951.26
<i>H.</i> spp.	2002	-7.99	0.38	5111	1523	11.25	<0.001	1955.70
O. latidens	2004	-7.54	0.13					1026.50
P. mexicanus	2004	-9.06	0.55	1383	457	10.60	0.001	1017.16
H. spp.	2004	-7.96	0.21	9783	3188	8.64	0.003	1019.13
O. latidens	2005	-7.68	0.14					904.78
P. mexicanus	2005	-8.92	0.57	1563	668	5.65	0.02	900.50
H. spp.	2004	-8.06	0.25	4630	2293	4.00	0.05	902.14

Table D.4: Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2001 to 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inter	<u>cept</u>	<u>Sl</u>	ope	$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
O. latidens	2001	-10.39	0.45					115.91
P. mexicanus	2001	-14.74	1.66	38789	10121	17.81	< 0.0001	100.11
<i>H</i> . spp.	2001	-9.40	0.61	-87536	60254	4.02	0.05	113.90
O. latidens	2002	-8.74	0.20					508.61
H. spp	2001	-10.68	0.58	23095	5633	16.66	< 0.0001	493.99
P. mexicanus	2002	-10.03	0.45	4337	1085	16.33	< 0.0001	494.32
O. latidens	2001	-9.29	0.29	13334	3950	9.28	0.002	501.37
P. mexicanus	2001	-9.78	0.43	12742	4068	8.87	0.003	501.78
<i>H</i> . spp.	2002	-9.95	0.69	5334	2707	4.48	0.03	506.17
O. latidens	2003	-7.74	0.12					1242.78
P. mexicanus	2003	-9.96	0.49	3323	657	27.42	< 0.0001	1217.48
O. latidens	2002	-8.59	0.24	4306	915	20.87	< 0.0001	1224.03
P. mexicanus	2002	-8.37	0.23	2398	643	13.30	0.0003	1231.59
<i>H</i> . spp.	2002	-9.00	0.42	5554	1652	13.15	0.0003	1231.74

Table D.5: Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	ear <u>Intercept</u>		<u>Slo</u>	<u>Slope</u>		<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
O. latidens	2002	-9.54	0.30					233.92
P. mexicanus	2002	-11.76	0.93	16265	5206	11.51	0.001	224.48
O. latidens	2003	-9.00	0.23					381.82
P. mexicanus	2003	-11.26	0.86	6910	2160	14.89	< 0.0001	369.06
O. latidens	2002	-9.95	0.46	10273	3480	8.56	0.003	375.39
O. latidens	2004	-8.13	0.15					823.98
P. mexicanus	2004	-10.39	0.56	2578	549	26.55	< 0.0001	799.73
P. mexicanus	2003	-9.89	0.48	5571	1255	25.75	< 0.0001	800.53
O. latidens	2003	-9.26	0.33	7017	1542	19.75	<0.0001	806.52
O. latidens	2005	-8.30	0.16					708.97
P. mexicanus	2005	-10.18	0.50	4957	1072	24.31	< 0.0001	686.91
Ips pini	2005	-9.01	0.29	9602	2624	13.27	0.0003	697.96
P. mexicanus	2004	-9.87	0.53	1865	548	12.76	0.0003	698.46
O. latidens	2004	-9.27	0.40	2678	907	9.08	0.003	702.14

Table D.6: Association of trees colonized by other bark beetles on the locations of trees colonized by *O. latidens* from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand G). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

lnsect	Year <u>Intercept</u> <u>Slope</u>		ope	$\chi^{2}$	P-value	AIC		
		Est.	SE	Est.	SE			
O. latidens	2002	-10.31	0.50					92.49
P. mexicanus	2002	-12.47	1.43	12433	6208	4.20	0.04	90.30
O. latidens	2003	-7.73	0.14					927.05
P. mexicanus	2003	-9.68	0.49	2700	584	22.34	<0.0001	906.84
P. mexicanus	2002	-8.84	0.33	7184	1654	18.69	< 0.0001	910.49
O. latidens	2004	-6.85	0.09					1996.65
P. mexicanus	2004	-8.45	0.41	1125	270	18.13	< 0.0001	1980.85
P. mexicanus	2003	-7.89	0.28	1511	366	17.05	<0.0001	1981.93
O. latidens	2003	-7.62	0.24	1544	413	14.45	0.0001	1984.53
O. latidens	2005	-7.64	0.13					1003.86
P. mexicanus	2005	-9.52	0.44	2503	496	27.04	< 0.0001	978.97
O. latidens	2004	-9.18	0.61	1353	498	7.78	0.01	998.23
<i>Н</i> . spp.	2004	-8.20	0.27	2899	1111	6.84	0.01	999.71
Table D.7: Association of trees colonized by other bark beetles on the locations of trees colonized by *P. mexicanus* from 2001 to 2003 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	ar <u>Intercept</u>		Sl	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2001	-8.37	0.13					1107.73
I. pini	2001	-8.91	0.23	35863	10566	10.50	0.001	1099.03
H. spp.	2001	-9.63	0.49	6688	2397	8.21	0.004	1101.32
P. mexicanus	2002	-7.88	0.10					1707.69
O. latidens	2002	-10.42	0.48	9434	1615	42.88	< 0.0001	1666.47
P. mexicanus	2001	-10.14	0.47	8669	1661	28.63	< 0.0001	1680.72
H. spp.	2002	-8.86	0.26	9040	2038	18.92	< 0.0001	1690.43
I. pini	2002	-9.01	0.32	23104	5783	16.78	< 0.0001	1692.57
I. pini	2001	-8.34	0.18	30580	8429	12.10	0.0005	1697.25
H. spp.	2001	-8.98	0.38	5873	1856	10.47	0.001	1698.88
P. mexicanus	2003	-8.32	0.13					1157.80
I. pini	2003	-9.88	0.40	23801	5198	22.42	< 0.0001	1137.17
H. spp.	2003	-9.85	0.42	16023	3799	20.12	< 0.0001	1139.46
O. latidens	2003	-9.35	0.31	6491	1571	17.70	< 0.0001	1150.27
H. spp.	2002	-9.07	0.32	7127	2567	7.39	0.01	1152.19
P. mexicanus	2002	-9.21	0.43	2142	943	5.72	0.02	1153.87

Table D.8: Association of trees colonized by other bark beetles on the locations of trees colonized by *P. mexicanus* from 2000 to 2005 in a lodgepole pine stand of southern British Columbia (Stand C). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Inter	cept	Sle	ope	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE	-		
P. mexicanus	2000	-9.77	0.45					109.67
<i>H</i> . spp.	2000	-11.55	0.91	17106	4442	12.47	0.0004	99.16
P. mexicanus	2001	-8.20	0.20					443.53
<i>H</i> . spp.	2001	-10.42	0.57	11716	2171	31.39	< 0.0001	413.93
O. latidens	2001	-8.80	0.28	9934	1908	19.69	< 0.0001	425.63
H. spp.	2000	-8.99	0.32	10103	2163	16.86	< 0.0001	428.46
P. mexicanus	2002	-8.76	0.28	6892	1616	12.71	0.0004	432.61
P. mexicanus	2002	-8.38	0.22					377.24
P. mexicanus	2001	-9.66	0.41	3188	563	25.39	< 0.0001	353.67
O. latidens	2002	-9.99	0.49	7902	1562	23.56	< 0.0001	355.51
H. spp.	2001	-10.29	0.59	10443	2340	20.87	< 0.0001	358.19
O. latidens	2001	-8.88	0.30	8895	2163	12.30	0.0004	366.76
P. mexicanus	2003	-9.07	0.32					203.48
O. latidens	2003	-10.08	0.55	21436	5885	12.11	0.001	193.28
P. mexicanus	2002	-9.92	0.50	2453	720	8.95	0.003	196.45
P. mexicanus	2004	-9.07	0.32					203.48
O. latidens	2004	-10.00	0.49	8842	1841	17.76	< 0.0001	187.64
P. mexicanus	2003	-10.68	0.70	7106	1809	16.72	< 0.0001	187.67
O. latidens	2003	-10.12	0.55	21955	5885	12.76	0.0003	192.63
P. mexicanus	2005	-9.43	0.38					148.03
O. latidens	2005	-11.52	1.00	29383	7742	20.02	< 0.0001	129.95
P. mexicanus	2004	-11.24	0.86	6498	1584	19.11	< 0.0001	130.86
O. latidens	2004	-10.39	0.60	9003	2202	13.00	0.0003	136.97

Table D.9: Association of trees colonized by other bark beetles on the locations of trees colonized by P. mexicanus from 2001 to 2005 in a lodgepole pine stand of southern British Columbia (Stand D). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<u>Intercept</u>		<u>Sle</u>	ope	$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2001	-8.59	0.22					404.67
P. mexicanus	2000	-9.23	0.34	13670	3959	10.81	0.001	395.60
O. latidens	2001	-9.12	0.36	7797	3489	4.51	0.03	401.90
D. murrayana	ae 2001	-9.65	0.64	10388	5406	3.86	0.05	402.55
P. mexicanus	2002	-7.23	0.11					1350.92
O. latidens	2002	-9.00	0.48	4705	1156	19.27	< 0.0001	1332.65
H. spp.	2002	-9.06	0.49	7709	1892	16.60	< 0.0001	1335.32
P. mexicanus	2001	-7.90	0.24	2951	812	13.21	0.0003	1338.71
O. latidens	2001	-7.58	0.18	5516	1846	8.20	0.004	1343.72
D. murrayana	<i>ie</i> 2002	-7.66	0.25	4344	2070	4.24	0.04	1347.68
P. mexicanus	2003	-6.44	0.07					2679.99
O. latidens	2003	-8.84	0.37	1901	267	54.53	< 0.0001	2625.27
P. mexicanus	2002	-7.62	0.27	1456	306	23.82	< 0.0001	2655.99
<i>H</i> . spp.	2003	-7.36	0.22	4056	834	23.26	< 0.0001	2656.54
H. spp.	2002	-7.48	0.32	4490	1274	12.38	0.0004	2667.42
O. latidens	2002	-7.27	0.27	2306	699	11.66	0.0006	2668.14
D. murrayana	ie 2002	-6.73	0.16	3006	1393	4.51	0.03	2675.29
P. mexicanus	2004	-6.92	0.10					1760.75
O. latidens	2004	-8.61	0.36	2891	553	27.02	< 0.0001	1734.48
P. mexicanus	2003	-8.08	0.38	663	200	11.56	0.0007	1749.84
H. spp.	2004	-7.33	0.17	4965	1566	9.88	0.002	1751.52
O. latidens	2003	-7.80	0.41	731	318	5.40	0.02	1756.00
P. mexicanus	2005	-7.23	0.11					1350.92
H. spp.	2004	-7.61	0.18	8968	2753	9.77	0.002	1342.15
O .latidens	2005	-8.40	0.41	2400	771	9.17	0.002	1342.75
O. latidens	2004	-8.32	0.41	1924	650	8.62	0.003	1343.31

Table D.10 Association of trees colonized by other bark beetles on the locations of trees colonized by *P. mexicanus* from 2001 to 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	r <u>Intercept</u>		<u>Sl</u>	<u>Slope</u>		<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2001	-9.60	0.30					235.26
O. latidens	2001	-10.53	0.49	19498	5459	10.13	0.001	227.15
P. mexicanus	2002	-8.42	0.17					680.03
O. latidens	2002	-9.84	0.39	6597	1305	25.55	< 0.0001	656.53
H. spp.	2001	-10.43	0.50	23889	4811	24.57	< 0.0001	657.51
I. pini	2001	-8.02	0.20	-38136	15209	7.68	0.01	674.41
P. mexicanus	2001	-9.21	0.36	10091	3551	7.40	0.01	674.68
I. pini	2002	-8.93	0.32	23242	10901	4.45	0.01	677.63
O. latidens	2001	-8.720	0.23	8206	3792	4.06	0.01	678.02
P. mexicanus	2003	-7.44	0.10					1621.76
O. latidens	2003	-8.37	0.28	1905	485	15.35	< 0.0001	1608.56
<i>H</i> . spp.	2002	-8.56	0.35	4962	1386	14.63	0.0001	1609.28
I. pini	2002	-7.97	0.19	24266	6660	13.02	0.0003	1610.89
O. latidens	2002	-7.92	0.20	2630	811	9.88	0.001	1614.03
P. mexicanus	2002	-7.75	0.18	1276	570	4.81	0.03	1619.10

Table D.11: Association of trees colonized by other bark beetles on the locations of trees colonized by *P. mexicanus* from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	ear <u>Intercept</u>		<u>Slo</u>	pe	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2002	-9.23	0.26					308.95
O. latidens	2002	-10.36	0.54	11687	3923	8.83	0.003	302.22
<i>H</i> . spp.	2002	-9.88	0.42	32195	12923	5.91	0.02	305.14
P. mexicanus	2003	-8.33	0.16					692.34
O. latidens	2003	-9.67	0.38	8115	1707	21.78	< 0.0001	672.80
P. mexicanus	2002	-9.79	0.43	11499	2597	20.93	< 0.0001	673.65
O. latidens	2002	-9.21	0.32	9583	2481	14.55	0.0001	680.03
H. spp	2002	-8.65	0.24	18186	8470	4.33	0.04	690.25
P. mexicanus	2004	-7.23	0.09					1829.13
P. mexicanus	2003	-8.26	0.25	3483	684	29.25	< 0.0001	1802.60
O. latidens	2004	-8.20	0.23	2697	530	26.99	< 0.0001	1804.86
O. latidens	2003	-7.91	0.19	4521	1004	19.38	< 0.0001	1812.46
I. pini	2004	-7.50	0.13	8529	2378	10.56	0.001	1821.29
H. spp.	2003	-7.47	0.13	7652	2476	8.21	0.004	1823.64
<i>H</i> . spp.	2004	-7.63	0.20	6768	2864	5.48	0.02	1826.37
P. mexicanus	2005	-8.11	0.15					840.23
O. latidens	2005	-9.89	0.45	5689	1165	27.10	< 0.0001	815.43
I. pini	2005	-8.78	0.26	9119	2386	14.41	0.0001	828.12
P. mexicanus	2004	-9.41	0.46	1568	484	11.20	0.001	831.33
O. latidens	2004	-8.96	0.35	2394	816	8.86	0.003	833.67
H. spp.	2004	-8.72	0.33	7063	3121	4.76	0.03	837.77
I. pini	2004	-8.36	0.20	8375	3921	3.79	0.05	838.74

Table D.12: Association of trees colonized by other bark beetles on the locations of trees colonized by *P. mexicanus* from 2002 to 2005 in a lodgepole pine stand of southern British Columbia (Stand G). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slo</u>	<u>Slope</u>		<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
P. mexicanus	2003	-7.38	0.12					1258.95
O. latidens	2003	-8.56	0.33	2288	548	18.39	< 0.0001	1242.75
P. mexicanus	2002	-8.19	0.26	5459	1392	15.16	< 0.0001	1245.99
O. latidens	2002	-7.67	0.16	6654	2303	7.72	0.01	1253.43
<i>H</i> . spp.	2003	-7.71	0.21	6049	3000	3.88	0.05	1257.26
P. mexicanus	2004	-6.63	0.08					2414.52
O. latidens	2004	-8.21	0.37	1389	301	22.44	< 0.0001	2394.49
P. mexicanus	2003	-7.52	0.25	1303	328	15.76	< 0.0001	2401.17
O. latidens	2003	-7.23	0.21	1218	366	11.35	0.0007	2405.59
H. spp.	2004	-6.97	0.16	1795	672	7.10	0.01	2409.83
H. spp.	2003	-6.87	0.14	4447	2101	4.33	0.04	2412.60
P. mexicanus	2005	-7.37	0.11					1273.69
O. latidens	2005	-8.61	0.31	2214	449	23.71	< 0.0001	1252.18
O. latidens	2004	-8.51	0.51	1018	426	5.91	0.02	1269.99
II. spp.	2004	-7.77	0.23	2134	966	4.87	0.03	1271.03
I. pini	2004	-7.58	0.16	3545	1608	4.64	0.03	1271.26
H. spp	2005	-7.55	0.15	1454	623	4.62	0.03	1271.27

Table D.13: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2001 to 2002 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<u>Intercept</u>		Sle	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
H. spp.	2001	-8.78	0.16					765.20
P. mexicanus	2001	-10.65	0.72	7248	2562	8.28	0.004	758.78
P. mexicanus	2000	-9.58	0.40	19118	7853	6.39	0.01	760.67
H. spp.	2002	-9.45	0.22					420.10
P. mexicanus	2002	-12.29	1.16	6268	2296	10.66	0.001	411.37
P. mexicanus	2001	-12.59	1.12	11765	3790	10.57	0.001	411.46
<i>H</i> . spp.	2001	-11.80	0.90	12623	4252	10.20	0.001	411.83
I. pini	2002	-11.39	0.80	37953	13522	8.76	0.003	413.26
O. latidens	2002	-11.82	1.03	8887	3466	8.12	0.004	413.91
I. pini	2001	-10.08	0.40	40343	17799	4.65	0.03	417.37

Table D.14: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2000 and 2001 in a lodgepole pine stand of southern British Columbia (Stand C). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE			
H. spp.	2000	-9.77	0.45					109.67
P. mexicanus	2000	-10.89	0.72	10712	2971	8.96	0.003	102.67
H. spp.	2001	-8.89	0.29					239.40
H. spp.	2000	-9.67	0.45	9970	3034	8.29	0.004	233.01
P. mexicanus	2001	-9.71	0.47	2338	785	6.89	0.01	234.41

Table D.15: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2001 to 2004 in a lodgepole pine stand of southern British Columbia (Stand D). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Year <u>Intercept</u>		<u>Sle</u>	<u>Slope</u>		P-value	AIC
		Est.	SE	Est.	SE			
H. spp.	2001	-10.25	0.50			······································		91.96
O. latidens	2001	-12.95	1.61	40341	16308	8.60	0.003	85.31
H. spp.	2003	-9.07	0.28					263.74
O. latidens	2003	-11.48	1.38	1913	1002	3.95	0.05	261.63
H. spp.	2004	-10.25	0.50					91.96
O. latidens	2004	-15.30	2.51	7705	3230	6.47	0.01	87.45
O. latidens	2003	-16.09	3.20	4313	2103	5.08	0.02	88.83
P. mexicanus	2003	-15.30	-3.29	2594	1511	4.20	0.04	89.71

Table D.16: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2002 to 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
H. spp.	2002	-8.53	0.18					612.23
P. mexicanus	2001	-9.40	0.38	10892	3740	7.73	0.01	606.55
I. pini	2002	-9.18	0.35	28507	11569	5.96	0.02	608.32
I. pini	2001	-9.01	0.29	27962	11710	5.56	0.02	608.72
<i>H.</i> spp.	2003	-7.89	0.13					1086.55
I. pini	2003	-9.25	0.34	12233	2346	34.68	< 0.0001	1053.96
I. pini	2002	-8.49	0.25	26986	8396	10.14	0.001	1078.50
P. mexicanus	2003	-8.70	0.46	1283	670	3.69	0.05	1084.95

Table D.17: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2003 and 2004 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
H. spp.	2002	-11.25	0.71					50.99
P. mexicanus	2002	-15.02	2.97	24881	15033	4.02	0.04	48.98
H. spp.	2004	-9.45	0.29					252.92
I. pini	2004	-10.07	0.41	17087	5873	6.15	0.01	248.84

Table D.18: Association of trees colonized by other bark beetles on the locations of trees colonized by *Hylurgops* spp. from 2004 and 2005 in a lodgepole pine stand of southern British Columbia (Stand G). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slc</u>	ope	$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
H. spp.	2004	-9.06	0.27					283.63
I. pini	2004	-9.83	0.46	10142	3668	7.65	0.01	278.02
D. murrayanae	2003	-9.54	0.36	18892	6439	6.58	0.01	279.08
P. mexicanus	2003	-10.93	0.94	2605	1136	5.47	0.02	280.19
H. spp.	2003	-9.96	0.54	14832	6445	4.87	0.03	280.79
H. spp.	2005	-9.39	0.32					209.89
P. mexicanus	2005	-12.89	1.28	4281	1285	12.57	0.0004	199.35
<i>H</i> . spp.	2004	-8.35	0.48	-12047	5938	6.02	0.01	205.90
I. pini	2005	-8.71	0.40	-36068	20339	5.25	0.02	206.67
O. latidens	2005	-10.90	0.88	2612	1246	4.36	0.04	207.56

Table D.19: Association of trees colonized by other bark beetles on the locations of trees colonized by *I. pini* from 2001 and 2003 in a lodgepole pine stand of southern British Columbia (Stand B). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
I. pini	2001	-11.35	0.58					76.10
P. mexicanus	2001	-20.12	4.73	29709	14064	6.91	0.01	71.18
I. pini	2003	-9.81	0.27					304.65
P. mexicanus	2003	-11.84	1.04	6915	3073	6.30	0.01	300.30

Table D.20: Association of trees colonized by other bark beetles on the locations of trees colonized by *I. pini* from 2002 and 2003 in a lodgepole pine stand of southern British Columbia (Stand E). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Intercept		Slope		$\chi^{2}$	P-value	AIC
		Est.	SE	Est.	SE			
I. pini	2002	-10.90	0.58					73.41
P. mexicanus	2001	-13.43	1.58	26225	11556	4.92	0.03	70.50
I. pini	2003	-9.44	0.28					273.33
H. spp.	2003	-14.22	1.68	8929	2654	20.89	< 0.0001	254.46
P. mexicanus	2002	-8.08	0.52	-9035	4088	9.95	0.002	265.40
H. spp.	2002	-12.11	1.34	11037	4895	7.15	0.01	268.20
O. latidens	2002	-8.42	0.51	-7790	4116	5.25	0.02	270.10
I. pini	2002	-10.39	0.59	40096	18285	4.81	0.03	270.54

Table D.21: Association of trees colonized by other bark beetles on the locations of trees colonized by *I. pini* from 2004 and 2005 in a lodgepole pine stand of southern British Columbia (Stand F). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	<b>Intercept</b>		<u>Slope</u>		$\chi^{2}$	<b>P</b> -value	AIC
		Est.	SE	Est.	SE			
I. pini	2004	-10.55	0.50					94.43
H. spp.	2003	-12.21	0.99	31800	9467	9.69	0.002	86.77
H. spp.	2004	-13.53	1.35	26674	8180	9.05	0.003	87.40
I. pini	2005	-9.86	0.35					175.77
O. latidens	2005	-13.43	1.57	10209	3636	11.81	0.001	166.01
P. mexicanus	2005	-13.11	1.46	7859	2850	10.71	0.001	167.10
P. mexicanus	2004	-13.78	1.84	4183	1670	9.72	0.002	168.09
O. latidens	2004	-12.62	1.31	6583	2491	9.25	0.002	168.57

Table D.22: Association of trees colonized by other bark beetles on the locations of trees colonized by *I. pini* from 2004 in a lodgepole pine stand of southern British Columbia (Stand G). The line in bold represents an intercept-only model; i.e., modeling a constant density of insects across the stand. Subsequent lines reflect whether the location of each listed insect and year provides inference on the location of the insect studied relative to this constant density. A positive estimate for a slope reflects positive spatial association, while a negative estimate reflects spatial inhibition at a between-tree scale. The response variable for each equation is  $log(\lambda)$ , where  $\lambda$  is the estimated density of trees colonized per square meter. Significant models are listed in order of best fit for each year.

Insect	Year	Intercept		Slope		$\chi^2$	<i>P</i> -value	AIC
		Est.	SE	Est.	SE	~ •		
I. pini	2004	-9.91	0.41					132.86
<i>H</i> . spp.	2003	-12.13	1.13	12281	4369	8.95	0.003	125.93
H. spp.	2004	-12.66	1.47	11209	4608	8.18	0.004	126.71
D. murrayar	nae 2004	-11.23	0.87	12443	5327	5.64	0.02	129.24
P. mexicanu	s 2003	-13.03	1.68	4098	1867	5.45	0.02	129.43
D. murrayai	nae 2003	-10.55	0.58	22986	9209	4.68	0.03	130.20

### APPENDIX E

R statistical code outlining the use of point process models in this thesis.

1. Read in data

```
StandA<-
read.csv("/home/koopmans/Documents/EndemicMPB/StandA/naboundA.csv",
header=T,na.string=".")</pre>
```

2. Establish Boundary

```
boundaryA<-owin(poly=list(x=c(-3, 770, 770, 605, 605, 500, 500, 315, 315, 155, 155, 55, 55, -3), y=c(50, 50, 190, 190, 325, 325, 300, 300, 350, 390, 390, 315, 315))) # each boundary was different and was derived at plot set up
```

3. Subset by year and species

```
A99<-StandA[StandA$Att.Year=="1999",] # Subset all attacks from 1999
mpbA99<-A99[A99$Att.spp=="MPB",] # mountain pine beetle (1999)
ilatA99<-A99[A99$Att.spp=="ILAT",] # Orthotomicus latidens (1999)
imexA99<-A99[A99$Att.spp=="IMEX",] # Pseudips mexicanus (1999)
ipinA99<-A99[A99$Att.spp=="IPIN",] # Ips pini (1999)
dmurA99<-A99[A99$Att.spp=="DMUR,] # D. murrayanae (1999)
hsppA99<-A99[A99$Att.spp=="HPOR" | A99$Att.spp=="HSPP"]
#Hylurgops species (1999)
```

4. Create a point process and density surface

```
ilatA99ppp<-ppp(x=ilatA99[!(is.na(ilatA99$absX)),"absX"],y=ilatA99[!
(is.na(ilatA99$absY)),"absY"],window=boundaryA) # cxcludes na values, incorporates
a density #surface for colonization by O. latidens</pre>
```

ilatA99d<-density.ppp(ilatA99ppp, eps=1) # density measured in 1 x 1 m spacing

5. Create a homogenous point process of mountain pine beetle attack

6. Create a model of mountain pine beetle attack in 1999 incorporating the location of trees attacked by *O. latidens* in 1999

ppmMPBilatA99<-ppm(mpbA99ppp,-1+ilat,covariates=list(ilat=ilatA99d))
7. Determine the coefficient estimate, standard error, and AIC value for the homogenous
model of mountain pine beetle attack</pre>

```
coef(mpbA99ppm)
sqrt(diag(vcov(mpbA99ppm)))
AIC(mpbA99ppm)
```

8. Compare the homogenous model and the model incorporating O. latidens attack and determine its coefficient estimate, standard error, and AIC value

```
anova(mpbA00ppm,ppmMPBilatA00,test="Chisq")
coef(ppmMPBilatA00)
sqrt(diag(vcov(ppmMPBilatA00)))
AIC(ppmMPBilatA00)
```

### APPENDIX F

Study of the effect of *Pseudips mexicanus* on host selection behaviour of *Dendroctonus* ponderosae in cut bolts using no-choice bioassays in the laboratory

# INTRODUCTION

Epidemic-level mountain pine beetle *Dendroctonus ponderosae* (Hopkins) are believed to land at random and sample the host to determine its suitability for reproduction (Hynum and Berryman 1980, Raffa and Berryman 1982, Pureswaran and Borden 2003). Random landing may be a successful method of host searching for mountain pine beetle at epidemic levels, as host defenses can be overcome by the attraction of conspecifics through aggregation pheromones (Geiszler et al. 1980a, Wood 1982a, Raffa and Berryman 1983). However, endemic level mountain pine beetle likely cannot rely on the help of mass attack by conspecifics to overcome the defenses of healthy trees, potentially making random landing energetically unfavorable.

Endemic-level mountain pine beetle may rely on secondary bark beetles for the establishment of populations capable of mass attacking trees (Carroll et al. 2006; Chapter 3). Host trees that also may be suitable for endemic level mountain pine beetle are potentially stressed by drought events, windthrow, root disease, and/or fire damage (Geiszler et al. 1980b, Tkacz and Schmitz 1986).

The different physiological conditions of hosts utilized by epidemic and endemic beetles, in concert with the sheer differences in population numbers, suggest that mountain pine beetle may rely on different host-seeking behaviour at different population densities. Mountain pine beetle at epidemic levels have been shown to use host volatiles in a synergistic manner with aggregation pheromones to locate potential host trees (Borden et al. 1998). Furthermore, volatiles of non-hosts have been shown to disrupt host-seeking behaviour (Borden et al. 1998, Huber et al. 2000, Huber and Borden 2003). Therefore, endemic mountain pine beetle may also be capable of utilizing volatiles emanating from potential hosts to locate trees which are most suitable for reproductive success.

I propose that at the endemic level, mountain pine beetle orient toward trees which have been previously infested with secondary bark beetles, or may be more likely to accept hosts that have been partially colonized by another species of bark beetle. In light of recent work indicating a close relationship between mountain pine beetle and *Pseudips mexicanus* (Hopkins) (Carroll et al. 2006), only one known assay has been conducted involving *P*. *mexicanus* related volatiles or pheromones as a primary attractant (Smith 2008). Smith found little response by mountain pine beetle to pheromones of *P. mexicanus*, but endemic mountain pine beetle appear to benefit from associations with this insect (Smith 2008).

In the present study, mountain pine beetle was introduced to lodgepole pine hosts, either colonized or uncolonized previously by *P. mexicanus*, in a no-choice assay. Some mountain pine beetle were starved to simulate endemic conditions, while other mountain pine beetle were fed prior to lab assays to simulate epidemic conditions. My hypothesis is that females of "endemic" mountain pine beetle will accept bolts previously colonized by *P. mexicanus* more readily than well-fed "epidemic" beetles. These results may lend information on the host acceptance behaviour of endemic level mountain pine beetle.

#### METHODS

Lodgepole pine trees used for host material were harvested from Telkwa, British Columbia. Trees lacked recent exposure to epidemic populations of mountain pine beetle and were obtained from healthy pine stands free of mountain pine beetle and secondary bark beetle attack, as well as any signs of infection. Trees were selected on the basis of similar growing conditions, health, vigour, and had a diameter at breast height of between 28 and 33 cm (dbh). The cut ends of all sections were sealed with hot parafin wax post-harvest to prevent desiccation of the phloem tissue.

Mountain pine beetles used in the host selection trials were obtained from colonized lodgepole pine trees harvested near Smithers, British Columbia. Trees contained teneral mountain pine beetle adults as well as late instar larvae. The colonized pine bolts were placed in emergence containers in a controlled environmental held at 22°C. Emerging beetles to be used in assays were collected daily and separated based on sex (Lyon 1958). Insects were stored at 7-8°C and were supplied with fresh pine phloem and moistened Kimwipes® until used in experimentation, at which point beetles simulating "endemic" populations were starved for a period of 48 hours prior to testing. "Epidemic" beetles were able to feed up until the point of experimentation.

Healthy, uninfested lodgepole pine logs were cut into ~30cm bolts and waxed on the ends to prevent desiccation over the course of experimentation. Treatment bolts were infested with *P. mexicanus* at a density of approximately 8 attacks/m<sup>2</sup>. *Pseudips mexicanus* were

collected in Lindgren funnel traps baited with a combination of racemic ipsdienol and ipsenol bubble cap lures (Savoie et al. 1998; Smith et al. 2009) obtained from Contech Inc., Delta, British Columbia. Male *P. mexicanus* were inserted into holes drilled in the bark and beetles were left overnight. Once all males had successfully entered and frass was visible at each hole, two female *P. mexicanus* specimens were introduced to each entrance hole. Bolts were kept at 24-25°C for ten days after female *P. mexicanus* introduction. Bolts were placed in test cages approximately ten hours prior to release of test mountain pine beetles at 4pm Pacific Standard Time.

Host selection trials were conducted in the LK. Barber Enhanced Forestry Labatory at the University of Northern British Columbia, Prince George, British Columbia, in a regulated environment free from competing volatiles, and inaccessible to external specimens. Mesh cages two by two by four feet were used as experimental arenas. The experiment was conducted in a 2 x 2 factorial design with endemic and epidemic populations of beetles, and treated and control bolts, with treated bolts containing colonization by *P. mexicanus*. There were seven replicates for each treatment, for a total of twenty-cight bolts. Ten starved (endemic) or unstarved (epidemic) female mountain pine beetles were introduced to the center of each cage, approximately 55 cm from experimental bolts at the end of the enclosure. Female mountain pine beetles were left overnight and cages checked thoroughly the following morning. Experimental bolts were subsequently placed in sealed containers until further examination. Examination of bolts included a summary of beetles in the container, any apparent entrance and exit holes on the bark of each bolt, and finally a thorough

examination of the galleries under the bark of each bolt.

# **RESULTS AND DISCUSSION**

No significant differences could be determined between starved or unstarved beetles and whether or not they chose to enter a host with the number of replicates conducted in this study. However, a trend in the data was noted. Although there appeared to be no difference in the number of starved beetles beetween control and treated hosts, unstarved beetles appeared to enter hosts with *P. mexicanus* less often than control hosts (Table E.1). This may indicate that starved or endemic level beetle may be less discriminatory in the hosts they colonize, compared to well-fed or epidemic beetles. Further replication may yield significant results suggesting that beetles with higher lipid content are more likely to avoid or reject hosts with secondary colonization in favour of hosts without other species present.

Table F.1: Number of female mountain pine beetle, found in uninfested (control) or infested(P. mexicanus) lodgepole pine bolts (n=10 insects introduced). Starved mountain pine beetlewere used to simulate endemic conditions, and unstarved beetles were used to simulateepidemic conditions. There were seven replications of each treatment.Treatment typeStarved D. ponderosae (SE)Control7.14 (0.34)P. mexicanus6.42 (0.72)4.42 (0.95)

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