

Management response to one insect pest may increase vulnerability to another

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Summary

1. Large-scale insect outbreaks provide an ideal system to examine the cascade of ecological effects of disturbance regimes across forested landscapes. A major outbreak of the mountain pine beetle *Dendroctonus ponderosae* continues to exert landscape-level mortality across forests of lodgepole pine *Pinus contorta* var. *latifolia* in western Canada. This outbreak, exacerbated in part by fire suppression and climate change, has affected more than 14 million ha of merchantable forest. Salvage and reforestation efforts are currently underway at landscape-level scales. An emerging concern is the migration of Warren root collar weevil *Hylobius warreni* from stands with a reduced host pool, i.e. those with a high per cent of mature, dead lodgepole pine, into young, replanted stands, resulting in significant levels of mortality to juvenile trees.

2. The impact of Warren root collar weevil in stands of young trees (9–11 years of age) replanted after salvage harvesting was examined in nine cutblocks (areas delineated for commercial timber harvest, c. 1 km in diameter). All cutblocks, sampled across the central interior of British Columbia, were located next to unsalvaged, mature stands.

3. Field data and aerial surveys revealed higher tree mortality from Warren root collar weevils along cutblock perimeters adjacent to unsalvaged, mature stands. Mortality decreased with increasing distance from the edge of the cutblocks. Additional mortality along these gradients was associated with increasing per cent of pine in the mature stand; more-so if the pine was dead. Moreover, the gradient of mortality became more pronounced with time as mountain pine beetle had attacked the adjacent mature stands. Weevils attacked the largest trees within the replanted cutblocks.

4. These gradients of tree mortality suggest migration of Warren root collar weevils from unsalvaged mature stands into adjacent replanted forests most probably in search of food.

5. *Synthesis and applications.* This study demonstrates how a management response to a large insect outbreak, itself mediated by anthropogenic factors, can predispose reforested stands to additional, unanticipated threats from other insects. Reforestation strategies following outbreaks of mountain pine beetle may need to include harvesting larger salvage blocks to minimize edge effects and reduce mortality from Warren root collar weevils. Moreover, the inclusion of deciduous non-host tree stock in planting mixes might reduce insect movement and limit tree mortality because of Warren root collar weevils.

Key-words: bark beetles, below-ground herbivory, *Dendroctonus ponderosae*, disturbance agents, *Hylobius warreni*, landscape disturbance, lodgepole pine, *Pinus contorta*, root feeding, root girdling

Introduction

Disturbance events play important roles in wide ranges of biotic assemblages and occur at all levels of ecological

organization. In forest ecosystems, insect disturbance agents often have cascading effects on other biological processes, such as altering habitat to affect predator–prey relationships (Matsuoka, Handel & Ruthrauff 2001) and altering host suitability to future herbivory (Negrón 1998; Raffa, Krause & Reich 1998). Disturbance events caused by forest insects are

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especially prone to cascade effects, where positive feedback can dominate population dynamics once phase-transition thresholds are breached (Raffa *et al.* 2008). Such impacts are evident in the mountain pine beetle *Dendroctonus ponderosae* Hopkins system, where an outbreak now extends over more than 14 million ha of British Columbia and north western Alberta, Canada (Kurz *et al.* 2008).

The mountain pine beetle is an eruptive forest insect native to western North America. Over the past few decades, altered disturbance regimes (e.g. fire suppression) and manifestations of climate change such as increasing winter temperatures (i.e. too high to kill substantive proportions of overwintering larvae) have created optimum conditions for outbreaks of this insect (Hicke *et al.* 2006; Taylor *et al.* 2006). Stands of mature lodgepole pine *Pinus contorta* var. *latifolia* Dougl. ex. Loud., the beetle's primary host, have now suffered up to 90% mortality in the central interior of British Columbia, where the outbreak first began to erupt (Aukema *et al.* 2006). Consequently, salvage harvesting operations are underway at unprecedented levels in British Columbia, especially in areas where insect populations have exhausted their host supply and collapsed. A significant potential threat to reforestation efforts, however, is the migration of Warren root collar weevil *Hylobius warreni* Wood from areas with a high per cent of mature, dead, lodgepole pine into nearby, recently planted, juvenile stands.

Warren root collar weevil is found throughout the boreal forests of North America. Adults weevils feed nocturnally on twigs, buds and foliage of both young and mature trees of a variety of conifers (Hopkins, Klingenberg & Aukema 2009), descending during dawn hours to rest in the duff layers consisting of moss, lichen and fine woody debris accumulated at the base of host trees. Both males and females are flightless throughout their life cycle, which may last up to 7 years. Adult females lay up to 25 eggs a year in the duff layer around the root collars at the bases of trees (Cerezke 1994). Upon eclosion, larvae feed on the phloem tissues of the root collar, protected by a hard casing comprised of a mix of frass and tree resin (Cerezke 1970). After 2 years of feeding at the root collar, larvae pupate prior to adult emergence. Although adult feeding is not detrimental to the host, larval feeding may girdle young trees at the root collar, inhibiting growth and/or causing mortality. Warren root collar weevils do not feed on dead trees.

Historically, Warren root collar weevil has not been a major forest pest. There are several reasons, however, why this insect may increase its impacts within pine ecosystems over the next decade given the massive salvage and replanting efforts continuing across the affected landscape following the outbreak of mountain pine beetle. First, insects may mature to adults post-harvesting. Following harvesting, larvae and eggs remaining on residual stumps may develop to maturity, yielding a supply of insects that may attack newly replanted forests (Cerezke 1973). Secondly, larval feeding disproportionately impacts young trees, which will quickly become the predominant age class on the landscape. Recent observations of young stands *c.* 4–12 years of age in the central interior of British Columbia have shown cumulative mortality levels as

high as 16% (Schroff, Lindgren & Gillingham 2006). Thirdly, reduced host availability (through mortality because of mountain pine beetle) may force weevils to concentrate on the remaining live, young trees. This would be especially problematic in situations where unsalvaged, mature stands of predominantly dead pine are located adjacent to cutblocks (areas delineated for commercial timber harvest) that have been harvested then replanted with young trees. Hence, there is great concern that Warren root collar weevils may migrate from areas with a high per cent of mature, dead lodgepole pine into reforested cutblocks, thereby increasing the per cent of young trees killed.

Here, we examine the hypothesis that salvage harvesting responses to mountain pine beetle attack may inadvertently predispose replanted stands to increased mortality from Warren root collar weevil. We pose three questions. First, is there a gradient of mortality from the edges of mature, unsalvaged stands heavily impacted by the outbreak of mountain pine beetle into young replantings? If so, what is causing this mortality? Is it caused by below-ground feeding by larval Warren root collar weevils? Secondly, are gradients of mortality into replantings mediated by the properties of adjacent, unsalvaged stands (e.g. tree species and live/dead composition, number of years since attack by mountain pine beetle)? Finally, do spatial patterns of mortality exist locally or at the scale of entire cutblocks? The answers to these questions, together with information on movement patterns and habitat discrimination among weevils (Klingenberg, Björklund & Aukema 2010), may provide the basis for new management strategies to limit emerging threats to reforestation.

Materials and methods

SITE SELECTION

Nine cutblocks were selected across four forest districts in the central interior of British Columbia, Canada (mean size \pm SD = 48.8 \pm 7.2 ha; Klingenberg 2008) where mountain pine beetle first began to erupt (Aukema *et al.* 2006). Each cutblock had been harvested then replanted with seedling lodgepole pine *c.* 1 year of age. At the time of study, the replanted trees were 9–11 years old, with a mean stocking density of 3,200 \pm 375 stems ha⁻¹. Prior to replanting, logging slash, including residual stumps, had been piled and burned. Each cutblock had been hand-planted with 95–100% lodgepole pine at *c.* 2 \times 2 m spacing, with some evidence of natural regeneration. In some cutblocks, small residual patches of unharvested trees were left to encourage natural regeneration (Sullivan & Sullivan 2001; Sullivan, Sullivan & Lindgren 2001).

All cutblocks exhibited moderate levels of Warren root collar weevil activity, assessed from aerial surveys and visual inspection. Each cutblock was located immediately adjacent to mature stands that were characterized by a high per cent of mature lodgepole pine that had been killed by mountain pine beetle. We could not locate any cutblocks next to the unaffected pine because of the magnitude of the epidemic of mountain pine beetle (Aukema *et al.* 2006). All sites were found within the sub-boreal spruce (SBS/SBPS) biogeoclimatic zones (an ecosystem classification scheme used in British Columbia; Meidinger & Pojar 1991) and were relatively flat and uniform in composition.

FIELD SURVEYS

Survey transects

In summer 2006, up to four 4×100 m long transects were established in each cutblock to find out if there were gradients of tree mortality into the cutblock from the edges of adjacent, unsalvaged mature stands (Fig. 1). The scale was selected with reference to previous research on Warren root collar weevils in young, reforested stands (Schroff *et al.* 2006). The transects were placed at random locations around the perimeter of each cutblock and marked with 24-cm wire 'pigtails'. Along each transect, every tree was measured for vigour (good, moderate, poor and dead), needle chlorosis, height, and its precise location was recorded. Tree pathogens such as comandra blister rust *Cronartium comandra* Peck, and insects such as spruce gall adelgids *Adelges cooleyi* Gillette (Hemiptera: Adelgidae), giant conifer aphids *Cinara* spp. (Hemiptera: Aphidae), aphid-tending ants including *Camponotus herculeanus* L. (Hymenoptera: Formicidae), northern pitch twig moth *Petrova albicapitana* Busck (Lepidoptera: Tortricidae), and terminal weevils such as *Pissodes terminalis* Hopping and *Pissodes strobi* Peck (Coleoptera: Curculionidae), were recorded when observed on host trees (primarily lodgepole pine and hybrid spruce). Because their impact was low compared with Warren root collar weevils, however, their occurrence is not reported further here. Each transect was revisited a year later and any newly deceased trees were identified.

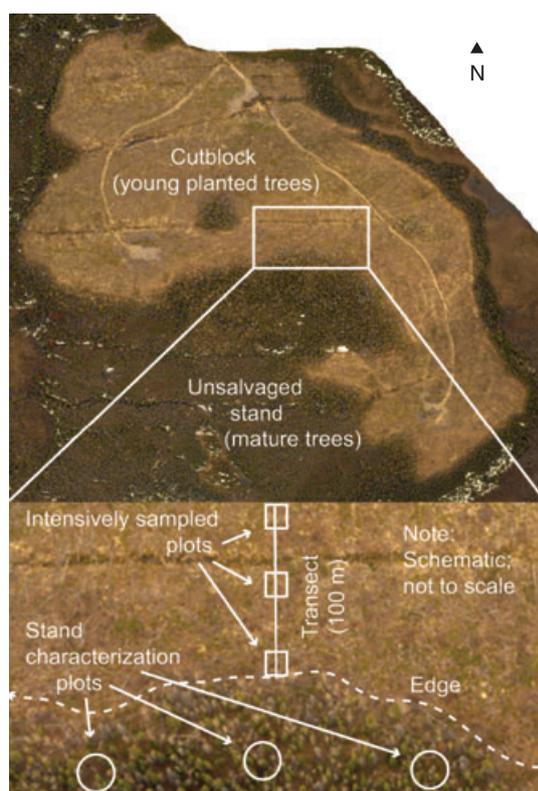


Fig. 1. Representation of the layout of transect (line) and intensive sampling plots (boxes) in a cutblock and stand characterization plots within adjacent mature, unsalvaged stand (circles). Inset figure (below) is schematic to demonstrate methods; scale bar is not to exact scale. White along cutblock edges is snow. Photo date 14 May 2007. For sizes of all cutblocks, see Klingenberg (2008).

Intensively sampled plots

Transects provide useful information on the location of dead trees, but not necessarily the causative agents of mortality. Injury by larvae of Warren root collar weevils, for example, can only be determined by careful excavation of the soil around the root collar of young trees and examination of feeding scars, girdling, and/or sap casings. Therefore, 8×8 m plots were established in 2006 for intensive sampling at 0, 50 and 100 m marks along each transect to determine whether mortality was correlated with weevil injury (Fig. 1). Weevil feeding was evaluated on all trees within each plot by looking for sap casings and/or the presence of larvae at the root collar (Cerezke 1994), and Warren root collar weevil was recorded as the causative agent of mortality if girdling was observed. Vigour, height, spatial location, length of terminal growth from previous year, length of terminal growth from 2 years previous, ground-level diameter, and diameter at breast height (1.3 m) was recorded for all trees together with their precise location. The trees within the intensive sampling plots were also examined for other insect pests and fungal pathogens (as above) but incidences were low and are not considered further here. Each intensive sampling plot was re-sampled a year later to record any changes in tree mortality and levels of larval feeding by Warren root collar weevil.

Characterization of stands killed by mountain pine beetle

Perpendicular to each transect, three circular plots 15 m in diameter were established in the mature, unsalvaged stands killed by mountain pine beetle (Fig. 1). The centre of the first plot was located 15 m into the stand from the edge of the beginning of the 100 m transect. The second and third plots were located 25 m on either side of the centre of the first plot, also 15 m from the stand edge (Fig. 1). Plot boundaries were established using a BAF #4 prism (Cruise Master Prisms INC., Sublimity, OR, USA). Variables recorded from each tree within each plot included species, diameter at breast height, and evidence of mountain pine beetle attack (never attacked, colonized, post-colonized and dead). In addition, the time since mountain pine beetle attack was estimated using the characteristics of the attacked tree including brood (if present), the amount of bark left on the tree, the colouration of needles, and the amount of needles left in the crown. Where there was evidence of attack over several years, an average estimated attack date of all trees surveyed in the plot was assigned. Because visual estimation methods are subjective (Saf-ranyik, Shrimpton & Whitney 1974; Shore & Safranyik 1992), especially where trees are killed rapidly by extremely high densities of mountain pine beetle, estimates of attack were compared with aerial survey records of mountain pine beetle attack (Aukema *et al.* 2006). Visual dating methods were highly consistent with these spatial records (M.D. Klingenberg, unpublished data).

Statistical analysis of transect and plot data

Generalized linear-mixed effects models were used to examine the fixed effects of variables characterizing the measurements of individual trees on binary response variables. Variables included tree height, vigour (dead, poor, moderate or good, fit as four separate 0/1 indicator variables) and tree position (distance from edge of adjacent mature stand). Response variables included tree status (live/dead), and presence/absence of feeding scars at the root collar of host trees in the intensively sampled plots. Random effects included site and transect nested within site. Regression models were constructed using a backward elimination procedure to remove a single least-significant variable in iterative model fits until all

remaining variables were significant using $\alpha = 0.05$. Separate regressions were developed for data collected in 2006 and 2007. In 2007, the same model framework was used to examine whether trees of varying vigour in 2006 were associated with tree death in 2007. All data analysis was performed in R v.2.5.0 (Ihaka & Gentleman 1996; R Development Core Team 2008).

AERIAL SURVEYS

Patterns of mortality within entire cutblocks

Patterns of tree mortality may be caused by multiple, and often interacting, mechanisms (Aukema *et al.* 2006). Although gradients of tree mortality from stand edges into the cutblocks might infer migration of Warren root collar weevils into the plots from neighbouring mature stands with reduced host availability, we were concerned that focusing solely on edge effects might miss important patterns of mortality within the cutblocks such as clusters or 'hot-spots'. If found, these might imply endemic increases of resident weevils developing from stumps left from logging slash (Cerezke 1994), even though such piles were apparently burned prior to planting. To study patterns of tree mortality in entire cutblocks, we used high-resolution aerial photographs of each of the nine cutblocks where transects and intensive plots were located [6496 × 4872 pixels with mean ground sampling distance (GSD) 20 cm pixel⁻¹; Klingenberg 2008]. All photos were imported into ARCVIEW v.9.2 (ESRI, 2008), where each young tree that had died over the past year (i.e. visibly red) was spatially referenced.

Statistical analysis of aerial survey data

The x and y coordinates for each dead tree in each cutblock were exported from Arcview into R v.2.5.0 for point pattern analysis using spatial point process regression models (spatstat package v.1.12–6). In brief, these models examine whether a response variable, λ , in this case the density of dead trees m⁻¹ across each cutblock, varies with spatially explicit covariates. Covariates to explore spatial trends included x and y terms (examining both linear and quadratic trends) as well as a newly defined variable, the distance to the nearest stand edge (usually the cutblock perimeter, but occasionally a residual harvest patch left within the cutblock). Regression parameters were estimated using maximum pseudolikelihood methods, and the significance of terms was judged by comparing the change in deviance between two nested models relative to a chi-square reference distribution (Berman & Turner 1992). The most basic model contained only an intercept, signifying a constant density of dead trees across the cutblock with no spatial trend (i.e. a homogenous Poisson process assuming complete spatial randomness). The best models retained significant spatial terms and had the lowest Akaike's Information Criterion (AIC) values (Akaike 1973).

Results

FIELD SURVEYS

Are weevils killing replanted trees?

Overall, we found that trees with feeding scars had a 17% probability of dying in a given year (Model A in Table 1). Within the intensively sampled plots, the annual mortality rate was 3%, judged by trees that had recently died and retained

red needles ($n = 38$). Of these, 87% exhibited partial or complete girdling by larvae of Warren root collar weevil. Seventeen per cent of the trees surveyed exhibited evidence of larval feeding by Warren root collar weevil.

Larval feeding activity decreased with distance from the mature unsalvaged stand. At the same time, feeding activity increased with tree diameter at ground level. After correcting for tree size, we also found feeding activity increased if the tree had been hand-planted vs. regenerating naturally (Model B in Table 1). Weevils selected the most dominant young trees in the cutblock, as tree height was positively correlated with the appearance of new feeding scars (Model C in Table 1).

Is mortality in transects associated with characteristics of neighbouring, unsalvaged, mature stands?

Along each transect, we observed 5% mortality on average. Mortality decreased with increasing distance away from the adjacent unsalvaged mature stand, and larger trees were more likely to be found dead (Model D in Table 1). Trees within each cutblock appeared to be spatially uniform in size, as there was no statistical relationship between tree height and distance away from the adjacent unsalvaged mature stand edge along the transect. The positive relationship between tree size and likelihood of death persisted across both years: analysis of the data collected in the second summer revealed that the probability of a tree's death was positively correlated with the tree's height and condition the previous year (Model E in Table 1).

On average, the mature stands were *c.* 90% pine, and of these trees, between 70% and 80% were dead. Stands had been attacked by mountain pine beetle 0–5 years prior to sampling. The inverse relationship between the likelihood of tree death and both distance from the cutblock perimeter and tree size remained consistent when the data on the neighbouring, mature, unsalvaged stands were included in model building. Moreover, these adjacent-stand variables helped to explain additional mortality observed within the replanted cutblocks. Tree mortality of young trees along each transect increased with increasing proportion of pine in the stand, increasing pine mortality within the stand, and the number of years since mountain pine beetle had attacked the unsalvaged, mature stands adjacent to each transect (Model F in Table 1).

It is possible that the higher number of dead trees along cutblock margins was simply an artefact of higher densities of trees around the cutblock perimeters, possibly because of natural ingress. Natural regeneration was observed along the transects and within the intensively sampled plots, which is characteristic of lodgepole pine forests in the central interior of British Columbia (Burton 2002). To exclude the possibility that higher tree densities along stand edges might in fact be creating conditions of constant relative mortality, we regressed tree density against distance from the mature stand edge. No significant gradients of tree density were observed within any of the nine cutblocks censused ($P > 0.05$), indicating that gradients of mortality were not statistical artefacts of tree density.

Table 1. Regression models to assess the effects of tree and stand characteristics on tree mortality and Warren root collar weevil feeding on young lodgepole pine trees within nine cutblocks in the central interior of British Columbia, Canada

Model	Data set ^a	Year	Trees (n)	Response variable ^b	Reforested cutblock				Adjacent mature stand ^d						
					Intercept	Larval feeding (1/0)	Transect distance (m)	Natural / planted ^c (1/0)	Ground-level diameter (mm)	Tree height (cm)	Tree vigour		Dead pine (%)	Years since death	
A	Plots within transect	2006	1117	Tree mortality	-5.28 (0.47)	3.69 (0.50)									
B	Plots within transect	2006	685	Larval feeding	-3.83 (0.42)		-0.0076 (0.0031)	0.97 (0.29)	0.069 (0.001)						
C	Plots within transect	2007	918	Larval feeding	4.68 (0.44)					0.0097 (0.0022)					
D	Transect	2006	2565	Tree mortality	-3.66 (0.35)		-0.0078 (0.0037)			0.0072 (0.0018)					
E	Transect	2007	2565	Tree mortality	-5.54 (0.37)					0.012 (0.0026)	2.12 (0.51)	2.77 (0.53)			
F	Transect	2006	2565	Tree mortality	-8.32 (1.04)		-0.0078 (0.0037)			0.0071 (0.0018)			0.04 (0.08)	0.025 (0.012)	0.64 (0.20)

Coefficient estimates are provided on the first line for each model, with standard errors of the estimates below in parentheses.

^aThe full data set includes the data collected from all trees along the 100 m transects; the reduced data set is restricted to trees sampled within the 8 × 8 m intensively sampled plots at points along the transects (see Methods).

^bThe binary yes/no response variables of tree mortality and larval feeding may be back transformed using $\exp(y/[1 + \exp(y)])$ to obtain the probability of a tree being dead or exhibiting feeding scars.

^cTree was estimated to be either naturally regenerated from the seedbank or planted by hand.

^dThese variables were recorded from the mature, unsalvaged stand adjacent to the studied cutblocks.

AERIAL SURVEYS

Do patterns of mortality persist at entire-cutblock scales?

We identified between 200 and 5000 dead trees in each of the nine cutblocks from the high-resolution, aerial photographs (Fig. 2). All dead trees were identified by the presence of red, necrotic needles, indicating that the trees had died within the past year. Graphically, it appears that there is a higher density of dead trees along the edges of the cutblock (adjacent to unsalvaged, mature stands of dead lodgepole pine). Spatial point process regression models of the densities of dead trees are summarized for each of the cutblocks in Table 2.

Within seven of the nine cutblocks (A–G), the density of dead trees was highest around the cutblock perimeters (i.e. a significant distance-to-margin covariate included in Table 2). This spatial trend was often apparent even accounting for a mortality gradient across a cutblock in the x or y direction. In the two cutblocks where no perimeter mortality was statistically significant (H,I), there were trends in the x and y directions, signifying a spatial trend in young tree mortality from at least one cutblock edge.

Discussion

Our findings, together with research demonstrating increased movement rates of Warren root collar weevil in a habitat with more dead trees (Klingenberg *et al.* 2010), are consistent with

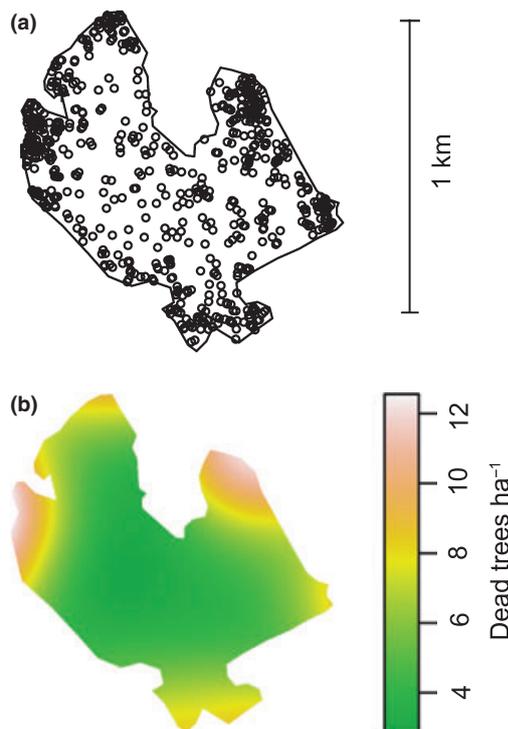


Fig. 2. Plot of (a) spatial location of dead trees, and (b) intensity surface of a representative cutblock (cutblock D in Table 1). Units for plot B are scaled to dead trees ha^{-2} .

the hypothesis that Warren root collar weevils are migrating out of mature, unsalvaged stands with reduced host pools (i.e. a high proportion of dead trees) into young, reforested stands in search of food. These results provide an example of how mitigation activities, in this case salvage harvesting and replanting, in response to one insect problem can inadvertently create a new pest challenge. In our study system, this effect is perhaps of greater concern because of the magnitude of the mountain pine beetle outbreak is due, in part, to previous management strategies such as fire suppression that have resulted in vast expanses of same-age hosts susceptible to mountain pine beetle (Taylor *et al.* 2006). Moreover, increasing temperatures consistent with anthropogenic impacts have allowed the mountain pine beetle to expand into new elevational and geographical ranges (Carroll *et al.* 2004; de la Giroday 2009; Robertson *et al.* 2009).

Tree mortality because of feeding by Warren root collar weevil larvae may become a significant concern as the outbreak of mountain pine beetle declines, and forests are salvaged and replanted. Over the four forest districts studied here, more than 115 million m^3 of pine had been harvested in the decade prior to this study. Lodgepole pine is a primary component of regenerating stands and also a primary host of Warren root collar weevil (Cerezke 1994), therefore the negative effects of this insect may occur at the landscape scale. Indeed, we do not know whether the absence of a distance effect in re-measured transects in 2007 (Model E in Table 1) occurred because the trend of increasing mortality is beginning to plateau, or whether the widespread trend can now only be observed at larger scales (e.g. entire cutblocks; Table 2).

Our results indicated that weevils selected trees that were planted by hand vs. trees that had naturally seeded. The roots of planted trees often have a smaller cross-sectional area, and they are thought to be at a higher risk of mortality from larval girdling (Robert & Lindgren 2006, 2010). It is standard procedure to hand plant reforested cutblocks in western Canada, and underlines the care needed in planting. Encouraging natural regeneration, using seedling production methods to increase the vigour of trees, may reduce the risk of mortality (Duke & Lindgren 2006; Robert & Lindgren 2006, 2010). Although Warren root collar weevil may only kill a per cent of young trees, larval feeding on the root collars frequently decreases stand productivity as trees lose vigour (Cerezke 1994). Not only are low-vigour trees likely to die the following year, but larval feeding may open infection corridors for fungal pathogens (Whitney 1961, 1962).

Although above-ground herbivory by mountain pine beetle may trigger large-scale movement by Warren root collar weevil because of declining host availability, mountain pine beetle may also indirectly benefit Warren root collar weevils by creating site conditions that favour insect development. For example, the sudden reduction in transpiration potential because of mountain pine beetle killing large tracts of mature forest has elevated the water table in many areas, and Warren root collar weevil prefers moist habitats (Cerezke 1994). Moreover, an increased duff layer following salvage harvesting favours

Table 2. Best models of the density of dead trees m^{-2} in nine cutblocks in the central interior of British Columbia, Canada

Block	Size (ha)	Residual harvest patches	Intercept	x	x ²	y	y ²	Distance to margin (m)	Null model ^a			Mortality gradient at entire-cutblock scale? ^d	
									Comparison ^b		Density ^c		
									χ^2	d.f.			P
A	56.2	No	-7.08 (1.35×10^{-1})			-3.76×10^{-3} (5.47×10^{-4})	-2.99×10^{-6} (4.69×10^{-7})	-1.33×10^{-3} (3.72×10^{-4})	56.2	3	< 0.0001	19	From all edges
B	39.5	No	-4.46 (4.06×10^{-2})			-4.70×10^{-4} (5.12×10^{-5})		-2.20×10^{-3} (3.04×10^{-4})	162.7	2	< 0.0001	71	From all edges
C	84.9	No	-9.98 (3.60×10^{-2})	-1.00×10^{-3} (2.70×10^{-4})		3.60×10^{-3} (5.90×10^{-4})		-5.10×10^{-4} (1.40×10^{-3})	1022.2	3	< 0.0001	4	From all edges
D	41.9	No	-6.76 (6.10×10^{-2})					-7.00×10^{-3} (6.10×10^{-4})	154.3	1	< 0.0001	6	From all edges
E	39.0	Yes	-5.09 (7.60×10^{-2})	-8.00×10^{-4} (1.70×10^{-4})		-5.70×10^{-4} (1.30×10^{-4})		-2.20×10^{-3} (7.80×10^{-4})	38.8	3	< 0.0001	58	From all edges
F	73.0	Yes	-7.10 (6.58×10^{-2})	-1.26×10^{-4} (6.21×10^{-5})		-2.74×10^{-3} (1.12×10^{-4})	-9.00×10^{-7} (4.10×10^{-8})	-1.06×10^{-3} (2.77×10^{-4})	1033.4	4	< 0.0001	38	From all edges
G	47.2	No	-9.11 (2.18×10^{-1})	1.80×10^{-4} (5.34×10^{-5})		1.20×10^{-3} (1.35×10^{-4})		-1.90×10^{-3} (5.80×10^{-4})	98.3	3	< 0.0001	2	From all edges
H	41.6	Yes	-5.14 (4.02×10^{-1})			2.24×10^{-3} (3.96×10^{-4})	3.92×10^{-7} (9.03×10^{-8})		99.0	2	< 0.0001	4	From one edge
I	15.5	Yes	-6.75 (1.54×10^{-1})	-1.10×10^{-3} (8.45×10^{-5})		-1.20×10^{-3} (1.91×10^{-4})			247.1	2	< 0.0001	16	From two edges

Coefficient estimates are provided on the first line for each model, with standard errors of the estimates below in parentheses. Coefficient estimates are recorded on a log-linear scale. For example, to estimate the density of dead trees at a particular location in cutblock B, the equation is $\log(\lambda) = -4.46 - 4.70 \times 10^{-04}(\text{distance in } y \text{ direction}) - 2.20 \times 10^{-03}(\text{distance to nearest margin})$.

^a Null model assumes no gradient and estimates a constant density (a homogeneous Poisson process, or only an intercept).

^b Comparison of null model with best spatial trend model. Significance indicates a spatial gradient of mortality at the cutblock scale.

^c Density of dead trees for the null model (assuming no spatial trend; converted to dead trees ha^{-1}).

^d Judged by sign and significance of spatial terms. A negative coefficient for a 'distance to margin' term indicates tree mortality decreases with increasing distance towards the plot centre.

Warren root collar populations, especially if slash is not burned prior to replanting (Cerezke 1994). Habitat modification associated with clear-cut harvesting affects many aspects of forest ecology, including insect communities (Niemelä, Langor & Spence 1993; Bengtsson, Persson & Lundkvist 1997; Heliölä, Koivula & Niemelä 2001; Lemieux & Lindgren 2004; Latty *et al.* 2006), and forest-management practices have been shown to mediate the dispersal patterns and population dynamics of other *Hylobius* species (Eidmann 1997; Leather, Day & Salisbury 1999; Rieske & Raffa 1999; Nordlander *et al.* 2003; Nordlander, Bylund & Björklund 2005).

Seven of the nine cutblocks exhibited higher gradients of mortality towards their entire perimeters. The two cutblocks that exhibited a gradient from one or two stand edges, but not the entire perimeter, both retained residual patches of mature, dead pine to serve as wildlife habitat after harvesting. For example, cutblock I (Table 2) retained eight such patches. Not surprisingly, this pine had also been recently killed by mountain pine beetle. We suspect that such residual patches of mature trees may obfuscate gradients of young tree mortality from cutblock margins, as weevils may create internal, opposing gradients by migrating from refugia. Current harvesting and reforestation practices attempt to mimic historical fire regimes (Bergeron *et al.* 2002) and encourage the implementation of smaller cutblocks (DeLong 2002), which are often replanted with high per cent of pine trees susceptible to Warren root collar weevil (Cerezke 1994). Smaller cutblocks with a high per cent of susceptible hosts may be prone to greater concentration of weevils, resulting in elevated mortality levels.

Conclusions

This study provides an example of how a response to one landscape-level insect outbreak can create new challenges to reforestation from another insect that may not have been a significant pest previously. At this time, it is unknown whether the impacts on reforestation efforts because of below-ground feeding by Warren root collar weevil will exist over the same spatial extent as the outbreak area for mountain pine beetle (> 14 million ha in British Columbia and Alberta). The work reported here focused on the region exhibiting early stages of the outbreak (Aukema *et al.* 2006) and hence the greatest salvage and reforestation efforts to date. If mortality continues, large-scale interventions such as fill-planting may be required to return the stand to ideal stocking densities.

Given the patterns of mortality to date, we make the following recommendation for forest-management strategies that could reduce the impact of Warren root collar weevil. As the ratio of perimeter to area decreases with increasing size of cutblock, we recommend consideration to harvest larger cutblocks, especially when located close to unsalvaged stands. This may not always be possible, however, because of local restrictions on the area that can be felled at one time or because of conflicts with wildlife management objectives. We recommend that sites prone to Warren root collar larval feeding should be identified by characterizing adjacent stands following eruptions of mountain pine beetle which would facilitate

select monitoring. We also recommend that post-harvest techniques, many of which are standard practice, should be continued. These include prescribed burning and scarification to remove excess slash and stumps because this will disrupt the development of populations of Warren root collar weevil remaining in stands. We encourage the incorporation of less susceptible host tree species such as deciduous species into prescribed planting mixes because this may reduce weevil impacts (Hopkins *et al.* 2009). Finally, in certain areas, the maintenance of high stocking standards and limitation of pre-commercial thinning treatments may maintain conditions less favourable to Warren root collar weevil development.

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