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RESEARCH ARTICLE

Incoming! Association of landscape features with dispersing mountain pine beetle populations during a range expansion event in western Canada

Honey-Marie C. de la Giroday · Allan L. Carroll · B. Staffan Lindgren · Brian H. Aukema

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Abstract Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is a forest insect that undergoes intermittent population eruptions, causing landscape-level mortality to mature pines. Currently, an outbreak covers over 16.3 million ha of British Columbia and Alberta in western Canada. Recent incursion into the jack pine (*Pinus banksiana* Lamb.) of northwestern Alberta threatens further range expansion through the boreal forest to central and eastern Canada. The spread from British Columbia into northwestern Alberta has been facilitated by above-canopy dispersal of the insect by meso-scale atmospheric currents. At these scales, dispersing *D. ponderosae* may behave like inert particles, causing terrain-induced tropospheric convective and advective currents to influence population dispersal and establishment. We use spatial point process regression models to examine the association of meso-scale variables, including landscape features and their orientations, habitat suitability, elevation and treatment efforts, with occurrence of *D. ponderosae* infestations in 2004, 2005, and 2006. Infestations of *D. ponderosae* primarily established in canyons and valleys, before moving into more open-sloped areas. Southwestern slopes of midslope ridges and small hills, southwest facing open slopes, and valleys that run in a northeast–southwest cardinal direction were positively associated with higher intensities of infestation. This study provides insight into the influences of complex terrain on landscape disturbance by a forest insect, and can be used to prioritize areas for potential management.

Keywords *Dendroctonus ponderosae* · Dispersal · Jack pine · Landscape features · Lodgepole pine · Mountain pine beetle · Mountains · Boreal forest · Valleys

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H.-M. C. de la Giroday (✉) · B. S. Lindgren · B. H. Aukema
University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada
e-mail: honeydelagiroday@gmail.com

A. L. Carroll
Department of Forest Sciences, University of British Columbia, 3034 Forest Sciences Centre, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

B. H. Aukema
Department of Entomology, University of Minnesota, 1980 Folwell Ave, St. Paul, MN 55108, USA

Introduction

Interactions between meso-scale atmospheric currents and the topography of a landscape can play an important role in governing the spread and impact of insect herbivores in forest ecosystems by directly influencing the dispersal capabilities of insect populations (Bjørnstad et al. 2002; Ims et al. 2004). In 2002, a massive outbreak of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) that originated in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) forests in the central interior of British Columbia began to spread into the Peace River region of British Columbia, a region not thought to be part of its historical distribution. Previously, the northern Rocky Mountains were thought to be a geoclimatic barrier to such range expansion.

The invasion of the Peace River region was facilitated by long-distance, airborne dispersal (Jackson et al. 2008; de la Giroday 2009; Robertson et al. 2009; Safranyik et al. 2010; Ainslie and Jackson 2011). Newly emerged beetles are attracted to dark objects on a light background (Shepherd 1966), and thus may orient towards the canopy, dispersing upward and downwind. This may allow beetles to move above the canopy and become incorporated into wind currents during warm, fair-weather periods (Chapman 1962; Safranyik et al. 1989). Once within meso-scale atmospheric currents, the movement of insects is similar to the drift of inert particles (Taylor 1974), although insects may maintain a degree of flight control (Lewis and Dibley 1970). In situations where long-distance dispersal dominates, alterations of wind velocity, turbulence, and direction determine the transport, deposition, and the establishment of insect populations where there is susceptible host and suitable climate. The descent of MPB from wind currents occurs via gravitational settling, active flight, rainout, and/or impaction (i.e. the contact of biota with objects). In particular, landscape features provide impactive surfaces for interception of insects (Defant 1951; Mason and McManus 1981; Ashmole et al. 1983; Antor 1994; Bullard et al. 2000). The greater the mass of an airborne object, the more likely it will impact a surface rather than be swept around the obstacle into lee-ward eddies (Westbrook and Isard 1999). Also, alterations in wind speed may cause increased settlement in areas where wind speed is reduced such as when the direction of motion is perpendicular to emergent landscape features (Ruel et al. 2001). Alternatively, wind speed(s) may increase, depending on fetch, in open areas, increasing the transportation distances of insects within valleys.

As the MPB moved into the Peace River region, insect populations moved *en masse* through a topographically complex landscape. This movement, coupled with relatively consistent directions of meso-scale winds in the region (Holt and Eaton 2008), may have caused predictable settling and establishment of infestations where landscape features and convective currents interacted. Despite the importance of topography on settlement patterns of insects exhibiting aeolian dispersal, the influence of topography and topographic orientation on the deposition patterns of MPB in these recent range expansion events has not been studied.

The primary objectives of the present study were threefold: (1) to examine the association of landscape features on the establishment and persistence of insect populations of sufficient size to kill mature trees in a newly-invaded area; (2) to determine whether the specific orientations of those features provided additional inference on locations of insect establishment; and (3) to examine the relative contributions of other landscape characteristics, including elevation, susceptible habitat and treatment/control tactics, on the annual establishment patterns of MPB during initial stages of invasion. Investigation of factors driving establishment of MPB infestations within this region allows retrospective examination of the invasion event(s) and may provide critical information to formulate strategies to mitigate further range expansion events of this eruptive forest herbivore.

Materials and methods

Study system

The MPB is a cryptic herbivore that spends all but a few days of its life cycle under the bark of mature pine trees. The forests of the Peace River region contain lodgepole pine, a primary host species of *D. ponderosae*, and jack pine (*P. banksiana* Lamb.), a “novel host” in which the MPB has been demonstrated in laboratory experiments to successfully reproduce (Safranyik and Linton 1983; Cerezke 1995). Typically, the insect exists for long periods at endemic levels, but may intermittently undergo drastic population eruptions (Zhang and Alfaro 2003; Gamarra and He 2008). At epidemic population phases, the insect must kill its host in order to reproduce, exerting positive feedback in a system with landscape-scale consequences (Raffa and Berryman 1983; Raffa et al. 2008). Outbreaks typically decline when the host supply is exhausted and/or lethal climatological events result in mortality of a large proportion of the population (Stahl et al. 2006).

We delineated our study area to encompass all outbreaking populations of MPB on the northeastern slopes of the Rocky Mountains within British Columbia from 2004 to 2006. This area includes the Peace River region from the Rocky Mountains to the border of the province of Alberta, an area approximately 3 million ha in size (Fig. 1). At the western edge of the study area, the terrain is dominated by the northern Rocky Mountains with strongly linear terrain features formed by erosion of folded and faulted sedimentary rocks. These linear features include large U-shaped valleys, produced by glacial erosion, separated by distinct ridges. The Hart Range, the primary mountain range in the region containing the Solitude and Murray Ranges, dissects

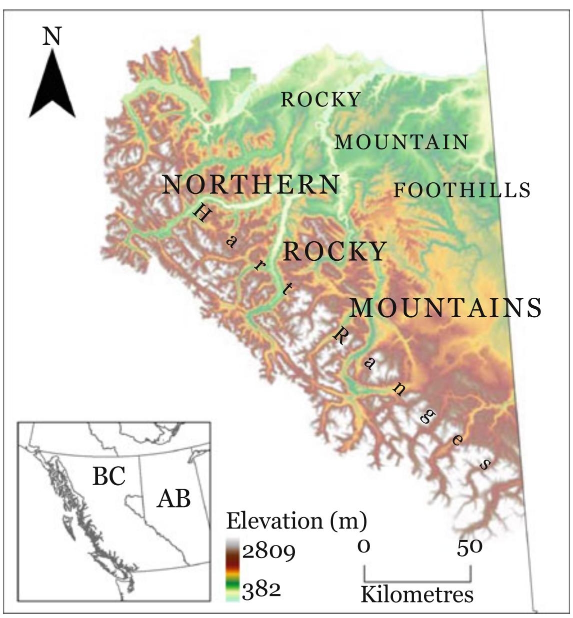

Fig. 1 Location of research area in the northeastern British Columbia. The research area includes a portion of the northern Rocky Mountains, including the Hart Ranges, and the Rocky Mountain Foothills, an area of undulate topography that eventually becomes a plateau at the eastern edge of the research area. The *inset map* shows the location of the research area in British Columbia

the area at a central belt of lower elevation in the Rocky Mountains. This range encompasses two low-lying passes, the Pine Pass (874 m), which is the lowest of six highway passes through the northern Rocky Mountains, and the Monkman Pass (1,092 m). The eastern portion of the research area is composed of flat-lying or gently dipping sedimentary rocks producing plateau topography.

Landscape feature data

Using digital elevation models (DEM; GeoBase 2007; horizontal accuracy = 90% of features within 10 m of true position; vertical accuracy = 90% of elevation points are within 5 m of their true elevation) composed of 1:250,000 map tiles and 73 m × 73 m resolutions, each pixel within the research area was classified into one of ten landscape feature types (Table 1) based on its relative elevation using a Topographic Position Index (TPI; see Supplementary Material A; Jenness 2006) tool v.1.3a, as an extension within Arcview v.3.2 (ESRI). A recommended circular pixel neighbourhood was used during classification (Jenness 2006). Three combinations of small and large neighbourhood sizes were examined, including 1,000 and 2,000 m, 1,000 and 3,000 m, and 1,000 and 6,000 m, respectively. Resulting TPI rasters were visually inspected and compared to the source digital elevation model. The first two TPI rasters resulted in a classification with a pixel resolution too coarse to accurately reflect the topography of the research area. The third classification scheme satisfactorily represented terrain within the region and was selected for use in statistical analyses.

Landscape feature orientation

Through exploratory analysis, landscape features exhibiting a positive spatial association with infestations were identified (see "Statistical methods" section). The orientation of these landscape features was calculated to allow investigation of the effects of orientation on the annual occurrence of MPB infestations. The orientation of landscape features was determined using azimuth or aspect according to the type of feature, with unidirectional landscape features having an aspect (e.g., open slopes facing southwest) and bidirectional, linear landscape features having an

Table 1 Average size and elevation of landscape features classified within study area of the Peace River region of British Columbia (see Fig. 4 for map)

Landform	Area (ha)	Percentage of landscape	Elevation (m)			
			Mean	Min.	Max.	Range
Plains	1,161,849	39.02	877	396	1,988	1,592
Open slopes	836,946	28.11	1,091	395	2,142	1,747
U-shaped valleys	237,761	7.98	964	382	1,806	1,424
Mountain tops/high ridges	168,347	5.65	1,619	764	2,808	2,044
Upper slopes/mesas	159,454	5.36	1,468	726	2,491	1,765
Midslope drainages/shallow valleys	158,742	5.33	1,238	396	2,138	1,742
Canyons/deeply incised streams	122,853	4.13	1,007	384	1,817	1,433
Midslope ridges/small hills in plains	116,685	3.92	1,219	477	2,121	1,644
Upland drainages/headwaters	13,852	0.47	1,608	860	2,332	1,472
Local ridges/hills in valleys	1,122	0.04	1,119	662	1,759	1,097
Total	2,977,611	100	1,059	382	2,808	2,426

azimuth (e.g. U-shaped valleys running in southwest to northeast orientation). These datasets were then converted to binary rasters (73 m × 73 m pixel size, similar to the DEM) where locations of a particular landscape feature with a specific orientation were noted by ones (i.e., presence) while the rest of the landscape was recorded as zeros (i.e., absence).

Susceptible host distribution data

A stand susceptibility index (SSI) dataset for the research area, produced by Shore et al. (2008), was used as a surrogate for habitat considered suitable for outbreaking populations of MPB in our analyses. SSI values are derived from a multiple regression model that allows a user to predict the susceptibility of a region to successful attack by MPB if they have data pertaining to the following four parameters: the relative abundance of pine, ages of dominant and codominant pine, stand density, and climatic conditions conducive to beetle populations (Shore and Safranyik 1992; Shore et al. 2000). Shore et al. (2008) used spatially-explicit forest survey data from the British Columbia Ministry of Forests, Lands and Natural Resource Operations to estimate the first three parameters. Since SSI was originally developed for use in British Columbia, west of the Rocky Mountains, climate suitable for the MPB was characterized by a "location" factor denoting a combination of the latitude, longitude and elevation of areas with historically high likelihood of outbreaks (Shore and Safranyik 1992). To extend the relevance of the SSI calculation to areas east of the Rockies, Shore et al. (2008) replaced the location factor with a climatic suitability index (Carroll et al. 2004). Climatic suitability averages were modeled for the region using methods developed by Safranyik et al. (1975) and Carroll et al. (2004) and historical daily weather data for BC obtained from Environment Canada Meteorological Services (2002). Resulting SSIs ranged between 0 and 100, and were categorized into five classes with class 0 being the lowest susceptibility to infestation by MPB (e.g., no trees) and class 5 being the highest (i.e., pine leading ages ≥60 years, suitable climate, etc.; Shore and Safranyik 1992). The surface for forest susceptibility was converted to a binary raster of "most susceptible (i.e. class 5)" versus "less."

Infestation data

Detailed annual survey maps of discrete outbreaking populations of MPB were obtained from forest licensees. Due to the significant economic threat, helicopter survey flights by licensees from 2004 to 2006 covered the entire research area. The surveys were conducted by identifying and recording locations of "red-attack" trees from helicopter using GPS, in concert with ground reconnaissance work in selected areas. Because MPBs in epidemic population phases must kill their host in order to reproduce, and foliage fades from green to red within 1 year after colonization (Safranyik et al. 1974), mapping "red-attack" can be used as a proxy for estimates of insect abundance (Aukema et al. 2006; Wulder et al. 2006). The surveys were conducted in 2004, 2005, and 2006 from approximately May to September. Centre point locations for each infestation were recorded in Universal Transverse Mercator (UTM) coordinates. Additional data collected for each infestation included its size, the approximate number of trees affected, ecological land classification scheme, land tenure, and any control strategy implemented. Infestations were either mapped as points or polygons. To examine the accuracy of infestation mapping completed in 2006, a small subset of infestations was ground-truthed in the region in 2007. We found that locations were accurately recorded; however ascertaining the accuracy of the estimates of the number of red trees was difficult to verify due to additional attack by MPB in 2007. For our analysis, polygon data were converted to point data based on the centroid of the polygon and combined with other point locations for infestations. A separate dataset of infestation treatment data was procured from licensees for 2005 and 2006. Treatments to reduce beetle populations included single tree treatments and harvesting of infested blocks. Polygonal and point treatment data were combined into a single point dataset using methods similar to those used for infestation data, such that all points had an affected area associated with them. A raster surface of distance from treatment location within the research area for 2005 and 2006 was produced.

Statistical methods

We used multivariate regression to examine the potential influences of landscape features, their orientation, habitat suitability, easting and northing, elevation, and, for 2005 and 2006, the distances from locations of treatment in the previous year on the density of discrete patches of trees killed by MPB in the study area for each year. Use of regression to gain inference on variables associated with the presence of an organism is not unlike habitat or species distribution models (e.g., Guisan and Zimmerman 2000; Elith and Leathwick 2009). Here, we utilize a type of spatial regression for an inhomogenous Poisson point process (Baddeley and Turner 2000, 2005) reflecting a density of insect infestations, λ, that changes conditional on spatially-explicit covariates

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

where λ is the conditional density at a given pixel, β are regression coefficients, and $x_1,\ldots,x_p$ are covariates. In this model, each covariate must contain information at all pixel points on the study surface. This technique represents a useful method to contend with spatial autocorrelation, as the spatial dependence is inherent within the point process. Coefficients are estimated using maximum pseudolikelihood methods (Baddeley and Turner 2000, 2005), and nested models may be compared by examining the change in deviance relative to a χ^2 reference distribution. Non-nested models can be compared by examining Akaike Information Criteria (AIC), with the lowest AIC value judged to be the best (Akaike 1973). Substituting covariate values into the resulting regression equation yields an estimated intensity at a given point on the pixel map of the study area (example provided in "Results" section). Our analysis was conducted as follows:

Step 1: We selected a "sensible" set of landscape features to include as covariates in formulating regression equations (rather than use all 10; Table 1, in addition to other covariates such as elevation, etc.). Our criteria were selecting those landscape features exhibiting a positive association with infestations. These were determined by exploratory contingency tests that examined whether the intensity across a landscape feature type was greater than would be expected by random chance for each of the 2004, 2005, and 2006 datasets. Analyses for each year were restricted to the area of infestation plus a 25 km buffer (Supplementary Material B).

Step 2: Fit multiple regression equations for each year (i.e., 2004, 2005, and 2006), providing inference on the influences of a variety of variables (landscape features identified in Step 1, elevation, relative location, etc.) on the intensity of MPB populations. The marginal effects of two covariates, namely those reflecting the Cartesian coordinates x and y (easting and northing), were difficult to estimate (e.g., inflated standard errors; Graham 2003) due to high correlation between x and y, as infestations settled in northeast bands across the entire research area (Fig. 2). To contend with this challenge, we reduced these two covariates to one dimension by defining a new variable, the distance from each infestation to a line of reference (138° bearing) along the Rocky Mountains,

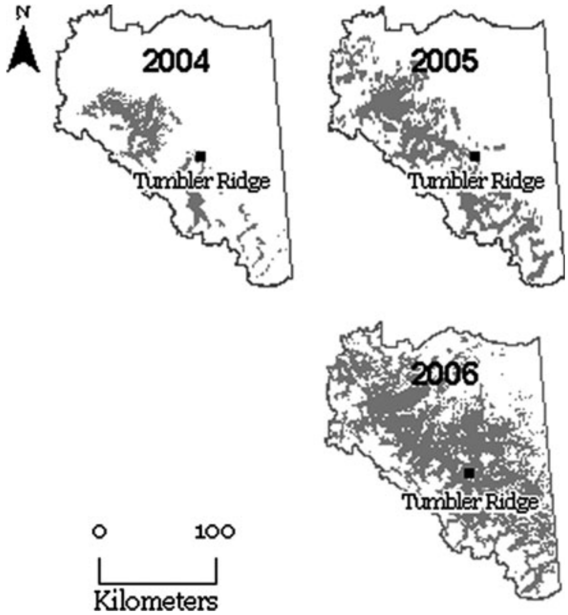

Fig. 2 Location of infestations (*shaded areas*) of MPB in the study area of the Peace River region of British Columbia in 2004, 2005, and 2006

perpendicular to the direction of spread (48° bearing; see Supplementary Material C). We refer to this variable as 'distance from line of reference' and use it in place of easting and northing variables. In sum, information-theoretic model selection procedures were used to distill a full model with the above variables (e.g., landscape features, elevation, relative location, etc.) into a final multiple regression equation that provided the best inference on the intensity of MPB populations for each year (i.e., 2004, 2005, and 2006). The final model in each year included at least one term for various landscape features (see "Results" section).

Step 3a: To identify spatial *orientations* of landscape features that could have influenced the intensity of infestations, we then returned to the initial infestation inventory datasets for each year and fit separate regression models using one of the eight (for aspects) or four (for azimuths) orientations for each type of landscape feature that was significant in the previous models. The best-fitting feature orientation was selected for each feature type in each year by examining AIC values. For example, if the final model in a given year in step 2 contained a term for "open slopes," eight separate univariate point process regression models were fit, regressing infestation intensity for that year against surfaces of north, northwest, west, southwest, south, southeast, east, and northeast aspects of open slopes. The best model of those eight was selected to continue to the next step.

Step 3b: We then returned to the final models from Step 2 and substituted any covariate(s) reflecting landscape features with the new covariate identified in Step 3a reflecting the feature's best-fitting orientation. This allowed a comparison between models with landscape features, and those with features restricted to a specific best-fitting orientation of landscape features. The model with the lowest AIC value was judged to fit the best.

All data were handled in Arcview v.9.2, ArcInfo Workstation, and Arcview v.3.2 while the spatstat package v.1.14-9 (Baddeley and Turner 2005) within R v.2.8.1 was used for statistical analyses (Ihaka and Gentleman 1996; R Development Core Team 2009).

Results

Spatial extent and topography of invaded area

The number of incipient-epidemic infestations increased annually within the Peace River region of British Columbia between 2004 and 2006 (Fig. 2). There were 10,536 infestations mapped in 2004 and 12,275 in 2005. These numbers approximately tripled to 35,084 infestations in 2006. In 2004, the mean area of patches of red trees killed by MPB was quite small; approximately one third of a hectare. However, the mean sizes of individual infestations increased to approximately 1 ha in 2006. Sizes of patches of dead trees became more variable due to expanding areas that were colonized, as the largest areas measured in 2006 were 2,440 ha, vs. 6 and 133 ha in 2004 and 2005 respectively. By 2006, the total area of trees killed by MPB had expanded to 35,084 ha. Patches of mortality were found in lodgepole pine forests between elevations of approximately 500–1,700 m. Infestations stretched from the western slopes of the Rocky Mountains in 2004 to the town of Tumbler Ridge, British Columbia (Fig. 2). By 2006, this extent had expanded two-fold in a northeasterly direction to encompass almost the entire Peace River region.

Dominant landscape features in the region included plains, open slopes, and U-shaped valleys (Fig. 3). A numerical summary of their areas and elevations are provided in Table 1. Together, plains and open slopes comprised more than 50% of the landscape in the Peace River region. Other landscape features such as canyons and deeply incised streams, upper slopes and mesas, and midslope ridges or small hills in plains each comprised no more than 6% of the area proportionally, but absolute area was always more than 100,000 ha in size. The smallest landscape features in size were local ridges or hills in valley bottoms, comprising 1,122 ha across the region (0.04% of the total area). Plains exhibited the lowest mean elevation (877 m) while mountaintops/high ridges had the highest (1,619 m). Most successful attacks were at 1,000 m in elevation each year.

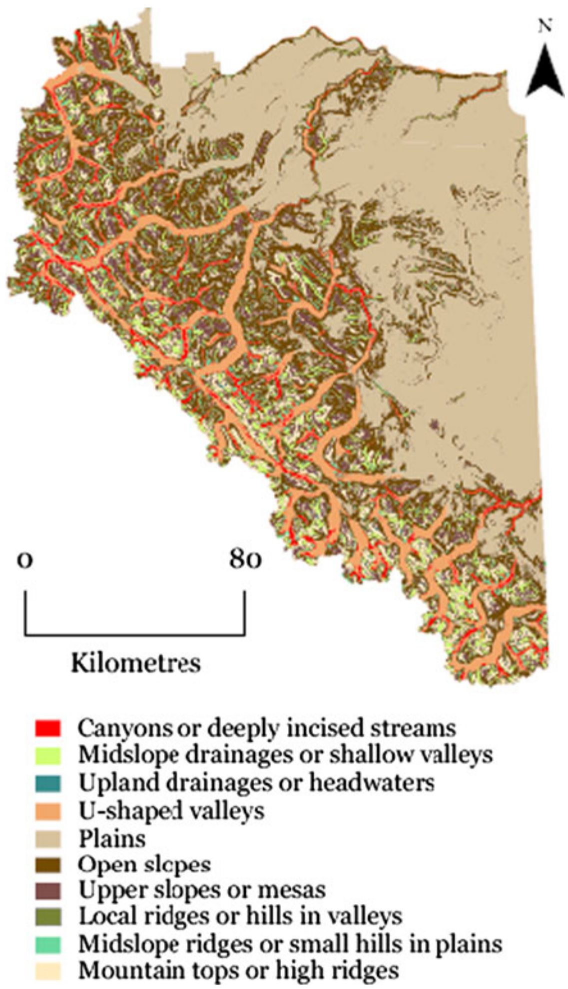

Fig. 3 Map of landscape features in the study area of the Peace River region of British Columbia

Most of the Peace River region across northeastern BC was considered highly unsuitable for outbreaking populations of MPB (Fig. 4), as two thirds of the landscape was classified as suitability class 0. The most susceptible habitat, i.e. class 5, occupied only 3% of the landscape (74,894 ha) (Table 2), although populations were found in lower suitability classes (Fig. 2). The most susceptible habitat is stratified across nine different landscape features. Of these, plains, open slopes, and U-shaped valleys comprised the largest proportion of highly susceptible habitat (49, 27, and 14% respectively). Upland drainages or headwaters, local ridges or hills in valleys, and upper slopes or mesas collectively comprised less than 1% of habitat classified as highly susceptible to outbreaking populations of MPB.

Landscape features associated with mountain pine beetle infestations

Exploratory analyses using contingency tests revealed that certain landscape feature had more (or less) infestation than would be expected if infestations were

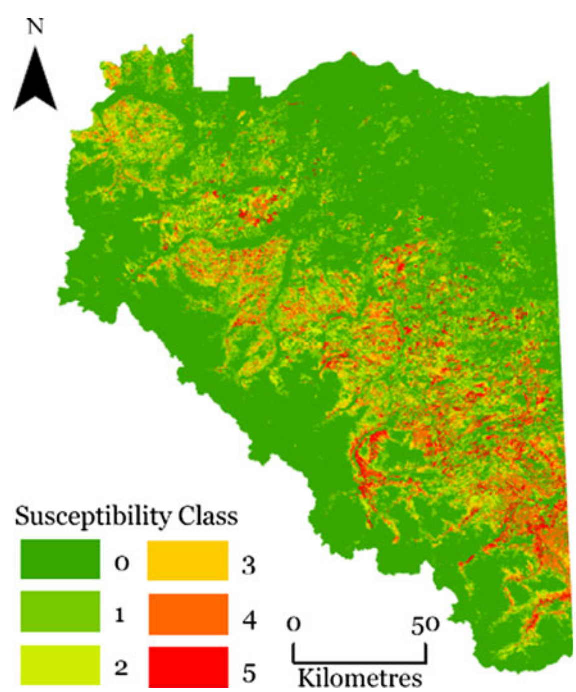

Fig. 4 Distribution of habitat susceptibility classes in the study area of the Peace River region of British Columbia

Table 2 Percentages of landscape features and total landscape with habitat considered highly susceptible to outbreaking populations of MPB in the Peace River region of British Columbia (habitat susceptibility class 5)

Landscape feature	Relative distribution (%)	Percent of landform type	Percent of landscape	Area (ha)	Orientation
Plains	48.749	3.142	1.226	36510.1	–
Open slopes	27.392	2.451	0.689	20515.2	Aspect
U-shaped valleys	14.397	4.535	0.362	10782.3	Azimuth
Midslope ridges, small hills in plains	3.447	2.213	0.087	2581.7	Aspect
Canyons, deeply incised streams	2.759	1.682	0.069	2066.6	Azimuth
Midslope drainages, shallow valleys	1.967	0.928	0.049	1473.3	Aspect
Upper slopes, mesas	0.628	0.295	0.016	470.6	–
Mountain tops, high ridges	0.606	0.270	0.015	454.0	–
Local ridges, hills in valleys	0.053	3.582	0.001	40.2	Aspect
Upland drainages, headwaters	7.000E−4	0.004	2.000E−5	0.5	–
Total	100.000	19.000	3.00000	74895.0	

Orientation indicates if and how the orientation of a landscape feature was determined with 'Aspect' being a unidirectional orientation and 'Azimuth' being bidirectional

distributed randomly in proportion to the relative abundance of each feature type. In 2004, canyons or deeply incised streams, local ridges or hills in valleys, midslope ridges or small hills in plains and U-shaped valleys had more area infested than expected. This pattern persisted into 2005, as midslope ridges or small hills in plains, and U-shaped valleys had greater areas infested than expected, along with canyons or deeply incised streams. In 2006, canyons or deeply incised streams, local ridges or hills in valleys, midslope ridges or small hills among plains, open slopes and U-shaped valleys exhibited a greater total area infested by MPB than expected. Although open slopes and plains occupied a large proportion of the landscape, in 2004–2005 they had proportionally less area infested than would be than would be expected by random chance. Landscape features including mountain tops or high ridges, midslope ridges or small hills in plains, upland drainages or headwaters, and upper slopes or mesas each contained fewer infestations across the landscape in all 3 years. Incidentally these areas also contained less susceptible habitat (Table 2).

The spatial point process regression models incorporating the most important landscape features from exploratory contingency tests indicated that increased intensities of infestation were associated with canyons or deeply incised streams and local ridges or hills in valleys in 2005, midslope ridges or small hills in plains in 2004 and 2006, open slopes in 2006, and U-shaped valleys in all 3 years (Table 3). In all 3 years, the presence of highly susceptible habitat was positively correlated with infestation intensity. In 2004, canyons or deeply incised streams were associated with lower densities of MPB.

After accounting for the effects of landscape features, we found, not surprisingly, that the intensity of infestations decreased with distance from the reference line drawn parallel to the crest of the Rocky Mountains (see "Statistical methods", step 2). Furthermore, there were fewer patches of beetle killed trees at higher elevations after taking the effects of landscape features and distance from the Rocky Mountains into account. Beetle control tactics appeared to be efficacious in minimizing local spread of MPBs from infestations established in the previous year. The intensity of infestations decreased with increasing distance from treatment sites in the previous year for both 2005 and 2006 (Table 3).

Influence of feature orientation on establishment patterns

In 2004 and 2005, the initial years of invasion, information on orientation of landscape features did not explain the location of MPB infestations as well as simply knowing the type of landscape feature and its location within the research area, as indicated by lower AIC values for the latter models ($\Delta AIC_{2004} = 63$;

Table 3 Multiple regression equations estimating the density of discrete beetle infestations as a function of landscape features, topography, distance from a source line, habitat susceptibility, and distance from control tactics in the previous year, 2004–2006, in the Peace River region of British Columbia

Year	Model parameters	Estimate (m)	Standard error (m)	*Z*	*P*-value	Model AIC
2004	Intercept	−7.82	7.92E−02	−98.7	<0.0001	311,275
	Distance from reference line	−5.03E−05	4.95E−07	−101.6	<0.0001	
	Canyons, deeply incised streams	−0.30	3.68E−02	−8.1	<0.0001	
	Midslope ridges, small hills in plains	0.60	4.11E−02	14.4	<0.0001	
	U-shaped valleys	0.22	2.69E−02	8.3	<0.0001	
	Elevation	−3.85E−03	5.36E−05	−71.8	<0.0001	
	Highly susceptible habitat	1.55	2.86E−02	54.1	<0.0001	
2005	Intercept	−8.76	7.44E−02	−117.7	<0.0001	355,544
	Distance from reference line	−3.96E−05	5.85E−07	−67.7	<0.0001	
	Canyons, deeply incised streams	0.14	3.23E−02	4.3	<0.0001	
	Local ridges, hills in valleys	0.82	0.20	4.1	<0.0001	
	U-shaped valleys	0.39	2.42E−02	16.0	<0.0001	
	Elevation	−2.39E−03	4.58E−05	−52.1	<0.0001	
	Highly susceptible habitat	0.89	2.96E−02	30.0	<0.0001	
	Distance from 2004 control tactics	−9.91E−05	1.46E−06	−67.9	<0.0001	
2006	Intercept	−11.60	4.22E−02	−275.4	<0.0001	1,011,290
	Distance from reference line	−5.44E−06	2.67E−07	−20.4	<0.0001	
	Midslope ridges, small hills in plains	0.45	2.42E−02	18.6	<0.0001	
	Open slopes	0.28	1.23E−02	22.9	<0.0001	
	U-shaped valleys	0.20	1.83E−02	11.2	<0.0001	
	Elevation	−1.18E−03	2.49E−05	−47.2	<0.0001	
	Highly Susceptible Habitat	0.98	1.90E−02	51.3	<0.0001	
	Distance from 2005 control tactics	−5.31E−05	7.79E−07	−68.2	<0.0001	

Log(λ) is the response variable for each model, where λ is the density of sites successfully attacked by MPB populations per square meter. For example, in 2004, the estimated density of beetle patches at sites 5 km from a line of reference parallel to the crest of the Rocky Mountains, in a canyon at 1,500 m elevation and in highly susceptible habitat would be $\exp^{(-7.82\ +\ 5000\ \times\ -0.0000503\ +\ -0.0296\ +\ 1500\ \times\ -0.00385\ +\ 1.55)}$ or 0.034 infestations per hectare or one patch of tree-killing beetles every 30 ha

$\Delta AIC_{2005} = 230$). This changed in 2006, however. Persistence of tree killing populations of *D. ponderosae* in the Peace River region in 2006 was associated with certain landscape features that commonly exhibited a southwest orientation ($\Delta AIC_{2006} = -7$). Interestingly, a southwest orientation was common for all three landscape features included in the 2006 model (Table 4). For 2006, southwestern slopes of midslope ridges or small hills in plains, southwest facing open slopes, and U-shaped valleys that run in a northeast–southwest cardinal direction, parallel to the assumed direction of beetle flight, positively influenced intensity. As previously established by initial models lacking feature orientation, elevation and distance from the northwestern edge of the research area, i.e., relative location, were inversely correlated to intensity of *D. ponderosae* infestations while distance from highly susceptible habitat was positively correlated. The intensity of infestations decreased with increasing distance from treatment in the previous year.

Discussion

Our results demonstrate not only that specific landscape features are associated with establishment of an invading organism, but that orientation of those landscape features can provide insight into continued spread and persistence of that organism. Initially, as

Table 4 Multiple regression equations estimating density of *D. ponderosae* infestations replacing the coefficient of landscape feature in Table 3 with a specialized coefficient that reflects the best-fitting orientation of the feature (see "Statistical methods", step 3)

Year	Model parameters	Estimate (m)	Standard error (m)	*Z*	*P*-value	ΔAIC[a]
2004	Intercept	−7.97	5.80E−02	−137.4	<0.0001	63
	Distance from reference line	−4.99E−05	4.23E−07	−117.9	<0.0001	
	Local ridges: west	1.06	0.45	2.4	0.00870	
	Midslope ridges: southwest	1.11	8.66E−02	12.8	<0.0001	
	U-shaped valleys: northeast–southwest	0.50	2.92E−02	17.2	<0.0001	
	Elevation	−3.72E−03	4.44E−05	−84.0	<0.0001	
	Highly susceptible habitat	1.58	2.84E−02	55.6	<0.0001	
2005	Intercept	−8.17	5.79E−02	−141.1	<0.0001	230
	Distance from reference line	−4.24E−05	5.31E−07	−79.8	<0.0001	
	Canyons/deeply incised streams: north–south	0.14	4.97E−02	2.7	0.00653	
	Local ridges/hills in valleys: south	1.00	0.38	2.6	0.00860	
	U-shaped valleys: northeast–southwest	0.17	2.84E−02	5.9	<0.0001	
	Elevation	−2.70E−03	3.97E−05	−67.9	<0.0001	
	Highly susceptible habitat	0.91	2.96E−02	30.7	<0.0001	
	Distance from 2004 treatment	−1.01E−04	1.46E−06	−69.0	<0.0001	
2006	Intercept	−0.12	3.67E−02	−312.2	<0.0001	7
	Distance from reference line	−6.04E−06	2.48E−07	−24.4	<0.0001	
	Midslope ridges/small hills in plains: southwest	0.76	5.28E−02	14.4	<0.0001	
	Open slopes: southwest	0.52	2.33E−02	22.4	<0.0001	
	U-shaped valleys: northeast–southwest	0.30	2.31E−02	12.6	<0.0001	
	Elevation	−1.19E−03	2.31E−05	−51.6	<0.0001	
	Highly susceptible habitat	0.97	1.90E−02	50.9	<0.0001	
	Distance from 2005 treatment	−5.40E−05	7.80E−07	−69.3	<0.0001	

Data are for the years 2004–2006 in the Peace River region of British Columbia. Other variables are the same as in Table 3

[a] Change in AIC compared to analogous model with full landscape feature in Table 3. Model explains the data the best if ΔAIC > 2 (Arnold 2010)

MPB crossed the Rocky Mountains into new areas of the province of British Columbia in western Canada, the majority of infestations were found on southeast/west facing ridges and in canyons and valleys, the latter of which could have been acting as conduits for further dispersal. By 2006, increased densities of infestations of MPB were consistently associated with mid-slope ridges, small hills, and open slopes that were primarily facing in a southwest direction.

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

An alternative explanation for increased associations of MPB with southwestern slopes, not mutually exclusive to the first, is that additional episodes of aeolian dispersal may have deposited higher numbers in the Peace River region on southwestern slopes, as wind is strongly unidirectional and blows from the west and southwest (Holt and Eaton 2008). MPB tend to accumulate on windward sides of barriers, as large insects (i.e., those with bodies greater than a 4 or 5 mm^2 surface area, like MPB) are less likely to be carried over top of a barrier to enter circulating leeward eddies because of their great inertia (Lewis and Dibley 1970). Hills that are relatively close to each other will also increase the amount of deposition on the windward slope of consecutive hills (Goossens 1996). However, given that features with a southwest orientation did not exhibit a positive association until 2 years after the initial range expansion event, it is more probable that site micro-climate difference between aspects caused the observed association as infestations established on these aspects would have spread more readily into adjacent stands.

In our study, as in others (e.g., Preisler and Mitchell 1993; Bentz and Munson 2000; Fettig et al. 2006; Nelson et al. 2006; Fettig et al. 2007; Trzcinski and Reid 2008) anthropogenic interventions against tree-killing eruptive herbivores decreased occurrences of infestations in the year following treatment. Management activities included single tree treatments using fall and burn, and harvesting of stands infested with MPB. These control tactics decrease the potential for short-distance dispersal to adjacent stands (Trzcinski and Reid 2008). Treatments may have been efficacious in this region potentially due to relatively low rates of increase among populations as a whole, either due to temperature or high levels of competition. Attacked hosts within the research area were noted to have greater than optimal levels of attack (i.e., 62 attacks/m^2; Raffa and Berryman 1983) resulting in lower per capita reproductive rates due to intraspecific competition (Safranyik and Carroll 2006).

The SSI has been an important planning and operational tool in the management of MPB populations in British Columbia over the past two decades (Shore et al. 2000). While the goal of our study was not to conduct a comparison among rating classes in a new landscape, our results indicate that, at minimum, the highest susceptibility rating scheme provides excellent inference on the population of tree-killing bark beetles in this system. While much research remains to be done concerning factors that mediate survival and spread in the boreal forest (Safranyik et al. 2010), our results suggest that components of the SSI, such as climatic suitability, will be important predictors in characterizing future range expansion.

In summary, our results indicate that, following the initial invasion event, the continuing spread of the MPB may potentially be facilitated by low-elevation valleys aligned along the dominant wind direction, acting as conduits of suitable habitat for the insect (e.g. Robertson et al. 2009). The orientation of landscape features also affects the probable establishment of MPB, either by influencing the susceptibility of hosts or by allowing populations on warmer and drier sites to have greater reproductive rates facilitating spread into adjacent stands. We note that simplification of polygonal data that potentially span more than one landscape feature into point forms characterized by one feature could bias our conclusions, although the majority of infestations during the invasion events were quite small, reducing the likelihood of such potential errors. Our statistical approach and these results may be of particular value in formulating management strategies as the insect progresses eastward through the boreal forests of Canada, or in other areas where the insect is at epidemic population phases, such as regions of the southern Rocky Mountains of Colorado. Predicting the potential spread of new infestations based on landscape features and their orientation, particularly low-lying valleys, in concert with new landscape-scale spread modeling approaches (e.g., Gamarra and He 2008; Zheng and Aukema 2010) may provide additional coarse-scale tools for directing control activities.

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