



Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate

Brian H. Aukema, Allan L. Carroll, Yanbing Zheng, Jun Zhu, Kenneth F. Raffa, R. Dan Moore, Kerstin Stahl and Stephen W. Taylor

B. Aukema (Brian.Aukema@nrca.gc.ca), Natural Resources Canada, Canadian Forest Service, Univ. of Northern British Columbia, 2019 Administration Building, 3333 University Way, Prince George, BC, Canada, V2N 4Z9. – A. Carroll and S. Taylor, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC, Canada, V8Z 1M5. – Y. Zheng, Dept of Statistics, Univ. of Kentucky, 873 Patterson Office Tower, Lexington, KY 40506, USA. – J. Zhu, Dept of Statistics, Univ. of Wisconsin, Medical Science Center, 1300 Univ. Ave., Madison, WI 53705, USA. – K. Raffa, Dept of Entomology, Univ. of Wisconsin, 345 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA. – R. D. Moore, Dept of Geography and Dept of Forest Resources Management, Univ. of British Columbia, Room 225, 1984 West Mall, Vancouver, BC, Canada, V6T 1Z2 – K. Stahl, Dept of Geography, Univ. of British Columbia, 1984 West Mall, Vancouver, BC, Canada, V6T 1Z2.

Insect outbreaks exert landscape-level influences, yet quantifying the relative contributions of various exogenous and endogenous factors that contribute to their pattern and spread remains elusive. We examine an outbreak of mountain pine beetle covering an 800 thousand ha area on the Chilcotin Plateau of British Columbia, Canada, during the 1970s and early 1980s. We present a model that incorporates the spatial and temporal arrangements of outbreaking insect populations, as well as various climatic factors that influence insect development. Onsets of eruptions of mountain pine beetle demonstrated landscape-level synchrony. On average, the presence of outbreaking populations was highly correlated with outbreaking populations within the nearest 18 km the same year and local populations within 6 km in the previous two years. After incorporating these spatial and temporal dependencies, we found that increasing temperatures contributed to explaining outbreak probabilities during this 15 yr outbreak. During collapse years, landscape-level synchrony declined while local synchrony values remained high, suggesting that in some areas host depletion was contributing to population decline. Model forecasts of outbreak propensity one year in advance at a 12 by 12 km scale provided 80% accuracy over the landscape, and never underestimated the occurrence of locally outbreaking populations. This model provides a flexible approach for linking temperature and insect population dynamics to spatial spread, and complements existing decision support tools for resource managers.

The spatiotemporal distributions of insect populations that erupt from low densities to outbreaks are affected by many factors, such as predators, pathogens, resource availability, habitat heterogeneity, climate, and dispersal. Teasing apart the relative contributions of these factors presents numerous biological and statistical challenges, however. For example, descriptive statistics (e.g. Ripley's K, Moran's I, autocorrelation functions) provide "snapshots" of spatial or temporal patterns, but do not provide inference into processes that drive them. Inference can be derived by modeling progression of the observed pattern, but space-time modeling presents unique challenges. First, as with any modeling exercise, the selection of variables is nontrivial. Environmental variables are frequently correlated, hence inference on a specific factor may be spurious if a correlated variable is driving the process (Wiens 1989, Aukema et al. 2005a). Second, simple "classical" linear regression models that improperly assume independence among spatially- or temporally-dependent observations risk biasing estimates

of the significance of model parameters (Legendre 1993, Knapp et al. 2003). Third, regression models that incorporate spatial or temporal effects explicitly, such as autoregressive models, may be computationally intensive (Augustin et al. 1996, He et al. 2003).

The mountain pine beetle is an eruptive herbivore that intermittently kills mature pines over large areas. In western North America, almost all pines may serve as hosts, although lodgepole pine *Pinus contorta* Douglas var. *latifolia*, is considered the primary host (Wood 1963, Furniss and Schenk 1969, Amman and Cole 1983). During outbreaks, insects colonize trees via pheromone-mediated mass attacks that, in concert with vectored fungi, collectively exhaust host defenses (Safranyik et al. 1975, Raffa and Berryman 1983). Females select host trees, and attract males via pheromones emitted while boring through the bark into the phloem. Females deposit eggs in niches along ovipositional galleries under the bark. Larvae develop through four instars, mining the phloem tissue and girdling the tree.

Development is typically univoltine and is highly temperature dependent: temperature thresholds for larvae ensure overwintering of predominantly cold-tolerant (i.e. late larval) life stages, and temperature thresholds for pupation and emergence of the adults in late summer ensure synchronicity necessary for successful tree colonization (Bentz et al. 1991, Powell et al. 2000).

Northwestern North America has experienced 4 or 5 outbreaks of mountain pine beetle over the past century (Safranyik 2004, Taylor et al. 2006). Currently, the provinces of Alberta and British Columbia in Canada are experiencing the largest mountain pine beetle outbreak on record, with mortality to mature lodgepole pine extending over a 9.2 million ha area in 2006. In a previous study, we examined the role of land tenure factors in the origin and spatiotemporal spread of this outbreak (Aukema et al. 2006). However, many other factors affect the onset, propagation, and duration of outbreaks, such as summer temperatures, insect overwintering ability, and dispersal.

In this paper, we examine such factors within the previous large-scale outbreak of mountain pine beetle in British Columbia, Canada, which occurred over an area known as the Chilcotin Plateau. The Chilcotin Plateau extends eastward from the Coast Mountains to the Fraser River, and is bounded to the north and south by the Nechako Plateau and Bridge River, respectively. The Coast Mountains block Pacific moisture, resulting in a much drier climate than coastal British Columbia. Temperatures range from $< -40^{\circ}\text{C}$ in winter to $> 30^{\circ}\text{C}$ in summer. Due to a combination of factors such as low site productivity, a smaller outbreak in the 1930s, and the effects of surface fires and/or historical fire suppression, the Plateau consisted primarily of lodgepole pine forests in age classes susceptible to mountain pine beetle by the early 1980s (Taylor and Carroll 2004). Here, we examine the outbreak from its endemic beginnings through the collapse period (1972–1986). We examine the contributions of temperature, through carefully selected variables that reflect aspects of the insects' phenology and development, and the spatial and temporal arrangements of neighboring mountain pine beetle populations, to the probability of local outbreaks. The model, conditioned on climatic data from 1972–1983, is used to forecast the extent of future outbreaks (1984–1986). Finally, we examine how spatial synchrony of these insects at local and regional scales changes with rise and collapse of the outbreak.

Methods

Study area and data preparation

We laid a grid of 469 cells averaging ca 12×12 km in size over the Chilcotin Plateau (Fig. 1). Cells were demarcated by dividing one degree latitude by one degree longitude into 5 (E–W) \times 10 (N–S) cells. The total study area measured 7 191 199 ha. The average elevation across the study region was 1345 m.

Tree mortality due to mountain pine beetle was estimated from aerial survey maps of the Forest Insect and Disease Survey (FIDS) performed by the Canadian Forest Service (1972–1986). Aerial survey maps are useful

proxies of mountain pine beetle abundance, as these insects generally kill their host tree to reproduce. Foliage of killed trees fades to red within twelve months (Safranyik et al. 1974), becoming visually apparent to aerial sketch mappers. Maps were digitized using ArcGIS (ESRI 2005) (Albers projection, NAD83) and intersected with the grid cells, so each cell contained a value of percent area killed by mountain pine beetle, for each year.

There are important limitations to consider when working with aerial survey data. To contend with potential survey bias (e.g. inclusion of unsuitable habitat and/or compensation for increased red vs green visual apparency), correction factors were implemented as described by Aukema et al. (2006). In brief, the percentages of pine stands killed within each polygon area were multiplied by 5, 20, or 30% depending on their classifications (low, medium, or severe ratings). This step was only included as a “best practice”, as the measure did not change the locations of polygons and had no bearing on our binary (presence/absence) response variable. Another potential limitation with survey data is the inability to preclude alternative causes of tree death without extensive ground-truthing. For this data set, however, there is no evidence of extensive mortality to lodgepole pine by causes other than mountain beetle during the selected years of study (i.e. no other causes were detected by FIDS). Spatial location errors are likely the greatest concern with sketch-mapped data, but

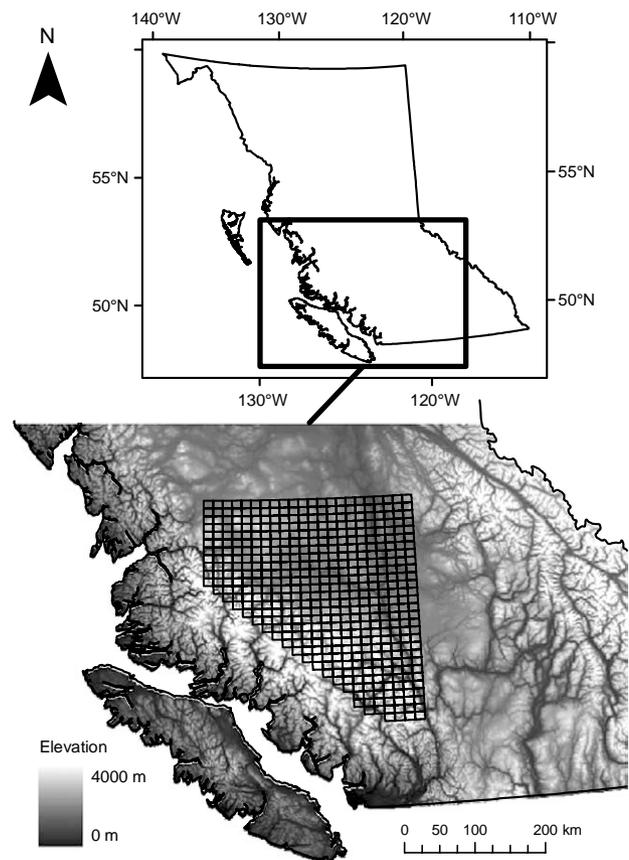


Figure 1. Map of lower British Columbia, Canada. Shaded areas indicate elevation. Grid indicates study area over the Chilcotin Plateau.

no errors were identified post-digitization and orthorectification. Finally, the relationship between mapped “red attack” and absolute insect populations is likely nonlinear. For example, in this paper, though we may term early years (e.g. 1972–1979) as “endemic” or “incipient”, we note that we are referring to a few locally outbreaking populations, since truly endemic populations may not kill enough trees to become visually apparent from the air. Despite these potential limitations, aerial survey data are useful for examining population trends at the landscape level (Aukema et al. 2006).

Statistical analysis

We used a spatial-temporal autologistic regression model to examine factors responsible for the spread of outbreaking mountain pine beetle populations (i.e. those that reached sufficient levels to kill trees). The response variable was a binary response: presence/absence of mountain pine beetle red attack anywhere in the cell for a given year. In brief, an autologistic model combines use of the response variable as a covariate (i.e. “auto” meaning “self”) with logistic regression (i.e. binary responses). In this case, the response variable was adapted to define spatial and temporal covariates (Table 1) to reflect biological properties of insect proliferation and dispersal. Temporal variables were individual cell responses, lagged by one and more years. Spatial effects were summed individual cell 0/1 values

within a given spatial neighborhood for that year. First-order neighborhoods encompassed the nearest four cells (N, S, E, W), while second-order neighborhoods encompassed the nearest eight cells by including the diagonals.

The regression also included climatic variables, defined according to known biology and phenology of the insect and a pioneering landscape ecology model of Safranyik et al. (1975). In model fitting, degree day variables for egg hatch (ddeg) and heat accumulation for univoltine development to next flight (dd) were included within two newly defined covariates incorporating the products of the variables P1a (0/1 indicator for conditions of 50% egg hatch before winter being met) and P1b (0/1 indicator for sufficient heat accumulation for univoltine development being met), i.e. $P1a \times P1b \times dd$ and/or $P1a \times P1b \times ddeg$. This ensured that degree day information was used if and only if both conditions of 50% egg hatch before winter (P1a) and sufficient heat accumulation (P1b) were met.

The density of climate stations was less than the resolution of the study grid (Fig. 1), so the available stations were used to interpolate daily temperature data for each cell over the region. In a previous application in British Columbia, the interpolation scheme, derived from that used in the DAYMET model (Thornton et al. 1997, Hasenauer et al. 2003), produced overall mean absolute errors of $<2^{\circ}\text{C}$ for both daily maximum and minimum temperatures (Stahl et al. 2006a). Details of the interpolation algorithm are provided in Supplementary material,

Table 1. Candidate variables for autologistic regressions examining the probability of an outbreaking population of mountain pine beetle in a 12×12 km cell on the Chilcotin Plateau of British Columbia, 1972–1986.

Variable type	Variable	Explanation and rationale
Temporal	lag1	Presence/absence of mountain pine beetle in a cell the previous year.
	lag 2	Same, two years previous.
	lag 3	Same, three years previous.
Spatial	1st nbhd	First-order neighborhood (nearest four neighbours).
	2nd nbhd	Second-order neighborhood (nearest eight neighbours).
	infestations	Number of discrete infestations in each cell. This differs from the response variable, the presence/absence of red attack in each cell.
Environmental	tmin	Minimum temperature over calendar year.
	tmax	Maximum temperature over calendar year.
	tmean	Mean temperature over calendar year.
	cold ^a	Number of days cold enough to cause lethal mortality to overwintering larvae, after Wygant (1940). Temperatures less extreme than -37°C can be lethal early and late in the year, and complete mortality occurs when larvae are exposed to temperatures $< -37^{\circ}\text{C}$ for short periods (Wygant 1940, Somme 1964, Stahl et al. 2006b).
	warm ^a	Mean August temperature. Development and emergence of new mountain pine beetle adults is closely governed by temperature. Peak flight occurs in a narrow window in summer (McCambridge 1971, Safranyik 1978, Safranyik and Carroll 2006).
	ddeg ^a	Accumulated degree days above 5.5°C from August to end of growing season.
	dd ^a	Accumulated degree days above 5.5°C from August in previous year to current July.
	Pl ^a	0/1 indicator variable: sufficient heat accumulation to hatch 50% of eggs before winter (306°C degree days).
	P1b ^a	0/1 indicator variable: sufficient heat accumulation to develop and emerge on a univoltine life cycle (833°C degree days).
	P2 ^a	0/1 indicator variable if minimum winter temperatures were higher than -40°C .
elevation	Mean elevation of cell, based on 25 sampled points (regular design) within cell. This may be a useful proxy for host tree distribution, as lodgepole pine do not grow at high elevations over our study area.	

^aDerived from Safranyik et al. (1975).

Appendix 1. Temperatures were interpolated to the centre of each grid cell at the 10th percentile elevation (i.e. the elevation capping the lowest 10% of the grid area). This elevation was chosen because it better represented the elevations of the pine stands in the western portions of the study domain, which includes portions of the Coast Mountains, than did the mean elevation for the grid cell. The eastern portions of the domain have less relief (Fig. 1), and the difference between the mean and 10th percentile elevations is not critical.

Model building was approached in three stages. First, we determined an appropriate spatial neighborhood structure(s) and time lag(s) to account for spatial and temporal dependencies. Second, these spatial and temporal variables were incorporated into models with only one environmental variable at a time to evaluate the effect of each covariate separately. Finally, we constructed a model using backward elimination of candidate variables from a full model. The maximum likelihood estimate of each covariate's slope coefficient (as well as the model's intercept) divided by the corresponding standard error yields a Z-ratio that provides an indication of the utility for each variable in explaining the probability of the appearance of a mountain pine beetle outbreak in a cell. High Z-ratios indicate good explanatory power. (In fact, Z-ratios exceeding a value of 1.96 could be considered a test of significance using $\alpha = 0.05$). Model comparisons were performed using Akaike's information criterion (Akaike 1973). Models with the lowest AIC values are judged to fit the best. Details of the statistical model and inference are provided in Supplementary material, Appendix 2.

Synchrony among mountain pine beetle populations was examined using smoothed nonparametric spatial covariance functions (snf function in package ncf v1.08, available from <<http://onb.ent.psu.edu>>; (Bjørnstad et al. 1999, Bjørnstad and Falck 2001)) within R v2.1 (Ihaka and Gentleman 1996, R Development Core Team 2006). In brief, these functions allow examination of decay in spatial correlation of fluctuating, spatially-referenced populations, from local to wider regional scales, by calculating correlations for all pairs of time series at numerous distances and then fitting a smoothing spline. Local synchrony is defined as the average correlation between time series as the distance approaches zero, while regional synchrony is the average correlation across the study area. We used the midpoints of our grid cells as spatial reference points, so local synchrony is an estimate at the shortest distance between grid cell centroids (ca 12 km; synchrony as distance approaches zero would equal 1). We examined the time series for each cell in two ways. First, we examined the overall synchrony of the buildup and collapse of the entire outbreak (1972–1986). Second, we examined the synchrony of the outbreak in 6 yr periods, incremented by one year each time, for a total of 10 windows (i.e. 1972–1978, 1973–1979, . . . , 1980–1986). Similar temporal windows were used in previous work and capture sufficient population processes to examine changing spatial dependencies through outbreak formation, progression, and collapse phases (Aukema et al. 2006). The covariance function, and hence estimates of regional synchrony, was evaluated to distances of 300 km, within the reliable estimation range of approximately two-thirds the distance across the study area (435 km) (Isaaks and

Srivastava 1989). Confidence intervals about the covariance function, estimates of local and regional synchrony, and differences between the latter were estimated using a bootstrap resampling technique with 1000 replications (Efron and Tibshirani 1993, Bjørnstad and Falck 2001).

Results

Overview of the outbreak

In 1972, surveyors mapped 33 discrete areas of tree mortality covering 476 ha over the Chilcotin Plateau (Fig. 2A). These areas exceeded >100 000 ha by 1980. By 1985, the outbreak tallied 10 000 areas of mature lodgepole pine mortality covering 700 000 ha. Although the total area infested (measured from survey polygons prior to overlaying on a grid) did not increase rapidly until the early 1980s, the proportion of cells with mountain pine beetle outbreak activity increased steadily throughout the 1970s (Fig. 2B). The outbreak collapsed by 1986.

Factors important to describing the spread of mountain pine beetle populations

In the first stage of model-building, we confined our examination to the spatial and temporal arrangements of insect populations, without environmental covariates (Table 2). The probability of a mountain pine beetle outbreak in a cell was best described by the presence of

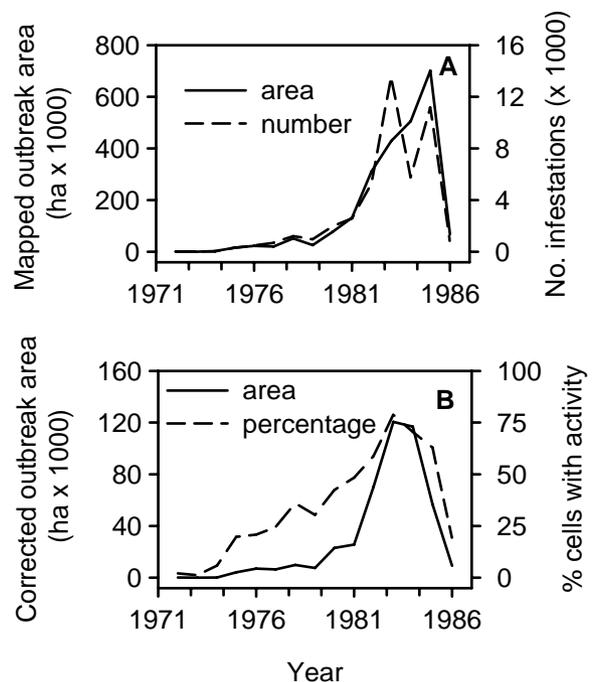


Figure 2. Area and number of discrete outbreaking populations of mountain pine beetle over the Chilcotin Plateau of British Columbia, 1972–1986 (A). Summary of polygon data from aerial sketch mapping of Forest Insect and Disease Survey (B). Polygon area corrected as in Aukema et al. (2006). These data form the basis of analyses.

Table 2. Summaries of autoregressive logistic models restricted to different spatial and temporal terms to examine the probability of occurrence of a mountain pine beetle outbreak in a 12 × 12 km cell on the Chilcotin Plateau of British Columbia, 1972–1986.

Model	Intercept	Spatial neighborhood		Temporal lag (yr 3)			AIC
		1st order	2nd order	1	2	3	
1	-3.38	1.61		0.51			3984.18
2	-3.37	1.59		0.50	0.10		3937.46
3	-3.38	1.60		0.54	0.23	-0.22	3977.99
4	-3.41	1.72	-0.10	0.55			3971.61
5	-3.38	1.73	-0.13	0.49	0.07		3989.20
6	-3.42	1.71	-0.10	0.54	0.24	-0.22	3953.92
7	-0.29						7684.20

Parameter estimates are maximum likelihood estimates. Lowest AIC indicates best model. Model 7, for comparison, contains no spatial or temporal terms.

outbreaking populations within the nearest 4 cells (i.e. distances of ca 18 km from the center of a cell) and outbreaking populations in the previous two years within the cell, according to the AIC values. These spatial and temporal terms were then incorporated into models with one environmental covariate at a time.

Each environmental covariate from Table 1 provided some inference on whether an outbreaking population would be detected (Table 3). In general, outbreak probability decreased with the number of severe cold days, or increases in elevation. Outbreak probability increased with any one of the quantitative temperature variables (i.e. minimum, maximum, or mean temperatures, as well as degree-day indices). Outbreak probability also increased with the number of discrete areas of mortality in a cell, even though the spatial term for presence/absence of mountain pine beetle outbreak activity in a local neighborhood was already contained in the model.

We finally included all environmental variables in a broader analysis to select the best possible model, displayed in Table 4. A back-transformation of the odds ratio from the intercept of this model (i.e. $e^{-3.768}/(1 + e^{-3.768})$) indicates that the baseline probability of finding an outbreaking population in a cell in a given year is 2.3% for the Chilcotin outbreak. The final model contains terms for all environmental covariates except maximum temperature.

Table 3. Summaries of autoregressive logistic models restricted to single environmental covariates (in addition to 1st order spatial and lag-1 and lag-2 temporal terms) to examine the probability of occurrence of a mountain pine beetle outbreak in a 12 × 12 km cell on the Chilcotin Plateau of British Columbia, 1972–1983.

Variable	MLE	SE	Z-ratio	Sign
cold	-0.018	0.0072	-2.52	-
P1a × P1b × dd	2.3×10^{-4}	4.9×10^{-5}	4.70	+
P1a × P1b × ddegg	0.0006	0.0001	4.96	+
tmax	0.021	0.0069	2.97	+
tmean	0.051	0.0138	3.72	+
tmin	0.007	0.0042	1.71	+
warm	0.022	0.0072	3.13	+
P2	0.079	0.0496	1.59	+
elevation	-2.3×10^{-4}	0.0001	-3.09	-
infestations	0.007	0.0053	1.37	+

Variable definitions are provided in Table 1. Parameter summaries include the maximum likelihood estimates (MLE) and the corresponding standard errors (SE). Sign summarizes whether the variable increases or decreases outbreak probability if inference was restricted to that term.

The highest Z-ratio was for the spatial neighborhood term, indicating that the proximity of mountain pine beetle outbreaks in neighboring cells is the best predictor of a cell to contain an outbreaking population. The presence of outbreaking populations in a cell within the previous two years also contributed to detecting outbreak populations.

The climatic variables with the highest Z-ratios in this model include “cold” and “warm”, both of which exceeded an absolute value of 1.96 and could be considered statistically significant in a hypothesis testing framework. The probability of outbreak is inversely related to the number of severe cold days, and increases with a term for mean August temperature when the beetles are most active. The remaining variables, even though they have “low” Z-ratios, are useful to the model as the model selection criterion, AIC, balances model complexity with explanatory ability. Outbreak probability increases with increasing degree day accumulation and minimum temperature, and decreases with increasing elevation. In contrast to the models with single environmental covariates (Table 3), our full model (Table 4) indicates that outbreak probability decreases with increasing mean temperature and winters without lethal cold temperatures (i.e. signs for coefficients “tmean” and “P2” changed from positive to negative).

Table 4. Summaries of the best autoregressive logistic model to examine the probability of occurrence of a mountain pine beetle outbreak in a 12 × 12 km cell on the Chilcotin Plateau of British Columbia, 1972–1983.

Variable	MLE	SE	Z-ratio	Sign
intercept	-3.768	0.5203	-7.23	-
cold	-0.033	0.0114	-2.87	-
P1a × P1b × dd	1.4×10^{-4}	0.0002	0.83	+
P1a × P1b × ddegg	4.3×10^{-4}	0.0004	0.99	+
tmean	-0.088	0.0524	-1.68	-
tmin	0.003	0.0108	0.27	+
warm	0.036	0.0162	2.24	+
P2	-0.056	0.0742	-0.76	-
elevation	-7.1×10^{-5}	0.0001	-0.60	-
infestations	0.006	0.0075	0.74	+
1st order neighborhood	1.452	0.0550	32.29	+
temporal lag 1	0.700	0.1038	6.74	+
temporal lag 2	0.502	0.1083	4.63	+

Variable definitions are provided in Table 1. Parameter summaries include the maximum likelihood estimates (MLE) and the corresponding standard errors (SE). Sign summarizes whether the variable increases or decreases outbreak probability, given all other terms in the model. The AIC for this model is 3098.13.

Forecasting outbreaks

As a tool to validate the final model, we can compare predictions to actual aerial survey maps and determine the percentage of cells classified correctly. Given the parameter values of the final fit with data from 1972 to 1983 (Table 4), we predict the outbreaks of mountain pine beetle in all cells for the year 1984, and then continue from these predictions for two additional years. This exercise results in one, two, and three year forecasts (post 1983, the last year of data provided to the model) for the years 1984, 1985, and 1986, shown in Fig. 3. The output of the model for the outbreak risk in each cell at a given time point is a probability distribution, from which can be quantified a mean predicted risk and associated measure of spread. A summary of the forecasts is provided in Table 5.

The predictive accuracy on 12×12 km cells across the 7.2 million ha study area for our model was 78.0% for 1984 (one year forecast), 69.0% for 1985 (two year forecast), and 30.5% for 1986 (three year forecast). The model never underestimated the number of cells with outbreak activity. In both 1984 and 1985, there was an environmental perturbation of lethal temperatures in the autumn that aided in suspension of the Chilcotin outbreak (Stahl et al. 2006b). While our model predicted 384 outbreaks in 1986, only 74 were recorded.

Landscape and regional synchrony

Not surprisingly, synchrony declined with distance (Fig. 4). Local outbreaking populations exhibited very high correlation in synchrony (0.82), while the region-wide synchrony during the outbreak was 0.30. The correlations between grid cells with outbreaking populations were always positive, even when separated by distances of up to 300 km.

We also examined how synchrony might change at local vs regional scales for different phases of the outbreak by estimating the covariance function for different temporal windows (Table 6). Landscape-level synchrony declined as the outbreak collapsed, while local synchrony started to increase earlier than the outbreak collapse. In the incipient years of the outbreak, 1972–1982, local synchrony was ca 0.6. This value increased to 0.8 during the highest epidemic years and outbreak collapse (i.e. years 1983–1986). The region-wide synchrony exhibited an opposite pattern, however. This is illustrated by the difference between the local and regional synchrony, which increased during the last three years (Table 6). From peak outbreak years to outbreak collapse, outbreaking populations exhibited increasingly similar characteristics at local rather than regional scales.

Discussion

The most striking feature of the mountain pine beetle outbreak on the Chilcotin Plateau is the strong spatial and temporal dependencies at small scales (< 18 km) (Table 4: spatial coefficient Z-ratio, 32.3; temporal coefficient Z-ratios, 6.7 and 4.6). These dependencies indicate the prevalence of positive feedback in a system where insects

gain the ability to colonize live trees at high densities, essentially engineering their resource (Raffa and Berryman 1983, Økland and Berryman 2004, Økland and Bjørnstad 2006) possibly due in part to density-dependent effects involving competitors or fungi that may mediate population phase transitions (Aukema et al. 2005b, Sallé et al. 2005, Safranyik and Carroll 2006). Thus, after incorporating temperature and elevational variation as covariates, the predominant factors contributing to the propagation of mountain pine beetle outbreaks are proximate, simultaneously outbreaking populations. Such populations either erupt from endemic populations in situ, or may be founded by dispersal from nearby outbreaking, source populations. These processes cannot be distinguished solely by examination of air photo patterns, as similar patterns may arise from multiple, confounding processes (Aukema et al. 2006). The most parsimonious explanation for such strong spatial and temporal dependence, given the spatial and temporal extent of the outbreak used for our model, is dispersal. If localized increases were primarily responsible for outbreaks, the observed landscape-level pattern would have been a more uniform rise in outbreaking populations at spatially disjunct locations, as evidenced in southern areas of the province in the current outbreak (Aukema et al. 2006). The importance of dispersal to the spread of epidemic populations is supported by beetle presence in novel habitats in north-eastern British Columbia (Safranyik and Carroll 2006), examination of spatio-temporal data in west-central British Columbia in the current outbreak (Aukema et al. 2006), mesoscale atmospheric transport models (Jackson et al. 2005), within-stand dispersal studies (Safranyik et al. 1992), observations of bark beetles on snowfields (Furniss and Furniss 1972), and isolated populations in previous outbreaks arising instantaneously 300 km from the nearest source (Cerezke 1989).

Temperature is the most important climatic factor considered here affecting outbreak progression, after accounting for spatial and temporal dependence that may be attributed to the effects of dispersal (and/or incipient eruptions) (Table 4). Temperature primarily affects two different aspects of insect biology: flight and colonization, and larval development. First, increased August temperatures contributed to outbreak formation (Z-ratio for “warm” coefficient of 2.24). Increased temperatures during this flight period may provide a shorter, more synchronized flight period leading to increased mass-attack success (Safranyik and Carroll 2006). Further, increased summer temperatures may provide indirect benefits to the herbivores by water-stressing potential host trees, thereby decreasing their resistance. Second, the low number of lethally cold days during the winter contributed to increased annual survivorship (Z-ratio for “cold” coefficient of -2.87). Larval mortality is strongly temperature dependent, with winter being the most critical time (Wygant 1940). The outbreak occurred following the well-documented 1976–1977 shift in the Pacific Decadal Oscillation (Mantua et al. 1997), which was associated with warmer winters and fewer occurrences of potentially lethal temperatures, and ended following early autumnal cold snaps in 1984 and 1985 (Safranyik and Linton 1991), during winters associated with strongly negative Arctic Oscillation indices (Stahl et al. 2006b).

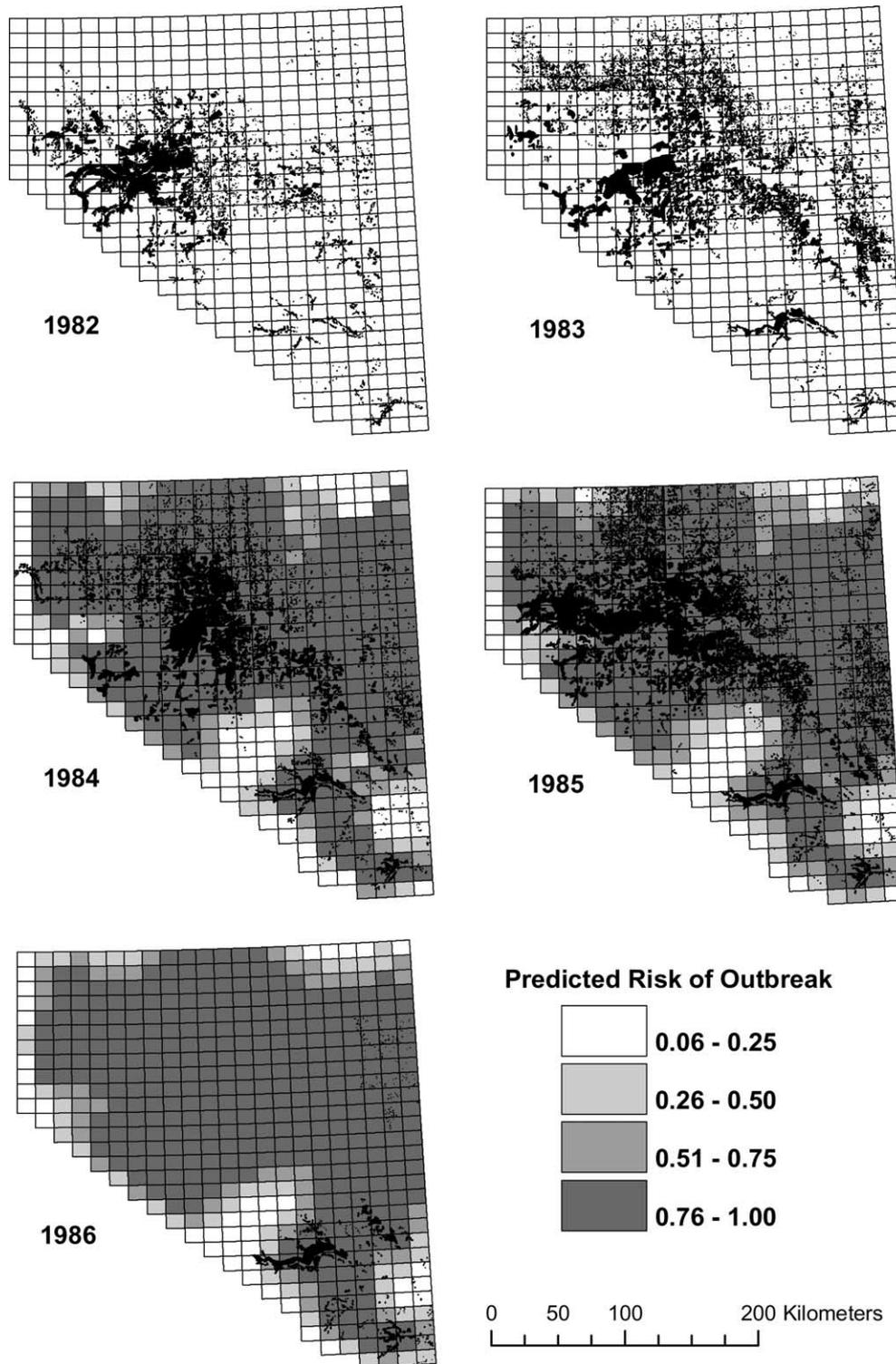


Figure 3. Comparison of forecasted outbreak probabilities for 1984, 1985, and 1986 using model in Table 4 to actual mapped infestations (black areas) on the Chilcotin Plateau of British Columbia, Canada. The model output provides a probability distribution from which a mean probability can be quantified. For ease of presentation, this mean predicted risk of outbreak for each cell is classified into one of four different outbreak probability categories. Mapped outbreaks for years 1982 and 1983 are provided for reference, as spatial arrangements of outbreaking populations on the lattice for those years influence predictions for 1984 onward via spatial neighbourhood and temporal lag terms.

Both flight/host procurement and overwintering/larval development benefit from increasing temperatures. This is particularly worrisome given current climate change scenarios

(Logan and Bentz 1999, Williams and Liebhold 2000, Carroll et al. 2004). It is well documented that temperature may generate spatial synchrony in similar density-dependent

Table 5. Predictions of the numbers of 12 × 12 km cells containing mountain pine beetle outbreaking populations on the Chilcotin Plateau of British Columbia, Canada, given climatic effects and spatial and temporal arrangements of outbreaking insect populations, from forecast of model in Table 4. The model provides a unique probability distribution of the outbreak risk for each cell. The mean of each distribution has been classified into four categories (low, moderate, high, extreme) for ease of presentation. Actual numbers are provided for model validation.

Year	Validation ^a	Risk of outbreak				Totals	
		Low 0–25%	Moderate 25–50%	High 50–75%	Extreme 75–100%	High + extreme (P > 50%)	All actual outbreaks
1984	Predicted risk	58	32	46	333	379	330
	Actual outbreaks	16	11	22	281	303	
1985	Predicted risk	46	39	57	327	384	295
	Actual outbreaks	9	19	35	232	267	
1986	Predicted risk	41	44	48	336	384	91
	Actual outbreaks	5	12	11	63	74	

^aValidation is the tally of the number of cells with predicted risk in the four categories compared to the number of cells experiencing actual outbreaks within each category. The number of cells across the predicted risk category sums to the study total, $n = 469$, while the total cells experiencing outbreaks is less than that.

populations over large regions, i.e. the Moran effect (Moran 1953, Liebhold et al. 2004). This effect may be even more pronounced when populations are linked by local or long-distance dispersal (Paradis et al. 1999), such as in mountain pine beetle (Peltonen et al. 2002). Such dispersal is dependent upon critical temperature thresholds in most eruptive insect herbivores, which could introduce further positive feedback into such systems by linking subpopulations (Moser and Dell 1979, Safranyik et al. 1992).

Some temperature variables displayed opposing signs between the single covariate models (Table 3) and the full model (Table 4). Examples include terms for mean temperature, and P2, the presence of minimum winter temperatures higher than -40°C . This contradiction may be indicative of nonlinear, indirect effects of temperature that are difficult to express with our coarse variables (Logan and Powell 2001). The contradiction may also be due to collinearity among variables. For instance, the number of days with lethal cold temperatures and the presence/absence of winter temperatures higher than -40°C (i.e. variables

“cold” and “P2” in Table 1), are highly correlated. In such cases of conflicting signs, we expect that inference may be derived from known insect biology and the effect studied in the single covariate model (Table 3). Although conflicting signs may occur in the full model, the goal of the full model is more prediction of the overall distribution of insect outbreaks given all covariates than inference from each covariate.

The predictive accuracy of our model approached 80% for a one year forecast. This high predictive capacity is surprising for two reasons. First, the primary purpose of the model was regression (i.e. examining the effects of various factors on outbreak propensity). The strong spatial and temporal autocorrelation identified provided an unexpected benefit for predicting future outbreaks as well. It is well documented that strong spatial dependence occurs within stands as local populations “switch” their attacks from focal to nearby trees in early stages of outbreak formation (Geiszler and Gara 1978, Mitchell and Preisler 1991, Powell et al. 1998). However, understanding the mechanisms behind emerging spatiotemporal dependence in population phase transitions, informed by phenomological models (Logan et al. 1998), remains the subject of current research. Quantifying such dependence would allow better forecasting and integration of processes across scales. The predictive capacity of our model is also surprising because it lacks information on host quality or abundance or management activities, since detailed annual estimates are not available. Host resources are an important factor in bark beetle dynamics (Coulson 1979, Raffa and Berryman 1983, Økland and Bjørnstad 2006). We have attempted to use elevation as a proxy for host abundance/susceptibility, as the outbreaks have historically occurred between 800 and 1400 m in British Columbia (Taylor et al. 2006). Host depletion during the late outbreak and collapse phases was evidenced by the disparities between local and region-wide synchrony trends (Table 6). At local scales (i.e. inside 18 km), populations were rising or falling together as hosts may have been depleted, resulting in a lower display of synchrony over the region as a whole (i.e. > 300 km) during the terminal years.

Likely host depletion, combined with environmental perturbations of cold autumnal temperatures (Stahl et al.

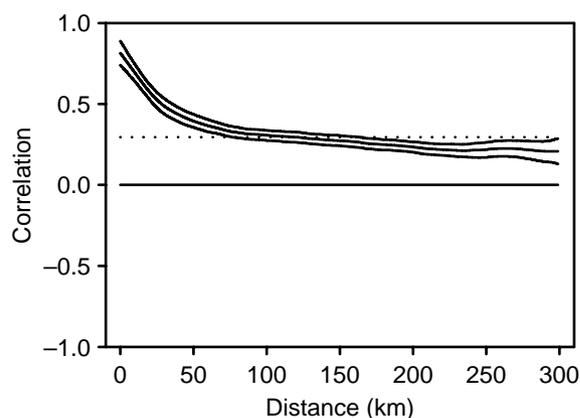


Figure 4. Nonparametric spatial covariance functions on tree mortality due to mountain pine beetle on the Chilcotin Plateau of British Columbia, Canada, 1972–1983. Y-axis represents correlation among presence/absence of mountain pine beetle outbreaking populations, as a function of distance (x-axis). Solid lines are covariance functions with 95% confidence intervals based on 1000 bootstrap replications. Dashed line indicates average synchrony across region.

Table 6. Spatial synchrony of tree mortality caused by mountain pine beetle on grid cells 12 × 12 km in size over the Chilcotin Plateau, British Columbia, Canada, estimated by nonparametric spatial covariance functions.

Temporal window	Local		Regional		Difference ^a	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
1972–1986	0.82	(0.74,0.89)	0.30	(0.27,0.32)	0.52	(0.44,0.60)
1972–1977	0.66	(0.44,0.85)	0.25	(0.20,0.30)	0.41	(0.20,0.61)
1973–1978	0.57	(0.39,0.77)	0.25	(0.20,0.30)	0.32	(0.12,0.51)
1974–1979	0.51	(0.34,0.67)	0.12	(0.09,0.17)	0.38	(0.21,0.55)
1975–1980	0.58	(0.43,0.72)	0.22	(0.17,0.28)	0.36	(0.19,0.53)
1976–1981	0.65	(0.51,0.78)	0.26	(0.21,0.31)	0.39	(0.26,0.54)
1977–1982	0.69	(0.58,0.80)	0.23	(0.18,0.27)	0.46	(0.34,0.58)
1978–1983	0.82	(0.72,0.90)	0.47	(0.41,0.53)	0.35	(0.24,0.44)
1979–1984	0.81	(0.72,0.90)	0.33	(0.29,0.37)	0.48	(0.38,0.58)
1980–1985	0.80	(0.71,0.88)	0.17	(0.14,0.20)	0.63	(0.54,0.71)
1981–1986	0.82	(0.74,0.90)	0.18	(0.15,0.21)	0.64	(0.56,0.73)

^aDifference between estimates of local and regional synchrony (see Methods).

2006b), coincided with the periods for which we were predicting outbreaks two- and three- years in advance (i.e. 1985 and 1986). These phenomena contributed to the decreasing predictive accuracy of our model (69 and 30% for two- and three-year forecasts). Even though the model contains coefficients for cold temperatures, the behaviour of the outbreak over the previous 10+ years, i.e. the time period on which the model was conditioned, indicated that terms for spatial and temporal dependence (reflective of building and dispersing populations) are the more critical factors (i.e. higher Z-ratios in Table 4). At the same time, it is possible that certain aerial survey correction factors, such as removing “grey attack” areas (Aukema et al. 2006) may have resulted in survey estimates that were too conservative. Retaining these areas, in which small outbreaking populations may have persisted, may have resulted in higher predictive accuracies. The fact that predictive accuracy ranged from 30 to 78% (over different time spans) yet never underestimated outbreak activity suggests that our covariates are fairly accurate predictors, but also that additional conditions must be met for populations of mountain pine beetle to erupt because the error was always in one direction.

Many modeling approaches have been used to study mountain pine beetle outbreaks, from simulation studies to spatial and aspatial process models (Powell et al. 1996, 1998, Barclay et al. 2005) at different scales (Thompson 1991, Safranyik et al. 1999, Riel et al. 2004). Our model presents a complementary tool for such decision support systems, in that it directly optimizes parameters using likelihood techniques, fully conditioned by previously observed data. Due to the generality of our approach and the strong space-time autocorrelation, forecasting is easily facilitated. It would not be difficult, for example, to recondition and/or extend this model to other areas of the current outbreak in the provinces of British Columbia and Alberta. Our approach may provide another useful tool in resource management and implementing strategies to mitigate the effects of eruptive herbivores.

Acknowledgements – This study was supported by funds from the Mountain Pine Beetle Initiative of Natural Resources Canada 7.05, Canadian Forest Service, the Government of Canada’s Climate Change Impacts and Adaptation Program via Grant

A676, the Ministry of Water, Land, and Air Protection via Contribution Agreement TBIO4025, and the British Columbia Forest Science Program grant Y081277. The authors thank the pilots and surveyors involved in the Forest Insect and Disease Survey. James Floyer, UBC, assisted with compilation of the climatic data and programming of the weather interpolation model, and Francis Wu, UBC, assisted with processing digital elevation data. Sandra Allen, Hollie Moore, and Honey Giroday, CFS and UNBC, provided technical assistance. The authors appreciate the insightful comments of three reviewers.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. – In: Petrov, B. N. and Csadki, F. (eds), 2nd International symposium on information theory. Akademiai Kiado, pp. 267–281.
- Amman, G. D. and Cole, W. E. 1983. Mountain pine beetle population dynamics in lodgepole pine forests. Part II: population dynamics. – USDA FS Intermountain Forest and Range Experiment Station General Technical Report INT-145.
- Augustin, N. H. et al. 1996. An autologistic model for the spatial distribution of wildlife. – *J. Appl. Ecol.* 33: 339–347.
- Aukema, B. H. et al. 2005a. Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the great lakes region: effects of weather and predators over short time scales. – *Popul. Ecol.* 47: 61–69.
- Aukema, B. H. et al. 2005b. Quantifying sources of variation in the frequency of fungi associated with spruce beetles: implications for hypothesis testing and sampling methodology in bark beetle-symbiont relationships. – *For. Ecol. Manage.* 217: 187–202.
- Aukema, B. H. et al. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. – *Ecography* 29: 427–441.
- Barclay, H. J. et al. 2005. Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability. – *Can. Entomol.* 137: 566–583.
- Bentz, B. J. et al. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera, Scolytidae) and simulation of its phenology. – *Can. Entomol.* 123: 1083–1094.

- Bjørnstad, O. N. and Falck, W. 2001. Nonparametric spatial covariance functions: estimation and testing. – *Environ. Ecol. Stat.* 8: 53–70.
- Bjørnstad, O. N. et al. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. – *Trends Ecol. Evol.* 14: 427–432.
- Carroll, A. L. et al. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. – In: Shore, T. L. et al. (eds), *Challenges and solutions. Proc. of the Mountain Pine Beetle Symp.*, Kelowna, BC, Canada October 30–31, 2003, Information Report BC-X-399, Canadian Forest Service, Pacific Forestry Centre, pp. 223–232.
- Cerezke, H. F. 1989. Mountain pine beetle aggregation semi-chemical use in Alberta and Saskatchewan, 1983–1987. – In: Amman, G. D. (ed.), *Proc. from the Symp. on the management of lodgepole pine to minimize losses to the mountain pine beetle*, Kalispell, Montana July 12–14, 1988, USDA Forest Service, Intermountain Research Station, Ogden, UT. General Technical Report INT-262.
- Coulson, R. N. 1979. Population dynamics of bark beetles. – *Annu. Rev. Entomol.* 24: 417–447.
- Efron, B. and Tibshirani, R. J. 1993. *An introduction to the bootstrap*. – Chapman and Hall.
- Furniss, M. M. and Schenk, J. A. 1969. Sustained natural infestations by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. – *J. Econ. Entomol.* 62: 518–519.
- Furniss, M. M. and Furniss, R. L. 1972. Scolytids (Coleoptera) on snowfields above timberline in Oregon and Washington. – *Can. Entomol.* 104: 1471–1478.
- Geiszler, D. R. and Gara, R. I. 1978. Mountain pine beetle attack dynamics in lodgepole pine. – In: Berryman, A. A. et al. (eds), *Forest insect and disease research/theory and practice of mountain pine beetle management in Lodgepole Pine Forests Symp. Forest Wildlife and Range Experiment Station, Univ. of Idaho and USDA Forest Service*, pp. 182–187.
- Hasenauer, H. et al. 2003. Validating daily climate interpolations over complex terrain in Austria. – *Agricult. For. Meteorol.* 119: 87–107.
- He, F. L. et al. 2003. Autologistic regression model for the distribution of vegetation. – *J. Agricult. Biol. Environ. Stat.* 8: 205–222.
- Ihaka, I. and Gentleman, R. 1996. R: a language for data analysis and graphics. – *J. Comput. Graph. Stat.* 5: 299–314.
- Isaaks, E. H. and Srivastava, R. M. 1989. *Applied geostatistics*. – Oxford Univ. Press.
- Jackson, P. L. et al. 2005. Modeling beetle movement by wind. – *Bull. Am. Meteor. Soc.* 86: 28–29.
- Knapp, R. A. et al. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. – *Ecol. Appl.* 13: 1069–1082.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – *Ecology* 74: 1659–1673.
- Liebholt, A. et al. 2004. Spatial synchrony in population dynamics. – *Annu. Rev. Ecol. Syst.* 35: 467–490.
- Logan, J. A. and Bentz, B. J. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. – *Environ. Entomol.* 28: 924–934.
- Logan, J. A. and Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). – *Am. Entomol.* 47: 160–173.
- Logan, J. A. et al. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. – *Theor. Popul. Biol.* 53: 236–255.
- Mantua, N. J. et al. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. – *Bull. Am. Meteor. Soc.* 78: 1069–1079.
- McCambridge, W. F. 1971. Temperature limits of the flight of mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). – *Ann. Entomol. Soc. Am.* 64: 534–535.
- Mitchell, R. G. and Preisler, H. K. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. – *For. Sci.* 37: 1390–1408.
- Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. – *Aust. J. Zool.* 1: 291–298.
- Moser, T. C. and Dell, T. R. 1979. Predictors of southern flight beetle activity. – *For. Sci.* 25: 217–222.
- Økland, B. and Berryman, A. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. – *Agricult. For. Entomol.* 6: 141–146.
- Økland, B. and Bjørnstad, O. N. 2006. A resource-depletion model of forest insect outbreaks. – *Ecology* 87: 283–290.
- Paradis, E. et al. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. – *Ecol. Lett.* 2: 114–120.
- Peltonen, M. et al. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. – *Ecology* 83: 3120–3129.
- Powell, J. et al. 1998. Theoretical analysis of “switching” in a localized model for mountain pine beetle mass attack. – *J. Theor. Biol.* 194: 49–63.
- Powell, J. A. et al. 1996. Local projections for a global model of mountain pine beetle attacks. – *J. Theor. Biol.* 179: 243–260.
- Powell, J. A. et al. 2000. Seasonal temperature alone can synchronize life cycles. – *Bull. Math. Biol.* 62: 977–998.
- R Development Core Team. 2006. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, <<http://www.R-project.org>>.
- Raffa, K. F. and Berryman, A. A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). – *Ecol. Monogr.* 53: 27–49.
- Riel, W. G. et al. 2004. A spatio-temporal simulation of mountain pine beetle impacts. – In: Shore, T. L. et al. (eds), *Challenges and solutions. Proc. of the Mountain Pine Beetle Symp.*, Kelowna, BC, Canada October 30–31, 2003, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, NRC Research Press, pp. 106–113.
- Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. – In: Kibbee, D. L. et al. (eds), *Theory and practice of mountain pine beetle management in lodgepole pine forests. Symp. Proc. Univ. of Idaho*, pp. 77–84.
- Safranyik, L. 2004. Mountain pine beetle epidemiology in lodgepole pine. – In: Shore, T. L. et al. (eds), *Challenges and solutions. Proc. of the Mountain Pine Beetle Symp.*, Kelowna, BC, Canada October 30–31, 2003, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, NRC Research Press, pp. 33–40.
- Safranyik, L. and Linton, D. A. 1991. Unseasonably low fall and winter temperatures affecting mountain pine beetle and pine engraver populations and damage in the British Columbia Chilcotin Region. – *J. Entomol. Soc. BC* 88: 17–21.
- Safranyik, L. and Carroll, A. L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. – In: Safranyik, L. and Wilson, B. (eds), *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine*. Natural Resources Canada, pp. 3–66.
- Safranyik, L. et al. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. – Canadian Forest Service Tech. Report 1.
- Safranyik, L. et al. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. – In: Baumgartner, D. M. (ed.), *Management of Lodgepole Pine Ecosystems Symp. Proc.*, Washington State Univ. Cooperative Extension Service, pp. 406–428.

- Safranyik, L. et al. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. – *J. Appl. Entomol.* 113: 441–450.
- Safranyik, L. et al. 1999. A population dynamics model for the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae). – Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-386 35.
- Sallé, A. et al. 2005. Fungal flora associated with *Ips typographus*: frequency, virulence, and ability to stimulate the host defence reaction in relation to insect population levels. – *Can. J. For. Res.* 35: 365–373.
- Somme, L. 1964. Effect of glycerol on cold hardiness in insects. – *Can. J. Zool.* 42: 87–101.
- Stahl, K. et al. 2006a. Comparison of approaches for spatial interpolation of daily air temperature in a large region with complex topography and highly variable station density. – *Agricult. For. Meteorol.* 39: 224–236.
- Stahl, K. et al. 2006b. Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. – *Clim. Res.* 32: 13–23.
- Taylor, S. W. and Carroll, A. L. 2004. Disturbance, forest age dynamics, and mountain pine beetle outbreaks in BC: a historical perspective. – In: Shore, T. L. et al. (eds), *Challenges and solutions. Proc. of the Mountain Pine Beetle Symp.*, Kelowna, BC, Canada October 30–31, 2003, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, NRC Research Press, pp. 41–51.
- Taylor, S. W. et al. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. – In: Safranyik, L. and Wilson, B. (eds), *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine.* Natural Resources Canada, pp. 67–94.
- Thompson, A. J. 1991. Simulation of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) spread and control in British Columbia. – Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-329.
- Thornton, P. E. et al. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. – *J. Hydrol.* 190: 214–251.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 385–397.
- Williams, D. W. and Liebhold, A. M. 2000. Spatial synchrony of spruce budworm outbreaks in eastern North America. – *Ecology* 81: 2753–2766.
- Wood, S. L. 1963. A revision of bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). – *Great Basin Nat.* 23: 1–117.
- Wygant, N. D. 1940. Effects of low temperature on the Black Hills beetle (*Dendroctonus ponderosae* Hopk.). – Summary of Ph.D. thesis submitted to New York School of Forestry, on file at USDA Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Download the Supplementary material as file E5453 from www.oikos.ekol.lu.se/appendix.