Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak

Brian H. Aukema, Allan L. Carroll, Jun Zhu, Kenneth F. Raffa, Theodore A. Sickley and Stephen W. Taylor

Eruptive herbivores can exert profound landscape level influences. For example, the ongoing mountain pine beetle outbreak in British Columbia, Canada, has resulted in mortality of mature lodgepole pine over >7 million ha. Analysis of the spatio-temporal pattern of spread can lend insights into the processes initiating and/or sustaining such phenomena. We present a landscape level analysis of the development of the current outbreak. Aerial survey assessments of tree mortality, projected onto discrete 12×12 km cells, were used as a proxy for insect population density. We examined whether the outbreak potentially originated from an epicenter and spread, or whether multiple localized populations erupted simultaneously at spatially disjunct locations. An aspatial cluster analysis of time series from 1990 to 2003 revealed four distinct time series patterns. Each time series demonstrated a general progression of increasing mountain pine beetle populations. Plotting the geographical locations of each temporal pattern revealed that the outbreak occurred first in an area of west-central British Columbia, and then in an area to the east. The plot further revealed many localized infestations erupted in geographically disjunct areas, especially in the southern portion of the province. Autologistic regression analyses indicated a significant, positive association between areas where the outbreak first occurred and conservation lands. For example, the delineated area of west-central British Columbia is comprised of three conservation parks and adjacent working forest. We further examined how population synchrony declines with distance at different population levels. Examination of the spatial dependence of temporal synchrony in population fluctuations during early, incipient years (i.e. 1990–1996) suggested that outbreaking mountain pine beetle populations are largely independent at scales >200 km during non-epidemic periods. However, during epidemic years (i.e. 1999–2003), populations were clearly synchronous across the entire province, even at distances of up to 900 km. The epicentral pattern of population development can be used to identify and prioritize adjacent landscape units for both reactive and proactive management strategies intended to minimize mountain pine beetle impacts.

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In forest systems, certain insects undergo region-wide population eruptions that impact landscape-level processes, such as nutrient cycling and ecological succession (McCullough et al. 1998), and likewise exert immense economic and sociopolitical impact (Holmes 1991). Population eruptions exhibit both temporal and spatial patterns over landscapes. Long-term temporal patterns can reveal whether the insect's eruptions are predominantly periodic (Myers 1998) or intermittent (Werner and Holsten 1983, Bakke 1989, Eisenhart and Veblen 2000, Alfaro et al. 2004). The spatial configurations of insect populations can provide insight into how outbreaks develop. Insect populations may erupt from an epicenter that then spreads, or from multiple simultaneous eruptions that coalesce (Johnson et al. 2004). Knowledge of temporal and spatial patterns may offer insights into processes driving insect outbreaks, and are valuable in prioritizing areas for appropriate management tactics. This is especially important in areas where land-use objectives may conflict, such as in parks/protected areas vs working forests. During the previous century, the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae), has reached epidemic levels 4–5 times in north-western North America (Taylor and Carroll 2004). The last outbreak in the 1980s caused mortality over ≈ 1.84 million ha of mature pine forests in western Canada. In recent years, mountain pine beetle populations have again increased to outbreak levels and killed pine over a ≈ 7.1 million ha region between 1999 and 2005 in British Columbia alone. This insect can breed within virtually all *Pinus* spp. in western North America (Wood 1963, Furniss and Schenk 1969, Amman and Cole 1983). However, based on the frequency, size, and severity of infestations, lodgepole pine *Pinus contorta* var. *latifolia*, is considered the insect's primary host. Trees that are between 60 and 160 yr are the most susceptible, as phloem thickness is generally the limiting factor in successful reproduction once host defenses are overcome (Amman 1972). Beetles colonize trees via a pheromone-mediated mass attack that effectively exhausts host defenses (Safranyik et al. 1975, Raffa and Berryman 1983). Additionally, fungi vectored by beetles rapidly invade tree tissues, and these might compromise expression of tree defenses (Safranyik et al. 1975). Females select hosts, and are joined by males as they bore through the bark into the phloem tissue. Mated females oviposit in niches chewed along vertical galleries. Following eclosion, larvae mine circumferentially around the bole, developing through four instars. The beetles typically overwinter as late-instar larvae, before completing development to adults during the following spring (Reid 1962). Development is temperature-dependent, which helps synchronize emergence and dispersal, and thus mass attack, in mid-summer for most populations (Evenden et al. 1943, Reid 1962, Bentz et al. 1991, Powell et al. 2000).

Extensive studies have investigated factors that facilitate increases in mountain pine beetle populations at the scales of trees and stands. Generally, these factors either act directly on the beetle, such as moderate winter temperatures that minimize overwintering mortality, or indirectly through reductions in tree defenses brought about by abiotic or biotic injury or stress, such as drought (e.g. Safranyik et al. 1975, Raffa and Berryman 1983). However, other than theoretical models (Logan et al. 1998), few studies have evaluated mountain pine beetle activity at the scale of landscapes (Perkins and Roberts 2003, McIntire 2004).

In this paper, we examine two aspects of the current mountain pine beetle outbreak in British Columbia. First, we investigate the spatial pattern of outbreak development. We investigate whether one specific origin can be detected, or whether the data suggest that the outbreak has originated from multiple, coalescing point sources. Further, we investigate whether outbreak locations are associated with parks and protected lands, i.e., areas of little to no historical management for eruptive insects due to access and/or value-based decisions (although important exceptions exist). Second, we examine the scales at which temporal synchrony is spatially dependent among the buildup and subsequent outbreak years. Specifically, we consider: does synchrony decline with distance? At what distance are population fluctuations independent? Does spatial dependence vary anisotropically, i.e. directionally? Such insights may be valuable in understanding what processes, such as dispersal, may lead to population spread at different scales over a landscape.

In this paper, we use the term "incipient years" for the period 1990–1996, in which 9mountain pine beetle populations were increasing across the province. "Epidemic years" include 1999–2003. We recognize that studies confined to individual forest districts, for example, may reveal localized outbreaks during incipient years, but our focus is at the provincial level. We use the term "epicenter" as an area in which the outbreak first occurred, as manifested by spatially concentrated visible mortality. This term does not imply that such areas are necessarily more favorable places for survival during endemic periods. We use the term "conservation areas" synonymous with "parks and protected natural areas." This is meant to avoid potential confusion regarding the term "protected." That is, lands are excluded from commercial activities of extraction of natural resources, and not "protected" in the sense of potential safeguarding forests from insects by aerial application of pesticides.

Methods

Data collection and processing

We delineated a study area in British Columbia that encompasses most mountain pine beetle infestations in the current outbreak. The area extended from the southern provincial border, 49°N, to 57°N, north of Fort St. John. The eastern border comprises the Rocky Mountains (i.e. the provincial boundary), while the western border corresponds to a line over the Coastal Mountains from ca 122°W to 130°W. This excludes habitats deemed largely unsuitable for mountain pine beetle outbreaks, such as Pacific maritime and boreal forests (although previous outbreaks have encompassed small areas within these excluded regions, e.g. Collis and Alexander 1966). This study area, 53 392 412 ha, was divided into 3 630 grid cells. Grid cells were demarcated by dividing one degree latitude by one degree longitude into 5 (E − W) × 10 (N–S) cells across the study area. On average, cells were 1.47×10^8 m^2 in size, or ca 12 × 12 km.

We estimated mortality due to mountain pine beetle from annual aerial survey maps of the Forest Insect and Disease Survey performed by the Canadian Forest Service (1990–1996) and the British Columbia Ministry of Forests (1999–2003). (Unfortunately, province-wide mapping was not performed during 1997–1998.) Each year, an aerial survey of the entire province was conducted, and areas of tree mortality, judged from red and/or grey crowns, were recorded on 1:250 000 NTS topographic maps (see Taylor and Carroll 2004). Because foliage of trees killed by mountain pine beetle fades to red within one year (Safranyik et al. 1974), such monitoring, in concert with ground-truthing, provides a useful record of mountain pine beetle activity at the landscape level.

The maps were digitized using ArcGIS (Anon 2004a) (Albers projection, NAD83). Surveyors assign each outbreak area a severity code: low (1–10% of stands killed), medium (11–29%), and severe (30%+). We implemented corrections proposed by colleagues developing the British Columbia Mountain Pine Beetle model for outbreak projections (Eng et al. 2004), and multiplied the infestation areas by the midpoints of the severity classes for low and medium and 30% for severe. This reduces potential observation errors of infestation extent, such as inclusion of unsuitable habitat, or overestimation of mortality due to the higher visual perceptibility of red foliage (Eng et al. 2004). These corrections ensured that in areas of heavy infestations, estimates of mortality do not exceed the total area of the grid cell over a three-year course of infestation. We excluded areas of grey trees (i.e. ≥3 yr post-infestation) from the analyses. The infestation polygons were overlaid onto grid cells such that each cell contained a value of percent area infested by mountain pine beetle for each year.

These values formed the bases of all analyses. Data processing was performed using AML macros in ArcInfo (Anon 2004a) and programming in R (Ihaka and Gentleman 1996, Anon 2004b).

Information on stands susceptible to mountain pine beetle was obtained from the 1990 provincial Forest, Recreation, and Range Resource Analysis (Anon 1995). We define susceptible stands as those ≥60 yr of age (Safranyik et al. 1975) and ≥60% pine composition. These inventory data were used to quantify the amount of susceptible hosts within parks/protected areas vs working forests in 1990; i.e. the beginning of the temporal window studied. We do not include annual estimates of host availability into our spatiotemporal analyses of mountain pine beetle populations (described in Statistical analysis, below) for two reasons. First, annual inventories do not exist. Second, we were unable to make sufficiently reliable projections of pine on the landscape post-1990 at the same spatial resolution as mountain pine beetle activity due to estimation error. Estimation error on pine abundance is propagated through the concomitant effects of fire, stand aging, mortality due to insects and disease, and management and salvage practices.

Statistical analysis

To estimate whether the current outbreak originated from a point source or rather erupted in multiple locations, we used cluster analysis techniques for time series (Swanson and Johnson 1999, Williams and Liebhold 2000, Okland and Bjornstad 2003). In brief, the time series of percent mortality due to mountain pine beetle for each grid cell were compared to one another aspatially, and split into k clusters based on similarity of each of k time-series patterns. The cluster types were then mapped back onto the study area. Examination of the resulting spatial pattern(s) may then provide insights into the process(es) driving the pattern(s), although it is recognized that different unique and/or simultaneous processes may yield similar patterns. For example, if dispersal is a significant process, one might expect that time series similar in temporal pattern might be spatially proximate. Hence, if the outbreak originated from a point source and then spread, we might expect a "bullseye" pattern in cluster types with outer rings exhibiting time lags in mortality. If the outbreak had multiple simultaneous origins, we might expect a spatial "checkerboard" pattern.

All data analyses were performed using R. We used and compared both hierarchical (mva package) and non-hierarchical (MASS package) clustering techniques. In agglomerative hierarchical techniques, a sorting algorithm or linkage method first groups similar time series and then successively merges similar resulting groups,

producing a dendrogram. There are a variety of linkage methods (Venables and Ripley 2002). The spatial patterns when remapping k clusters were similar for all methods; hence, we only report those obtained using Ward's minimum variance method. Choosing the most appropriate number of k clusters to map is partially subjective, and often a "moderate" number is selected (Johnson and Wichern 1982). To inform our decision, we used two non-hierarchical cluster methods: K-means (MacQueen 1967) and non-metric multidimensional scaling (Kruskal 1964a,b). Mapping clusters obtained by the K-means methods were similar to that of hierarchical clustering, so are not reported. In non-metric multidimensional scaling, the best number of clusters is chosen based on the "elbow" of a stress plot. A stress plot examines stress, which is a quantitative measure of the goodness of fit, vs the number of dimensions, which are representations that try to match the observed distances between every pair of N items in q dimensional space (Kruskal 1964a, Cox and Cox 2001, Venables and Ripley 2002). Grid cells with no mountain pine beetle activity were excluded from these analyses.

We identified the region where the outbreak first occurred (i.e. the epicenter; see Results), and tested whether this region had a greater association with conservation areas than each of the other regions characterized by the distinct time series patterns. When hypothesis testing in regression frameworks, it is critical to contend with any violations of model assumptions, such as independence when using spatially correlated data, which may subsequently bias test results (e.g. Legendre et al. 2002). Because the mapped regions were of different spatial arrangements and sizes (i.e. the area where the outbreak first occurred was the smallest and quite contiguous; see Results), we adjusted for differences in sample size and potential spatial dependencies as follows. For cells of a given non-epicenter time series pattern, the same number of cells as contained in the epicenter was sampled from an area 100×60 km (comparable to the size of the epicenter; see Results). If there were not enough cells of the required pattern type in the area, the entire sample was discarded and a new area and sample was chosen. This sample was then pooled with the cells from the epicenter. An autologistic regression was performed in which the response was a Bernoulli trial of cell association with a time series characteristic of the epicenter (i.e. one if so, and zero otherwise. All zero cells were of another specific type of time series pattern, depending on the comparison of interest). The predictors were a binary indicator variable of conservation area (i.e. one if present any-where in cell, and zero otherwise) and a first-order spatial neighborhood term to contend with spatial' autocorrelation. A Bayesian model with a flat prior was used for inference of the model parameters. Monte Carlo samples from the posterior distribution of the

model parameters were generated using a Metropolis-Hastings algorithm. Based on the posterior distributions, we constructed 95% credible intervals for the model parameters. A positive coefficient for the conservation area term that does not overlap zero indicates that conservation lands are more significantly associated with the time series characteristic of the epicenter than with the other time series. This test was performed 100 times with new resamples, possibly with replacement, for each comparison to a different time series type.

To estimate the scale at which mountain pine beetle populations operate synchronously, we examined smoothed nonparametric covariance functions in R (sncf function in package ncf, available from < http:// onb.ent.psu.edu >;; Bjornstad et al. 1999, Bjornstad and Falck 2001). The covariance function used the midpoint of each grid cell as the spatial reference. We examined the spatial dependence of synchrony for two time periods characterizing the building or incipient years (1990–1996) when elevated populations of mountain pine beetle were first detected in BC, and outbreak or epidemic years (1999–2003) during which time populations expanded dramatically. The maximum distance was set at 900 km, since estimates near the maximum distance in the study area (1 370 km) may be poor (Isaaks and Srivastava 1989). Confidence intervals around the covariance function were constructed using a bootstrap resampling technique with 1 000 replications (Efron and Tibshirani 1993, Bjornstad and Falck 2001). Due to elevational variation such as mountains, we might expect the spatial covariance to vary with direction. Hence, we also examined anisotropic nonparametric spatial covariance functions, using the reprojections of the data onto eight intervals from $0°$ (N–S) to $180°$ (i.e. $0°$–$22.5°$, etc.). Distance for these analyses was truncated to 600 km, again to avoid problems of tail bias (Isaaks and Srivastava 1989).

Results

By 1990, British Columbia had extensive areas of mature pine available to potentially sustain mountain pine beetle outbreak populations (Taylor and Carroll 2004). Within our study area, 11.1% of the land had stands considered susceptible to mountain pine beetle (Fig. 1A). Approximately 10.5% of the study area, 5.6×10^6 ha, fell within designated conservation areas, with historically little management activity directed against mountain pine beetle (Fig. 1B). Of these conservation areas, 8.5%, or 473 566 ha, contained susceptible pine.

Annual aerial survey maps of the mountain pine beetle outbreak in British Columbia are shown in Fig. 2, for 1990–1996 (incipient years) and 1999–2003 (epidemic years). During the incipient years, a total of 64 974 infestations averaging 4.3 ha in size were mapped, with

A.
Susceptible pine

B.
Conservation areas
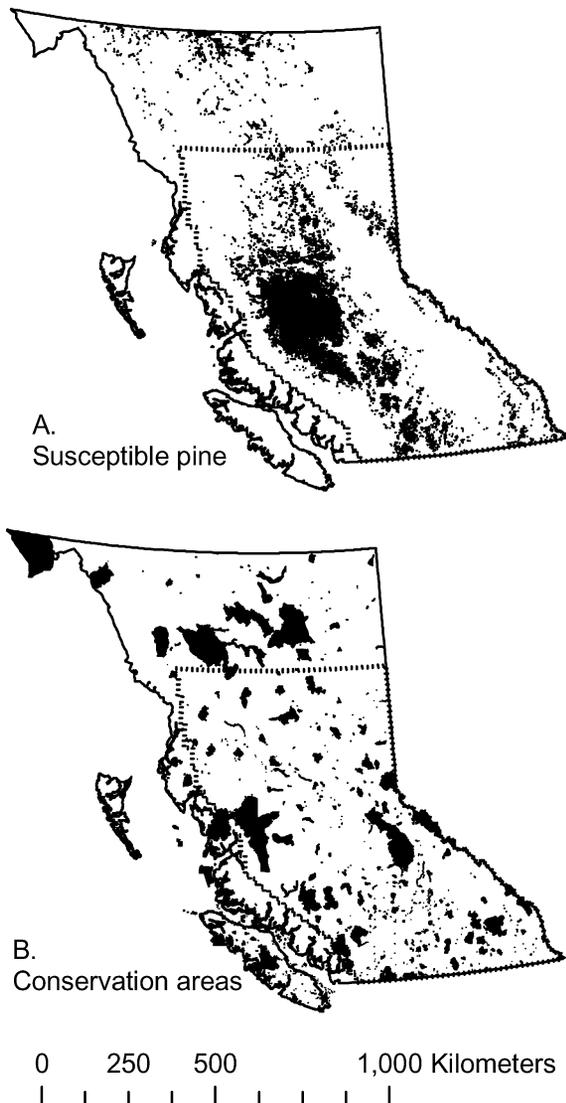
0   250   500   1,000 Kilometers

Fig. 1. Map of British Columbia, Canada. The study area, which encompasses most historical mountain pine beetle populations, is delineated by a dashed line in each figure. Stands ≥60% pine and ≥60 yr of age considered susceptible to mountain pine beetle at the start of the study, 1990. Conservation areas (parks and protected areas).

the largest encompassing 2022 ha. During the years 1999–2003, surveyors mapped 54805 infestations with an average size of 124.7 ha, with the largest encompassing an area of 162814 ha. Currently, the cumulative area affected has reached >7 million ha.

After overlaying the survey polygons on a grid and implementing corrections (see Methods), the time series of mountain pine beetle mortality within individual grid cells were divided into four distinct patterns based on the results of cluster analyses. The stress at four dimensions using multidimensional scaling (Fig. 3) is <2.5%, which indicates that four groupings are an "excellent" fit

(Kruskal 1964a). The dendrogram prepared using agglomerative hierarchical clustering also suggested the presence of four distinct clusters, as indicated by the four vertical lines intersecting the dotted cut-off line in Fig. 4. Analyses used to sort the time series into distinct patterns were performed without any knowledge of spatial location. Subsequently plotting these time series patterns on a map allows us to examine patterns of outbreak development.

What is the spatial pattern of outbreak development?

Our mapped results indicate that the current mountain pine beetle epidemic began to intensify first in an area of west-central British Columbia (Fig. 5). Two lines of evidence support this finding. First, the time series in this region, i.e. cluster type I, exhibit the earliest increase in area of tree mortality from 1999 to 2003. On average, the amount of tree mortality in each grid cell rapidly increased from 2% in 1999 to 23% of land area in 2002. In the other cluster of time series characterizing other locations (II–IV), especially cluster types II and III, the percentage of land area with mountain pine beetle-caused mortality did not begin to increase quickly until 2000 or 2001. This was a full year after the areas characterized by cluster type I. Second, it appears that the infestation had begun to decline in that region: the trend in cluster type I demonstrates a decrease in area of tree mortality, from 23% in 2002 to 15% in 2003. All other infestations, i.e. cluster types II, III, and IV, show an increasing trend in mountain pine beetle populations in 2003. The magnitude of these responses, in concert with their geographical location, suggests radial spread from an epicenter very offset from the geographical center of cluster type I. That is, the increasing pattern in cluster type II, i.e. up to 10% of pine forests killed by mountain pine beetle in 2003, directly to the east of land areas characterized by the time series pattern I, suggests spread of mountain pine beetle eastward (i.e. into the local Vanderhoof and Quesnel forest districts).

In addition to the evidence for a primary origin for the outbreak in an area of west-central British Columbia, the southern and eastern portions of the province demonstrated isolated localized increases in mountain pine beetle activity (Fig. 5). For example, there are a number of infestations of cluster type III in which 1% of the pine-dominated forests, or ca 1.5 km^2 in each grid cell, contained trees killed by mountain pine beetle by 2003. Many of these infestations are in a "checkerboard" pattern, and not in a solid block such as cluster type I. Dividing the time series into higher numbers of aspatial clusters (e.g. lowering the dashed line in Fig. 4) did not change the spatial patterns observed (results not shown). Increasing the number of time series patterns always
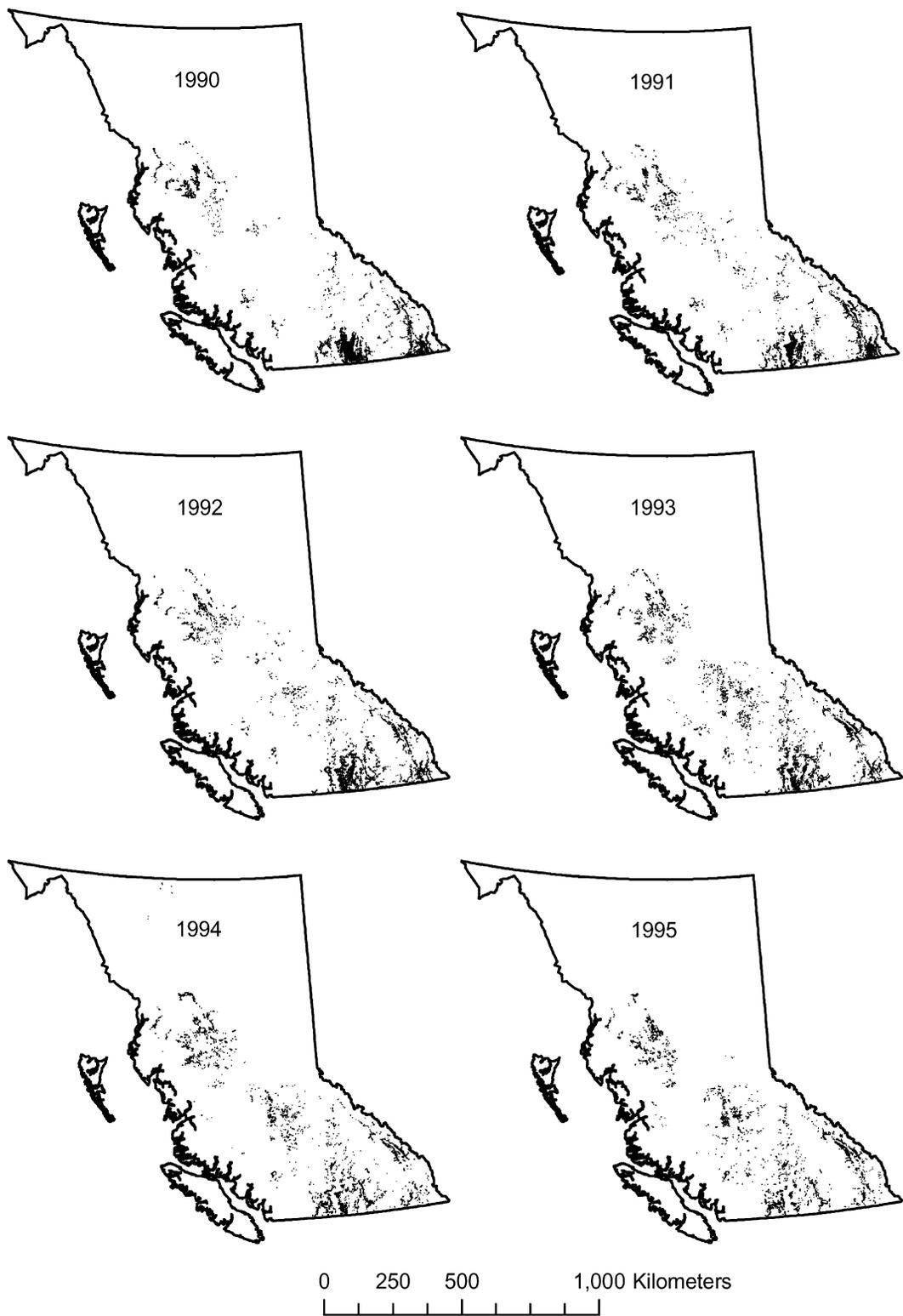
Fig. 2. Tree mortality due to mountain pine beetle, 1990–1996 and 1999–2003, from the annual aerial Forest Insect and Disease Surveys. Figure reflects original polygon maps prior to being overlaid on a grid.
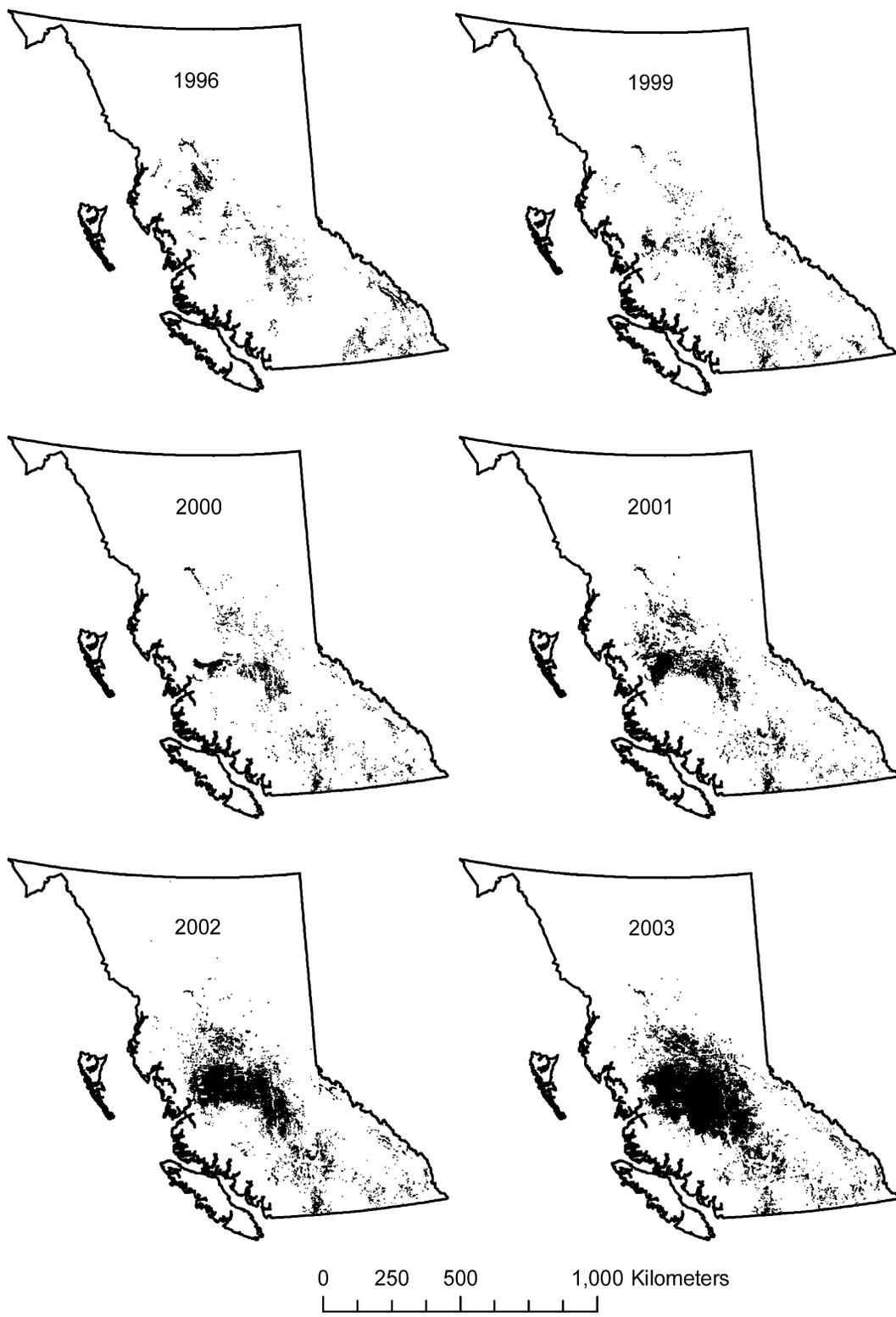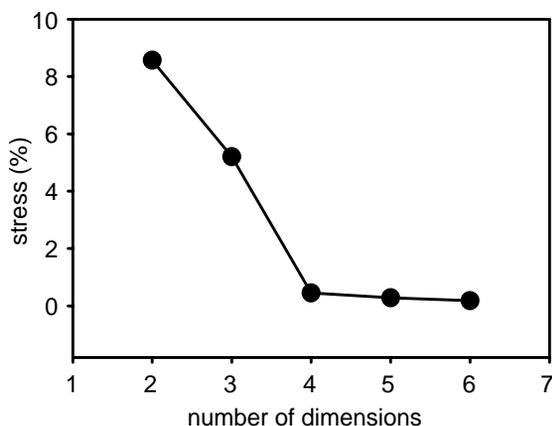
Fig. 2. Continued.

Fig. 3. Stress plot for multidimensional scaling analysis of time series data of tree mortality caused by mountain pine beetle, 1990–2003, on grid cells 12 × 12 km in size in British Columbia, Canada. The optimal number of clusters, i.e. types of time series patterns, corresponds to the elbow of the stress plot.

yielded a region of high mortality in the vicinity of cluster type I in west-central BC. Similarly, increasing the number of clusters only increased the number of geographically isolated outbreaks of mountain pine beetle in the southern portions of the province.

Does the presence of conservation land increase the probability that infestations will be characterized by the time series of cluster type I?

Hereafter, we term the region characterized by cluster type I in Fig. 5 as the "epicenter" of the outbreak.
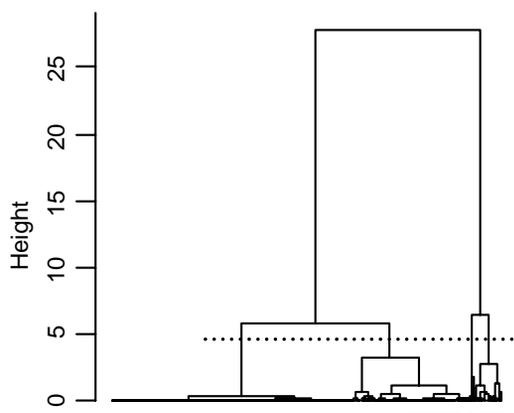

Fig. 4. Dendrogram from hierarchical cluster analysis of time series data of tree mortality caused by mountain pine beetle, 1990–2003, on grid cells 12 × 12 km in size in British Columbia, Canada. Dendrogram uses Ward's minimum distance linkage method with Euclidean distances. The horizontal dotted line cuts the dendrogram into four clusters (i.e. vertical lines dropping from the cut line. Four clusters are suggested by other clustering techniques as well (see Fig. 3, Results)). Grid cell identifiers are not labeled on x-axis.

We tested the hypothesis that the epicenter contained more conservation area than each of the other cluster types using autoregressive tests on resampled data that accommodated differences in sample size and spatial arrangement (Table 1). The epicenter contained more conservation lands than any of the cells in cluster type II, as evidenced by 100/100 positive tests of this hypothesis. The epicenter also contained more conservation lands than cells in either cluster types III or IV, although each of these tests demonstrated positive associations <95% of the time. None of the tests for any region indicated that they contained more conservation lands than the epicenter.

Observed distribution of conservation areas and host availability among the regions

The distribution of conservation areas vs the working forest, and the distribution of 23susceptible pine within these lands, are listed in Table 2. The epicenter is the only geographical region that has more conservation area than working forest (62.2 vs 37.8%). All other regions, i.e. cluster types II, III, and IV (Fig. 5), have less than 20% conservation lands by area. The composition of susceptible pine also differs among these regions. The amount of susceptible pine in the epicenter is distributed relatively evenly between conservation and working forest lands, whereas in regions characterized by cluster types II, III, and IV, >90% of the susceptible pine is located in working forests. The relative coverages of pine within the entire regions characterized by the epicenter and cluster II are close to 50%, and considerably less in other regions (21.3 and 8.8% for areas associated with cluster types III and IV, respectively). In the epicenter, however, the relative coverage of susceptible pine in conservation lands is higher than the relative coverage in conservation areas associated with cluster type II (42.2 vs 20.7%).

Within the epicenter, did insect populations first intensify within specific areas?

The provincial-level cluster analysis indicated that the 31 cells within the epicenter were characterized by time series that uniformly exhibited increasing populations of mountain pine beetle in 1999, and decreasing populations by 2002. To examine whether there were potential differences in time series behavior within this epicenter, we applied hierarchical cluster analysis to the encompassed cells. Three distinct groups of time series could be distinguished (Fig. 6), which we term A, B, and C to avoid confusion with the cluster types from the provincial-level examination shown in Fig. 5. Again, this
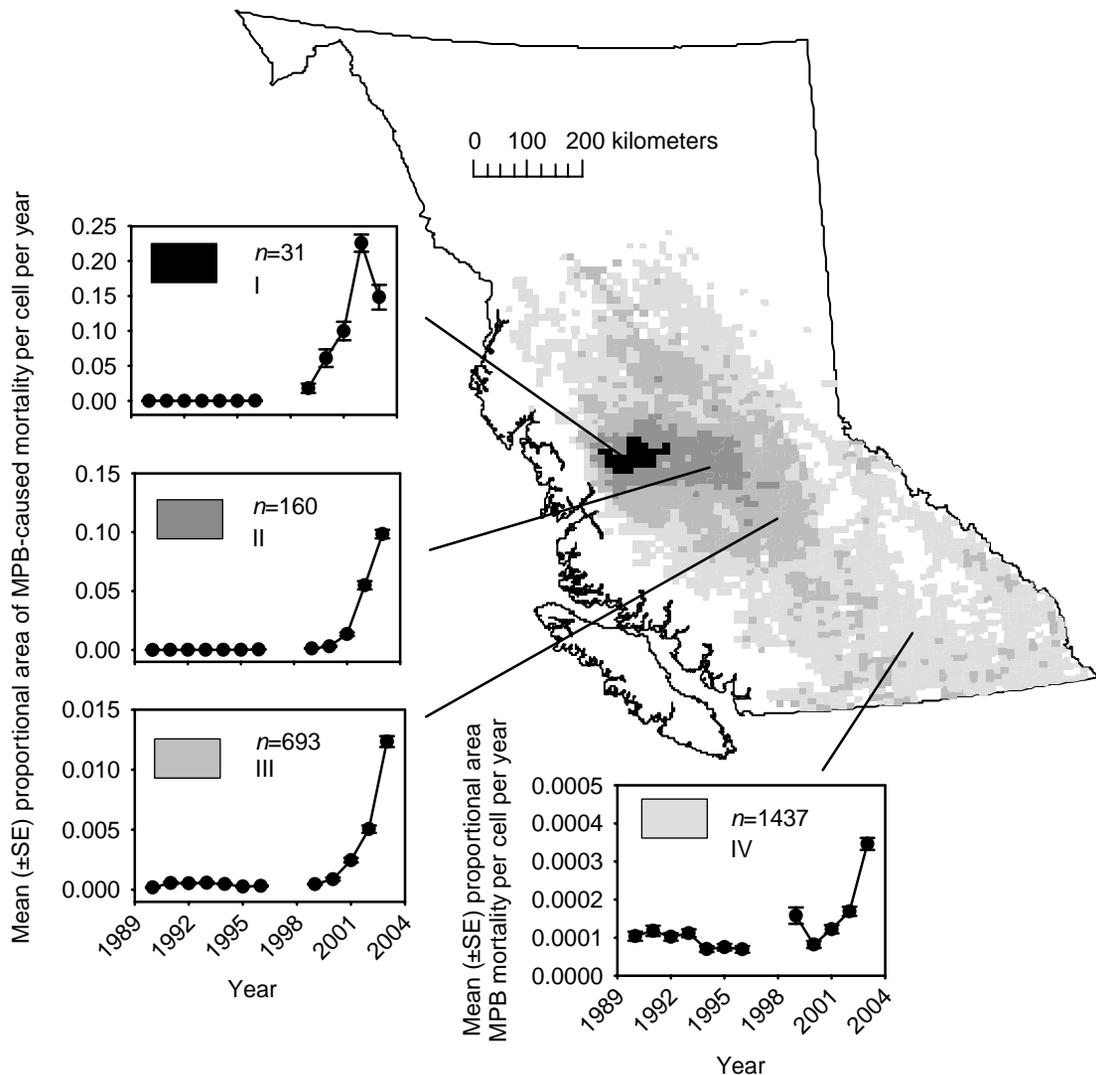
Fig. 5. Time series patterns (means ± SE) of tree mortality caused by mountain pine beetle, 1990–2003, on grid cells 12 × 12 km in size in British Columbia, Canada, based on hierarchical cluster analysis for κ = 4 clusters. Note different scales for y-axes. The reader is cautioned that the labels of the patterns, i.e. types I to IV, are strictly categorical. Outbreak progression between types, i.e. populations in I causing II and III and then IV, is not necessarily inferred. See text for details.

cluster analysis was performed without any knowledge of spatial location before the results were plotted on a map.

Table 1. Comparison of the association of conservation lands within the epicenter to regions characterized by other time series patterns (see Fig. 5). Positive association infers that there is more conservation land in the epicenter than the other region; a negative association indicates less. Table displays summary of 100 autologistic regressions based on resamples to account for differences in sample size and spatial arrangement (see Methods).

Comparison: epicenter vs	positive	negative	no relationship
Cluster type II	100	0	0
Cluster type III	93	0	7
Cluster type IV	84	0	16

A map of the epicenter and the associated time series is displayed in Fig. 7. Although all cells had increasing populations of mountain pine beetle in 1999, cells characterized by Type A in the northwest area of the epicenter had the greatest percentage of cell area affected, 8% (Fig. 7A). These populations had reached their peak, 18% cell mortality, by 2000, while other populations in regions characterized by Types B and C peaked at 25% in 2002 before declining (Fig. 7A).

The distribution of land tenures and susceptible pine within the epicenter are shown in Fig. 7B. The epicenter comprises portions of the working forests (local Nadina, Vanderhoof, and Quesnel forest districts), as well as areas of three conservation lands: North Tweedsmuir Provincial Park, South Tweedsmuir Provincial Park, and

Table 2. Distribution of stands susceptible to mountain pine beetle ($\geq 60\%$ pine composition and ≥ 60 yr of age) in 1990, within conservation areas and working forests, across the different regions identified by cluster analysis (see Fig. 5).

	Total	Conservation areas		Working forest	
	ha	ha	(%)[*]	ha	(%)[*]
A. Cluster type I ("epicenter")					
Susceptible pine	224 783	120 956	(53.8)	103 826	(46.2)
Cluster area	460 259	286 504	(62.2)	173 755	(37.8)
Relative area of susceptible pine[†]	48.8%	42.2%		59.8%	
B. Cluster type II					
Susceptible pine	1 156 815	89 891	(7.8)	1 066 924	(92.2)
Cluster area	2 378 801	434 287	(18.3)	1 944 515	(81.7)
Relative area of susceptible pine[†]	48.6%	20.7%		54.9%	
C. Cluster type III					
Susceptible pine	2 214 431	129 879	(5.9)	2 084 553	(94.1)
Cluster area	10 400 581	809 095	(7.8)	9 591 485	(92.2)
Relative area of susceptible pine[†]	21.3%	16.1%		21.7%	
D. Cluster type IV					
Susceptible pine	1 924 642	109 200	(5.7)	1 815 442	(94.3)
Cluster area	21 794 770	1 884 478	(8.6)	19 910 292	(91.4)
Relative area of susceptible pine[†]	8.8%	5.8%		9.1%	

*Percent of total, across the columns.
†Percent of area, down the rows.

the Entiako Park and Protected Area. The three parks are relatively evenly divided by area across the entire epicenter (Table 3). The susceptible pine, however, is more concentrated in eastern portions of the epicenter regions. Within the three parks, North and South Tweedsmuir Parks contain <20% of the susceptible pine (Table 3). On a relative scale, susceptible pine covered more than half of the areas of Entiako Park and Protected Area (79.1%) and the working forests (59.8%) (Table 2) bounded within the epicenter.

The distribution of land tenure within the regions characterized by each cluster type is shown in Fig. 7C. Region A, which had the greatest initial tree mortality, is comprised of 97% conservation area. Predominantly,
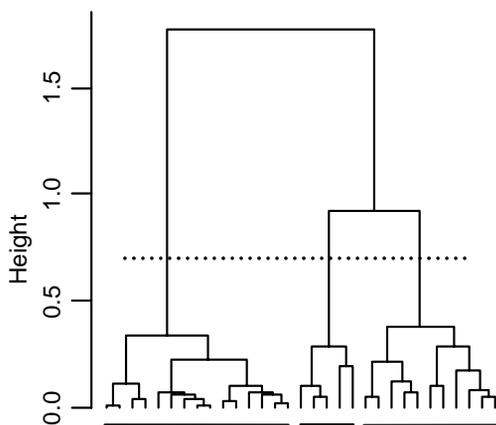

Fig. 6. Dendrogram from hierarchical cluster analysis restricted to the 31 grid cells comprising the "epicenter" of time series data of tree mortality caused by mountain pine beetle, 1990–2003. Dendrogram uses Ward's minimum distance linkage method with Euclidean distances. Three 9cluster types are below the horizontal dotted line. Grid cell identifiers are not labeled on x-axis.

this is North Tweedsmuir Provincial Park (Fig. 7B). Eighty-five percent of the area covered by time series associated with cluster B is conservation land, containing lands from all three of the provincial parks. Regions associated with time series C had one-third conservation area, and two-thirds working forest (Fig. 7C).

Are mountain pine beetle populations synchronous?

The time series patterns in Fig. 5 differ in magnitude, but not direction. Overall, each time series demonstrates an increasing pattern of mountain pine beetle activity across the study area. Spatial covariance functions, which estimate spatial synchrony as a function of distance, are shown for both the early, incipient years of population growth (1990–1996) (Fig. 8A) and the following epidemic years (1999–2003) (Fig. 8B). As expected, the covariance functions for both time periods demonstrate that spatial synchrony declines with increasing distance. The average regional synchrony, however, differs greatly between incipient and epidemic years. In incipient years, the average province-wide synchrony is very close to zero (Table 4). That is, populations of mountain pine beetle across the province were largely asynchronous and temporally independent. Populations were only positively correlated in time at scales of <200 km, as the average local synchrony (i.e. estimate near distance =0) of 0.53 decayed to zero around this distance. In contrast, the average synchrony across the province during epidemic years was 0.38. Local correlations were higher, ca 0.71, and decayed to the province-wide average over distances up to 300 km. In the temporal window of epidemic years, on average, all populations of mountain pine beetle seem to be increasing. Even at distances of 900 km, the spatial synchrony

Fig. 7. Epicenter of mountain pine beetle outbreak, 1990–2003. A) Time series patterns (means ± SE) of tree mortality caused by mountain pine beetle, 1990–2003, on 12 × 12 km grid cells, mapped according to cluster type. B) Conservation areas and associated susceptible pine coverage within epicenter. C) Relative distribution of land tenure within each area characterized by each cluster type.
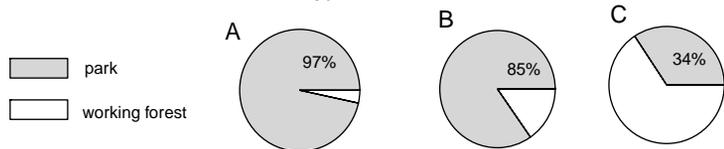

A. Time series cluster types and associated map
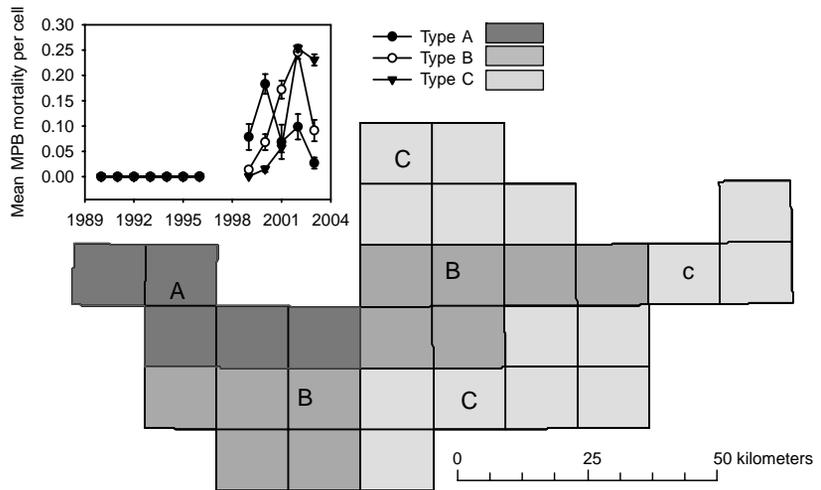
B. Park and pine coverage
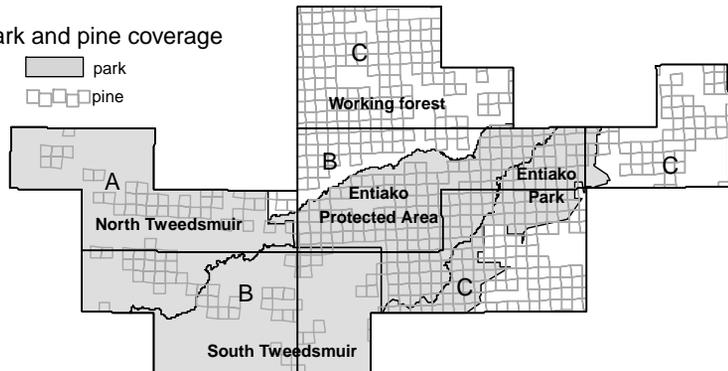
C. Land tenure within each cluster type

did not decay to zero. Directionality did not change the nature of the synchrony for either time period. The covariance functions did not exhibit significant waves.

Correlations were close to zero in all directions in incipient years, but positive in all directions in epidemic years.

Table 3. Distribution of land among conservation areas and working forest susceptible to mountain pine beetle ($\geq$60% pine composition and $\geq$60 years of age) in 1990, within the epicenter (cluster type I in Fig. 5) of the mountain pine beetle outbreak. See Fig. 7A&B for a map of the epicenter.

	N. Tweedsmuir		S. Tweedsmuir		Entiako	
	ha	(%)[*]	ha	(%)[*]	ha	(%)[*]
Susceptible pine	23 035	(19.0)	12 347	(10.2)	85 574	(70.7)
Epicenter area	96 433	(33.7)	81 828	(28.6)	108 243	(37.8)
Relative area susceptible pine[†]	23.9%		15.1%		79.1%	

[*]Sums to 1, across the columns.
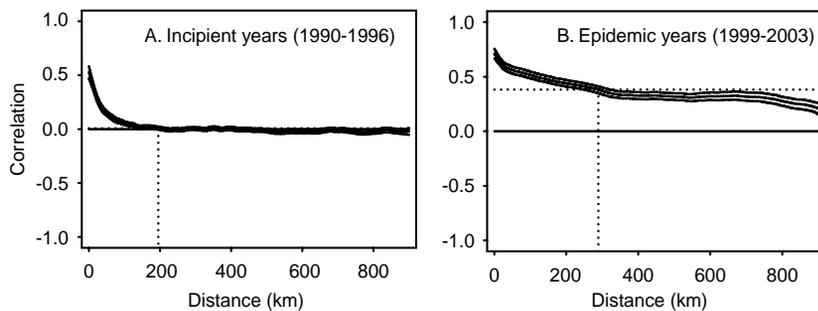[†]Percent of area, down the rows.

Fig. 8. Nonparametric spatial covariance functions. Solid lines are covariance functions with 95% confidence intervals based on 1 000 bootstrap replications. A) Tree mortality caused by mountain pine beetle during incipient years, 1990–1996. Dashed lines indicate distance (vertical lines) at which average regional synchrony (horizontal lines) is reached (see Table 4). B) Tree mortality caused by mountain pine beetle during epidemic years, 1999–2003.

Discussion

The current mountain pine beetle outbreak in British Columbia initiated in an area encompassing portions of several large, contiguous conservation areas and the adjacent working forest in the west-central region of the province. This is an area where there is no evidence for previous outbreak occurrence (Taylor et al. 2005), so host availability was high (Table 2). As populations simultaneously increased before declining within this epicenter, they continued to increase in adjacent areas, suggesting eastward expansion into neighboring forest districts (Fig. 5). Determining the processes driving these spatiotemporal patterns is challenging, however. Processes frequently act at different spatial scales to affect landscape-level patterns (Wiens 1989, Wu and Loucks 1995, He et al. 2002, Aukema 2004). Moreover, different processes may show similar landscape-level signatures.

An example of this problem is the difficulty of separating the potentially interacting effects of insect dispersal from anthropogenic activities, such clear-cut harvesting, when examining the spatiotemporal pattern of outbreak development within the epicenter. Initial mortality was the highest in Region A of the epicenter (Fig. 7A), an area with 20% susceptible pine located predominantly within a section of North Tweedsmuir Provincial Park. It is possible that beetles migrated eastward from this region into areas with more pine and exacerbated an apparent epicenter effect of population development. The slower rates of increase in

Regions B and C (Fig. 7A) in conjunction with their locations to the east of Region A (Fig. 7B) are consistent with a dispersal effect. An alternative, but not mutually exclusive explanation, is that the slower rates of increase in Regions B and C may have been due to greater management interventions against the insects, as those regions had greater areas of working forest considered amenable to aggressive control tactics (Fig. 7C). Clear-cut harvesting is not permitted in National and Class A Provincial Parks and protected areas in British Columbia, including Tweedsmuir (Anon 1988). We note, however, that within the epicenter, access challenges and/or concerns of endangered species habitat conservation preclude management interventions in many areas of working forest, and that intervention activities such as prescribed burns were directed against the beetle within Tweedsmuir Park in the years following detection of an initial 5 000 ha outbreak in 1994. At a province-wide level, it is possible that aggressive tactics applied at the stand level within jurisdictions such as the Vanderhoof and Quesnel forest districts to the east of the epicenter delayed outbreaks for a year or two in those regions (regions associated with cluster type II in Fig. 5).

The localized buildup of such populations without significant immigration cannot be discounted, as localized eruptions in spatially disjunct populations were prevalent throughout the southern portion of British Columbia (Fig. 5). It is highly unlikely that these southern populations simply arose from random dispersal from areas such as provincial parks within the

Table 4. Spatial synchrony of tree mortality caused by mountain pine beetle on grid cells 12 × 12 km in size in British Columbia, Canada, estimated by isotropic nonparametric spatial covariance functions. See also Fig. 8.

	Incipient years (1990–1996)		Epidemic years (1999–2003)	
	Value	95% CI	Value	95% CI
Average correlation				
local synchrony*	0.53	{0.47, 0.58}	0.71	{0.67, 0.76}
regional synchrony†	0.009	{0.004, 0.013}	0.38	{0.35, 0.41}
Distance of decay (km)				
to regional average	196	{135, 220}	289	{250, 320}
to zero	211	{181, 315}	NA	NA

*Correlation where distance is very near zero (synchrony at distance 0 would be 1).
†Correlation across entire province-wide study area.

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northern epicenter. Although beetles may be transported hundreds of kilometers by advective wind currents during peak flight periods, this atmospheric transport is generally unidirectional. For example, atmospheric models have suggested that outbreak populations from the central interior of the province are sources of new infestations east of the Rocky Mountains (Jackson et al. 2005). The absence of waves in the anisotropic covariance functions supports the hypothesis that the Rocky Mountains do not necessarily serve as a complete E−W dispersal barrier at the current, unprecedented population pressure. During non-outbreak conditions, however, relatively few mountain pine beetles leave the stand (Safranyik et al. 1989, 1992), and previous comparative studies with other eruptive herbivores have characterized mountain pine beetles as poor dispersers (Peltonen et al. 2002). Hence, the building outbreak in the southern portion of the province was likely predominantly due to localized increases.

Spatial synchrony may occur without dispersal of subpopulations (Ranta et al. 1995, Grenfell et al. 1998, Blasius and Stone 2000). For example, mobile predators or parasitoids may induce synchrony in herbivore populations (Ydenberg 1987, Bjornstad and Bascompte 2001). Insect predation and parasitism, however, are generally not considered significant factors in mountain pine beetle dynamics (Amman and Cole 1983, Moeck and Safranyik 1984). Another frequent cause of spatial synchrony is correlated density-independent, environmental factors acting at a landscape-level scale, which may synchronize spatially disjunct populations with the same density-dependent population structure (Moran 1953, Ranta et al. 1997, Koenig 2002). This is termed the Moran effect (Royama 1992). In the mountain pine beetle system, however, it is difficult to determine the density-dependent population structure driving populations for three reasons. First, our analyses encompass a short window of the ongoing outbreak, which makes determining first- or second-order processes intractable. Examining population processes using longer time series is an area of current focus. Second, population estimates of mountain pine beetle are indirect, via corrected estimates of tree mortality within each cell. Observation or measurement error can affect estimates of growth rate (Haydon et al. 1999). Third, estimates of mountain pine beetle populations would have to be rescaled by the total amount of susceptible pine available each year, instead of using the absolute land area in each cell. This is challenging, since detailed forest inventories are not performed annually. However, lodgepole pine is one of the most abundant tree species in our study area, and small scale variability in relative forest composition is likely negligible at the provincial extent studied. Further, rescaling responses to susceptible pine likely would not significantly affect the current results, since the increasing landscape-level trend in mountain pine beetle populations would still be apparent (Bjornstad et al. 1999).

The high level of spatial synchrony noted for epidemic years is likely due, in part, to a Moran effect. The most probable environmental factor is temperature, which is more spatially synchronous than precipitation (Koenig 2002, Peltonen et al. 2002). Temperature synchronizes the developmental stages of mountain pine beetle at shorter, i.e., intra-annual, resolutions (Bentz et al. 1991), which is essential for coordination of flight and subsequent mass attack (Reid 1962, Safranyik et al. 1975). Indeed, there has been both an amelioration of extreme winter minimum temperatures and an increase in summer heat accumulation relevant to mountain pine beetle development throughout the southern half of British Columbia during the last several decades (Carroll et al. 2004). It is important to note, however, that temperature or other climatic factors may have different effects during different population phases of bark beetles (Okland and Berryman 2004). Currently, we are working on elucidating factors that affect the transition between incipient and outbreak dynamics, and examining how climatic factors may influence population synchrony and spread.

In addition to ecological factors such as dispersal and Moran effects, the larger distances exhibiting positive spatial synchrony in epidemic than incipient populations of mountain pine beetle may be due to the greater spatial extent of the outbreak. That is, beetle populations may occur across larger distances during outbreak than endemic or incipient years. In the present study, however, the spatial extent of mountain pine beetle infestations was similar for all years (Fig. 2). It is important to note that our estimates of synchrony are derived from measures of high density populations (i.e., mass attacked trees). Spatial synchrony of latent, endemic populations that are unable to kill healthy trees has not been characterized at landscape level scales, and is a focus of our current efforts.

Summary and conclusions

The apparent epicentral nature of outbreak initiation and spread, combined with estimates of expansion rates, can be used to identify and prioritize adjacent landscape units for either reactive, direct control efforts, or proactive tactics aimed at reducing forest susceptibility to future mountain pine beetle epidemics. Because issues surrounding land tenure add a value-laden and hence sensitive dimension to such discussions, we note the following three points.

First, because landscape-level signatures may be driven by multiple, and often interacting, processes, management practices against eruptive herbivores must safeguard against biases that target only one process. For

example, we do not necessarily advocate management interventions against mountain pine beetle in conservation areas to prevent dispersal into adjoining areas, since localized increases may be equally responsible for infestations in neighboring areas.

Second, dispersal of insect populations is not by itself a threat to forests. Mortality of dispersing beetles is exceptionally high (Schmid 1969) as survivors must land in areas with suitable numbers, climate, and habitat to initiate new infestations. Effective dispersal remains 10one of the least understood features of bark beetle biology.

Third, insect outbreaks depend on many factors, such as the spatial arrangement of incipient populations, extent of synchrony, climatic suitability, topography, host availability and susceptibility, and disturbance histories including previous outbreaks and fire. Anthropogenic impacts, such as fire suppression or application of different management strategies, any of which may depend on access or land tenure, may also affect insect populations. Knowledge of such factors, how they interact, and the spatiotemporal patterns of outbreak development is critical to natural resource management, and decisions to implement strategies intended to minimize herbivore impacts. Such knowledge must be incorporated into discussions among stakeholders with potentially diverse interests in forest ecology and management.

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