

Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada

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Received 21 April 2008; revised 18 October 2008; accepted 26 November 2008; published 17 February 2009.

[1] We present evidence of high spatial synchrony in an area affected by mountain pine beetle (MPB, *Dendroctonus ponderosae*) across large distances in British Columbia, Canada, in a study of a spatially explicit database of an area affected by MPB-caused tree mortality for the period 1959–2002. We further show that large-scale climatic patterns (Pacific Decadal Oscillation (PDO) and, to a lesser degree, Arctic Oscillation (AO)) are strongly related to the observed MPB synchrony, and that they probably operate through controlling the frequency of extreme cold winter temperatures that affect MPB larvae survival. A smaller portion of the data's variability is linked to the onset of the two largest outbreaks in the studied period and might be attributed to dispersal from outbreak-prone areas or else to differences in microhabitat (e.g., host availability) in these regions. The onset of a warm PDO phase in 1976 favored MPB outbreaks by reducing the occurrence of extremely low winter temperatures province-wide. Likewise, the exceptionally high and persistent AO values of the late 1980s and 1990s enhanced MPB activity in the southern and northern parts of the region. Summer warmth cannot be discarded as an important agent at smaller scales.

Citation: Macias Fauria, M., and E. A. Johnson (2009), Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada, *J. Geophys. Res.*, 114, G01012, doi:10.1029/2008JG000760.

1. Introduction

[2] Mountain pine beetle (MPB, *Dendroctonus ponderosae*) is a destructive biotic agent endemic in western Canadian forests. It attacks all pine species in the region [Taylor *et al.*, 2006] although MPB outbreaks have occurred principally in lodgepole pine (*Pinus contorta*) stands. A large MPB outbreak has occurred in British Columbia (BC) during the last decade, with 2 to 8 million hectares of pine forest affected annually [Taylor *et al.*, 2006] and significant consequences for the global carbon budget [Kurz *et al.*, 2008]. MPB populations have occurred east of the Canadian Rocky Mountains, raising concerns of a potential MPB outbreak throughout the boreal forest of North America [e.g., Logan and Powell, 2001; Carroll *et al.*, 2004; Moore *et al.*, 2005].

[3] MPB population dynamics are characterized by endemic and epidemic phases [Safranyik and Carroll, 2006]. In endemic phases, populations are maintained at low densities and are able to attack only stressed trees within the forest. During epidemic phases, the densities of MPB populations are high enough to produce mass attacks mediated by pheromones [Borden, 1982] on healthy mature

trees. This enables MPB populations to grow exponentially, causing tree mortality over areas of thousands of hectares.

[4] Apart from the dispersal phase by mature adults, all life stages of MPB occur within the subcortical tissues of their host trees, where they feed on the phloem tissue in the inner bark, excavating mines and tunnels [Safranyik and Carroll, 2006]. Adult and healthy trees with a thick phloem provide the best conditions for beetles to develop and reproduce [Amman, 1972; Amman and Cole, 1983; Safranyik *et al.*, 1974; Shore and Safranyik, 1992].

[5] Winter mortality and host availability have been proposed as critical factors controlling MPB population dynamics in its northern distribution limit in British Columbia [Taylor and Carroll, 2003; Carroll *et al.*, 2004; Moore *et al.*, 2005; Stahl *et al.*, 2006]. Reduced frequencies of extremely low cold season temperatures (<−37°C) and an increased average age of forest stands have been proposed to explain the expansion of MPB in BC [Taylor *et al.*, 2006; Stahl *et al.*, 2006]. Other climate parameters, such as a warm growing season, spring drought, aridity, and variability of growing season precipitation, that affect the biology of the beetle (e.g., warm daily August temperatures facilitate the flight of adult beetles [Aukema *et al.*, 2008]) and/or the fitness of the host (hydric stress weakens trees) are known to affect MPB populations [Safranyik *et al.*, 1975; Carroll *et al.*, 2004].

[6] Changes in the dynamics of the Pacific Decadal Oscillation (PDO) teleconnection are directly linked to reduced occurrence of extremely cold winter temperatures in the region [Stahl *et al.*, 2006]. The PDO is a large-scale climatic pattern defined by the leading mode of monthly sea

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surface temperature anomalies in the North Pacific Ocean, poleward of 20°N [Hare, 1996; Zhang *et al.*, 1997]. It is manifested by El Niño-like changes in the sea surface temperature distribution over the tropical and North Pacific, which are evident at decadal timescales, and it is strongly linked to atmospheric circulation over North America and the North Pacific, as commonly expressed by the Pacific North American (PNA) index [Mantua *et al.*, 1997]. PDO events have persisted for 20 to 30 years during the twentieth century. Warm (cool) PDO phases are characterized by a strengthened (weakened) Aleutian Low, enhancing (reducing) warm air advection onto the west coast of North America which causes positive (negative) temperature anomalies over northern North America [Minobe, 1997; Mantua and Hare, 2002]. In particular, Stahl *et al.* [2006] reported a reduced frequency of cold events in British Columbia during El Niño and positive PDO winters to be consistent with a deepening of the Aleutian Low, an amplification and eastward displacement of the Canadian Ridge, and a northward displaced polar jet stream inhibiting the outflow of cold Arctic air over BC. The PDO is related to the sea surface temperatures, precipitation, and convection variability in the Indian Ocean and tropical Pacific, and its spatial climatic patterns are similar to the El Niño–Southern Oscillation (ENSO) pattern [Mantua *et al.*, 1997; Zhang *et al.*, 1997].

[7] The Arctic Oscillation (AO) has also been reported to be an important low-frequency climatic pattern controlling the occurrence of Canadian winter temperature extremes. AO is the dominant pattern of nonseasonal sea level pressure variations north of 20°N, and is characterized by sea level pressure anomalies of one sign in the Arctic and opposite sign at midlatitudes [Trenberth and Paolino, 1981; Wallace and Gutzler, 1981]. Although it has a weaker influence in western than in eastern Canada, it has been reported to influence the occurrence and duration of warm winter spells in both southeastern and northern British Columbia [Shabbar and Bonsal, 2004], as well as the occurrence of winter cold spells in that region [Stahl *et al.*, 2006].

[8] The regional-scale relationships between these teleconnections and winter cold mortality events raise the possibility that British Columbia MPB populations might be spatially synchronized by these large-scale climatic patterns. However, synchrony between disjunct animal populations can also originate through other processes, such as dispersal of individuals or the effect of mobile natural enemies (predators or viruses [e.g., Ydenberg, 1987]): these different processes can give rise to similar landscape-level signatures [e.g., Aukema *et al.*, 2006], making their identification difficult.

[9] In this study we show evidence of large-scale synchrony in MPB activity in British Columbia using a spatially explicit database of area affected by MPB-caused tree mortality for the period 1959–2002. We further show the strong and significant link between area affected by MPB and the PDO, which is suggested to operate through the occurrence of minimum winter temperatures and thus through beetle larvae cold mortality. We also present evidence for two minor but significant sources of variability in the data: one related to the two major outbreak events that occurred during the period on record and attributed to

dispersal from outbreak-prone areas or to differences in host availability in these regions, and the other to the control of the occurrence of cold mortality events by the Arctic Oscillation. Our results show evidence that external climatic forcing is an important synchronizer of the area affected by mountain pine beetle in the region.

[10] The study is structured as follows:

[11] 1. Spatiotemporal study of the spatially explicit database of area affected by MPB-caused tree mortality in British Columbia.

[12] 2. Analysis of the relationship between the area affected by MPB and temperature and precipitation data for the region, as well as its relationship with the Pacific Decadal Oscillation and the Arctic Oscillation. Relationships were studied at different temporal scales using low- and high-pass filters.

[13] 3. Assessment of the relationship between these two teleconnection patterns and climatic variables relevant to MPB populations.

2. Data

2.1. Area of Tree Mortality Caused by MPB

[14] Records of area affected by MPB-caused tree mortality in British Columbia consisted of province-wide aerial overview surveys of forest insect outbreaks conducted by the Canadian Forest Service (1959–1996) and by the British Columbia Ministry of Forests (1999–2002). Province-wide surveys were not done in 1997 and 1998: 1997 was interpolated by averaging the values for 1995, 1996, and 1999, and 1998 by averaging the values for 1997, 1999, and 2000. To assess the robustness of the relationships, analyses were repeated for the periods of continuous data 1959–1996 and 1999–2002 separately, and for the period 1959–2002 without the years 1997 and 1998. Only the results using the full record 1959–2002 with the two interpolated years are shown in this study as all analyses yielded similar results. Data are available at the British Columbia Natural Disturbance Database site (<http://cfs.nrcan.gc.ca/subsite/disturbance/>) and consist of annual maps of presence/absence of MPB-caused tree mortality, with a cell size of 2.5×2.5 km (Figure 1). Areas include all stands where lodgepole pine was detected across all severity classes: thus, not all lodgepole pine in infested areas were killed, and infested areas may contain other nonsusceptible tree species, as well as nonforested portions. Ideally, information on area affected by MPB-caused mortality should have been weighted according to the availability of susceptible (mature) pine within each cell. Unfortunately, annual inventories of stand composition in British Columbia do not exist [Aukema *et al.*, 2006]. Thus, assessment of the relative influence of host availability on MPB populations was not performed due to lack of appropriate data. Moreover, the relationship between mapped MPB area and absolute insect populations is likely nonlinear: presence of MPB on a given cell refers to locally outbreaking populations, and endemic populations may not be visible from the air [Aukema *et al.*, 2008]. Nonetheless, Aukema *et al.* [2006, 2008] showed this data to be useful for examining population trends at the landscape level. Values of area affected by MPB in BC were log_e transformed in order to reduce the correlation between the mean and the variance, a common procedure when dealing with

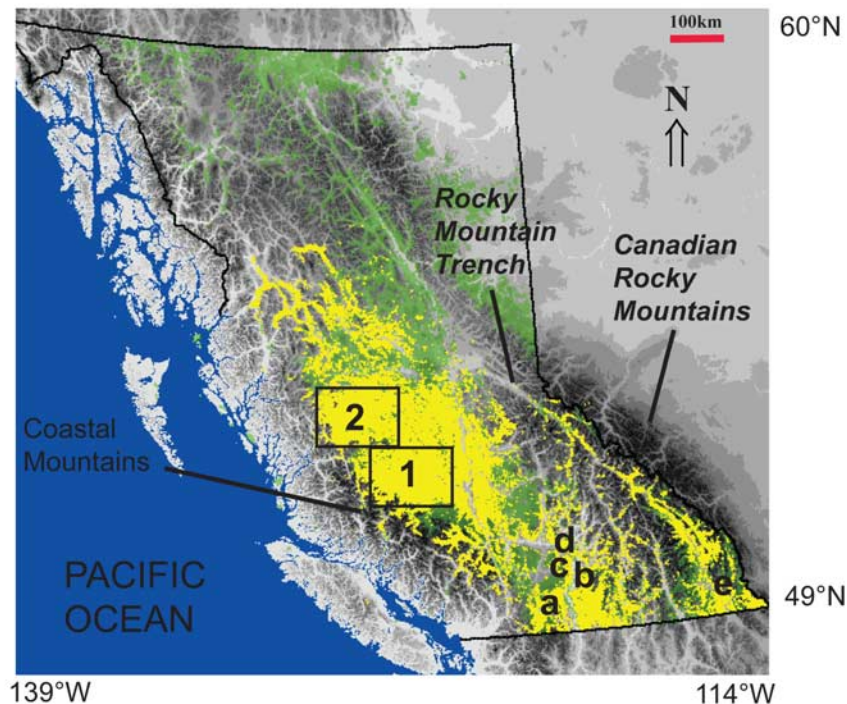


Figure 1. Map of British Columbia, showing the total number of 2.5×2.5 km cells with presence of area affected by tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) during the period 1959–2002 (yellow). The distribution area of lodgepole pine (*Pinus contorta*) is shown in green. Grayscale indicates altitude above sea level (increasing from white to black). The area affected by the Chilcotin Plateau outbreak from late 1970s to 1985 is highlighted by rectangle number 1. The area affected by the current outbreak (ongoing since late 1990s) is highlighted by rectangle number 2. Location of the meteorological stations where daily winter temperature data was analyzed (see Methods) are shown as letters: a, Princeton ($49^{\circ}27'N$, $120^{\circ}30'W$, 700 m.a.s.l.); b, Vernon ($50^{\circ}15'N$, $119^{\circ}17'W$, 482 m.a.s.l.); c, Westwold ($50^{\circ}28'N$, $119^{\circ}45'W$, 610 m.a.s.l.); d, Kamloops ($50^{\circ}40'N$, $120^{\circ}20'W$, 345 m.a.s.l.); e, Fernie ($49^{\circ}30'N$, $115^{\circ}03'W$, 1001 m.a.s.l.); m.a.s.l., meters above sea level.

population-related data [e.g., Koenig, 1999]. Annual estimates of the number of cells with presence of MPB-caused tree mortality in BC showed very high similarity with total annual area affected by MPB in BC (in hectares; $r^2 = 0.95$; Figure 2), and thus allowed these data to be treated as a spatially explicit database of area affected by MPB.

2.2. Climatic Data

[15] We used the interpolated 50-km gridded monthly climatic data set for Canada (CanGrid [Zhang *et al.*, 2000]), which spans the period 1900–2005 for maximum, minimum and mean temperatures, and precipitation sum. Temperature data are monthly means of daily maximum and minimum temperatures, and the monthly mean temperature is the average of the monthly maximum and minimum temperatures. Precipitation data are totals of daily precipitation. These data have undergone rigorous quality control, and have been adjusted for identified inhomogeneities caused by station relocation and changes in instrumentation and observing practices [Zhang *et al.*, 2000]. Spatially explicit gridded climatic data allowed direct comparison with gridded MPB data: however, the use of monthly climatic averages potentially masks the occurrence of key climatic parameters occurring on a daily scale, such as days

with temperatures causing cold mortality in MPB. In order to investigate if mortality-causing cold events (as defined by Wygant [1942]) occurred in southern BC (the warmest area in our study region), we used daily meteorological data from five weather stations located in southern BC (Kamloops, Westwold, Vernon, Princeton, and Fernie, Figure 1; Environment Canada).

[16] Seasonal (winter, spring, summer, and fall) and annual Pacific Decadal Oscillation indices were obtained from the Website of the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) at the University of Washington (<http://jisao.washington.edu/pdo/>). AO indices were obtained from the National Oceanic and Atmospheric Administration (NOAA; <http://www.cpc.noaa.gov/>).

3. Methods

3.1. Arrangement of Gridded Data

[17] In order to overlay and compare the spatially explicit data sets of MPB-caused tree mortality and Canadian precipitation (P) and temperature (T), data were georeferenced to Polar Stereographic projection (CanGrid's original projection was Polar Stereographic, whereas MPB original projection was the provincial standard Albers NAD 1983).

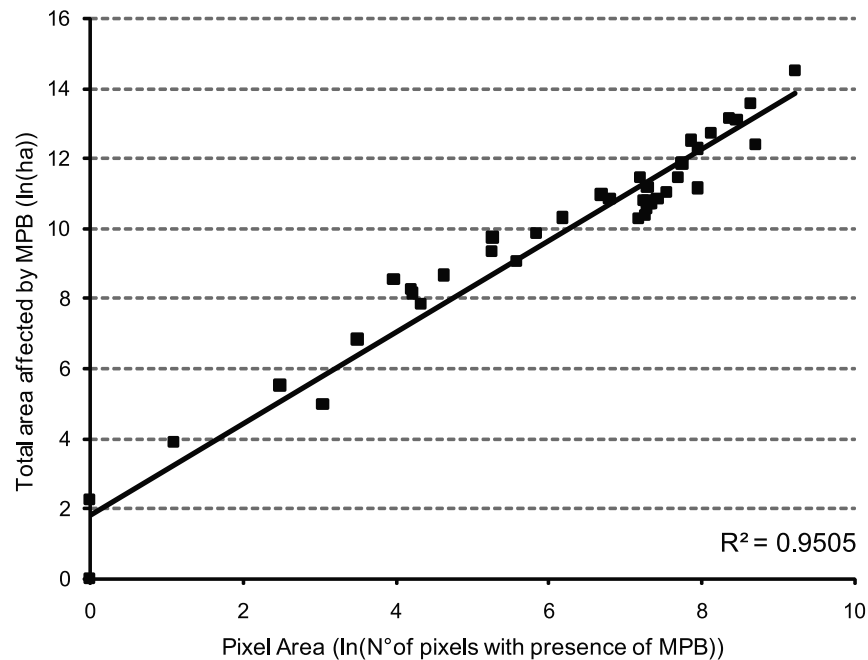


Figure 2. Plot showing the relationships between annual totals of area affected by mountain pine beetle in British Columbia and the estimates of area affected computed by the presence/absence cells shown in Figure 1 (period 1959–2002).

Second, MPB data were resized to 50×50 km cells (283 cells in total): each new cell contained the sum of all 2.5×2.5 km cells with presence of MPB-caused tree mortality contained within it. This permitted a direct comparison with the Canadian P and T data set.

[18] The aggregation of MPB across 50×50 km spatial units is expected to smooth out fine-scaled spatial variability in the data, such as local sampling variance and demographic stochasticity [e.g., Bjørnstad *et al.*, 1999a; Peltonen *et al.*, 2002], enabling the study of potential large-scale patterns. Nonetheless, and with the exception of the comparison with the Canadian P and T data set, all analyses performed in this study with the MPB gridded data were repeated at 2.5×2.5 km, 10×10 km, 20×20 km, 50×50 km, and 100×100 km cell sizes to exclude potential size-related biases and to test the robustness of our results. Only the results corresponding to the 50×50 km grid will be shown in this study, as its scale matches with the scale of the climatic data.

3.2. Spatiotemporal Study of MPB Data

[19] The study of synchrony in MPB data was approached in several ways. Aggregated 50×50 km cells were used as a proxy for time series of MPB subpopulations. According to Liebhold and Kamata [2000], spatial synchrony is the process by which populations in spatially disjunct locations fluctuate in a similar manner. Population fluctuations can be recorded as a time series composed of abundances or log abundances [e.g., Koenig, 1999], or growth rates [e.g., Royama, 1992; Bjørnstad *et al.*, 1999b]. Bjørnstad *et al.* [1999a] argued that growth rates (i.e., the first-differenced time series of log abundance) are more robust estimates of interpopulation synchrony. However, abundance values were used in this study because (1) the data

we dealt with were not actual population numbers, their relationship with population numbers being most likely nonlinear [Aukema *et al.*, 2008], and (2) to allow comparison with several previous studies, as abundances have previously been used in the study of spatial synchrony with data sets of the exact same type as the one used in this study for mountain pine beetle and other forest insect populations [e.g., Peltonen *et al.*, 2002; Økland *et al.*, 2005; Aukema *et al.*, 2006, 2008].

[20] First, pairwise cross correlations were computed between all cells in which there was at least one year with presence of MPB-caused tree mortality (i.e., more than 40,000 pairs in the 50×50 km grid). Intercell distances were calculated by taking the midpoint of each grid cell as the spatial reference. Then, spatial synchrony was assessed by computing the relationship between intercell correlation and distance. We used noncentered smoothed nonparametric covariance functions (NCF), developed by Bjørnstad *et al.* [1999a, 1999b] (<http://asi23.ent.psu.edu/onb1/>) to explore how synchrony decreased with increasing distance. The NCF uses a smoothing spline to produce continuous estimates of spatial covariance as a function of distance [e.g., Peltonen *et al.*, 2002]. Confidence intervals for the NCF were calculated by bootstrap resampling with 1000 replications [Bjørnstad *et al.*, 1999b].

[21] Second, time-space plots were obtained by plotting the annual estimate of area affected by MPB along a N-S axis in British Columbia, from the border with the U.S.A. at 49°N to the northernmost cell with recorded MPB activity ($\sim 57^\circ\text{N}$). Each latitudinal band (50 km latitudinal bands in the case of the 50 km grid) consisted of the sum of all the cells with area affected by MPB-caused tree mortality. The same was done for the W-E axis, from the Rocky Mountains in the east to the Coast Mountains in the west (Figure 1).

Such analyses aimed at condensing the information contained in the 42 maps of annual area affected by MPB into a comprehensive and reduced format, in order to investigate (1) if MPB outbreaks have occurred synchronously over the province or have started from a single focus and (2) if the range of MPB activity has changed during the study period and, if so, when.

[22] Third, principal component analysis was performed on the MPB data set to analyze the data's main modes of variability. PCA was applied to the variance-covariance matrix stemming from the time series of the cells where at least one year of MPB activity was recorded for the period 1959–2002.

3.3. MPB and Climate: Gridded Data Sets

[23] The annual area of MPB-caused tree mortality for each cell with at least one year of recorded MPB activity during the period 1959–2002 was correlated (Pearson linear correlation) with the corresponding climatic record (T and P) on that cell. Thus, a gridded correlation map was obtained between area affected by MPB and each climatic variable analyzed (i.e., minimum, mean, and maximum previous fall, and current year winter, spring, summer, and annual temperature, as well as total precipitation). In addition, two cold season temperature grids were computed: one for the minimum temperatures from December to February and another from November to March. Because we were not working with population data but with a rather coarse (spatially and temporally) data set of area affected by tree mortality caused by mountain pine beetle, temporal lags between climate and the mountain pine beetle data were not accounted for, as in the work of *Aukema et al.* [2008].

[24] Likewise, the gridded MPB data were correlated with the Pacific Decadal Oscillation and the Arctic Oscillation for the fall of the previous year, and the current year winter, spring, summer, and annual indices. These teleconnection indices were correlated with each of the cells with at least one year of recorded MPB activity, producing a correlation map between the area affected by MPB and each seasonal and yearly index.

[25] The gridded P and T data sets were also correlated with PDO and AO indices for the period analyzed 1959–2002, producing correlation maps of the influence of these large-scale climatic patterns on Canadian climate. Temperature and precipitation anomalies were also computed as the difference from the 1959–2002 climatological mean.

[26] Finally, the spatial synchrony of a set of climatic parameters reported to be linked to MPB in BC [*Carroll et al.*, 2004; *Aukema et al.*, 2008] was analyzed using the NCF [*Bjørnstad et al.*, 1999a, 1999b]. The climatic parameters were cold season (defined as November to March) minimum temperatures, spring precipitation, and August mean temperature. The objective of this analysis was to compare the spatial synchrony patterns of these climatic parameters with those of MPB data, as when populations either do not share the same pattern of density dependence or are subject to nonlinear dynamics (as it is the case in MPB populations), synchrony in climate must be greater than between populations [*Grenfell et al.*, 1998, 2000] and its NCF curve decline slower than that for population estimates [*Peltonen et al.*, 2002].

[27] When calculating more than one significance test, as it is the case in gridded data intercorrelations, significance levels should normally be adjusted to account for multiplicity, using Monte-Carlo methods to estimate field significance [e.g., *Livezey and Chen*, 1983; *Katz*, 1988; *Katz and Brown*, 1991; *Mason and Goddard*, 2002]. The impact of multiplicity is assumed to be important given the large number of tests involved in the spatially explicit data (hundreds). However, field significance tests were not performed in this study because our aim was to see overall spatial patterns of correlation. Significance levels in the correlation analyses performed with gridded data in this study should thus be interpreted as general patterns of relationship.

3.4. MPB and Climate: Provincial Totals

[28] Provincial totals of area affected by MPB were compared to the PDO and AO seasonal and annual indices. Frequency analyses were limited by the relatively short length of the series (44 years). To assess the interannual and interdecadal variability associated with the relations between area affected by MPB and climatic data, 7-year centered unweighted moving averages were computed (as in the work of *Macias Fauria and Johnson* [2006]), generating 38-yearlong low-pass-filtered series and the corresponding 38-yearlong high-pass-filtered series (computed by subtracting the low-pass-filtered series from the original ones). In this case, multiplicity was not an issue and thus significances can be interpreted in a more restrictive sense.

[29] Many of the time series in this study are autocorrelated. Autocorrelation in time series may hamper the assumption of independent observations in estimating the level of statistical significance for Pearson correlations: it reduces the effective data size by an amount not known a priori [*von Storch and Zwiers*, 1999]. Significance of interseries Pearson correlations was computed using a combination of autoregressive (AR) modeling and Monte-Carlo methods. For any given pair of series, the autocorrelation order of both was calculated using the *Burg* [1978] method, a method of AR spectral estimation based on minimizing the forward and backward (least squares) prediction errors. Several AR models were computed for a maximum AR order of 30, more than the maximum AR order needed when dealing with a ~40 year time series. The best AR model (i.e., the best model order) for each time series was then selected using the Akaike Information Criterion [*Akaike*, 1974]. Once the AR model order of each series was estimated, 1000 surrogate series with the same AR characteristics were generated and their correspondent correlations calculated: the empirical probability distribution of the correlation coefficients was then easily calculated and, hence, significances at $p < 0.05$, $p < 0.02$ and $p < 0.01$.

4. Results

4.1. MPB Synchrony

[30] Nonparametric covariance function showed synchrony declining with distance up to distances of ~300 km (Figure 3a). Local synchrony (defined as the average correlation between time series as the distance approaches zero) was extremely high (0.92; Table 1). The region-wide synchrony (defined as the average correlation across the study area) was 0.32 (Table 1), remarkably high considering

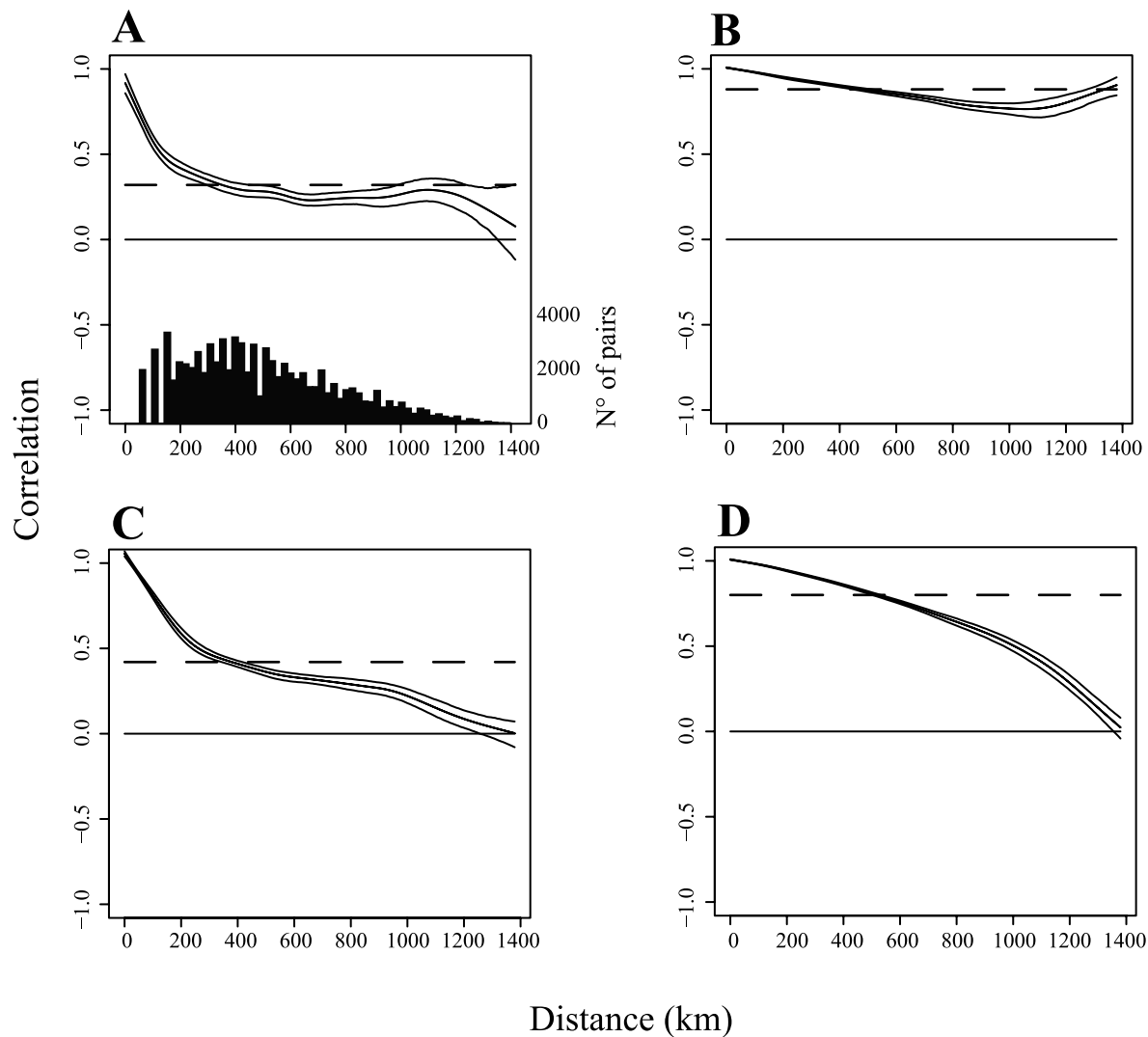


Figure 3. Nonparametric spatial covariance function on (a) tree mortality due to mountain pine beetle in British Columbia, Canada, 1959–2002; (b) minimum winter temperatures, calculated as November to March, for the same period and area; (c) spring precipitation for the same period and area; and (d) August mean temperatures for the same period and area. The y axis represents the correlation among 50×50 km cells; the x axis represents distance between the cells. Solid lines are smoothed covariance functions with 95% confidence intervals based on 1000 bootstrap replications. Dashed lines indicate average synchrony across the region. The bottom of Figure 3a shows the number of correlation pairs per distance (right y axis).

maximum intercell distances of >1400 km. Intercell correlations were always positive, and close to the regional mean even at distances of >1100 km. The shape and absolute values of the nonparametric covariance curve were largely similar to those found by Aukema *et al.* [2008] for the period 1972–1983 in the Chilcotin Plateau (see Figure 1 for location) and by Aukema *et al.* [2006] for the period 1999–2003 over the whole province (Table 1), and suggest high synchrony over the whole study area. Time-space plots (N-S and W-E transects) were an efficient way of compacting the information contained in the annual maps of MPB-caused tree mortality in BC (Figures 4 and 5), and showed different centers of MPB activity, which were corroborated by close inspection of the annual maps. A northern area of MPB has been moderately active since the early 1970s, with peaks

of area affected in the late 1980s and 1990s. This area corresponds to the northwest area of MPB activity (centered at $\sim 54^{\circ}$ – 56° N, $\sim 125^{\circ}$ – 130° ; Figure 1), and it is not clearly visible in the W-E transect because it mostly shares longitude with other active MPB areas located in central BC. Likewise, the southernmost area has also shown moderate to intense activity since the early 1960s, with peaks in the late 1980s and 1990s. This area can be divided into two main centers of action when seen in the W-E transect (Figure 5): an eastern center, which corresponds to the mountain regions of southeastern BC (former Nelson Forest Region; BC Ministry of Forests), and a central region, corresponding to south central BC (former Kamloops Forest Region; BC Ministry of Forests). Finally, the two most extensive MPB outbreaks in the record are clearly distinguishable both in the

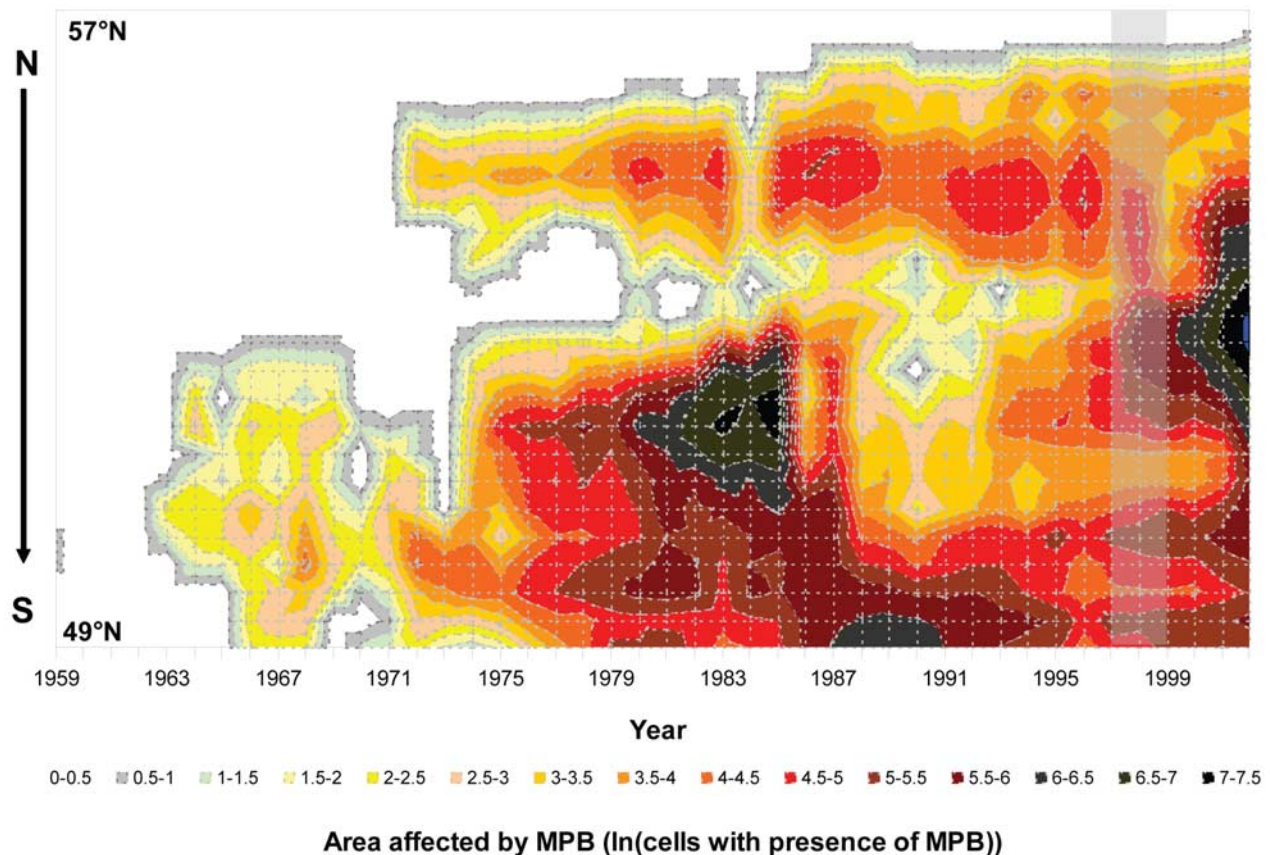


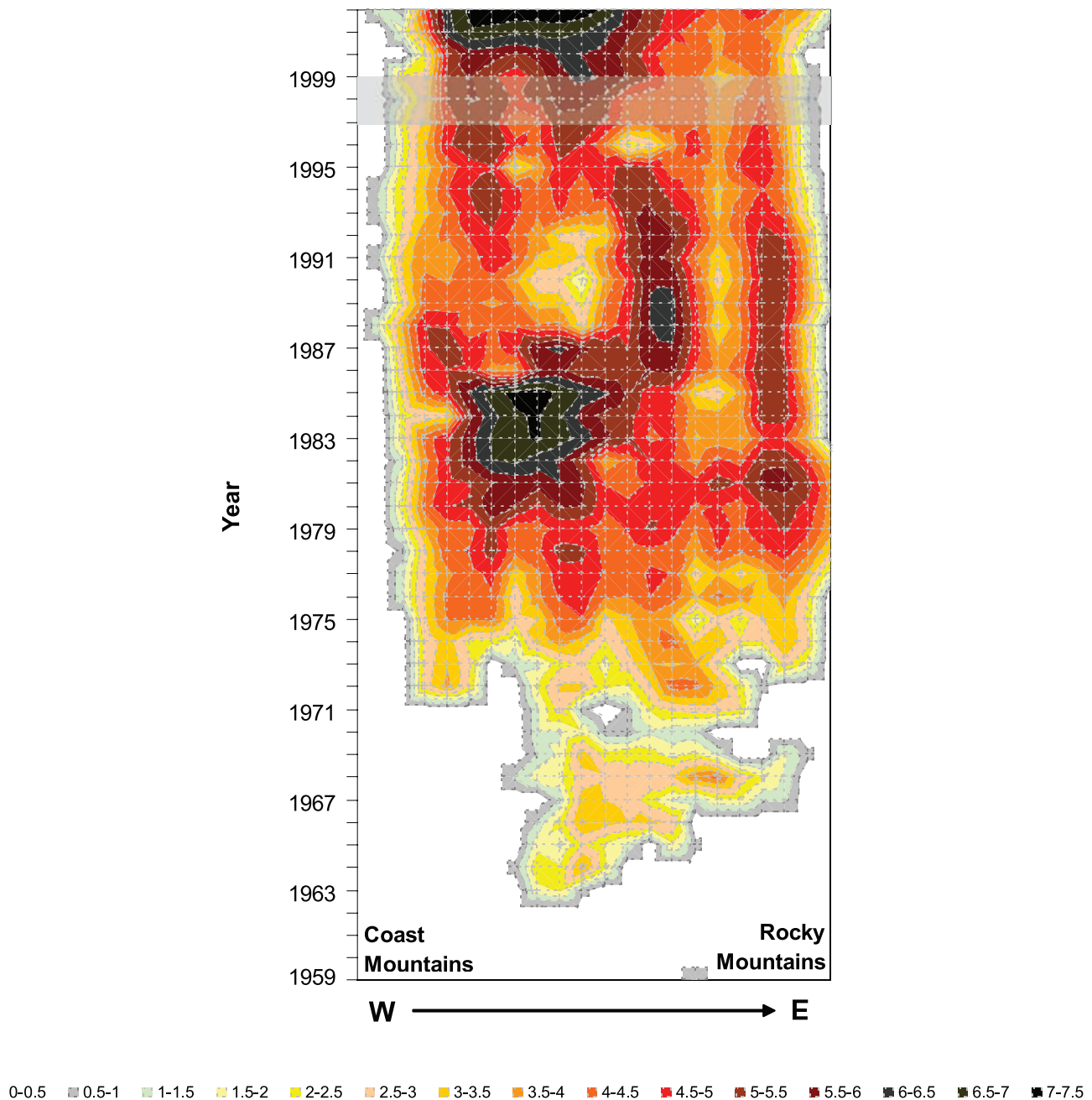
Figure 4. Time versus space plot across a N-S gradient depicting the natural logarithm of the annual totals of 2.5×2.5 km cells with area affected by mountain pine beetle across 50 km latitudinal bands (color scale; period 1959–2002). Gray-shaded area shows interpolated values for 1997 and 1998 (see text). The maximum number of cells with area affected by MPB per square (i.e., per latitudinal band per year) is 15,200, which represents a natural logarithm value of 9.6.

N-S and W-E transects: the Chilcotin outbreak [Safranyik and Linton, 1998; Stahl *et al.*, 2006] ended abruptly after 1985 and started in the late 1970s over a wide region of ~ 400 km wide in both N-S and W-E directions. The plots suggest that at least two areas in this outbreak were especially active independently (Figures 4 and 5), and the number of cells with MPB-caused tree mortality increased synchronously over a vast region. Similarly, the current outbreak (1999 to present) seems to have started synchronously over a wide region, and it is difficult to identify an epicenter of the outbreak in the data, a result found by Aukema *et al.* [2006]. In this case, the difficulty increases because two key years in the start of the outbreak are missing (1997 and 1998). The same analysis was performed with 2.5×2.5 km cells with the aim of analyzing the start of the outbreaks with the highest possible resolution (Figures S1a and S1b, available as auxiliary material), confirming our observations that the two large outbreaks started independently over a large number of cells distributed over a vast region.¹ Finally, the time-space plots also showed that the range of area affected by MPB abruptly expanded northward in the early 1970s, as previously

reported by Carroll *et al.* [2004], and that since then it has expanded in that direction ~ 100 km, with a minor 'jump' in the late 1980s.

[31] The principal components analysis identified three main modes of variability in the MPB data set. The first principal component explained 45.7% of the total variance and its loadings were very highly and positively related with all the cells of the MPB-caused tree mortality data in BC (Figure 6a). It thus represented the common variability in the data, and its scores (Figure 7b) formed virtually the same time series as the annual totals of area affected by MPB in BC ($r^2 = 0.99$). The second component (Figure 6b) explained 18.6% of the total variance and was mainly related to the timing of the two main outbreaks (Figure 7c), being negatively related to the Chilcotin outbreak of the early 1980s and positively related to the current outbreak. The loadings of the third component (Figure 6c) explained 13.7% of the total variance and represented the synchronous variability of the northernmost and southernmost areas already identified in the time-space plots; cells with positive scores in the third component (Figure 7d) showed high MPB activity in the late 1980s and 1990s in these areas. The remaining principal components had low explained variance (below 5%) and will not be further discussed here.

¹Auxiliary materials are available in the HTML. doi:10.1029/2008JG000760.



Area affected by MPB ($\ln(\text{cells with presence of MPB})$)

Figure 5. Time versus space plot across a W-E gradient depicting the natural logarithm of the annual totals of 2.5×2.5 km cells with area affected by mountain pine beetle across 50 km longitudinal bands (color scale; period 1959–2002). Gray-shaded area shows interpolated values for 1997 and 1998 (see text). The maximum number of cells with area affected by MPB per square (i.e., per longitudinal band per year) is 15,600, which represents a natural logarithm value of 9.7.

4.2. MPB Relationships With Monthly Temperature and Precipitation

[32] Both the scores of the first principal component of the data (representing the common variability in area affected by MPB) and the annual estimates of the total area affected by MPB related very strongly to winter minimum temperatures averaged over British Columbia (Table 2). Correla-

tions were significant at all the studied timescales (i.e., when using unfiltered, low-, and high-pass-filtered series). Minimum temperatures of the period November to March were more strongly related to annual estimates of MPB activity than those of the period December to February. Likewise, annual mean temperatures in BC, and especially annual minimum temperatures, showed significant relation-

Table 1. Spatial Synchrony of Tree Mortality Caused by Mountain Pine Beetle Estimated by Nonparametric Spatial Covariance Functions^a

Period	Region	Cell Size (km)	Local Synchrony		Regional Synchrony		Dist. Reg. (km)
			Estimate	95% C.I.	Estimate	95% C.I.	
1959–2002	British Columbia	50 × 50	0.92	(0.86, 0.97)	0.32	(0.29, 0.35)	348
1990–1996 ^b	British Columbia	12 × 12	0.53	(0.47, 0.58)	0.009	(0.004, 0.013)	196
1999–2003 ^b	British Columbia	12 × 12	0.71	(0.67, 0.76)	0.38	(0.35, 0.41)	289
1972–1986 ^c	Chilcotin Plateau	12 × 12	0.82	(0.74, 0.89)	0.30	(0.27, 0.32)	-

^aResults from previous studies on mountain pine beetle synchrony by *Aukema et al.* [2006, 2008] are shown for comparison. Local synchrony, synchrony extrapolated at distance equal to 0 km. Regional synchrony, regional mean cross correlation. 95% C.I., 95% confidence intervals. Dist. Reg., the shortest intercell distance in which the function equals the regional mean correlation.

^bIn the work of *Aukema et al.* [2006].

^cIn the work of *Aukema et al.* [2008].

ships with the area affected by MPB, probably because of the relationships between cold season T and MPB. Other climatic parameters previously reported to be important for MPB activity, such as spring and summer precipitation or summer temperature, did not show significant relationships with total area affected by MPB over the studied period (Table 2). Spatially, mean minimum temperatures during the cold season were positively correlated with our estimates of area affected by MPB over 91.5% of the MPB range in the province. Cold season minimum temperatures were the only climatic parameter with widespread positive correlations with MPB-caused tree mortality. Significant ($p < 0.05$) correlations occurred scattered regularly over ~25% of the range, including the regions in the southern part of British Columbia (Figure 8a), despite the strong thermal gradient between the southern and northern areas (Figure S2). Analysis of daily temperature data from meteorological stations in southern BC (Figure 9; period 1950–2000) indicated that beetle larvae mortality-causing events have occurred in interior southern British Columbia. Daily temperatures $< -37^{\circ}\text{C}$, traditionally

considered the 100% winter larvae mortality threshold [Wygant, 1942], occurred during the decade of the 1960s in all the studied stations, and Westwold and Fernie reached these temperatures also in the 1970s. One $< -37^{\circ}\text{C}$ event occurred in Princeton in the 1990s. Moreover, $< -28^{\circ}\text{C}$ daily events, considered a threshold for initial winter larvae mortality [e.g., *Moore et al.*, 2005], have occurred yearly in all the stations during the studied period.

4.3. Temperature and Precipitation Synchrony and Trends

[33] Whereas spatial synchrony in winter minimum temperatures was high across all distances (Figure 3b), it decreased with increasing distances in August mean temperatures and especially spring precipitation (Figures 3c and 3d). Overall, all climatic parameters had higher synchrony than MPB data, but at large distances (> 900 km), MPB synchrony was larger than synchrony in spring precipitation and similar to August mean temperature synchronies.

[34] Mean annual temperatures increased $\sim 1.2^{\circ}\text{C}$ on average in British Columbia during 1959–2002. The strongest

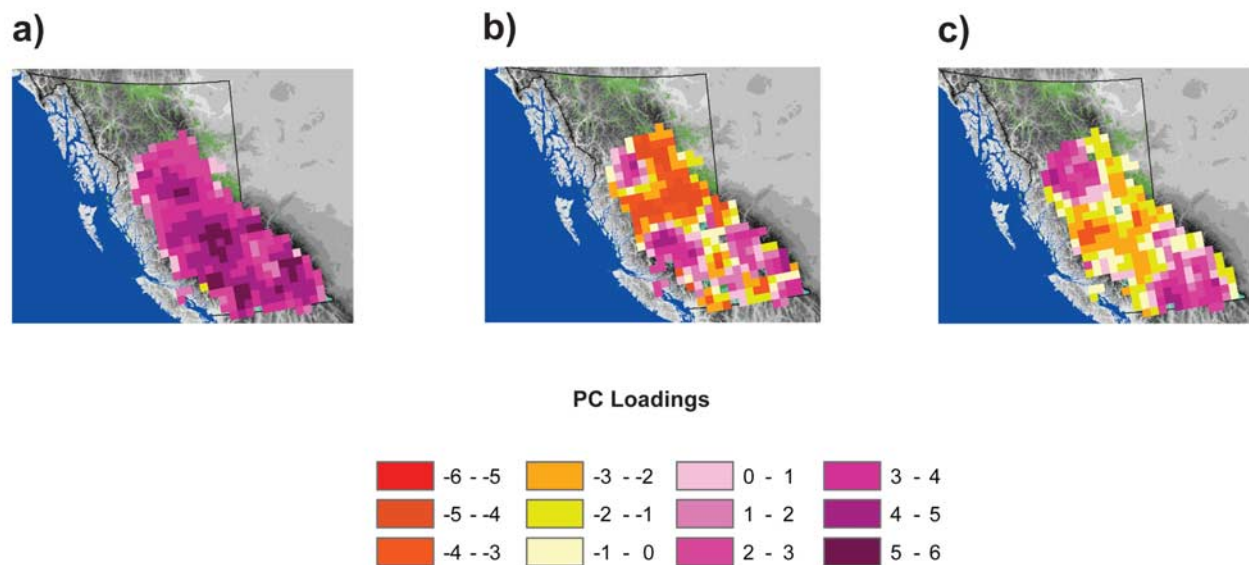


Figure 6. Principal component loadings for (a) the first, (b) the second, and (c) the third principal components from the variance-covariance matrix of the area affected by mountain pine beetle in British Columbia during the period 1959–2002. Altitude above sea level is shown in grayscale. Pine distribution is shown in green; area affected by MPB is shown in cyan.

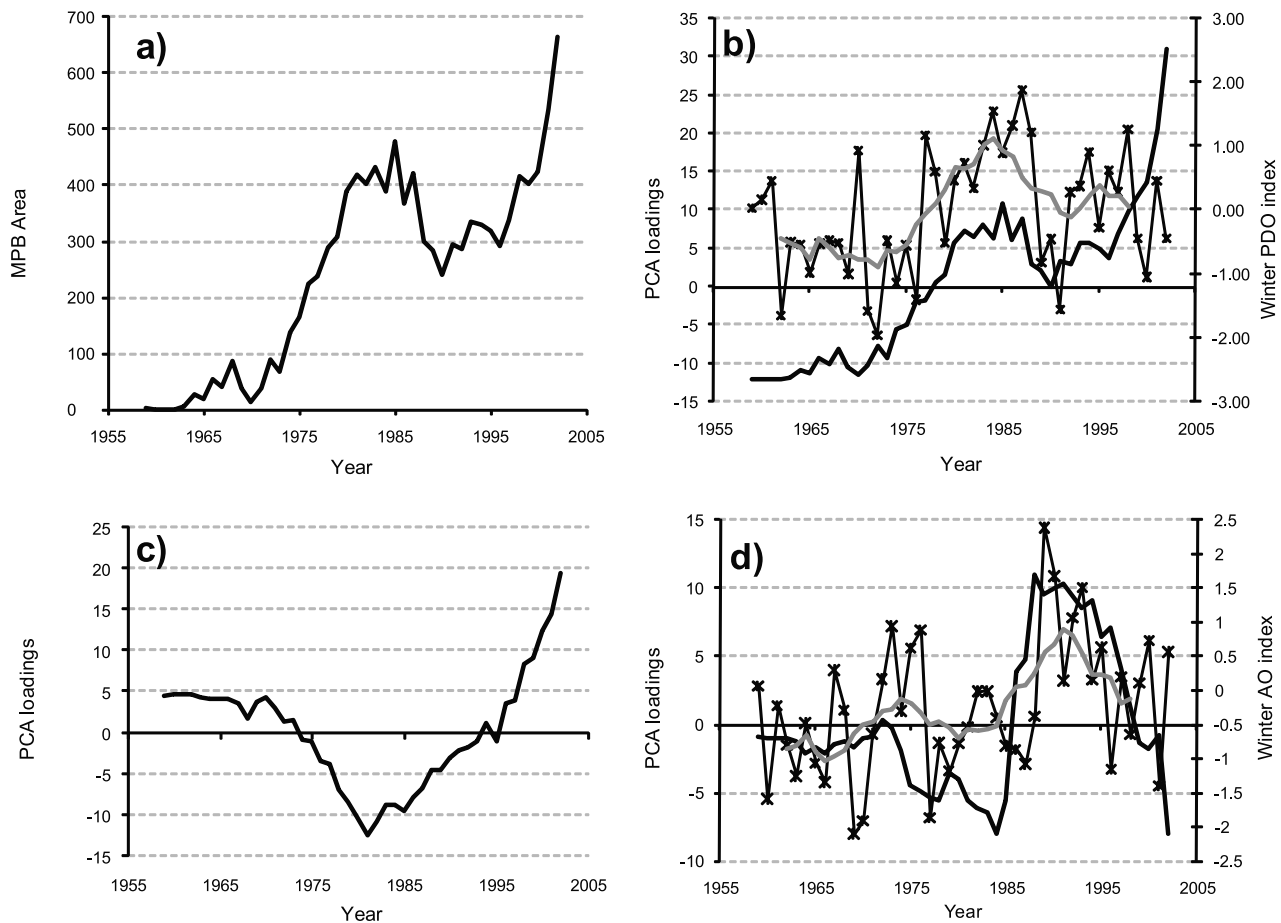


Figure 7. (a) Annual totals of MPB activity in British Columbia expressed as the sum of the \log_e of the number of cells with MPB activity in each 50×50 km cell; (b) scores of the first principal component of the mountain pine beetle variability (45.7% of the total variance; thick black line), Pacific Decadal Oscillation winter index (thin black line with marks), and a 7-year running average of the winter Pacific Decadal Oscillation index (thick gray line); (c) scores of the second principal component of the mountain pine beetle variability (18.6% of the total variance); (d) scores of the third principal component of the mountain pine beetle variability (13.7% of the total variance; thick black line), Arctic Oscillation winter index (thin black line with marks) and a 7-year running average of the winter Arctic Oscillation index (thick gray line). Period 1959–2002.

trends occurred in spring and winter (e.g., $>2^\circ\text{C}$ in winter minimums, $>1.5^\circ\text{C}$ in spring minimums; Figure 10) and the weakest in summer and autumn ($\sim 0.8^\circ\text{C}$ in both seasons). Positive anomalies over the baseline period 1959–2002 occurred in minimum, maximum, and mean temperatures, and showed a marked gradient in the SW-NE axis for all of Canada (e.g., Figure 11b). Overall, annual temperatures showed two subperiods within the study period, mainly due to the trends in the winter temperatures (Figure 10): while the first half of the period was characterized by lower than average temperatures and even decreasing trends, temperatures abruptly increased after 1976 (vertical gray line of Figure 10) and remained higher than average, with a steady increasing trend since then: this pattern was especially marked in the winter season. Precipitation anomalies showed a patchy pattern (not shown), with a general trend toward increased P in spring and summer, and decreasing P during fall and winter months (Figure S3).

4.4. Temperature and Precipitation Relationships With PDO and AO

[35] PDO and minimum, maximum and mean winter and spring temperatures in western Canada were highly correlated, with a maximum over the Yukon and Northwest Territories (winter; Figure 11a) and over British Columbia for spring. In southernmost BC, although positive, correlations were not significant (Figure 11a). Interestingly, the areas with the largest winter minimum temperature increases largely overlapped with the areas where correlations of winter T and winter PDO were highest, suggesting that winter temperature anomalies in western Canada during the last decades were at least partially caused by the positive phase of this large-scale climatic pattern. Correlations between province-averaged winter minimum temperatures and winter PDO indices showed high agreement at all the studied timescales ($r_{\text{unfiltered}} = 0.59$, $p < 0.001$; $r_{\text{low-pass}} =$

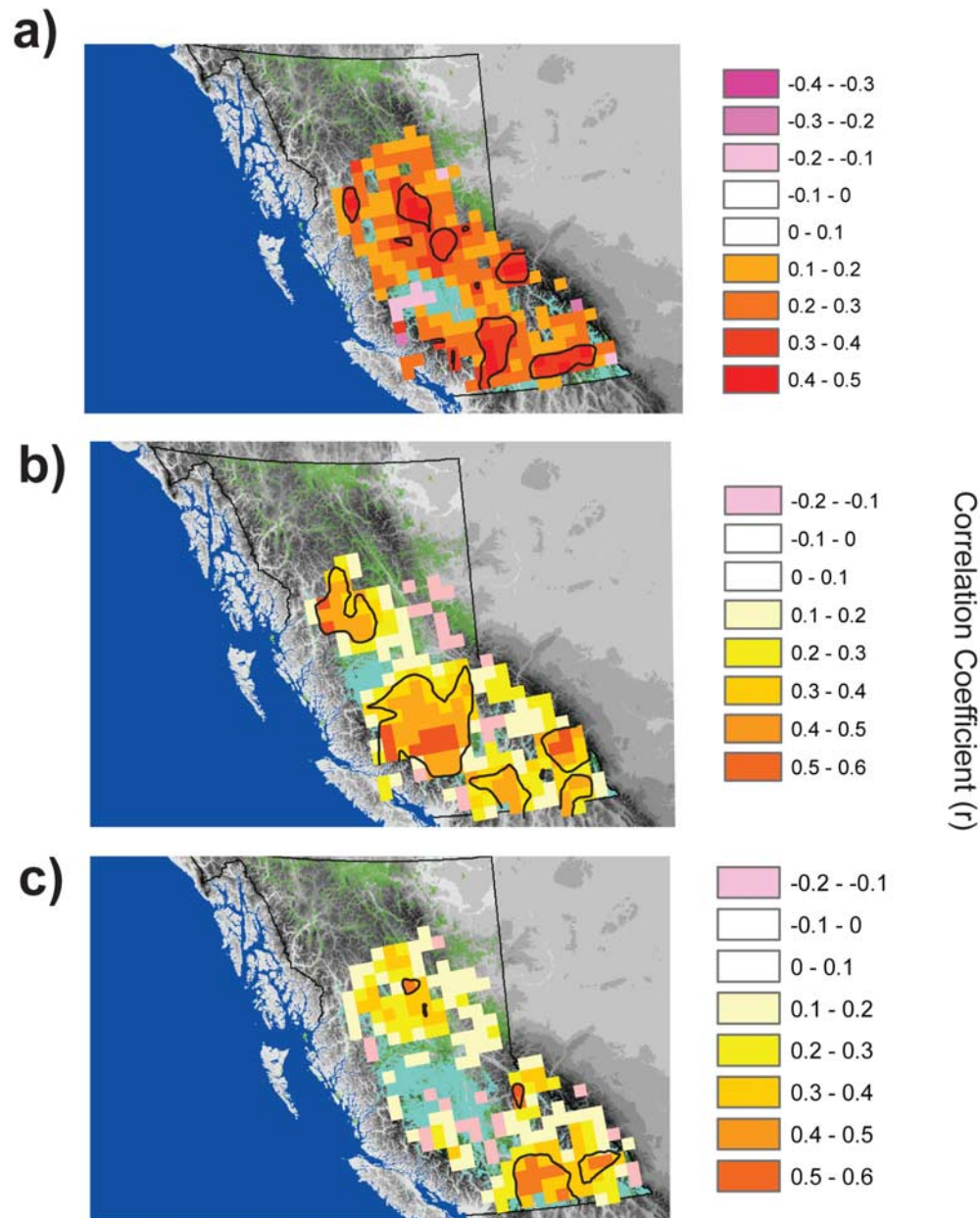


Figure 8. Pearson correlation coefficients between the 50×50 km cells with presence of area affected by mountain pine beetle-caused tree mortality and (a) cold season (defined as November to March) minimum winter temperatures, (b) the winter index of the Pacific Decadal Oscillation, and (c) the winter index of the Arctic Oscillation. Areas with $> 95\%$ significance are marked with a thick black line. Significances computed as described in Methods. Period 1959–2002. Altitude above sea level is shown in grayscale. Pine distribution is shown in green; area affected by MPB is shown in cyan.

0.77, $p < 0.05$; $r_{\text{high-pass}} = 0.60$, $p < 0.001$). PDO did not show significant relationships with summer temperatures in British Columbia (except for the coastal line), and was slightly positively related to spring and summer precipitation, especially in the southern interior in spring (not shown). Finally, the AO indices did not show significant patterns over western Canada but rather over the eastern and northeastern part of the country (not shown).

4.5. MPB Relationships With PDO and AO

[36] Both the scores of the first principal component and the area affected by MPB-caused tree mortality in British Columbia showed strong relationships with PDO indices (Table 2). Correlations were especially significant ($p < 0.01$) at low frequencies, and were positive for PDO indices of all seasons of the year, probably due to the high temporal persistence of the PDO. Winter and yearly PDO indices were the only ones related significantly with area affected

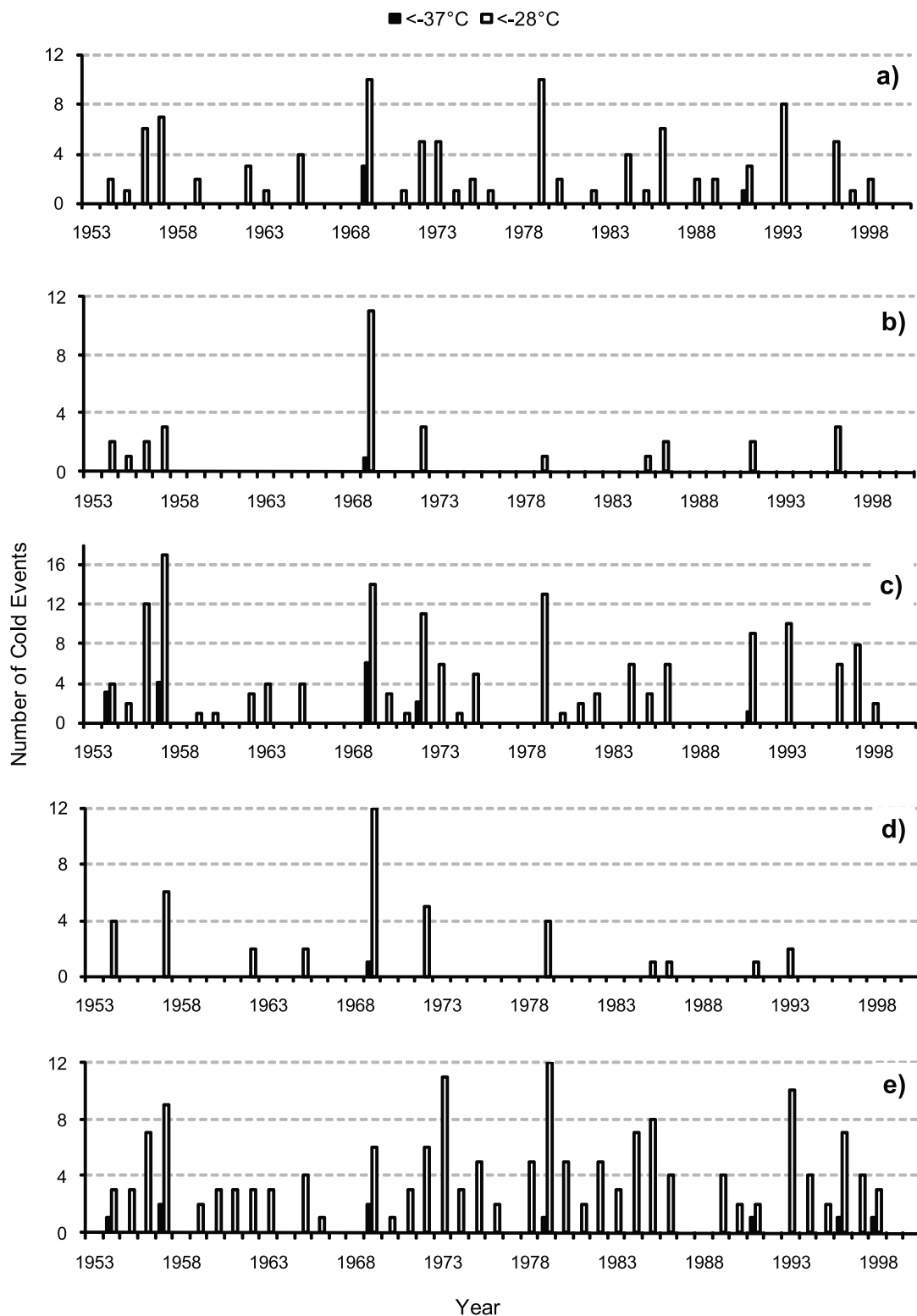


Figure 9. Occurrence of cold mortality events ($<-28^{\circ}\text{C}$ and $<-37^{\circ}\text{C}$ as defined by Wygant [1942]) in five southern British Columbia meteorological stations during the period 1950–2000; (a) Princeton, (b) Vernon, (c) Westwold, (d) Kamloops, and (e) Fernie. See Figure 1 for location of the stations on a map.

by MPB when using the unfiltered series. Correlations for the high-frequency series were low and nonsignificant. Spatially, winter PDO showed positive correlations over $\sim 80\%$ of the province (Figure 8b). Significant ($p < 0.05$)

correlations occurred over $\sim 46\%$ of the MPB range. Interestingly, the areas affected by the present outbreak did not show high correlations with PDO. This was due to the fact that these areas had not been affected by MPB during the

Table 2. Climate Versus MPB Correlations^a

	Min T Dc-Fb				Min T Nv-Mc				Min T yr				Max T sm				Mean T sm				P sp				P sm			
	U	L	H	U	L	H	U	L	U	L	H	U	L	H	U	L	U	L	H	U	L	H	U	L	U	L	H	U
MPB totals (ln)	***	0.47	0.77	0.37	***	0.53	0.88	0.41	***	0.51	0.86	0.41	***	0.51	0.86	0.41	***	0.51	0.86	0.41	***	0.51	0.86	0.41	***	0.51	0.86	0.41
PC1 (scores)	***	0.47	0.81	0.35	***	0.51	0.87	0.34	***	0.49	0.84	0.30	***	0.49	0.84	0.30	***	0.49	0.84	0.30	***	0.49	0.84	0.30	***	0.49	0.84	0.30
PC3 (scores)	N.S.	0.08	0.48	0.02	N.S.	0.10	0.49	-0.01	N.S.	0.21	0.55	-0.01	N.S.	0.21	0.55	-0.01	N.S.	0.21	0.55	-0.01	N.S.	0.21	0.55	-0.01	N.S.	0.21	0.55	-0.01

^aPearson correlation coefficients between MPB-related temporal data and climate for the period 1959–2002. U, unfiltered series; L, low-pass-filtered series; H, high-pass-filtered series (see Methods for the filtering technique); ***, significant correlation with $p < 0.01$; **, significant correlation with $p < 0.05$; N.S., nonsignificant correlation; MPB totals (ln), natural logarithm of the annual total number of cells affected by tree mortality caused by mountain pine beetle; PC1 and PC3, scores of the first and third principal components of the variance-covariance matrix applied to the mountain pine beetle data; Min T Dc-Fb, mean minimum temperature for the period December–February; Min T Nv-Mc, mean minimum temperature for the period November–March; Min T yr, mean annual minimum temperature; Mean T yr, annual mean temperature; Max T sm, mean maximum summer temperature; Mean T sm, mean summer temperature; P sp, precipitation total in spring; P sm, precipitation total in summer; Pacific Decadal Oscillation index for year (yr), winter (wt), spring (sp), summer (sm), and autumn (fil); AO, Arctic Oscillation index for year (yr), winter (wt), and summer (sm). Significance of correlation coefficients was computed taking into account autocorrelation in the series (see Methods). Correlations between the scores of PC2 and climate variables are not shown as all of them were low and nonsignificant.

period on record until 1999, and thus the actual time series in those cells largely consisted of a period with no area affected by MPB (1959–1996) followed by 4 years with large values of area affected (1999–2002). When analyzing the spatial coverage of the relationships between the PDO and the area affected by MPB for 1999–2002, the correlations appeared again over the areas affected by the outbreak, though with high uncertainty about their significance given the short period (Figure S4).

[37] Analyses of PDO versus area affected by MPB were performed using grids of smaller and larger cells. As a rule, spatial agreement between area affected by MPB and the Pacific Decadal Oscillation indices increased with increasing cell size (e.g., ~56% of the total area affected by MPB showed significant correlations ($p < 0.05$) with PDO when using the 100×100 km gridded data).

4.6. Climate and the Second and Third Modes of MPB Variability

[38] The second principal component (18.6% of the total variance) did not show any statistically significant relationship ($p < 0.05$) with climate when tested over minimum, maximum and mean seasonal temperatures, total seasonal precipitation, and both the indices of PDO and AO. The third principal component (13.7% of the total variance) showed significant relationships with the winter and annual indices of the AO, especially at low frequencies, as well as with summer temperatures (Table 2). Spatially, the regions of positive and high correlation with the AO index coincided with the spatial loadings of this component (Figure 8c), whereas no significant correlations were identified with summer temperatures when using the gridded T data (Figure S5).

5. Discussion

5.1. MPB Synchrony

[39] Large-scale synchrony in the records of area affected by MPB was suggested given (1) the large distances over which correlation between cells was positive (Figure 3a and Table 1), (2) the high variance explained by the first principal component of the variance-covariance matrix of the MPB data (45.7%), and (3) its regularly distributed, high and positive loadings over the whole MPB range in the province (Figure 6a). Persistent positive intercell correlations at distances up to >1000 km (Figure 3a) might be related to the existence of synchronous variability between the northernmost and the southernmost populations in British Columbia, visible in the time-space plot (Figure 4) and in both the spatial loadings and temporal scores of the third principal component (Figures 6c and 7d; 13.7% of the total variance). *Aukema et al.* [2006, 2008] found similar synchrony patterns during the period 1972–1983 and 1999–2003 (Table 1), which they named epidemic. Spatial synchrony measured over a longer term (1959–2002) appeared to be more similar to those periods than to the period 1990–1996, identified as endemic by *Aukema et al.* [2006] and characterized by both lower activity and spatial synchrony. The two large outbreak periods contained in the study data are probably favoring such high spatial synchrony.

[40] We found multiple and synchronous loci of origin of MPB activity during the period analyzed (Figures 4 and 5

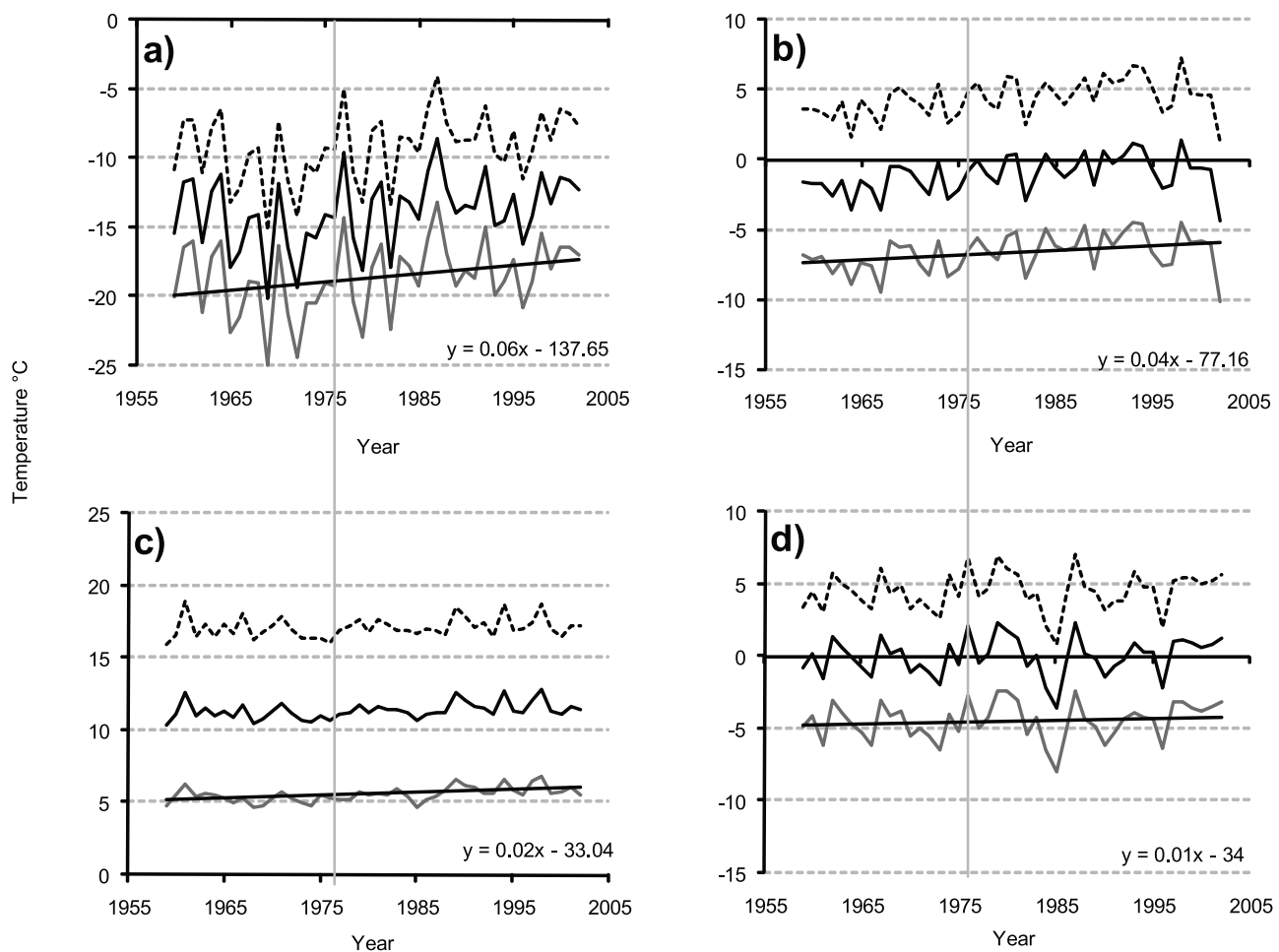


Figure 10. Seasonal temperature records (1959–2002) for maximum (dashed black line), mean (continuous black line) and minimum (continuous gray line) temperatures averaged over British Columbia; (a) winter; (b) spring; (c) summer; (d) autumn. A linear fit and the corresponding equation has been adjusted to each of the seasonal minimum temperatures. Vertical gray line indicates the year 1976, in which the PDO phase change occurred (see text for details).

and Figure S1), suggesting this species to exist at low density levels during nonoutbreak situations across the region. Visual inspection of maps of annual area affected further suggested this. This result agrees with a study by Økland *et al.* [2005], who reported MPB outbreaks in northwestern U.S.A. to have arisen independently in spatially separated subareas. Moreover, Peltonen *et al.* [2002], in a study of six different forest insect outbreak species (MPB among them), concluded that dispersal ability did not have a pronounced effect on synchrony at scales larger than 100 km.

[41] Despite this general pattern, particularly active regions of MPB activity were observed that eventually formed the two largest outbreaks in the record (the Chilcotin outbreak in the 1980s and the present outbreak), and that were captured by the second principal component (Figures 6b and 7c; 18.6% of the total variance). The present MPB data are most probably missing the spatiotemporal dynamics of endemic beetle populations, not allowing us to conclude whether the buildup of these major outbreaks was due to dispersal from outbreak-prone areas (as suggested by Aukema *et al.* [2006]) or else if differences in microhabitat

(e.g., host availability) and/or microclimate (e.g., especially warm sites) caused the outbreaks to start at different years, independently of dispersal.

5.2. MPB and Climate

[42] We found significant correlations between area affected by MPB activity and winter minimum temperatures (Table 2). Moreover, the significant relationships of PDO versus MPB and winter and spring T suggest that PDO may influence MPB activity through the occurrence of minimum temperatures that affect larvae mortality. The broad spatial coverage of such correlations (Figure 8) and the occurrence of MPB lethal minimum winter temperatures even in the southernmost parts of the province (Figure 9) further reinforce this idea. The susceptibility of MPB to cold events in late autumn and early spring [e.g., Stahl *et al.*, 2006] was reflected in their stronger relationship to winter minimum temperatures computed from November to March.

[43] A significant part of the variability in MPB (third PC, 13.7% of the total variance) was significantly related to the winter and annual AO indices (Table 2 and Figure 8c). The annual AO index mainly reflects the winter variability and

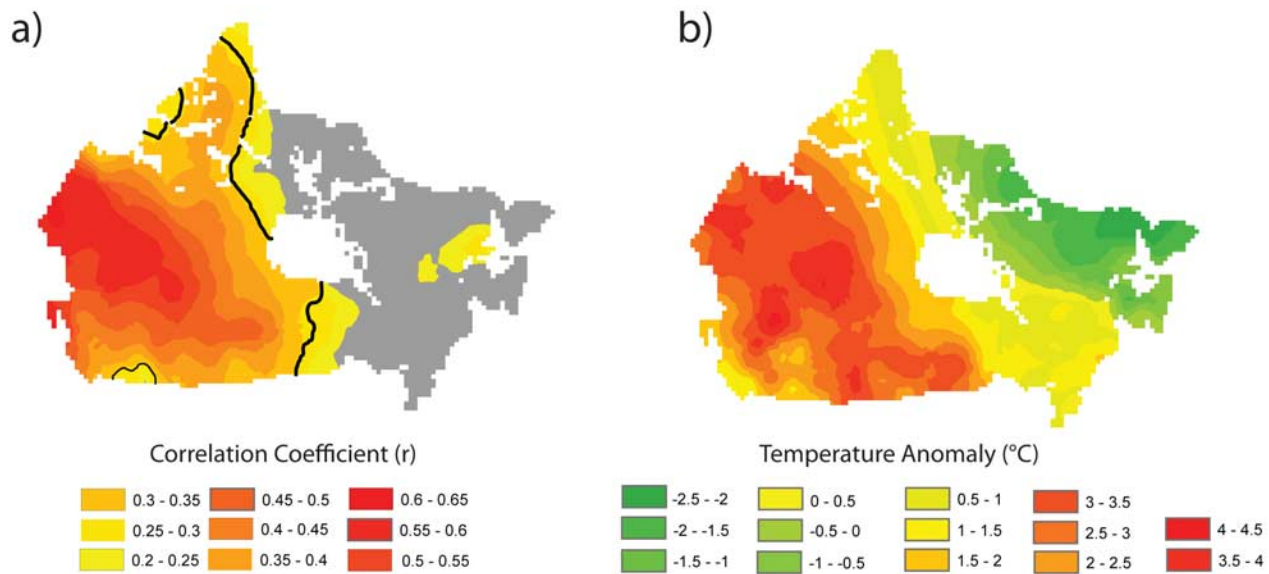


Figure 11. (a) Pearson correlation coefficients between minimum winter temperature in Canada and the winter index of the Pacific Decadal Oscillation during the period 1959–2002. Areas with >95% significance are marked with a thick black line; (b) winter minimum temperature anomalies for the period 1959–2002 in Canada.

was thus interpreted as a cold season signal. Peaks of area affected in the regions with high third PC loadings (northernmost and southernmost BC) coincided with the high and positive AO events of the late 1980s and 1990s (Figures 4 and 7d). The winter AO has been shown to be important in controlling the occurrence of extreme temperature events in British Columbia, especially in its southernmost and northernmost areas [Shabbar and Bonsal, 2004; Stahl *et al.*, 2006]. The lack of correlation between monthly temperature averages and winter AO might be because the AO is not the main driver of winter temperatures in the region and thus other analyses (such as the synoptic frequency analysis cited above) were required. Stahl *et al.* [2006] provide a good description of the synoptic-scale types of winter extreme cold events in British Columbia associated with both the PDO and the AO, which may also apply to the southernmost region of BC, where monthly winter minimum temperatures are not significantly related to winter PDO (Figure 11a), despite the fact that winter PDO is related to MPB in the area (Figure 8b). Finally, the significant relationships between the scores of the third PC and summer temperature might indicate subregional influence of this climatic variable on MPB.

[44] The coarse frequency analysis showed significant relationships occurring at all the studied timescales between MPB and winter minimum temperatures and between winter minimum temperatures and PDO. The stronger significance found at low frequencies in the relationships between MPB and PDO, and MPB and AO (Table 2) might be related with the dynamics of both PDO and AO. Whereas extreme cold temperatures directly affect MPB populations, the occurrence of a PDO or AO event only changes the probabilities of a set of climatic events to occur: during a cool PDO (or negative AO) winter, the probabilities of an Arctic air outbreak (the main cause of extreme cold temperatures in the region)

occurring in British Columbia are significantly higher than during a warm PDO (or positive AO) year, and in the case when an Arctic outbreak occurs, there are more chances that it will be extremely cold during a cool PDO year than during a warm one [Stahl *et al.*, 2006]. PDO and AO may thus be seen as low-frequency climate frameworks that influence the probability of occurrence (and thus the frequency) of climatic parameters relevant to MPB survival: the high temporal persistence of the PDO, characterized by 20–30 year phases during the twentieth century [Mantua and Hare, 2002], and the existence of an important low-frequency component in the AO [e.g., Shabbar and Bonsal, 2004], further support this idea.

[45] The synchronizing effect of density-independent stochastic factors (climate), also known as the Moran effect [Moran, 1953], has been shown in a large number of studies [e.g., Ranta *et al.*, 1997; Koenig, 1999; Bjørnstad *et al.*, 1999b]. The Moran effect was initially predicted to operate over spatially segregated populations with identical density-dependent and approximately linear dynamics [Moran, 1953; Bjørnstad *et al.*, 1999a]. This is not the case of the MPB populations in British Columbia, which are known to have nonlinear dynamics [Raffa and Berryman, 1983]. But the Moran effect has also been proposed as a potential cause for spatial synchrony in disjunct populations exhibiting far from linear dynamics and/or not showing identical density-dependent dynamics (including the mountain pine beetle [e.g., Aukema *et al.*, 2006]): previous studies have demonstrated, both theoretically and empirically, that populations far from Moran's ideal conditions can also be synchronized by spatially correlated climate [e.g., Grenfell *et al.*, 1998, 2000; Peltonen *et al.*, 2002]. Moreover, the extremely high spatial synchrony in winter minimum temperatures reinforced the idea of this climatic parameter to be an important synchronizer of MPB in the region (Figure 3b), as it

satisfies the need for a larger spatial synchrony in environmental factors to influence populations with nonlinear dynamics [e.g., *Koenig*, 2002]. The lower synchrony of spring P and the drop in synchrony of August mean T at large distances potentially exclude them as candidate synchronizer forces at a provincial scale. Moreover, the different patterns of temperature synchrony between August and winter cautions against the assumption that spatial synchrony in weather variables does not vary substantially among months [*Peltonen et al.*, 2002].

5.3. Climatic Trends in British Columbia and MPB

[46] Temperatures increased in BC during the studied period (1959–2002), especially in winter and spring (Figure 10), coinciding with the overall increase in area affected by MPB-caused tree mortality. The onset of a warm PDO phase in 1976 matches with the start of a period of large MPB outbreaks (Figures 7a and 7b): winter minimum temperatures showed two very different dynamics prior to and after the PDO regime phase shift in 1976, with higher overall values and even opposed trends after 1976 (Figure 10). Within the region of the last major outbreak, 100% mortality events (as defined by *Wygant* [1942]) have not occurred since the winter of 1996–1997 [*Stahl et al.*, 2006]. The spatial coincidence of the greatest T anomalies with the areas most strongly correlated with the PDO suggests that part of the warming trend in western North America is directly related to the onset of a warm PDO phase in 1976. Moreover, the exceptionally persistent and positive phase of the AO in the late 1980s and 1990s further enhanced MPB activity in parts of the province. The extent to which the observed T and P trends are linked to anthropogenic climate change is beyond the scope of this study and will not be further discussed. Studies on the influence of anthropogenic climate change on the AO and PDO remain inconclusive: while there is some evidence that increasing greenhouse gas concentrations will lead to a more positive AO [*Shindell et al.*, 1999; *Hoerling et al.*, 2001], observations and climate models cannot provide a definitive answer on this yet, and have failed to predict the shift of the AO to a neutral state since the late 1990s [e.g., *Overland and Wang*, 2005]. As for the PDO, too little is known so far about its mechanisms to state whether its dynamics are being affected by global warming [e.g., *Mantua and Hare*, 2002]. The same uncertainties apply to potential predictability of future dynamics of both teleconnections.

5.4. Future of MPB Outbreaks in Canada

[47] The onset of a cool PDO phase would probably reduce the decreasing trend in cold mortality events in British Columbia and hence the likelihood of large MPB outbreaks in BC. PDO data up to 2006 do not show evidence of a return of PDO to a negative phase (<http://jisao.washington.edu/pdo/>).

[48] The possibility of the current MPB outbreak spreading eastward and northward of the Canadian Rocky Mountains and into the boreal forest as a consequence of climate warming has been suggested [e.g., *Logan and Powell*, 2001; *Carroll et al.*, 2004]. Our results suggest that there is a strong relationship between the area affected by MPB in British Columbia and temperature, so that theoretically the range of MPB could expand with rising temperatures.

Indeed, time-space plots showed a northward expansion of the area affected by MPB during the studied period (Figure 4), already reported by *Carroll et al.* [2004]. However, the short temporal length of observations prevents us from stating an unprecedented MPB range expansion northward, and in any case, the data showed northward expansion of the detectable outbreaking populations [e.g., *Aukema et al.*, 2006], and not an expansion in the range of the species. The thermal gradient between the regions west of the Rocky Mountains and the boreal forest is very large, and temperatures lethal to MPB occur tens of times per year in these areas [*Stahl et al.*, 2006]. The Canadian Rocky Mountains may be more important in acting as a shelter against Arctic air invasions into British Columbia [*Stahl et al.*, 2006] than as a cold and high barrier that MPB populations have difficulties crossing (as suggested by *Moore et al.* [2005]). Only very intense Arctic air invasions are able to cross the mountains and produce cold mortality events in BC. Temperature data suggest that the actual barrier (an air mass barrier) might be located east of the Rocky Mountains past the areas in the eastern slopes of the range affected by Chinook winds which have in the past already been colonized by MPB [*Carroll et al.*, 2004; *Moore et al.*, 2005].

[49] Moreover, area burnt by wildfire, which controls the stand age distribution in the boreal forest [*Johnson*, 1992], has increased in the Canadian boreal forest during the last decades (Figure 12a), especially in its western part [*Stocks et al.*, 2002; *Gillett et al.*, 2004; *Kasischke and Turetsky*, 2006]. This has occurred in relation with the onset of the positive PDO phase in 1976 [*Macias Fauria and Johnson*, 2006; *Skinner et al.*, 2006]; host availability (i.e., mature stands) might have thus been reduced in that area, to an unknown extent that we presently have no data to quantify. This is exactly the opposite of what has occurred in British Columbia (Figure 12b), and has been suggested as a factor favoring MPB outbreaks in that region [e.g., *Taylor and Carroll*, 2003; *Moore et al.*, 2005].

5.5. Data and Analysis Constraints

[50] Results were partly constrained by the quality of the data available. The data analyzed in this study are not data on population numbers, but rather a proxy of MPB activity, as described in the Data section. In studies with spatially explicit data, cells are spatially fixed, whereas pine beetle populations are not. Thus, a given cell might have been free of MPB for a period of time and then colonized by MPB coming from a nearby cell. Thus, fixed cells, even if they contained actual population numbers, would not necessarily be accounting for real subpopulation fluctuations. Another limitation, already exposed, is the lack of host availability data: a given area might have had the right climatic conditions, but might have been lacking host individuals (either due to past resource depletion or to lack of pine in that particular region). These data constraints stress the difficulties of finding explicit and significant correlations between climate and the time series formed by these cells, and indicate why the relationships of area affected by MPB and climate increased with increasing cell sizes, from small cells to regional averages, as this integrated microhabitat differences and averaged out some of the constraints explained.

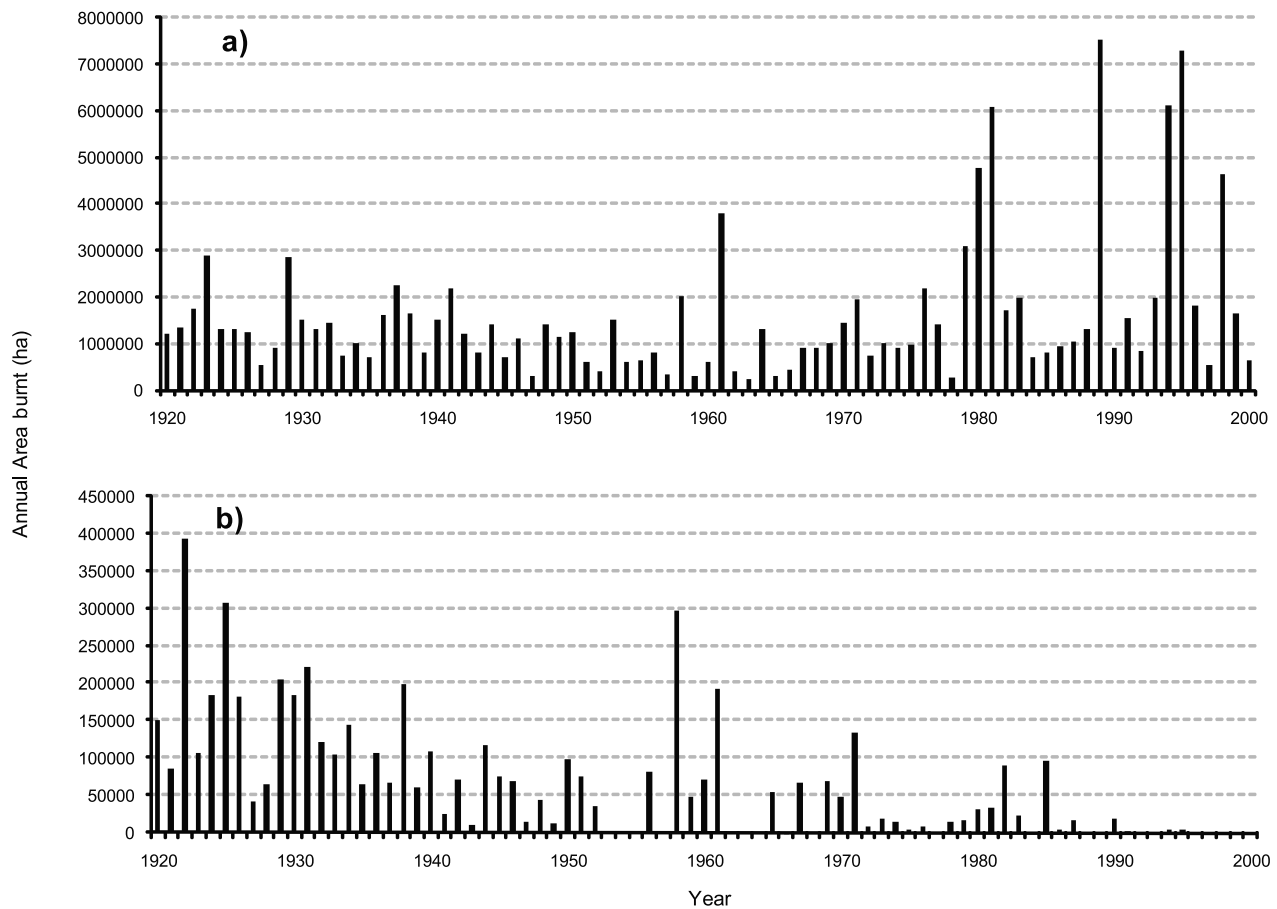


Figure 12. Estimates of annual totals of area burned (in hectares) for the period 1920–2000 over (a) the whole of Canada and (b) British Columbia. Data from *Van Wagner* [1988, 1991] and *Stocks et al.* [2002].

[51] Computational limitations due to the large amount of data used together with the lack of a daily gridded data set implied that analyses were done using climatic data averaged over time (i.e., monthly values). In this respect, the lack of correlations between climatic parameters reported to be important to MPB populations, such as spring drought or August warmth [e.g., *Carroll et al.*, 2004; *Aukema et al.*, 2008], might be in part due to the nature and scale of the methods used in the current study [e.g., *Thomson and Shrimpton*, 1984]. For example, the role of drought, reported to be important in preoutbreak situations [*Raffa et al.*, 2008], would probably not show up in correlation analysis. In any case, this limitation also applied to the study of cold season temperatures on MPB.

[52] It is also important to stress that both evidence of significant correlation with relative short time series and descriptive spatial statistics are not by themselves absolute proofs to infer causality of the relationships identified. Moreover, significance of correlations between gridded data sets should be treated with caution due to the potential effect of multiplicity [e.g., *Livezey and Chen*, 1983; *Katz*, 1988; *Katz and Brown*, 1991; *Mason and Goddard*, 2002].

[53] Finally, the use of temperature mortality thresholds for individual weather stations does not represent the wide range of temperatures experienced in the rugged and

heterogeneous landscape of southern British Columbia on a given winter day, but informs of generalized extreme cold weather in the region. Moreover, phloem temperatures may not be as extreme as air temperatures [*Bolstad et al.*, 1997] due to lag times associated with heat conduction and the insulating effects of snow cover over the lower portion of a tree trunk [*Stahl et al.*, 2006]. Therefore, threshold values of -37°C and -28°C are only indicative of cold temperatures close to known mortality values for mountain pine beetle, but should not be taken as absolute values in the present study.

6. Conclusions and Significance

[54] Spatially explicit records of area affected by MPB-caused tree mortality in British Columbia showed high synchrony across large distances. Spatiotemporal analysis of area affected by MPB activity further indicated high common variability, as seen both in time-space plots and in principal component analysis. Moreover, MPB activity seemed to start synchronously from largely separated loci located over distances of a few hundred kilometers.

[55] We showed evidence that large-scale climatic patterns (PDO and to a lesser degree the AO) are a main agent in the observed MPB synchrony and total area affected by MPB,

and suggested that they mainly operate through controlling the frequency of extreme cold winter temperatures that affect MPB larvae survival. Taken together the first (PDO-linked) and third (AO-linked) principal components, the percent of variance explained in MPB activity that can be linked to climatic variability was 59.4.

[56] A smaller portion of the data's variability (18.6%) was linked to the onset of the two largest outbreaks in the studied period and might be attributed to dispersal from outbreak-prone areas or else to differences in microhabitat (e.g., host availability) and/or microclimate (e.g., especially warm sites) in these regions.

[57] The onset of a warm PDO phase in 1976 favored MPB outbreaks by reducing the occurrence of extremely low winter temperatures. Likewise, the exceptionally high and persistent AO values of the late 1980s and 1990s enhanced MPB activity in the region. In this study we found no evidence of an influence of spring drought and summer temperature in MPB populations at a regional scale in BC.

[58] A PDO shift to a cool phase would probably stop or reduce the current outbreak of MPB by increasing the chances of cold mortality events in BC. In the absence of this, a cold spell is still possible but less probable (e.g., the cold spell of 1985/1986, probably related to a negative Arctic Oscillation configuration [Stahl et al., 2006]).

[59] **Acknowledgments.** This study was funded by an NSERC Discovery grant given to E. A. Johnson. We thank Mary L. Reid and M. Kurtis Trzcinski at the University of Calgary for their discussions on MPB biology, and John Moore and Aslak Grinstead at the University of Lapland and Samuli Helama at the University of Helsinki for help on time series analysis. We also thank Jordi Carreras and Albert Ferré at the University of Barcelona for their help in ArcGIS. We also want to thank the comments provided by an anonymous reviewer and by Barry Cooke, as they have helped to improve this manuscript.

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