Ecology, 93(10), 2012, pp. 2175–2185

Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains

TERESA B. CHAPMAN,[1,3] THOMAS T. VEBLEN,[1] AND TANIA SCHOENNAGEL[2]

[1]*Department of Geography, University of Colorado, Campus Box 260, Boulder, Colorado 80309 USA*
[2]*INSTAAR, University of Colorado, Boulder, Colorado 80309 USA*

Abstract. The current mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak in the southern Rocky Mountains has impacted ~750 000 ha of forest. Weather and habitat heterogeneity influence forest insect population dynamics at multiple spatial and temporal scales. Comparison of forest insect population dynamics in two principal host species may elucidate the relative contribution of weather and landscape factors in initiating and driving extensive outbreaks. To investigate potential drivers of the current MPB outbreak, we compared broadscale spatiotemporal patterns of MPB activity in lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) from 1996 to 2010 in Colorado and southern Wyoming with regional weather fluctuations, and then tracked the annual meso-scale progression of the epidemic in lodgepole pine with respect to weather, topographic, previous MPB activity, and forest stand attributes. MPB activity in lodgepole pine compared to ponderosa pine showed higher magnitude and extent of spatial synchrony. Warm temperatures and low annual precipitation favorable to beetle populations showed high regional synchrony across areas of both pine species, suggesting that habitat interacts with weather in synchronizing MPB populations. Cluster analysis of time series patterns identified multiple, disjunct locations of incipient MPB activity (epicenters) in lodgepole pine, which overlapped an earlier 1980s MPB outbreak, and suggests a regional trigger (drought) across this homogenous forest type. Negative departures from mean annual precipitation played a key role in subsequent spread of MPB outbreak. Development of the outbreak was also associated with lower elevations, greater dominance by lodgepole pine, stands of larger tree size, and stands with higher percentage canopy cover. After epidemic levels of MPB activity were attained, MPB activity was less strongly associated with stand and weather variables. These results emphasize the importance of considering differences in patterns of MPB dynamics for different host pine species even under similar regional-scale weather variation and the nonstationarity of outbreak dynamics over time.

Key words: bark beetle; Dendroctonus ponderosae; *epicenter; epidemic; lodgepole pine* (Pinus contorta); *ponderosa pine* (Pinus ponderosa); *Rocky Mountains, USA; spatial synchrony.*

INTRODUCTION

In the context of current warming trends, a major challenge for ecological research is the determination of the relative roles played by weather vs. underlying biophysical factors in the spread and consequences of ecological disturbances such as wildfire and bark beetles. In western North America, multiple outbreaks of several bark beetle species have caused wide-scale tree mortality in conifer forests since the early 1990s (Raffa et al. 2008). Of interest to ecologists and land managers is identification of potential mechanisms driving forest insect population eruptions across diverse landscapes. Recent research has emphasized the critical role of habitat heterogeneity and geographic variation in the landscape in influencing driving factors of insect outbreaks (Peltonen et al. 2002, Johnson et al. 2004, Liebhold et al. 2006). While scientists have identified weather variables that accelerate and facilitate forest insect development, the interaction between host tree stress, habitat structure, weather, and the onset of insect outbreaks is less understood, especially at the landscape scale (Raffa et al. 2008).

Weather-related mechanisms and population processes, such as dispersal, can drive synchronous fluctuations in insect populations with similar density-dependent structures (Liebhold et al. 2004). The potential of synchronous weather changes to synchronize populations over large distances, even at continental to global scales (Koenig 2002), was first modeled by Moran (1953) and is known as the "Moran effect" (Liebhold et al. 2004). Habitat similarity among populations can influence the magnitude and distance of synchrony of populations affected under regional driving mechanisms (Liebhold et al. 2006). Bark beetles attacking multiple host species in the same region may provide insight into the relative role of habitat structure

Manuscript received 11 June 2011; revised 16 April 2012; accepted 18 April 2012. Corresponding Editor: J. Franklin.
[3] E-mail: teresa.chapman@colorado.edu

on both weather- and dispersal-related drivers of synchronizing populations.

This study focuses on the spatiotemporal population dynamics of one native bark beetle species, the mountain pine beetle (MPB; Coleoptera: Scolytidae: *Dendroctonus ponderosae*), in the southern portion of its range, the Rocky Mountains of Colorado and southern Wyoming, USA (see Plate 1). Primary host species in this region include lodgepole pine (*Pinus contorta* var. *latifolia*), ponderosa pine (*Pinus ponderosa*), and limber pine (*Pinus flexilis*). Spatiotemporal landscape-scale studies of MPB dynamics have combined beetle populations in different host species (Peltonen et al. 2002, Okland et al. 2005, Aukema et al. 2006) or focused on patterns exclusively in lodgepole pine (Aukema et al. 2008, Fauria and Johnson 2009). The aim of the current research is to compare the spatiotemporal patterns of MPB activity within lodgepole and ponderosa pines from 1996 to 2010 to infer potential driving mechanisms and population processes of MPB population eruptions. Then, focusing on the development of a major MPB outbreak in lodgepole pine, a meso-scale analysis examines the "top-down" influence of local weather on patterns of MPB activity and the "bottom-up" influences of topography, forest structure variability, and previous MPB outbreak on the progression of an epidemic.

The typically univoltine (i.e., single year) life cycle of MPB is under direct temperature control (Bentz et al. 1991). Warmer temperatures during the August peak emergence and flight period favor beetle activity, increase stress to attacked trees (Safranyik and Carroll 2006), and speed phenological development of the beetle (Bentz et al. 1991). Extreme cold temperatures in fall, winter, and spring can increase larval mortality (Bentz et al. 1991), but cold fall and spring temperatures may be particularly influential in curtailing outbreaks because they occur when the beetles are not completely cold-hardened (Thompson 2009). Water stress lowers a tree's defenses by reducing the effectiveness of its oleoresin system and lowering the production of monoterpenes (Lusebrink et al. 2011). When warm temperatures and drought co-occur with widespread host availability, local beetle populations can erupt due to multiple positive feedbacks, including inefficacy of host defenses under increased beetle populations (Raffa et al. 2008, Boone et al. 2011).

Four stages of MPB populations are recognized: endemic, incipient epidemic, epidemic, and post-epidemic (Safranyik and Carroll 2006). The epicenter hypothesis (Royama 1992) predicts that local populations remain at endemic levels until favorable weather increases larval survival, enabling the population to escape regulation, reach very high densities, and supplement neighboring populations with dispersal. When there is a driving mechanism, such as synchronous regional weather variation across similar habitats, local increases in populations and dispersal act together to create wide-spread epidemic populations (Royama 1992).

Spatial synchrony in a broad sense measures the scale at which populations, both nearby and distant, are increasing or decreasing coincidently (Liebhold et al. 2004). It has been measured using cross correlations between population growth variables through time (Bjørnstad et al. 1999). Research addressing mechanisms of synchrony in multiple forest insect populations with various dispersal abilities, including MPB, suggests that weather is the main exogenous force (Peltonen et al. 2002), and the synchrony of populations should mirror the synchrony in influencing weather variables (the Moran effect; Moran 1953). The more rapid decline in population synchrony with increasing distance compared to the decline in weather synchrony with increasing distance has been attributed to variation in non-meteorological, bottom-up influences among populations (Peltonen et al. 2002), such as forest composition and habitat quality (Johnson et al. 2004, Liebhold et al. 2006).

Spatial pattern of outbreak development may reveal the relative importance of weather and dispersal in driving insect epidemics (Johnson et al. 2004, Aukema et al. 2006). The degree to which population increases in distant areas are due to long-distance dispersal or emergent local population growth remains uncertain (Chen and Walton 2011). Studies agree that short-distance dispersal (<2 km) is the most dominant form of MPB infestation spread (Safranyik et al. 1992, Chen and Walton 2011). Researchers theorize that rapid population growth, regardless of source populations, will initially depend on favorable local weather (Aukema et al. 2008, Chen and Walton 2011). Dispersal from epicenters, particularly long-distance dispersal by wind, becomes increasingly important in the spread of the epidemic and can lead to temporally sustained outbreaks and range expansion (Robertson et al. 2009). Multiple, disjunct locations of increased MPB-caused tree mortality (epicenters) in the onset of an epidemic may reflect the influence of regionally favorable weather in triggering and/or sustaining population growth (Aukema et al. 2006, Fauria and Johnson 2009). Epicenter locations are associated with higher habitat quality and connectivity (Johnson et al. 2004) and sometimes with protective land-management practices, such as wilderness areas (Aukema et al. 2006). Stand age, tree diameters, and tree density strongly influence stand susceptibility to beetle attack; mature, larger trees in denser stands are preferentially attacked in both lodgepole and ponderosa hosts (Negron and Popp 2004, Safranyik and Carroll 2006). Weather differences at locations of outbreak initiation previously have not been quantified. These epicenters may also be associated with previous outbreaks and be non-transient (Johnson et al. 2004, Fauria and Johnson 2009). Thus, we explore the possibility that MPB outbreak progression may be influenced by local weather, topographic, forest structure variability, and/or the presence of previous MPB outbreak.

To address the relative roles of top-down and bottom-up influences on the spatiotemporal patterns of recent MPB activity in southern Rocky Mountain region we asked: (1) How does the spatial synchrony of MPB activity compare between the host species and with spatial synchrony of regional weather variation? (2) What were the regional weather conditions conducive to the development of the MPB outbreak? (3) And, did the current MPB epidemic originate at multiple locations or diffuse from a single location? Then in the lodgepole pine host only, we asked: (4) How was the development of the MPB outbreak associated with spatial patterns of local weather variation, topographic variables, forest attributes, or previous MPB outbreak?

Methods

The study area in the southern Rocky Mountains of Colorado and southern Wyoming extends from 37°–42.5° N and 109°–105° W, and includes land that is either within U.S. Forest Service (USFS) Region 2 or Rocky Mountain National Park (RMNP). It spans ~2500–4000 m in elevation and includes both monotypic lodgepole pine forests and mixtures of lodgepole pine with Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasciocarpa*), and aspen (*Populus tremuloides*). In these subalpine forests high-severity fire is the key broadscale disturbance that creates even-aged populations of lodgepole pine (Sibold et al. 2006). In a small portion of the lower elevations of its range, lodgepole pine can be mixed with Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine.

Although ponderosa pine forests occur at elevations as low as ~1600 m, our study area is limited to USFS lands and RMNP, where ponderosa pine forests occur mainly between ~2500 and 2900 m. The vegetation composition of ponderosa pine forests varies from low-elevation, open stands with a grassy understory to denser, more even-aged stands at higher elevations, where it is found with Douglas-fir. The ponderosa pine zone is characterized by a mixed-severity fire regime resulting in a relatively fine-grain mosaic of stand ages and composition (Sherriff and Veblen 2007) in comparison with typically large patches of homogeneous forest structure in the subalpine zone (Sibold et al. 2006).

Data processing

Spatial analyses were implemented in ArcInfo 9.3 Geographic Information System (GIS) with Python programming language (*available online*)[4] and conducted in the North American Datum 1983 Universal Transverse Mercator Zone 13 North projection. The distributions (in 100 × 100 m grids) of lodgepole and ponderosa pine were determined from a regional vegetation database compiled from U.S. Forest Service vegetation layers and a RMNP vegetation layer (Appendix A). Vegetation layers were created from manual photo interpretation of 1-m resolution color aerial photographs taken in 2002 (scale 1:24 000 and 1:12 000, respectively). Vegetation attributes used were: (1) dominant tree species cover, (2) size class depicting mean diameter at breast height (dbh) for the dominant canopy species, and (3) cover class estimating the percent canopy cover.

A time series of Aerial Detection Survey (ADS) maps from 1996 to 2010 indicating tree mortality attributed to MPB was used to estimate the presence of MPB (U.S. Forest Service 2010; Appendix A). Mortality caused by MPB is detected by the change in the color of the needles from green to red, which occurs the year following attack by beetles, resulting in a one-year lag between tree mortality detection and MPB attack. ADS maps (scale 1:24 000) delineate polygons of insect-caused forest mortality by host and insect species and are created by manually digitizing areas during forest flyovers. From the ADS polygons, we created two grids (100 × 100 m resolution) of MPB presence in lodgepole or ponderosa pine.

Grids recording MPB presence for each host were overlaid with the corresponding pine distribution grid for cross-validation. Pixels of MPB that overlaid pixels of pine presence are referred to as MPB presence; ones that did not were omitted from the analysis (74.5% ± 3.0% of total reported area included each year, mean ± SD). To determine an index of MPB activity, the area of MPB-caused tree mortality (MPB presence) was divided by the area of pine (pine presence) for each host category within 8 × 8 km grid cells. A resolution of 8 km captures landscape-scale patterns of MPB activity, while averaging the effects of small-scale patch dispersion within the 2-km short-dispersal range of MPB (Safranyik et al. 1992). MPB activity pixels that did not document the presence of MPB from 1996 to 2010 in at least one year and did not have at least 200 ha pine presence were excluded. Grids (8 × 8 km) of MPB presence in the 1980s were created from georectified hand-drawn ADS maps of an MPB outbreak in Colorado in 1982–1985.

We used weather variables generated by the Parameter-elevation Regressions on Independent Slopes Model (PRISM) in which monthly weather data are estimated over a contiguous grid at a resolution of 0.0416 decimal degrees latitude and longitude (~4 km) cells (Daly et al. 2002; Appendix A). To evaluate the potential relationship of MPB activity with weather, we used mean annual precipitation (Annual PPT), August mean maximum temperature (August maxT), October mean minimum temperature (October minT), January mean minimum temperature (January minT), and March mean minimum temperature (March minT). Weather analyses were adjusted to account for the one-year lag between infestation and needle fade as well

---

[4] www.python.org

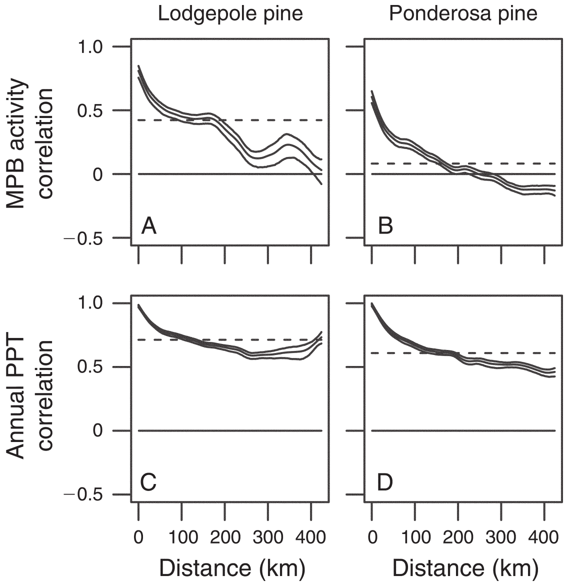

FIG. 1. Pairwise cross correlations between time series in relationship to distance (nonparametric covariance function estimates) of (A) the log of mountain pine beetle (MPB, *Dendroctonus ponderosae*) activity (measured by hectares of tree mortality per hectares of host area) in lodgepole pine (*Pinus contorta*; 554 grid cells, ~150 000 pairs), (B) ponderosa pine (*Pinus ponderosa*; 430 grid cells, ~90 000), (C) annual precipitation for the lodgepole pine grid cells, and (D) annual precipitation for the ponderosa pine grid cells, in the southern Rocky Mountains of Colorado and southern Wyoming, USA. Upper and lower 95% confidence intervals were determined with 500 bootstrap resamples. Dashed horizontal lines indicate average correlation (regional synchrony). Local synchrony is the *y*-intercept. Data sources: USFS region 2 aerial detection surveys 1996–2010 (U.S. Forest Service 2010), R2VEG (USDA 1998, data in Figs. 1–4 were obtained by request from specific National Forests) and ROMOVEG (USGS 2009), and SNCF R package (Bjørnstad et al. 1999).

as the univoltine life cycle of MPB life cycle: thus Annual PPT, August maxT, and October minT were analyzed from 1994 to 2008 and January minT and March minT from 1995 to 2009. Climate averages and standard deviations for each grid cell were created for the 30 years (1964–1993) preceding the current MPB activity. Each grid cell (8 × 8 km) of MPB activity was assigned the average value of the four nearest climate cells using a bilinear interpolation for every year.

Analytical methods

Spatial synchrony of MPB activity was quantified using a nonparametric spatial covariance function with a smoothing spline (Bjørnstad et al. 1999) in R (*available online*).[5] The logarithm of MPB activity in each year was used to calculate cross correlations between all pairs in the time series. The midpoint of each grid cell provides the spatial reference. Confidence intervals around the covariance functions were created from 500 bootstrap resamples. The maximum distance for the spatial correlation was the width of the study area (424 km). We compared the distance and magnitude of spatial synchrony for MPB activity in lodgepole and ponderosa pine and corresponding weather variables.

The spatial development of MPB activity through time in lodgepole and ponderosa pine was analyzed separately with a spatial K-means cluster analysis, using the Hartigan and Wong (1979) algorithm in R (see footnote 5) and the 15-year time series of MPB activity as the input. The number of clusters was subjectively determined based upon the most parsimonious number of clusters with the most distinct time series patterns. Cluster types were mapped onto the study region in a GIS for visual interpretation of the spatial arrangement. The MPB activity (mean ± SE) of each cluster type was calculated and plotted.

To determine if the spatiotemporal pattern of MPB activity reflects differences in local weather, topographic variables, forest attributes, or previous MPB outbreak, we employed several methods. First, to determine the meso-scale weather influences on the location of outbreak progression, we graphically explored differences in Annual PPT between cluster types for each year of the study. Second, to assess relationships between topographic and forest structure variables with MPB presence, GIS spatial overlays were performed. MPB presence in lodgepole pine grids (100 × 100 m) in each year of the time series were overlaid with grids of the same resolution for each of the variables for the entire study extent. Four stand variables were analyzed by this method: elevation, composition, dbh, and canopy cover. The expected area was based on an overlay of the lodgepole pine presence grid with each variable, resulting in the distribution of that variable across the covertype. The expected area assumes that MPB will be found in proportionally similar distributions if the pattern is random. The observed area was based on an overlay between cumulative MPB presence during years of subjectively differentiated weather signatures: 1996–2001, 2002 –2005, and 2006–2010. Third, to quantify the percentage overlap between previous 1980s MPB outbreak and the current outbreak, we overlaid the results of the cluster analysis with the grid of 1980s MPB presence.

RESULTS

How does the spatial synchrony of MPB activity compare between host species and with spatial synchrony of regional weather variation?

Regional synchrony of MPB activity varied between lodgepole and ponderosa pine (Fig. 1A, B). MPB activity in lodgepole pine had a higher regional synchrony (0.42, $n = 554$) with positive spatial correlation up to 424 km for the 15-year time series, indicating that populations across the entire study area increased and subsequently decreased coincidently. MPB activity in ponderosa pine had a lower regional synchrony (0.08,

---

[5] www.r-project.org

$n = 430$) with negative spatial correlation at distances >248 km, indicating that MPB activity in some localized areas increased simultaneously with decreases elsewhere. The local synchrony (i.e., as the distance approaches 0 km) was also higher in lodgepole pine than in ponderosa pine (0.80 and 0.58, respectively), suggesting that neighboring MPB populations in lodgepole pine behaved more similarly and possibly had greater dispersal between 8-km cells.

Regional synchrony of annual precipitation and temperature variables in areas of both host species showed both a high magnitude and extent of spatial synchrony. The regional synchrony of Annual PPT in lodgepole pine hosts was 0.71 and in ponderosa pine hosts was 0.61 (Fig. 1C, D). Analyzed weather variables showed high local synchrony (>0.97) and high regional synchrony (spatial correlations >0.59) across areas of lodgepole pine and ponderosa pine (Appendix B).

What were the regional weather conditions conducive to the development of the MPB outbreak?

In contrast to MPB presence in ponderosa pine, which remains low until a modest upsurge in 2010, MPB presence in lodgepole pine began a sharp acceleration into a regional epidemic in 2003 (Fig. 2A). In the distribution of lodgepole pine, Annual PPT is below average in 1994 and in 2001–2002 but returns to near average in 2003–2010 (Fig. 2B). The 2001 and 2002 years of below Annual PPT coincided with a four-year period (2000–2004) of above average August maxT, and throughout the 15-year period August maxT was above or near average in each year (Fig. 2C). During the 15-year time period of elevated MPB presence, minimum temperatures considered were either above average or near average (Fig. 2D–F). January minT did not fall more than 0.5 SD below average in any year, and in 2003 was ~4°C above average (Fig. 2E). In the lodgepole pine area, October minT fluctuated around the average through 2002, and in 2003 shifted into a much warmer phase through 2009 (Fig. 2D). Similarly, March minT was warmer in 2003–2007 and did not fall far below average for the entire length of the study (Fig. 2F). Although Annual PPT and August maxT return to average after 2002 and 2003, respectively, and remain near average for at least three years (Fig. 2B, C), there is no corresponding decline in MPB presence in lodgepole pine (Fig. 2A).

Did the current MPB epidemic originate at multiple locations or diffuse from a single location?

Time series of MPB activity in lodgepole and ponderosa pine identified through cluster analysis showed distinct spatiotemporal trends in MPB activity both between and within pine hosts during the years 1996–2010 (Fig. 3). Four distinct cluster types for MPB activity in lodgepole pine (cluster types Lp I–IV) and three distinct cluster types for MPB activity in ponderosa pine (cluster types Pp I–III) were identified. Cluster

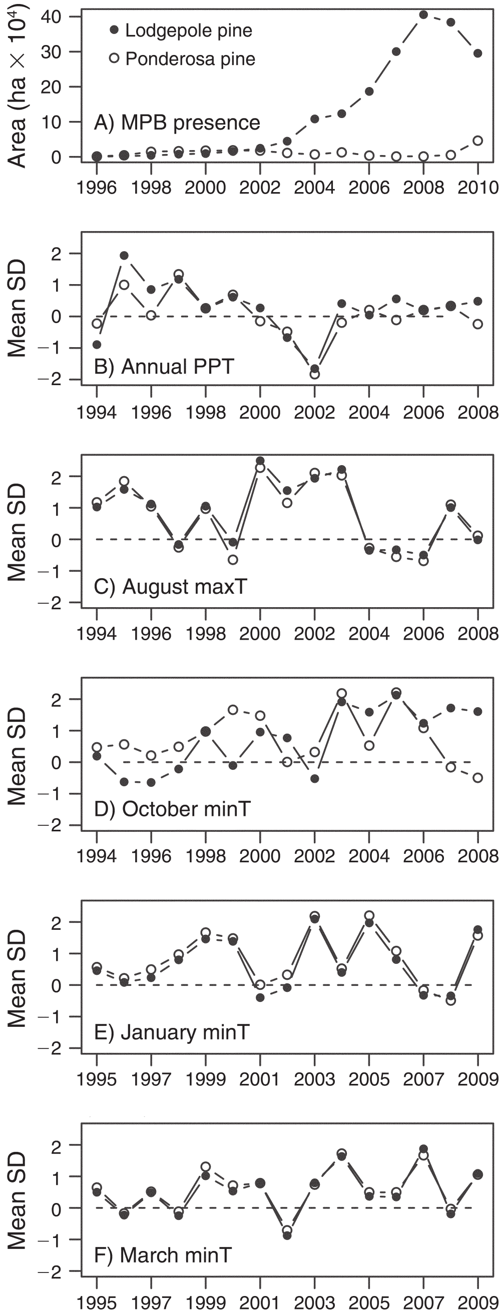

FIG. 2. Plots of (A) MPB presence (area in hectares of current year MPB-caused tree mortality) in the southern Rockies from 1996 to 2010 in lodgepole pine and ponderosa pine, and annual mean standard deviations of weather variables from the 30-year period prior to increased beetle activity (1964–1993) for areas of MPB activity in lodgepole pine ($n = 554$ 8 × 8 km grids) and in ponderosa pine ($n = 430$ 8 × 8 km grids), (B) annual precipitation (PPT), (C) August mean maximum temperature (maxT), (D) October mean minimum temperature (minT), (E) January mean minimum temperature, and (F) March mean minimum temperature. Values shown are the man standard deviation of the parameter for each year. Data sources: PRISM gridded climate 1964–2009 (Daly et al. 2002), USFS region 2 aerial detection surveys 1996–2010 (U.S. Forest Service 2010), and R2VEG (USDA 1998) and ROMOVEG (USGS 2009).

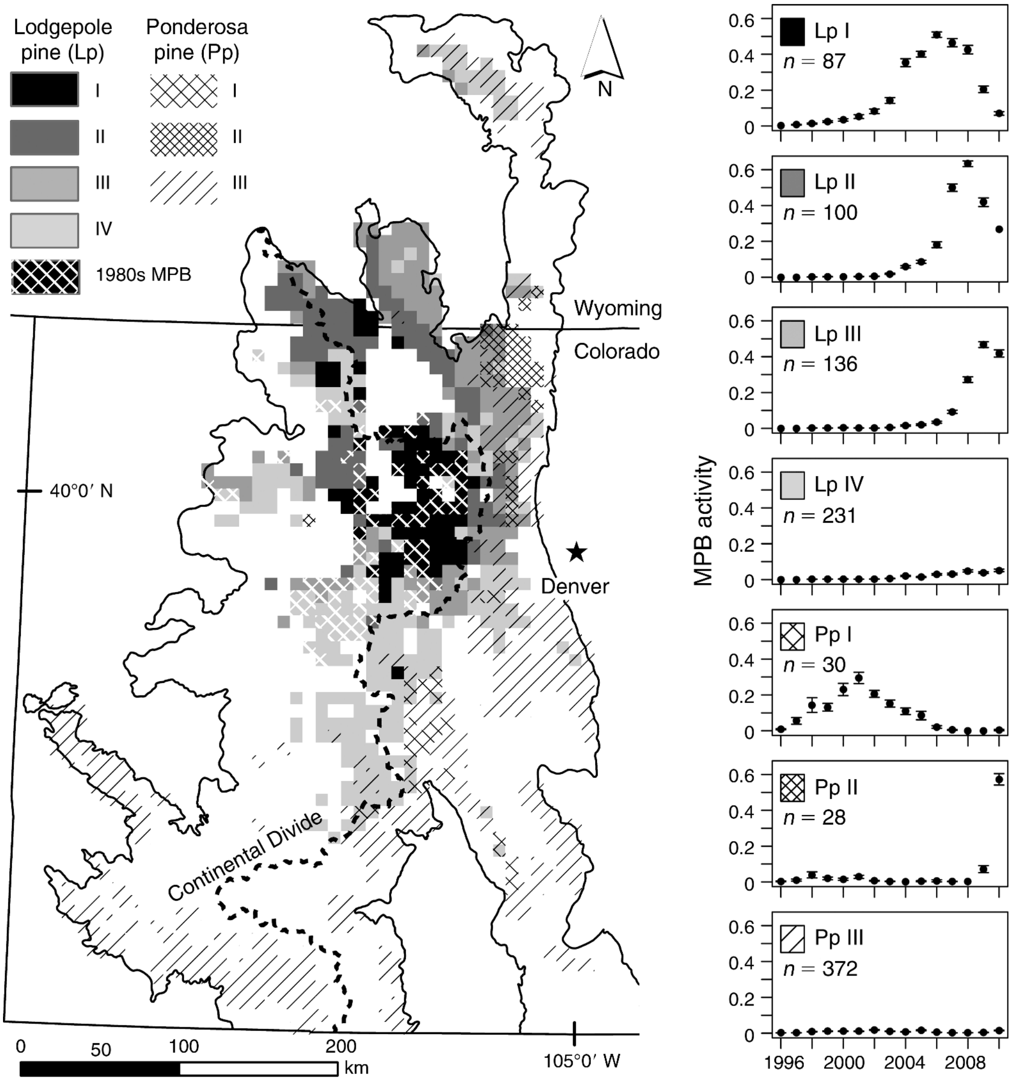

FIG. 3. K-means cluster analysis of time series of MPB activity in 8 × 8 km pixels, defined as the area of MPB presence weighted by the total pine area, in lodgepole pine ($k = 4$) and in ponderosa pine ($k = 3$) of the southern Rocky Mountains in Colorado and southern Wyoming, USA. Time series of MPB activity for each cluster type (lodgepole pine; Lp I–IV and ponderosa pine; Pp I–III) are graphically presented in association with the spatial location. Areas of current outbreak overlay areas of 1980s MPB presence. Data sources: R2VEG (USDA 1998), ROMOVEG (USGS 2009), USFS aerial detection surveys 1982–1985 and 1996–2010 (U.S. Forest Service 2010).

types Lp I–III show a gradual wave of increasing MPB activity, with each type characterized by a later peak (Fig. 3). Cluster type Lp I showed the earliest signs of elevated tree mortality from 1996 to 2002, reached a peak between 2005 and 2006, and began declining in 2007 (Fig. 3). These areas of earliest MPB activity did not indicate a single origin of the current epidemic, but instead multiple epicenters of elevated, incipient beetle populations of MPB activity across a broad central region of Colorado. These epicenters were widespread on the western side of the continental divide with at least one epicenter on the eastern side of the divide and were separated by distances as great as 100 km (Fig. 3). Cluster type Lp II began to show increases in MPB activity in 2004 and peaked in 2007. Cluster type Lp III exhibited a similar slight increase in 2007 and started declining in 2010. Most of cluster type Lp IV Lp was found either on the eastern side of the continental divide or farther south and only showed a minor increase in MPB activity after 2006. Together these cluster patterns revealed that the outbreak originated in multiple, disjunct locations, and diffused across time to cover the entire area of lodgepole pine.

The mapped clusters of temporal trends in MPB activity in ponderosa pine revealed two spatially and temporally distinct and less severe outbreaks (Fig. 3). Cluster type Pp I consisted of scattered areas that exhibited a peak in MPB activity in 2000 and 2001 and then began to decline. This pattern was on the eastern side of the continental divide, was separated by distances up to ~100 km, and was not proximate to areas of early MPB activity in lodgepole pine (Fig. 3). Cluster type Pp II did not show a sharp increase in MPB activity until 2010 and was proximate to areas of epidemic MPB in lodgepole pine on the northeastern slope of the Front Range.

How was the development of the MPB outbreak in lodgepole pine associated with spatial patterns of topographic variables, forest attributes, local weather variation, or previous MPB outbreak?

The spatiotemporal patterns of MPB outbreak in lodgepole pine became less predictable and more random over time with regard to topographic, forest, weather, and previous MPB outbreak variables. The outbreak grew from lower to higher elevations, from stand composition and structures historically associated with MPB to stands with attributes less associated with MPB, from locally drier to locally wetter weather, and from areas previously attacked by MPB in the 1980s to areas with less known previous MPB outbreak. From 1996 to 2001, MPB presence occurs more often than expected between 2500 and 2900 m and less often than expected at 2900–3900 m (Fig. 4A). Over time, however, the differential occurrence of MPB with elevation declined. Initially, in 1996 to 2001 higher than expected MPB presence is associated with stands with larger tree diameters, higher percentage canopy covers, and greater lodgepole pine forest composition (Fig. 4B–D). Only forest composition remained nonrandom over time, with pure lodgepole stands preferentially infested with respect to mixed stands. MPB presence became increasingly random with respect to diameter class and canopy cover, as stands with smaller trees and lower percentage canopy covers were attacked.

Lodgepole pine included in cluster type Lp I (epicenters) received less annual precipitation than lodgepole pine included in cluster type Lp II. Median values of Annual PPT in cluster type Lp I were lower in all 15 years than cluster type Lp II (Appendix C). Cluster type II Lp consistently had the highest levels of annual mean precipitation in comparison to all other cluster types (Appendix C). Although the 1980s MPB outbreak was centered toward the southern extent of the current outbreak, 39% of the epicenter cluster type Lp I overlapped it (Fig. 3). Cluster types Lp II and III, both of which are characterized by high but later peaking MPB activity and are located toward the northern end of the current outbreak, overlapped the 1980s outbreak

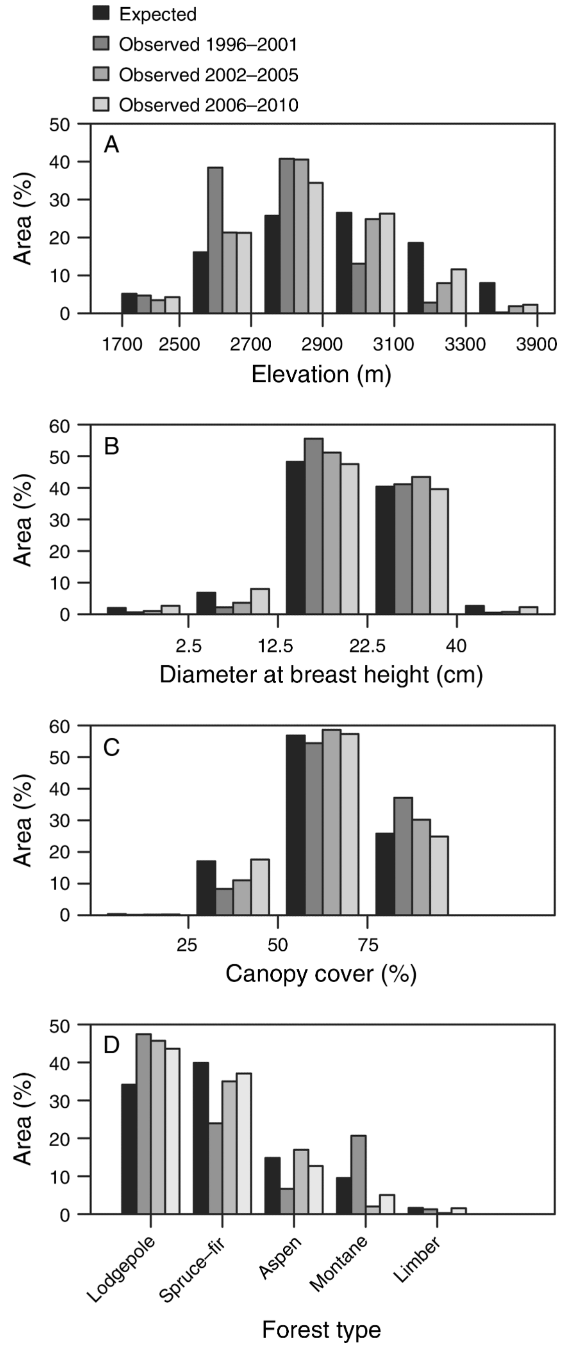

FIG. 4. Spatial overlay analysis of MPB presence and topographic and forest structure variables. MPB presence in lodgepole pine grids (100 × 100 m) in each year of the time series were overlaid with grids of the same resolution for each of the variables for the entire study extent to create the observed MPB presence. The expected area was based on an overlay of the lodgepole pine presence grid with each variable, resulting in the distribution of that variable across the covertype. Values for (A) elevation, (B) diameter at breast height, (C) canopy cover, and (D) forest type are represented as the percentage in each bin of total expected areas and observed areas of MPB presence for three time periods during the outbreak: 1996–2001, 2002–2005, and 2006–2010. The group of years is based on different weather signatures during the 15-year period (Fig. 2). Percent departures are determined by negative or positive deviations from the expected percentage in each range. Data sources: R2VEG (USDA 1998), ROMOVEG (USGS 2009), USFS aerial detection surveys 1996–2010 (U.S. Forest Service 2010), and national elevation data set (USGS 2010).

←

by 15% and 7%, respectively (Fig. 3). Cluster type Lp IV showing only minor increases in MPB activity and located to the south overlapped 37.5% with the 1980s MPB outbreak.

Discussion

At a broad scale, weather conditions from 1994 to 2009 were highly favorable to MPB activity and are reflected in the spatiotemporal development of the MPB epidemic in lodgepole pine forests in Colorado and southern Wyoming. Specifically, the linkage of MPB activity to weather is illustrated by the following patterns: (1) MPB activity increased synchronously over large distances that are greater than the beetle's annual dispersal ability; (2) weather variability was highly synchronous throughout the region; (3) synchronous weather fluctuations included conditions known to be favorable to MPB activity; (4) the initiation of the outbreak occurred in multiple locations across a wide spatial extent, suggesting a regional driving factor rather than a single, local triggering event; and (5) over time, the outbreak in lodgepole pine spread from lower to higher elevations and from stands with previously studied attributes of higher susceptibility to stands of formerly lower susceptibility (e.g., smaller trees). At later stages in the outbreak, the continuation of MPB activity appears less dependent on the initial severe drought that triggered the outbreak and more dependent on the lack of extreme cold that could induce high beetle mortality. Despite the lessening of drought conditions, the area of MPB presence in lodgepole pine continued to increase at a steep rate. Although a single outbreak constitutes a sample size of one, multiple epicenters of beetle activity separated by extensive distances in the development of the outbreak strengthen the argument that weather was regionally driving population sizes.

The strong influence of weather on MPB activity in ponderosa forests is also inferred from the synchronously favorable weather over broad areas and widely separated areas of elevated MPB activity. However, dissimilarity in spatiotemporal patterns of MPB activity between hosts implies that MPB population dynamics in these two pine species can operate differently. During the initial stages of the outbreak (1996–2001), patterns of MPB activity in lodgepole pine and ponderosa pine were separated by extensive distance and the continental divide. Despite similarity in regional weather fluctuations affecting areas of both lodgepole and ponderosa pine, either local habitat conditions or the responses of MPB populations to weather did not result in an outbreak in ponderosa pine from 1996 to 2008 of comparable magnitude to the outbreak in lodgepole pine. However, after 2008, a localized but intense increase in MPB activity in ponderosa pine initiated in the northern Front Range in areas overlapping with epidemic populations in lodgepole pine.

The most notable difference between MPB activity in lodgepole and ponderosa pine hosts is the magnitude and range of spatial synchrony. Some previous research found that bark beetle species have generally lower regional synchrony than other erupting forest insect populations (Peltonen et al. 2002, Okland et al. 2005). However, research comparing time periods of incipient and epidemic populations of MPB reported high levels of synchrony during outbreaks (Aukema et al. 2006), particularly when focusing exclusively on MPB in lodgepole pine (Aukema et al. 2008). The discrepancy in these previous results may be due to aggregating MPB activity in hosts that have very different spatiotemporal patterns of insect epidemiology. Ponderosa pine is a suitable host species of MPB, and may provide greater MPB brood survival and productivity than other suitable hosts (Amman 1982). To date research has not found genetic differences between MPB in different hosts in the same geographic region (Mock et al. 2007). We suggest that the apparently greater synchronization of MPB activity in lodgepole forests under regionally favorable weather is most likely due to the largely homogeneous structure of the host forests (Fig. 4). Most lodgepole forests in north-central Colorado established after fires in the second half of the 19th century (Sibold et al. 2006) creating vast areas of tree size classes known to be most susceptible to MPB attack 100–150 years later (Safranyik and Carroll 2006). Ponderosa pine is characterized by both low-severity fires and patches of high-severity fires, creating a more diverse landscape mosaic across broad regions (Sherriff and Veblen 2007).

Previous studies have also suggested that temperature may be more influential than precipitation in synchronizing distant MPB populations because of its generally higher synchrony and slower decline over distance (Peltonen et al. 2002, Fauria and Johnson 2009). However, the current study found high levels of regional synchrony in mean annual precipitation, especially across host lodgepole pine forests. This finding suggests that precipitation, in addition to winter and summer temperatures, may be influential in conjunction with temperature in contributing to MPB synchrony. The weather condition most likely triggering the initiation of incipient MPB populations in lodgepole was drought. In 2001–2002 many regions of Colorado experienced one of the most severe droughts in the past 500 years (Pielke et al. 2005). Warming trends across Colorado since 1900, with a steeper rise in temperatures in the last 50 years (Ray et al. 2008), in combination with continued annual and supra-annual variability in precipitation will likely continue to be conducive to MPB epidemics.

Time series analysis revealed epicenters with the earliest increases in MPB activity. Elevated MPB activity in these areas would have been highly influenced by favorable weather conditions such as severe droughts in 1994 and 2001–2002. Time series maps show that MPB activity was elevated across large areas west of the continental divide prior to 2003. The marked increase in MPB activity represented by cluster type Lp II after the 2002 drought probably also reflects strong contributions

PLATE 1. (Left) Mountain pine beetle damage to lodgepole pine on the western side of the Continental Divide in Rocky Mountain National Park (USA), demonstrating the severity of mortality in this region. (Right) Mountain pine beetle attacking a lodgepole pine, which is trying to pitch out the beetle with resin production. Photo credits: Michael Wente.

due to dispersal from neighboring epicenters and localized population growth under favorable weather. The last areas of lodgepole pine to experience high MPB activity (cluster types Lp III and IV) reflect continued massive dispersal of beetles under near average precipitation conditions but continued lack of extreme cold events. The localized MPB activity in ponderosa pine in southern Colorado (cluster type Pp I) was also most likely triggered by extreme warm and dry weather in the late 1990s and early 2000s. However, it appears that the post-2008 rise in MPB activity in northern Colorado in ponderosa pine (cluster type Pp II) is directly related to the surge of beetles moving eastward in wind currents and aggregating with previously low local populations. The temporal lag in peak MPB activity of Lp I–IV and Pp II cluster types may demonstrate traveling waves of outbreak (Johnson et al. 2004).

Epicenters of MPB activity in lodgepole pine appear to be associated with drier habitats at lower elevations that may be more conducive to higher endemic MPB populations in water-stressed hosts. This is implied by greater MPB activity at lower elevations during 1996–2001 following the 1994 triggering drought, and is further substantiated by the overlap of the 1980s MPB outbreak with the epicenters of the current outbreak. Despite substantial tree mortality from 1980 to 1986 in the overlap area (Lessard et al. 1987), large populations of lodgepole pine were still vulnerable to attack during the more severe current outbreak. The growth of the outbreak in cluster type Lp II areas, which includes moister habitats (Appendix C), may have been facilitated by the extreme drought of 2001–2002 in combination with beetle dispersal from epicenters. Cluster type II areas do not greatly overlap with the 1980s outbreak, and the spread of the epidemic into these forests may have marked a threshold as typically less susceptible forests (wetter, higher elevation) became susceptible to attack during extreme drought.

Extremely cold winter temperatures increase beetle mortality and may curtail outbreaks (Lessard et al. 1987, Aukema et al. 2008, Fauria and Johnson 2009, Thomson 2009). In Colorado, minimum temperatures have significantly warmed during the 20th century (Ray et al. 2008), and the current epidemic is concurrent with 15 years when mean minimum temperatures in the critical months of October, January, and March did not fall below approximately –0.5 standard deviations from the 30-year average. Although our study only examined mean temperatures, hourly phloem temperatures measured on lodgepole pines at ~40° S in our study area from 1991 to 2004 showed that minimum winter temperatures did not approach levels shown in experimental studies to be lethal to MPB (Malm 2009). Cold thresholds for killing beetles during fall and spring are less extreme than winter thresholds because larvae are still feeding and may not be sufficiently cold-hardened (Thomson 2009). Warm October temperatures can also enhance winter survival, as larvae can reach more advanced instar stages, which increases their cold tolerance (Bentz et al. 1991). The last MPB outbreak in lodgepole in central Colorado from 1980 to 1986 is thought to have ended abruptly following lethal October temperatures in 1983 and 1984 (Lessard et al. 1987, Malm 2009). In the present study, the persistently high mean minimum temperatures in January, October, and March appeared highly favorable to MPB populations by potentially reducing cold-induced mortality in all seasons.

In conclusion, broadscale regional weather variation seems to be the dominant extrinsic driver influencing MPB activity in Colorado and southern Wyoming in both lodgepole and ponderosa pine forests. Warm winter temperatures may create a prolonged period of reduced larval mortality, while regionalized droughts and warm summer temperatures may trigger MPB populations to switch from endemic to incipient-epidemic and, in the case of lodgepole pine, to epidemic population levels. However, the effect of weather drivers appears conditioned by the bottom-up influences of habitat heterogeneity and landscape-level variation in host composition during the initiation of outbreaks.

This spatiotemporal analysis showed that MPB activity in lodgepole and ponderosa pine hosts differed considerably over the period from 1994 to 2010. Lodgepole pine forests tend to be more homogeneous in forest composition and age structure, whereas ponderosa pine forests tend to have a more heterogeneous forest composition and age structure. This heterogeneity in forest structure potentially results in distinct intrinsic factors that significantly affect the growth and spread of local MPB populations. The current study showed that MPB activity in ponderosa and lodgepole pine hosts was distinctive during the onset of the current outbreak in lodgepole pine, suggesting that patterns observed in one host forest type cannot be simply extrapolated to the other host type. Recent outbreak in ponderosa pine will likely have a different development pattern than has been seen in lodgepole pine and will require additional study. Understanding the drivers of MPB activity in forests dominated by each host species requires host-specific studies and may be complicated by the positive feedbacks of epidemic MPB populations.

ACKNOWLEDGMENTS

We thank the USDA Forest Service and Rocky Mountain National Park for providing GIS data for this project. This research was supported by National Science Foundation award 0743498.

LITERATURE CITED

Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology 11:590–593.

Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. D. Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. Ecography 31:348–358.

Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickley, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography 29:427–441.

Bentz, B. J., J. A. Logan, and G. D. Amman. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Canadian Entomologist 123:1083–1094.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427–432.

Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research 41:1174–1188.

Chen, H., and A. Walton. 2011. Mountain pine beetle dispersal: spatiotemporal patterns and role in the spread and expansion of the present outbreak. Ecosphere 2:1–17.

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99–113.

Fauria, M. M., and E. A. Johnson. 2009. Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. Journal of Geophysical Research 114:G01012.

Hartigan, J. A., and M. A. Wong. 1979. A K-means clustering algorithm. Applied Statistics 28:100–108.

Johnson, D. M., O. N. Bjørnstad, and A. M. Liebhold. 2004. Landscape geometry and travelling waves in the larch budmoth. Ecology Letters 7:967–974.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. Ecography 25:283–288.

Lessard, G., D. Hildebrand, and D. E. Haneman. 1987. Forest pest conditions in the Rocky Mountain Regions 1986. USDA Forest Service, Rocky Mountain Region, Timber, Forest Pest and Cooperative Forest Management, Lakewood, Colorado, USA.

Liebhold, A. M., D. M. Johnson, and O. M. Bjørnstad. 2006. Geographic variation in density-dependent dynamics impacts the synchronizing effect of dispersal and regional stochasticity. Population Ecology 48:131–138.

Liebhold, A. M., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution, and Systematics 35:467–490.

Lusebrink, I., M. I. Evenden, F. G. Blanchet, J. E. K. Cooke, and N. Erbilgin. 2011. Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. Journal of Chemical Ecology 37:1013–1026.

Malm, K. 2009. Phenological predictions and the relationship to population growth rates for mountain pine beetle populations in northern Colorado. Thesis. University of Colorado, Boulder, Colorado, USA.

Mock, K. E., B. J. Bentz, E. M. O'Neill, J. P. Chong, J. Orwin, and M. E. Pfrender. 2007. Landscape-scale genetic variation in a forest outbreak species, the mountain pine beetle (*Dendroctonus ponderosae*). Molecular Ecology16:553–568.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. Australian Journal of Zoology 1:291–298.

Negron, J. F., and J. B. Popp. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. Forest Ecology and Management 191:17–27.

Okland, B., A. M. Liebhold, O. N. Bjørnstad, N. Erbilgin, and P. Krokene. 2005. Are bark beetle outbreaks less synchronous than forest Lepidopteran outbreaks? Oecologia 146:365–372.

Peltonen, M., A. M. Liebhold, O. N. Bjørnstad, and D. W. Williams. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83:3120–3129.

Pielke, A. E., Sr., N. Doesken, O. Bliss, T. Green, C. Chaffin, J. D. Salas, C. A. Woodhouse, J. J. Lukas, and K. Wolter. 2005. Drought in Colorado: an unprecedented drought or a routine drought? Pure and Applied Geophysics 162:1455–1479.

Raffa, K. F., B. H. Aukema, J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Ray, A. J., J. J. Barsugli, and K. B. Averyt. 2008. Climate change in Colorado. Western Water Assessment Conservation Board. http://wwa.colorado.edu/CO_Climate_Report/index.html

Robertson, C., T. A. Nelson, D. E. Jelinski, M. A. Wulder, and B. Boots. 2009. Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. Journal of Biogeography 36:1446–1458.

Royama, T. 1992. Analytical population dynamics. Chapman and Hall, London, UK.

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 *in* L. Safranyik and B. Wilson, editors. The mountain pine beetle: a synthesis of its biology, management, and impacts on lodgepole pine. Canadian Forest Service, Pacific Forestry Centre, Natural Resources Canada, Victoria, British Columbia, Canada.

Safranyik, L., D. A. Linton, R. Silversides, and L. H. McMullen. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology 113:441–450.

Sherriff, R. L., and T. T. Veblen. 2007. A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. Ecosystems 10:311–323.

Sibold, J. S., T. T. Veblen, and M. E. Gonzalez. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography 32:631–647.

Thomson, A. J. 2009. Climate indices and mountain pine beetle-killing temperatures. Forestry Chronicle 85:105–109.

USDA. 1998. R2VEG. USDA Forest Service Region 2 Integrated Resource Inventory. http://www.fs.usda.gov/detail/r2/landmanagement/gis/?cid=stelprdb519523

U.S. Forest Service. 2010. USDA Forest Service, Rocky Mountain Region—Aerial Survey Data Download. http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629

USGS [U.S. Geological Survey]. 2009. Rocky Mountain National Park vegetation mapping project—spatial vegetation data. http://biology.usgs.gov/npsveg/ftp/vegmapping/romo/romogeodata.zip

USGS [U.S. Geological Survey]. 2010. The national map. http://nationalmap.gov/viewer.htm

SUPPLEMENTAL MATERIAL

Appendix A

Information on GIS data layers used in the analysis (*Ecological Archives* E093-206-A1).

Appendix B

Results of spatial synchrony in MPB activity and climate variables (*Ecological Archives* E093-206-A2).

Appendix C

Descriptive boxplots of annual mean precipitation for each cluster type (I–IV) of MPB activity in lodgepole pine (*Ecological Archives* E093-206-A3).