Factors Influencing the Spatial and Temporal Dynamics of Engelmann Spruce Mortality during a Spruce Beetle Outbreak on the Markagunt Plateau, Utah

R. Justin DeRose and James N. Long

Abstract: Host conditions are known to influence spruce beetle population levels, but whether they influence the spatial and temporal patterns of beetle-caused mortality during an outbreak is unknown. Using dendrochronological techniques, we quantified the spatiotemporal dynamics of a modern (late 1980s through the early 2000s) spruce beetle outbreak in Engelmann spruce on the Markagunt Plateau, Utah. Erupting beetle populations occurred in multiple areas across the Plateau over the course of ~8 years. Early in the outbreak, the timing of spruce mortality was strongly and predictably related to latitude, slope, aspect, stand structure, host species composition, and site productivity potential. Exogenous forcing from landscape-scale drivers such as winter minimum temperatures, summer maximum temperatures, and landscape-wide host suitability probably contributed to spruce beetle population success and heightened spruce mortality. As the outbreak progressed, the timing of spruce mortality became less well correlated to stand and environmental variables. The outbreak subsided when suitable host material was depleted, including smaller spruce in remote stands at the fringe of the spruce-fir zone. Tests for spatial and temporal autocorrelation of beetle-cased spruce mortality did not provide strong evidence for the common perception that spruce beetle outbreaks originate in a specific location (epicenter) and then "spread" across the landscape; rather, support for positive spatial synchrony of multiple, building populations during development of the outbreak was found. Based on these results, silvicultural intervention before the onset of an outbreak might mitigate Engelmann spruce losses; however, the same is almost certainly not true later in an outbreak of this scale and magnitude. FOR. SCI. 58(1):1–14.

Keywords: *Dendroctonus rufipennis*, *Picea engelmannii*, silviculture, spatial covariance function, spruce-fir, time-series analysis

POPULATIONS OF SPRUCE BEETLE (*Dendroctonus rufipennis* Kirby) represent a pervasive natural disturbance process in Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) forests of western North America. Veblen et al. (1994) determined that spruce beetles were a more dominant disturbance agent than stand-replacing fire in spruce communities in Colorado. Several studies have documented the effects of epidemic spruce beetle populations on Engelmann spruce communities (Schmid and Hinds 1974, Veblen et al. 1991, DeRose and Long 2007), but, despite their importance in structuring Engelmann spruce-subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests, there has been limited study of what factors might influence the spatiotemporal pattern of Engelmann spruce mortality over the course of an outbreak.

Like mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, it is likely that the conditions necessary for a spruce beetle outbreak to occur include (1) an endemic population of spruce beetles, (2) suitable weather, (3) susceptible and available host material, and (4) escape from natural enemies (Raffa et al. 2008). The simultaneous occurrence of these conditions is influenced by the multiscale interaction of various processes so that once beetle populations build to epidemic numbers, thresholds associated with multiple conditions must be surpassed before an outbreak can occur (Raffa et al. 2008). Inciting or risk factors such as wind (Schmid 1981), logging activities (Reynolds and Holsten 1994), or avalanches (Hebertson and Jenkins 2007) fell trees and facilitate the building of endemic beetle populations to epidemic levels. In addition, recent work has suggested that warm weather was probably responsible for epidemic beetle populations in Alaska, regardless of other risk factors (Berg et al. 2006). Pheromone-mediated mass attack for the spruce beetle can occur once the temperature threshold for daily flight is met (i.e., ~16°C; Dyer 1973). During late spring or early summer, adults begin boring into the bark where they mate. Afterward females deposit eggs in galleries constructed in the phloem, and larvae feed horizontally, consuming phloem. A 2-year (semivoltine) life cycle is considered typical, with brood passing the first winter as prepupae and a second as adults (Schmid and Frye 1977, Hansen et al. 2001a). Relatively warm conditions, such as those at low elevations or southerly bole aspects, can accelerate development to a 1-year (univoltine) life cycle with the adult stage being reached before the first winter (Massey and Wygant 1954, Schmid and Frye 1977).

Manuscript received June 17, 2010; accepted January 19, 2011. http://dx.doi.org/10.5849/forsci.10-079.

R. Justin DeRose, Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230—Phone: (801) 625-5795; rjustinderose@gmail.com. James N. Long, Utah State University—james.long@usu.edu.

Acknowledgments: We acknowledge the Ecology Center, the T.W. Daniel Endowment, and the Intermountain Region Digital Image Archive Center for support of this study. This research was also supported by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah. Approved as journal paper no. 8168.

Furthermore, relatively warm summer weather can shift a local population from the semivoltine to univoltine cycle, resulting in accelerated beetle population growth and host mortality (Werner and Holsten 1985, Hansen et al. 2001b, Hansen and Bentz 2003). Conversely, winters with extremely low temperatures can drastically reduce the survival of larvae (Frye et al. 1974).

Availability of susceptible host is important for sustaining a spruce beetle outbreak (Reynolds and Holsten 1994). In the central and southern Rocky Mountains, this is typically mature Engelmann spruce >30 cm dbh because the spruce beetle prefers large trees for successful brood production (Schmid and Frye 1976). However, individual trees are not sufficient to maintain epidemic populations; extensive and dense Engelmann spruce stands must be present on the landscape for large outbreaks to occur. Schmid and Frye's (1976) spruce beetle hazard ratings consider susceptible stands to have large average spruce diameter (>40 cm mean dbh), high densities (>14 $m^2\ ha^{-1}$ basal area [BA]), and a large percentage of spruce (>65%). In Alaska, slower growing white spruce (*Picea glauca* [Moench] Voss) (i.e., low radial increment) and trees on drier sites have been found to be more vulnerable to spruce beetle attack (Hard 1985, 1987, Doak 2004), and this may also be true for Engelmann spruce in the Rocky Mountains. Reduced spruce radial increment may be a result of increasing stand density, climatic stress such as drought, or growth differences associated with topographic position (e.g., warmer southwest-aspect versus cooler northeast-aspect stands). Stand susceptibility characterizes the likelihood that spruce beetle populations will shift from endemic to epidemic populations (Schmid and Frye 1976, Hard et al. 1983). It is possible that attributes associated with susceptibility may also influence the spatial pattern and timing of spruce beetle-caused spruce mortality during an outbreak. For example, spruce beetle might preferentially attack large dbh spruce throughout the course of an outbreak, or perhaps host size becomes inconsequential once beetle populations are at epidemic levels.

Large-scale natural disturbances exhibit various spatiotemporal patterns. During the course of a spruce beetle outbreak, beetle populations might originate from an epicenter and then move across the landscape in a spreading pattern, or, alternatively, growing spruce beetle populations might simultaneously arise in seemingly spatially independent areas within the landscape. Indeed, Okland et al. (2005) have demonstrated synchrony in timing between spatially disjunct spruce beetle outbreaks in Oregon. Under this scenario, as populations build, they may eventually coalesce and finally collapse, having exhausted the host resource. There is limited detailed information about the possible role of forest structure, composition, or environmental factors in explaining the spatiotemporal patterns of Engelmann spruce mortality during a spruce beetle outbreak. By identifying factors influencing patterns of spruce beetle outbreaks, it may be possible to devise silvicultural recommendations for the purpose of mitigating spruce beetle-caused Engelmann spruce mortality.

Beginning in the late 1980s, a spruce beetle outbreak occurred on the Markagunt Plateau in the Dixie National Forest and Cedar Breaks National Monument. The spruce beetle killed ~93% of the Engelmann spruce >5 cm in dbh over an area of at least 250 km^2 (DeRose and Long 2007). Virtually every beetle-killed spruce is still standing after the outbreak; therefore, we had the opportunity to reconstruct the timing and pattern of Engelmann spruce mortality using dendrochronological techniques. In this article, because actual spruce beetle populations were not monitored, the quantity of spruce beetle-killed Engelmann spruce is used as a proxy for putative beetle populations and to discriminate between two distinct population phases: early and late outbreak. We tested two hypotheses: the timing of the outbreak would be influenced by forest structure, composition, and environmental factors such that, early in the outbreak, host conditions would be tightly correlated with spruce mortality and later in the outbreak, the spruce beetle would be less discerning, and host conditions would not be tightly coupled with spruce mortality; and the outbreak had an epicenter and exhibited a spreading spatiotemporal pattern across the plateau. Finally, we explored the possibility that some of the significant factors identified in the analysis could be silviculturally manipulated to influence the spread or eruption of spruce beetle outbreaks.

Methods

Study Area

The Markagunt Plateau is located within the Dixie National Forest in southwestern Utah on the western edge of the Colorado Plateau (Figure 1). The relatively recent (late 1980s through the early 2000s) spruce beetle outbreak killed most of the mature spruce on the plateau. Before the outbreak, the high-elevation plateau was dominated by Engelmann spruce forests, which also commonly include subalpine fir, aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), and limber pine (*Pinus flexilis* James). Although blue spruce (*Picea pungens* Engelm.) occurs on the plateau, it was present in only one of our plots and was not used for analysis; therefore, spruce in this study refers only to Engelmann spruce.

Precipitation on the plateau comes in two broad peaks: a larger one in the form of winter snow from cold Pacific air and a smaller one during the summer as a result of the southwestern monsoon (Mock 1996, DeRose and Long 2009). Long-term data from the Blowhard weather station located on the western edge of the Markagunt Plateau (Utah State University 2010) showed that mean annual precipitation for the period 1965–2005 was 739 mm (range 431–1202 mm) and for the same period minimum daily temperature was −30.5°C and maximum daily temperature was 32.2°C. Data from the Blowhard station were also used to portray possible relationships between temperatures and putative spruce beetle population levels based on known limitations to spruce beetle physiology (Hansen et al. 2001a), in particular, whether summer average (July, August, and September) maximums or winter average (January, February, and March) minimums might have influenced beetle populations via shifts in life cycle duration or winter-related mortality and, consequently, spruce beetle-caused spruce mortality (Miller and Werner 1987).

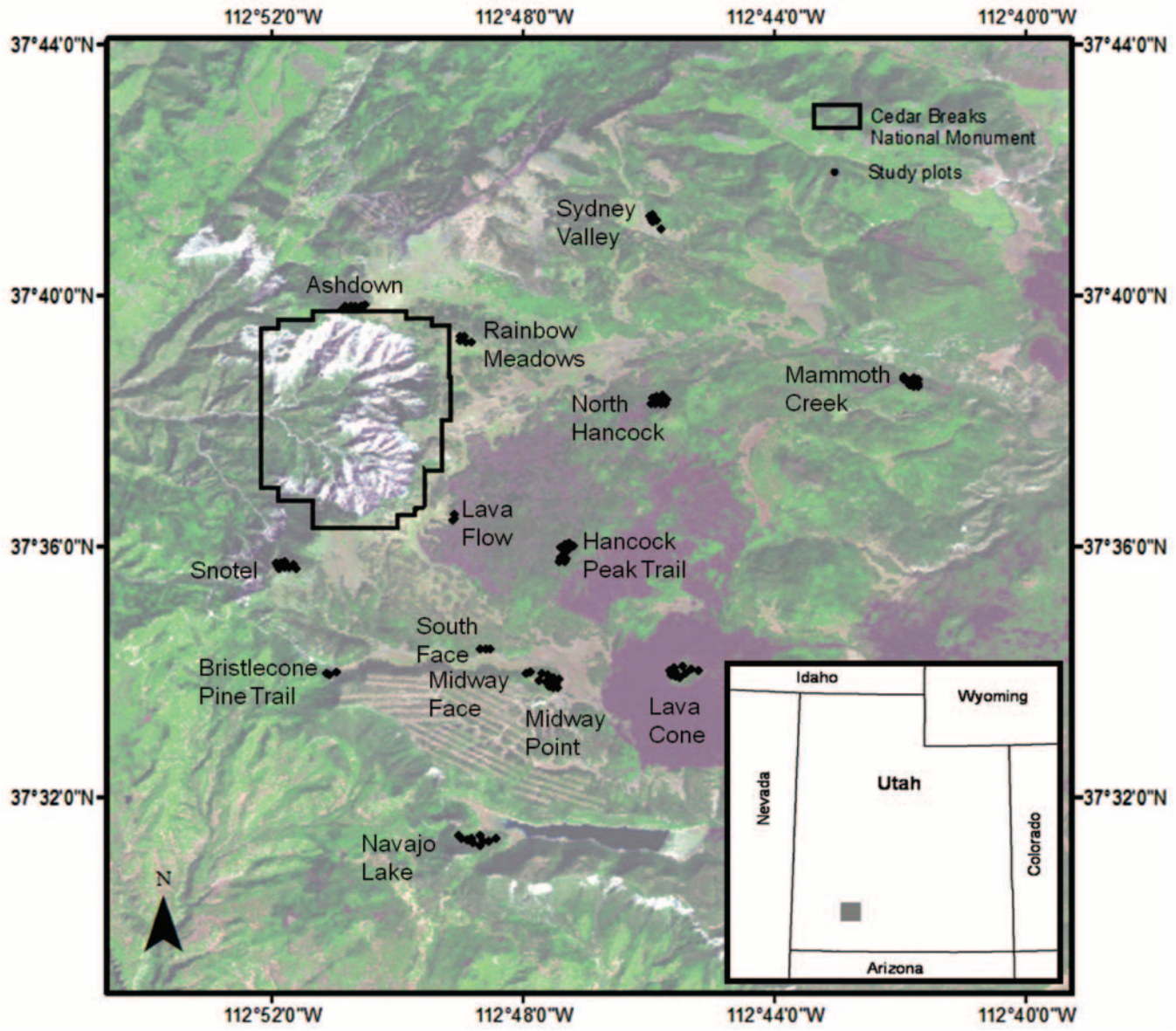

Figure 1. Location of study stands on the high elevation Markagunt Plateau in southern Utah, USA. Background is a 1991 (prespruce beetle outbreak) Landsat Thematic Mapper image showing the 7,4,3 band combination, where purple areas indicate lava flow, darker green areas indicate dense spruce forest, and lighter green areas indicate aspen forest.

Data Collection

We used restricted random sampling to select a number of stands across the plateau to characterize spruce–fir conditions. The plateau was gridded, and random points were located within each grid. If there was no spruce forest in a grid, no stand was measured. To differentiate distinct stand boundaries areas of relatively homogeneous overstory forest structure were scrutinized on aerial photos. We chose stands that showed no signs of human disturbance (i.e., logging). For each stand a number of plots were measured using a grid sampling approach with a random starting point, and plots were located at least 100 m apart (Figure 1). Within each plot individual tree variables and environmental conditions were measured.

Spatial data for each plot were collected with a global positioning sensor. Waypoints were recorded when error was estimated to be <3 m. Elevation, slope, and aspect were recorded for each plot. Variable radius plots (basal area factor [BAF] of 3–8 m^2, held constant in each stand) were used to characterize forest structure and composition. For each tree on the plot, dbh and height were measured and species and status (live or dead) were noted. For every dead spruce, the cause of death was noted, specifically whether or not it was killed during the recent spruce beetle outbreak. The presence or absence of beetle galleries and beetle emergence holes were assessed in identifying the cause of death. In the rare case that spruce was not killed by the recent outbreak, we determined whether mortality was due to earlier spruce beetle activity or some other cause. These trees were rare (13 of the 637 sampled trees) and were not included in the analysis. Increment cores were taken near the base of every tree, and special care was taken when

removing them from the tree to maintain the integrity of the outermost rings. The presence of rot on the cores was noted. Cores were stored in paper straws, which were labeled and allowed to dry before preparation and analysis.

Increment Core Preparation

Increment cores from Engelmann spruce were prepared using standard dendrochronological techniques (Stokes and Smiley 1968) and were visually crossdated against a locally developed Englemann spruce master chronology. This chronology consisted of trees from a previously existing spruce chronology (Briffa and Schweingruber 1992) combined with increment cores we opportunistically collected from any live spruce found on the plateau. Program COFECHA (Holmes 1983) was used to check dating of all tree-ring series. The calendar year of the outermost crossdated ring was assumed to be the year in which spruce beetle-caused mortality occurred. We did not quantify how many rings were not produced before actual tree death. Previous studies have indicated this error to be in the range of 1–2 years (Mast and Veblen 1994), which probably also applies to this study.

Timing of Spruce Beetle-Caused Spruce Mortality

The dependent variable, chosen to describe the spatiotemporal dynamics of spruce beetle-caused mortality during the spruce beetle outbreak, was crossdated year of death (D_y) for individual Engelmann spruce trees determined to have been killed during the beetle outbreak. To explore the first hypothesis, that D_y was influenced by structure, composition, and environmental factors, the time-series data were used to split our data into two populations: spruce beetle-caused spruce mortality early in the outbreak ($n = 94$ trees); and spruce beetle-caused spruce mortality late in the outbreak ($n = 536$ trees; note that 7 trees were removed because of missing data). Because we used prisms to sample each stand in this study, we used the prism BAF to characterize an area equivalent to 1 ha. For each stand, we defined the "early outbreak" as the time period in which a total of <2.0 m^2 ha^{-1} year^{-1} BA of Engelmann spruce had been killed in that stand; similarly, "late outbreak" was defined as the time period after >2.0 m^2 ha^{-1} year^{-1} BA of Engelmann spruce had been killed in the stand. By making an assumption that endemic population levels occurred early in the outbreak and epidemic populations later, our definition is an attempt to estimate spruce beetle population pressure on Engelmann spruce both early and late during the outbreak.

After dividing the data into early and late outbreak groups, we modeled the influence of a suite of independent variables on D_y for each data set (Table 1). Generalized linear models were used for both analyses, and the stepAIC procedure as part of the package MASS (Venables and Ripley 2002) was used in R (R Development Core Team 2008). The stepAIC function steps through all the independent variables, in both a forward and backward selection procedure, to produce a model based on minimizing the Akaike information criterion. If independent variables were highly covaried one of them was eliminated before the analysis and not reported here. The independent variables were chosen to characterize the possible influence of structural, compositional, environmental, and spatial attributes on D_y. Most of these variables have precedent in the spruce beetle literature. Because measurements for this study were conducted after the spruce beetle outbreak, the independent variables describing stand conditions have necessarily been reconstructed. The response to disturbance in high-elevation, spruce–fir forests is slow, as represented by newly established trees, growth release of advance regeneration, and nonhost radial growth (Veblen et al. 1991, DeRose and Long 2010); therefore, the reconstructed stand attributes are assumed to be a reasonable reflection of immediate preoutbreak conditions.

Variables calculated for individual trees included dbh,

Table 1. Mean ± SD and range of the independent variables tested for their influence on timing of spruce beetle-caused Engelmann spruce mortality.

Variable	Mean ± SD (range)
Individual tree ($n = 637$ trees)	
dbh (cm)	46.3 ± 16.3 (6.5–106.5)
Diameter increment (mm)	0.16 ± 0.29 (0.01–2.57)
Presence/absence of rot	0.12 ± 0.32 (0–1.0)
Plot ($n = 101$ plots)	
QMD_p (cm)	43.7 ± 10.0 (22.3–65.2)
$ESQMD_p$ (cm)	46.7 ± 10.4 (23.3–71.7)
SDI_p	936 ± 336 (408–1825)
$ESSDI_p$	610 ± 259 (55–1347)
SDI_r	0.53 ± 0.21 (0.14–0.93)
$\%SDI_p$	0.67 ± 0.23 (0.07–1.0)
Latitude (northing)	37.5976 ± 0.0435 (37.5206–37.6883)
Longitude (easting)	112.8012 ± 0.0436 (112.8658–112.6953)
AV	0.68 ± 0.33 (0–1.0)
Slope (%)	12.1 ± 13.6 (0–50)
Elevation (m)	3035 ± 149 (2619–3251)
Stand ($n = 14$ stands)	
SI (m)	22.1 ± 2.65 (16.2–25.9)
SDI_s	905 ± 146 (507–1159)
$ESSDI_s$	533 ± 158 (151–808)
$\%SDI_s$	0.59 ± 0.15 (0.15–0.82)

diameter increment (mean radial increment of the last 10 years of growth), and the presence/absence of root rot. These variables were investigated because it typically is assumed that spruce beetle prefers larger dbh trees (Schmid and Frye 1976) and might also preferentially attack slower growing trees (Hard 1985). The presence of root rot fungus is one possible cause of decreased radial increment in white spruce (Lewis 1997), so we included a rot presence/absence variable in our predictor data set.

Structural variables calculated for each plot included quadratic mean diameter (QMD_p), stand density index (SDI_p), and SDI ratio (SDI_r). QMD_p reflects stand structure with higher values typically indicating older, even-aged stands (Schmid and Frye 1976). To assess the effects of relative density on spruce beetle susceptibility, we calculated SDI_p using the summation method (Shaw 2000), which is a measure of relative stand density largely independent of age and site quality (Jack and Long 1996). Finally, SDI_r was calculated as the ratio of the SDI summation method to the original SDI calculation which is based on QMD (Reineke 1933). SDI_r has been shown to effectively differentiate even-aged, two-aged, and multi-aged stand structure (Ducey 2009). SDI was also calculated for each stand by averaging across plots (SDI_s).

Forests heavily dominated by spruce are thought to be especially susceptible to spruce beetle attack (Schmid and Frye 1976); therefore, we calculated compositional variables for each plot including QMD of spruce ($ESQMD_p$), SDI of spruce ($ESSDI_p$), and the percentage of spruce SDI ($\%SDI_p$). These three variables were also calculated for each stand by averaging across plots, $ESQMD_s$, $ESSDI_s$, and $\%SDI_s$, respectively (Table 1).

In addition to structural and compositional variables, we included latitude and longitude for each plot in the analysis. We also included the slope, elevation, and aspect value (AV) to test whether these environmental factors might influence the spatiotemporal patterns of spruce beetle-killed Engelmann spruce. A linear value of AV ranging from 0 to 1.0 was calculated and is interpreted as 0 = warm southwesterly aspects to 1.0 = cool northeasterly aspects (Roberts and Cooper 1989). To characterize site potential productivity, site index (SI) was calculated for each stand (n = 14) using the heights and ages of 10 dominant trees (Alexander 1967).

Analyzing Spatiotemporal Patterns

Temporal patterns of Engelmann spruce mortality were graphically portrayed by summing the BA ($m^2\,ha^{-1}$) of beetle-killed trees year by year for each of the stands, dividing by the number of plots, and displaying them as a time series (Table 2). The time series for each stand was defined as the period between the first and last D_y, including any intervening years with no spruce mortality. The time series and their associated locations were then analyzed for spatial synchrony using the nonparametric covariance function (NCF) (Bjornstand 2001) to explore the second hypothesis, that the spatial pattern of the outbreak was characterized as starting at an epicenter and spreading across the landscape. Analysis of spatial synchrony is typically used to test for the variation of temporal characteristics in spatially disjunct populations (Okland et al. 2005). This is done by calculating all possible combinations of pairwise correlations between time series of different populations or stands in this study and arranging them over the geographical distances between populations.

We used the R package ncf (Bjornstand 2009) to fit the NCF smoothing spline to our data, calculated confidence intervals using bootstrap resampling of 1,000 iterations, and defined the maximum lag distance as the maximum distance between stands (~20 km). Although the NCF method of spatiotemporal analysis has typically been used to examine spatial synchrony between seemingly disparate geographic populations (e.g., Okland and Bjornstad 2003), we used this approach to test for spatial synchrony in the time series of spruce beetle-killed trees between stands that were killed during the Markagunt Plateau outbreak.

To further explore the second hypothesis, we sought to detect possible spatial autocorrelation by calculating Moran's I for the entire D_y data set. Moran's I is interpreted like a Pearson correlation coefficient (Legendre and Fortin 1989) for which large, significant values indicate departure from spatial randomness. To detect possible temporal shifts in spatial autocorrelation of Engelmann spruce mortality we

Table 2. Median ± SD, range, and sample size for D_y time series by stand.

	Median ± SD	Range	No. trees	No. plots
Ashdown	1996 ± 2.2795	1988–2000	66	9
Bristlecone Pine Trail	1999 ± 3.1355	1991–2002	20	3
North Hancock	1996 ± 2.3246	1987–2001	49	10
Hancock Peak Trail	1998 ± 2.2239	1990–2004	76	10
Lava Cone	1997 ± 2.3425	1990–2002	61	10
Lava Flow	1997 ± 2.1368	1991–2001	17	3
Midway Face	1999 ± 2.8284	1991–2002	15	3
Midway Point	2000 ± 2.4624	1991–2006	94	10
Mammoth Creek	1998 ± 3.2593	1991–2007	39	10
Navajo Lake	2000 ± 2.8781	1987–2006	60	10
Rainbow Meadows	1996 ± 1.088	1994–1998	17	5
South Face	2000 ± 0.301	1999–2000	11	3
Snotel	1997 ± 2.7789	1988–2006	93	10
Sydney Valley	1996 ± 1.5082	1994–2001	19	5
Totals			637	101

also grouped D_y into running 5-year classes from 1987–1991, 1988–1992, …, to 2003–2007, calculated Moran's *I* for each group, and plotted these over the temporal sequence of 5-year class midpoints.

Results

Factors Influencing Timing of Spruce Mortality Early in the Outbreak

Among the variables we tested, six were predictive of D_y early in the outbreak (<2.0 m^2 ha^{-1} $year^{-1}$ BA) (Table 3). Moreover, the final model accounted for 71% of the variability in D_y, which suggested that the variables we measured probably exerted an influence on whether spruce were infested and killed early in the outbreak. Latitude, $ESSDI_s$, AV, and SI exhibited a strong negative relationship to D_y (Table 3), indicating that higher values of the factors were associated with earlier D_y. For example, trees killed early in the outbreak were more likely to occur in stands with higher proportions of Engelmann spruce on warmer sites with higher productivity potential. Slope and SDI_s were positively correlated with D_y, which suggested that spruce were likely to be killed earlier on level sites or in low-density stands, respectively (Table 3).

Factors Influencing the Timing of Spruce Mortality Late in the Outbreak

Among the predictor variables we tested, seven were influential in the prediction of D_y late in the outbreak (>2.0 m^2 ha^{-1} $year^{-1}$ BA); however, the amount of explained variation (45%) decreased substantially compared with that in the early outbreak model. Of the D_y predictors late in the outbreak, four were also influential in the early outbreak model: latitude, dbh, SI, and AV (Table 4). Latitude and AV had relationships with D_y similar to those in the early outbreak model and therefore are interpreted similarly. Although not strongly influential in the early model, dbh was strongly negatively related to D_y late in the outbreak, which suggested that later in the outbreak larger trees were killed before smaller trees. The relationship between SI and D_y was positive for the late outbreak model, i.e., spruce on lower-quality sites were killed earlier than those on high-quality sites. Elevation was negatively correlated with D_y so that higher-altitude spruce were more likely to be killed before lower-altitude spruce. SDI_p was negatively correlated with D_y, which suggested that spruce occurring in dense plots were more likely to be killed sooner during the late outbreak. Finally, SDI_r was also negatively correlated with D_y, which suggested that spruce in structurally simple stands (even-aged) were killed earlier than spruce in structurally complex (multiaged), later in the outbreak.

Table 3. Variables indicated by stepAIC for prediction of the timing of spruce beetle-caused spruce mortality early in the outbreak (<2.0 m^2 ha^{-1} $year^{-1}$ BA).

Variable	Estimate	SE	*T* value	*P* value
Intercept	1.348	2.238	6.022	<0.0001
Latitude	−3.558	5.930	−5.999	<0.0001
dbh	1.716	1.172	1.465	0.1465
Slope	5.520	1.519	3.634	<0.0001
SDI_s	5.977	1.771	3.376	0.0011
$ESSDI_s$	−1.078	1.259	−8.563	<0.0001
SI	−2.302	1.098	−2.096	0.0389
AV	−1.265	7.044	−1.795	0.0761

$n = 94$.

Table 4. Variables indicated by stepAIC for prediction of the timing of spruce beetle-caused spruce mortality late in the outbreak (>2.0 m^2 ha^{-1} $year^{-1}$ BA).

Variable	Estimate	SE	*T* value	*P* value
Intercept	2.458	1.268	19.384	<0.0001
Latitude	−1.183	3.387	−3.492	0.0005
dbh	−3.205	5.232	−6.127	<0.0001
Elevation	−6.709	7.413	−8.200	<0.0001
SDI_p	−6.751	2.487	−2.715	0.0068
SDI_r	−1.503	4.017	−2.622	0.0090
SI	2.840	4.945	5.742	<0.0001
AV	−5.658	3.158	−1.792	0.0737

$n = 536$.

Spatiotemporal Patterns

D_y indicated that individual Engelmann spruce were killed over the course of the outbreak from 1987 through 2007 (Figure 2). The first spruce killed in each stand represented the precursor to the outbreak, and D_y varied by 12 years, from 1987 to 1999. BA mortality for these stands ranged from 0.3 to 2.6 m^2 ha^{-1} $year^{-1}$. D_y for the last beetle-killed spruce from each stand varied by 9 years (1998–2007) with a large variation in BA mortality, from 0.3 to 5.4 m^2 ha^{-1} $year^{-1}$ (Figure 2).

The shift from early to late outbreak (2.0 m^2 ha^{-1} $year^{-1}$ BA killed) was characterized by a variable range of D_y between individual trees within each of the stands (8 years, from 1991 to 1999) and in magnitude of BA mortality by 0.3 to 10 m^2 ha^{-1} $year^{-1}$. Although the timing of D_y varied considerably over the period of the outbreak, the overall time series indicated the following: early spruce mortality plateau-wide began in the late 1980s and continued through late 1990s; increased mortality was seen during the mid 1990s and early 2000s, reaching as high as 16 m^2 ha^{-1} $year^{-1}$ in one stand, but included many years with no mortality; and a sharp decline in spruce mortality was seen from the early to mid 2000s (Figure 2).

Regardless of the considerable variability, the NCF for time series of beetle-killed trees exhibited high spatial synchrony (positive correlation on average) at all distances between stands on the plateau (Figure 3). Overall, synchrony decreased with increasing distance, but positive correlations were maintained on average, which suggested nonindependence of the timing of beetle-killed trees between stands. However, spatial synchrony beyond ~12–13 km is suspect, given that the confidence intervals included zero, which indicated the possibility of spatial independence beyond this distance. This result appeared to contradict the influence of latitude on D_y found in both the early and late population models.

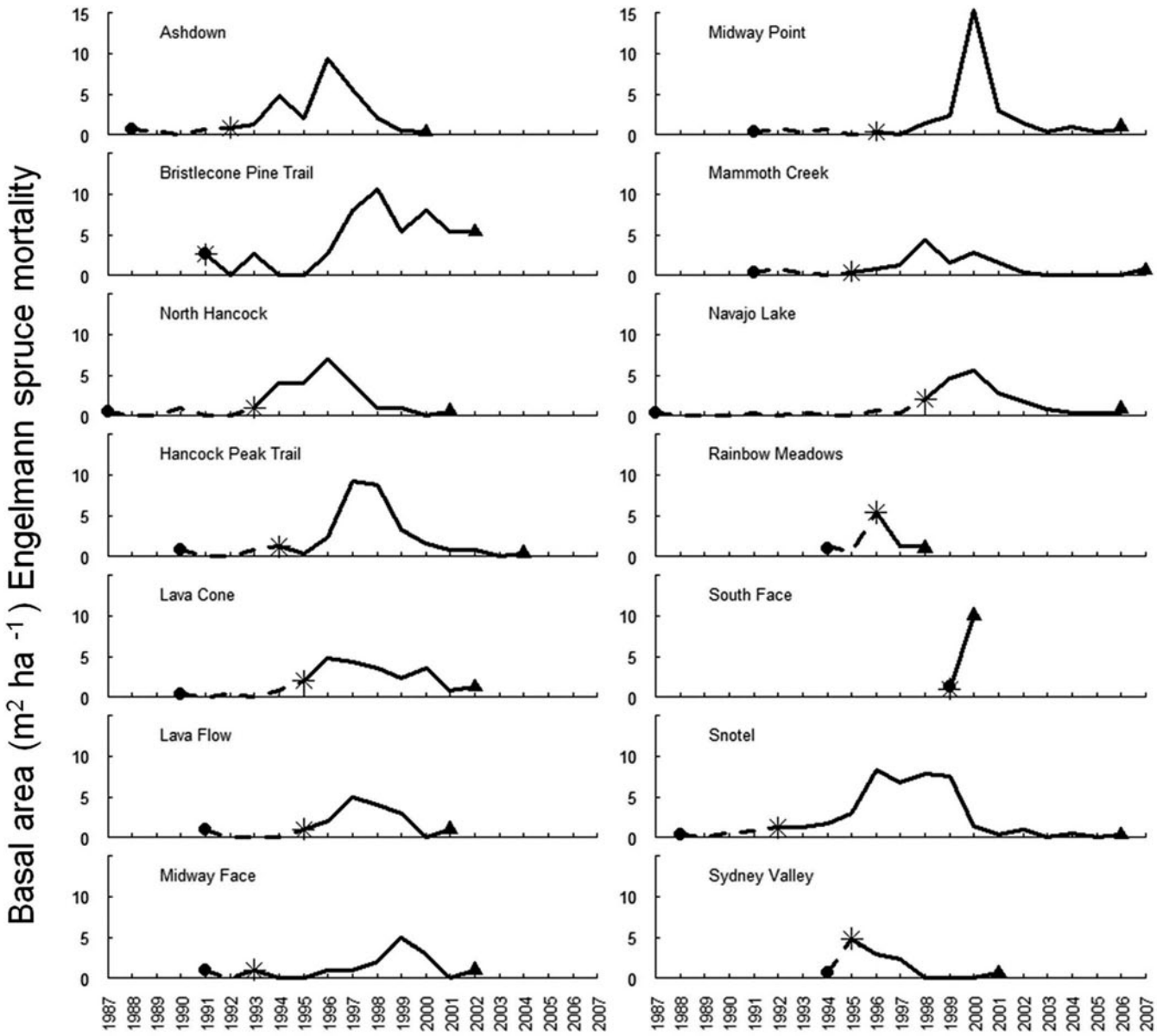

Figure 2. Time-series panels of Engelmann spruce basal area per year killed by the spruce beetle for each stand on the plateau ($n = 14$). Dotted line traces annual basal area mortality from circle (first year spruce killed by spruce beetle) to asterisk (year when >2.0 m^2 ha^{-1} BA of spruce killed by beetle), solid line continues time series to the triangle (last year spruce beetle-killed spruce in the stand).

Over the temporal range of observed Engelmann spruce mortality in this study (1987–2007), Moran's I indicated that the spatial locations of D_y were significantly different from random ($I = 0.2$, SD = 0.006, $P < 0.0001$). However, when grouped into running 5-year classes, Moran's I was only significant over the period from 1996 to 2000 (Figure 4), which suggested that earlier and later during the outbreak spatial autocorrelation of D_y was random or independent. From the mixed results of the NCF and Moran's I analyses, it was impossible to reject or accept the second hypothesis: that the outbreak spatiotemporal pattern spread out from an epicenter.

Discussion

In general, the results supported the first hypothesis. Both the early and late outbreak models suggested that forest structure, composition, environment, and spatial location influenced the timing of spruce mortality. Moreover, stand and environmental variables were more tightly correlated to D_y early in the outbreak compared with later in the outbreak ($R^2 = 0.71$ versus 0.45).

Early Outbreak

The first aerially mapped spruce beetle activity on the Markagunt Plateau occurred in 1988 within the Brian Head Ski Resort, but activity was also located in other areas on the plateau by 1991 (e.g., Mammoth Creek and Midway Face; Munson and DeBlander 1992). This was not inconsistent with this study in which spruce beetle-infested trees were identified as early as 1987 in multiple stands across the plateau (e.g., Ashdown and Navajo Lake in Figure 1 and Table 2) although mortality was low (Figure 2). Thus,

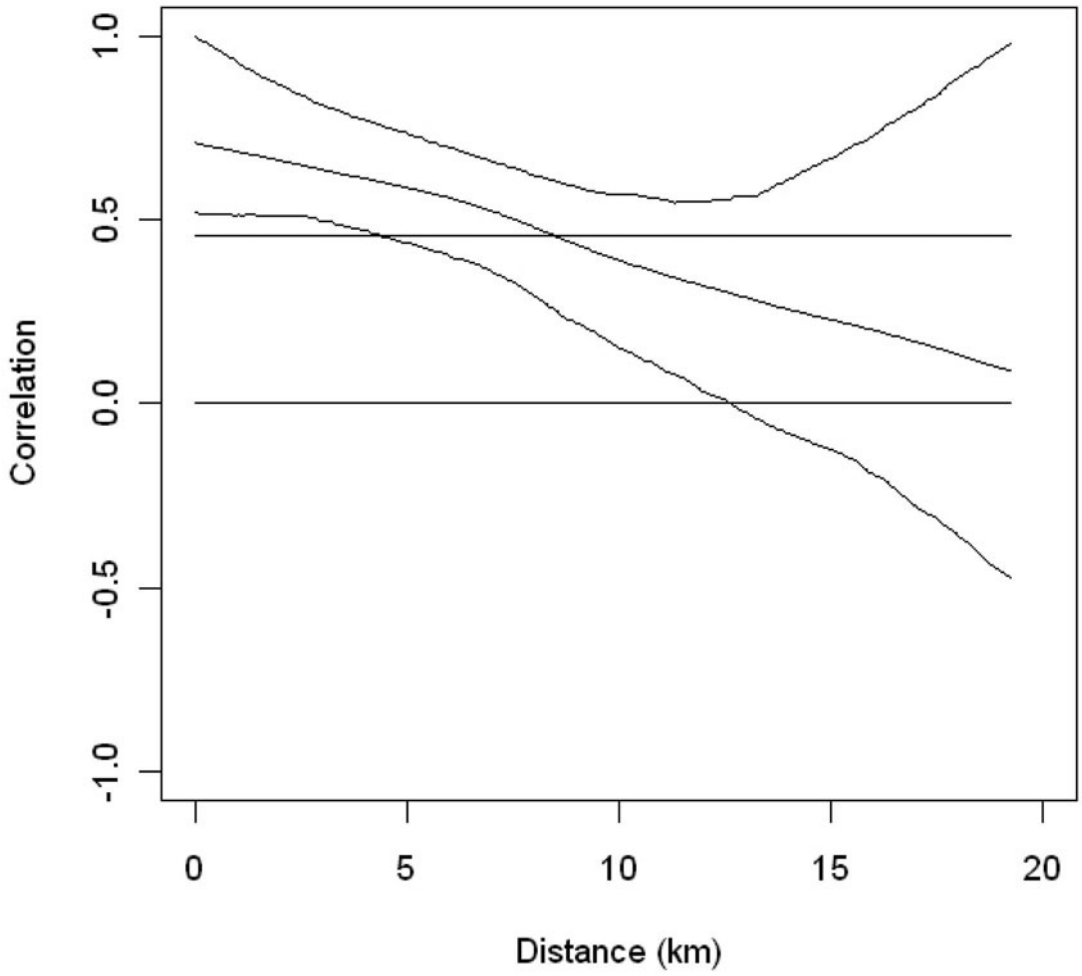

Figure 3. Positive correlation of the time-series from individual stands (Fig. 2) between sites ($n = 14$) indicating spatial synchrony of spruce beetle-caused spruce mortality. Note the confidence interval crosses zero indicating possible spatial independence at distance > 12–13 km.

endemic beetle populations were prevalent across the plateau, probably reproducing primarily in downed trees even though they were not detected by our sampling approach.

Spruce beetle populations during the early outbreak phase (<2.0 m^2 ha^{-1} year^{-1} BA killed) predictably killed spruce in particular stand and environmental conditions. Spruce in low-density stands with a high proportion of spruce were more likely to be attacked early in the outbreak. It is also probable that stands of high spruce density contribute to the maintenance of endemic beetle populations through nonoutbreak periods, and it is therefore not surprising to see early beetle activity there. Interestingly, spruce in high SDI stands were less likely to be killed earlier. This result might be due to the likelihood that stands with the highest SDI are heavily stocked, especially in the smaller size classes, with subalpine fir, and this results in very large estimates of SDI.

Beetles also began attacking trees from higher SI stands earlier. In addition, spruce on warmer sites (lower AV value) were more likely to be killed earlier during the outbreak, which may be a result of the tight physiological limitations imposed on the spruce beetle by temperature (Miller and Werner 1987). For example, Engelmann spruce on warm sites might be better habitat than spruce on cool sites because exposed boles maintain higher temperatures, increasing the likelihood that beetles will switch to a univoltine cycle. Furthermore, spruce trees on warm aspects are likely to exhibit drought stress before trees on cooler aspects, potentially increasing the likelihood of successful attack (Berg et al. 2006). Evidence of early beetle activity on warm sites has been described for other bark beetles as well. Nelson et al. (2007) found that "hot spots," areas of early mountain pine beetle activity, were typically found on warmer sites. Likewise, Powers et al. (1999) found mortality associated with Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) epidemics was associated with warmer aspects.

Late Outbreak

The transition to the late outbreak phase (>2.0 m^2 ha^{-1} year^{-1} BA killed) occurred between 1991 and 1999. During this ~10-year period spruce beetle populations continued attacking Engelmann spruce, eventually killing almost every spruce tree >5 cm dbh across the entire landscape (Table 2).

A possible factor contributing to the increase in mortality associated with the late outbreak phase is that an unusually

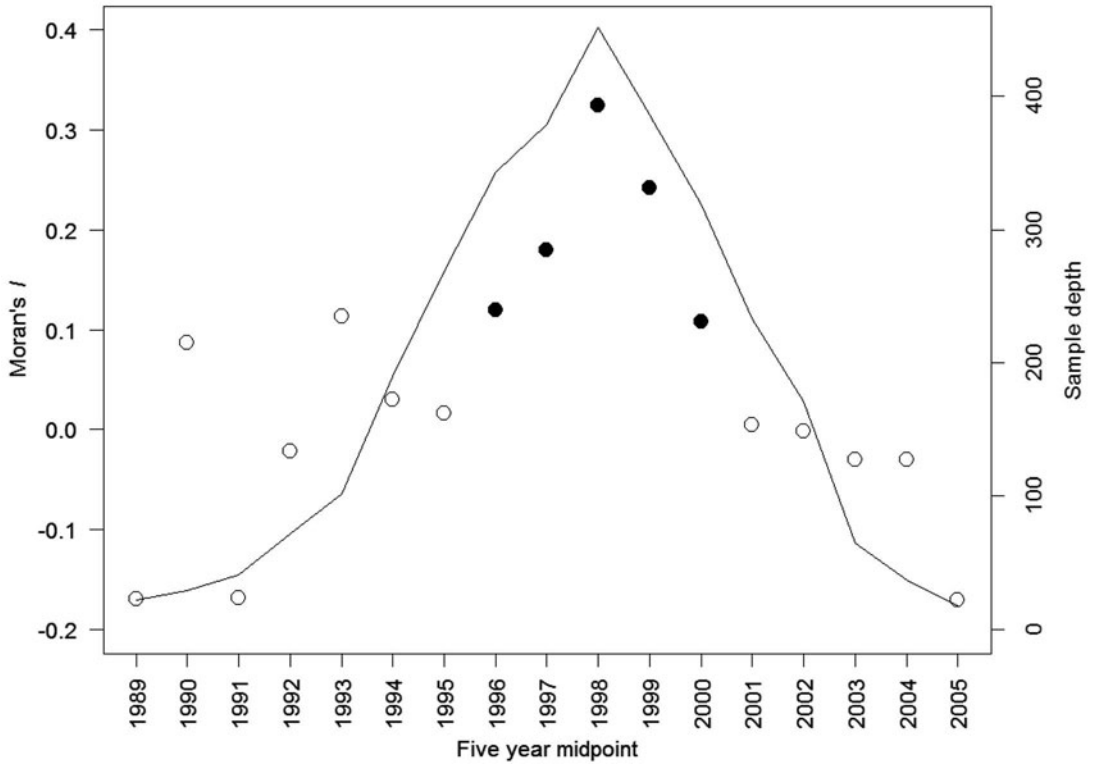

Figure 4. Moran's *I* for running 5-year classes over the course of the spruce beetle outbreak. Filled circles indicate significant values of Moran's *I*. Significant values indicate nonrandom spatial autocorrelation, whereas insignificant values (open circles) indicate a pattern not different than random. Sample size for each 5-year class is indicated by the solid line.

warm summer temperature anomaly triggered a switch from semivoltine to univoltine beetle populations (Werner and Holsten 1985, Hansen et al. 2001b, Berg et al. 2006). Such a switch would result in accelerated spruce beetle population growth (Hansen and Bentz 2003). Although we cannot establish causality, average summer maximum (~1995–2003) and average winter minimum temperatures (~1991–2000) that have increased relative to their long-term means appeared to coincide with the increase in spruce beetle-caused mortality across the Markagunt Plateau (Figure 5). It is possible this temperature anomaly was a catalyst for the accelerated spruce beetle activity on the plateau that led to the shift from early to late outbreak phases during the mid to late 1990s. The Engelmann spruce stands on the Markagunt Plateau were many centuries old before the recent outbreak (R.J. DeRose 2009, unpublished data) and have been susceptible, i.e., have had high hazard, for a long time. Therefore, although susceptible host was historically present, it is likely that the beetle populations, which were also historically present (see references in Hebertson and Jenkins 2008), did not begin to build until incited by temperature anomalies. Moreover, there was a lack of lethal winter temperatures beginning in 1991 (Frye et al. 1974, Miller and Werner 1987) (Figure 5).

This is not the first study to find temperature anomalies before and coincident with bark beetle outbreaks. Changes in temperature have been cited as factors contributing to unprecedented outbreaks of both the spruce beetle in Alaska (Berg et al. 2006) and the ongoing mountain pine beetle outbreak in British Columbia (Aukema et al. 2006). That observed spruce beetle-caused spruce mortality could be explained by considering temperature anomalies further suggests that they are an important factor for the landscape-wide, relatively synchronous signal in building spruce beetle populations as opposed to more local triggers such as logging and wind throw. That is, weather effects are regional and, thus, favorable temperatures should be expected to contribute to beetle population success across a landscape (Raffa et al. 2008). For example, a ~300-year dendrochronological history of the Kenai Peninsula, Alaska, shows that regionalized spruce beetle outbreaks are associated with runs of relatively warm summers, whereas windthrow events do not necessarily result in widespread outbreaks (Berg et al. 2006).

Later in the outbreak, once cumulative spruce mortality in a given stand was > 2.0 m^2 ha^{-1} year^{-1} BA, mass-attacking spruce beetle populations were probably less demanding about host conditions, as demonstrated experimentally by Wallin and Raffa (2004) and by our analysis. For example, during the late outbreak phase, spruce in stands of lower SDI_r (uneven-aged stands) or on sites with lower SI were killed earlier (Table 4). As the outbreak progressed, beetle population pressure was intense enough to eventually affect all Engelmann spruce on the landscape. The incredible beetle pressure might also explain why they attacked such small trees (as small as 6.5 cm dbh, data in this study) and relatively rare Engelmann spruce in marginal spruce forest types (e.g., mixed-conifer with <7% spruce composition) (Table 1).

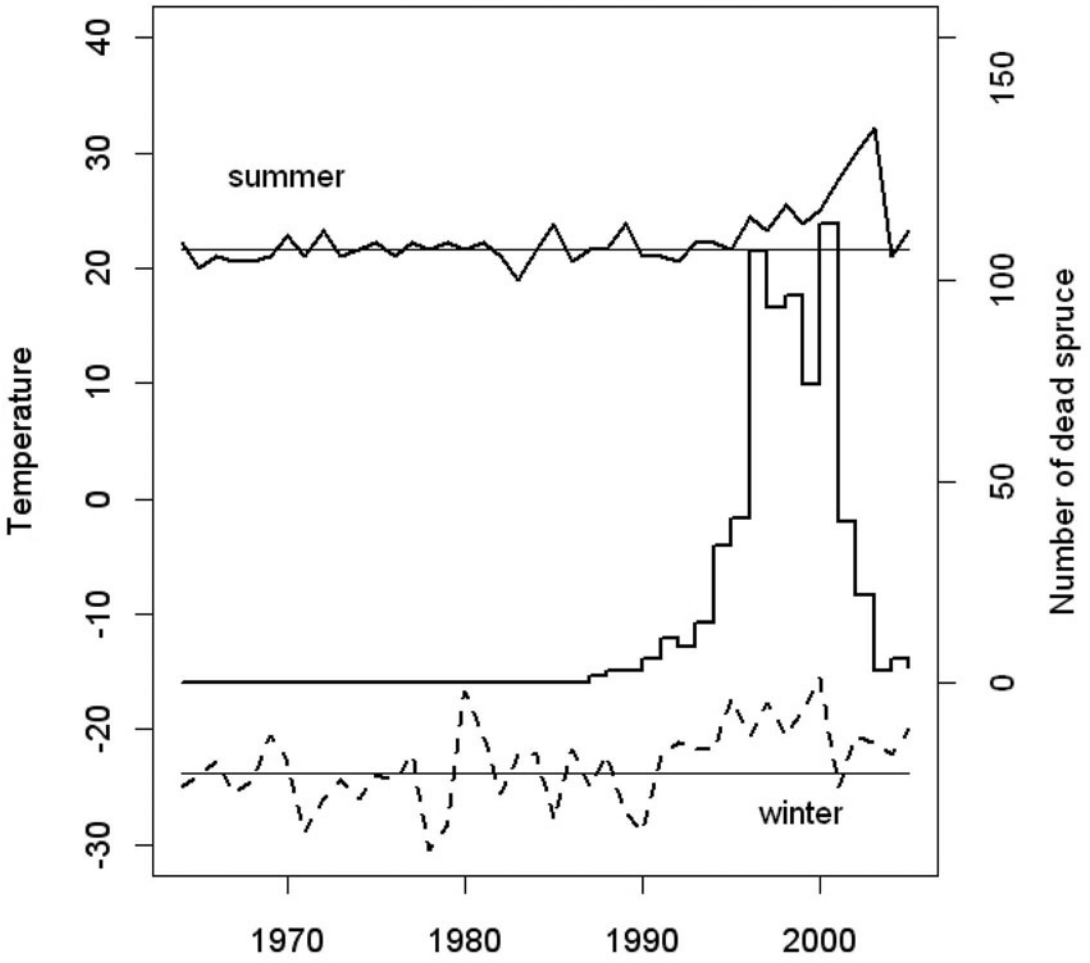

Figure 5. Summer seasonal average maximum (July, August, and September; solid line) and winter seasonal average minimum (January, February, and March; dashed line) temperatures for the period 1964–2005 plotted with long-term averages (calculated for the period 1964–1995) to show the deviation from the temperature record in ~1995. The frequency distribution of the number of spruce beetle-killed Engelmann spruce by year across the Markagunt Plateau measured in this study is juxtaposed with the temperature records to show the possible cause of spruce beetle population eruptions. Warm summers increase the likelihood of univoltine broods, whereas mild winters reduce the likelihood of cold-related brood mortality.

Outbreak Collapse

Finally, between 1998 and 2007 Engelmann spruce mortality subsided, suggesting that spruce beetle populations did as well, probably because of increasingly rare suitable hosts. The end of the outbreak was also associated with a return to normal temperature regimes (Figure 5), and there is anecdotal evidence that cooler temperatures are associated with the end of outbreaks despite remaining susceptible hosts (Berg et al. 2006). Spruce mortality became rare after ~2003 (Figure 2) and occurred primarily in remote stands and in drainages at the fringe of the spruce-fir zone, presumably because these were essentially the only remaining live spruce on the landscape.

The early and late outbreak model results were largely consistent with the spruce beetle hazard rating (Schmid and Frye 1976). However, in contrast with Schmid and Frye (1976), trees that occurred on sites of lower potential productivity were killed earlier than those on sites of high potential productivity in the late outbreak model. This inconsistency is attributed to the observation that, at least initially during the Markagunt Plateau outbreak, spruce beetles preferentially attacked dense spruce-dominated stands that occurred on lesser slopes (interpreted as moist valley bottoms in Schmid and Frye 1976) and are more likely to occur on more productive sites. When the outbreak develops, perhaps the sheer number of spruce beetles ensures successful mass attack, regardless of potential productivity.

Stand hazard ratings commonly include large individual spruce as a hazard factor; however, we found that dbh was significant in the late outbreak model but not in the early model. This seemingly counterintuitive result is most likely due to the fact that before the outbreak much of the plateau was dominated by mature (i.e., large) spruce and therefore other structural and compositional variables emerged as influential in the prediction of D_y early in the outbreak. Then, later in the outbreak, as the beetle was relegated to less suitable forest conditions, it probably chose the larger dbh spruce before the smaller.

Ecologically and silviculturally it is worthwhile to be

able to relate spruce beetle population levels to BA killed, which is why we set the threshold delineation between early and late outbreak (2.0 m^2 ha^{-1} $year^{-1}$ BA killed). For example, the potential influence of beetle populations on spruce forests could be interpreted directly using tree or stand BA. For management, the number and size of trees affected by the spruce beetle for a given area can be calculated with standard prism plots and dbh measurements. Furthermore, BA is a convenient measure for field foresters. If a 2.0-m prism were used for inventory, an average of ≤ 1 spruce beetle-killed trees per plot would indicate a relatively low population level, whereas an average of ≥ 2 attacked trees per plot would certainly be a cause for concern.

Spatiotemporal Outbreak Patterns

The spatiotemporal development of the outbreak on the landscape was ambiguous. Temporal patterns of D_y for both early and late populations were predictably related to stand conditions, but spatial patterns were much more difficult to discern. Latitude emerged as a predictor of D_y for both the early and late models; i.e., mortality occurred earlier at more northerly locations and later at more southerly locations. This finding is in contrast to the nonindependence (up to 12–13 km) of the complete stand-by-stand time series analysis indicated by the NCF results (Figure 3), which showed at least some overlap in mortality for stands all across the plateau (Figure 2). This is also in contrast to the spatial independence indicated earlier and later in the outbreak by Moran's *I*, but not during the most severe years (1996–2000) (Figure 4). However, it appeared possible that the temporal analysis of Moran's *I* might have been influenced by sample size (Figure 4) and should be interpreted collectively with the NCF analysis. Taken together, both the reconstructed NCF spatiotemporal patterns and Moran's *I* spatial correlation coefficient of spruce beetle-caused spruce mortality indicated that the outbreak did not simply spread across the landscape from a single epicenter nor did it simply erupt in seemingly independent stands on the landscape as indicated by the spatial synchrony results. In other words, there is spatial dependence, just not necessarily resulting from an epicenter. Rather, it appears that there was some combination of both spatiotemporal patterns and, when viewed over the landscape extent, the growth and spread of the outbreak was ultimately a result of the local relationship between stand conditions and spruce beetle dynamics, the latter influenced by favorable weather.

The US Forest Service Forest Health Protection Aerial Detection Survey (ADS) maps, which were produced annually from 1991 to 2007, generally supported our results regarding the spread of the spruce beetle outbreak (US Forest Service 2007). The ADS layers include polygons of forest health problems (e.g., spruce beetle infestation) drawn onto maps during low elevation flyovers. Although the ADS data are notably less accurate than our sampling method with respect to individual tree timing of death, they have the advantage of covering the entire Markagunt Plateau. These maps show small pockets of spruce beetle activity in the early 1990s ranging from the Bristlecone Pine Trail stand in the south to Sydney Valley in the north (Figure 1). In each successive year into the mid 1990s, these pockets enlarged and appeared north and northeast of our sites. During the late-1990s most of the growing pockets had coalesced over the center of the Plateau (e.g., Hancock Peak Trail) (Figure 1). The early 2000 ADS maps indicated patches of beetle infestation on the southernmost parts of the Plateau (e.g., Navajo Lake) (Figure 1) and the furthest east areas of spruce occurrence (e.g., Mammoth Creek) (Figure 1). By the mid to late 2000s, the only beetle activity indicated on the Plateau was in the south and east. Presumably, there was no living available spruce in the center and northern areas of the Plateau (Ashdown and Rainbow Meadows) (Figure 1).

It is possible that the relative nonindependence indicated by the analyses (NCF and the overall Moran's *I*) and corroborated by the ADS data could have resulted from spruce beetle dispersal from nearby populations during the outbreak. There was a maximum distance of $\sim$18 km between stands in this study, and spruce beetle dispersal is possible across such distances, especially if aided by wind (Schmid and Frye 1977, Byers 2000). Such interstand dispersal has been found for building mountain pine beetle populations (Aukema et al. 2006). Confirmation of this mechanism for spread of an outbreak requires monitoring of individual beetles. It is possible that during the progression of the Markagunt Plateau outbreak, once beetle populations had erupted, they were likely to disperse further and contribute to enhanced mortality in increasingly distant stands. Another possible explanation is that the plateau is too small for there to be truly "independent" populations and therefore geographic extent convoluted the NCF results. An alternative, but not mutually exclusive, possibility is that relative spatial synchrony indicated an overriding environmental factor that incited the beetle populations to build. Spatial synchrony also suggests that the erupting populations were not incited by a specific event such as logging or blowdown, as is commonly suggested for spruce beetle (Schmid and Frye 1977, Reynolds and Holsten 1994) but rather a plateau-wide factor such as temperature anomalies, drought, and/or relatively homogeneous forest conditions (Raffa et al. 2008).

Using a simplistic example, consider an outbreak that had been initiated as a result of a specific event, such as spruce blowdown in a single location, on a landscape composed of homogeneous spruce conditions. Under these circumstances, one reasonable expectation might be that a beetle population would build at an epicenter focused on the wind-thrown area. As the population grew, Engelmann spruce mortality would spread outward and proceed through a connected, homogeneous spruce landscape until conditions for beetle survival stopped. If, more realistically, the landscape were much more heterogeneous, we might expect the pattern of spread from the epicenter to be discontinuous, with beetle-caused mortality proceeding faster in stands with structure, composition, and site conditions conducive to the beetle. In addition, although not studied here, the connectivity of infested stands and uninfested stands with high susceptibility might also influence the spatiotemporal pattern of spread. For example, Shore et al. (2009) identified critical thresholds between mountain pine beetle-infested

lodgepole pine stands into uninfested stands of jack pine (*Pinus banksiana* Lamb.) to indicate possible scales where large increases in connectivity occurred. In a spruce beetle example, Bebi et al. (2003) found that historic spruce beetle disturbance was higher in stands that had a high percentage of nearby spruce stands (900 m^2 neighborhood) than in those in a more heterogeneous environment.

In contrast, if an outbreak in a homogeneous environment were incited by an overriding, landscape-wide factor such as temperature, building beetle populations could occur in multiple places (foci) at the same time. As these populations grew, spruce mortality would spread from multiple foci to highly susceptible and connected stands, ultimately coalescing on the landscape. However, if temperature-incited population growth occurred in a heterogeneous environment, variation in the timing of building populations would result because of insufficient or less-suitable host in some areas. The variation in the timing of the initial building populations would translate into variation in the timing of mortality among the multiple foci and then finally in the spatial pattern of Engelmann spruce mortality as the populations "spread" on the landscape. Populations with suitable host would attack and kill spruce much more rapidly, increase in population levels faster, and potentially contribute via dispersal to other populations. Populations with less-suitable hosts would grow much slower, take longer to overcome the host resource on the site, and subsequently move slower on the landscape, creating much more complicated spatiotemporal patterns.

Over the course of the Markagunt Plateau outbreak, spruce beetle population growth, most likely incited by temperature anomalies, proceeded over fairly homogeneous forest conditions (Table 1). Initial building of the seemingly independent (i.e., spatial synchrony) beetle populations actually occurred over a period of ~12 years (Figure 2) during which stand and environmental conditions conducive to beetle reproduction are predictable (Table 3). Although temperature anomalies probably incited the populations to build, the 12-year variability in the timing of initial beetle activity among the stands was probably a result of whether endemic populations had suitable host conditions to build in (Table 3). Once incited, warm temperature anomalies persisted (Figure 5), and beetle populations continued to build, increasing mass attack pressure on Engelmann spruce. Continued warm temperatures probably also allowed enhanced beetle population numbers that could disperse to stands with less suitable hosts and, as a result, D_y was less predictable later in the outbreak (Table 4). In time and with ongoing amenable temperature conditions (Figure 5), the spruce beetle continued to attack spruce, even in marginally suitable habitats (i.e., >7% spruce composition) (Table 1), until it effectively exhausted the host resource.

Silvicultural Options to Deter Spruce Beetle

Early in the outbreak, the timing of Engelmann spruce mortality was reasonably predictable using stand and environmental variables (Table 3). In light of the factors associated with the timing of spruce mortality, recommendations for management to mitigate losses to spruce beetle can be made. The early outbreak model (Table 3) reveals variables that cannot be manipulated by active management: latitude, slope, SI, and AV. However, an understanding of the relationship between these factors and spruce mortality could be used to identify stands in which current beetle populations might initially build (e.g., lesser slopes, high SI, or warmer sites) and to prioritize spruce regeneration treatments based on the highest susceptibility. In addition, dbh, SDI_s, and $ESSDI_s$ can all be modified by traditional silvicultural thinning or regeneration practices and, in combination with the identification of susceptible stands, could be used to modify stand structure and composition so as to reduce stand susceptibility (see Bentz and Munson 2000, Hansen et al. 2010).

Once spruce beetle populations have shifted to outbreak levels, they are probably less discriminating with respect to stand structure and composition and will mass-attack spruce trees as small as 6.5 cm dbh even in stands of low spruce density. Indeed, stand variables in this study were less well correlated to timing of attack during the late outbreak period than earlier. Raffa et al. (2008) characterized this loss of correlation as the crossing of a "threshold" in multiscale systems, after which causal relationships are "masked." The late outbreak loss of causal relationships suggests that silvicultural intervention is unlikely to influence landscape spruce beetle-caused spruce mortality and therefore silvicultural manipulation during a fully developed outbreak is futile.

Summary and Conclusions

The analysis of crossdated, spruce beetle-killed Engelmann spruce provided an unusually detailed look at the spatiotemporal dynamics of spruce beetle activity during the Markagunt Plateau outbreak. Both the abundance and spatial variability of suitable host conditions on the landscape and temperature anomalies appeared to strongly influence spruce beetle-caused spruce mortality. Our results do not provide strong evidence for the common perception that spruce beetle outbreaks originate in a specific location and then "spread" across the landscape. We found evidence, for example, of positive spatial synchrony of multiple, building populations during development of the Markagunt Plateau outbreak. Future studies that combine the data precision of dendrochronological approaches with a full characterization of entire landscapes could further understanding of how spruce beetle outbreaks develop.

Our results indicate that stand and environmental variables can be used to identify stands that are most likely to be infested first as outbreaks develop. Thus, our models can be used for strategic and tactical planning for the purpose of mitigating stand and landscape susceptibility to spruce beetle outbreaks. However, our results also suggest that modification of stand structure and composition to mitigate spruce beetle-caused spruce mortality must be done early, i.e., before an outbreak or during the early outbreak phase or not at all because stand variables become less well correlated to timing of attack as cross-scale thresholds are surpassed during the late outbreak phase.

Literature Cited

ALEXANDER, R.R. 1967. *Site indexes for Engelmann spruce in the central Rocky Mountains.* US For. Serv. Res. Paper RM-32. 7 p.

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.

BEBI, P., D. KULAKOWSKI, AND T.T. VEBLEN. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84:362–371.

BENTZ, B.J., AND A.S. MUNSON. 2000. Spruce beetle population suppression in northern Utah. *West. J. Appl. For.* 15:122–128.

BERG, E.E., D.J. HENRY, C.L. FASTIE, A.D. DE VOLDER, AND S.M. MATSUOKA. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manag.* 227:219–232.

BJORNSTAND, O.N. 2001. Nonparametric spatial covariance functions: Estimation and testing. *Environ. Ecol. Stat.* 8:53–70.

BJORNSTAND, O.N. 2009. *R package 'ncf': Spatial nonparametric covariance functions.* Version 1.1. Available online at cran.r-project.org/web/packages/ncf/index.html; last accessed January 2011.

BRIFFA, K.R., P.D. JONES, AND F.H. SCHWEINGRUBER. 1992. Tree-ring density reconstructions of summer temperature patterns across western North America since 1600. *J. Clin.* 5:735–754. Data archived at the World Data Center for Paleoclimatology, Boulder, CO. Available online at www.ncdc.noaa.gov/paleo/treering.html; last accessed January 2011.

BYERS, J.A. 2000. Wind-aided dispersal of simulated bark beetles flying through forests. *Ecol. Mod.* 125:231–243.

DEROSE, R.J., AND J.N. LONG. 2007. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. *For. Ecol. Manag.* 244:16–23.

DEROSE, R.J., AND J.N. LONG. 2009. Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. *Ecoscience* 16:28–38.

DEROSE, R.J., AND J.N. LONG. 2010. Regeneration response and seedling bank dynamics of a *Dendoctronus rufipennis*-killed *Picea engelmannii* landscape. *J. Veg. Sci.* 21:377–387.

DOAK, P. 2004. The impact of tree and stand characteristics on spruce beetle (Coleoptera: Scolytidae) induced mortality of white spruce in the Copper River Basin, Alaska. *Can. J. For. Res.* 34:810–816.

DUCEY, M.J. 2009. The ratio of additive and traditional stand density indices. *West. J. Appl. For.* 24:5–10.

DYER, E.D.A. 1973. Spruce beetle aggregated by the synthetic pheromone Frontalin. *Can. J. For. Res.* 3:486–494.

FRYE, R.H., H.W. FLAKE, AND C.J. GERMAIN. 1974. Spruce beetle winter mortality resulting from record low temperatures in Arizona. *Environ. Entomol.* 3:752–754.

HANSEN, E.M., AND B.J. BENTZ. 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). *Can. Entomol.* 135:697–712.

HANSEN, E.M., B.J. BENTZ, AND D.L. TURNER. 2001a. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* 133:805–817.

HANSEN, E.M., B.J. BENTZ, AND D.L. TURNER. 2001b. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* 133:827–841.

HANSEN, E.M., J.F. NEGRON, A.S. MUNSON, AND J.A. ANHOLD. 2010. A retrospective assessment of partial cutting to reduce spruce beetle-caused mortality in southern Rocky Mountains. *West. J. Appl. For.* 25:81–87.

HARD, J.S. 1985. Spruce beetles attack slowly growing spruce. *For. Sci.* 31:839–850.

HARD, J.S. 1987. Vulnerability of white spruce with slowly expanding lower boles on dry, cold sites to early seasonal attack by spruce beetles in south central Alaska. *Can. J. For. Res.* 17:428–435.

HARD, J.S., R.A. WERNER, AND E.H. HOLSTEN. 1983. Susceptibility of white spruce to attack by spruce beetles during the early years of an outbreak in Alaska. *Can. J. For. Res.* 13:678–684.

HEBERTSON, E.G., AND M.J. JENKINS. 2007. The influence of fallen tree timing on spruce beetle brood production. *W. North Am. Nat.* 67:452–460.

HEBERTSON, E.G., AND M.J. JENKINS. 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae, Scolytinae) outbreaks in Utah and Colorado. *Environ. Entomol.* 37:281–292.

HOLMES, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43:69–78.

JACK, S.B., AND J.N. LONG. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. *For. Ecol. Manag.* 86:205–220.

LEGENDRE, P., AND M.-J. FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107–138.

LEWIS, K.J. 1997. Growth reduction in spruce infected by *Inonotus tomentosus* in central British Columbia. *Can. J. For. Res.* 27:1669–1674.

MASSEY, C.L., AND N.D. WYGANT. 1954. *Biology and control of the Engelmann Spruce beetle in Colorado.* US Dept. of Agric. Circular No. 944. 35 p.

MAST, J.N., AND T.T. VEBLEN. 1994. A dendrochronological method of studying tree mortality patterns. *Phys. Geog.* 15:529–542.

MILLER, L.K., AND R.A. WERNER. 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Can. J. Zool.* 65:2927–2930.

MOCK, C.J. 1996. Climatic controls and spatial variations of precipitation in the western United States. *J. Clim.* 9:1111–1125.

MUNSON, A. S., AND V. DEBLANDER. 1992. *A biological evaluation of spruce beetle activity on Midway Face-Dixie National Forest, Cedar City Ranger District.* US For. Serv. Rep. No. 3420, Forest Pest Management Group, Ogden, Utah.

NELSON, T.A., B. BOOTS, M.A. WULDER, AND A.L. CARROLL. 2007. Environmental characteristics of mountain pine beetle infestation hot spots. *BC J. Ecosyst. Manag.* 8:91–108.

OKLAND, B., AND O.N. BJORNSTAD. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Pop. Ecol.* 45:213–219.

OKLAND, B., A.M. LIEBHOLD, O.N. BJORNSTAD, N. ERBILGIN, AND P. KROKENE. 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? *Oecologia* 146:365–372.

POWERS, J.S., P. SOLLINS, M.E. HARMON, AND J.A. JONES. 1999. Plant-pest interactions in time and space: A Douglas-fir bark beetle outbreak as a case study. *Land. Ecol.* 14:105–120.

R DEVELOPMENT CORE TEAM. 2008. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

RAFFA, K.F., B.H. AUKEMA, B.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.

REINEKE, L.H. 1933. Perfecting a stand-density index for even-aged forests. *J. Agr. Res.* 46:627–638.

REYNOLDS, K.M., AND E.H. HOLSTEN. 1994. Relative importance of risk factors for spruce beetle outbreaks. *Can. J. For. Res.* 24:2089–2095.

ROBERTS, D.W., AND S.V. COOPER. 1989. *Concepts and techniques of vegetation mapping.* US For. Serv. Gen. Tech. Rep. INT-257, p. 90–96.

SCHMID, J.M. 1981. *Spruce beetles in blowdown.* US For. Serv. RN-RM-141. 4 p.

SCHMID, J.M., AND R.H. FRYE. 1976. *Stand ratings for spruce beetles.* US For. Serv. RN-RM-309. 4 p.

SCHMID, J.M., AND R.H. FRYE. 1977. *Spruce beetle in the Rockies.* US For. Serv. Gen. Tech. Rep. RM-49. 38 p.

SCHMID, J.M., AND T.E. HINDS. 1974. *Development of spruce–fir stands following spruce beetle outbreaks.* US For. Serv. Res. Paper RM-131, 16 p.

SHAW, J.D. 2000. Application of stand density index to irregularly structured stands. *West. J. Appl. For.* 15:40–42.

SHORE, T., A. FALL, C. BURNETT, AND W. RIEL. 2009. *Characterization of the jack pine forests of western Canada for susceptibility to infestation by the mountain pine beetle.* Project No. 6.03. Natural Resources Canada, Can. For. Serv. Mountain Pine Beetle Information.

STOKES, M.A., AND T.L. SMILEY. 1968. *An introduction to tree-ring dating.* University of Chicago Press, Chicago, IL.

US FOREST SERVICE. 2007. *Forest Health Protection Aerial Detection Survey*. Available online at www.fs.fed.us/r1–r4/spf/fhp/aerial/gisdata.html; last accessed January 2011.

UTAH STATE UNIVERSITY. 2010. *Utah Climate Center.* Available online at climate.usurf.usu.edu/index.php; last accessed January 2011.

VEBLEN, T.T., K.S. HADLEY, E.M. NEL, T. KITZBERGER, M. REID, AND R. VILLALBA. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* 82:125–135.

VEBLEN, T.T., K.S. HADLEY, M.S. REID, AND A.J. REBERTUS. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72:213–231.

VENABLES, W.N., AND B.D. RIPLEY. 2002. *Modern applied statistics with S.* 4th ed. Springer, New York.

WALLIN, K.F., AND K.F. RAFFA. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecol. Monogr.* 74:101–116.

WERNER, R.A., AND E.H. HOLSTEN. 1985. Factors influencing generation times of spruce beetles in Alaska. *Can. J. For. Res.* 15:438–443.