

Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska

ROSEMARY L. SHERRIFF,^{1,5} EDWARD E. BERG,² AND AMY E. MILLER^{3,4}

¹Geography Department, Humboldt State University, Arcata, California 95521 USA

²U.S. Fish and Wildlife Service, Kenai National Wildlife Refuge, Soldatna, Alaska 99669 USA

³National Park Service, Alaska Regional Office, Anchorage, Alaska 99501 USA

⁴Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309-0450 USA

Abstract. We used tree ring data (AD 1601–2007) to examine the occurrence of and climatic influences on spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska and found evidence of regional-scale outbreaks dating from the mid-1700s, related to climate variability at multiple temporal scales. Over interannual time scales (~1–3 years), El Niño years, combined with severe late-summer drought, appeared to contribute significantly to spruce beetle outbreaks in the study area. Over multidecadal time scales (up to ~40 years), cool-phase Pacific Decadal Oscillation (PDO) conditions tended to precede beetle outbreaks, regardless of the phase of El Niño-Southern Oscillation (ENSO). All sites showed low-severity disturbances attributed to spruce beetle damage, most notably during the 1810s. During other major periods of disturbance (i.e., 1870s, 1910s, 1970s), the effects of spruce beetle outbreaks were of moderate or higher severity. The highly synchronized timing of spruce beetle outbreaks at interannual to multidecadal scales, and particularly the association between cool-phase PDO conditions and beetle disturbance, suggests that climate (i.e., temperature, precipitation) is a primary driver of outbreaks in the study area. Our disturbance chronologies (mid-1700s to present) suggest that recent eruptions (1990s to present) in south-central and southwest Alaska are within the historical *geographic* range, but that outbreaks since the 1990s show greater spatiotemporal synchrony (i.e., more sites record high-severity infestations) than at any other time in the past ~250 years.

Key words: Alaska Peninsula; *Dendroctonus rufipennis*; dendroecology; El Niño-Southern Oscillation (ENSO); forest disturbance; Kenai Peninsula; Pacific Decadal Oscillation (PDO); tree rings; white spruce (*Picea glauca*).

INTRODUCTION

In recent years, we have gained substantial insight into the interactive effects of climate and disturbance on forest dynamics across a variety of time scales. Above-average temperatures and prolonged drought over the last half century have been identified as contributing factors to reduced growth in mature and old-growth forests at high latitudes (Barber et al. 2000), increased tree mortality at mid-latitudes (Adams et al. 2009, van Mantgem et al. 2009), and an increasing incidence of wildfires (e.g., Westerling et al. 2006) and bark beetle (*Dendroctonus* spp.) outbreaks (e.g., Berg et al. 2006, Aukema et al. 2008, Hebertson and Jenkins 2008, Macias Fauria and Johnson 2009) in forests across western North America. The capacity for forested ecosystems to maintain their functional and structural characteristics under future warming is unknown (e.g., Raffa et al. 2008, Bentz et al. 2010, Turner 2010), but an understanding of past climate–disturbance interactions provides a basis for identifying when disturbance-

adapted ecosystems depart from a historical regime into a new trajectory (Lenton et al. 2008).

A number of recent studies have highlighted the importance of interactions of short-term (seasonal to interannual) and long-term (decadal to centennial) climate variability, related to broad-scale ocean–atmosphere patterns in both the Pacific (i.e., El Niño Southern Oscillation, ENSO; Pacific Decadal Oscillation, PDO) and Atlantic (i.e., Atlantic Multidecadal Oscillation, AMO) Basins, on drought and wildfire activity at ecosystem (e.g., Schoennagel et al. 2007), regional (e.g., Meyn et al. 2010), and subcontinental to hemispheric (e.g., Kitzberger et al. 2007) scales. Bark beetles are an additional important agent of mortality in western forests (Raffa et al. 2008), and have life-history traits that make them responsive to temperature (Werner and Holsten 1985, Miller and Werner 1987). Host susceptibility and host-mediated effects on bark beetles are likewise influenced by climate variables (temperature, precipitation), and yet only a few studies to date have explored the relationship between climate and bark beetle outbreaks prior to the late 20th century (e.g., Zhang et al. 1999, Hebertson and Jenkins 2008), and none to our knowledge has explicitly tested

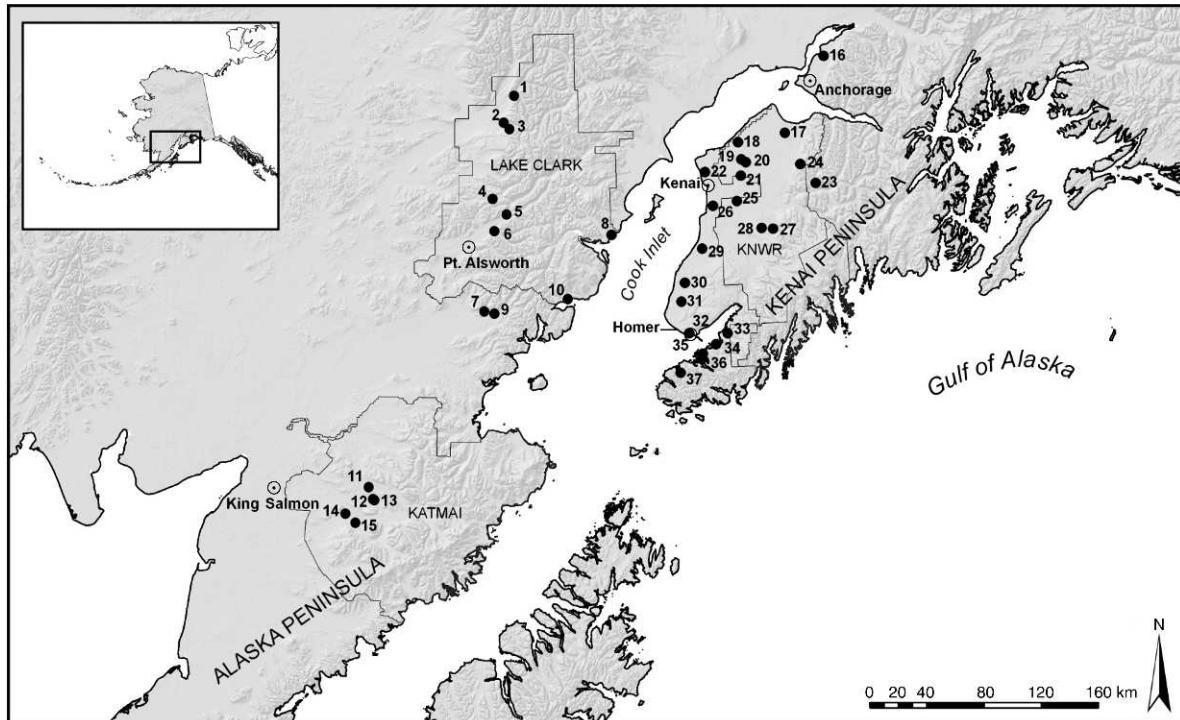


FIG. 1. Location of the study area in south-central and southwest Alaska, USA.

temporal relationships between beetle disturbance and broad-scale climate patterns (ENSO, PDO). The spatial and temporal scales at which climate synchronizes bark beetle outbreaks, similar (or dissimilar) to wildfires (i.e., Kitzberger et al. 2007), is largely unknown, and largely reflects the paucity of long-term, regional data sets on bark beetle outbreaks.

The spruce beetle (*Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytinae)) is one of the most widely distributed bark beetles in North America, ranging from Newfoundland and Interior Alaska to southern Arizona. In south-central and southwest Alaska, >1.5 million ha of spruce forest have been affected by the spruce beetle since 1989, and nearly half of the damage has occurred on the Alaska and Kenai Peninsulas. Mean annual temperature in south-central Alaska has increased by $\sim 1.5^{\circ}\text{C}$ in the last half century, largely driven by increases in winter temperatures and the shift to a warm-phase PDO that occurred in 1976 (Hartmann and Wendler 2005). Although there is evidence to suggest that above-average summer temperatures may have triggered the recent spruce beetle outbreak on the Kenai Peninsula (Berg et al. 2006), we have little understanding of whether climate-beetle relationships observed during the last few decades are representative of those in the long-term record.

Using analysis tools developed to examine temporal synchrony in regional fire regimes, we investigated the spatiotemporal occurrence of, and climatic influences

on, historic (18th–20th centuries) spruce beetle outbreaks in south-central and southwest Alaska. Our study represents one of the most extensive spatiotemporal data sets on spruce beetle disturbance in North America, and is the first study, to our knowledge, to examine regional synchrony of spruce beetle outbreaks, and synchrony between spruce beetle disturbance and climate indices across a range of temporal scales. Specifically, we examine (1) whether spruce beetle outbreaks in south-central and southwest Alaska have occurred synchronously across the study area, and at what temporal scale(s); (2) whether there are detectable relationships between regional spruce beetle outbreaks and climate variables (temperature and precipitation) in the historic record; and (3) whether historic spruce beetle outbreaks were synchronous with broad-scale climate patterns (ENSO, PDO) at interannual (0–5 year) and multidecadal (10–40 year) scales.

METHODS

Study area and field collections

We sampled 37 sites on the western Kenai Peninsula and the northern Alaska Peninsula that span a region of $\sim 300 \times 300$ km, extending from Bristol Bay to the Kenai Mountains (Fig. 1). The study area encompasses two climatic zones (Western Regional Climate Center 2009) that are influenced alternately by storms originating in the North Pacific and Bering Sea, and by cold air masses in Interior Alaska. Most of the precipitation falls as rain

between July and October, with the highest mean rainfall in August. Mean annual precipitation ranges from 378 mm on the northern Alaska Peninsula to 621 mm on the southern Kenai (1961–1990; Western Regional Climate Center 2009), and mean annual temperature over most of the area is $\sim 1^{\circ}\text{C}$ (PRISM; *available online*).⁶ Across the study area, white spruce (*Picea glauca* (Moench) Voss) and resin birch (*Betula neoalaskana* Sargent) dominate in well-drained uplands, grading into Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and Lutz spruce (*P. × lutzii* Little [*glauca* × *sitchensis*]) along the coast.

We used tree ring records at each site to identify growth releases associated with spruce beetle disturbance, following Veblen et al. (1991) and Berg et al. (2006). We sampled mature white, Sitka, and Lutz spruce between 1994 and 2002 (Kenai Peninsula) and 2005 to 2008 (Alaska Peninsula) in representative low-elevation, closed-canopy stands (10–50 ha) below tree-line affected by varying levels of recent spruce beetle disturbance (Appendix A: Table A1). Spruce densities ranged from 650 to 1500 stems/ha at most sites, with trees >20 cm diameter at breast height (dbh) comprising between 50% and 90% of basal area and median tree ages of >140 years. Tree mortality ranged from 10% to >95% in individuals >12 cm dbh (A. E. Miller and E. E. Berg, *unpublished data*). At each site, we preferentially cored large-diameter live and dead trees at a distance of at least 10 m from one another, and away from areas of obvious wind damage, selective cutting, or fire (median of 85 cores per site and 3097 cores total; Appendix A: Table A1).

Tree cores were subsequently evaluated for growth releases and tree death dates associated with past spruce beetle outbreaks (see *Dendroecological analysis*). Tree death dates were attributed to spruce beetle only when we found evidence of blue stain and/or beetle galleries on outer wood. Our assumption that growth releases evident in large-diameter trees can be attributed to past spruce beetle outbreaks while they were understory or subcanopy trees is supported by the following, as outlined by Berg et al. (2006): (1) the spruce beetle is the leading agent of mortality in white spruce in Alaska (Werner et al. 2006) and the only forest insect known to preferentially attack large-diameter mature spruce, resulting in accelerated growth in understory trees (Veblen et al. 1991, Werner et al. 2006); (2) fires, which have an estimated return interval of 400–600 years on the Kenai Peninsula, and for which we have almost no historic evidence on the Alaska Peninsula, are typically stand replacing and leave few surviving trees (Berg and Anderson 2006); (3) a climate signal (e.g., warming), if evident, should be expressed regionally, across elevation gradients and particularly at open-canopy, treeline sites

(Fritts 1976), whereas a spruce beetle signal should be confined to more productive, closed-canopy sites where beetles are active; (4) wind damage tends to be highly localized and sporadic, and thus would be unlikely to result in regionally synchronous growth releases; and (5) selective logging is uncommon in the region, and can be readily identified through the presence of old stumps (E. E. Berg, *unpublished data*). The northern spruce engraver beetle (*Ips perturbatus*), although present at our sites, is not a significant source of mortality in the study area and is not known to preferentially kill mature spruce at a stand scale (Økland et al. 2005, Werner et al. 2006).

Dendroecological analysis

Tree cores were processed using standard dendrochronological techniques, and cross-dated chronologies from each site were used to detect growth releases (release years) using JOLTS (R. L. Holmes, University of Arizona; *available online*),⁷ following Berg et al. (2006). We identified release years associated with spruce beetle in individual trees by comparing a ratio of mean ring width for a 10-year window prior to and following each annual tree ring. For each tree in each site, we excluded the first 10 years from each series (tree core) and defined a growth release as a doubling ($\times 2.0$) of the ring-width ratio. We also excluded 10 years following the first year of a growth release to ensure that release dates were independent. For all trees at each site, we then calculated the probability of observing a release event in a given five-year period using a binomial statistical model described by Ross (1988) using a minimum sample size of 20 trees per year at each site. We first estimated the overall probability of a tree releasing across all years of sampling by calculating the ratio of the total number of releases in all trees to the total number of tree years available for a release at a site (with the exclusion of the years previously mentioned). For each five-year period, we then calculated the number of trees with a release and the number of trees available for release, and used the binomial model to compare these values to the overall probability of a tree releasing across all years of sampling (value from the line above [cf. Berg et al. 2006]). We also evaluated the correspondence of site-level release years with tree death dates, for trees that showed evidence of beetle-related mortality (i.e., blue stain and spruce beetle galleries on outer wood; see *Testing for regional synchrony in spruce beetle outbreaks*).

To verify that the ≥ 10 -year release events we observed in our disturbance chronologies were not actually a response to climate (e.g., extreme warming), we ran the same JOLTS analysis described in the previous paragraph on independent tree ring series (six chronologies [Driscoll et al. 2005]) developed from treeline sites

⁶ (<http://prism.oregonstate.edu>)

⁷ (<http://www.ltrr.arizona.edu/pub/dpl/Jolts.zip>)

located within a 5–10 km radius of several of our beetle sites on the Alaska Peninsula. In closed-canopy stands, the death of mature trees from spruce bark beetle should favor growth only in neighboring trees, and thus only a proportion of trees within a stand would be expected to show a growth release. Tree growth at open-canopy, treeline sites is typically more sensitive to climate variability than at closed-canopy, mesic sites (Fritts 1976), and the tree cores (Driscoll et al. 2005), collected at the upper limit of treeline, were expected to show a climate signal, if present. We assumed that if both open, treeline and closed-canopy, lower-elevation, mesic sites showed the same release date, the release could be interpreted as a response to climate. However, if only the closed-canopy, low-elevation sites showed a release, we interpreted the release to be disturbance related.

Testing for regional synchrony in spruce beetle outbreaks

At each site, we examined the timing and severity of spruce beetle outbreaks by documenting (1) site-level release event years, as indicated by the binomial model; (2) the correspondence of site-level release years with tree death dates, for trees that showed evidence of beetle-related mortality (i.e., blue stain and spruce beetle galleries on outer wood; tree death dates 1910–2003); and (3) severity levels, measured as the percentage of trees with growth releases by decade.

We examined evidence of both site-level effects (i.e., synchrony of growth releases and spruce beetle-caused tree death dates) and regional-level synchrony of spruce beetle outbreaks across sites using a modified Ripley's K function (Ripley 1977) for a single dimension, *time*, using K1D software (D. Gavin, University of Oregon, unpublished software). The modified bivariate (BEK) and multivariate (MEK) Ripley's K functions are temporal variations of spatial point pattern analysis that have been recently used to evaluate temporal synchrony among fire events in sedimentary records (e.g., Gavin et al. 2006, Ali et al. 2009), and temporal lags between drought–tree mortality events (Bigler et al. 2007) and climate–fire events (Schoennagel et al. 2007). The analyses identify similarities in the timing of events (e.g., tree death dates and beetle-caused growth release years) within a defined temporal window ($\pm t$ years). The bivariate K function (BEK) gives the number of events in record 2 (e.g., growth release years) occurring within $\pm t$ years (the temporal window) of each event in record 1 (e.g., tree death dates), and scaled by $T/(n_1n_2)$, where T is the length of the record and n_1 and n_2 are the number of events in records 1 and 2, respectively (Gavin et al. 2006). The multivariate expression of the K function (MEK) is implemented by comparing events in one record to the aggregated events in all other records. To our knowledge, this study is the first to apply the methodology to evaluate temporal synchrony of insect outbreaks and climate–insect interactions. A detailed description of the equations for BEK and MEK with example applications are found in Gavin et al. (2006)

and Bigler et al. (2007), and in the K1D user's manual (*available online*).⁸

To evaluate whether release event years could be attributed to spruce beetle damage at the site level, we used the bivariate expression of the K function (BEK) to examine temporal synchrony of the initiation of beetle-caused tree death dates (D) and significant release event years (R) attributed to outbreaks, where release events coincide with (year = 0) or follow (e.g., lag year = 1–10) tree death dates. For graphical interpretation of the results, the K function was transformed to an L function, which stabilizes the means and variances of the K function over t years, expressed by $L_{RD}(t) = K_{RD}(t) - t$ (Gavin et al. 2006, Bigler et al. 2007). A 95% confidence envelope for the $L_{RD}(t)$ values was calculated by 1000 Monte Carlo simulations of randomized tree death dates. Within a window of t years, values of $L_{RD}(t)$ above the upper confidence limit indicate synchrony between release event years and beetle-caused death dates (i.e., releases coincide with or follow tree death dates more often than expected), values below the lower confidence limit indicate asynchrony (i.e., release years coincide with or follow death dates less often than expected), and values within the confidence envelope indicate independence between the two records.

To test for regional synchrony in outbreak histories, we used (1) the Kruskal-Wallis nonparametric test to compare equality of median outbreak intervals among sites (i.e., as a measure of the similarity or dissimilarity of the median outbreak intervals across the 37 sites), and (2) the bidirectional multivariate expression of the K function (MEK) to test for temporal synchrony in spruce beetle outbreaks (release event years) across sites (Gavin et al. 2006). We used MEK to evaluate the likelihood that release events occurred at multiple sites by chance (Gavin et al. 2006) by comparing release event years (R) from each site to the aggregated release events (A) of all other sites, in which 37 K functions are calculated and averaged together to give each site equal importance in the final K function (K1D user's guide [see footnote 8]; D. Gavin, *personal communication*). The bidirectional approach implies that events in each site are evaluated for synchrony irrespective of direction; i.e., release events at one site occur prior to, co-occur with, or follow events of all other sites. The multivariate K function was transformed to an L function expressed by $L_{RA}(t) = K_{RA}(t)/2 - t$ for graphical interpretation, and a 95% confidence envelope for the $L_{RA}(t)$ values was calculated as described previously. As with the bivariate function (BEK), values of $L(t)$ above, below, or in between the confidence limit indicate synchrony, asynchrony, or independence between event years, respectively. For example, if $L(0)$ through $L(100)$ are above the upper confidence limit, release years among sites are

⁸ (http://geography.uoregon.edu/gavin/K1D_1.pdf)

interpreted to occur synchronously at time scales over a range of $t = 0$ –100 years.

Finally, we inferred the severity of past spruce beetle outbreaks by using criteria from growth releases measured in trees that survived the outbreak that began in the 1990s (severity levels: low < 30% tree mortality; moderate is 30–70% tree mortality; high > 70% tree mortality). Based on observations of growth releases since the 1990s, release events affecting $\geq 30\%$ to $\geq 50\%$ of the live trees within a single decade or sustained across multiple decades were classified as moderate to high severity, respectively. Release events affecting <30% of the live trees were classified as low severity. Our estimates may underrepresent the severity of past outbreaks if recorder trees were removed by subsequent disturbance, but nevertheless enable us to compare severity levels across outbreak periods.

Spruce beetle outbreaks and climate

Climate data sets.—To examine the long-term relationship between spruce beetle outbreaks and climate, we compared our disturbance chronologies (AD 1601–2007) with four annual climate reconstruction records: (1) a tree ring record (MT index; 1769–2003) that correlates positively with spring–summer (April–July) temperatures on the Alaska Peninsula (King Salmon, Alaska; 1947–2000 [Driscoll et al. 2005]), (2) a tree ring record (POn index; 1676–2003) that correlates positively with late summer (August) precipitation on the Alaska Peninsula (King Salmon, Alaska; 1947–2000 [Driscoll et al. 2005]); (3) a tree ring record of the El Niño–Southern Oscillation (ENSO index; 1408–1978) that reflects a measure of the average winter (December, January, and February) sea surface temperature (SST) anomalies in the equatorial Pacific Ocean (Niño-3 region [D’Arrigo et al. 2005]); and (4) a tree ring record of the Pacific Decadal Oscillation (PDO index; 1790–1979 [D’Arrigo et al. 2001]) that reflects a measure of the variability in the dominant decadal mode of North Pacific average summer (April–August) SSTs (Mantua et al. 1997). The ENSO index includes ENSO-sensitive tree ring records from subtropical North America calibrated on Niño-3 Pacific SSTs and accounts for 79% of variance in the instrumental record (1950–1978 [D’Arrigo et al. 2005]). The PDO index includes tree ring records from PDO-sensitive regions of coastal Alaska, the Pacific Northwest, and two subtropical locations in North America, and accounts for 53% of the instrumental variance (1900–1979 [D’Arrigo et al. 2001]). Both ENSO and PDO are characterized by oscillations of warm (positive) and cool (negative) phases of SSTs that influence temperature and precipitation at periodicities of 2–6 years (ENSO [Diaz and Markgraf 2000]) and 20–30 years (PDO [Mantua et al. 1997]), respectively. Temporal autocorrelation in the ENSO record (D’Arrigo et al. 2005) is significant and negative only for lag year 2. PDO typically exhibits decadal variability, although significant temporal autocorrelation is only ~ 4 years in

the D’Arrigo et al. (2001) reconstruction record. For the 1950–1990 period of record, we found the 10-year average window for evaluating releases to be long enough to smooth the 2–6 year periodicity in ring widths associated with the ENSO cycle (ENSO phases often include ~ 1 –2 years in phase of El Niño or La Niña and ~ 1 –5 years neutral [Diaz and Markgraf 2000]) and short enough to detect releases that last for only ~ 10 years (see Berg et al. 2006).

In south-central and southwest Alaska, warm-phase ENSO (El Niño) and PDO conditions tend to produce significantly warmer winter and spring (November–March) temperatures than average, whereas cool-phase ENSO (La Niña) and PDO conditions tend to produce significant cooling in the instrumental record (Papineau 2001). Precipitation is highly variable during warm and cool phases of ENSO, but winter and summer precipitation show a general increase during the warm phase of the PDO and a decrease during the cool phase (Bond and Harrison 2000, Hartmann and Wendler 2005). The period of overlap between the ENSO and PDO reconstructions and our beetle records ends in 1978. We extended the ENSO and PDO reconstructions (D’Arrigo et al. 2001, 2005) from 1978 to 2005 using methods described in Schoennagel et al. (2007). The procedure involved adjusting the standard deviation and mean of each climate reconstruction, calculated over the period of overlap between the two time series (instrumental and tree ring records of ENSO or PDO), to reflect the detrended instrumental record. The reconstructed time series was replaced by the instrumental record during the 1950–2005 time period, when the correlation between the two records was high (cf. Schoennagel et al. 2007).

Beetle–climate analysis.—Using BEK and aggregated release event years (A) from all sites, we tested for synchrony between spruce beetle outbreaks and climate events (C) over the period of record (AD 1790–2005). Climate events included (1) the highest and lowest 25% annual reconstructed climate values of each index (POn, MT, ENSO, and PDO indices); and (2) warm (positive) and cool (negative) phase combinations of ENSO and PDO (i.e., +ENSO/+PDO, +ENSO/–PDO, –ENSO/+PDO, and –ENSO/–PDO). For two-way phase combinations, phase years were defined as all positive or negative values of the ENSO or PDO index. BEK assumes a one-directional relationship between the two events, in which the initiation of release events coincide with (year = 0) or follow (e.g., lag year = 1–50) climate events. Using a randomization of the climate time series, we conducted Monte Carlo simulations with 1000 replicates to determine the 95% confidence envelopes for $L_{AC}(t)$ values, as described previously. Within a temporal window of t years, values of $L(t)$ indicate synchrony, asynchrony, or independence between climate events and release years. Finally, we used Superposed Epoch Analysis (SEA [Grissino-Mayer 1995]; described in Appendix B) to compare release

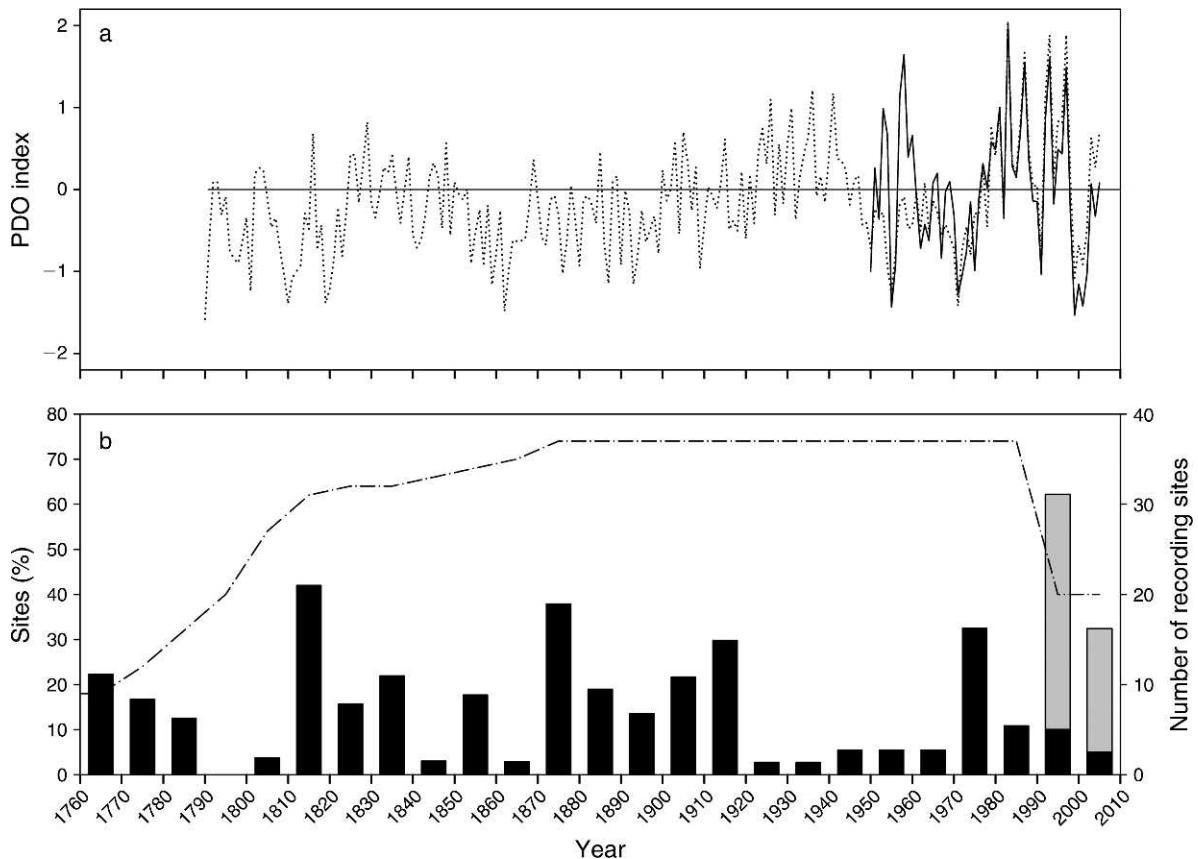


FIG. 2. (a) The tree ring index of Pacific Decadal Oscillation (PDO) (1790–2005, dotted line; see *Methods: Climate data sets*) and the instrumental index of PDO (1950–2005, solid line). Values above (below) 0 suggest warm-phase (cool-phase) PDO conditions. (b) The percentage of sites initiating significant growth releases in 10-year periods shown by black bars (left axis) with the number of recording sites through time shown as a dashed line (right axis). Gray bars represent the percentage of sites with spruce beetle-induced tree mortality since 1990 (left axis; Appendix A).

and nonrelease years with each climate index. This approach is analogous to that used to evaluate fire–climate relationships at interannual scales (e.g., Grissino-Mayer 1995, Schoennagel et al. 2007).

RESULTS

Regional synchrony in spruce beetle outbreaks

Across the nine sites where tree death dates (1910–2003) associated with spruce beetle damage (i.e., blue stain, galleries) could be clearly assessed, BEK analysis indicated that site-level growth releases initiated synchronously and lagged tree death dates by 0 to 10 years (95% confidence level; 12 release events, 21 death dates). Thus, growth releases recorded since 1910 can be attributed directly to spruce beetle-related mortality, with isolated trees showing beetle-related death dates as early as 1884 (Berg et al. 2006). Additional evidence comes from the comparison of release events from our disturbance chronologies with those from the open treeline chronologies of Driscoll et al. (2005); i.e., a lack of concordance in release events between the two chronologies suggests that climate was not the primary

driver of significant releases at our sites. At least two of six sites sampled by Driscoll et al. (2005) recorded significant releases in the 1930s and 1940s, and all six sites showed a release related to late-20th century (1990s) warming (data not shown), but none of these periods appeared as widespread release events in our disturbance chronologies (Fig. 2; Appendix C: Fig. C1).

Over the ~250-year record of spruce beetle outbreaks (70 release events between 1761 and 2003; Fig. 3a), all sites showed at least one significant site-level release event, with 30% or more sites initiating site-level releases in the decades spanning the 1810s, 1870s, 1910s, and 1970s (Fig. 2; Appendix A: Table A1). Across all sites, intervals between significant release event years ranged from 10 to 165 years, with a mean of 48 years (median of 44.5 years). The initiation of beetle-caused release events was highly synchronized across all sites at interannual to centennial time scales (MEK analysis of 70 release events across 37 sites; Fig. 3b), and median outbreak intervals across sites were indistinguishable (KW test, $P = 0.304$; Appendix D). The confidence intervals in the MEK analysis are close to 0 when the lag year (t) is at or

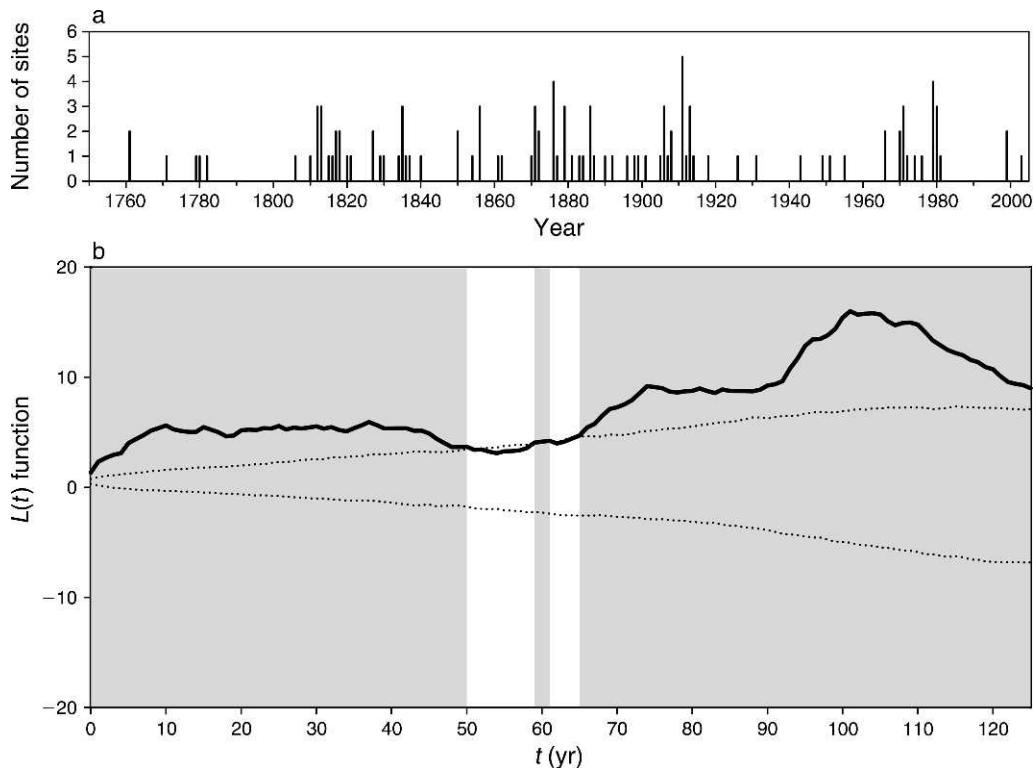


FIG. 3. Multivariate expression of the K function (MEK) analysis of temporal synchrony in the initiation of growth release events attributed to spruce beetle outbreaks across 37 sites. (a) The release event years and the number of sites recording release event years from 1761 to 2003 ($n = 70$ events) used in the analysis. (b) The K function transformed to the L function (solid black line), $L_{RA}(t)$, where values >0 indicate synchrony and values <0 indicate asynchrony in outbreak events, R represents the release event years from each site, and A represents the aggregated release event years of all other sites. The dotted lines represent the 95% confidence envelope based on 1000 Monte Carlo simulations. The gray shaded area represents years of significance.

near 0 because there are generally more release events that co-occur across sites in a given year, or within a few years of one another, than over any other time period (Fig. 3a). The widening confidence intervals with window size in the MEK analysis are also an indication of a slight trend in the number of release events over time (i.e., slightly higher frequency of release events in the 19th century than the 20th century; Fig. 3a). These factors tend to make it more difficult to get a significant result over long time scales (D. Gavin, *personal communication*). The simulation envelopes (i.e., 1000 Monte Carlo simulations) address the nonstationarity in the data, and the results of the MEK analysis show synchrony in release events among sites to be strong across time scales.

All sites exhibited low-severity ($<30\%$ of trees showing sustained growth release) disturbances attributed to spruce beetle damage over the period of record, and most prominently during the 1810s, when 23 of 37 sites recorded a release event (Berg et al. 2006; see Appendix C: Fig. C1). During other major release periods (i.e., 1870–1880s, 1900–1910s, 1970s), the tree ring evidence suggests that spruce beetle outbreaks were of moderate or higher severity across the study area ($\geq 30\%$ of the trees with growth releases within 1–2

decades) (Berg et al. 2006; see Appendix C: Fig. C1). Spruce beetle damage dating from the 1990s or later was evident at 35 of 37 sites, with 76% of the sites showing high-severity infestations ($>70\%$ tree mortality and $>50\%$ of the surviving trees showing a release; 28 sites; Appendix A: Table A1).

Relationship between climate and spruce beetle disturbance

The relationship between climate and release events attributed to spruce beetle outbreaks was evident across a range of temporal scales. At interannual time scales, BEK and SEA analyses revealed significant relationships between the timing of release years and tree ring records of late summer (August) precipitation (POn index [Driscoll et al. 2005]) and warm-phase ENSO conditions (NINO3 index [D'Arrigo et al. 2005]). BEK analysis indicated that release events tend to lag the lowest annual values of the POn index, correlated with dry late summer conditions in the instrumental record (significant synchrony in lag years -1 to -3 within 95% confidence; Fig. 4b) and the highest values of the ENSO index, correlated with warm-phase (El Niño) conditions (significant synchrony in lag year -2 within 95% confidence; Fig. 4c). Results of SEA were consistent

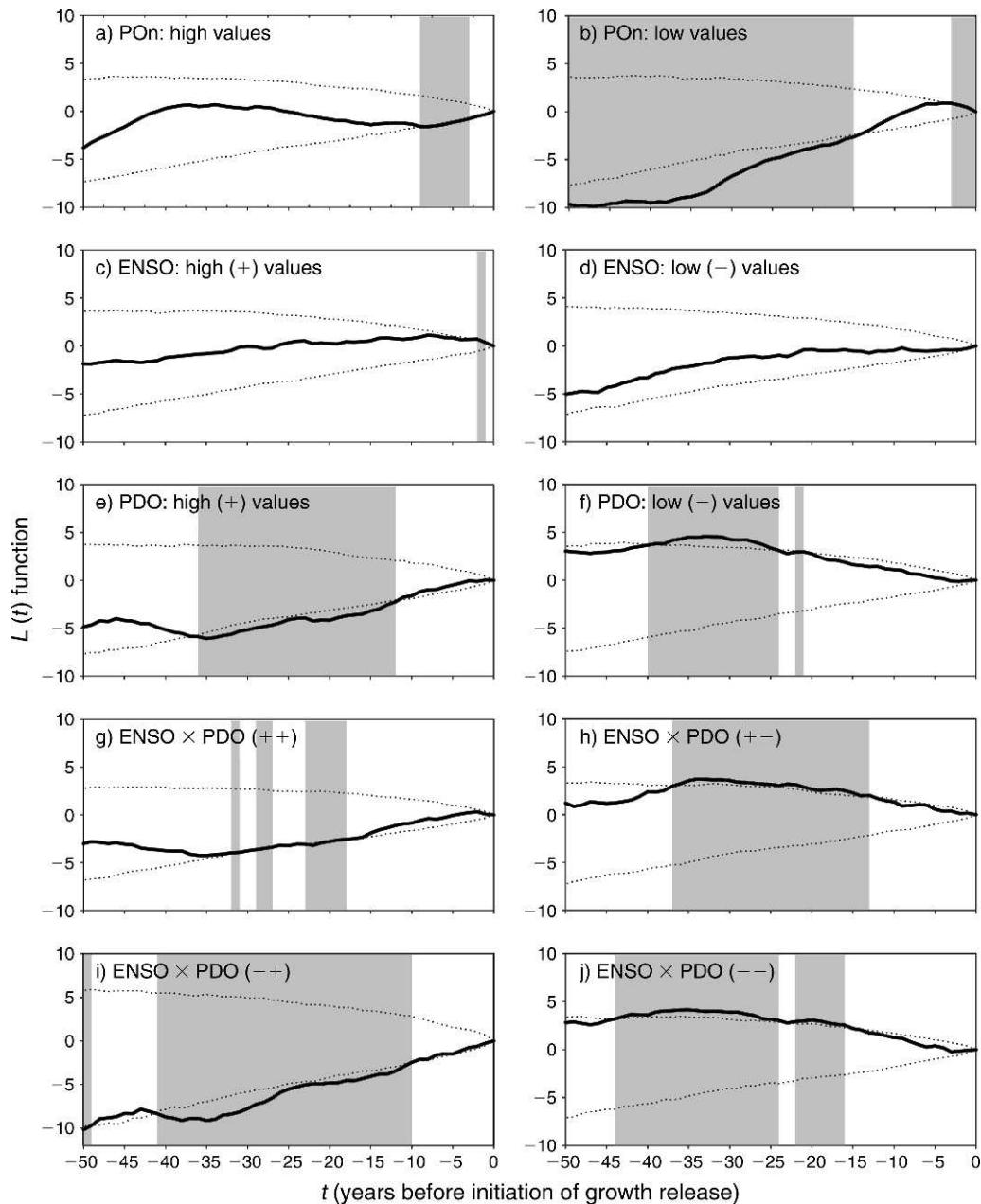


FIG. 4. (a–f) Bivariate expression of the K function (BEK) analysis of the temporal association for corresponding time periods between initiation of release events from all 37 sites (1761–2003) and extreme climate events (highest/lowest 25% of annual reconstructed climate values [see *Methods: Climate data sets*]) and (g–j) two-way phase combinations of ENSO and PDO indices. The (+) symbol indicates the warm-phase and the (–) symbol indicates the cool-phase of ENSO or PDO. $L_{AC}(t)$ values (solid line) above the upper 95% confidence interval (dotted line) denote synchrony between climate and release events; values below the lower confidence interval denote asynchrony (A, aggregated release event years from all 37 sites; C, climate event years). Years of significant synchrony or asynchrony are shaded gray.

with trends shown by BEK, in that release events tended to co-occur with below-average values in the POI index (i.e., significance in lag years -1 , 0 , and 1 within 95–99% confidence; Appendix B: Fig. B1a), warm-phase years in the ENSO index (significance in lag years -1 and -2 within 95% confidence; Appendix B: Fig. B1d), and cool-phase years in the PDO index that correlate with

cooler, drier conditions in the instrumental record (significance in years -5 and 1 within 95% confidence; Appendix B: Fig. B1c). Conversely, BEK analysis indicated that release events tended to occur less frequently than expected (asynchronously) with the highest values of the POI record, correlated with wet late-summer conditions (significant asynchrony in lag

years -3 to -9 within 95% confidence; Fig. 4a) and were independent of the lowest values of the ENSO index that correlate with cool-phase (La Niña) conditions (Fig. 4d). We found no detectable relationship between release events and climate events in the MT index (not shown), which correlates with warmer than expected spring–summer (April–July) temperatures on the Alaska Peninsula (Driscoll et al. 2005).

At multidecadal scales, BEK analysis revealed a tendency for release events to follow cool phases of the PDO for up to ~ 40 years (synchronous significance in lag years -21 and -24 to -40 ; Fig. 4f), whereas fewer than expected release events tended to follow warm phases of PDO during a similar time lag (asynchronous significance in lag years -12 to -36 ; Fig. 4e). The phase of the PDO also appeared to control the outcome of phase interactions (+/–) with ENSO, wherein release events showed significant synchrony with cool (–) phase and asynchrony with warm (+) phase PDO conditions, regardless of the phase of ENSO (Fig. 4g–j). No significant synchrony was detected between 70 randomly generated release events and the climate indices tested previously (Appendix E).

DISCUSSION

The present study expands upon current knowledge regarding historic spruce beetle activity and provides the context for present-day climate–disturbance interactions in south-central and southwest Alaska. Our findings indicate that (1) major spruce beetle outbreaks in south-central and southwest Alaska, as inferred from sustained growth releases recorded across a range of sites, occurred in the 1810s, 1870s, 1910s, and 1970s and were synchronous across the period of record, and (2) these outbreaks tended to occur within multidecadal periods characterized by cool (–) phase PDO conditions and, over shorter time scales, following one to a few years of warm (El Niño) phase ENSO and drier-than-average summer conditions, as inferred from reconstructed climate indices (D'Arrigo et al. 2001, 2005, Driscoll et al. 2005). We base our interpretation of spruce beetle disturbance on the assumption that even during high-severity outbreaks, spruce beetles do not normally kill all trees in a stand, and that the extended growth release observed in surviving trees reflects a period of increased growth following the death of neighboring trees. All sites in our study showed between $\sim 10\%$ and 60% of trees releasing during the periods identified as outbreaks, suggesting localized canopy disturbances rather than a uniform warming signal. For those sites where we could unequivocally identify spruce beetle damage as the cause of tree death, we found that significant site-level growth releases tended to be synchronous with (i.e., within 0–10 years of) tree death dates, indicating that the releases were in response to spruce beetle damage. The mean interval between release events over the 250-year record was 48 years, in agreement with previously published regional estimates for the late 20th century (30–50 years

[Holsten et al. 2001]). Major spruce beetle outbreaks coinciding with these time periods are likewise reported from historical accounts in the southern Rocky Mountains (1850s–1880s, 1890s, 1900s, 1970s [Baker and Veblen 1990]) and central British Columbia, Canada (1810s–1820s, 1960s, 1980s [Zhang et al. 1999]). The striking similarity in the timing of these outbreaks suggests that they may relate to environmental variables (e.g., climate) exhibiting similar patterns of synchrony across different regions (e.g., Koenig 2002).

Climate variables (e.g., temperature, precipitation), disturbance (e.g., wind, fire, and timber harvest), stand conditions (e.g., forest composition and structure, tree age, tree chemistry, tree physiology), and biological agents (e.g., pathogens and defoliators) that predispose trees to attack are thought to be the primary controls on bark beetle irruptions (Werner et al. 2006, Raffa et al. 2008). The early stages of beetle attack are critical, and whether beetles are effective in overcoming host defenses depends in large part on their local population density, weather (e.g., temperature, precipitation, and wind, as they affect dispersal), and physiological stresses on the host (Hard 1987, Raffa et al. 2008). In south-central Alaska, the massive spruce beetle outbreak in the 1990s has been attributed to both an aging forest, characterized by high-density stands of large-diameter, slow-growing spruce, and a warming trend that enabled the spruce beetle to proliferate while leaving drought-stressed trees susceptible to beetle attack (Werner et al. 2006).

This study is the first, to our knowledge, to examine long-term relationships between bark beetle disturbance and climate across a range of temporal scales. A comparison of release event years in our disturbance chronology with those in the treeline chronologies of Driscoll et al. (2005) indicates that release events in our chronologies cannot be attributed directly to warming. The 20th century growth releases that appear in the Driscoll et al. (2005) treeline record from the northern Alaska Peninsula (AD 1930–1940 and AD 1990), and in a recently published tree ring chronology from a treeline mountain hemlock (*Tsuga mertensiana*) site on the western Kenai Peninsula (AD 1920–1940 [Daigle and Kaufman 2009]), are consistent with a regional warming signal that is absent in our disturbance chronologies. Instead, the similarity in the frequency of outbreak intervals among our 37 sites, and the highly synchronized timing of outbreaks across a range of temporal scales, suggest the importance of both short- and long-term climate variability as a driver of regional spruce beetle outbreaks.

Our results indicate that interactions between spruce beetle outbreaks, as indicated by significant growth releases in our closed-canopy sites, and climate variables (e.g., temperature, precipitation) inferred from tree-growth response in adjacent treeline sites (PON index [Driscoll et al. 2005]) and records of ENSO (D'Arrigo et al. 2005) and PDO (D'Arrigo et al. 2001), are scale

dependent and potentially complex. A key finding of our study is that broad-scale ocean–atmospheric patterns in the Pacific Basin (ENSO, PDO) appear to interact to enhance or moderate the effects of regional climate patterns on spruce beetle outbreaks at interannual to multidecadal scales in Alaska. Land surface air temperatures surrounding the Gulf of Alaska are dominated by the Aleutian Low during the winter and spring, which in turn is strongly associated with large-scale North Pacific SST anomalies described by the PDO (Bond and Harrison 2000, Wilson et al. 2007). Under warm-phase PDO conditions, prominent low-pressure anomalies in atmospheric flow occur at roughly three times the frequency seen under cool-phase conditions, and result in marked increases in winter (November–March) precipitation (Bond and Harrison 2000). Summer precipitation patterns are similar, although less pronounced. Under cool-phase PDO conditions, the opposite occurs: enhanced sea level pressure variance from the Bering Sea to the Gulf of Alaska results in high-pressure ridges that block winter storms, bring in cold arctic air, and lead to reduced rain and snow (Overland et al. 1999, Bond and Harrison 2000). These positive pressure anomalies associated with the November–March Aleutian Low correspond closely with the cool-phase PDO periods of 1900–1924 and 1947–1976 (Overland et al. 1999), suggesting that these periods would have been characterized by below-average winter–spring temperatures and precipitation that could predispose host trees to beetle attack.

At interannual time scales, ENSO and PDO reconstructions revealed the strongest associations with spruce beetle outbreaks during and following years recorded as warm-phase ENSO and cool-phase PDO; i.e., spruce beetle outbreaks tended to initiate during and following years of late-summer drought (low August precipitation; Fig. 4b and Appendix B: Fig. B1a), warm (El Niño) phases of ENSO (Fig. 4c and Appendix B: Fig. B1d), and cool phases of PDO (Appendix B: Fig. B1c). At longer time scales (up to ~40 years), we found a strong pattern of cool-phase PDO conditions preceding spruce beetle outbreaks, regardless of the phase of ENSO. Our results suggest that both temperature and precipitation are important drivers of spruce beetle outbreaks in south-central and southwest Alaska, but it is difficult to discern the degree to which one (temperature or precipitation) may be more influential than another, nor can we necessarily assume that all sites respond similarly to a common driver (e.g., warming [Barber et al. 2000, Driscoll et al. 2005]). However, the tendency of up to 40-year periods of cool-phase PDO conditions to occur prior to outbreaks suggests that extended periods of decreased winter precipitation (i.e., snowpack) associated with cool-phase PDO, and short-term periods of warmer temperatures associated with warm-phase ENSO, both contribute to widespread spruce beetle outbreaks. First, short-term periods of warm winter temperatures and deeper snowpacks

associated with warm-phase ENSO could enhance overwinter survival of beetle larvae (Miller and Werner 1987, Werner et al. 2006). Second, warm summer temperatures could accelerate development of early larval stages, reducing generation time from a two-year to one-year life cycle and increasing the number of mature beetles in any single year (Werner and Holsten 1985). Third, one to a few years of warm-phase ENSO during extended periods of cool-phase PDO interactions could extend the snow-free season through earlier snowmelt dates (Vincente-Serrano et al. 2007), both facilitating earlier emergence and dispersal of beetles in the spring (Werner and Holsten 1985), and reducing soil moisture, thereby enhancing drought stress and the susceptibility of trees to beetle attack (Hard 1987, Barber et al. 2000). In south-central Alaska, late-spring conditions are conducive for spruce beetle attack because the already depleted photosynthates required for production of defensive compounds are being put toward tree growth. Frozen soils and low springtime precipitation limit water availability to roots, resulting in reduced translocation and resin exudation. As a result, trees growing on cold, dry sites have been found to record higher beetle attack densities than those growing on warmer sites (Hard 1987), and similar reductions in tree defenses and/or increases in attack densities are expected to occur in years of low late-summer precipitation.

The regional increase in spruce beetle disturbance that began in the late 1980s in Alaska followed a regime shift from cool- to warm-phase PDO conditions in 1976 (Papineau 2001, Hartmann and Wendler 2005). The shift has resulted in an increase in temperature and total winter precipitation in south-central and southwest Alaska, but no change in snowfall, and thus a higher percentage of winter precipitation is now falling as rain (Hartmann and Wendler 2005). Mean annual temperature across much of the study area hovers near 0°–1°C, and a shift in winter precipitation from snow to rain has likely resulted in decreased snowpacks at low elevation, a shorter snow season and earlier snowmelt, and increased early-summer drought. In south-central and southwest Alaska, recent years of widespread spruce beetle activity occurred during and following the warm-phase ENSO/PDO years of 1987–1988, 2002–2003, and 2006–2007 (Alaska Department of Natural Resources; *available online*).⁹ In British Columbia, mountain pine beetle outbreaks also initiated following the onset of the warm-phase PDO in 1976, presumably due to increased overwinter survival of larvae during milder winters, and/or accelerated development during warmer summers (Macias Fauria and Johnson 2009). In our study area, the warm-phase PDO/ENSO phase combination observed during recent outbreaks contrasts with historic reconstructions that indicate spruce beetle outbreaks

⁹ (<http://forestry.alaska.gov/insects/surveys.htm>)

initiated more often than expected during cool-phase PDO conditions (i.e., -PDO/+ENSO). We believe that warm-phase PDO conditions could have supported spruce beetle outbreaks in the past, but that only a limited number of warm-phase PDO/ENSO periods occurred during our ~250 year record, and recent warming trends may have shifted beetle-climate interactions by facilitating earlier emergence and dispersal of beetles, enhancing beetle reproduction and/or reducing soil moisture that leads to drought stress and greater susceptibility of trees to beetle attack.

The sustained warming that has occurred in recent decades suggests that historic (~mid-18th-mid-20th centuries) relationships between climate and spruce beetle outbreaks may be changing. In high-latitude forests and other climatically sensitive ecosystems, continued warming could lead to a shift in the frequency, severity, location, and extent of insect outbreaks from historic levels (Raffa et al. 2008, Bentz et al. 2010), and potentially to a large-scale forest dieback (Lenton et al. 2008). Our reconstructions indicate that the spruce beetle outbreak that occurred in Alaska in the 1990s was within the historical *geographic* range, but that it showed greater spatiotemporal synchrony, particularly in high-severity infestations, than at any other time in the past ~250 years. Our research represents an important step in our understanding of the potential divergence between historic and present-day spruce beetle disturbance, and the role played by climate in controlling the timing and extent of an outbreak.

ACKNOWLEDGMENTS

We thank M. Bowser, C. Lindsay, M. Shephard, D. Shepard, P. Bradway, J. Carbone, D. Manthorne, and A. Starr for field and lab assistance for collections from the Alaska Peninsula. Logistical support was provided by the National Park Service, Pedro Bay Native Corporation, and Pedro Bay Native Council. We also thank contributors to the Kenai field and lab work, who are acknowledged in Berg et al. (2006). Funding for the project was provided by the National Park Service. We thank Daniel Gavin and three anonymous reviewers for helpful comments on the manuscript.

LITERATURE CITED

- Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Illegas, D. D. Breshears, C. B. Zou, P. A. Troch, and T. E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences USA* 106:7063–7066.
- Ali, A. A., C. Carcaillet, and Y. Bergeron. 2009. Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology* 15:1230–1241.
- 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.
- Baker, W. L., and T. T. Veblen. 1990. Spruce beetles and fire in the nineteenth-century subalpine forests of western Colorado, U.S.A. *Arctic and Alpine Research* 22:65–80.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602–613.
- Berg, E. E., and R. S. Anderson. 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska over the last two millennia as determined from soil charcoal. *Forest Ecology and Management* 227:275–283.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. DeVolder, 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. *Forest Ecology and Management* 227:219–232.
- Bigler, C., D. G. Gavin, C. Gunning, and T. T. Veblen. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116:1983–1994.
- Bond, N. A., and D. E. Harrison. 2000. The Pacific decadal oscillation, air-sea interactions and central North Pacific winter atmospheric regimes. *Geophysical Research Letters* 27:731–734.
- Daigle, T. A., and D. S. Kaufman. 2009. Holocene climate inferred from glacier extent, lake sediment and tree rings at Goat Lake, Kenai Mountains, Alaska, USA. *Journal of Quaternary Science* 24:33–45.
- D'Arrigo, R. D., E. R. Cook, R. J. Wilson, R. Allan, and M. E. Mann. 2005. On the variability of ENSO over the past six centuries. *Geophysical Research Letters* 32:L03711.
- D'Arrigo, R. D., R. Villalba, and G. Wiles. 2001. Tree-ring estimates of Pacific decadal climate variability. *Climate Dynamics* 18:219–224.
- Diaz, H., and V. Markgraf, editors. 2000. *El Niño and the Southern Oscillation: multiscale variability and global and regional impacts*. Cambridge University Press, Cambridge, UK.
- Driscoll, W. W., G. C. Wiles, R. D. D'Arrigo and M. Wilmking. 2005. Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve, Alaska. *Geophysical Research Letters* 32:L20703 (1–4).
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, New York, New York, USA.
- Gavin, D. G., F. S. Hu, K. Lertzman, and P. Corbett. 2006. Weak climate control of stand-scale fire history during the late Holocene. *Ecology* 87:1722–1732.
- Grissino-Mayer, H. D. 1995. *Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico*. Dissertation. University of Arizona, Tucson, Arizona, USA.
- 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. *Canadian Journal of Forest Research* 17:428–435.
- Hartmann, B., and G. Wendler. 2005. The significance of the 1976 Pacific climate shift in the climatology of Alaska. *Journal of Climate* 18:4824–4839.
- Hebertson, E. G., and M. J. Jenkins. 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology* 37:281–292.
- Holsten, E., P. Hennon, L. Trummer, and M. Schultz. 2001. *Insects and diseases of Alaskan forests*. U.S. Forest Service Alaska Region Technical Report R10-TP-87, Anchorage, Alaska, USA.
- Kitzberger, T., P. M. Brown, E. K. Heyerdahl, T. W. Swetnam, and T. T. Veblen. 2007. Continental-scale synchrony in wildfires and climate in western North America over the past

- 5 centuries. *Proceedings of the National Academy of Sciences USA* 104:543–548.
- Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. *Ecography* 25:238–288.
- Lenton, T. M., H. Held, E. Kriegler, J. W. Hall, W. Lucht, S. Rahmstorf, and H. J. Schellnhuber. 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences USA* 105:1786–1793.
- Macias Fauria, 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.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *American Meteorological Society* 78:1069–1079.
- Meyn, A., S. W. Taylor, M. D. Flannigan, K. Thonicke, and W. Cramer. 2010. Relationship between fire, climate oscillations, and drought in British Columbia, Canada, 1920–2000. *Global Change Biology* 16:977–989.
- Miller, K. L., and R. A. Werner. 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Canadian Journal of Zoology* 65:2927–2930.
- Økland, B., A. M. Liebhold, O. N. Bjørnstad, N. Erbilgin, and P. Krokene. 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? *Oecologia* 146:365–372.
- Overland, J. E., J. M. Adams, and N. A. Bond. 1999. Decadal variability of the Aleutian low and its relation to high-latitude circulation. *Journal of Climate* 12:1542–1548.
- Papineau, J. M. 2001. Wintertime temperature anomalies in Alaska correlated with ENSO and PDO. *International Journal of Climatology* 21:1577–1592.
- 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.
- Ripley, B. D. 1977. Modeling spatial patterns. *Journal of the Royal Statistical Society B* 39:172–212.
- Ross, S. M. 1988. *A first course in probability*. Third edition. Macmillan, New York, New York, USA.
- Schoennagel, T. L., T. T. Veblen, D. Kulakowski, and A. Holz. 2007. Multidecadal climate variability and climate interactions affect subalpine fire occurrence, western Colorado (USA). *Ecology* 88:2891–2902.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.
- van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.
- 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.
- Vincente-Serrano, S. M., M. Grippa, T. L. Toan, and N. Mognard. 2007. Role of atmospheric circulation with respect to the interannual variability in the date of snow cover disappearance over northern latitudes between 1988 and 2003. *Journal of Geophysical Research* 112:D08108.
- Werner, R. A., and E. H. Holsten. 1985. Factors influencing generation times of spruce beetles in Alaska. *Canadian Journal of Forest Research* 15:438–443.
- Werner, R. A., K. F. Raffa, and B. L. Illman. 2006. Dynamics of phytophagous insects and their pathogens in Alaskan boreal forests. Pages 133–146 in F. S. Chapin, M. W. Oswood, and K. Van Cleve, editors. *Alaska's changing boreal forest*. Oxford University Press, New York, New York, USA.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- Wilson, R., G. Wiles, R. D'Arrigo, and C. Zwick. 2007. Cycles and shifts: 1,300 years of multi-decadal temperature variability in the Gulf of Alaska. *Climate Dynamics* 28:425–440.
- Zhang, Q., R. I. Alfaro, and R. J. Hebda. 1999. Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada. *Forest Ecology and Management* 121:215–225.

APPENDIX A

Sample site information (*Ecological Archives* E092-124-A1).

APPENDIX B

A description and the analysis of Superposed Epoch Analysis (SEA) used to evaluate climate conditions during and prior to release events from 1761 to 2003 (*Ecological Archives* E092-124-A2).

APPENDIX C

Site-level information on spruce beetle activity for sites on the Alaska Peninsula (*Ecological Archives* E092-124-A3).

APPENDIX D

Histogram of median spruce beetle outbreak intervals for 37 sites in southwest and south-central Alaska (*Ecological Archives* E092-124-A4).

APPENDIX E

Interannual to multidecadal scale analysis of climate conditions during and prior to randomly selected release events and extreme climate events (*Ecological Archives* E092-124-A5).