

Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a Sky Island mountain range



Christopher D. O'Connor^{a,c,*}, Ann M. Lynch^{b,c}, Donald A. Falk^{a,c}, Thomas W. Swetnam^c

^a University of Arizona, School of Natural Resources and the Environment, 325 Biosciences East, Tucson, AZ 85721, USA

^b U.S. Forest Service, Rocky Mountain Research Station, 1215 E. Lowell St., Tucson, AZ 85721, USA

^c University of Arizona, Laboratory of Tree-Ring Research, 1215 E. Lowell St., Tucson, AZ 85721, USA

ARTICLE INFO

Article history:

Received 22 July 2014

Received in revised form 18 October 2014

Accepted 21 October 2014

Keywords:

Dendroctonus rufipennis

Fire exclusion

Drought

Mixed-conifer

Temperature

Dendrochronology

ABSTRACT

The spruce beetle (*Dendroctonus rufipennis*) is known for extensive outbreaks resulting in high spruce mortality, but several recent outbreaks in the western United States have been among the largest and most severe in the documentary record. In the Pinaleno Mountains of southeast Arizona, U.S.A., an outbreak in the mid-1990s resulted in 85% mortality of Engelmann spruce >7 cm diameter. To put this outbreak into historical perspective, we used dendrochronology to examine the effects of host species' distribution and growth rates on spruce beetle outbreak initiation, frequency and size over three centuries. We used multiproxy records of understory spruce growth release, snag death dates, failed attack scars, and historical records to identify 12 distinct outbreak events over a 319-year period of reconstruction. Outbreaks were defined by spatial criteria, affecting 25% or more of sites, instead of mortality-based criteria that could not be assessed in older outbreak events. We also tested outbreak associations with summer temperature and spring drought as they relate to thresholds associated with larval development and host stress, respectively. In the decades following fire exclusion in adjacent mixed-conifer forest, the area occupied by Engelmann spruce and corkbark fir doubled in size, coinciding with the first widespread outbreaks in the reconstructed period and a doubling of outbreak duration. Outbreaks lagged spruce establishment by 40–90 years depending on forest type and time since fire, and were correlated significantly with several years of antecedent warm summer temperatures followed by up to a decade of persistent spring drought. Mean annual growth increment, a factor associated with host susceptibility, was significantly higher in recently colonized mixed-conifer forest than in historically spruce- and fir-dominated sites. Increasing size and severity of outbreaks appears to have been influenced by host range expansion due to fire exclusion, coupled with increasing incidence of warm summer temperatures associated with persistent spring water stress. The combined effects of expansion of spruce into mixed-conifer forest and climatic trend toward warmer, drier conditions have the potential to promote extensive spruce beetle outbreaks across the host range of the western United States.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Subalpine spruce-fir forests comprised primarily of Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and corkbark or subalpine fir (*Abies lasiocarpa* vars. *arizonica* or *bifolia* (Hook.) Nutt.), are the highest elevation forest type in the southwestern United States and comprise approximately 8.4% of the evergreen forests of Arizona, New Mexico, Colorado, Utah, and Nevada (Prior-Magee et al., 2007; Vankat, 2013). Species dynamics in spruce-fir forest are mediated by fire, insect outbreaks, avalanches,

rockslides, and blow-down events (Veblen et al., 1994; Bebi et al., 2003; Kulakowski et al., 2003; Bigler et al., 2005). Infrequent mixed- and high-severity canopy fires at 200–1000-year intervals (Arno, 1980; Romme and Knight, 1981; Kipfmüller and Baker, 2000; Anderson et al., 2008; Morris et al., 2013; O'Connor et al., 2014) are the typical stand-replacing disturbances in this forest type because mature stands tend to form closed canopies with low canopy base heights that retain abundant dead fuels in the lower canopy (Burns and Honkala, 1990). Fires in spruce-fir forests in the southwestern United States have been associated historically with extreme drought conditions that tend to occur during combined negative phases of the El Niño Southern Oscillation and Pacific Decadal Oscillation at centennial to millennial

* Corresponding author. Tel.: +1 520 621 0059; fax: +1 520 621 8801.

E-mail address: occonnorc@email.arizona.edu (C.D. O'Connor).

timescales (Schoennagel et al., 2005; Sibold and Veblen, 2006; Margolis and Swetnam, 2013). During extended periods between fires, spruce beetle (*Dendroctonus rufipennis* Kirby) and western balsam bark beetle (WBBB) (*Dryocoetes confusus* Swaine) are the most important drivers of forest species composition, structure and age distribution of upper elevation forests (Schmid and Hinds, 1974; Aplet et al., 1988; Veblen et al., 1991a; Vankat, 2013).

Over the past two decades, the size and severity of spruce beetle outbreaks have increased throughout the western states (Dymerski et al., 2001; DeRose and Long, 2007, 2012; Raffa et al., 2008). A variety of factors at local and regional scales have been identified as potential contributors to recent outbreak extent and severity, including large contiguous stands of mature spruce (Berg et al., 2006; DeRose et al., 2009), warmer than average mean winter and summer temperatures (Berg et al., 2006; Hebertson and Jenkins, 2008; Raffa et al., 2008; Bentz et al., 2010; DeRose and Long, 2012), persistent drought and increased vapor pressure deficit (DeRose and Long, 2012; Williams et al., 2013; Hart et al., 2014a), and decadal to multidecadal scale climate variability (Sherriff et al., 2011; Hart et al., 2014a).

While regional climate and stand characteristics may act as precursors to spruce beetle outbreak (Hart et al., 2014b), an inciting factor that allows the endemic beetle population to move into incipient and outbreak modes is generally considered necessary (Schmid and Frye, 1977). Conditions necessary for a spruce beetle population to transition from simply being present in the system to becoming a significant agent of spruce mortality may require synchrony among a series of stand-level and regional climate conditions (Raffa et al., 2008), a situation analogous to spreading fire in which conditions appropriate for fire ignition and spread occur more frequently than spreading fire itself.

Patterns of spruce beetle outbreak size and severity are poorly understood, due mainly to the short length of the historical record and the relatively long time intervals between repeated outbreaks on the same landscapes. Several recent studies have examined potential natural controls on outbreak size, severity, and inciting factors (Berg et al., 2006; Hebertson and Jenkins, 2008; Sherriff et al., 2011; DeRose and Long, 2012; Hart et al., 2014a); however, no spatially explicit reconstructions of spruce beetle outbreak history have examined changes in outbreak size, frequency, and duration through time as a function of changes to stand conditions, host range distributions, and regional climate patterns.

Here we employ a spatially explicit gridded sampling design to reconstruct changes to the distribution, age structure, and stand characteristics of a spruce-fir forest in relation to spruce beetle outbreaks on an isolated mountain range in southeastern Arizona, USA. We use demographic reconstructions of tree establishment, species composition, spatial extent, and age structure to track changes to spruce population characteristics over a 319-year period between stand-replacing fires. We develop a multiproxy reconstruction of spruce beetle outbreaks based on (1) growth release events in surviving trees, (2) encapsulated scars from failed spruce beetle attacks, (3) death dates from spruce beetle-killed trees, and (4) historical documentation of outbreak events, to reconstruct the spatial and temporal components of major spruce beetle outbreaks. We then examine relationships between the size and severity of spruce beetle outbreaks and changes to the distribution of host species. Lastly we test associations between spruce beetle outbreak initiation and seasonal temperature and moisture conditions.

2. Study area

The spruce-fir forest of the Pinaleño Mountains, located at 32° 41' N, 109° 53' W, represents the southernmost extent of the forest type in North America (Stromberg and Patten, 1991) and is

situated at the top of a vertical gradient spanning approximately 2100 m (McLaughlin, 1993). The study area above 2835 m (9300 ft.) is located on gently sloping Typic Dystrochrepts with sandy loam texture underlain with large gneissic material (NRCS, 2012). Vegetation is dominated by Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.), with occasional Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), southwestern white pine (*Pinus strobiformis* Engelm.), and aspen (*Populus tremuloides* Michx.) (Fig. 1). Engelmann spruce in the Pinaleño Mountains exhibits little introgression with white spruce (*Picea glauca* (Moench) Voss), which is common further north (Haselhorst and Buerkle, 2013). The forest surrounding the study area along the central plateau of the range is primarily mixed-conifer forest dominated by Douglas-fir and southwestern white pine with additional components of white fir (*Abies concolor* (Gor. & Glend.) Lindl. ex Hildebr.) and ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.). The mixed-conifer forest transitions abruptly to pine and oak forest (*Quercus* spp.) on the steep slopes below 2135 m (O'Connor, 2013).

The contemporary spruce-fir forest originated from a stand replacing fire in 1685 that also burned parts of the surrounding mesic mixed-conifer forest with high severity (O'Connor et al., 2014). Small patches of surviving spruce and fir began to repopulate the upper elevation forest shortly after the fire, and much of the spruce-fir zone was under closed canopy conditions by the mid to late 1700s (O'Connor et al., 2014). No fires entered the spruce-fir forest for 311 years until the 1996 Clark Peak fire burned 143 ha of spruce-fir forest with high severity (Froehlich, 1996). Shortly thereafter the 2004 Nuttall Complex Fire burned over the majority of the remaining spruce-fir forest with more than 70% moderate to high burn severity (Fig. 1).

The adjacent mixed conifer forest underwent a significant change in fire frequency following EuroAmerican settlement of the region and subsequent livestock grazing and timber extraction starting in the late 1870s (Bahre, 1998). The interruption of historic fire regimes in inland dry forests of the southwestern United States concurrent with EuroAmerican settlement is documented in fire history studies throughout the region (e.g. Grissino-Mayer et al., 1995, 2004; Swetnam and Baisan, 1996; Swetnam et al., 2001; Brown and Wu, 2005; Fulé et al., 2009). Prior to 1880, median fire return intervals for fires greater than 100 ha ranged from 3.4 years in the driest mixed-conifer sites to 23.9 years in the most mesic mixed-conifer sites. After 1880 the median fire return interval for dry and mesic mixed-conifer forests increased to more than 50 years in the few areas that recorded fire, and more than 100 years over the majority of the forest type (O'Connor et al., 2014). This change in fire frequency resulted in a significant increase in stem densities and a shift toward more shade tolerant, fire-sensitive species (Grissino-Mayer et al., 1995; O'Connor, 2013).

Spruce beetle activity in the Pinaleño Mountains is documented from an outbreak detected in 1952 that had already been active for several years, resulting in a loss of approximately 18–20% of spruce timber volume (Bennett, 1953), and another outbreak from 1999 to 2002 that was preceded by a series of defoliation events by other insects (Koprowski et al., 2005). Cumulative insect damage resulted in mortality of 83% of Engelmann spruce and 63% of corkbark fir greater than seven cm diameter at breast height (DBH) throughout the spruce-containing forest extent (O'Connor, 2013). The endemic population of spruce beetles began to increase in the spruce-fir forest following a winter storm in 1993 that caused a modest amount of tree breakage and blowdown (Frank and Fairweather, 1994). Beetle population density then increased rapidly in an approximately 200 ha patch of old growth spruce-fir forest where trees were defoliated in 1996–1999 by *Nepytia janetae* (Rindge), a native Geometrid moth that was previously unknown as a forest pest (Lynch unpublished). Bark beetle-related mortality

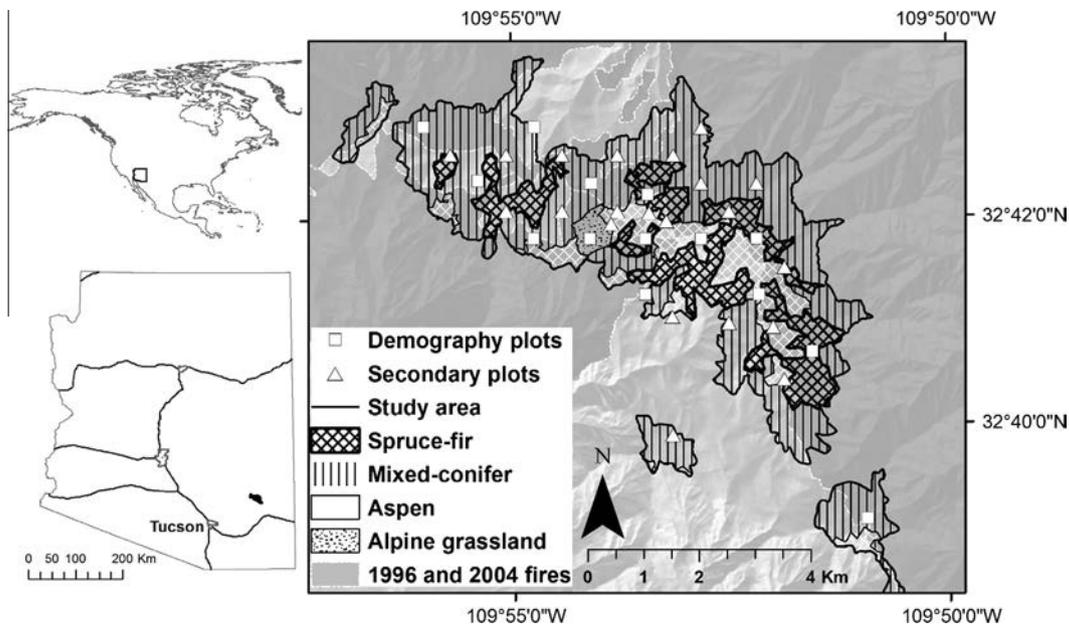


Fig. 1. Location and sampling design of spruce-containing forest in the Pinaleno Mountains, Arizona, USA. Study area denotes elevation above 2835 m. Distributions of forest types are from LANDFIRE biophysical setting generalized to a minimum patch size of 6.75 ha (LANDFIRE, 2013). Fire extents are from the USFS Monitoring Trends in Burn Severity database (MTBS, 2013).

was first noted in 1999 (Wilson et al., 1999; USDA Forest Service, 2000). The same year, the introduced spruce aphid *Elatobium abietinum* (Walker) was first detected in the Pinaleno Mountains, damaging spruce of all size classes (Lynch, 2009). From 1999 to 2002 the bark beetle outbreaks and spruce aphid infestation spread throughout the extents of spruce and corkbark fir (Lynch, 2009).

3. Methods

To reconstruct the spatial and temporal dimensions of spruce-containing forest and bark beetle outbreaks, we used tree establishment and growth records from a primary grid of 14 fixed area (0.05 ha) tree demography plots spaced 1-km apart, supplemented with a secondary grid of 21 fixed sample size plots offset 500 m from demography plot locations. In demography plots, we used increment cores or cross sections to collect samples from all living and dead trees greater than 19.5 cm DBH. We collected samples from trees with DBH range of 1–19.4 cm in a sub-plot equal to one third the total plot area (0.017 ha), and seedlings <1 cm DBH were cut at the soil surface within the sub-plot. In fixed sample size plots, we collected increment cores or cross sections from the 10 spruce trees and 10 non-spruce trees >15 cm DBH nearest plot center. The 15 cm DBH threshold in fixed sample-size plots was used to filter for trees likely to have survived the mid-20th century spruce-beetle outbreak. At least one, and up to three increment cores were collected from the side of each living tree perpendicular to hill slope, at a height of less than 20 cm from mineral soil. More than one core was collected from trees with ring anomalies such as branch traces, injury, rot, or other deformation that obscured pith location. Radial cross-sections were collected from stumps and fallen logs, and quarter wedges were removed from standing snags as close to the root collar as possible. In addition to sampling for dendrochronology, we recorded tree species, condition class, and DBH or diameter at the root crown (for stumps).

3.1. Sample processing

Increment cores and cross-sections were mounted and sanded with progressively finer grits until individual cell structure was

observable. Samples were cross-dated using a combination of visual pattern matching (Yamaguchi, 1991) and skeleton plots (Stokes and Smiley, 1968; Speer, 2010). A master chronology developed from Douglas-fir within the spruce-fir zone had the highest series inter-correlation among all high elevation species and was used to validate crossdating (Speer, 2010). On samples that did not include pith, concentric ring pith locators (Applequist, 1958) were used to estimate pith dates if ring curvature indicated pith was within 10 years of the innermost ring. Crossdating of samples prior to ring-width measurement allowed us to account for occasional locally absent rings and other growth anomalies limited to specific plot locations or individual trees. After samples were crossdated, ring-width measurements were recorded with J2X measuring software on a Velmex TA system® with sensor accuracy of one micron (VoorTech, 2010). Initial crossdating of individual trees was checked with COFECHA crossdating analysis software (Holmes, 1983). Samples that did not correlate with the plot-level chronology at a level of 0.3 or higher were removed from the analysis (Grissino-Mayer, 2001).

Bark beetle outbreaks are usually inferred in dendrochronological reconstructions by growth releases in surviving understory trees (Veblen et al., 1991b; Eisenhart and Veblen, 2000; Berg et al., 2006). Raw ring width measurements from individual trees at each plot location were analyzed for growth releases with the program JOLTS (Holmes, 1999). Growth releases were recorded as a minimum 50% increase (JOLTS ratio of 1.5) in the 10-year running mean of ring widths at the individual tree level. Previous spruce beetle outbreak reconstructions using the 10-year running mean of ring widths have used more conservative growth release criteria (100–250% increase in ring width growth) to define an outbreak (Veblen et al., 1991b; Berg et al., 2006). In calibrating the growth release criteria to two known events and locations, we found that the less conservative 50% growth increase criteria tended to detect outbreak 1–4 years sooner than the more conservative criteria (supplemental Fig. 1). Earlier detection coincided more closely with aerial and ground spruce beetle surveys (Bennett, 1953; Lynch, 2009), spruce death dates, and failed-attack scars.

A minimum time between releases of 15 years was used to focus on initiation of outbreaks and to distinguish between discrete

outbreak events. Tree-level growth releases were composited by site to determine the proportion of outbreak-recording sites. We used a threshold of at least 25% of sites with 10% or more trees recording growth release over a five-year period to identify spatially significant spruce beetle outbreaks. The criterion of 25% or more of sites recording release was used to filter out background growth release events recorded in only one or a few sites. Growth releases occurring within 500 m and up to five years after fire or known logging operations were excluded from the analysis (O'Connor et al., 2013).

Use of a 10-year running mean excluded the first and last decades of measurement series, and caused a problem with detecting growth releases associated with the most recent insect outbreaks in the 16 plots affected by the 2004 high-severity fire. To reconstruct the spatial and temporal progression of insect-caused tree mortality for the 1990s insect outbreaks, we combined growth release records from unburned plots with tree death dates determined from the last ring of growth. Samples with charred outer rings were not used for the analysis of tree death dates. We did not attempt to differentiate between bark beetle, defoliator, or pathogen-caused mortality in the 1990s series of outbreaks.

Failed attack scars are commonly found on trees in the early and late stages of spruce beetle outbreak when the beetle population is not sufficient to overcome tree defenses, or in trees too small in diameter for successful brood development (Schmid and Frye, 1977) (Fig. 2). Scars form as a result of lesions caused by spruce beetle attack and larval gallery formation that are then encapsulated in callus tissue and incorporated into an annual growth ring. Lesions are highly variable in size, ranging from one to several centimeters in length, and tend to be aggregated around the lower bole of the tree (Schmid and Frye, 1977). Although two previous studies are known to have used failed-attack scars to infer outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in ponderosa pine (Craighead, 1925; Blackman, 1931), this is the first study we are aware of to use failed attack scars to corroborate growth release evidence of spruce beetle outbreak.

3.2. Reconstruction of dynamic host range distributions

We used a spatial reconstruction of spruce and corkbark fir establishment following the 1685 stand-replacing fire to verify the potential for spruce beetle or WBBB outbreaks at each plot location through time. An interpolated surface of spruce and corkbark fir establishment was generated through inverse distance weighting of earliest establishment dates from the four nearest plots with a power function of two (ESRI Inc., 2012). Inverse distance weighting is a deterministic method for multivariate spatial interpolation that relies on a network of neighboring point values to generate a continuous interpolated probability surface (Shepard, 1968). Minimum inner ring dates were substituted for establishment dates if pith was not present or could not be estimated within 10 years.

To test for differences in spruce growth rates in mixed-conifer and spruce-fir forest, we limited our analysis to spruce establishing after 1880 to maximize similarity of climate and fire exclusion conditions. As an additional precaution, we excluded the first 30 years of each tree-ring series to remove the effects of juvenile growth. Mean ring-width measurements were separated into two groups by geographic location inside or outside the pre-1870 spruce extent. We used a two-tailed *t*-test with unequal variance to assess the significance of differences in mean ring widths between trees in the two groups.

3.3. Spatial reconstruction of bark beetle outbreaks

To reconstruct the approximate size and spatial distribution of spruce beetle outbreaks recorded in at least 25% of recording sites,

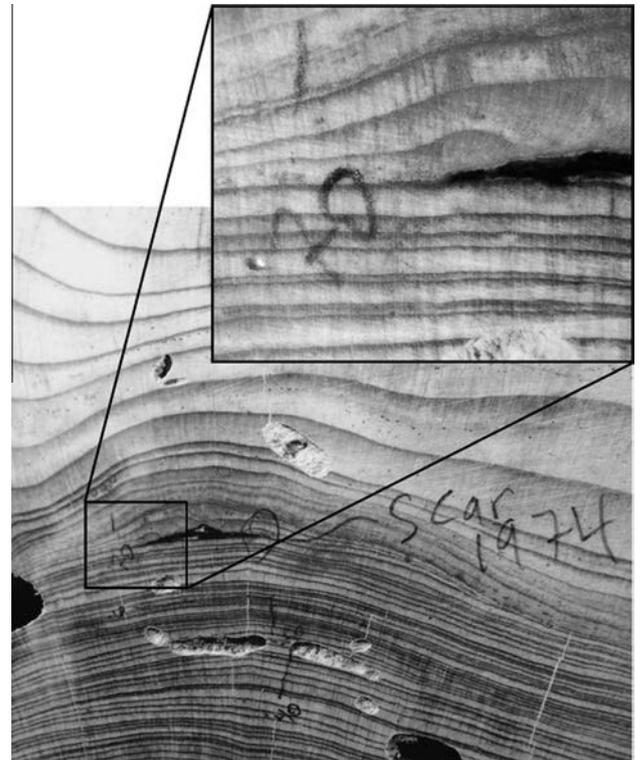


Fig. 2. A scar formed in 1974 from a failed spruce beetle attack on a suppressed understory Engelmann spruce in the Pinaleno Mountains, Arizona. Upper right: magnified image of scar region. From the position of the wound within the ring, it appears that attack occurred early in the growing season, i.e., probably May or June. The failed attack occurred four years prior to the onset of a growth release in 1978.

we used the spatial sampling grid with composited growth release events attributed to each sampling location. An outbreak was attributed to a plot location if 10% or more of trees (minimum of two trees) exhibited a growth release over a five-year period. The approximate spatial extent of outbreak events was determined through inverse distance weighting of outbreak presence or absence. A small number of neighboring plots (4), a conservative signal decay function (power function of two), and a maximum interpolation distance of 750 m were used to limit the possibility of over-predicting outbreak area (Hessl et al., 2007). Interpolated surfaces were clipped to the spruce range extent above 2835 m elevation.

3.4. Outbreak periodicity analysis

We used wavelet analysis (Torrence and Compo, 1998) to identify significant periodicity in the sequence of spruce beetle outbreaks over the reconstructed period. The unfiltered series of growth release events generated from all trees in the JOLTS analysis was square root transformed to partially offset right-skewness resulting from the loss of sample depth in the early part of the series. We used a zero-padded Morlet wavelet with six parameters, a scaling width of 0.25, and starting scale of two. A cone of influence was generated to identify extraneous periodicities resulting from series-length edge effects. Wavelet analysis and figure generation used the Interactive Wavelet Plot tool (Torrence and Compo, 2014). Significance of identified patterns of periodicity were tested against a theoretical red-noise spectrum, which is a conservative series that accounts for temporal autocorrelation and is appropriate for time series exhibiting increasing power with decreasing frequency (Torrence and Compo, 1998). Power series cut-offs of 75%, 50%, 25% and 5% were used to assess the strength and consistency of outbreak periodicity through time.

3.5. Outbreak initiation and climate

The approximate onset of spruce beetle outbreak was designated as the first year of concurrent growth release in 25% of spruce-containing sites. Year of outbreak initiation was analyzed statistically against seasonal records of precipitation and summer temperature, as well as annual forest drought stress to identify associations to local and regional climate conditions. We used superposed epoch analysis (SEA) (Lough and Fritts, 1987) with EVENT software (Holmes and Swetnam, 1994) to test for significant climate associations to outbreak initiation within ten years before and after the initial year of growth release. SEA tests for departures from the range of annual values in a continuous climate variable in relation to a series of event years (Swetnam, 1993). Values of a climate variable prior to, during, and after outbreak initiation were compared with the distribution of values for the full time domain. We tested the statistical significance of outbreak initiation correlations to the climate variables with 1000 bootstrapped random event years compared to actual event years (Holmes and Swetnam, 1994). The relationship between outbreak initiation and summer temperatures, known to affect larval development (Hansen et al., 2011), was tested using mean maximum summer temperature (June–August) from 1896 to 2008 (PRISM, 2013) and tree-ring reconstructed mean annual temperature from the southern Colorado Plateau (Salzer and Kipfmüller, 2005). Effects of host drought stress during the period of beetle flight (Massey and Wygant, 1954) were tested with spring precipitation anomaly (January–June, PRISM, 2013), regional tree-ring reconstructed annual Forest Drought Severity Index (FDSI) (Williams et al., 2013), and Palmer Drought Severity Index (Cook and Krusic, 2004, grid point 105). Availability of summer temperature and spring precipitation records were limited to the period 1896–2012. Tree-ring reconstructed annual PDSI, mean temperature, and FDSI were available for the entire reconstructed period.

4. Results

We collected samples from 654 trees in 35 plots, including 296 Engelmann spruce, 111 corkbark fir, 103 Douglas-fir, 76 southwestern white pine, 33 aspen, 29 white fir, and six ponderosa pine. We were able to crossdate 87% of samples (709 of 815) and to assign or estimate pith date on 76% of samples (617 of 815). From 591 measured series we detected 1205 growth release events, averaging 2.04 growth release events per tree. One or more drought-associated incomplete or locally absent growth rings were recorded in 9.8% of spruce and 7.2% of corkbark fir samples.

Immediately following the stand-replacing fire in 1685, the distribution of Engelmann spruce was restricted to a few small areas on north facing fire-sheltered canyons and surrounding springs (Fig. 3a). By 1780 spruce seedlings had infilled between separated populations, forming a nearly contiguous forest covering approximately 340 ha in the highest elevation sites and spreading to an isolated peak southeast of the main spruce–fir forest. Slow expansion of the original spruce population into mesic sites that experienced infrequent fire (O'Connor et al., 2014) continued from 1820 to 1870, including two additional isolated spruce populations to the south and west of the main spruce–fir forest, reaching a peak distribution of approximately 1095 ha after 185 years. With the interruption of the historical fire regime in surrounding mixed-conifer forest in the 1870s (O'Connor et al., 2014), the area occupied by spruce seedlings doubled in approximately 60 years from 1095 ha to 2168 ha by expanding into mixed-conifer forest to the southeast and west from 1871 to 1930, eventually occupying 89% of the area above 2835 m (Fig. 3a). At the time of sampling, mean DBH of spruce sampled from plots containing spruce prior to 1880

(32.2 cm) was nearly identical to that of spruce in the mixed-conifer forest where spruce established after 1880 (32.5 cm). However, mean ring width (0.15 cm) of spruce establishing after 1880 in the spruce–fir forest was significantly less than that of spruce that established in mixed-conifer forest after 1880 (0.22 cm) (two-tailed paired *t*-test with unequal variance $p < 0.001$; juvenile growth is excluded in the comparison). Prior to 1880, five demography plots comprising the historical spruce–fir zone contained Engelmann spruce. By 1996, the additional 9 demography plots in the mixed-conifer forest also contained spruce. Basal area of live spruce in mixed-conifer forest in 1996, prior to the most recent spruce beetle outbreak, varied with proximity to the spruce–fir forest. Spruce basal area in two plots near the historical spruce–fir forest exceeded 40 m²/ha, whereas mean spruce basal area throughout the mixed-conifer forest was 16.0 m²/ha, and in the three most distant plots spruce basal area was less than 2 m²/ha (Supplemental materials Table 1). For reference, a study from Utah documented more than 93% mortality of overstory spruce (>10 cm DBH) in stands with spruce basal area as low as 10 m²/ha (DeRose and Long, 2007).

Corkbark fir followed a similar pattern of wave-form range expansion (Frelich, 2002) following stand replacing fire, although establishment of fir typically lagged that of spruce (Schmid and Hinds, 1974; Aplet et al., 1988) (Fig. 3b). Corkbark fir was slow to expand out from three original sites also occupied by Engelmann spruce prior to 1750. The first large expansion of corkbark fir extent occurred from 1840 to 1885, approximately 50 years after spruce establishment over the same general area. The extent of corkbark fir more than doubled from 1886 to 1930 (from 880 ha to 2080 ha) coinciding with fire exclusion in surrounding mixed-conifer forest, and continued to expand into other sites already occupied by spruce over the next 40 years (Fig. 3b). Prior to 1880, corkbark fir was also limited to the historic spruce–fir zone and by 1996 eight of the nine demography plots located in the mixed-conifer forest also contained corkbark fir. Bark beetle outbreaks prior to 1996 do not appear to have negatively affected the overall spatial extent of spruce or corkbark fir over the past 300 years.

4.1. Spruce beetle outbreak dynamics

Twelve growth release events affecting 25% or more of spruce-inhabiting sites were detected from 1700 to 2008 (Table 1). The first growth release did not occur until 94 years after the fire in 1685 and 77 years after confirmed spruce establishment. While the interval between outbreaks remained relatively constant before and after fire exclusion (mean interval 19.3–20.2 years), outbreak duration was significantly shorter over the first two centuries of spruce range expansion following the 1685 fire than in the subsequent 100 years (3.4 years vs. 9.9 years, paired *t*-test with unequal variance $p = 0.025$) (Table 1).

Failed attack scars were recorded in 18% of spruce cross sections and were not recovered from increment cores. 75% of growth releases recorded in 25% or more of sites (9 of 12 events) were corroborated with failed spruce beetle attack scars (Fig. 2). The three growth release events not corroborated by failed attack scars were short duration and relatively small in size (1824–1829, 1842–1845, 1866–1868) (Figs. 4a and 6). The high rate of decomposition limited the use of tree death dates to corroborate spruce beetle outbreaks prior to 1920 (Fig. 4b). All outbreaks recorded after 1920 are corroborated with growth releases, tree death dates, and failed attack scars, and two of the five outbreaks are recorded in Forest Service insect survey records (Fig. 4). Growth releases at individual sites were common throughout the reconstructed period (Fig. 4d); however the 25% filter clearly demarcates large-scale spruce beetle outbreaks (Fig. 4c).

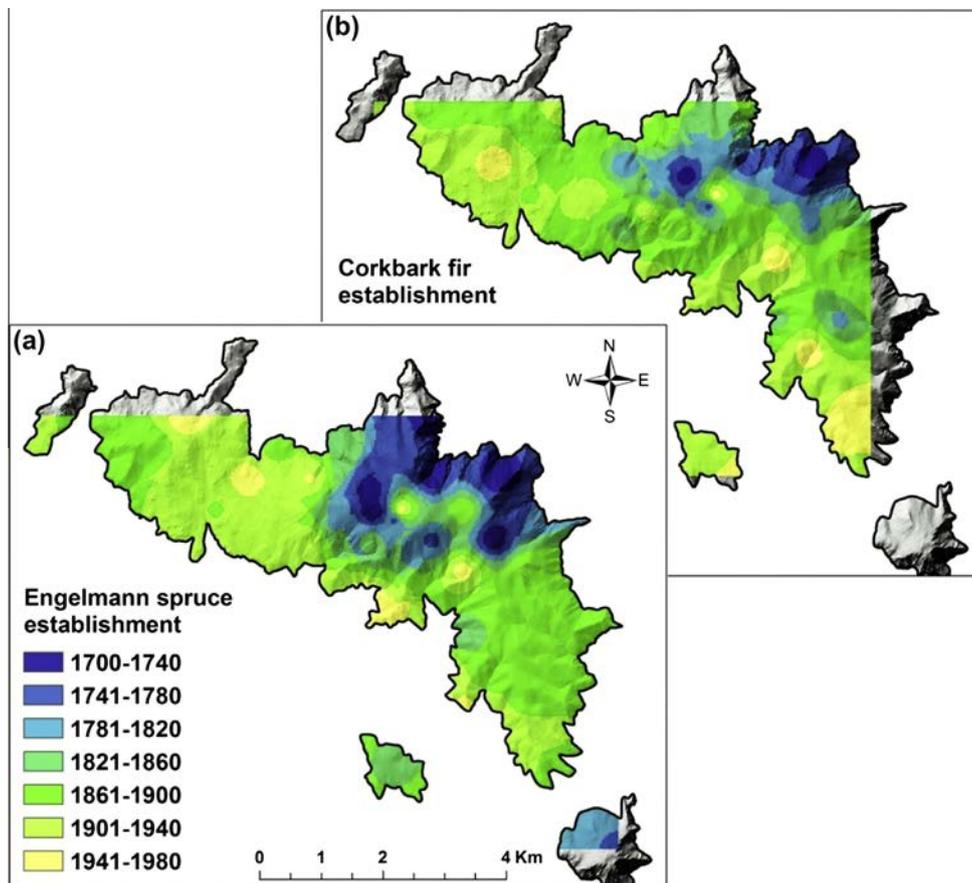


Fig. 3. Temporal progression of Engelmann spruce (a) and corkbark fir (b) tree establishment following stand-replacing fire in 1685. Colors associated with windows of seedling establishment apply to both figures. Interpolated stand age surfaces are generated from inverse distance weighting of minimum tree establishment dates from 44 spruce (a) and 37 corkbark fir (b) gridded point locations. The interpolation algorithm used four nearest point locations with a power function of two.

Table 1

Spruce beetle outbreak events 1779–1996. Horizontal line at 1880 indicates the division between outbreaks occurring pre and post forest changes as a result of fire exclusion in surrounding mixed-conifer forest and the start of range expansion of Engelmann spruce and corkbark fir. The 1880–1890 outbreak is included in the pre-fire exclusion period because this outbreak occurred within the historical fire return interval of the mixed-conifer forest.

Outbreak start	Outbreak end	Duration (years)	Interval (years)
1779	1783	4	
1803	1806	3	24
1824	1829	5	21
1842	1845	3	18
1866	1868	2	24
1880	1890	10	14
1896	1910	14	16
1923	1932	9	27
1940	1944	4	17
1949	1966	17	9
1972	1981	9	23
1996	2002	6	24
Pre 1890	Mean	4.6*	20.2
	Std. dev.	2.9	4.3
Post 1890	Mean	9.8*	19.3
	Std. dev.	4.9	6.6

* Indicates significant difference $p < 0.01$.

4.2. Outbreak periodicity through time

A wavelet power spectrum with periodicity of 16–25 years was the only consistent temporal pattern identified over the full period of reconstruction (Fig. 5a). The 16–25 year period accounts for more

than 75% of the power spectrum from approximately 1790–1850 and again from 1880 to 2008. Focusing on the time period with greatest wavelet resolution from 1860 to 2008, a peak periodicity of 21.5 years (Fig. 5c) is significantly different from the red noise spectrum over the entire period and accounts for more than 95% of the power spectrum from 1885 to 1950 and again from 1975 to 1985 (Fig. 5b). Shorter periodicities of two to four years are present within individual decades but are not contiguous over the analysis period. Longer periodicities of 70–100 years are present after 1820 but are part of the cone of influence and attributable to edge effects of the analysis (Torrence and Compo, 2014).

4.3. Spatial reconstruction of outbreak events

After 1780, outbreaks occurring in two or more sites were common. Outbreaks tracked the expansion of the spruce population starting 94 years after stand replacing fire, and remained relatively small, affecting the same 3–7 sites over the next century (Fig. 6). The 1880–1890 outbreak was approximately twice the size of any previous event in the record, and was the first to affect all three spatially distinct satellite spruce populations outside of the main spruce-fir forest. After 1890, outbreaks tended to alternate between smaller and larger events. Records of repeated outbreaks in sites where suitable host trees persisted for several centuries provide evidence for relatively low outbreak severity for at least the first 260 years following stand-replacing fire. The outbreak that began in 1949 was the longest and one of the most widespread events affecting the spruce population. During this outbreak trees within individual sites exhibited staggered release dates every

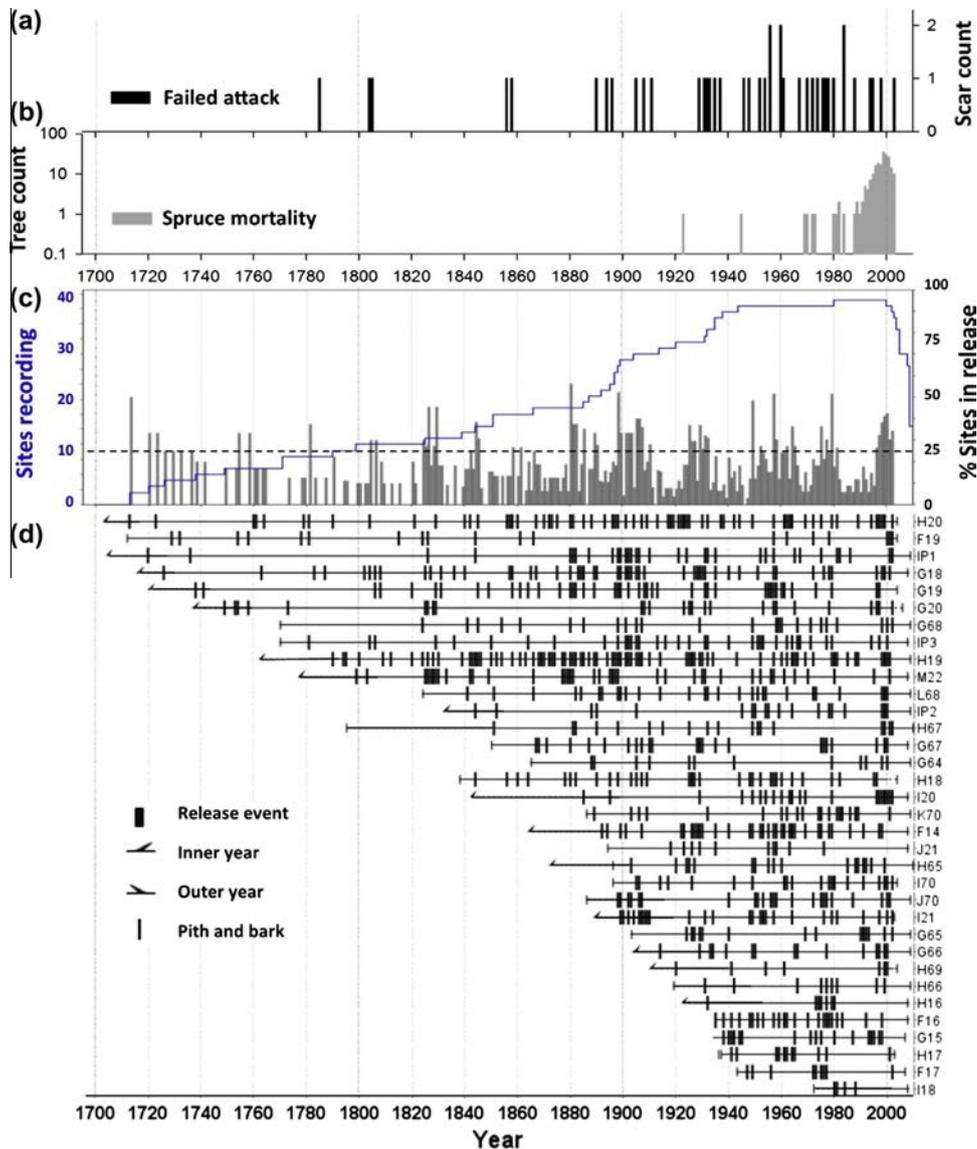


Fig. 4. Multiproxy reconstructions of spruce beetle outbreaks in the Pinaleno Mountains 1700–2008. (a) Bark beetle failed attack scars within individual growth rings of surviving trees. (b) The outer growth ring of beetle-killed trees. (c) Index plot of 34 composited site records recording growth release; the dashed horizontal line intersecting the y-axis to the right indicates 25% of sites in release (used to differentiate outbreaks from other ecological factors). The number of sites recording on the left y-axis is a measure of changing sample depth (spruce occupancy) over time. The earliest growth release attributed to spruce beetle outbreak is in 1779 with nine sites (26% of sites) containing spruce. (d) Site-level record of growth release events occurring in two or more trees over a 5-year period.

3–5 years from 1949 to 1966. The early part of this outbreak was documented in 1952 by aerial and ground surveys (Bennett, 1953). The outbreak continued at a low level for more than a decade, eventually affecting approximately three times the area of the original aerial survey boundary. A single site that hosts corkbark fir but not spruce exhibited a growth release during the 1949–1966 outbreak, suggesting that a concurrent outbreak of WBBB, noted as a minor mortality agent in the Bennett (1953) report, may have also occurred during this period. A spruce beetle outbreak detected from growth releases from 1972 to 1981 (Fig. 6) was not noted in aerial surveys but is corroborated by a series of spruce death dates and failed attack scars (Fig. 4a and b).

Growth release and death date records of the most recent spruce beetle outbreak from 1996 to 2002 are confounded by concurrent damage from *N. janetae* from 1996 to 1999 (which also affected corkbark fir) and spruce aphid from 1999 to 2002, both of which caused significant mortality of understory spruce (Lynch, 2009) and may have delayed the growth release of surviving understory spruce and corkbark fir. Defoliation damage from

N. janetae was limited to the oldest stands of spruce and corkbark fir, whereas damage from spruce aphid occurred throughout the spruce extent. During the most recent spruce beetle outbreak, 94% of spruce-inhabited sites recorded growth releases and mortality of overstory spruce. Corkbark fir mortality from WBBB was also recorded from 1993 to 2003 in 23% of sites. By 2002 the number of sites containing living spruce greater than 15 cm DBH was reduced from 97% to 72% of sites, and then further reduced to 49% of sites following the 2004 fire. In spruce-fir forest unaffected by the 2004 fire, the proportion of corkbark fir to Engelmann spruce increased by 16–44% of total live stems, resulting in an overall shift from spruce to corkbark fir dominance (44% of plots spruce dominant vs. 56% of plots corkbark fir dominant) for the first time in the historical record.

4.4. Climate conditions associated with widespread outbreaks

The six outbreaks recorded from 1896 to 2010 were consistently associated with a temporal sequence of several years of

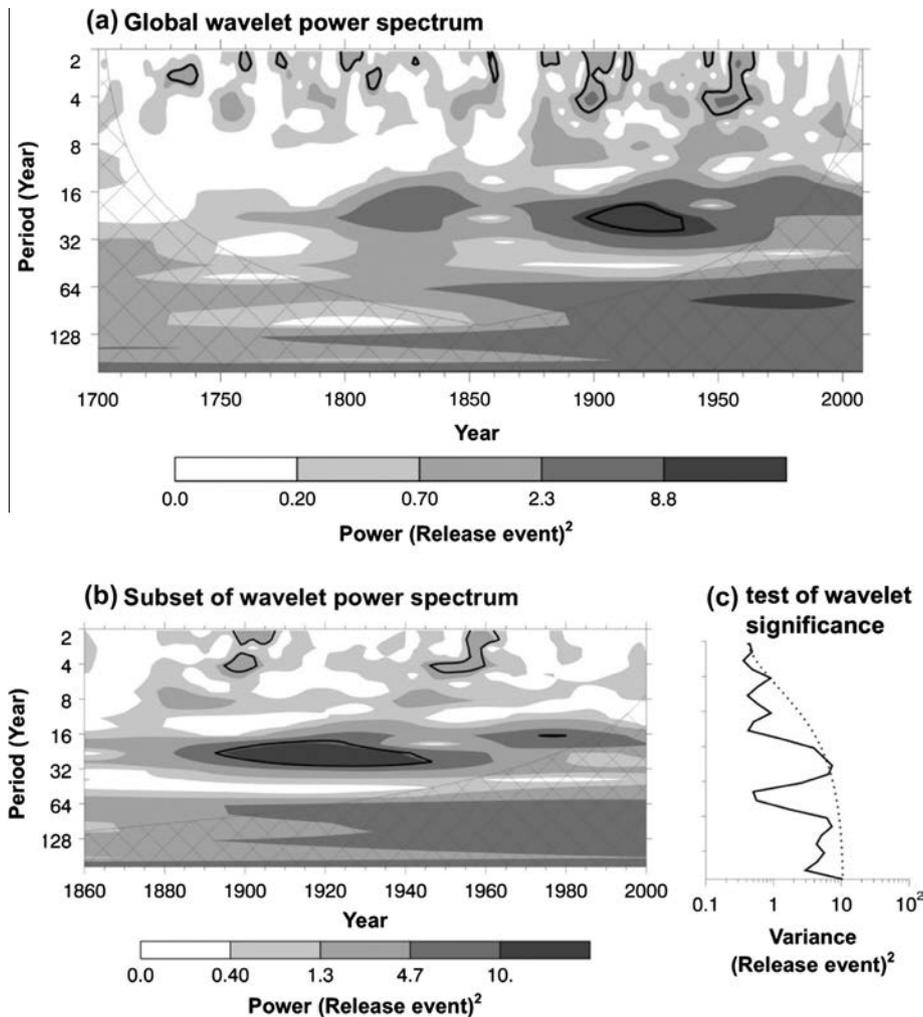


Fig. 5. (a) Wavelet power spectrum of spruce beetle outbreaks for the period 1700–2010. Contour levels represent the proportion of wavelet power above 75%, 50%, 25%, and 5% above each level, respectively. The cross-hatched region is the cone of influence, where zero padding has reduced the variance. Black contour is the 5% significance level, using a red-noise background spectrum. (b) Subset of the reconstructed period (1860–2000) in which the spectral peak of 21.5 years is significant at the 5% level. (c) The global wavelet power spectrum (black line); the dashed line is the significance for the global wavelet spectrum at the 5% significance level (Torrence and Compo, 1998).

antecedent warm summer temperatures, followed by below average spring precipitation and persistent forest drought stress (negative FDSI) during the decade after outbreak initiation (Fig. 7). Mean maximum summer (June to August) temperatures 0.4–1.2 °C above the 114-year mean were associated with each of the five years prior to outbreak initiation (Fig. 7a). Following outbreak initiation, summer temperature no longer expressed a consistent pattern. Conversely, regional FDSI and spring (January–June) precipitation showed no consistent pattern prior to spruce beetle outbreak but the year of outbreak detection and following decade were associated with persistent drought (Fig. 7b and c). Values of FDSI and spring precipitation were below average for eight of the ten years following outbreak initiation, punctuated by up to two years of significantly low precipitation (95% confidence) and one year of significantly high drought stress (99% confidence) in comparison to the 114-year mean of each variable. A significant period (>95 confidence) of high moisture eight years prior to outbreak detection occurred over the entire period of reconstruction (Figs. 7b, c and 8).

Comparable seasonal reconstructions of temperature and precipitation are not available for the southern Arizona spruce-fir forest type prior to 1896; however, outbreaks prior to 1896 did not exhibit consistent relationships with annual tree-ring

reconstructed temperature from the southern Colorado Plateau (Salzer and Kipfmüller, 2005) or annual tree-ring reconstructed PSDI. Outbreaks were associated with persistent negative values of regional FDSI prior to 1896; however the pattern associated with forest drought and outbreak occurrence was different than the 20th century pattern. From 1770 to 1896, outbreaks were associated with moderate forest drought stress before, during, and after growth release. The period of drought stress following outbreak was shorter (up to six years) than that associated with outbreaks over the 20th–21st centuries (Fig 8).

5. Discussion

Spruce beetle outbreaks tracked the size and age distribution of available spruce following the stand-replacing fire in 1685. Outbreaks were generally smaller and of shorter duration prior to the onset of fire exclusion when the extents of spruce and corkbark fir were approximately half of their post-fire-exclusion maximum. The continuous expansion of the spruce-fir forest range after 1685, with accelerated expansion after 1880, and relative stand dominance of Engelmann spruce over corkbark fir suggest that outbreak severity remained relatively low for almost three centuries following stand-replacing fire.

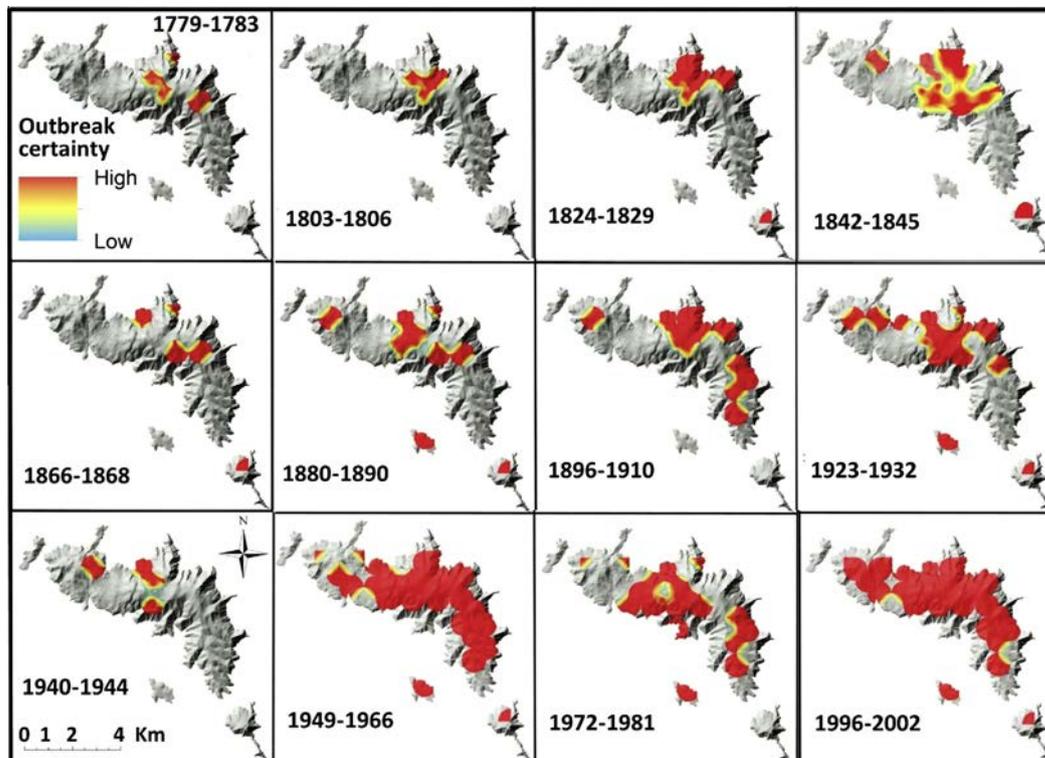


Fig. 6. Spatial progression of spruce beetle outbreaks recorded in 25% or more of sites from 1779 to 1996. Outbreak events are reconstructed from growth releases detected in a minimum of 10% of trees over a five-year period at each of 34 spruce-containing sites. An interpolated outbreak certainty surface is generated from inverse distance weighting of the four nearest point locations with a power function of two at a maximum distance of 750 m (Hessl et al., 2007). The underlying surface is the spruce extent in the Pinaleno Mountains circa 1995.

The most recent spruce beetle outbreak beginning in 1996 was concurrent with outbreaks of a defoliator, a foliage-feeding aphid, and an outbreak of WBBB in corkbark fir. The combined effects of multiple damage agents, dense mature forest conditions, and climatic stressors resulted in the largest and highest severity spruce beetle outbreak in the reconstructed period. The individual effects of spruce beetle, western balsam bark beetle, *N. janetae*, and spruce aphid in the recent mortality cannot be definitively separated. However, defoliation contributed to mortality only within the ~200-ha area defoliated by *N. janetae*, and only during the initial years of the bark beetle outbreaks, perhaps serving as an inciting event. Spruce aphid damage throughout the spruce extent may have played a role in subsequent mortality, but the majority of spruce mortality resulted from spruce beetle attack (Lynch, unpublished data). Outbreaks of similar or higher severity have been documented in other western North American forests (e.g. Berg et al., 2006; DeRose and Long, 2007), and the species has the capacity to deplete mature host resources (Furniss and Carolin, 1977). The 2004 fire further reduced the spatial extent of spruce-fir forest, leaving the majority of spruce and corkbark fir in mixed-conifer forest, outside of the pre-fire exclusion range of either species.

5.1. Effects of fire exclusion on Engelmann spruce and corkbark fir distribution

Over much of the 20th century, fire exclusion in the southwestern United States had the most obvious effects on fire-dependent pine and mixed-conifer forest types where forest structure has changed dramatically (e.g. Minnich et al., 1995; Allen et al., 2002; O'Connor, 2013). An increase in the proportion of spruce and corkbark fir in mixed-conifer forests has been documented in several locations where steep ecological gradients allow different forest types to coexist in close spatial proximity (Habeck and Mutch,

1973; Cocks et al., 2005; Mast and Wolf, 2006). Median fire return intervals of approximately 10–25 years (O'Connor et al., 2014) would have maintained a relatively open structure in mixed-conifer forest of the Pinaleno Mountains. Engelmann spruce probably recruited in the mixed-conifer forest after low and mixed-severity fires, but would have succumbed to the relatively frequent surface fires, preventing it from persisting in the mixed-conifer ecosystem. In upper ecotone mixed-conifer forests of northern Arizona, where the interruption of presettlement fire regimes did not occur until approximately 1920, a similar pulse of Engelmann spruce establishment in the mixed-conifer forest occurred immediately following fire exclusion (Mast and Wolf, 2006).

Discussion of the expansion of shade tolerant subalpine species into the mixed-conifer ecosystem in past studies has focused on the increased risk of high-severity fire in mixed-conifer forest with the increase in ladder fuels, and potential for spread of canopy fire from mixed-conifer to spruce-fir forest as a result of changes to the amount and vertical distribution of fuels (Grissino-Mayer et al., 1995; Swetnam et al., 2009). In this study we identify a series of additional factors that may contribute to the size and severity of biotic disturbances affecting spruce colonizing mixed-conifer forest. Spruce expansion into mixed-conifer forest was accompanied by a significant increase in growth rates, reducing the amount of time necessary for these trees to attain a size suitable for spruce beetle colonization. Younger large diameter spruce in the mixed-conifer forest contributed a significant new resource for spruce beetle following fire exclusion. It should be noted however that Hard (1985) found that small faster growing trees were less prone to attack by spruce beetle than large trees with slower radial growth, and Schmid and Frye (1976) found that increased heterogeneity of species and age classes reduced the likelihood of successful spruce beetle attack in Colorado. Testing the associations between a suite of stand conditions and outbreak risk, Hart et al. (2014b) found only

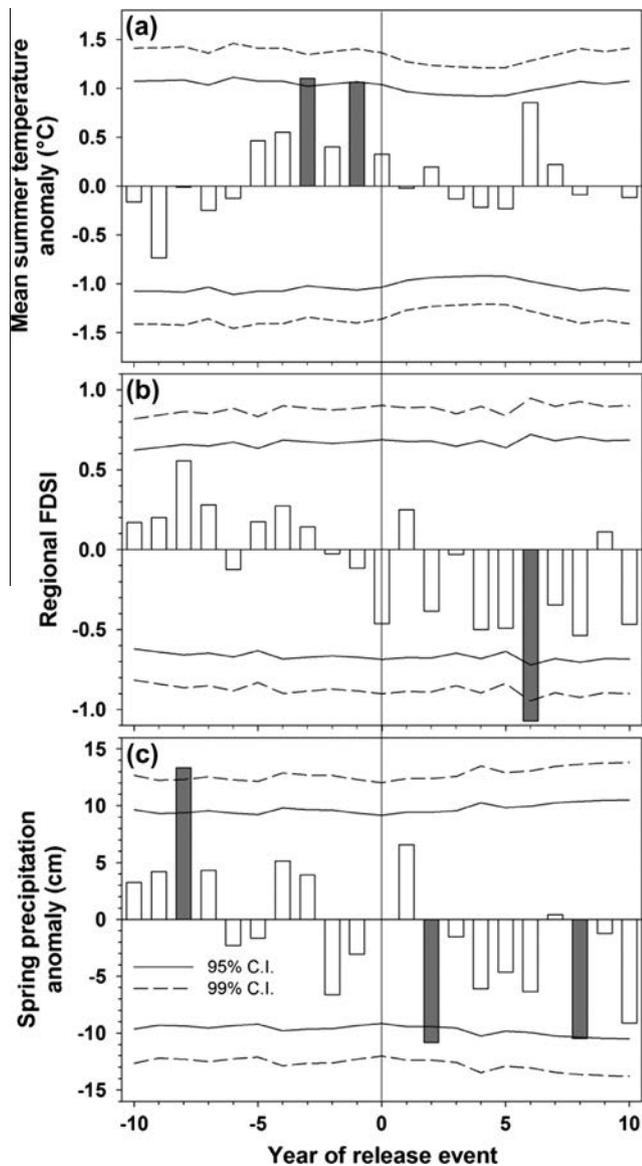


Fig. 7. Associations between spruce beetle outbreaks and significant seasonal climate variables from 1896 to 2008, as determined using superposed epoch analysis. (a) June–August maximum temperature anomaly in relation to initial growth release, (b) Regional Forest Drought Severity Index (FDSI) (Williams et al., 2013) in relation initial growth release. (c) January–June precipitation anomaly in relation to initial growth release. The vertical line at year zero indicates the year for which 25% or more of sites were experiencing growth release. Bars to the left of this line are years prior to growth release, while bars to the right are after growth release. Shaded bars are statistically significant ($p \leq 0.05$) deviations from 114-year mean value of the climate series. Confidence intervals of 95% and 99% are indicated by solid and dashed lines respectively.

weak evidence to support stand composition and age as risk factors contributing to outbreak likelihood, instead identifying minimum spruce DBH of 25.4 cm as the most robust indicator of outbreak risk. Given the complexity of beetle–host interactions, an increase in the abundance and size of available spruce in the mixed-conifer forest may not necessarily predispose a stand to attack. However, if an outbreak begins and builds population in older stands with larger diameter trees, the availability of spruce in the mixed-conifer forest may facilitate spill-over and sustain an outbreak.

5.2. Outbreak reconstruction methods and outbreak frequency

Tree-ring growth thresholds used to reconstruct spruce beetle outbreaks in previous studies (Veblen et al., 1991b; Eisenhart

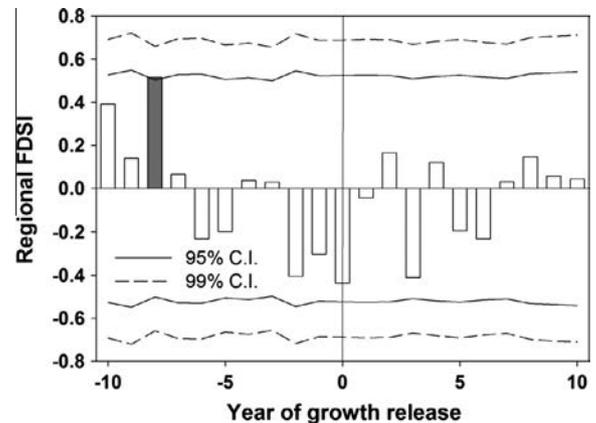


Fig. 8. Association of six spruce beetle outbreaks with regional Forest Drought Severity Index 1770–1896 (Williams et al., 2013). Vertical line at year zero indicates the year for which 25% or more of sites were experiencing growth release. Shaded bars are statistically significant ($p \leq 0.05$) deviations from the 126-year mean value of FDSI. Confidence intervals of 95% and 99% are indicated by solid and dashed lines respectively.

and Veblen, 2000; Berg et al., 2006; DeRose and Long, 2012; Hart et al., 2014a) were found here to be overly conservative for capturing the onset of documented outbreaks in the early 1950s and mid-1990s. The 50% increase in tree-ring growth over a 10-year period used in this study identified growth changes on average 1–2 years earlier than the more conservative 100% increase method used by Berg et al. (2006) and 1–4 years earlier than the 250% threshold used by Veblen et al. (1991b) (Supplemental Fig. 1). A potential problem with a lower growth release threshold is a potential increase in Type 1 error (false positives). We addressed this potential source of error, which is more likely to indicate a growth release at an individual site, by using a spatial threshold requiring a minimum of 25% of all spruce-containing sites to exhibit a similar growth release within a five-year window. In previous studies, a high proportion of understory trees in release, possibly indicating high mortality of overstory trees, was used to indicate outbreak occurrence without reference to spatial scale of the growth release signal. The rapid rate at which dead trees decomposed limited our ability to estimate the severity of past spruce beetle outbreaks; however we were able to estimate past outbreak size, and we used the threshold of 25% of sites to differentiate spatially important outbreak events from endemic-phase insect activity.

The use of multiple proxy records, including spatial reconstructions of host distribution and inclusion of failed attack scars and tree death dates, improved the temporal and spatial resolution of two documented outbreaks and corroborated the growth release records of ten other undocumented events. While other insects cannot be unequivocally ruled out as potential causes of growth release in spruce-containing mixed-conifer forests, concurrent spruce beetle outbreaks in the adjacent spruce-dominated forest suggest that spruce beetle-related mortality was the most likely cause of growth release in both forest types.

Using changes in the growth patterns of surrounding trees remains an imperfect method to detect the initiation of spruce beetle outbreaks. Determining the specific year of growth change is subject to the methods used and the minimum threshold defined as a growth release. Moving average window methods with or without tree growth trend removal (Veblen et al., 1991b; Berg et al., 2006), detection of changes to growth trend (Rodionov and Overland, 2005; Hart et al., 2014a), and correction for non-insect-induced growth changes (*sensu* Swetnam and Lynch, 1993) can all be applied to the same tree-ring sample and produce a range of outbreak onset dates depending on the amount of trend removal and threshold of growth release. Adding to the uncertainty, the

degree of outbreak severity and other environmental stressors can result in loss of needles in attacked trees and subsequent growth release in surrounding trees over a variable period of one to four years (Schmid and Frye, 1977) with some reported release events occurring up to seven or more years post outbreak (Sherriff et al., 2011). Continued development of improved methods to detect growth trend changes in tree-ring series and to isolate the causes of these changes, such as the recent work of Druckenbrod et al. (2013), will further improve our ability to define the temporal windows of past spruce beetle outbreaks and relate these to local and environmental conditions that may provide improved predictive power to assess future outbreak risks. Calibration of reconstruction methods to more temporally precise proxy records such as documented dates of bark beetle attack, tree death dates and failed attack scars will help improve the accuracy of these approaches.

The temporal progression of spruce-fir stand development and spruce beetle outbreaks documented here is similar to the model proposed by Schmid and Hinds (1974). Following a high severity fire in 1685, spruce-fir forest was relegated to a few relict populations that provided progeny that eventually colonized most of the upper elevation area. Growth releases detected at multiple sites within the limited area occupied by spruce approximately 100 years after stand-replacing disturbance suggests that the stand conditions necessary for spruce beetle outbreak were achieved considerably faster in southern Arizona than the 200-year window proposed for the southern Rocky Mountains and Utah based on size and structural traits (Schmid and Hinds, 1974). The 100-year period to develop appropriate size and structure for spruce beetle outbreak in the highest elevation sites is consistent with the findings of Bebi et al. (2003) and Hart et al. (2014b) that risk of spruce beetle outbreak was low for the first 60–70 years following high-severity fire. Spruce beetle is one of a few aggressive bark beetle species capable of depleting its host resources once an outbreak is established (Furniss and Carolin, 1977; Raffa et al., 2008). The rapid growth rate of spruce in mixed-conifer forest would make these trees vulnerable more quickly than in older dense stands of spruce where outbreaks were historically more likely to initiate (Reynolds and Holsten, 1994).

In the literature, intervals between repeated outbreaks vary considerably with geographic location, host spruce species, and method of outbreak documentation. Dendrochronologically reconstructed outbreaks in white spruce (*Picea glauca* (Moench) Voss) averaged once every 52 years on the Kenai Peninsula of Alaska (Berg et al., 2006), whereas historical documents and surveys limited to the 20th century suggest outbreak intervals of 30–50 years in Sitka (*Picea sitchensis* (Bong.) Carr.) and white spruce in Alaska (Werner et al., 2006). In Engelmann spruce and subalpine fir forests of British Columbia and northwestern Colorado, dendrochronologically reconstructed outbreaks were recorded at approximately 100-year intervals (Veblen et al., 1994; Zhang et al., 1999), and in a multisite reconstruction from the Colorado Front Range, outbreak return intervals in Engelmann spruce forests varied from 40 to 60 years (Hart et al., 2014a). In a review of literature documenting outbreaks in Utah and Wyoming, Jenkins et al. (2014) found the average outbreak interval to be 19 years within a given geographic region, an interval similar to the peak wavelet frequency of growth release events over the majority of the period of reconstruction in this study. Spruce beetle outbreaks are dependent on coincidence of suitable host resources with an inciting event that allows a population to build (Massey and Wygant, 1954; Furniss and Carolin, 1977), and appropriate temperature and precipitation conditions to promote the transition from incipient to outbreak population levels and behavior. In the Pinaleno Mountains, synchrony of outbreak conditions appears to have occurred at approximately 20-year intervals for most of the past two centuries. Variability in outbreak size and severity through time on a given landscape depends on dynamic

stand and environmental conditions during outbreak initiation. Differences between outbreak detections in historical documents and dendrochronological reconstructions may be attributable to the variety of methods used to detect an outbreak, or differences in the definition of what an outbreak entails. Depending on the filtering criteria selected in a dendrochronological analysis, less severe outbreaks may be indistinguishable from background noise or to the contrary, a relatively low severity outbreak over a large area may be detected from growth release records while remaining unreported in forest surveys.

5.3. Spruce beetle physiology and climate associations to outbreak initiation

Studies of two spruce beetle outbreaks during exceptionally warm winter and summer conditions (Berg et al., 2006; DeRose and Long, 2012) indicate that a physiological shift from semivoltine to univoltine reproductive life cycles (Werner and Holsten, 1985; Hansen et al., 2001, 2011) may have contributed to the severity of recent spruce beetle outbreaks. In both studies similar temperature anomalies were not associated with previous outbreaks, although the authors did not test for patterns of summer temperatures specific to developmental thresholds for the onset or bypassing of larval diapause between third and fourth instar life stages that is responsible for the univoltine life-cycle shift (Hansen et al., 2011). Above average winter temperatures have been associated with outbreak conditions at higher latitudes due to a reduction in overwintering beetle mortality (Hebertson and Jenkins, 2008); however the lowest recorded temperature in the instrumental record (1895–2014) for the spruce-fir forest of the Pinaleno Mountains (-20.7°C) (PRISM, 2013; CRL, 2014), is well above the threshold for spruce beetle mortality (-40°C) (Frye et al., 1974; Holsten et al., 1999). Minimum winter temperatures prior to the instrumental record were probably cooler, but the lowest recorded temperature in Arizona is -40°C in the White Mountains, which experience colder extremes than the Pinaleno Mountains (NCDC, 2014).

Although host susceptibility to spruce beetle outbreaks is associated with several factors, including stand conditions and host size and stress, outbreak initiation is generally associated with an inciting event that allows endemic spruce beetle populations to build (Massey and Wygant, 1954; Furniss and Carolin, 1977). In this study, the six most recent spruce beetle outbreaks were associated with persistent warm summer temperatures followed by extended drought. Prior to the most recent outbreak, mean monthly summer temperatures of $15.5\text{--}17.8^{\circ}\text{C}$ during the period of spruce beetle flight, gallery excavation, and larval development (Massey and Wygant, 1954; Schmid and Frye, 1977), were within the $15\text{--}17^{\circ}\text{C}$ threshold triggering a shift in developmental cycle from semi-voltine to univoltine life cycle for a portion of the developing beetle population (Werner and Holsten, 1985; Hansen et al., 2001; Régnière et al., 2012). Mean summer temperatures associated with outbreaks on the Kenai Peninsula in Alaska ($10.5\text{--}11.5^{\circ}\text{C}$), also associated with a shift in voltinism, were considerably lower than those in the Pinaleno Mountains of Arizona. A multi-year period of temperatures favorable to spruce beetle larval development and population growth followed by several years of persistent drought stress sets up an ideal temporal sequence for a spruce beetle population shift from an endemic or incipient stage to an outbreak stage. Although temperature may synchronize spruce beetle larval development and facilitate outbreak initiation through acceleration of the spruce beetle life cycle (Bentz et al., 2010), drought may be what enables outbreaks to persist. If accelerated spruce beetle development does not coincide with an abundance of susceptible hosts shortly after outbreak initiation, the outbreak may not develop because host conditions are not favorable. Likewise if tree drought stress is not preceded by two or more

years of warm summer conditions that facilitate a developmental shift from the semivoltine life cycle for a portion of the spruce beetle population, beetle abundance may not be sufficient to overcome even diminished host defenses. This asynchrony between conditions favorable to spruce beetle development and detrimental to host spruce is documented in the record of failed spruce beetle attacks over the period of reconstruction.

Although data were not available to reconstruct summer temperatures prior to 1896, earlier outbreaks were associated with shorter periods of forest drought stress following outbreak initiation (Fig. 8). Consistently shorter periods of drought following outbreak initiation may have contributed to shorter outbreak durations prior to the 20th century. The increase in outbreak duration after 1880 may also be attributable to the increased distribution and growth rate of available host trees, allowing beetle populations to spread over a larger area over several years or to re-infest the same sites as beetle population dynamics change over the course of an outbreak (Bentz et al., 2010). The increase in the number of trees available to record growth release events as a result of fire exclusion may also be a factor in the record of longer outbreak duration in the 20th century.

Given the uncertainty with respect to temporal lags between outbreak initiation and survivor growth release, associations between spruce beetle outbreak and single year climate anomalies need to be interpreted carefully. During the six most recent outbreaks a consistent pattern of an anomalously wet spring several years prior to each of the 20th century outbreaks may be coincidental, or indicative of extreme winter storms or other weather events that contributed to the availability of damaged host material. No tree or bark beetle physiological signal has been identified to explain significant rainfall or snowfall as a trigger for spruce beetle outbreak, although wet periods prior to outbreaks have been observed in studies of other western bark beetle species (Powell, 1969). An opposite pattern of severe drought six and seven years prior to growth release in spruce on the Markagunt Plateau of Utah was reported by DeRose and Long (2012), suggesting that the relative contribution of antecedent drought or excessive moisture to outbreak initiation may vary by region.

5.4. Spruce growth response to climate

Annual patterns of moisture and temperature were unlikely to cause the patterns of growth release observed in spruce populations of the Pinaleno Mountains. In a study of Engelmann spruce growth response to climate in Sky Islands of southern Arizona and New Mexico (Buckley, 1989), ring width had a strongly significant positive response to previous winter and spring (December–March) precipitation, and on south-facing slopes, a short-term significant positive response to early monsoon (June) precipitation. The response of spruce growth to temperature was a somewhat weaker negative response to spring (March) and pre-summer (May and June) warm temperatures. These results suggest that while the Engelmann spruce growth pattern in this system is dominated by the winter and spring precipitation signal, early summer temperatures can mediate growth to some degree. A persistent change in seasonal conditions from dry winter and hot summer (reduced growth) to wet winter and cool summer (optimal growth) conditions could produce a change in ring width patterns resembling a growth release; however, the six growth release events in which seasonal precipitation and temperature records were available were not associated with conditions that would increase spruce growth.

5.5. Western balsam bark beetle in the spruce-fir forest

During the most recent spruce beetle outbreak, significant mortality of corkbark fir was caused by a concurrent outbreak of WBBB.

Outbreaks of WBBB are generally considered secondary to spruce beetle outbreaks because susceptibility of corkbark fir to mortality from WBBB is generally limited to trees >200 years of age and with DBH > 32 cm (Bleiker et al., 2003). Mortality from WBBB has also been associated with prior infection by *Armillaria* root fungus that is typically found in older senescing corkbark fir in the southwestern states (Negrón and Popp, 2009). These conditions associated with “old” corkbark fir have been present only during the past 50 years in the Pinaleno Mountains, suggesting that corkbark fir has only recently become susceptible to outbreaks of WBBB and making it unlikely that WBBB contributed to growth release events prior to the 1950s.

6. Conclusions and summary

Spatial and temporal reconstruction of spruce-fir demography and disturbance yielded several consistent patterns relating forest dynamics, spruce beetle outbreaks, and fire over the past three centuries. Initial spruce beetle outbreaks occurred approximately 90 years after spruce establishment following a stand-replacing fire in 1685. Outbreaks became progressively larger as spruce colonized additional extent and matured (Fig. 6). For two centuries, the distribution of spruce and therefore spruce beetle outbreak size were limited by regular surface fires in adjacent mixed-conifer forest. Cessation of surface fires in the mixed-conifer forest with Euro-American land uses starting in the late 1800s resulted in a doubling of the area occupied by Engelmann spruce over an approximately 40-year period. Accelerated spruce growth rates in the mixed-conifer forest resulted in a shorter time for newly established saplings to reach a diameter suitable for beetle attack.

After the initial outbreak in the 1780s, widespread and probably relatively low severity outbreaks occurred at approximately 20-year intervals for over two hundred years in this system regardless of host distribution and stand conditions, suggesting that once a suitable host population is established, conditions favorable to spruce beetle outbreaks may occur more frequently at the southern range limit of the spruce-fir forest than in higher latitude forests. Outbreaks over the last century were associated with a pattern of several years of above-normal summer temperatures prior to outbreak paired with persistent spring drought and forest stress during outbreak. The association with warm temperatures suggests that a switch from semivoltine to univoltine life cycle may promote outbreak initiation, but once a successful outbreak begins, the univoltine life cycle is no longer necessary. Instead, outbreak persistence appears to be associated with drought-driven prolonged host tree stress. Longer outbreak duration over the past century may also be related to the increased abundance and spatial extent of suitable host trees following fire exclusion.

The legacy of spruce and corkbark fir in mixed-conifer forest poses a challenge for restoration efforts to return natural fire resilience to mixed-conifer forests. The majority of the area occupied by spruce and corkbark fir after the 2004 fire was historically mesic mixed-conifer forest where fire return intervals ranged from 10 to 25 years prior to 1880 (O'Connor et al., 2014). Returning fire to these forests may reduce available spruce and corkbark fir seed sources and potentially slow the rate of recovery of the upper elevation forest. Climate conditions for the next century are projected to be unfavorable for spruce establishment and survival (Rehfeldt, 2004; Notaro et al., 2012), so the rate of seedling establishment over the next few decades is likely to determine the composition of the upper elevation forest for the foreseeable future.

Warmer temperatures and increased forest drought stress projected for the region (Seager and Vecchi, 2010; Garfin et al., 2013; Williams et al., 2013) will continue to affect the developmental rates of multiple insect pests (Raffa et al., 2008; Bentz et al.,

2010) and may lead to persistent conditions favorable to accelerated insect development and reduced host defenses. With a diminished climatic limitation to insect population development, host range distribution and density may become the most significant limits to the size and severity of future insect outbreaks (Bentz et al., 2010). Future outbreak dynamics in this mountain range will depend on the effects of restoring fire to the mixed-conifer forest and success of reestablishment of spruce-fir forest within the perimeter of the 2004 fire.

In spruce-fir and mixed-conifer forests throughout the southwestern United States, warmer temperatures are also expected to lengthen the window of favorable fire conditions (Crimmins, 2011; Williams et al., 2013). The 20th century incursion of spruce into mixed-conifer forests following fire exclusion increases the risk of crown fire and portends a future of more frequent and potentially larger and more destructive spruce beetle outbreaks. Emergent endemic insect populations such as *N. janetae* and introduced exotic insects such as spruce aphid may also alter the complex disturbance dynamics of upper elevation forest types. Climate- and fire-mediated interactions between multiple disturbance agents suggest that the forests of the future may bear little resemblance to those of the 20th century, let alone those of the past.

Acknowledgements

Support for this project was provided by the Rocky Mountain Research Station, U.S. Forest Service through Research Joint Venture Agreement 07-JV-11221615-317 and the Coronado National Forest through Cost-Reimbursable Agreement 09-CR-11030515-039. We thank Craig Wilcox, Carl Edminster, and David Meko for their thoughtful insights. Numerous field and shop assistants helped make this work possible: Alexis Arizpe, Jesse Minor, Rebecca Minor, Tyson Swetnam, Laura Marshall, Jacqueline Dewar, Benjamin Schippers, Rolland O'Connor, Anastasia Rabin, Kyle Miller, Alicia Durnin, Joshua Farella, Ali Jaffery, Anna Penalozza-Issaian, Josue Sanchez, Julia Guiterman, Kenneth LeRoy, Elliot Breshears, Matthew Lee and Jason Klotz. Additional field assistance was provided by Matthew Littrell and the Coronado National Forest LiDAR crew. Comments from two anonymous reviewers made substantial improvements to the clarity and consistency of this manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.10.021>.

References

- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433.
- Anderson, R.S., Allen, C.D., Toney, J.L., Jass, R.B., Bair, A.N., 2008. Holocene vegetation and fire regimes in subalpine and mixed conifer forests, southern Rocky Mountains, USA. *Int. J. Wildland Fire* 17, 96–114.
- Aplet, G.H., Laven, R.D., Smith, F.W., 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. *Ecology* 69, 312–319.
- Applequist, M., 1958. A simple pith locator for use with off-center increment cores. *J. For.* 56, 141.
- Arno, S.F., 1980. Forest fire history in the northern Rockies. *J. For.* 78, 460–465.
- Bahre, C.J., 1998. Late 19th century human impacts on the woodlands and forests of southeastern Arizona's sky islands. *Des. Plant* 14, 8–21.
- Bebi, P., Kulakowski, D., Veblen, T.T., 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84, 362–371.
- Bennett, R.K., 1953. Bark beetle infestation conditions, Mt. Graham Ranger District, Coronado National Forest, Arizona, season of 1953. USDA Agricultural Research Administration, Bureau of Entomology and Plant Quarantine, Forest Insect Laboratory, Albuquerque NM. 11p.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60, 602–613.
- Berg, E.E., David Henry, J., Fastie, C.L., De Volder, A.D., Matsuoka, S.M., 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Klauane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manage.* 227, 219–232.
- Bigler, C., Kulakowski, D., Veblen, T.T., 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology* 86, 3018–3029.
- Blackman, M.W., 1931. The Black Hills Beetle (*Dendroctonus ponderosae* Hopk.). *Bull. N.Y. State Coll. For.* 97.
- Bleiker, K., Lindgren, B., Maclauchlan, L., 2003. Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleoptera: Scolytidae). *Can. J. For. Res.* 33, 1538–1543.
- Brown, P.M., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86, 3030–3038.
- Buckley, B.M., 1989. Dendroclimatic aspects of Engelmann spruce in southern Arizona and New Mexico. M.A. Thesis, Arizona State University. 131p.
- Burns, R.M., Honkala, B.H., 1990. Silvics of North America: Volume 1. Conifers. USDA Forest Service Agriculture Handbook 654, Washington, DC.
- Cocke, A.E., Fulé, P.Z., Crouse, J.E., 2005. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. *J. Appl. Ecol.* 42, 814–823.
- Cook, E.R., Krusic, P.J., 2004. The North American Drought Atlas. Lamont-Doherty Earth Observatory and the National Science Foundation. Lamont-Doherty Earth Observatory and the National Science Foundation, Palisades, NY, USA. <<http://iridl.ldeo.columbia.edu/SOURCES/LDEO/TRL/NADA2004/pdsi-atlas.html>> (accessed 01.13).
- Craighead, F., 1925. The *Dendroctonus* problems. *J. For.* 23, 340–354.
- Crimmins, M.A., 2011. Interannual to decadal changes in extreme fire weather event frequencies across the southwestern United States. *Int. J. Climatol.* 31, 1573–1583.
- CRL, 2014. University of Arizona Conservation Research Laboratory Mount Graham Red Squirrel Project Minimum Temperature Records. <<http://ag.arizona.edu/research/redskquirrel/oldsite/min-temp-rawdata2.htm>> (accessed 09.10.14).
- DeRose, R.J., Long, J.N., 2007. Disturbance, structure, and composition: spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. *For. Ecol. Manage.* 244, 16–23.
- DeRose, R.J., Long, J.N., 2012. Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. *Can. J. For. Res.* 42, 1649–1660.
- DeRose, R.J., Long, J.N., Shaw, J.D., 2009. Relationships between forest structure, composition, site, and spruce beetle occurrence in the Intermountain West. In: McWilliams, W., Moisen, G., Czaplewski, R., (Eds.), Forest Inventory and Analysis (FIA) Symposium Proc. RMRS-P-56CD. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 14p.
- Druckenbrod, D.L., Pederson, N., Rentsch, J., Cook, E.R., 2013. A comparison of times series approaches for dendroecological reconstructions of past canopy disturbance events. *For. Ecol. Manage.* 302, 23–33.
- Dymerski, A.D., Anhold, J.A., Munson, A.S., 2001. Spruce beetle (*Dendroctonus rufipennis*) outbreak in Engelmann spruce (*Picea engelmannii*) in central Utah, 1986–1998. *West. N. Am. Nat.* 61, 19–24.
- Eisenhart, K.S., Veblen, T.T., 2000. Dendroecological detection of spruce bark beetle outbreaks in northwestern Colorado. *Can. J. For. Res.* 30, 1788–1798.
- ESRI Inc., 2012. ArcMap. V. 10.1. Redlands, CA.
- Frank, M.S., Fairweather, M.L., 1994. Annual Southwestern Region forest insect and disease conditions report 1993. R-3 94-3, 30 p.
- Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge Univ Pr, Cambridge, UK.
- Froehlich, G., 1996. Biological Assessment and Evaluation for Clark Peak Fire Suppression and Rehabilitation. US Forest Service, Safford Ranger District, Graham County, Arizona, USA.
- Frye, R., Flake, H., Germain, C., 1974. Spruce beetle winter mortality resulting from record low temperatures in Arizona. *Environ. Entomol.* 3, 752–754.
- Fulé, P.Z., Korb, J.E., Wu, R., 2009. Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. *For. Ecol. Manage.* 258, 1200–1210.
- Furniss, R.L., Carolin, V.M., 1977. Western Forest Insects. U.S. Department of Agriculture Forest Service. U.S. Government Printing Office, Washington, D.C., U.S., 658p.
- Garfin, G.M., Overpeck, J., Wilder, M., 2013. Assessment of Climate Change in the Southwest United States. 531p.
- Grissino-Mayer, H.D., 2001. Research report evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57, 205–221.
- Grissino-Mayer, H.D., Baisan, C.H., Swetnam, T.W., 1995. Fire history in the Pinaleno Mountains of southeastern Arizona: effects of human-related disturbances. In: Debano, L.F., Ffolliott, P.F., Gottfried, G.J., Hamre, R.H., Edminster, C.B., (Eds.), Biodiversity and management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Gen. Tech. Rep. RM GTR-264, pp. 399–407.
- Grissino-Mayer, H.D., Romme, W.H., Lisa Floyd, M., Hanna, D.D., 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85, 1708–1724.

- Habeck, J.R., Mutch, R.W., 1973. Fire-dependent forests in the northern Rocky Mountains. *Quatern. Res.* 3, 408–424.
- Hansen, E.M., Bentz, B.J., Turner, D.L., 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* 133, 827.
- Hansen, E.M., Bentz, B.J., Powell, J.A., Gray, D.R., Vandygriff, J.C., 2011. Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *J. Insect Physiol.* 57, 1347–1357.
- Hard, J.S., 1985. Spruce beetles attack slowly growing spruce. *For. Sci.* 31, 839–850.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D., Kulakowski, D., 2014a. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95, 930–939. <http://dx.doi.org/10.1890/13-0230.1>.
- Hart, S.J., Veblen, T.T., Kulakowski, D., 2014b. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? *For. Ecol. Manage.* 318, 44–53.
- Haselhorst, M.S.H., Buerkle, C.A., 2013. Population genetic structure of *Picea engelmannii*, *P. glauca* and their previously unrecognized hybrids in the central Rocky Mountains. *Tree Genet. & Genom.* 9, 669–681.
- Hebertson, E.G., Jenkins, M.J., 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environ. Entomol.* 37, 281–292.
- Hessl, A.E., Miller, J., Kernan, J., Keenum, D., McKenzie, D., 2007. Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. *Prof. Geogr.* 59, 87–104.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Holmes, R.L., 1999. Program JOLTS: finding growth surges or suppressions in trees. Laboratory of Tree-Ring Research software library, University of Arizona, Tucson, AZ. <<http://www.ltrr.arizona.edu/software.html>>.
- Holmes, R.L., Swetnam, T.W., 1994. Program EVENT user manual: superposed epoch analysis in fire history studies. Laboratory of Tree-Ring Research, University of Arizona, Tucson AZ. online access: <<http://www.ltrr.arizona.edu/software.html>>.
- Holsten, E.H., Their, R.W., Munson, A.S., Gibson, K.E., 1999. The spruce beetle. *Forest Insect and Disease Leaflet* 127, 11p.
- Jenkins, M.J., Hebertson, E.G., Munson, A.S., 2014. Spruce beetle biology, ecology and management in the Rocky Mountains: an addendum to spruce beetle in the Rockies. *Forests* 5, 21–71. <http://dx.doi.org/10.3390/f5010021>.
- Kipfmuehler, K.F., Baker, W.L., 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. *J. Biogeogr.* 27, 71–85.
- Koprowski, J.L., Alanan, M.I., Lynch, A.M., 2005. Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.* 126, 491–498.
- Kulakowski, D., Veblen, T.T., Bebi, P., 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *J. Biogeogr.* 30, 1445–1456.
- LANDFIRE, 2013. LANDFIRE 1.1.0: Biophysical setting layer. <<http://landfire.cr.usgs.gov/viewer/>> (Accessed 14.01.12).
- Lough, J., Fritts, H., 1987. An assessment of the possible effects of volcanic eruptions on North American climate using tree-ring data, 1602 to 1900 AD. *Clim. Change* 10, 219–239.
- Lynch, A.M., 2009. Spruce aphid, *Elatobium abietinum* (walker) life history and damage to Engelmann spruce in the Pinaleno Mountains, Arizona. In: Sanderson, H.R., Koprowski, J.L., (Eds.). *The Last Refuge of the Mt. Graham Red Squirrel: Ecology of Endangerment*. University of Arizona Press, Tucson, AZ, pp. 318–338.
- Margolis, E.Q., Swetnam, T.W., 2013. Historical fire–climate relationships of upper elevation fire regimes in the south-western United States. *Int. J. Wildland Fire* 22, 588–598. <http://dx.doi.org/10.1071/WF12064>.
- Massey, C.L., Wygant, N.D., 1954. Biology and control of the Engelmann spruce beetle in Colorado. USDA Forest Service, Circular No. 944, Washington, DC. 35p.
- Mast, J.N., Wolf, J.J., 2006. Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, USA. *For. Ecol. Manage.* 236, 241–250.
- McLaughlin, S.P., 1993. Additions to the flora of the Pinaleno Mountains, Arizona. *J. Arizona-Nevada Acad. Sci.* 27 (1), 5–32.
- Minnich, R.A., Barbour, M.G., Burk, J.H., Fernau, R.F., 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conserv. Biol.* 9, 902–914.
- Morris, J.L., Brunelle, A., DeRose, R.J., Seppä, H., Power, M.J., Carter, V., Bares, R., 2013. Using fire regimes to delineate zones in a high-resolution lake sediment record from the western United States. *Quatern. Res.* 79, 24–36.
- MTBS, 2013. Monitoring Trends in Burn Severity. <<http://www.mtbs.gov/dataaccess.html>> (accessed 14.01.13).
- NCDC, 2014. National Oceanic and Atmospheric Administration National Climate Data Center State Climate Extremes Committee Website. <<http://www.ncdc.noaa.gov/extremes/scec/records>> (accessed 15.10.14).
- Negrón, J.F., Popp, J.B., 2009. The flight periodicity, attack patterns, and life history of *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), the western balsam bark beetle, in north central Colorado. *West. N. Am. Nat.* 69, 447–458.
- Notaro, M., Mauss, A., Williams, J.W., 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. *Ecol. Appl.* 22, 1365–1388.
- NRCS, 2012. Soil Survey Staff, USDA Natural Resources Conservation Service. <<http://websoilsurvey.nrcs.usda.gov/>> (accessed 14.01.12).
- O'Connor, C.D., 2013. Spatial and temporal dynamics of disturbance interactions along an ecological gradient. PhD Dissertation, School of Natural Resources & the Environment, University of Arizona, 204p.
- O'Connor, C.D., Falk, D.A., Lynch, A.M., Wilcox, C.P., 2013. Growth and demography of Pinaleno Mountain high elevation forests. Final Report for U.S. Forest Service, Rocky Mountain Research Station, Research Joint Venture Agreement 07-JV-11221615-317, 57p.
- O'Connor, C.D., Falk, D.A., Lynch, A.M., Swetnam, T.W., 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, U.S.A. *For. Ecol. Manage.* 329, 264–278.
- Powell, J., 1969. Historical study of the relation of major mountain pine beetle outbreaks in western Canada to seasonal weather. Forest Research Laboratory, Forestry Branch Information Report A-X-23. Calgary, Alberta, p. 18.
- Prior-Magee, J.S., Boykin, K.G., Bradford, D.F., Kepner, W.G., Lowry, J.H., Schrupp, D.L., Thomas, K.A., Thompson, B.C., 2007. Ecoregional gap analysis of the southwestern United States: the Southwest regional gap analysis project final report. <<http://fws-nmcfwru.nmsu.edu/swregap/report/SWReGAP%20Final%20Report.pdf>> (accessed 04.11.13)
- PRISM, 2013. PRISM Climate Group, Oregon State University. <<http://prism.oregonstate.edu>> (accessed 14.01.13).
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517.
- Régnière, J., Powell, J., Bentz, B., Nealis, V., 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *J. Insect Physiol.* 58, 634–647.
- Rehfeldt, G.E., 2004. Interspecific and intraspecific variation in *Picea engelmannii* and its congeneric cohorts: biosystematics, geneecology, and climate change. USDA Forest Service, Rocky Mountain Research Station Gen. Tech. Rep. RMRS-GTR-134. Fort Collins, CO. p. 1–22.
- Reynolds, K.M., Holsten, E.H., 1994. Relative importance of risk factors for spruce beetle outbreaks. *Can. J. For. Res.* 24, 2089–2095.
- Rodionov, S., Overland, J.E., 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES J. Mar. Sci.* 62, 328.
- Romme, W.H., Knight, D.H., 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62, 319–326.
- Salzer, M.W., Kipfmuehler, K.F., 2005. Reconstructed temperature and precipitation on a millennial timescale from tree-rings in the Southern Colorado Plateau, USA. *Clim. Change* 70, 465–487.
- Schmid, J.M., Frye, R.H., 1976. Stand ratings for spruce beetles, USDA For. Serv. Res. Note RM-309. USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. 4p.
- Schmid, J.M., Frye, R.H., 1977. Spruce beetle in the Rockies. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Gen. Tech. Rep. GTR RM-49. Fort Collins, CO. 44p.
- Schmid, J.M., Hinds, T.E., 1974. Development of spruce-fir stands following spruce beetle outbreaks. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Res. Paper RM-131. Fort Collins, CO. 21p.
- Schoennagel, T., Veblen, T.T., Romme, W., Sibold, J., Cook, E., 2005. ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. *Ecol. Appl.* 15, 2000–2014.
- Seager, R., Vecchi, G.A., 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proc. Natl. Acad. Sci.* 107, 21277–21282.
- Shepard, D., 1968. A two-dimensional interpolation function for irregularly-spaced data. In: Blue, R.B., Rosenberg, A.M. (Eds.), *Proceedings of the 1968 23rd Association for Computing Machinery national conference*. ACM, pp. 517–524.
- Sherriff, R.L., Berg, E.E., Miller, A.E., 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* 92, 1459–1470.
- Sibold, J.S., Veblen, T.T., 2006. Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale climatic variation. *J. Biogeogr.* 33, 833–842.
- Speer, J.H., 2010. *Fundamentals of Tree-Ring Research*. University of Arizona Press, Tucson, AZ.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago, IL.
- Stromberg, J.C., Patten, D.T., 1991. Dynamics of the spruce-fir forests on the Pinaleno Mountains, Graham Co., Arizona. *Southwest. Nat.* 36, 37–48.
- Swetnam, T.W., 1993. Fire history and climate-change in giant sequoia groves. *Science* 262, 885–889.
- Swetnam, T.W., Baisan, C.H., 1996. Fire histories of montane forests in the Madrean Borderlands. In: Ffolliott, P.F., DeBano, L.F., Baker, M.B., Gottfried, G.J., Solis-Garza, G., Edminster, C.B., Neary, D.G., Allen, L.S., Hamre, R.H., (Eds.), *Effects of fire on Madrean Province ecosystems: a symposium proceedings*. General Technical Report RM-GTR-289. December 1996. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO., pp. 15–36.
- Swetnam, T.W., Lynch, A.M., 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monogr.* 63, 399–424.
- Swetnam, T.W., Baisan, C.H., Kaib, J.M., 2001. Forest fire histories of the sky islands of la frontera. In: Webster, G.L., Bahre, C.J. (Eds.), *Changing Plant Life of La Frontera: Observations on Vegetation in the United States/Mexico Borderlands*. University of New Mexico Press, Albuquerque, pp. 95–119.

- Swetnam, T.W., Baisan, C.H., Grissino-Mayer, H.D., 2009. Tree-ring perspectives on fire regimes and forest dynamics in mixed-conifer and spruce-fir forests on Mt. Graham. In: Sanderson, H.R., Koprowski, J.L., (Eds.). *The Last Refuge of the Mt. Graham Red Squirrel: Ecology of Endangerment*. The University of Arizona Press, Tucson, pp. 55–67.
- Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* 79, 61–78.
- Torrence, C., Compo, G.P. 2014. Interactive Wavelet Plot. Accessed June 11, 2014. <http://paos.colorado.edu/research/wavelets/>.
- USDA Forest Service, 2000. Forest insect and disease conditions in the Southwestern Region, 1999. 34p.
- Vankat, J., 2013. *Vegetation Dynamics on the Mountains and Plateaus of the American Southwest*. Springer, Dordrecht; Springer Netherlands.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991a. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72, 213–231.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991b. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. *Can. J. For. Res.* 21, 242–254.
- Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., Villalba, R., 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* 82, 125–135.
- VoorTech, 2010. Measure J2X. 4.X. VoorTech Consulting, Holderness, NH.
- Werner, R.A., Holsten, E.H., 1985. Factors influencing generation times of spruce beetles in Alaska. *Can. J. For. Res.* 15, 438.
- Werner, R.A., Holsten, E.H., Matsuoka, S.M., Burnside, R.E., 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *For. Ecol. Manage.* 227, 195–206.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3, 292–297.
- Wilson J.L., Fitzgibbon R., Dudley S. 1999. Evaluation of a spruce and western balsam bark beetle outbreak on Mt. Graham, Safford Ranger District, Coronado National Forest. USDA Forest Service, Southwestern Region, Arizona Zone Entomology and Pathology, Specialist Report, December 1999. 23p.
- Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21, 414–416.
- Zhang, Q., Alfaro, R.I., Hebda, R.J., 1999. Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada. *For. Ecol. Manage.* 121, 215–225.