



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



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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.

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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

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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 Pinaleno 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 strobus* Engelm.), and aspen (*Populus tremuloides* Michx.) (Fig. 1). Engelmann spruce in the Pinaleno 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 Pinaleno 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

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