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ORIGINAL ARTICLE

Fire history and moisture influences on historical forest age structure in the sky islands of southern Arizona, USA

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ABSTRACT

Aim The purpose of this study was to examine the influence of moisture and fire on historical ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) age structure patterns.

Location We used a natural experiment created over time by the unique desert island geography of southern Arizona.

Methods We sampled tree establishment dates in two sites on Rincon Peak and another site in the Santa Catalina Mountains. The influence of regional moisture patterns was investigated by examining synchrony among tree age peaks and periods of favourable moisture. The influence of fire was investigated by examining the relationship between local fire histories and age peaks.

Results Tree age peaks (recruitment events) were synchronized with periods of reduced fire frequencies, suggesting that periods of reduced fire activity allowed time for young trees to develop fire-resistant characteristics. For example, two age peaks (1670s–1680s and 1770s–1780s) in the Rincon Peak-north site coincided with a period of reduced fire frequency. These age peaks were absent in the Rincon Peak-south site where fires were more frequent during that time. All three sites had age peaks in the early 19th century, coinciding with regional climate variability (i.e. El Niño Southern Oscillation patterns) that reduced fire activity.

Main conclusions Historically prior to fire suppression, the survivorship, and thus cohort establishment, of ponderosa pine was ultimately determined by local fire history patterns. The importance of fire as a tree establishment regulator highlights the need to use fire at appropriate intervals not just to restore but to maintain healthy forests.

Keywords

age structure, climate, desert sky islands, forests, frequent fires, *Pinus ponderosa*, ponderosa pine, regeneration, restoration, southern Arizona

INTRODUCTION

In forested ecosystems, understanding tree age structure patterns and the processes that shape that structure is fundamental to sustainable management. The age structure of a forest is a function of natality and mortality over time. Forest regeneration and mortality are both strongly influenced by disturbances and climate (Bergeron & Gagnon, 1987; Engelmark *et al.*, 1994; Fraver & Palik, 2012). In many areas, natural disturbance patterns have been altered, leading to increased forest density and more severe fires (Covington *et al.*, 1997). Given predicted climate changes (Seager *et al.*, 2007), it is critical to understand how both climate and disturbances historically influenced age structure patterns, particularly in dry forests, as they may face the greatest climate change impacts (Moore *et al.*, 1999; Allen *et al.*, 2002; Savage *et al.*, 2013).

In the southwest United States, studies have found tree establishment to be episodic (Weaver, 1951; Cooper, 1960; Mast *et al.*, 1999). The timing of age peaks (i.e. periods of higher than normal tree establishment) has been linked to both climate and fire history patterns (Savage *et al.*, 1996; Brown & Wu, 2005). Climate is important because survivorship of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) seedlings depends on moisture availability, especially in the dry months of May and June (Barton, 1993; Feddema *et al.*, 2013). Indeed, successful regeneration requires favourable conditions, including adequate moisture and temperature, over multiple years (Savage *et al.*, 1996). For example, southwest United States pine forests experienced a regeneration pulse in the first three decades of the 20th century (Pearson, 1933; Mast *et al.*, 1999). This pulse was due to a number of factors including favourable moisture, temperature, a lack of fire and decreased grass competition caused by increased livestock grazing (Pearson, 1933; Savage *et al.*, 1996). Climate–age peak linkages in the 20th century have also been documented in South American forests (Villalba & Veblen, 1997) and elsewhere across the United States (Mast *et al.*, 1998; Mast & Wolf, 2004; Brown, 2006; Taylor, 2010; Swetnam & Brown, 2011).

Although it is clear that climate influences ponderosa pine regeneration, historically there were other factors, particularly fire, which were also very important (Mast *et al.*, 1998; Meunier *et al.*, 2014). Prior to fire suppression policies, most ponderosa pine seedlings and saplings were probably killed by frequent surface fires (Barton, 1993). The importance of frequent fires as an ecological thinning mechanism was first stressed by Weaver (1943). Harper (1977) further proposed that successful regeneration required safe sites where seedlings and saplings were protected from fires and grass competition. The importance of these safe sites was re-emphasized by White (1985) who believed these fine-scale patches were created by intense spot fires that eliminated grass competition. At a stand level, Arno *et al.* (1995) found that in Montana, ponderosa pine age peaks coincided with periods of reduced fire activity. Similarly, Barton *et al.* (2001) found that in southeastern Arizona, 19th-century age peaks coincided with periods of reduced fire frequency. Furthermore, Brown & Wu (2005) and Meunier *et al.* (2014) found that ponderosa pine age peaks coincide with temporal 'fire-safe periods'.

It is clear that both climate and fire can influence ponderosa pine age structure patterns. However, given 20th-century fire regime changes and predictions of changes in climate patterns in the Southwest, further investigations are needed to determine how these two factors interacted and which one, if any, was the limiting factor in determining historical age structure patterns. One strategy for further investigation is to use closely spaced sites with relatively similar climate, thereby allowing us to hold climate constant while varying fire histories. Such 'natural experiments' (Diamond, 1986) exist in the sky islands of southern Arizona, where isolated conifer forests experienced similar regional moisture patterns but different fire histories due to local topographic differences (Iniguez *et al.*, 2009).

A natural experiment is provided by the fire histories from Rose Canyon, in the Santa Catalina Mountains, and Rincon Peak, in the Rincon Mountains, of southern Arizona (Fig. 1). These two study areas at similar elevations are located 40 km apart and share a similar climate pattern and similar vegetation (i.e. ponderosa pine forest). Within these two study areas (Fig. 1), there are three sites with distinct fire history patterns: Rincon Peak-north (RPN), Rincon Peak-south (RPS) and Catalina Rose Canyon (CRC). Fires spread throughout the Rincon Peak study area at intervals of 9–14 years between 1650 and 1763, but no fires were recorded in RPN between 1763 and 1819 (Iniguez *et al.*, 2009). After 1819, widespread fires (i.e. fires recorded by ≥ 2 plots) were notably absent both in RPN and RPS until 1867. Therefore, RPN had at least two long fire intervals while RPS experienced only one. Fire intervals in CRC also varied between 1650 and 1900, but all fire intervals were less than 20 years (Iniguez *et al.*, 2008).

Objectives

The goal of this study was to investigate the influence of moisture (e.g. drought variability) and fire history on age structure patterns under pre-settlement (i.e. prior to 1900) conditions. This research was intended to answer the question of whether age structure patterns were historically determined by moisture or fire frequency patterns. Our hypothesis was that if age structure was determined by regional moisture patterns, we would expect temporal synchrony between age peaks across sites. That is, broad-scale favourable moisture conditions should produce age peaks during approximately the same time periods across all sites, regardless of local fire history differences. If age structure was controlled by fire history patterns, we would expect synchrony between age peaks and local periods without fires or with lower fire frequencies but not necessarily synchronized with favourable moisture conditions.

MATERIALS AND METHODS

Study area

The Rincon Peak study area is within Saguaro National Park and has an elevation range from 2100 to 2550 m a.s.l. (Fig. 1). The Rose Canyon study area is within the Santa Catalina Ranger District, which is part of the Coronado National Forest and ranges in elevation between 2100 and 2600 m a.s.l. No timber harvesting has occurred on Rincon Peak due to the steep topography and lack of roads (Baisan & Swetnam, 1990). The Santa Catalina study area experienced limited timber harvesting, from a small area, in the early to mid-20th century to supply local home construction. Wildfires have been actively suppressed for the past century on both study areas.

The two study areas are within the Madrean Archipelago: a system of coniferous 'islands' separated by low-elevation

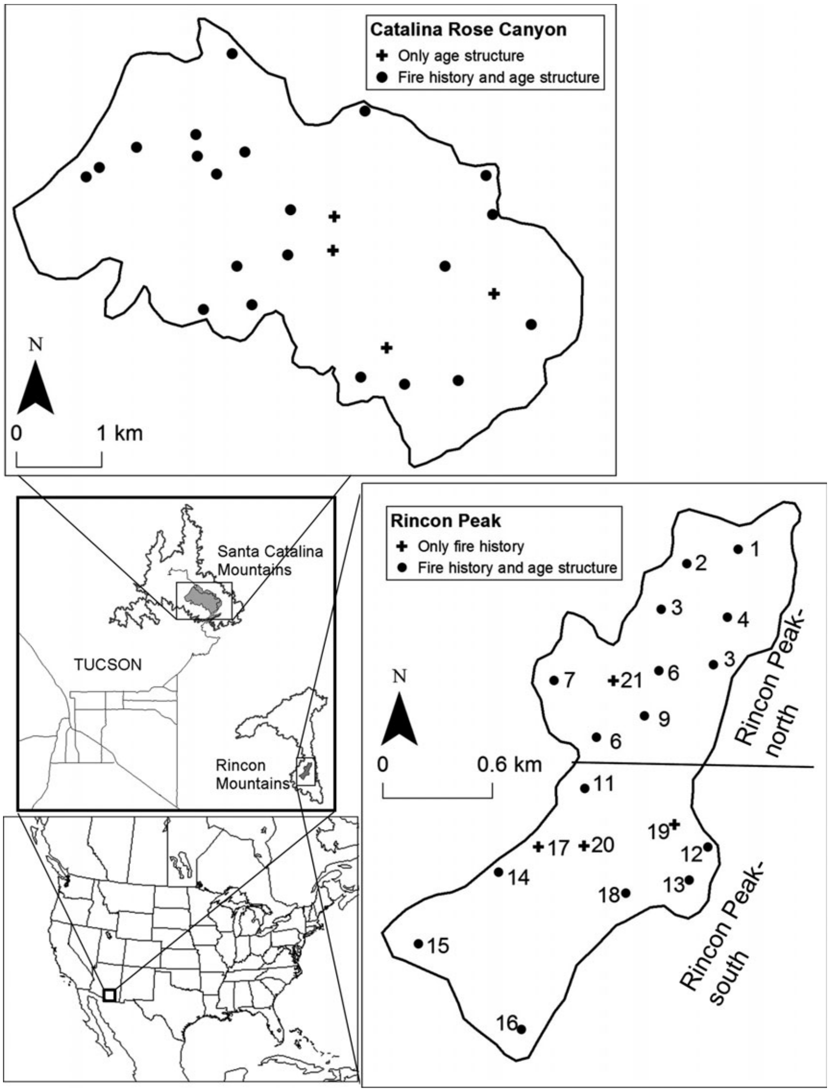

Figure 1 Location of fire history and age structure plots in Rincon Peak and Santa Catalina Mountains in southern Arizona. The two study areas were separated into three sites: Rincon Peak-north, Rincon Peak-south and Catalina Rose Canyon. At each plot we collected fire history, age structure or both.

desert 'seas'. The mountains are a northern extension of the Sierra Madre Occidental of northwestern Mexico (Warshall, 1995). The Madrean Archipelago is located at the junction of four major floristic regions: the Sonoran desert, the Chihuahuan desert, the Sierra Madre and the Rocky Mountains. The region has a bimodal precipitation pattern. In winter, high elevations (> 1500 m) typically receive snow while lower elevation areas receive rainfall. In summer, tropical moisture promotes monsoonal weather that produces localized thunderstorms. Average precipitation at the Palisades ranger station (elevation 2400 m) within the Rose Canyon study area was 78 cm between 1965 and 1981 (http://www.wrcc.dri.edu/summary/Climsmaz.html).

The vertical relief and geographical position of these mountains combine to produce a diverse mosaic of plant communities stratified along elevation/moisture gradients (Whittaker & Niering, 1965, Niering & Lowe 1984). The composition of the ponderosa pine belt varies with elevation. At high elevations, ponderosa pine forests include Douglas fir (*Pseudotsuga menziesii* var. *glauca* Beissn. Franco), southwestern white pine (*Pinus strobiformis* Engelm.) and Gambel oak (*Quercus gambelii* Nutt.). At lower elevations, ponderosa pine forms both pure pine and pine-oak communities. The latter includes Madrean evergreen oaks such as silverleaf oak (*Quercus hypoleucoides* A. Camus), Arizona white oak (*Q. arizonica* Sarg.) and netleaf oak (*Q. rugosa* Née). Other communities that surround ponderosa pine stands in our study areas include chaparral communities dominated by oaks, juniper species (*Juniperus* spp.), pinyon pine (*Pinus discolor* Bailey & Hawksw) and pointleaf manzanita (*Artostaphylos pungens* K. Kunth).

We delineated study area boundaries based on the extent of pine forest and major ridgelines. Pine species were the targeted population for both the age structure and fire history reconstructions; therefore, we used pine forest distributions as lower elevation boundaries. We also used ridgelines as lateral boundaries to separate areas with distinct topographic characteristics. We delineated boundaries using a combination of digital elevation maps, 1:24,000 topographic maps, digital orthophoto quarter quadrants and field reconnaissance. The Santa Catalina study area was larger (1800 ha) than the Rincon Peak study area (310 ha). To collect fire history and age structure samples, we used a geographically stratified random sampling framework. To ensure complete spatial coverage, we divided each study area into geographical units of equal size. We then randomly selected multiple points from each unit based on the unit size and availability of forested stands (see Iniguez *et al.*, 2008, 2009 for more details).

Field methods

In the field, we located each plot to within 10 m using global positioning systems and collected fire history and/or age structure information. We collected fire-scar samples within 2 ha circular plots. First, we located all fire-scarred trees within the plot, and collected two to nine of the best-preserved samples. We used chainsaws to collect the fire-scar samples, cutting full or partial cross sections (Arno & Sneck, 1977). When available, pith dates from fire scarred trees were also added to the age structure database. Additional fire history sampling methods are described in Iniguez *et al.* (2008, 2009). Overall, we sampled 20 fire history plots in RP and 21 in RC (Fig. 1).

Tree age samples were also collected at each plot. Four plots on Rincon Peak lacked live conifer trees due to a historical stand-replacing fire, so fire scar information was only collected at those plots. At each forested plot, we used a 0.1 ha plot to measure the diameter of all trees $\geq$ 10 cm at breast height and cored at least five of the largest trees. Tree age samples were also collected at six and four randomly selected plots within Rincon Peak and the Rose Canyon site, where 20–25 trees were cored just outside the 0.1 ha plot (Fig. 1). Tree age sampling focused on trees that appeared to have established prior to 1900; usually trees with yellow bark or large branches. To determine if the visual estimates of ages were generally correct, we also cored at least two smaller trees. Trees were cored as close to the ground as possible by angling the increment borer downwards. For each core, we noted tree species, coring height and plot numbers.

Laboratory methods

Fire-scarred samples and tree cores were catalogued, sanded and dated. Each sample was dried for at least a week and progressively sanded to a high polish. We dated samples using dendrochronological techniques (Stokes & Smiley, 1968) to assign each fire scar and pith date a calendar year. We estimated missing piths by overlying concentric circle transparencies to match the curvature of the innermost rings (Liu, 1986). We estimated only pith dates that were within 20 years of the innermost ring.

The year of establishment for every tree was estimated depending on pith date, growth rate and coring height. Initial growth rates for each tree were estimated by matching the rings near the pith of each tree core with transparencies of concentric circles with known ring frequency (rings cm^{-1}). Using this method, each tree core was assigned to one of three growth categories: fast growing (2–7 rings cm^{-1}), moderate growing (8–12 rings cm^{-1}) or slow growing (13+ rings per inch). We then harvested seedlings from each growth rate category and determined the average number of years it took seedling to reach heights of 10, 20 and 30 cm, which provided a vertical growth rate estimate. For each cored tree, we estimated an establishment date (i.e. year of germination) by subtracting, from the pith date, the estimated number of years it took the tree to reach the coring height. This estimate was based on the coring height and horizontal growth rate. On average, fast growing trees reached a height of 20 cm in 2 years and slow growing trees took 5 years. So, the establishment date for fast growing trees was estimated 2 years prior to the pith date for cores taken 20 cm above the ground. Corrections were typically 2–5 years because most trees were growing fast and cores were taken fairly close to the ground.

Analysis

We identified tree age peaks by comparing observed versus expected age structure patterns. To reflect correction factors of establishment dates and assess long-term processes, we aggregated annual establishment dates into decadal age classes. For each site, we determined the expected decadal frequency by fitting the observed frequency (within the period of analysis) with an exponential model that reflected the decrease in available samples of older trees due to mortality and decay (Bergeron & Gagnon, 1987). In a sense, the expected frequency is the null hypothesis in that it is the age structure we would expect to find if tree establishment was constant over time but adjusted for a decrease in sample size with increasing time since the present. The exponential model was then used as the expected frequency for each site. We also calculated the standard deviation of the expected frequency and used it as a threshold to identify age peaks. A similar method was used by Bergeron & Gagnon (1987) to analyse age structure pattern in *Pinus resinosa* (Ait.) forests. That is, we defined an age peak when the observed frequency in a decade, or series of consecutive decades, was at least one standard deviation greater than the expected.

To evaluate the impact of wildfires on age structure, we examined synchrony between age structure and fire history patterns. To analyse fire history patterns, we constructed a plot composite by aggregating all fire-scarred trees within a plot (Dieterich, 1980). Fire years within a plot were identified when a fire was recorded by at least one tree in that plot. We graphed the fire chronology for each plot using the fire history program FHX2 (Grissino-Mayer, 2001). We identified widespread fire years when two or more plots recorded a fire within that study area (Farris *et al.*, 2010).

We compared age structure patterns to climate conditions using the tree-ring reconstructed summer (July–August) Palmer Drought Severity Index (PDSI) based on grid point

105 in southern Arizona (Cook *et al.*, 1999). In general, positive PDSI values indicate wet conditions and negative values indicate dry conditions. For each decade, we calculated the PDSI average, number of years with positive (wet) values, maximum number of consecutive years with positive PDSI values and the number of years with PDSI values greater than +1.0 (moderate wet).

RESULTS

Overall, we determined tree establishment dates for a total of 607 trees; 499 (82%) were ponderosa pine and the rest were either southwestern white pine or Douglas fir (Table 1). The analysis was restricted to the time period between 1650 and 1900 because: (1) few fire-scarred or cored trees pre-dated 1650 and (2) human-induced fire suppression after 1900 disrupted the natural fire regime (Iniguez *et al.*, 2008). Using our age peak criteria, we identified four distinct age peaks in RPN and two in RPS (Figs 2a & 3a). The CRC site had the oldest age peak in the 1650s and another age peak from 1800 to 1869 (Fig. 4a).

Age peaks in Rincon Peak-north

The two oldest age peaks on Rincon Peak occurred in the 1670–1680s and 1770–1780s and were found exclusively in RPN during decades of reduced fire activity and drought conditions (Fig. 2a). The climate during the period between 1670 and 1689 was relatively dry (Fig. 2c); especially in the 1670s, which had 3 years with positive PDSI values (Table 2). During this same period, however, RPN and RPS differed significantly in regard to fire history. For example, a fire in 1684 was recorded in both RPN and RPS, but this fire burned a smaller portion in the RPN site (recorded in four of nine plots) where the age peak occurred (Fig. 2b). In the RPS site, where the age peak was not found, the 1684 fire was more extensive (recorded in seven of nine plots) (Fig. 3b). In addition, the RPS site also experienced a fire in 1691 that did not burn in RPN (Figs 2b & 3b).

Table 1 Number of tree establishment dates by species and study site in the Rincon Peak and Santa Catalina study areas in southern Arizona. The Rincon Peak study area included the Rincon Peak-north (RPN) and Rincon Peak-south (RPS) sites while the Santa Catalina study area included the Catalina Rose Canyon (CRC) site.

All	RPN	RPS	CRC	Total
Pinus ponderosa	97	113	289	499
Pinus strobiformis	29	18	7	54
Pseudotsuga menziesii	24	8	22	54
Total	150	139	318	607
Youngest (establishment year)	1932	1926	1946	
Oldest (establishment year)	1485	1378	1646	
1650–1900 (period of analysis)				
Pinus ponderosa	85	86	275	446
Pinus strobiformis	19	12	3	34
Pseudotsuga menziesii	21	5	7	33
Total	125	103	285	513

A century later, the 1770s–1780s age peaks, found in RPN only, also corresponded with an extended period of reduced fire activity. In terms of moisture, the 1770s–1780s age peaks established during a dry period (Fig. 2c) as there were only 5 years with positive PDSI values between 1770 and 1789 (Table 2). In terms of fire history, this age peak coincided with a period of minimal fire activity at the RPN site. That is, between 1763 and 1819, the only fire recorded in RPN, where the age peak occurred, was a 1775 fire which scarred only two of nine plots (Fig. 2b). Conversely, no age peak was found between 1770 and 1789 at the RPS site, which burned not only in 1775 but also in 1786, 1798 and 1806 (Fig. 3b).

Age peaks in the 1810s and 1830s at RPN coincide with both favourable moisture and a lack of widespread fires (Fig. 2a). Reconstructed PDSI values show that 15 of the 20 years during the 1810s and 1830s had positive PDSI values suggesting favourable conditions for regeneration (Table 2). The fire in 1819 was the only widespread fire in RPN between 1775 and 1867 (Fig. 2b). Despite similar fire history and moisture condition, the 1810s age peak occurred in RPN, but not in the RPS site. Although numerous trees established between the 1819 and 1867 fires in RPN, only the 1830s met the age peak criteria. The 1830s age peak in RPN occurred during a wet period which included 9 years of positive PDSI values and an absence of fires (Fig. 2c). The 1830s age peak in RPN was also synchronized with age peaks in both RPS and the Santa Catalina Mountains. No age peaks occurred in RPN after 1840, despite favourable moisture and fire conditions. Ponderosa pine establishment declined in RPN after the 1830s, while the establishment of Douglas fir and southwestern white pine increased (Fig. 2a).

Age peaks in Rincon Peak-south

The RPS site had two age peaks between 1650 and 1900 (Fig. 3a). The first age peak included three consecutive decades starting in the 1830s. The timing of this age peak was synchronized with age peaks in the RPN and CRC sites (Figs 2 & 4). The 1830s included 9 years with positive PDSI values, and 6 years with PDSI value > 1 (Table 2). Similarly, half of the years in the 1840s and 1850s had positive PDSI values. These three decades were also synchronous with a lack of widespread fires (i.e. fires that scarred ≥ 2 plots) on Rincon Peak between 1819 and 1867 (Figs 2b & 3b). Three fires were recorded between 1819 and 1867, but all three occurred on separate years and each scarred one plot suggesting these were all small fires (Farris *et al.*, 2010). The 1880s age peak on RPS was not synchronized across sites. This age peak established during a period when moisture conditions were variable and fire was recorded in only one plot within the site (Fig. 3b).

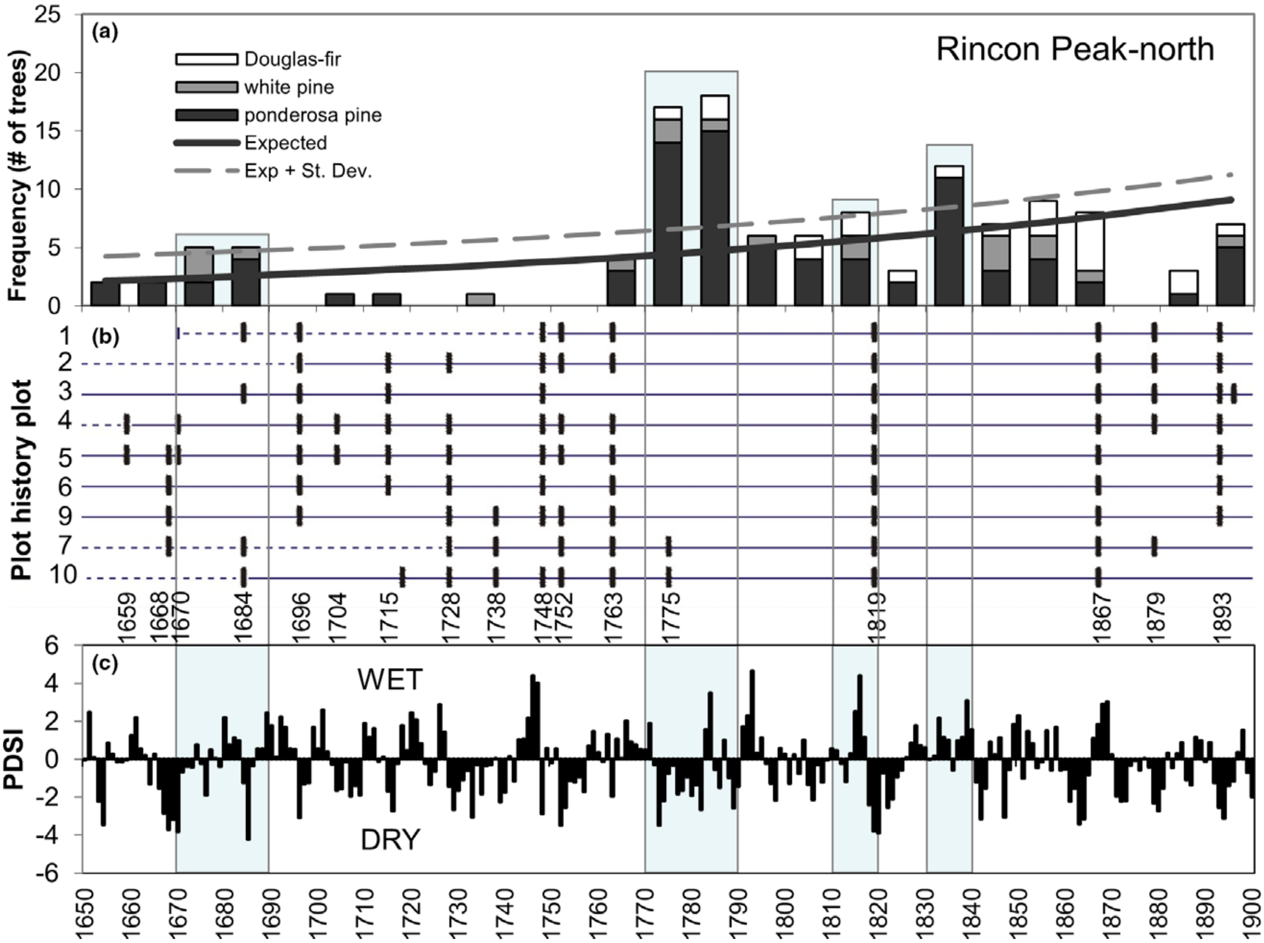

Figure 2 Age structure, fire history and summer Palmer Drought Severity Index (PDSI) reconstructions for the Rincon Peak-north site in the Rincon Mountains. Age structure (a) cohorts (highlighted) were identified when tree establishment per decade was one standard deviation above the expected mean. Composite fire chronologies (b) for individual fire history plot are shown as horizontal lines and fire events are shown as vertical dashes. Fire history plot numbers correspond to locations in Fig. 1. Moisture patterns (c) represent summer (July–August) PDSI.

Age peaks in the Catalina Rose Canyon site

The 1650s age peak in CRC was the earliest age peak found within the three sites (Fig. 4a). It was difficult to assess the influence of fire history on this age peak because our fire history sample depth was low during this period (i.e. few trees were recording) (Fig. 4b). Reconstructed PDSI indicate relatively dry conditions during the 1650s, although 4 of 10 years had positive PDSI values (Table 2). A later age peak in CRC, on the other hand, included seven consecutive decades from 1800 to 1869 (Fig. 4a). This long age peak in CRC was also synchronized with age peaks at the other two sites. Moisture patterns varied during this time with periods of drought from 1818 to 1821, but mostly favourable moisture conditions in the 1810s, 1830s and 1850s (Table 2, Fig. 4c). This age peak in CRC also coincided with a pattern of reduced widespread fires (i.e. fires that scarred ≥ 2 plots). For example, fire frequencies diminished from two to three widespread fires per decade prior in 1800 to as little as one fire per decade between 1830 and 1860. In addition, two of the longest intervals between widespread fires (i.e. 1836–1851 and 1857–1870) were also recorded during this time period in CRC (Fig. 4b).

DISCUSSION

Age structure patterns and PDSI

Tree regeneration is influenced by seasonal to annual moisture patterns, especially in dry southwest ponderosa pine forests. Seasonal drought during the pre-monsoon months of May and June can kill young seedlings without well-developed roots (Schubert, 1974; Barton, 1993). Furthermore, Savage *et al.* (1996) suggest that large pulses of ponderosa pine regeneration were a function of 4 years of favourable temperature and moisture conditions. Ponderosa pine seedlings need at least two consecutive years of above average moisture to develop deep roots and the ability to survive droughts (Schubert, 1974; Savage *et al.*, 1996). Our results, based on tree-ring drought reconstructions for southern

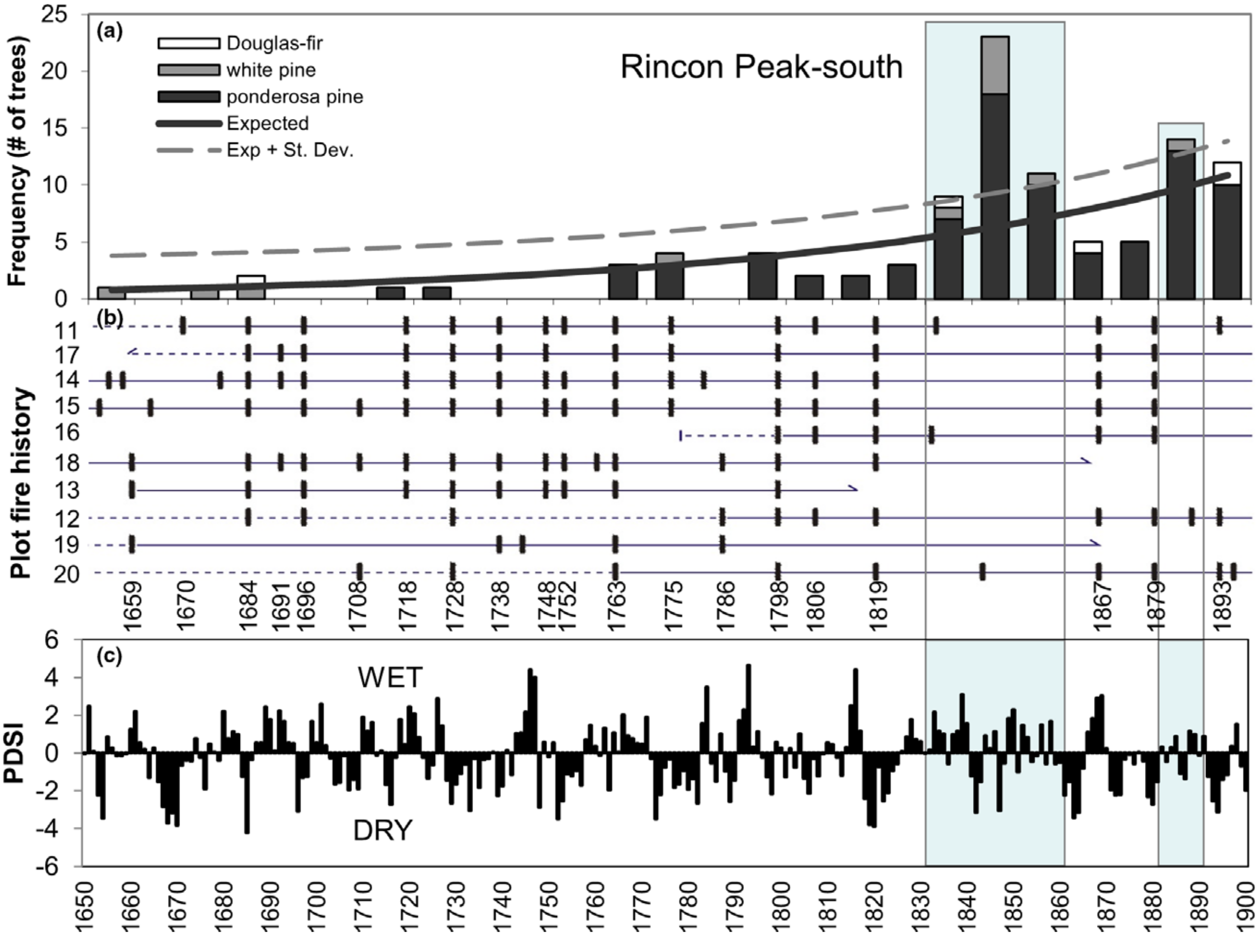

Figure 3 Age structure, fire history and summer Palmer Drought Severity Index (PDSI) reconstructions for the Rincon Peak-south site in the Rincon Mountains. Age structure (a) cohorts (highlighted) were identified when tree establishment per decade was one standard deviation above the expected mean. Composite fire chronologies (b) for individual fire history plots are shown as horizontal lines and fire events are shown as vertical dashes. Fire history plot numbers correspond to locations in Fig. 1. Moisture patterns (c) represent summer (July–August) PDSI.

Arizona, show that consecutive years with positive (wet) PDSI values occurred in all but one decade (1730s) between 1650 and 1900, suggesting consistent decadal conditions favourable for tree regeneration occurred regularly. A pattern of consistent regeneration is also suggested by tree establishment in every decade between 1650 and 1900 in CRC and in 22 of 25 decades in Rincon Peak. Consistent favourable moisture conditions and tree establishment in most decades indicates that moisture patterns did not limit tree regeneration at decadal scales. In other words, although moisture patterns influence regeneration, they were not the primary determining factor responsible for the episodic age structure patterns, at least in these sites.

Age structure patterns and fire

Tree age structure patterns in southern Arizona pine forests appeared to be determined primarily by fire history. The majority of historical fires in ponderosa pine forests were surface fires, non-lethal to most mature trees (Swetnam & Baisan, 2003). Surface fires, however, did kill most young trees that lack fire-tolerant characteristics such as thick bark and an elevated canopy (Barton, 1993). As a result, tree establishment was inversely related to fire frequency (Meunier *et al.*, 2014). For instance, in this study, most age peaks occurred when the particular site experienced fewer and/or smaller fires. In some instances, age peaks were synchronous between sites, particularly between 1810 and 1859. Other age peaks, such as the 1670s–1680s and 1770s–1780s age peaks in RPN and the 1880s peak in RPS, were not synchronous between sites but did coincide with fewer fires at that particular site. This highlights the significance of fire as a thinning agent and the important relationship between fire-free periods and age peaks. Similar increases in pine establishment during periods of decreased fire activity have also been reported in Mexican pine forests with frequent fire regimes (Fulé & Covington, 1997; Cortez-Montaño *et al.*, 2012).

It is possible that some age peaks were also related to severe stand-replacing fires. For example, low tree survivorship

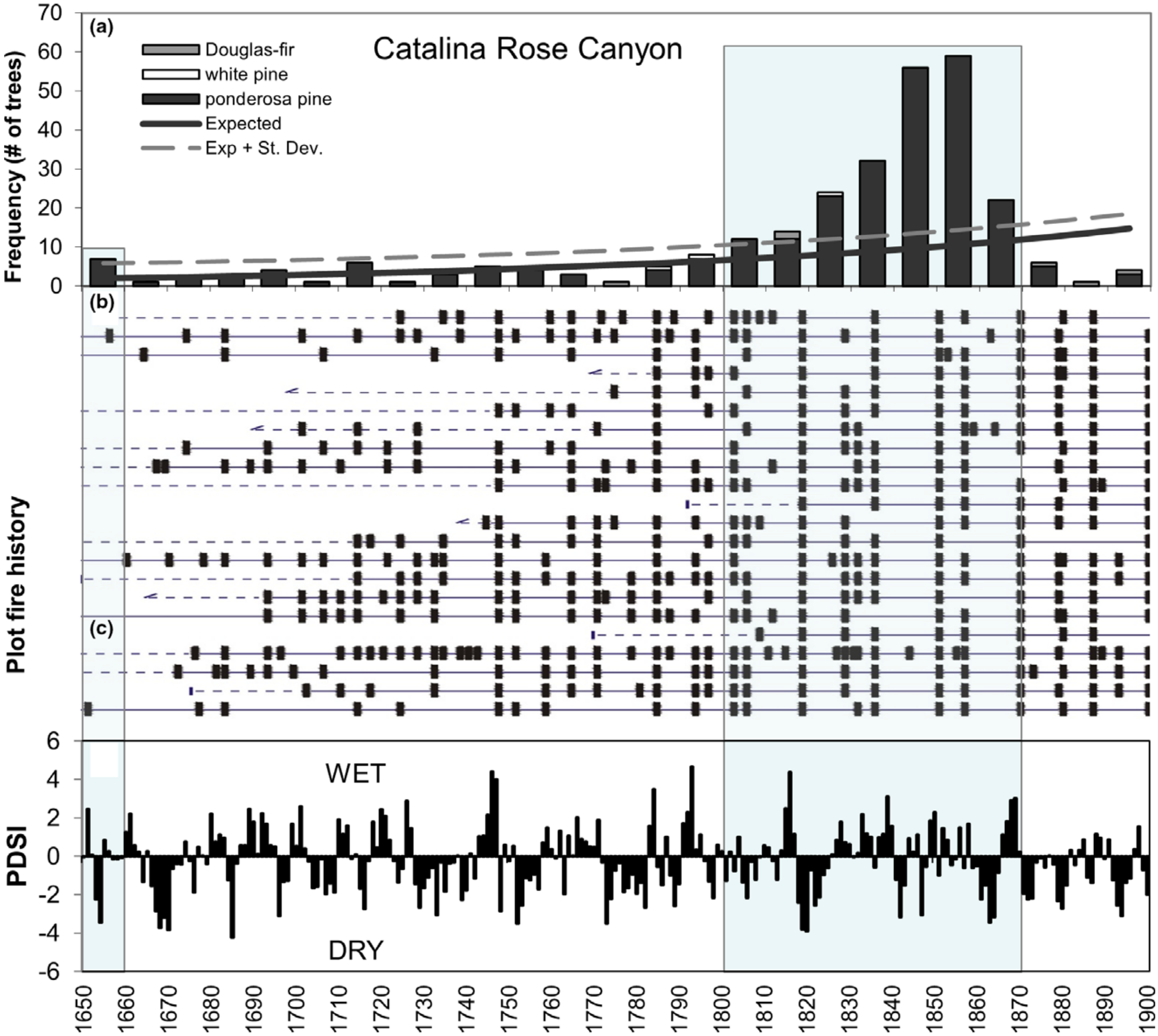

Figure 4 Age peaks, fire history and moisture conditions for the Rose Canyon site in the Santa Catalina Mountains in southern Arizona. (a) Cohorts (shaded) were identified when tree establishment per decade was one standard deviation above the expected mean. (b) Composite fire chronologies were composed from multiple trees within each fire history plot and are shown as horizontal lines and with vertical dashes representing a recorded fire event. Moisture patterns (c) represent summer (July–August) Palmer Drought Severity Index (PDSI).

prior to the 1770s–1780s age peak in RPN and the 1830–1869 age peak in RPS suggests that regeneration may have established after stand-replacing fires in 1763 and 1819 respectively. Although these stand-replacing fires were small (< 100 ha), they may have fragmented fuel connectivity between RPN and RPS resulting in the fire history differences observed between the two sites (Iniguez *et al.*, 2009). Other peaks, however, were probably not related to stand-replacing fires. For example, the 1830s peak in RPN and the 1880s peak in RPS were both preceded by the establishment of trees that had survived previous fires, suggesting that they must have been low-severity surface fires. Therefore, although an age peak could follow a severe stand-replacing fire, an age peak alone is not a sufficient indicator of fire severity. Other studies have used ponderosa pine age peaks (recruitment pulses) to infer past stand-replacing events (e.g. Kaufmann *et al.*, 2000; Sherriff & Veblen, 2006). The results presented in this study, however, suggest that fire severity inferences based on ponderosa pine age structures alone are inappropriate. These kinds of inferences (i.e. high severity events associated with subsequent age peaks) are much more definitively established when multiple lines of evidence are used, including age structures, fire scars and tree deaths or ring growth changes in surviving trees (e.g. Margolis *et al.*, 2007; Brown *et al.*, 2008).

Recent work by Dugan & Baker (2015) found that most age cohorts in their study area at the Grand Canyon were associated with fire quiescence. However, they also argued

Table 2 Moisture patterns for decades when age peaks occurred in the Rincon Peak and Santa Catalina study areas in southern Arizona. Moisture conditions are based on summer (July–August) Palmer Drought Severity Index (PDSI) values reconstructed from tree-ring chronologies for grid point 105 (Cook *et al.*, 1999). In general, positive PDSI values suggest wet conditions, and negative values indicate drought conditions. In addition, PDSI values greater than +1 indicate moderate wet conditions. Moisture patterns were only evaluated for decades corresponding with age peaks found in this study.

First year of decade	No. of sites with an age peak	Avg. PDSI	No. of positive PDSI years	Max no. of years with consecutive positive PDSI	No. of years with PDSI > 1
1650	1	−0.24	4	2	1
1670	1	−0.66	3	2	0
1680	1	0.27	7	4	4
1770	1	−0.91	2	2	1
1780	1	−0.54	3	2	2
1800	1	−0.55	3	0	1
1810	2	0.17	6	4	3
1820	1	−0.73	4	4	1
1830	3	0.97	9	6	6
1840	2	−0.39	5	3	3
1850	2	0.49	5	2	3
1860	1	−0.28	4	4	4
1880	1	−0.35	5	2	2

that the establishment of many cohorts was also preceded by either severe fire or drought. They further suggested that such disturbances create the necessary growing space for new cohort establishment. Their data showed that, in most plots, previously established trees survived these disturbances. Hence, these disturbances appear to have caused relatively small patches of tree mortality, which in most cases were smaller than their 1-ha plots. It is therefore important to note that most age structure and fire history studies in the southwest have not found historical evidence for large patches (> 100 ha) of stand-replacing fires in ponderosa pine forests, such as those associated with recent wildfires.

Climate–fire frequency–age structure relationship

In this study, moisture patterns do not appear to limit tree establishment at decadal scales. Climate, however, clearly influenced fire and thus indirectly influences age structure patterns. For example, all three sites had at least two decades of significant tree establishment between 1810 and 1859. Similarly, other ponderosa pine sites across the Southwest have also had age peaks at this time (Mast *et al.*, 1999; Barton *et al.*, 2001; Brown & Wu, 2005). The first half of the 19th century included one of the wettest periods in our analysis. The period 1837–1846, for example, was the Southwest's second wettest 10-year period in the past 1000 years (Ni *et al.*, 2002). The regional age peak in the early to mid-19th century also coincides with a period of reduced fire activity across the Southwest (Swetnam & Betancourt, 1998; Grissino-Mayer & Swetnam, 2000). This suggests that longer fire intervals, due to reduced El Niño Southern Oscillation (ENSO) amplitude, may have produced synchronous peaks across Southwest forests (Brown & Wu, 2005; Swetnam & Brown, 2011). This emphasizes that longer fire intervals, not just moisture conditions, produced age peaks at both local and regional scales.

CONCLUSIONS

Our results show that historical episodic tree age structure patterns in ponderosa pine forests were related to fire history. That is, tree age peaks were historically synchronized with local periods of reduced fire frequencies. In some cases, age peaks were only observed at sites where fires were absent or less frequent because of local factors. For example, the 1770s–80s age peak in Rincon Peak occurred during less than ideal moisture conditions and only in RPN during a local period of reduced fire activity. At other times, however, periods of low fire frequency were a result of regional patterns. For example, regional climate variability (i.e. ENSO patterns) in the early 19th century may have reduced fire frequencies across all sites and produced synchronized age peaks among all three sites, as well as other sites in the Southwest (Mast *et al.*, 1999; Barton *et al.*, 2001; Brown & Wu, 2005; Swetnam & Brown, 2011). Regardless of the reason, reductions in fire activity typically produced age peaks. We therefore conclude that historical age structure patterns were controlled directly by fire processes, which in turn were sometimes synchronized with regional climate variations.

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BIOSKETCHES

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Tom Swetnam and **Christopher Baisan** have collaborated on numerous projects focusing on reconstructing disturbance dynamics and linking them to climate and humans. They have used tree-ring to reconstruct forest fires, insect outbreaks and tree demography from local to global scales.

Author contributions: J.M.I., T.W.S. and C.H.S. conceived the idea; J.M.I. and C.H.S. led the data collection; J.M.I. did the data analysis. Writing was led by J.M.I. with significant contributions by T.W.S. and C.H.S.

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