ORIGINAL RESEARCH   **Open Access**

Pre-Columbian red pine (*Pinus resinosa* Ait.) fire regimes of north-central Pennsylvania, USA

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Abstract

Background: Fire-dependent vegetation communities in the northeastern USA have undergone significant transitions since social and ecological disruptions associated with Euro-American colonization of North America. There is much interest, though little information available, about historical fire regimes of fire-adapted vegetation communities in the northeastern USA in pre-Columbian times (i.e., pre-1492 CE). We intensively investigated a red pine (*Pinus resinosa* Ait.)—oak (*Quercus* spp.) forested landscape in north-central Pennsylvania, USA, for exceptionally old red pine remnants (stumps, snags) where previous research had suggested the potential to develop fire-scar and tree-ring chronologies which extend to time periods prior to 1492.

Results: Tree-ring and fire-scar chronologies recovered from red pine trees extend back to 1370 and 1402, respectively. Red pine trees were broadly distributed across this landscape (34.4 km^2 area) prior to 1492, and frequent fire (i.e., mean fire return intervals of 4.1 years at landscape scale, 9.7–11.7 years at smaller spatial scales (0.5–7.1 km^2)) was observed in the time period prior to sustained contact between Indigenous peoples and Euro-American colonizers circa 1609.

Conclusions: This study resulted in the longest fire-scar record in eastern North America and offers unique foundational ecological information regarding pre-Columbian fire regimes of northeastern USA fire-adapted forest communities. Fire scars provide physical evidence that fire was an important ecological component of this landscape before and after 1492 and that the current period of reduced fire activity is unprecedented in the 500 years prior to fire exclusion practices that were widely adopted circa 1915. Beyond fire scars, the spatial and temporal extent of the red pine tree-ring record provides evidence that red pine, a fire-dependent species, was historically a more important component of this landscape than it is today. The conservation of red pine vegetation communities will require incorporating recurring fire into management plans, for the successful regeneration and perpetuation of red pine, and to sustain associated flora and fauna of conservation concern.

Keywords: Fire regimes, Northeastern USA, Pennsylvania, Pre-Columbian, Red pine

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Resumen

Antecedentes: Las comunidades dependientes del fuego en el noreste de los EEUU han sufrido transiciones significativas desde las disrupciones sociales y ecológicas asociadas con la colonización euroamericana de Norteamérica. Existe mucho interés, aunque poca información disponible, sobre los regímenes históricos del fuego en comunidades adaptadas al fuego en tiempos precolombinos (i.e. pre- 1492). Investigamos intensivamente un paisaje forestal de pino rojo (*Pinus resinosa* Alt.) y roble (*Quercus* spp.) en el centro-norte de Pennsylvania, EEUU, en el cual había remanentes excepcionalmente añosos de pinos rojos (muertos en pie o tocones) sobre los cuales investigaciones previas habían sugerido su potencial para desarrollar cronologías de anillos decrecimiento y cicatrices de fuego que se extendían a períodos previos a 1942.

Resultados: Las cronologías de anillos de crecimiento y cicatrices de fuego del pino rojo se extendieron desde 1370 y hasta 1402, respectivamente. El pino rojo estaba ampliamente distribuido a través de este paisaje (en un área de 34,4 km^2) antes de 1492, y fuegos frecuentes [(i.e. retorno del fuego a intervalos de cada 4,1 años a escala de paisaje, y a intervalos de 9,7 años a menores escalas espaciales (0,5 – 7,1 km^2)] fueron observados en el período previo al contacto sostenido entre los pueblos indígenas y los colonizadores euroamericanos ocurrido alrededor de 1609.

Conclusiones: Este estudio resultó en el registro más extenso de cicatrices de fuego en el este de Norteamérica y ofrece una información ecológica fundacional en relación a los regímenes de fuego precolombinos en las comunidades forestales adaptadas al fuego en Noreste de EEUU. Las cicatrices de fuego proveen evidencia física de que el fuego fue un componente ecológico importante antes y después de 1492, y que el período actual de actividad reducida de fuegos no tiene precedentes en los 500 años previos a las prácticas de exclusión que fueron ampliamente adoptadas alrededor de 1915. Más allá de las cicatrices, la extensión espacial y temporal de los registros de anillos de crecimiento del pino rojo proveen evidencia de que este pino, una especie dependiente del fuego, fue un componente más importante de este paisaje de lo que es hoy. La conservación de las comunidades vegetales de pino rojo requiere de la incorporación de fuegos recurrentes en sus planes de manejo para su regeneración y perpetuación exitosa, y también para sostener la flora y fauna asociadas como valor de conservació.

Background

Fire-dependent vegetation communities of the northeastern USA (Northeast) face a multitude of conservation challenges in the wake of widespread timber exploitation and twentieth century fire-exclusion policies. Perhaps utmost is a lack of detailed knowledge regarding fire's role and ecological context in times prior to the major disruptions associated with Euro-American colonization of North America, i.e., pre-Columbian or pre-1492 CE. Tree-ring and fire-scar chronologies developed from dead trees (i.e., remnant wood in the form of stumps or snags) have the capacity to provide such information. These archives provide sub-annually precise, spatially explicit fire occurrence information that can be analyzed across a range of spatial scales (e.g., tree to landscape) (Farris et al. 2010; Marschall et al. 2019; Rolstad et al. 2017), allowing for improved understanding of historical fire regimes, vegetative community structure and composition, and associated ecological processes and vegetation community outcomes (Swetnam et al. 1999). Such records can also help clarify the relative influences of climate and Native American land use practices as fire regime controls (Abrams and Nowacki 2021; Oswald et al. 2020). Other biological archives, such as sedimentary pollen and charcoal records, offer valuable long-term information as well, but at temporal and spatial scales too coarse to infer site-specific information to inform modern management decisions, and are less able to detect fires of low-to-moderate intensity (Abrams and Seischab 1997; Remy et al. 2018; Stocks and Kauffman 1997).

Relative to other regions of North America (especially the western USA), fire-scar chronologies are scarce in the Northeast (Margolis et al. n.d). Multiple ecological and social factors contribute to this disparity, including a lower prevalence of fire-adapted tree species that persist for long periods post-mortem, differences in land use history, a more humid climate, historical emphasis of wildland fire research in the western USA, and sampling biases. Of the fire-scar chronologies that exist for this region, very few precede the early to mid-1600s (Table 1, Fig. 1).

Existing research indicates that considerable potential exists to develop temporally long fire-scar chronologies using red pine (*P. resinosa* Ait.) remnant wood (e.g., Brose et al. 2013, 2015; Kipfmueller et al. 2021; Mann et al. 1994; Marschall et al. 2019). Red pine is an ideal tree species for fire-scar chronology development due to its abilities to survive and record low-to-moderate severity fires (Hauser 2008), and to persist as remnant wood for centuries post-mortem. In addition, red pine is a fire-dependent species, requiring recurring fire for successful

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Table 1 Published fire history sites within the eastern range of native red pine (*Pinus resinosa* Ait.)

Site	Time span (no. years)	Earliest fire scar (year)	Tree species	Reference
Tioga[a]	1370–2016 (646)	1402	PIRE	
BSL	1665–1856 (191)	1683	PIRE	Guyette and Dey 1995a
COS	1636–1994 (358)	1662	PIRE	Guyette and Dey 1995b
SGN	1656–1861 (205	1669	PIST	Dey and Guyette 1996b
PPU	1634–1875 (241)	1643	PIST	Dey and Guyette 1996a
PMT	1577–2015 (438)	1693	PIRE	Abadir et al. 2019
RSR	1800–1987 (187)	1815	PIRE	Engstrom and Mann 1991
BXT	1687–2010 (323)	1799	PIRE	Abadir et al. 2019
BRF	1450–1851 (401)	1584	PIRE	Mann et al. 1994
LBH	1601–2011 (410)	1633	PIRE	Brose et al. 2013
SLR	1530–2011 (481)	1623	PIRE	Brose et al. 2013
UDR	1578–1914 (336)	1635	PIRE	Brose et al. 2013
100	1643–2014 (371)	1745	PIRI	Stambaugh et al. 2018
SHR	1556–2011 (455)	1710	PIRI	Stambaugh et al. 2018
ACR[b]	1841–2017 (176)	1848	PIRI	Saladyga and Standlee 2018
084	1610–2014 (404)	1704	PIPU, PIRI	Stambaugh et al. 2018
107	1619–2013 (394)	1646	PIRI	Marschall et al. 2016
088	1547–2013 (466)	1560	PIRI	Marschall et al. 2016
170	1614–2015 (401)	1629	PIRI, PIPU	Stambaugh et al. 2018
081	1628–2014 (386)	1634	PIPU, PIRI	Stambaugh et al. 2018
053	1563–2013 (450)	1595	PIPU	Stambaugh et al. 2018
CMP	1652–2018 (366)	1702	PIRI	Howard et al. 2021
SVM	1600–2000 (400)	1616	QUAL	Shumway et al. 2001
PKK	1770–2010 (240)	1868	PIPU, PIRE, QURU	Hessl et al. 2011
RK	1660–2005 (345)	1671	PIPU, PIRI	Aldrich et al. 2014
KM	1598–2005 (407)	1638	PIPU, PIRI	Aldrich et al. 2014
MM	1687–2003 (316)	1704	PIPU, PIRI	Aldrich et al. 2010

Time span defined by earliest and latest tree ring years reported

PIRE Pinus resinosa Ait., *PIST Pinus strobus* L., *PIPU Pinus pungens* Lamb., *PIRI Pinus rigida* Mill

[a] This study, [b] data from nine nearby study sites combined

regeneration and to perpetuate as a community component (Stambaugh et al. 2019). Relative to the Great Lakes region, natural-origin Northeast red pine forests (i.e., not artificially regenerated) have received little attention in terms of their long-term ecological processes, including fire regime characteristics. This difference may be due to the low abundance and economic importance of red pine in the Northeast compared to other portions of its range (Burns and Honkala 1990).

In north-central Pennsylvania, red pine stands of natural origin are rare and little is known about their present or historical disturbance ecologies. Here, similar to other sites in the central and northern Appalachians, red pine is found in small, discrete, nearly pure stands, and as sparsely scattered individuals. Stands of red pine are typically found on or near ridgetops where edaphic factors regulate competing vegetation and

provide favorable light and seed bed conditions (Cook et al. 1952; Stephenson et al. 1986). Remnant wood of centuries-old red pine are often found at sites with very few or no living red pine individuals, suggesting a deep-time presence of a fire-dependent species, and the loss of the species to succession over time due to changing disturbance regimes, poor regeneration conditions, and increasing competition. The stands that do remain may be relicts of an era of different land use, fire regimes, and climate.

Information regarding pre-Columbian fire regimes and associated ecological processes is urgently needed to inform the conservation of remaining red pine communities. Decades of fire exclusion and other land use changes have led to current conditions in which these communities are failing to regenerate and are now succeeding to mesophytic, closed-canopied forests
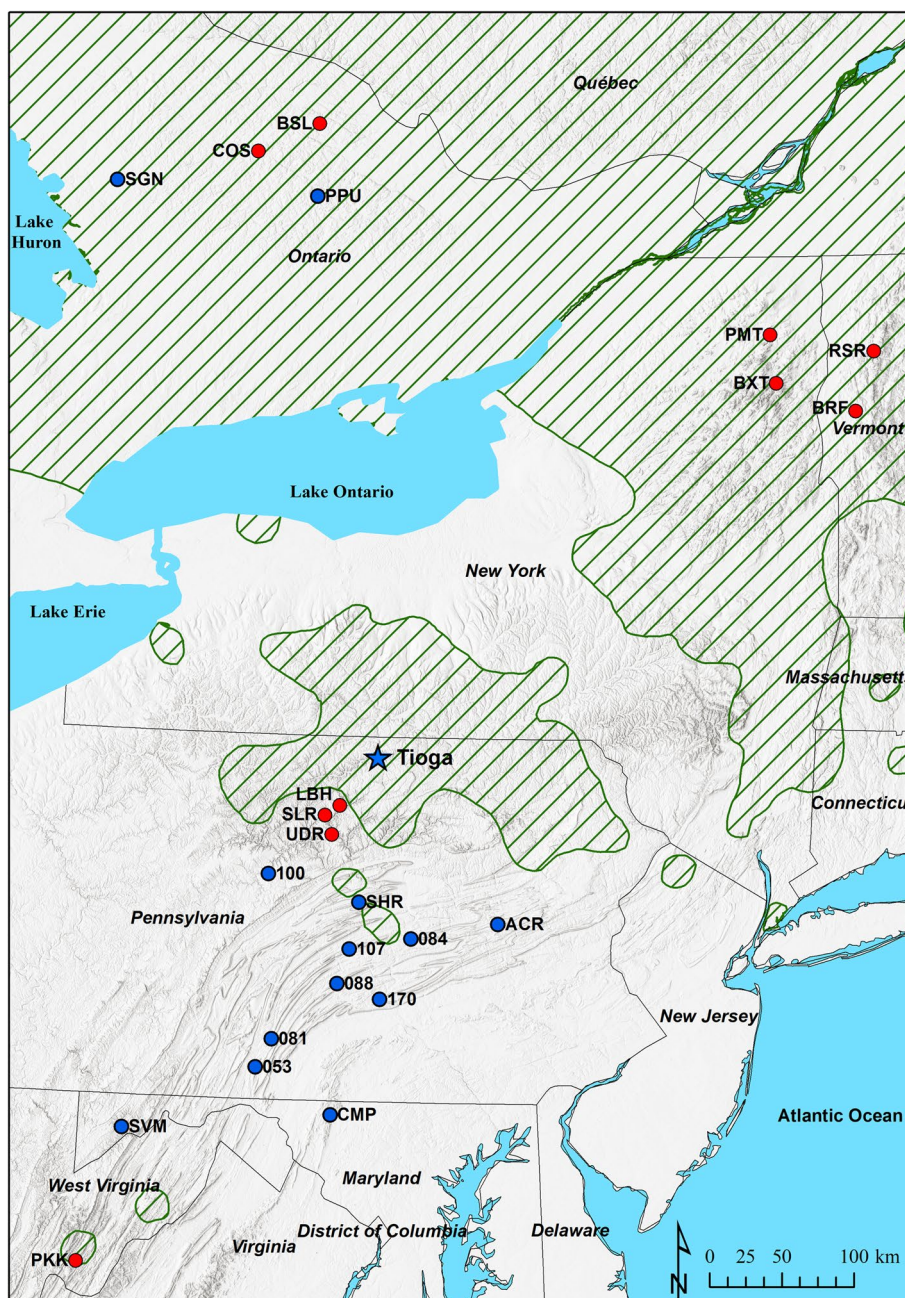
Fig. 1 Regional published tree-ring and fire-scar-based fire history studies in relation to the current study (blue star). Red circles indicate studies with red pine (*Pinus resinosa* Ait.) included as a sampled species, and blue circles indicate studies of other species only. Site names in bold; red pine native distribution is indicated by green hash marks (Little 1971). Refer to Table 1 for study citations

dominated by hardwood tree species, with light levels too low to foster robust ground-layer vegetation communities (Held and Jones-Held 2014; Nowacki and Abrams 2008).

Not far from the focal landscape in this study, fire-scarred red pines at three sites in the upper Pine Creek watershed in north-central Pennsylvania (study sites LBH, SLR, UDR, Fig. 1) revealed high levels of fire activity in the earliest portions of their records, the early 1600s, followed by an extended period of low fire activity until Euro-American colonization of the region (Brose et al. 2013, 2015). However, questions remained as to whether this early frequent fire regime was typical or anomalous compared to the preceding time period.

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In the landscape included in this study, fire-scar chronologies previously developed extend to 1620 AD (Marschall et al. 2019; Stambaugh et al. 2018). Results from these studies showed that before fire suppression and exclusion efforts began circa 1915, fires occurred on average every two to three years at the landscape scale and were generally dormant season, small-scale events, with fire extent and scarring synchrony modulated by antecedent drought (Marschall et al. 2019). Fire frequency from the seventeenth to twentieth centuries was closely associated with changes in human populations and culture (Stambaugh et al. 2018).

Based on these previous studies, documenting pre-Columbian-aged red pines was hypothesized to be possible in this landscape if additional, focused field surveying and collection efforts were made. Previous collections allowed for a robust master ring-width chronology to be constructed from 192 live and dead red pines which spanned the period of 1580–2016 (Marschall et al. 2019). However, samples collected from four trees did not crossdate with the master chronology despite being good candidates for tree-ring dating based on numbers of tree-rings per sample (range = 165–340 rings), ring-width variability, and the presence of fire scars that could be additional verification of dating. Considering these traits, and their physical characteristics (highly solar bleached and heavily eroded external surfaces), we surmised that

the samples were likely too old for their tree-ring records to sufficiently overlap with the master chronology. If this was correct, these red pine remnants and their fire scars could represent an opportunity for the development of the oldest fire-scar chronology in eastern North America.

The overarching goal of this research was to construct the longest annually resolved record of fire in the Northeast (i.e., pre-Columbian) to provide new information on historical fire regimes and ecologies of the region. The specific objective of this study was to resurvey and expand collections in areas with previously documented oldest wood ages, thereby further extending the existing tree-ring and fire-scar chronologies. With an extended fire record, we hoped to contribute to the limited information available regarding pre-Columbian vegetation and fire regime characteristics to support the conservation of fire-dependent vegetation communities in the region.

Methods

Study site

Most (approximately 75%) of the 34.4 km^2 study site (hereafter Tioga) is administered by the Pennsylvania Game Commission (PGC, State Gameland 037), with one small inholding owned by the US Corps of Engineers and one privately owned parcel. Located in north-central Pennsylvania (Tioga county), USA, this landscape
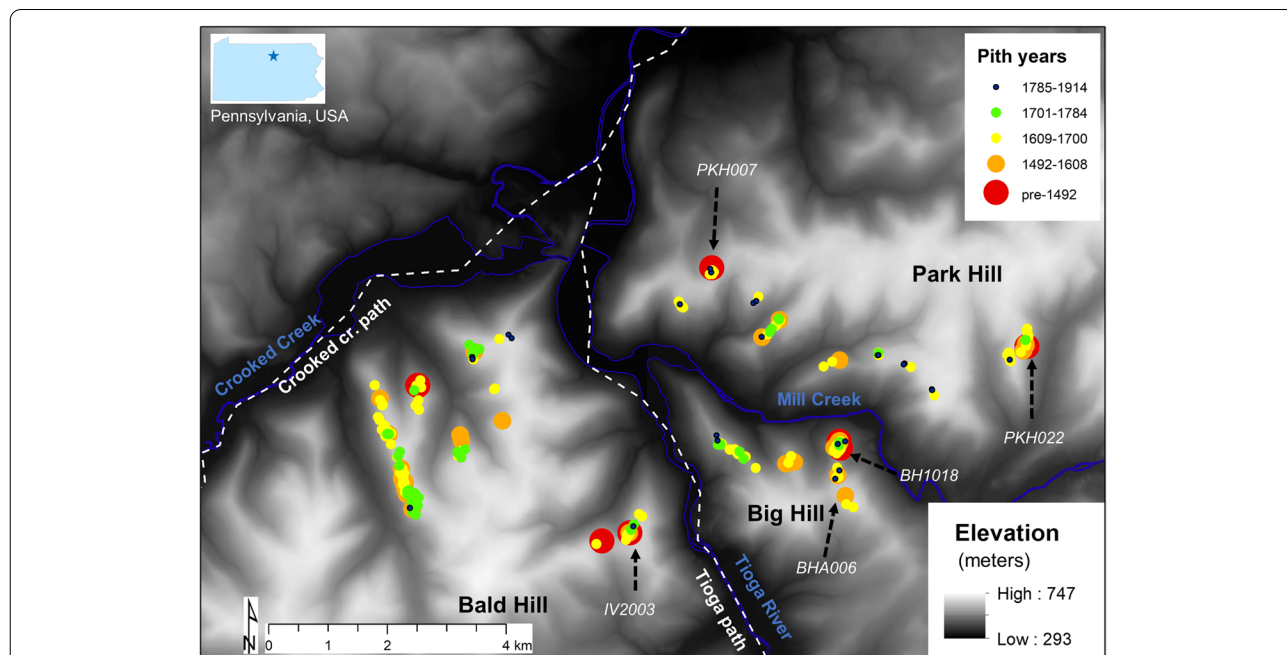

Fig. 2 Map showing the temporal and spatial distribution of 267 fire-scarred red pine (*Pinus resinosa* Ait.) trees sampled across a landscape in north-central Pennsylvania, USA. White dashed lines indicate approximate locations of documented Native American paths (Wallace 1965), white italicized sample numbers and black-dashed arrows indicate locations for the four oldest trees in the study, and one tree of special interest (BHA006) which recorded nine fires between 1535 and 1564, a period for which very few fire scars have been recovered in the eastern USA

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lies within the Deep Valleys section of the Appalachian Plateaus Province (Fig. 1, Sevon 2000) and is within the southern limits of the Wisconsin glaciation (Rayburn and Breaker 1981). The landscape is dominated by uplands of three separate mountains (Big, Bald, and Park Hills) and is bisected north-to-south by the Tioga River and two of its tributaries, Crooked and Mill Creeks (elevation range: ~350–650 m) (Fig. 2). Valley bottoms range from approximately 200 to 600 m wide and today are occupied by two flood control reservoirs and agriculture fields. Upland soils are primarily well-drained, very stony loams formed in glacial till and derived from sandstone and shale parent materials (Rayburn and Breaker 1981). The climate is humid continental with warm, humid summers, and cold, snowy winters. Mean monthly temperatures range from −9.4 °C (January) to 27.2 °C (July), and the area records the lowest annual rainfall in Pennsylvania with a mean annual precipitation of 88.5 cm (https://www.uscli matedata.com/climate/tioga/pennsylvania/united-states/uspa3301).

According to PGC inventory records, upland forests are primarily even-aged (~80–120 years) with closed-canopies (i.e., fully stocked), and overstories dominated by chestnut oak (*Quercus montana* Willd.) and northern red oak (*Q. rubra* L), and smaller components of white oak (*Q. alba* L.) and eastern white pine (*Pinus strobus* L.). This dry-oak forest type is dominant on ridgetop to mid-slope topographic positions (e.g., Fig. 3), and transitions to mesophytic northern hardwoods-hemlock (*Tsuga canadensis* L.) in the lower elevations. The midstory of the upland forests is dominated by shade-tolerant tree species such as red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), black gum (*Nyssa sylvatica* Marshall), and black birch (*Betula lenta* L.), while understory vegetation is comprised largely of mountain laurel (*Kalmia latifolia* L.) and *Vaccinium* species, with scattered areas of scrub oak (*Q. Ilicifolia* Wangenh). Sparsely interspersed among the matrix of oak-dominated uplands are small (~0.5–5 ha), nearly-pure stands of living red pines, most of which are located on or near west-facing ridgetop topographic positions. In addition, solitary live red pine trees are occasionally found throughout the studied landscape, also primarily on west-facing aspects. Remnant red pine trees (stumps, snags, logs) are distributed throughout the landscape across a wider variety of aspects and topographic positions and are much more common than live individuals. Several red pine remnants exhibiting evidence of historical turpentine collecting practices (i.e., "box cuts," Fig. 3A) were observed throughout the study area.

Early written descriptions of the region provide evidence that upland forest composition and structure were different than what currently exists. An early surveyor of what is currently Athens, Pennsylvania (approximately 40 km east of the study site), described the region's uplands as "pine plains…covered with a dense growth of pitch pine (*P. rigida*), with some yellow pine (*colloquial term for red pine*) and scrub oak…" (Murray 1908, italicized text is ours). Other accounts exist of fire-maintained agricultural fields near Native American settlements in the region (Murray 1908). At the time of European contact, the study area was at the southern extent of the Seneca (Onondowahgah) Nation

Fig. 3. **A** Red pine (*Pinus resinosa* Ait.) remnants (circled, and in foreground) are abundant in the studied landscape, though the modern forest is nearly entirely comprised of hardwood tree species (e.g., *Quercus montana* Willd., *Q. rubra* L., *Acer rubrum* L.). Multiple red pine remnants exhibiting evidence of historical turpentine collecting practices (i.e., "box cuts") were observed in the study area (e.g., foreground, tree-ring record of 1755–1905). **B** Small (e.g., 0.5–5.0 ha), nearly pure, stands of red pine are scattered throughout the hardwood-dominated forest on west-facing slopes

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territory (Jones 2010). Based on what is known about how the Iroquois chose settlement sites (Jones 2008), it is likely that the study landscape was primarily used by the Seneca as hunting territory. The nearest known Seneca population centers were at Diahoga (now Athens, PA) and present-day Painted Post, NY (approximately 30 km north of the study site). Documented Native American travel corridors passed through the study area, including the Tioga Path (which bisects the study site) and a path through the Crooked Creek valley along the northwest perimeter of the study site (Fig. 2) (Wallace 1965).

Sample collection and preparation

In 2018 and 2019, we revisited the study area to increase sampling intensity and lengthen existing tree-ring and fire-scar records (Marschall et al. 2019). New field surveys and sample collection efforts targeted only tree remnants suspected to be in the oldest age-class. Surveys for these oldest trees were informed by the physical characteristics of the oldest crossdated samples from the previous studies, including the four undated remnant trees that were suspected to be exceptionally old. These

physical characteristics included lighter grey exterior color (likely due to increased exposure and solar bleaching), exaggerated exterior wood erosion, and shapes indicative of large tree size.

In the field, we cut cross-sections (approximately 5–10 cm thick) from the lowest and most solid portions of pine remnants using a chainsaw. Multiple cross-sections were collected when needed to ensure that the most complete tree-ring and fire-scar record of individual remnants was captured (e.g., Fig. 4). Tree locations were recorded using a GPS device, and sample orientation relative to north and height above ground was recorded. Cross-sections were transported to the Center for Tree-Ring Science at the University of Missouri for preparation, tree-ring and fire-scar analyses, and archiving.

In the laboratory, cross-sections were stabilized with glue and tape when necessary, then polished with belt and orbital sanders using successively finer sandpaper (80–1200 grit) until wood cellular detail was visible. Wood samples from remnant trees were identified as red pine based on a comparison of wood anatomical features (e.g., early/latewood transition, distribution of resin ducts) from samples previously collected from living red pine

Fig. 4 Sample number IV2003, a red pine (*Pinus resinosa* Ait.) remnant which contained the oldest known fire scars in eastern North America. White dashed lines indicate where the two cross-sections pictured at left were removed. This sample spanned the years 1370–1710 and had fire scars (indicated by white arrows) from 19 different fire events

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in the study area (Marschall et al. 2019). We measured tree-ring widths sequentially to 0.01-mm precision using a Velmex TA measuring system (Velmex, Bloomfield, NY, USA). Ring-width series were plotted and visually dated using an existing ring-width master chronology for the site (Center for Tree-Ring Science, University of Missouri, unpublished data) and standard dendrochronology methods (Speer 2010; Stokes and Smiley 1968). Year of tree establishment was identified based on the pith year from the lowest cross-section collected from each tree. When absent, we estimated pith dates based on ring-curvature using a concentric circle diagram and the average width of the inner-most five rings, following methods described by Applequist (1958) and Speer (2010). Aspect, elevation, and slope measurements for each tree location were derived from 10-m resolution digital elevation model data (ArcMap GIS, version 10.6.1) and plotted against tree establishment dates (i.e., pith year) to visually assess potential groupings or relationships.

Fire scars were identified by visible cambial injury without evidence of mechanical wood-removal, and the presence of woundwood tissue and traumatic resin canals (Smith and Sutherland 1999), and were assigned to the year which exhibited cambial response. When possible, we assigned seasonality to fire scars based on scar positions either within or between the annual rings (Kaye and Swetnam 1999). Assigned fire-scar positions were dormant (between annual rings), early earlywood, middle earlywood, late earlywood, latewood, and undetermined. Years for which any fire scars were assigned seasonality other than dormant (growing season fire scars) were tallied.

Fire history analyses

Historical fire regime characteristics were assessed at multiple spatial scales: landscape scale (defined by the spatial extent of all sampled trees), groupings of trees located on the same landform (landform scale, i.e., Bald, Big, or Park Hills), and individual trees (tree scale, ~1 m^2). We chose to group trees by landform to facilitate appropriate comparisons of our findings to previous fire history research in this landscape and elsewhere in terms of study site size. Site areas for landscape and landform spatial scales were calculated separately in the ArcGIS (version 10.6.1) environment by measuring convex-hull polygons drawn around recording tree locations. Trees were considered to be recording for all years for which tree rings were present.

Fire frequency statistics were calculated, summarized, and graphically displayed using the computer software program FHAES v. 2.0.2 (Brewer et al. 2016). Analyses at the landscape scale were based on the site-composite record from all trees in the study and were limited to the

time period prior to the advent of modern fire exclusion practices (pre-1915, Decoster 1995), and with at least three trees recording. Analyses at the landform scale were based on their respective landform-composite fire-scar records and were restricted to the time period preceding that which was previously reported (i.e., pre-1620, Marschall et al. 2019). Individual tree mean fire interval (Tree MFI) was calculated for trees with at least three fire scars.

Fire frequency statistics calculated included mean fire interval (MFI), interval ranges, Weibull median interval, and lower/upper exceedance intervals (LEI/UEI; statistically long or short interval thresholds). For each year in which a fire scar was identified (fire year), the percentage of trees scarred relative to the total number recording (scarring synchrony) was calculated. The number of fire years per decade (11-year moving sum) was calculated at the landscape scale and plotted along with 11-year moving-average values for Palmer Drought Severity Index (PDSI, Palmer 1965; grid point 254, Cook et al. 2004) and 11-year moving mean for the percentage of recording trees scarred at the landscape scale. The distributions of composite intervals and Tree MFIs were assessed via histograms at all spatial scales.

Fire history analyses were conducted for the entire period of record prior to 1915 (Pre-1915), and separately for four culturally distinct sub-periods: Pre-1609, the period before local Native American tribes were in direct and sustained contact with European colonizers of North America; 1609–1700, the period of Native American inhabitation directly after Euro-American contact, dominated by inter-tribal interactions and warfare related to the fur trade (Richter 1983); 1701–1784, the period of Native American inhabitation directly preceding Euro-American colonization, dominated by an alliance among Native groups and conflict with and among French, British, and American colonists (Richter 1983); and, the period of Euro-American colonization (EAC), 1785–1914, which followed the cessation of Native lands in 1784 (Florin 1977) and subsequent Euro-American settlement of the region. When fire intervals spanned sub-periods, they were included in the period which contained the majority of years. Tree MFIs were grouped for mean calculation per time period based on establishment years because trees of the same cohort are exposed to similar climate and disturbance factors at similar stages of development.

Drought/fire analyses

We tested for associations between historical fire events and drought conditions using superposed epoch analysis (SEA) considering fire records compiled at the landscape and landform spatial scales. Drought

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condition data consisted of reconstructed summer season PDSI (Palmer 1965) for southern New York (grid point 254, Cook et al. 2004). For landscape-scale analyses, SEA was conducted based on the composite fire-scar record for all recorded fire years prior to 1915, and separately for fire records filtered to include only years in which at least two trees and 10% were scarred. These tests were conducted separately for fire records from the entire time record (Pre-1915), and for all sub-periods. For landform-scale analyses, SEA was limited to the Pre-1609 sub-period, conducted separately for site-composite fire records compiled by landform, and restricted to fire records which contained at least three fire years. SEA was conducted separately on unfiltered fire records, and records were filtered to include only fire years which were recorded by at least two trees, and fire years recorded on multiple landforms. For all SEA, lagged conditions of 6 years prior and 4 years after fire events were considered. Drought conditions were considered significantly different than expected at the 0.05 alpha level with confidence intervals derived by bootstrapping data for 1000 simulated events.

Results

Newly crossdated tree-ring and fire-scar chronologies
Samples from 79 new trees were collected, 71 of which were successfully crossdated. Calendar years covered by the new samples spanned the period 1518–1904, extending the previously developed chronology by 63 years (Fig. 5). The lengthened chronology provided sufficient overlap to crossdate the four previously undatable samples of suspected advanced age (IV2003, BH1018, PKH022, and PKH007). These four trees provided the oldest tree-ring series in the data set, resulting in the entire tree-ring record from 267 trees spanning calendar years 1370–2016 (646 years; Fig. 5). Pith was present on 166 of the trees sampled and estimated for 101. The number of rings missing to pith ranged from 8 to 97 ($\bar{x} = 33$) with actual and estimated pith dates ranging from 1338 to 1913 (Fig. 6). The spatial extent of all trees sampled (landscape scale) included an area of 34.4 km^2.

Compiled fire-scar record
From the newly dated trees ($n = 75$), we identified and dated 250 fire scars resulting in 79 unique fire years from 1402 to 1877. Twenty-six of these fire years preceded the previously reported fire record (i.e., Pre-1590; Marschall et al. 2019) and 10 new fire years were identified in the period of overlap (1590–1877). After the incorporation of the new fire scars from the new samples, the extended fire-scar chronology represented a total of 1285 fire scars and 155 unique fire years spanning the period 1402–1966 (565 years).

Tree establishment
Seven of the trees sampled were established prior to 1492 and were spatially dispersed across the landscape (Fig. 2). There was an abrupt increase in tree establishment coincident with the beginning of the 1609–1700 sub-period and in the mid-1700s (Fig. 6). Most (n=150, 56.2%) of the 267 trees were established during the 1609-1700 period (Table 2), approximately two-thirds (n=98) of which were established during the first half of this period (between 1609 and 1655) (Fig. 6A). Relative to the 1609–1700 sub-period, few trees were established in the Pre-1609 and later sub-periods (Table 2). No clear relationships among slope, elevation, aspect, and date of tree establishment were apparent, although we note that very few trees were established on aspects other than west-facing after the beginning of the EAC sub-period (Fig. 6B).
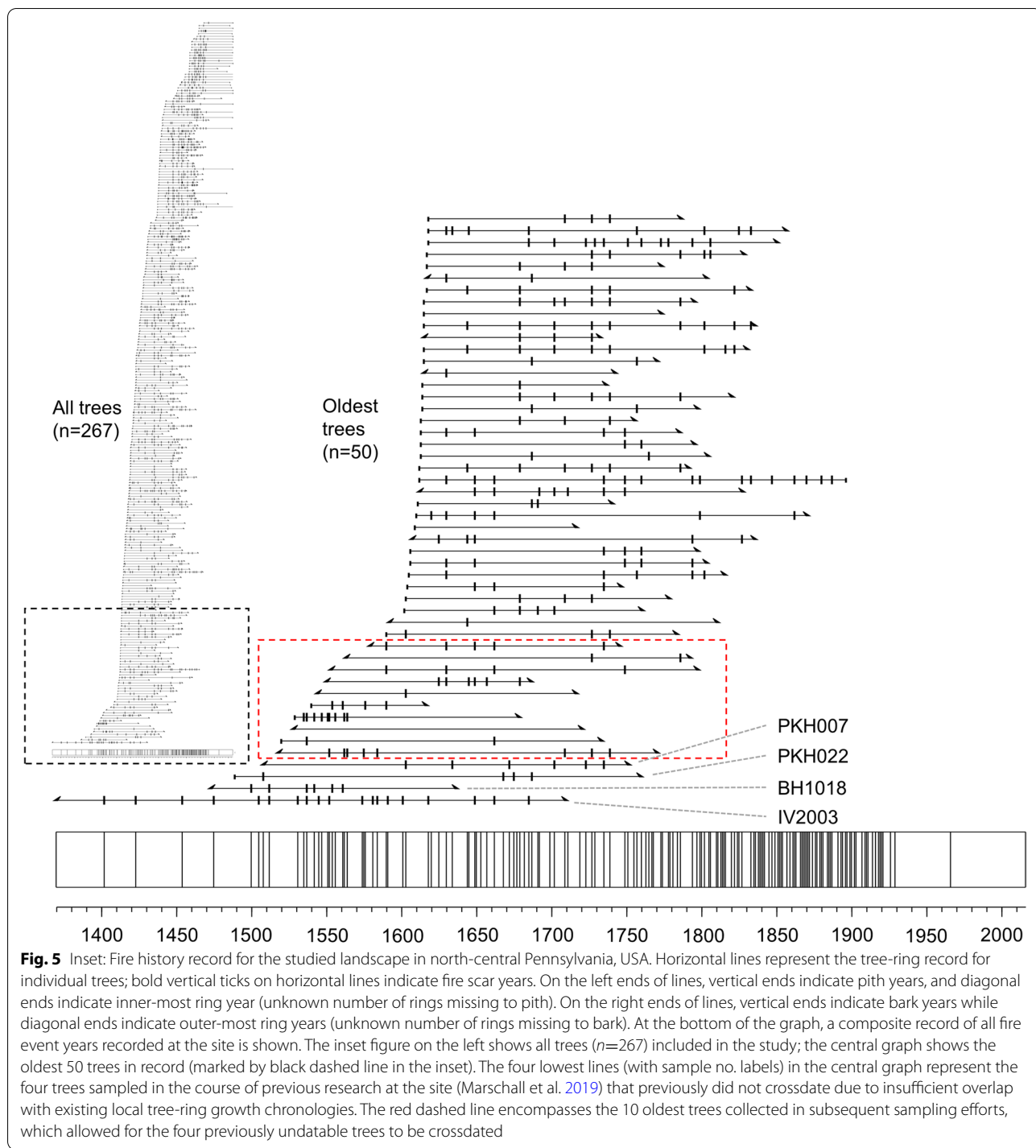
Fire regime characteristics
Landscape scale (entire period of analyses)
During the Pre-1915 time period (1370–1914), 1265 fire scars were identified representing 147 unique fire years. Sample depth and time period restrictions resulted in the exclusion from analyses of four fire years prior to 1500 (1402, 1423, 1454, 1475; all on the same tree (IV2003)), and eight fire years after 1914, resulting in a total of 143 fire years included in landscape-scale analyses. Fire intervals were negatively skewed during this period and all sub-periods (Fig. S1) and ranged from 1 to 19 years with MFI and WMI values of 2.9 and 2.6 years respectively (Table 2). LEI/UEI values were 0.7 and 5.6 years respectively. The percentage of trees scarred ranged from 0.5 to 64.1 ($\bar{x} = 10.9$), and was negatively skewed during this time period and all sub-periods (Fig. S2).

Landscape scale (by sub-periods)
Based on the landscape-scale composite record, fire frequency was steady through the Pre-1609 and 1609–1700 sub-periods (MFIs 4.1 and 4.2 years, respectively), increased slightly during the 1701–1784 sub-period (MFI = 3.5), and then greatly increased during the EAC sub-period (MFI = 1.9). Annual fire (i.e., fire interval = 1) was detected in all periods and the range of fire intervals steadily narrowed through time, from 1 to 19 years (Pre-1609) to 1 to 8 years during EAC sub-period. LEI/UEI values were similar during sub-periods prior to EAC, ranging from 0.7 to 1.2 (years) and 6.1 to 8.0 respectively. LEI was longer than 1 year only during the 1609–1700 and 1701–1784 periods, indicating these were the only periods in which annual fire was statistically not expected. During the EAC sub-period, LEI reduced to 0.6, and UEI shortened substantially (3.3 years) (Table 2).

The mean percentage of trees scarred was highest during the Pre-1609 sub-period (17.8%), and lowest during

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Fig. 5 Inset: Fire history record for the studied landscape in north-central Pennsylvania, USA. Horizontal lines represent the tree-ring record for individual trees; bold vertical ticks on horizontal lines indicate fire scar years. On the left ends of lines, vertical ends indicate pith years, and diagonal ends indicate inner-most ring year (unknown number of rings missing to pith). On the right ends of lines, vertical ends indicate bark years while diagonal ends indicate outer-most ring years (unknown number of rings missing to bark). At the bottom of the graph, a composite record of all fire event years recorded at the site is shown. The inset figure on the left shows all trees (*n*=267) included in the study; the central graph shows the oldest 50 trees in record (marked by black dashed line in the inset). The four lowest lines (with sample no. labels) in the central graph represent the four trees sampled in the course of previous research at the site (Marschall et al. 2019) that previously did not crossdate due to insufficient overlap with existing local tree-ring growth chronologies. The red dashed line encompasses the 10 oldest trees collected in subsequent sampling efforts, which allowed for the four previously undatable trees to be crossdated

the 1609–1700 sub-period (5.5%), after which it steadily increased during the 1701–1784 (7.9%) and EAC (11.0%) sub-periods (Table 2, Fig. 7), at which point this value was nearly equal to the average over the entire time period (1370–1914, 10.9%).

Landform scale (Pre-1609 sub-period)

For the sub-period analyzed at the landform spatial scale (Pre-1609), the earliest years recorded by trees at Bald, Big, and Park Hill landforms were 1370, 1473, and 1489 respectively, with corresponding earliest fire years
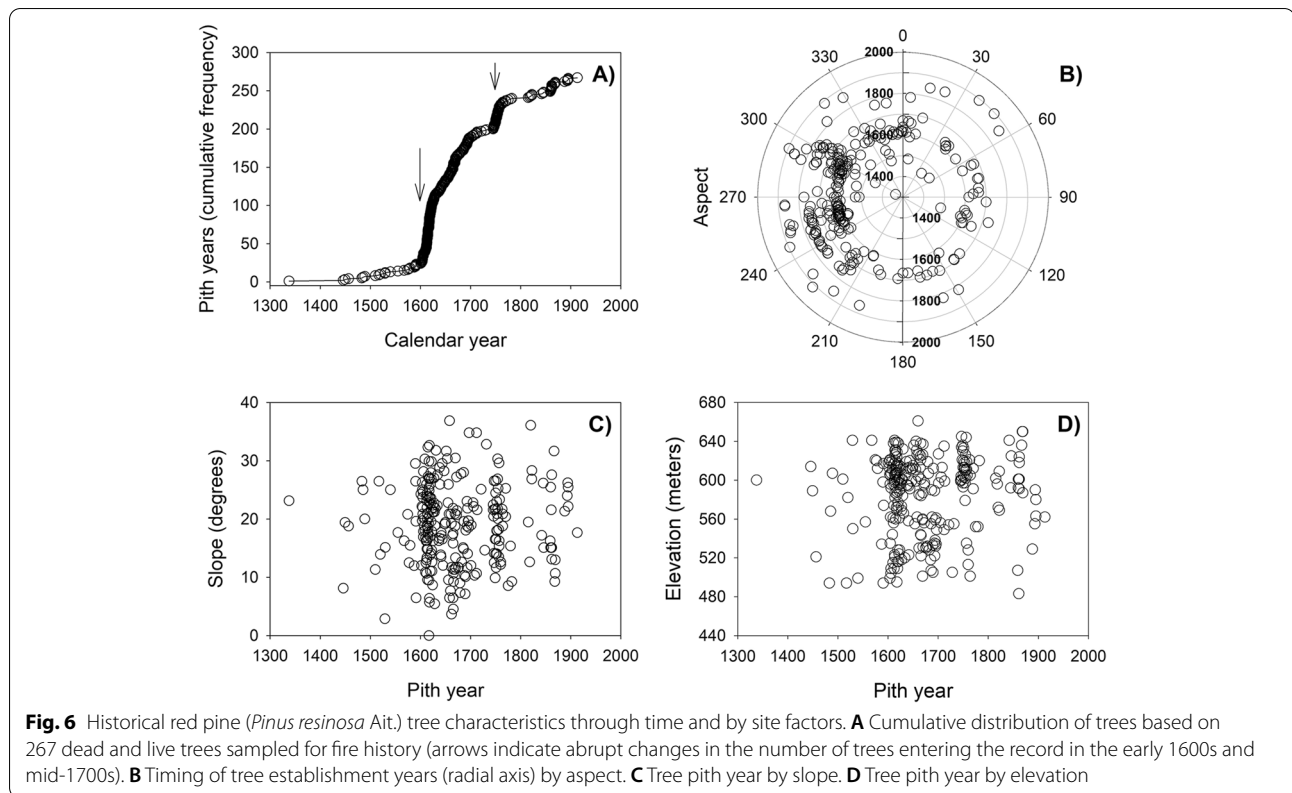
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Fig. 6 Historical red pine (*Pinus resinosa* Ait.) tree characteristics through time and by site factors. **A** Cumulative distribution of trees based on 267 dead and live trees sampled for fire history (arrows indicate abrupt changes in the number of trees entering the record in the early 1600s and mid-1700s). **B** Timing of tree establishment years (radial axis) by aspect. **C** Tree pith year by slope. **D** Tree pith year by elevation

Table 2 Fire frequency, scarring synchrony, seasonality, and tree establishment information for different cultural time periods. Statistics are provided for the entire period of record prior to 1915 and four sub-periods

Time period	1370–1914	1370–1608	1609–1700	1701–1784	1785–1914
Fire-regime statistics					
Fire years (*n*)	147	30	23	24	70
MFI[a] (years)	2.9	4.1	4.2	3.5	1.9
Range[a] (years)	1–19	1–19	1–15	1–10	1–8
WFI[a] (years)	2.6	3.3	3.7	3.2	1.7
LEI/UEI[a] (years)	0.7/5.6	0.9/8.0	1.2/7.6	1.2/6.1	0.6/3.3
Tree MFI[b] (*n*)	22.1 (199)	32.4 (26)	24.8 (104)	15.9 (49)	10.2 (20)
Scarred[a] (%)	10.9	17.8	5.5	7.9	11.0
Establishment (*n*)	267	38	150	52	27
Fire scar seasonality					
Scars (*n*)	1265	46	145	357	717
U (%)	40.8	50.0	48.3	40.6	38.8
D (%)	55.8	39.1	51.7	54.1	58.4
E (%)	1.3	6.5	0	1.40	1.3
M (%)	0.7	2.2	0	0.8	0.7
L (%)	0.9	2.2	0	2.80	0
A (%)	0.5	0	0	0	0.8
GSFY (%)	11.6	10.0	0	16.7	14.3

Fire years, number of unique fire years; *MFI*, mean fire interval; *Range*, range of fire interval length; *WFI*, Weibull median interval; *LEI/UEI*, lower/upper exceedance interval; *Tree MFI*, mean fire interval based on individual tree fire-scar chronologies, included in individual time periods based on pith year; *Scarred*, mean percentage of trees scarred during fire events (scarring synchrony); *Establishment*, number trees entering record (based on pith years); *Scars*, total number of fire scars; seasonality codes based on position within the tree-ring: *U*, fire scars with undeterminable seasonality; *D*, dormant; *E*, early earlywood; *M*, middle earlywood; *L*, late earlywood; *A*, latewood; *GSFY*, fire year in which at least one growing season fire scar (not dormant or unidentified) was identified; [a]calculated for time period with at least three trees recording, [b] calculated only for trees with three or more fire scars
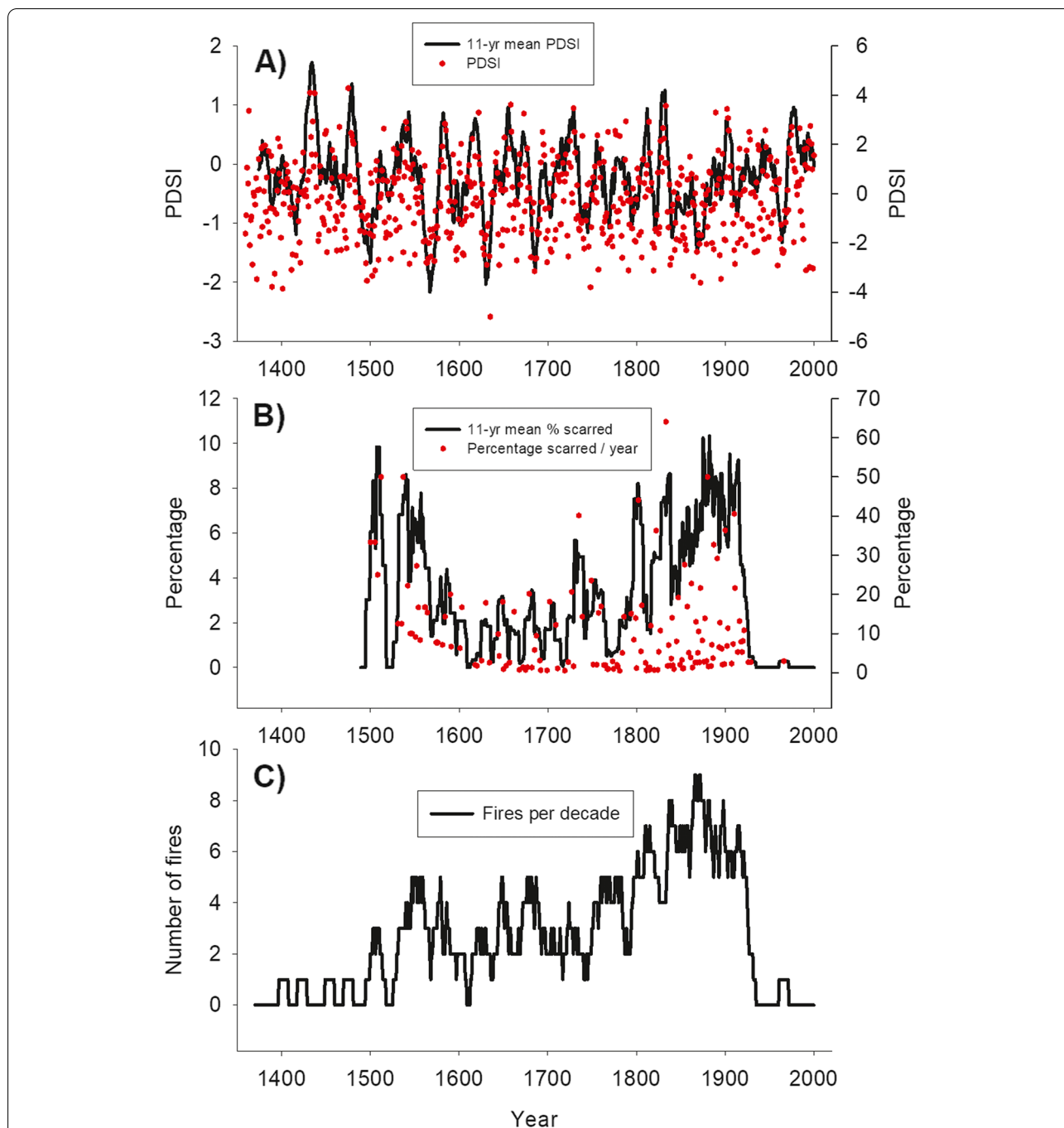
Fig. 7 Time series plots for drought and fire regime metrics for the entire time period recorded by red pine (*Pinus resinosa* Ait.) tree rings for the time period 1370–2016 across the entire study area. **A** 11-year moving mean and annual values for Palmer Drought Severity Index (PDSI, Cook et al. 2004) for the closest grid point (no. 254) in south-central New York. **B** 11-year moving mean and annual values for the percentage of trees recording scarred per fire year. **C** Number of fires detected per decade (11-year moving sum)

identified as 1402, 1500, and 1508 (Fig. 8). Twenty-three trees were recording at the landscape scale at the end of the Pre-1609 sub-period, and at that time the recording area for each landform (Bald, Big, Park Hills) was 7.1 km², 0.5 km², and 1.6 km² respectively (Table 3). During this

sub-period, Bald and Big Hills had 10 trees recording, and Park Hill had three (Table 3, Fig. 8). Trees located on Bald and Big Hills recorded 18 and 15 fire years respectively during the Pre-1609 sub-period, with only 2 fire years recorded at Park Hill. There were 26 fire years
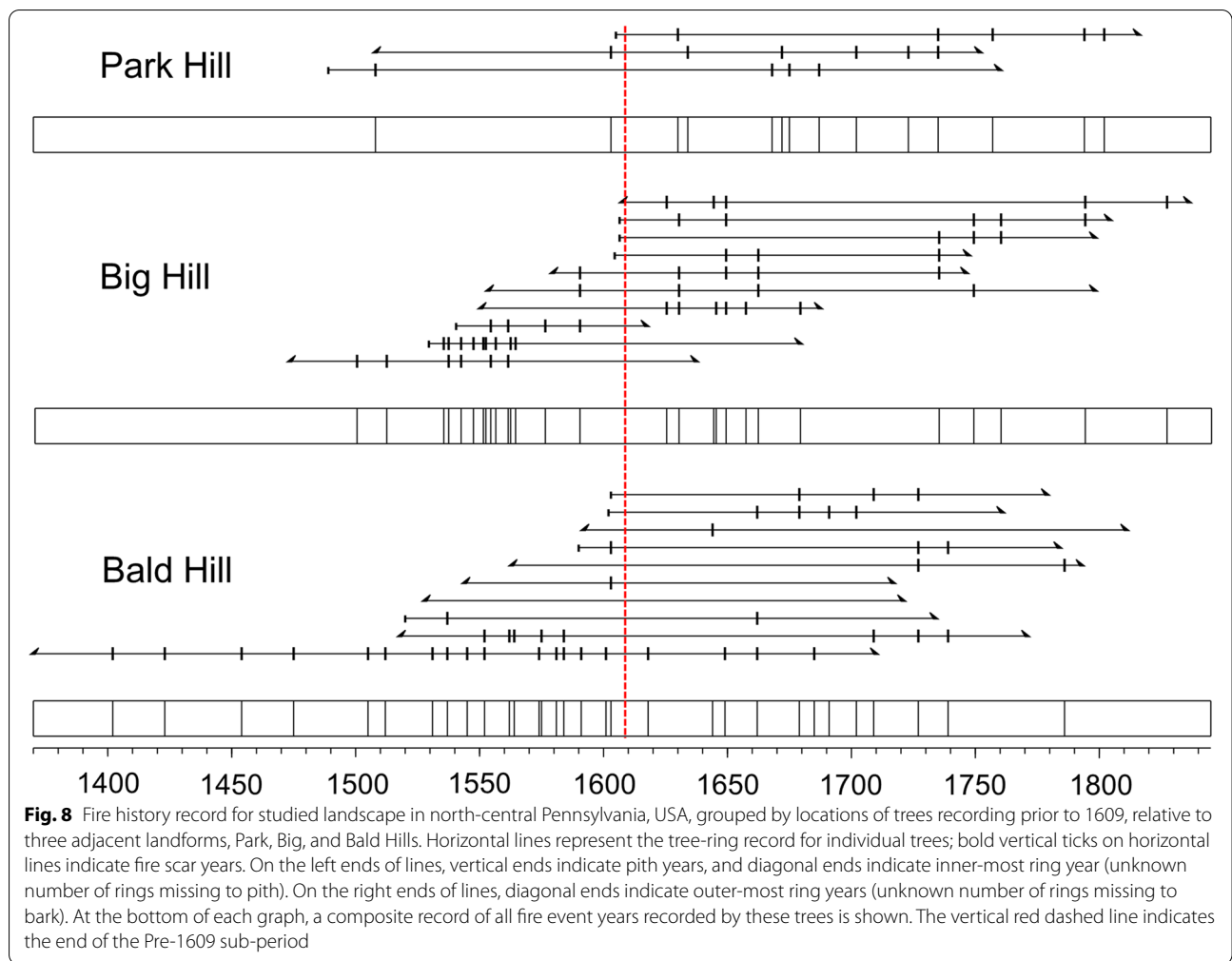
Fig. 8 Fire history record for studied landscape in north-central Pennsylvania, USA, grouped by locations of trees recording prior to 1609, relative to three adjacent landforms, Park, Big, and Bald Hills. Horizontal lines represent the tree-ring record for individual trees; bold vertical ticks on horizontal lines indicate fire scar years. On the left ends of lines, vertical ends indicate pith years, and diagonal ends indicate inner-most ring year (unknown number of rings missing to pith). On the right ends of lines, diagonal ends indicate outer-most ring years (unknown number of rings missing to bark). At the bottom of each graph, a composite record of all fire event years recorded by these trees is shown. The vertical red dashed line indicates the end of the Pre-1609 sub-period

Table 3 Fire frequency and scarring synchrony for trees recording prior to 1609, compiled by landform

Landform	Time span (years)	Site area (km^2)	No. trees recording	Fire years (*n*)	MFI (yearz)	Range (years)	LEI/UEI (years)	WFI (years)	Scarred[a] (%)
Park Hill	1489–1608	1.6	3	2	na	na	na	na	na
Big Hill	1473–1608	0.5	10	15	9.7	2–24	3.5/16.5	8.9	23.2
Bald Hill	1370–1608	7.1	10	18	11.7	1–31	2.4/21.5	9.0	32.7

Fire years, number of unique fire years; *MFI* mean fire interval (years), *Range* range of fire interval length (years), *WFI* Weibull median interval (years), *LEI/UEI* lower/upper exceedance interval, *Scarred* mean percentage of trees scarred during fire events (scarring synchrony); [a]calculated for time period with at least three trees recording

in the period of overlap between the three landforms (1490–1608), 76.9% (*n*=20) of which were only detected on one landform; the remainder of fire years (*n*=6) were detected on two landforms.

Fire frequency and scarring synchrony statistics were only calculated for Bald and Big Hills due to the low number of fires recorded at Park Hill. Fire intervals were negatively skewed at both landforms (Fig. S3), with intervals ranging from 1 to 31 and 2 to 24 years. MFI/WFI values were similar at the two landforms, 11.7/9.0 and 9.7/8.9 years at Bald and Big Hills respectively, and LEI/UEI values of 2.4/3.5 and 21.5/16.5 in the same order (Table 3). Values for the mean percentage of recording trees scarred were 32.7% and 23.2% at Bald and Big Hills respectively (Table 3), and both exhibited a negatively skewed distribution (Fig. S3).

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Individual tree fire-scar records (entire period of analyses)

At the individual tree scale, the number of scars recovered from individual trees was negatively skewed (Fig. S4), ranged from 0 to 19 ($\bar{x} = 5.0$), and the number of rings ranged from 70 to 340 ($\bar{x} = 165$). Tree MFI values ranged from 3.6 to 68.0 years ($\bar{x} = 22.1$ years) for trees with at least three scars ($n=199$), and their distribution was negatively skewed (Fig. S4).

Individual tree fire-scar records (by sub-periods)

The MFI of individual trees was positively correlated with landscape-scale MFI over time, except between the Pre-1609 and 1609–1700 sub-periods when landscape MFI remained nearly constant (4.1 and 4.2 years respectively), though Tree MFI was lower in the 1609–1700 sub-period (24.8 vs. 32.4 years). After 1700, Tree MFI steadily decreased along with landscape-scale MFI (Table 2).

Individual tree fire chronologies provide findings at a different spatial scale than those of site-composite records, allowing for additional inferences regarding fire regime characteristics (Fig. 5). For instance, the oldest tree in the record (IV2003, Fig. 4) not only contained the longest tree-ring series (340 years), but also the most fire scars ($n = 19$ (1402–1685), Tree MFI = 15.7) of all trees sampled. Four of these fire years (1402, 1423, 1454, 1475) occurred Pre-1492, resulting in an MFI calculated for that time period of only 24.3 years. Another exceptionally interesting tree, BHA006 (Fig. 2) recorded nine fires between 1535 and 1564, a time period for which very few fire scars have been recovered in the eastern USA, with a Tree MFI of 3.6 years (lowest value for all trees analyzed).

Fire seasonality

Seasonality was determined for 59.2% of fire scars, most of which were identified as dormant season, and was similar across time periods (see Table 2 for seasonality detailed by sub-period). During the Pre-1915 time period, 55.8% of fire scars occurred in the dormant season, and of the remaining scars, 1.3% occurred in the early earlywood, 0.7% in the middle earlywood, 0.9% in the late earlywood, and 0.5% in the latewood (the remaining portion of fire scar had unidentified seasonality). In total, 17 fire years (11.6%) contained at least one growing season fire scar (i.e., not dormant or unidentified) (Table 2). The only time sub-period with no growing season fire scars was the 1609–1700 sub-period (Table 2).

Fire and drought associations

During the Pre-1915 period, at the landscape scale, SEA indicated conditions were drier than statistically expected during the year of fire (lag = 0) for fire years in which at least two trees were scarred, and three years prior (lag = -3) for fire years for which at least 10% of

the recording trees were scarred. During the 1609–1700 sub-period, conditions were wetter than expected 6 years before fire years (lag = −6), and during the 1701–1784 sub-period, conditions were wetter than expected 3 years after fire events (lag = +3).

Fire records from Big and Bald Hills contained sufficient fire years (≥ 3) during the Pre-1609 time period to conduct SEA analyses. Drought conditions were drier than expected two and three years prior to fire years (lag = −2 and −3) at Bald Hill; no other associations with drought were detected at the landform scale.

Discussion

This study resulted in the longest fire-scar record in eastern North America and offers unique foundational ecological information regarding pre-Columbian fire regime characteristics of Northeastern fire-adapted forest communities. At multiple spatial scales (individual trees, landforms, and landscape), fire scars provided physical evidence of frequent, recurrent fires prior to the major disruptions associated with sustained contact between Native Americans and Euro-American colonizers. Beyond fire scars, the spatial and temporal extent of the red pine tree-ring record provides physical evidence that the fire-dependent red pine-dominated ecotype was historically a more important component of the forest community than today, and further implicates frequent fire as a deep-time influence on vegetation communities in the Northeast.

There is great interest regarding the historical importance of fire in forests of the Northeast. Conceptual ideas of ecology and historical human land use in the Northeast, the relative controls of Native American fire-use versus climate on fire regimes, and the appropriateness of fire as a modern-day natural community management tool are all influenced by understanding the role of fire prior to Euro-American colonization (Abrams and Nowacki 2021; Leonard et al. 2020; Oswald et al. 2020). The findings documented in this study provide indisputable physical evidence that fire was an integral ecological component in this landscape prior to the impacts of colonization, and that the cessation of fire in the twentieth century is a major departure from the preceding 500+ years (Fig. 5). Because fires of low severity or small extent can go undetected by fire-scar studies (Farris et al. 2010), it is likely that the historical fire frequency was even more frequent than reported here.

During the Pre-1609 sub-period, fire occurred frequently at the landscape scale (approximately every four years) and occurred throughout the study area. Calculated as a mean per sub-period (MFI), fire frequency remained fairly stable throughout the sub-periods preceding EAC, and then, similar as reported in other related

studies in the region (e.g., Abadir et al. 2019; Brose et al. 2013, 2015; Marschall et al. 2016; Stambaugh et al. 2018), increased substantially with the commencement of EAC (Table 2, Fig. 7). This pattern of increased fire frequency coincident with EAC has also been observed in other eastern US regions (e.g., Abadir et al. 2022; Guyette et al. 2002; Hutchinson et al. 2019; Stambaugh et al. 2020). Our findings both support and diverge from the conceptual model of Brose et al. (2001) which posits that Appalachian fire regimes consisted of periodic low-intensity fires prior to EAC and settlement, after which high-severity, stand-replacing fires dominated. In support, we found that fire frequency measured as a mean calculated per time period (i.e., MFI) at the landscape scale varied very little among the different pre-EAC periods (i.e., MFI range 3.5–4.2 years), and then greatly increased post-EAC (1.9 years) (Table 2). Our fire frequency findings diverge, however, when considered at the decadal scale rather than by period mean, as we found high variability in fire frequency (i.e., not periodic) during the pre-EAC periods (including annual fire and decades without fire at landform and landscape spatial scales) as opposed to the relatively constant rate of fire occurrence we observed after EAC (Fig. 7).

Fire frequency calculated at the landform scale (Bald and Big Hills) for the Pre-1609 sub-period (MFIs: 11.7 and 9.7 years respectively, Table 3) was very similar to MFI values reported previously for the same landforms for the period of 1620–1794 (MFIs: 9.8 and 9.7 years), though the numbers of samples and the spatial extent included by sample locations were lower (Marschall et al. 2019). Because fire frequency increases with spatial extent following power-law behavior (Falk et al. 2007; Malamud et al. 2005; Marschall et al. 2019), we interpret the Pre-1609 landform-scale MFI values reported here likely to be conservative. Further, though the quantity and distribution of sampled trees recording in the Pre-1609 sub-period did not allow for stand-scale (~1 km^2) fire frequency analyses, based on the relationship between spatial extent and fire frequency, it is likely that the stand-level fire frequencies reported previously here for the time period of 1620–1794 (Marschall et al. 2019; MFIs 14.5 to 18.2 years) are also conservative estimates for stand-level fire frequencies in the Pre-1609 sub-period.

We observed considerable differences in scarring synchrony (i.e., mean percentage of trees scarred per fire year) at the landscape scale among the pre-EAC sub-periods. Fire-scarring synchrony has been included in fire-scar based fire regime reconstructions to describe fire extent (Farris et al. 2010), within fire perimeter scarring variation (e.g., degree of scarring, Marschall et al. 2019), and as a scalar of fire severity (Guyette et al. 2016),

and offers a more nuanced description of fire activity across a study area than fire frequency alone. Our data show relatively high synchrony across the landscape in the Pre-1609 sub-period (Fig. 7B), followed by the lowest synchrony in the entire record during the 1609–1700 sub-period. Though sample depth is lower during the Pre-1609 sub-period (Fig. 5), the fire years with high synchrony values (e.g., 1512, 1537, 1552) were detected on separate landforms (i.e., Big Hill and Bald Hill), suggesting these Pre-1609 sub-period fires were more widespread than most in the record (Marschall et al. 2019).

In addition to the lowest levels of landscape scale fire frequency and scarring synchrony, and increased uniformity in the season of fire (Table 2), we documented an abrupt increase in red pine establishment during the 1609–1700 sub-period (Table 2, Fig. 6), suggesting it was a unique period of reduced and irregular fire activity, and increased red pine regeneration, relative to all other sub-periods reported here. Successful regeneration of red pine and other eastern North American hard pines (subgenus *Diploxylon* Koehne: e.g., pitch pine, Table Mountain pine (*Pinus pungens* Lamb)) is dependent on periods of frequent fire (Stambaugh et al. 2019) associated with periods of less frequent fire of sufficient length to allow for seedling survival and recruitment to the forest overstory. We interpret these records to indicate that prior to sustained Euro-American colonization influence, red pine regenerated continuously across the landscape in uneven-aged stands due to recurring frequent fires with high spatial heterogeneity (Marschall et al. 2019). Later, circa 1600, increased and widespread red pine regeneration was successfully established and recruited into the overstory as fire frequency and extent decreased, which likely resulted from changes to Seneca population demographics and culture caused by European disease and warfare (Abrams and Nowacki 2021; Cronon 1983; Richter 1983). This large cohort of red pine was likely able to establish and persist up to the logging era (mid-to-late 1800s) due to recurring, spatially heterogeneous fires in the interim (Marschall et al. 2019). This phenomenon of increased tree establishment and forest density directly after Native American depopulation has been observed elsewhere in the central Appalachian Mountain region (de Graauw and Hessl 2020) and supports the hypothesis that the open forest communities dominated by pyrophyllic tree species encountered by early Euro-American colonizers (Hanberry et al. 2020; Thomas-Van Gundy and Nowacki 2013) were the result of long-term Native American land use and management practices.

The fire-scar chronology presented in this study suggests that fire has long played an important role in the development of the vegetation communities found here and at similar sites in the Northeast. The ubiquitous

spatial distribution and ages of remnant red pine wood (i.e., stumps, snags) found here, especially when compared to the scarcity and restricted distribution of live red pine (nearly exclusive to west-facing aspects, Fig. 6B), indicate that the species was historically much more prevalent than in modern times. Physiological traits and seedbed requirements of red pine (Hauser 2008), its association with frequent fire regimes across varied North American ecosystems (Margolis et al. n.d), and the positive relationship between successful regeneration and frequent fire (Stambaugh et al. 2019) indicate that frequent, recurrent fire existed here long before our tree-ring record begins in the 1300s.

Historical observations of fire-maintained, open-canopy pine forest communities (i.e., "pine plains" (Murray 1908)) are in stark contrast to the dense hardwood forests that dominate the region today. However, such historical descriptions do comport with what would be expected under the frequent historical fire regime documented by our fire-scar chronology, as well as the density and broad distribution of red pine remnants in our study landscape. In today's north-central Pennsylvania forests, native red pine is exceedingly scarce. Prior to this and other nearby red pine fire history studies (Brose et al. 2013, 2015), many professional forest managers of the region were generally unaware of its presence, and questions remained whether the species was native to the region or only existed as trees planted during reforestation efforts in the 1930s to 1940s (pers. communication with multiple regional forest and habitat management professionals from Pennsylvania Game Commission and Pennsylvania Bureau of Forestry). In addition, red pine is not included as a component in Pennsylvania Natural Heritage Program's plant community classifications (Zimmerman et al. 2012), nor is the species referenced in management guides for the Pennsylvania Game Commission, who manage most of the land included in this study. Improved understanding of the historical presence and distribution of red pine, provided by studies such as this, is critical to the restoration and perpetuation of these ecosystems.

Evidence suggests that historical fire regimes in Pennsylvania were largely driven by anthropogenic ignitions. Lightning-ignited wildfires are very rare in Pennsylvania, as most lightning occurs during the humid summer and is typically accompanied by precipitation, and historical fire regimes closely track changes in human occupancy and culture (Brose et al. 2013, 2015; Marschall et al. 2016; Stambaugh et al. 2018). We did not find a statistically significant association between drought and fire occurrence at the landscape scale, though we did find fire years in which at least two trees and at least 10% of recording trees were scarred, to be associated with drought. These are similar to findings by Marschall et al. (2019) in which only fire years with elevated values of fire extent or scarring synchrony for the time period of 1620–1914 were associated with drought. We interpret these results to provide further evidence that fire occurrence was not historically dependent on drought conditions, though fire extent and scarring synchrony were.

Historically, frequent and widespread fires promoted more open forest communities (such as woodlands or savannas) in the eastern USA than what currently exists (Hanberry and Abrams 2018; Hanberry et al. 2020). These fire-maintained open conditions facilitated regeneration conditions favorable to fire-dependent tree species (e.g., red pine) and their associated robust ground-flora vegetation communities (Nowacki and Abrams 2008). During field work conducted for this research, we observed no evidence of any red pine trees regenerating since the beginning of fire exclusion practices circa 1915. This complete lack of red pine regeneration suggests that, without human intervention, this fire-adapted vegetation community will continue to decline and eventually will no longer exist in this landscape.

Due to the lack of fire since the early twentieth century, native red pine forests, like other hard pine communities in the eastern USA, are succeeding to mesophytic (mostly hardwood) forests (Cook et al. 1952; Hanberry et al. 2020; Nowacki and Abrams 2008). Additionally, as forest density increases due to lack of fire, hard pine forest communities are increasingly vulnerable to outbreaks of southern pine beetles (*Dendroctonus frontalis*), which are expanding northward from the southeastern USA as climate change creates more favorable conditions in the Northeast (Dodds et al. 2018). In addition to promoting increased resiliency to pests and climate change, using prescribed fire to maintain fire-adapted hard pine ecosystems promotes high biodiversity values and critical habitat for many species of conservation concern (Harper et al. 2019).

The abundance and spatial extent of red pine remnants found in this study area, along with the temporally consistent record of frequent fire, definitively show that red pine and wildland fire were both important components in this landscape in pre-Columbian times, and support the use of prescribed fire as an appropriate and necessary management tool for the conservation of red pine. Landscapes such as the one studied here, consisting primarily of publicly owned and managed lands where living, native red pine trees are present to serve as a seed source, offer a unique and compelling opportunity to restore and conserve this rare and dwindling natural community.

Conclusions

Fire-scar and tree-ring chronologies developed from red pine trees spatially distributed across this studied landscape indicate that frequent fire was an important ecosystem process in this landscape in pre-Columbian times. The current period of fire exclusion is unprecedented in the 500+ years prior to the advent of modern fire-exclusion practices in 1915, and the conservation of red pine vegetation communities will require fire as part of their management to perpetuate and to sustain associated flora and fauna species of conservation concern.

Our findings indicate that iterative, intensive, and adaptive sampling of remnant wood can provide a framework for lengthening fire-scar records at other sites in the eastern USA where remnant wood exists. We exhaustively sampled in this landscape over a 3.5-year time period with primary research goals building over time, along with a progressing ability to successfully target oldest wood age-classes at this site. That such efforts bore fire scars of exceptional age suggests that similarly intensive and targeted sampling elsewhere in red pine communities may also produce deeper-time fire-scar chronologies (e.g., pre-Columbian). The fire-scar record reported here represents a single element of a complicated story regarding the historical ecology of fire-adapted communities in the eastern USA. Efforts to restore and sustain these declining and disappearing natural communities will benefit from increased recognition of, and understanding from, diverse information sources such as Indigenous Traditional Ecological Knowledge (ITEK), additional tree-ring data, and other natural archives (e.g., soil seedbanks, pollen/charcoal sedimentary records). We hope that the physical evidence of historical fires reported here will encourage and support such efforts.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-022-00135-6.

Additional file 1: Figure S1. Histograms of fire intervals compiled at landscape scale for different time sub-periods: A) Pre-1915, B) Pre-1609, C) 1701-1784, D) 1609-1700, E) 1784-1914.

Additional file 2: Figure S2. Histograms of percentage of trees recording fire-scarred at landscape scale for different time sub-periods: A) Pre-1915, B) Pre-1609, C) 1701-1784, D) 1609-1700, E) 1784-1914.

Additional file 3: Figure S3. Histograms of fire return intervals and percentage of trees recording that were scarred for the time sub-period, Pre-1609: A) fire return intervals based on the composite fire scar record for samples located on Big Hill. B) fire return intervals based on the composite fire scar record for samples located on Bald Hill. C) percentage of trees recording located on Big Hill that were fire scarred. D) percentage of trees recording located on Bald Hill that were fire scarred.

Additional file 4: Figure S4. Histograms of A) number of fire scars identified per tree sampled, and B) mean fire interval calculated for individual trees with at least three fire years recorded (*n*=199).

Availability of data and materials

The datasets used or analyzed during the current study will be made available upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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