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Successful hard pine regeneration and survival through repeated burning: An applied historical ecology approach

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ABSTRACT

Forest inventories commonly report fire-adapted pine populations severely reduced from pre-EuroAmerican times due to the combined effects of past land uses and altered fire regimes. Relatively little information exists about the fire ecology and management of hard pine ecosystems in the northeastern U.S. The objective of this study was to determine what burning frequencies best promote regeneration and recruitment of three hard pine species native to the northeastern U.S. We used data from dendrochronological fire history studies to derive historical fire years, pine regeneration years, and individual tree survival information. For all tree species, pith calendar years ranged from 1530 to 1932 with the majority of regeneration occurring prior to 1754 (the earliest dates of EuroAmerican settlement). The number of years from fire occurrence at a site to regeneration (pith year) ranged from 0 (i.e., regeneration occurred in year of fire, n = 9) to 130 with a median of 8 years. Frequency distributions of regeneration following fire were similarly shaped across species, all being strongly negatively skewed (i.e., most regeneration occurred soon after fires) and increasing abruptly (> 100% increase) from 0 to 1 year since fire and then declining following a negative exponential curve. The number of years from regeneration to the next fire ranged from 0 to 172 years with a median of 14 years. Frequency distributions of hard pine survival were negatively skewed, with the exception of red pine. Overall, these data suggest that these species exhibit relatively high regeneration in the years immediately following fire events and a subsequent decrease with time since fire. Although other factors may affect the regeneration of pine following fire, it appears that significant statistical relationships can be established and used to develop effective fire frequency guidelines for successful hard pine regeneration.

1. Introduction

Throughout eastern North America, fire-adapted pines occur in diverse climatic and physiographic settings from hot subtropical coastal plains of the southeastern U.S. through the warm/cool continental climes of the mountainous Appalachians to the cold boreal forests of glaciated Canada (Wright and Bailey, 1982; Keeley and Zedler, 1998). Today, these pines are icons of historically fire-dependent and fire-maintained ecosystems (Brose and Waldrop, 2006; Stambaugh et al., 2017). Fire management and research has long occurred for some pine species, most notably longleaf pine (*Pinus palustris*) (Wahlenberg, 1946), slash pine (*P. elliottii*) (Heyward, 1939), and jack pine (*P. banksiana*) (Eyre, 1938; Eyre and LeBarren, 1944). However, the fire ecology is comparably less well understood for other species and there is increasing need for information to fill species and geographical voids (USDA Forest Service, 2015; Anderson et al., 2016; Lafon et al., 2017).

Pre-EuroAmerican settlement forests with fire-adapted pines were extensive in the central Appalachians and Lake States regions (Whitney, 1990; Abrams and Ruffner, 1995; Abrams and McCay, 1996), extending northward into eastern Canada (Bergeron et al., 2001). In some cases, these ecosystems represent unique conservation opportunities such as restoring fire-adapted and early successional species and habitats (Radeloff et al., 2000; Lampereur, 2013) and maintaining species and genetic diversity (Gibson and Hamrick, 1991). Little information exists

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about the fire ecology and management of pine ecosystems in the central Appalachians in particular – a region where fires now occur infrequently compared to the past (Abrams and Nowacki, 1992; Hardy et al., 2001; Guyette et al., 2012).

Most of the hard pines (subgenus Pinus) in the central Appalachians and northward are considered to occur in fire-prone environments (Schwilk and Ackerly, 2001; Keeley, 2012) and be fire-adapted: shortleaf pine (*Pinus echinata*; Carey, 1992), pitch pine (*P. rigida*; Gucker, 2007), red pine (*P. resinosa*; Hauser, 2008), jack pine (*P. banksiana;* Carey, 1993), and Table Mountain pine (TMP) (*P. pungens*; Reeves, 2007). Fire-adapted characteristics among these pines include enhanced regeneration in early successional conditions (exposed mineral soil, reduced tree competition, high light conditions), ability to sprout from axillary buds and/or stems (pitch, shortleaf, and TMP), relatively thick bark, high fire-scar tolerance, and cone serotiny, among others. Moreover, some encourage fire though the retention of low dead branches and production of volatile foliage (jack, pitch, and TMP). Historical fire regimes associated with these species ranged from frequent to infrequent, from surface to stand-replacing events (Heinselman, 1981; Wright and Bailey, 1982), from localized to regional in extent (Drobyshev, 2008; Stambaugh et al., 2018), and originated from both anthropogenic and lightning ignitions (Welch and Waldrop, 2001; Muzika et al., 2015). Historical observations by Chapman (1952) and Goodlett (1954) are corroborated by forest inventories that show the decrease of fire-dependent pine populations since EuroAmerican settlement due to the combined effects of past land-use practices and fire regime alterations (Ahlgren, 1974; Nowacki and Abrams, 1992; Oswalt, 2012). In Pennsylvania, Thompson et al. (2013) recorded an 11% pine decrease within the Central Appalachian Broadleaf Forest – Coniferous Forest Province. Similarly, a wholesale decline in pine was reported across all physiographic units studied by Abrams and Ruffner (1995). Hard pines in the central Appalachians often occur in limited groups, in co-dominant to suppressed canopy positions (Oliver and Larson, 1996) and with little regeneration indicating future succession towards further population declines (Mann et al., 1994; Fraver and Palik, 2012).

For fire-adapted species and ecosystems, there is no surrogate management treatment that fully mimics the effects of fire (e.g., heat, litter and vegetation consumption) (Bergeron et al., 2001). Prescribed fire management of fuels and vegetation often focuses on fire frequency as the primary fire regime factor (Peterson and Reich, 2001). Fire frequency is also a primary component of fire management and planning including long-term optimization, capacity, and budget needs (Rachmawati et al., 2015). Little information is available describing schedules of burning that best promote successful pine regeneration (Stambaugh et al., 2007). Here, we use the term 'regeneration' to describe the general process of accumulating new trees. Regeneration relies on both establishment (i.e., the process of initiating new trees) and recruitment (the process related to survival and ingrowth). In northern conifer forests, peaks in hard pine regeneration are not random, but often occur when specific site conditions (e.g., following fire; Bergeron and Brisson, 1994; Fraver and Palik, 2012) and/or optimal climate conditions exist (Kullman, 1986). Pine regeneration is strongly linked to the timing of disturbance events because conditions needed for regeneration are often met within a few months of dispersal and seeds lying on the ground have low survival after the first growing season due to predation and loss of viability (Keeley and Zedler, 1998). Though frequent fire may encourage regeneration, it can also cause mortality during early developmental stages. Therefore, there is a need for further examination of species-specific responses to fire frequency and how fire frequency is associated with regeneration and recruitment success.

The objective of this study was to determine burning frequencies that best promote regeneration and recruitment of fire-adapted pines. We used an approach to analyzing historical fire and tree characteristics following the methods of Stambaugh et al. (2007). We considered three pine species widely distributed throughout the central Appalachians and beyond. Through this retrospective analysis, which encompasses multiple time periods, cultural fire uses, fire event types and characteristics, and climate conditions, we hope to provide a synthesis of fire frequency information that can be used to guide hard pine fire management and perhaps circumvent the need for fire frequency experiments that require long time periods.

2. Methods

For this analysis, we utilized a database of pine tree-ring records which provided regeneration years (pith dates), historical fire event years, and information on tree survival. Fire scar and regeneration dates represented absolute calendar years derived using standard dendrochronological dating methods (Stokes and Smiley, 1968). Trees within the database consisted of those that grew at different times during the last four centuries and that survived repeated fires of varying severities. Conditions of trees that died and have since decomposed are unknown. Datasets came from 12 fire scar history sites across an approximately 65,000 km^2 area in three ecological provinces of central Pennsylvania (Brose et al., 2013; Marschall et al., 2016; Stambaugh et al., 2018) (Fig. 1). Each study site, approximately 1 km^2 in area, consisted of a collection of 28 to 58 living and remnant (e.g., stumps, snags) pine trees sampled for fire scars. Trees were selected opportunistically in an attempt to maximize time span coverage, range of tree sizes, and fire scarring. Samples consisted of tree cross-sections cut near ground-level and, in some cases, at multiple levels depending on wood decay and fire scarring conditions.

Fire event, tree regeneration, and tree survival data were developed by study site. Sites varied in many characteristics such as site conditions (e.g., soils, aspects, slope), site histories (e.g., land uses), and stand conditions (e.g., stand ages, growth rates, tree sizes). We feel that data from many different sites is a strength of this study in that any significant relationships that associate fire to tree regeneration and survival must emerge regardless of these other conditions.

For each tree at a site, data included: pith (i.e., establishment) year, number of years from pith to previous fire at the site, and number of years from pith to next fire at the site (Fig. 2). Pith dates reflected the first year of growth of the stem. Due to the sprouting ability of pitch, Table Mountain, and shortleaf pines, it is not known whether these stems initiated from seedlings or sprouts. When the pith was missing, pith year was estimated by dividing the distance to the pith (determined using a pith indicator; Speer, 2012) by the average ring-width

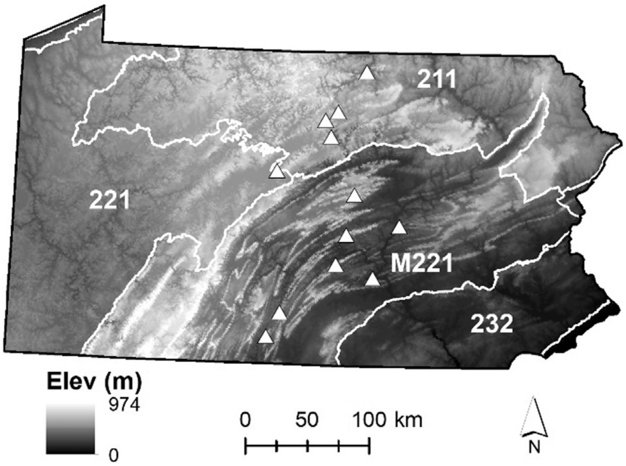

Fig. 1. Elevation map of Pennsylvania showing locations of the twelve study sites (white triangles) within Ecological Provinces (Cleland et al., 2007). Province codes are: 211 = Northeastern Mixed Forest, 221 = Eastern Broadleaf Forest, M221 = Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow (also shown, 232 = Outer Coastal Plain Mixed Forest).

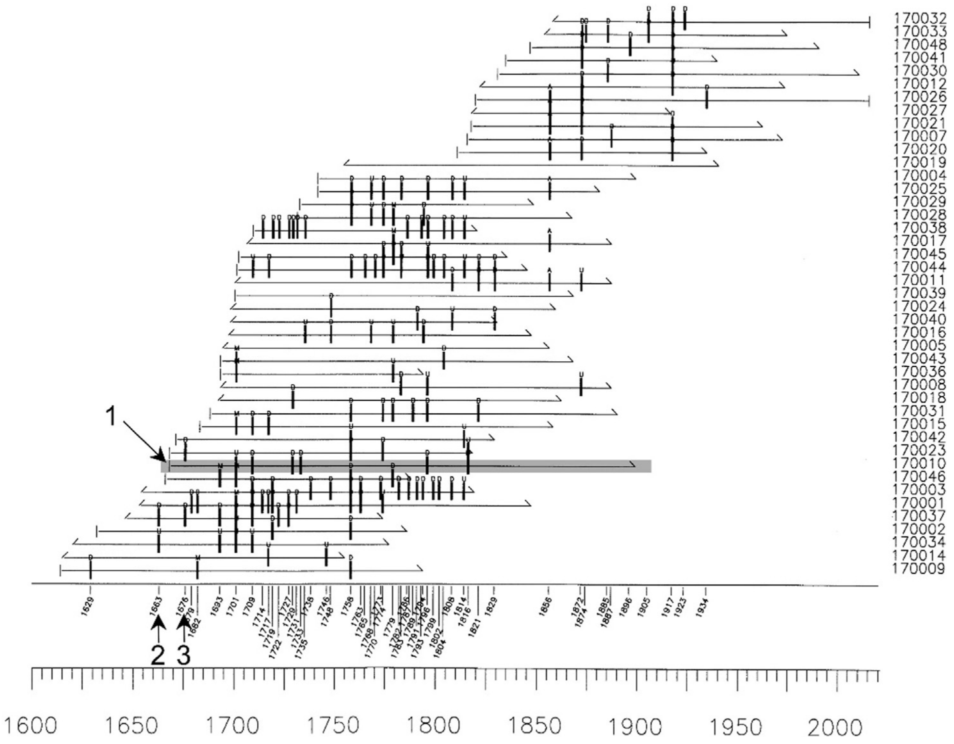

Fig. 2. Example of site-level fire scar history data and chart from State Gameland 170 (Stambaugh et al., 2018), one of twelve sites used in the historical fire and pine regeneration and survival analysis (see Brose et al., 2013, Marschall et al., 2016, and Stambaugh et al., 2018 for all charts). On this chart, horizontal lines represent the periods of 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 while diagonal ends indicate inner ring year (rings missing to center). On the right ends of lines, vertical ends indicate bark years while diagonal ends indicate outer ring years (rings missing to bark). A composite of all fire years at the site is given at the bottom of charts. The highlighted sample provides an example of the individual tree data: (1) pith year, (2) number of years from fire to pith (i.e., regeneration), and (3) number of years from pith to next fire scar at the site.

of the three innermost rings. In cases where multiple samples were available from the same tree, we utilized the one closest to the ground. Through this process, data were obtained from a total of 550 trees of which 187 were pitch pine (6 sites), 286 were red pine (4 sites), 31 were TMP (1 site), and 46 were mixed-pines (1 site). Mixed pines represented sites where pitch, Table Mountain, and shortleaf pines co-occur, but species of remnant wood were not differentiated.

Data analyses were conducted by species to limit the influence of variability among species in fire-adapted traits and growing conditions. Frequency distributions of pith years were constructed using decadal bins to inspect temporal patterns in tree regeneration. Additionally, frequency distributions were constructed to characterize the relationship between a) years from site-level fire to tree-level regeneration, and b) years from individual tree regeneration to next fire at the site (i.e., survival). Quantiles were used to further stratify and describe proportions of trees regenerating and surviving following fire events. We fit empirical distribution functions (EDFs) to 'years from fire to regeneration' and 'years from regeneration to next fire', and tested model goodness-of-fit for lognormal, Weibull, and gamma distributions. EDFs were tapered to 30-year periods for both 'years from fire to regeneration' and 'years from regeneration to next fire'. Goodness-of-fit test statistics included Kolmogorov-Smirnov (K-S), Cramer-von Mises, and Anderson-Darling which were considered significant at $p > 0.10$. Significant models for regeneration and survival may improve predictions in future studies to model tree regeneration and disturbance dynamics (e.g., simulation, prediction). All analyses were performed using SAS software v.9.4 (SAS Institute Inc., Cary, NC, USA). For 'years from fire to regeneration' and 'years from regeneration to next fire', thresholds (θ) < 0 were iteratively attempted to determine which model maximized goodness-of-fit significance. Negative thresholds produced distributions within the range of data (0–30 years) that were consistent with the fire ecology of pine regeneration given that little to no regeneration occurs during the calendar year of the fire (i.e., year = 0) because new seedlings are vulnerable to mortality by fire. Although certain hard pines can resprout after death of the shoot, germinants/first year seedlings have low sprouting potential and survival in the year of the fire (Garren, 1943; Stambaugh et al., 2007).

3. Results

For all tree species, pith calendar years ranged from 1530 to 1932 with an average year of 1711. For all species, 71% of the regeneration occurred prior to 1754 (the earliest dates of EuroAmerican settlement) and 8% occurred in the decades following the beginning of expansive industrialized logging circa 1850 (Stambaugh et al., 2018). Frequency of pitch and red pine regeneration was negatively skewed towards earlier years with a mode of 1668 and 1614, respectively (Fig. 3) while frequency of TMP and mixed-pines were positively skewed to normal. For all species, an abrupt increase in regeneration appeared to occur at approximately 1580–1600. From the years 1600–1900, regeneration was lowest in the decades of 1780, 1790, 1850, 1870, and 1880.

A total of 414 trees had data on fires at the site prior to regeneration (Fig. 4). The number of years from fire to regeneration (pith year) ranged from 0 (i.e., regeneration occurred in year of fire, n = 9) to 130 with a median of 8 years. Frequency distributions of regeneration were similarly shaped across species, all being strongly negatively skewed (i.e., most regeneration occurred soon after fires) and increasing abruptly (> 100% increase) from 0 to 1 year since fire and then declining following a negative exponential (Table 1, Fig. 4) . The composite of regeneration for all species showed highest amounts of regeneration in the first few years following fires.

A total of 540 trees had data on years from regeneration to the next fire at the site (Fig. 5). The number of years from regeneration to the next fire ranged from 0 to 172 years with a median of 14 years. Frequency distributions of survival were negatively skewed, with the exception of red pine (Fig. 5). Red pine survival was equally distributed across years from regeneration to the next fire and therefore could not be fit with an EDF (Table 1).

Pitch pine was the only species with regeneration in the year of a fire. For both pitch pine and mixed pine, regeneration was highest one year post-fire and then declined negative-exponentially with time since fire. Based on quantiles, 50% of all pitch pines regenerated within the first 5 years of a fire and 75% regenerated within 11 years. Only 1% of pitch pines regenerated at > 20 years following a fire. In terms of survival, 50% of pitch pines were found to have survived a fire within five

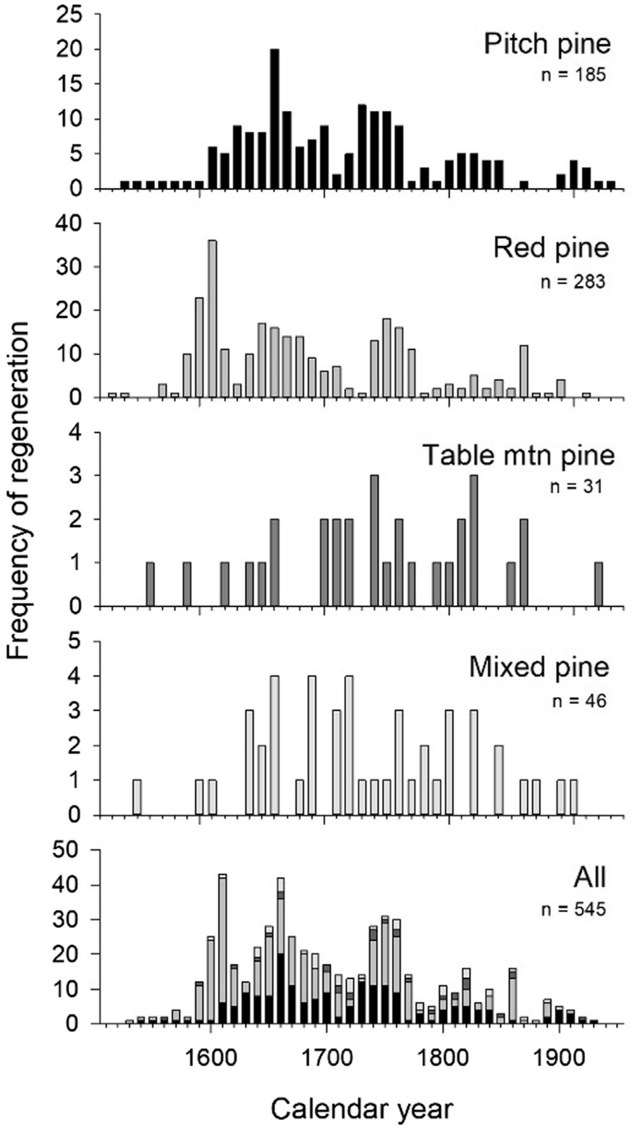

Fig. 3. Frequency distributions of pith dates of hard pines since year 1520. Note y-axis scale differences for species.

years of their regeneration.

Red pine, TMP, and mixed-pine regeneration was absent in the year of fires. Regeneration was highest for red pine and TMP at 8 and 5 years post-fire, respectively. Mixed pines had a more strongly negatively skewed distribution and regeneration limited to the first ten years following fires (Fig. 4). For red pine, 50% of trees regenerated within the first 11 years of a fire and 75% within the first 20 years. Fifty percent of red pines showed to have survived a fire within 21 years of their establishment. Red pine was the only species whose survival distribution did not fit any EDF (Fig. 5). For TMP, 50% of trees regenerated within the first 7 years following fire and 75% occurred within the first 11 years. Fifty percent of TMPs showed to have survived a fire within 7 years of their regeneration.

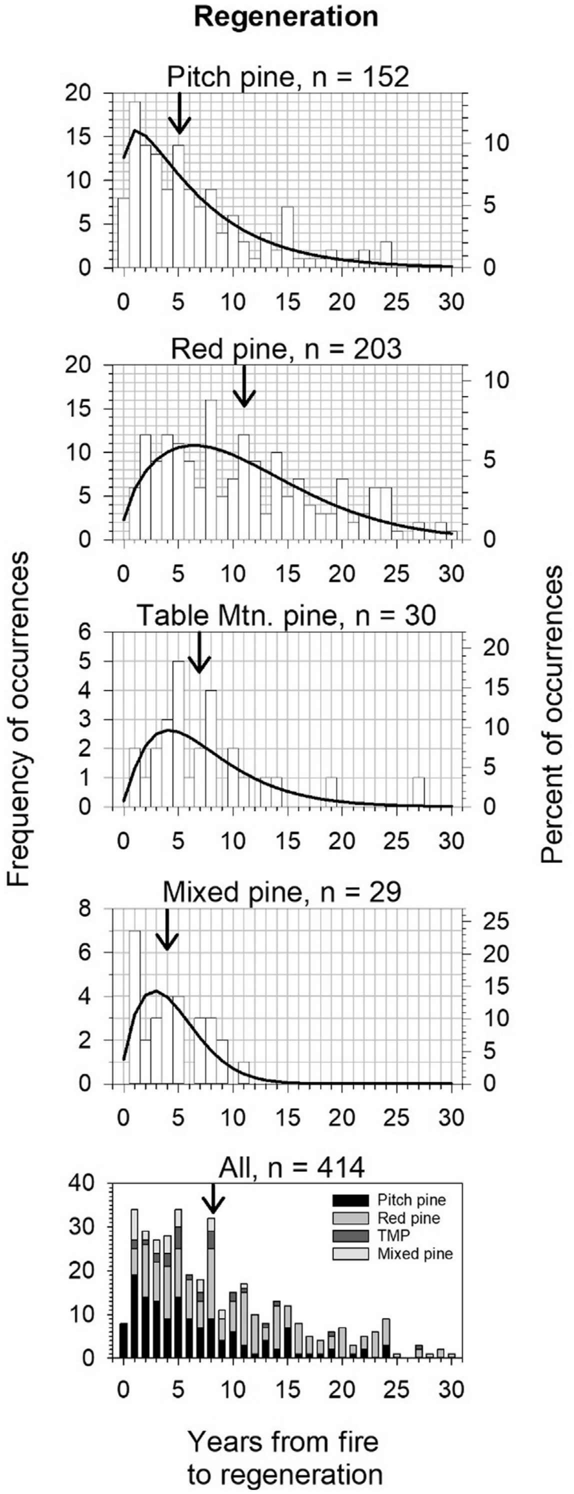

Fig. 4. Frequency distributions of tree regeneration by years since fire (white bars, left axis). Black lines represent best-fit distribution functions (Table 1) that estimate percent of tree occurrences in years since fire (right axis). Arrows indicate location of the 50% quantile.

4. Discussion

These data support that successful regeneration of these hard pine species is dependent on periods of frequent fire. Relatively high regeneration occurred in the years immediately following fire events and decreased with time since fire. Decreased regeneration with time since fire is expected to be related to site factors known to limit regeneration (e.g., decreasing exposed mineral soil, increasing litter cover and depth, competition for growing space). Factors operating at larger spatial scales may further significantly affect the regeneration of pine following fire. For example, Bergeron and Brisson (1994) found that increases in red pine regeneration following fires in Quebec were promoted by increased precipitation and cooler temperatures. In Newfoundland, red pine regeneration and root growth were significantly higher in burned stands (Mallik and Roberts 1994). Despite

Table 1
Parameters for empirical distribution functions and goodness-of-fit test results for regeneration and survival of pitch pine (*Pinus rigida*), red pine (*P. resinosa*), Table mountain pine (*P. pungens*), and mixed pine species across central Pennsylvania, USA.

		Parameters					Goodness-of-fit test		
	Distrib.	Threshold (θ)	Scale (σ, ζ)	Shape (α, c)	Mean	sd	*K-S* Stat (p-value)	*C-V M*	*A-D*
Years from fire to regeneration									
Pitch pine	Gamma	−0.23	5.47	1.24	6.56	6.1	0.07 (0.11)	0.089 (0.18)	ns
Red pine	Weibull	−0.23	12.65	1.57	11.13	7.39	na	0.098 (0.11)	ns
Table mountain pine	Weibull	−0.23	8.65	1.52	7.57	5.23	na	0.073 (0.24)	0.447 (0.25)
	Gamma*	−0.23	3.39	2.28	7.51	5.13	0.12 (> 0.25)	0.050 (> 0.5)	0.312 (> 0.5)
Mixed-pine	Weibull	−0.23	5.29	1.67	4.5	2.91	na	0.094 (0.12)	ns
Years from regeneration to next fire									
Pitch pine	Lognormal	−1.2	1.85	0.86	8.06	9.72	0.065 (> 0.15)	ns	ns
Red pine	none								
Table mountain pine	Lognormal*	−1.2	2.04	0.69	8.6	7.61	0.140 (> 0.15)	0.050 (> 0.50)	0.289 (> 0.50)
	Gamma	−1.2	4.25	2.3	8.57	6.44	ns	0.998 (0.12)	0.552 (0.16)
Mixed pine	Lognormal	−1.2	1.94	0.6	7.17	5.52	0.118 (> 0.15)	0.067 (0.31)	0.439 (0.29)
	Weibull	−1.2	9.29	1.98	7.03	4.34	na	0.040 (> 0.25)	0.279 (> 0.25)
	Gamma*	−1.2	2.5	3.27	7	4.53	0.109 (> 0.25)	0.046 (> 0.50)	0.306 (> 0.50)

K-S = Kolmogorov-Smirnov, *C-v M* = Cramer-von Mises, *A-D* = Anderson-Darling, na = not applicable, ns = not significant.
* = model shown in Figs. 4 and 5.

fire's ability to create conditions favorable for pine regeneration, regeneration following fire may not be immediate due to lack of seed production or dispersal to receptive seedbeds, and hence synchrony is needed between seed availability and seedbed receptivity for successful seedling establishment.

During the last four centuries, dramatic changes in fire regimes occurred across the U.S. due largely to anthropogenic influences (Guyette et al., 2012; Taylor et al., 2016; Stambaugh et al., 2018). These anthropogenic influences had wide-ranging effects on hard pine communities, especially when resulting in altered fire frequency and severity from prior times. It is not clear whether or not past anthropogenic influences confound the ability to determine fire regime conditions conducive to promoting hard pines. We surmise that the sources of historical ignitions (whether human or lightning) had little influence on determining actual pine regenerative response, which is preset by ecophysiological traits.

Our fire data, likely generated from primarily anthropogenic fires, may be expected to be most aligned with those fire conditions with fire management prescriptions. For example, do the fire regimes that promote hard pines differ between anthropogenic and lightning-dominated ignitions? Certainly, the historical forest conditions (e.g., fire regimes, vegetation structure and composition) are likely very different than those that have existed during approximately the last 150 years (Nowacki and Abrams, 2008). Historically, relatively frequent burning over multiple centuries would have led to more open forest conditions such as savannas, barrens, or woodlands (Batek et al., 1999; Hanberry and Abrams, 2018). Currently, these sites primarily consist of closed-canopy forests dominated by deciduous hardwood and mixed-conifer species, and infrequent fire in modern times has led to litter accumulation that has altered seedbanks to favor hardwood regeneration, especially shade-tolerant mesophytic tree species (Nowacki and Abrams, 2008). Few locations exist where the long-term effects and processes of repeated burning may be observed, making historical data especially valuable.

Low representation of pith dates across all species after 1850 was likely due to multiple factors including land uses that have caused their decline such as logging that removed seed sources, and too frequent and intense fires followed by fire suppression (Chapman, 1952; Goodlett, 1954; Nowacki and Abrams, 1992). Pine regeneration during the same year of fire may occur if fires burn (1) prior to seedfall and (2) in a heterogenous pattern with variable intensity and severity due to site-level topographical variation, the presence of rock outcrops, streams, and other natural fire breaks, or lack of continuous fuel to support fire spread. Only pitch pine was observed to regenerate in the same year as a fire, which may reflect its ability to tolerate fire and survive by adaptation (e.g., ability to resprout).

These data represent only the trees that survived past fires, not those that have died and decomposed, and thus, become unavailable for sampling. However, focusing our analysis strictly on conditions associated with survivors may be particularly valuable for understanding successful management of hard pine communities. Based on comparable results among species, the results here appear plausible to guide the use of fire to successfully regenerate pine that are capable of growing to maturity in management systems that incorporate repeated use of prescribed fire. Further, conditions of historical fires are within the range of those of prescribed burning because they were not significantly associated with drought and there was no evidence for stand-replacing events (Stambaugh et al., 2018).

Though not analyzed here, most trees survived repeated and relatively frequent burning throughout their lives (Stambaugh et al., 2018). Frequent burning following regeneration did not appear to eliminate regeneration. If this was the case, then we would have expected survival distributions to be more positively skewed towards longer intervals. Although burning soon after regeneration may seem counterintuitive for promoting regeneration, it appears to have been more commonly associated with survival than longer periods without fire. This suggests that additional processes, such as reducing competing vegetation, may be as important to pine regeneration success as is the direct impact from fire. Further, site conditions (e.g., stand density) may serve to further influence hard pine survival through repeated fires. For example, probability of pine survival following fires would be higher in more open canopy conditions than closed because hard pines are generally shade intolerant species.

5. Conclusion

This study presents a new, retrospective approach to understanding hard pine tree regeneration and survival across a wide range of time, sites, fire events, and burning frequencies. The approach utilized commonly reported metrics in fire scar history datasets such as fire events and tree pith dates, and therefore, could be broadly applicable across large regions for various species using existing data archives, e.g., the International Multiproxy Paleofire Databank. Application of this method elsewhere should consider the various factors of fire regimes, species ecology, and other forest conditions that may be important to data analysis and interpretation.

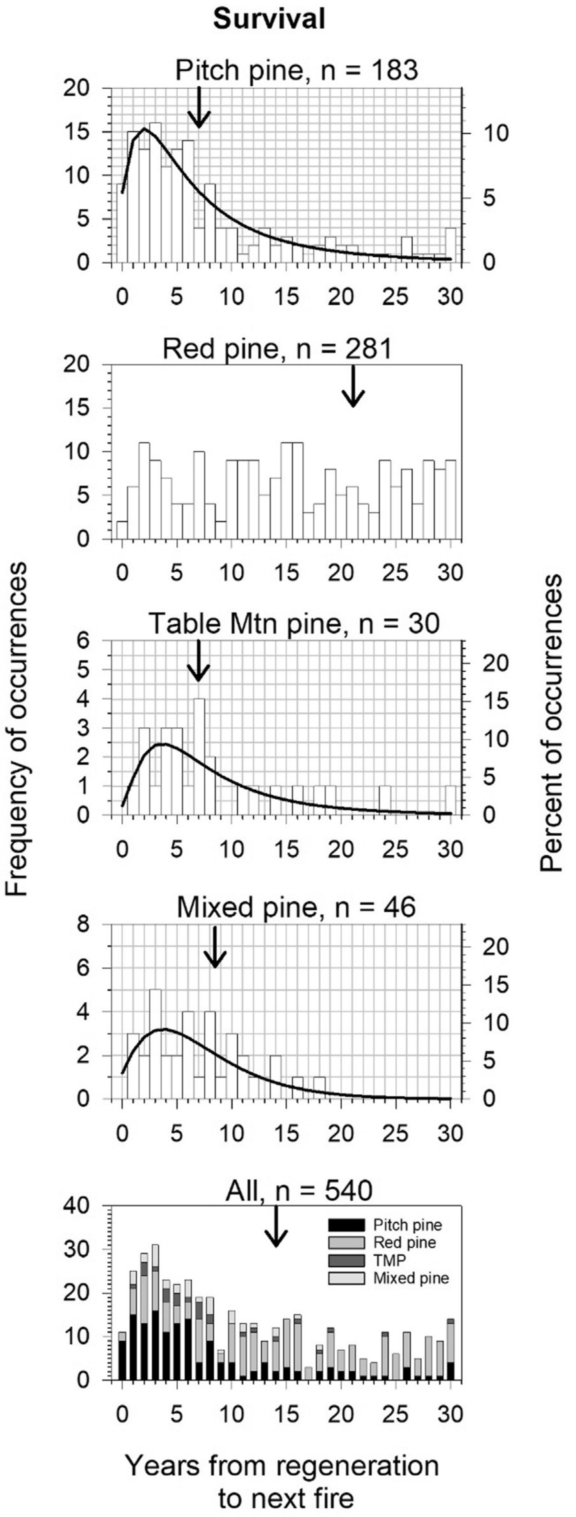

Fig. 5. Frequency distributions of years from tree regeneration to next fire occurring at the site. Black lines represent best-fit distribution functions (Table 1) that estimate percent of trees surviving at the time of the next fire occurring at the site (right axis). Arrows indicate location of the 50% quantile.

Results from this study demonstrate that (1) pine regeneration is directly linked to fire, (2) fire frequency was high during periods of successful pine regeneration and recruitment, and (3) pine regeneration subsided during recent periods of fire suppression. Fire frequency is significantly related to the successful regeneration and recruitment of hard pines, however it may be misconceived that all fires promote fire-dependent species or that managing based on a static fire interval promotes hard pines. Relatively frequent fires promoted regeneration of hard pine species considered here, while slightly less frequent fires promoted their survival following establishment. Based on our approach and findings, further determination of species-specific fire regimes may be possible elsewhere and aid in refining burning prescriptions for hard pine communities.

Frequent fires set the stage for successful pine regeneration and survival by creating favorable seed beds, reducing competing vegetation (especially woody hardwood trees and shrubs), and creating more open stand conditions that lead to higher light levels for improved pine seedling and survival. A relatively longer fire-free period is needed for pine survival and growth into the overstory. Pine bark grows thicker during this fire-free period conferring increasing resistance to topkill or death from subsequent fires. This study suggests that continued frequent burning was critical for promoting pine success, especially in competition with hardwood and shrub sprouts.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.01.012.

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