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RESEARCH

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Fire history and tree invasion in an Ozark glade, barrens, and woodland complex

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Abstract

Background In the Ozark Plateau, glade and barrens communities provide habitat and species diversity within the broader landscape of hardwood forests and oak-pine woodlands. In the past, frequent surface fires burned through the extensive oak-pine woodlands of the region, and it is likely that these fires burned into adjacent barrens and glades, helping keep them clear of woody vegetation. Following fire protection in the twentieth century, many of these barrens and glades have been invaded by shrubs and trees. However, we generally lack empirical evidence of the role that fire played in maintaining these open habitats historically. Therefore, we aimed to assess the role of past fire in shaping vegetation at Devil's Knob-Devil's Backbone Natural Area, an area that includes invaded glade and barrens communities surrounded by oak-pine woodlands and forest. Our objectives were to (1) characterize the past fire regime at the site; (2) assess whether the timing of tree invasion aligns with the timing of fire protection at the site; and (3) assess the drivers of spatial and temporal patterns of tree invasion within the glades and barrens.

Results We collected fire-scarred shortleaf pine samples from the wooded slopes surrounding the glades and barrens and we collected cores from trees within the barrens and glades. The reconstructed fire scar record spanned the period 1670–2018, with a composite mean fire interval of 2.6 years prior to the onset of fire protection in the 1930s. Tree establishment dates from within the glades and barrens demonstrated that large pulses of tree recruitment aligned with the onset of fire protection, indicating that fire was an important ecological process that maintained open habitat in the glade and barrens communities. Analysis of tree age and corresponding environmental site conditions within the glades and barrens indicated that the majority of red cedar (*Juniperus virginiana*) establishment occurred later in the 1960s on topographic positions with higher amounts of insolation.

Conclusion Our results support the view that frequent fire played an important role in maintaining these glades and barrens in the past and that prescribed burning can be used to restore and maintain these habitats in the future.

Keywords Barrens, Dendrochronology, Fire history, Glade, *Juniperus virginiana*, Woody plant invasion

Resumen

Antecedentes En las mesetas de Ozark, las comunidades de claros en bosquetes y planicies áridas proveen de hábitat y diversidad de especies dentro de un amplio paisaje de bosques de maderas duras y de roble-pino. En el pasado, fuegos frecuentes de superficie quemaban los extensos paisajes de estos bosques de robles y pinos de la región, y es probable que esos fuegos llegaran a quemar los claros y planicies áridas adyacentes a esos bosques, ayudándolas a clarear esas áreas de vegetación arbustiva. Luego de la protección contra el fuego iniciada en el siglo XX, muchos de esos claros y planicies áridas fueron invadidas por vegetación arbustiva y arbórea. En general, se carece de evidencia

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empírica del rol que el fuego tuvo para mantener históricamente esos hábitats abiertos. Por ese motivo, buscamos determinar el rol de fuegos pasados en el modelado de la vegetación en el Área Natural conocida como *Devil's Knob-Devil's Backbone*, un área que incluye comunidades invadidas de claros y planicies áridas rodeadas de bosques de robles y pinos. Nuestros objetivos fueron: (1) caracterizar el régimen de fuegos pasados en el área; (2) determinar si el período de tiempo de invasión de árboles y arbustos coincide con el período de protección contra el fuego en esa área, y (3) determinar los patrones espaciales y temporales que conducen a la invasión de árboles tanto dentro de los claros como en las planicies áridas.

Resultados Colectamos muestras de escaras de fuego en muestras de pinos de hoja corta de las laderas arboladas que rodean a los claros y áreas de planicies áridas, y colectamos también tarugos de troncos de árboles en ambos lugares. El registro reconstruido de las escaras de fuego abarcó el período entre 1670-2018, con un intervalo medio de fuegos de 2,6 años previo al inicio del período de protección que comenzó en 1930. Los datos de establecimiento de árboles dentro de las áreas de claros y planicies áridas demuestran que grandes pulsos de reclutamiento de árboles se alinea con el inicio de la protección contra el fuego, indicando que el mismo fue un proceso ecológico importante que mantuvo el hábitat de las comunidades de los claros y de planicies áridas. El análisis de la edad y el correspondiente a las condiciones ambientales de esos sitios de claros y planicies indican que establecimiento de la mayoría del cedro rojo (*Juniperus virginiana*) ocurrió ya adentrados los años 1960 en posiciones topográficas con altos índices de insolación.

Conclusiones Nuestros resultados apoyan la visión de que fuegos frecuentes jugaron un rol muy importante en el mantenimiento de esos claros y planicies áridas en el pasado, y que las quemas prescriptas pueden ser usadas para restaurar y mantener esos hábitats en el futuro.

Background

Glades and barrens are a focus of conservation efforts in the Ozark Region because they function as islands of contrasting grassland habitat within the broader matrix of closed canopy hardwood forests and shortleaf pine-oak woodlands. Glades and barrens are ancient ecosystems that support a high diversity of heliophytic understory plant species that are adapted to thin soils and high light conditions and are not found in disturbance-created openings in adjacent forests (Heikens 1999; Ware 2002). In the Interior Highlands, glades and barrens have historically been combined into an overarching concept of "glades" (Nelson 2010), but they are generally distinguished in the broader Southeast. Barrens are treeless, or nearly so, with perennial grassland vegetation in shallow soil over bedrock (DeSelm 1989, 1994; Baskin and Baskin 1999; Heikens 1999; Nelson et al. 2013). Glades are characterized by extensive areas of exposed bedrock, gravel, and very thin soils supporting an annual grass dominated zone, often with hydro-xeric (winter wet) hydrology, and usually on flat or gently sloping sites (Baskin and Baskin 1999; Heikens 1999). Glades and barrens generally occur as a mosaic or complex along gradients of soil depth, moisture, slope, and aspect, but they differ in regard to their physiognomy, species composition, vulnerability to woody plant encroachment, and the degree to which edaphic site factors maintain their openness (DeSelm 1989, 1994; Baskin and Baskin 1999; Heikens 1999; Nelson et al. 2013).

Glades and barrens in the Ozarks are home to a suite of rare and endemic species. These include yellow coneflower (*Echinacea paradoxa* (J.B.S. Norton) Britt.), Trelease's larkspur (*Delphinium treleasei* Bush), Bush's skullcap (*Scutellaria bushii* Britton), and Missouri bladderpod (*Physaria filiformis* Bush ex K.C. Davis) (Nelson 2010). These unique plant communities provide habitat and food resources for native fauna like the eastern collared lizard (*Crotaphytus collaris* (Say, 1823)), southern coal skink (*Eumeces anthracinus pluvialis* (Cope, 1880)), tarantula (*Aphonopelma hentzi* (Girard, 1852)), and greater roadrunner (*Geococcyx californianus* (Lesson, 1829)) (Nelson 2010). Glades (inclusive of barrens) account for approximately 0.7% of the Ozark landscape, yet they provide habitat for 17% of the species with viability concerns in the Ozark-Ouachita Highlands (Nelson 1997, USDA 1999). The Ozark Plateau contains the highest acreage of glades in eastern North America (Nelson 2012). However, many former glade and barrens habitats have been degraded by tree invasion during the twentieth century, which has driven a decline in glade and other grassland obligate species (Miller et al. 2017; Brewster et al. 2018).

One possible driver of the observed tree invasion in glades and barrens is the decline of fire in the Ozarks (Beilmann and Brenner 1951; Foti 2004). In the past, fires burned through adjacent pine-oak woodlands and into these habitats, checking the growth of trees and promoting non-woody vegetation cover. Consequently, the decline of fire in the late twentieth century removed

this control and may have initiated the wave of woody encroachment. However, direct evidence of these historical fires in glades and barrens is limited. There could be a combination of factors, other than or in addition to fire, that might have kept trees from establishing at any one glade and barrens site, including soil characteristics, climate, hydrology, and grazing (Baskin and Baskin 2000; Noss 2012). The uncertainty about the causes of tree invasion in glades and barrens has led to disagreement about how and even whether managers should restore the open condition of these habitats. Therefore, we need direct evidence of the timing of woody invasion, along with the characteristics of past fire regimes and other environmental changes like droughts and grazing. Information on the role of past wildfire regimes in this landscape would help us understand how fire shaped vegetation in the past and could help justify and inform the use of fire to restore and maintain glade and barrens ecosystems in the Ozarks in the future (Swetnam et al. 1999).

Fire-adapted natural communities are distributed throughout the Ozark Plateau, including shortleaf pine (*Pinus echinata* Mill)-oak (*Quercus* spp. L) forests, woodlands, and savannas, and prairies, barrens, and glades (USDA 1999). Historically, these communities were likely maintained, at least in part, by fires that burned across the landscape pushing fire-intolerant species to less fire-prone landscape positions, reducing tree density in woodland sites, and creating openings for heliophytic shrubs and herbaceous plants (Foti et al. 1999; Guyette et al. 2006; Nelson 2012). Vegetation reconstructions from the early nineteenth century demonstrate that the distribution of both fire-tolerant and fire-intolerant species and communities were shaped by fire (Batek et al. 1999; Nelson 2012). Furthermore, the Ozark fire regime and resulting vegetation patterns were likely influenced by anthropogenic fire use for millennia (Jurney 2012). Lightning ignitions do occur in the region (Yang et al. 2007), but they represent a small fraction of contemporary fires and past fire frequency has consistently responded to fluctuations in human populations and associated land use (Guyette et al. 2002). Tree-ring fire history reconstructions have found that fire was less frequent in the Ozarks during the eighteenth century when population density was lower. Then fire frequency increased during the late eighteenth century following the migration of the southeastern tribes into the region and then the arrival of Euro-Americans in the middle of the nineteenth century (Guyette et al. 2006; Stambaugh and Guyette 2006). However, pollen records, travel descriptions, and the presence of fire-adapted plant and animal species support the conclusion that fire played an important role in shaping vegetation and maintaining endemic species in the Ozarks even during periods of reduced human population (Foti et al. 1999; Nanavati and Grimm 2020).

During the twentieth century, fire-protection policies, land use changes, and human population growth greatly reduced the frequency of fire in Ozark landscapes (Strausberg and Hough 1997; Fowler and Konopik 2007). Fire protection altered vegetation communities across the region, with woodlands growing denser and composition shifting from fire-adapted pine and oak species to less fire-tolerant hardwoods and red cedar (*Juniperus virginiana* (L.) Antoine) (Foti 2004; Hanberry et al. 2012). At the same time, formerly treeless habitats such as prairies, glades, and barrens were invaded by trees and shrubs that shade out the understory vegetation (Baskin and Baskin 2000; Miller et al. 2017). Red cedar is a species that is particularly successful at invading these formerly open grasslands, as its seeds are broadly distributed by birds and it is well adapted to compete on thin, droughty soils. Once established, red cedar shades out understory vegetation, alters soil chemistry, and shifts fuels and potential fire regimes (Van Els et al. 2010; Williams et al. 2013; Nunes Biral et al. 2019). Red cedar also exhibits allelopathic properties and creates system feedbacks that make it difficult to restore sites to their former open conditions (Miller et al. 2017; Bennion 2023). Consequently, the successful establishment of red cedar and hardwoods leads to a decline in the endemic grassland biodiversity that characterizes glade and barrens communities (Ware 2002).

Tree-ring reconstructions can provide multi-century records of fire frequency, seasonality, and extent. Previous fire history studies in the Ozark Region reveal that pine-oak woodlands and forests experienced low-severity surface fires at short intervals (2–22 years), with fire frequency varying spatially and temporally in response to topography, climate, and human activities (Guyette and Spetich 2003; Guyette et al. 2006; Stambaugh and Guyette 2006). Most of these reconstructed fires occurred in the trees' dormant season. However, contemporary experimental studies by Bones et al. (2026) in loblolly or shortleaf pine-dominated woodlands in Alabama, Mississippi, South Carolina, and Tennessee indicate that prescribed burns during the early and late growing season more effectively reduce woody vegetation than fires in the dormant or mid growing season, though they do not specifically define these seasons or state whether they describe dormancy of the herbaceous or woody components of the communities. Despite a depth of information on past fire regimes in oak-pine woodlands and forests in the Ozarks, glades and barrens are components of the landscape that lack direct fire history information. Few tree-ring fire history studies have been conducted in glades and barrens

because they contained few trees in the past to record fire scars. However, two fire history studies have been conducted in the woodlands surrounding Ozark glades, which found that fire was frequent with return intervals from 3 to 5.7 years (Guyette and McGinnes Jr 1982, Jenkins, Guyette, and Rebertus 1997).

In addition to fire scars, tree establishment patterns can be used to examine the past influence of wildfire and other disturbance processes on vegetation dynamics. If a disturbance event is responsible for vegetation change, then we would expect the disturbance timing to align with a shift in tree establishment. For example, Stambaugh et al. (2014) documented an increase in oak establishment followed by red cedar cohorts after the onset of fire protection in Oklahoma. In other regions, climatic variability, land use, fire protection, and insect outbreaks have been linked to shifts in the rate and composition of tree establishment providing insight into the historical processes that shaped vegetation (Frelich and Reich 1995; Savage et al. 1996; Brose and Waldrop 2006; Kipfmueller et al. 2021). Recently, studies have used dendrochronology to examine red cedar invasion along the Midwestern prairie-forest boundary (DeSantis et al. 2011; Jones 2016; Hoff et al. 2018), but limited work has been done assessing tree invasion in glade and barrens habitats within the eastern deciduous forest proper (but see Copenheaver et al. 2004).

This study aims to combine tree establishment data with fire history data from a woodland-glade-barren complex to assess the role that fire played in keeping glades and barrens open and then initiating the shift towards woody invasion during the twentieth century. Previous research shows that fire declined during the twentieth century and that glades and barrens were invaded during this same period. However, there have not been studies combining fire history and woodland-glade-barrens dynamics that directly link woody encroachment to changes in the fire regime. It is essential to understand the degree to which fire-maintained glades and barrens historically in order to inform and guide the use of prescribed fire for their restoration and management. Furthermore, managers need information on the character of past fire regimes to guide the frequency, seasonality, and temporal variability of prescribed burns in pine-oak woodlands, barrens, and glades. Therefore, our study aims to address this need by focusing on Devil's Knob-Devil's Backbone Natural Area (DKDB), a forest-woodland-barrens-glade landscape in the Ozark Mountains that has experienced significant woody vegetation changes. We hypothesize that the decline of fire in the twentieth century has facilitated tree invasion within the glade and barrens communities within this mosaic. Our objectives were the following:

1. Characterize the frequency, seasonality, climate drivers, and temporal variability of past fires in the oak-hickory-pine forest/woodland that surrounds the glade/barrens complex at DKDB.
2. Investigate the timing of tree invasion in the glades and barrens and its relation to fire protection.
3. Assess the effect of abiotic site conditions on tree invasion within the glade and barrens complex.

Methods

Study area

Devil's Knob-Devil's Backbone Natural Area is a unit of Arkansas's State System of Natural Areas managed by the Arkansas Natural Heritage Commission (AHNC). It is located along the southern portion of the White River Hills Level IV Ecoregion of the Ozark Highlands, Izard County, Arkansas (36.002528°, − 92.051507°) (Woods et al. 2004). The natural area encompasses 332.7 hectares, with an elevation range of 121–322 m. The site consists of two elevated knobs connected by a flat bench or "backbone" and surrounding woodlands and forests (Fig. 1) (ANHC 2016). Historically, the glade and barrens habitat likely covered most of the two knobs and the backbone. The knobs are composed of dolomite and their stony slopes currently host woodlands of red cedar, Ashe's juniper (*Juniperus ashei* Buchholz), winged elm (*Ulmus alata* Michx.), smoketree (*Cotinus obovatus* Raf.), and chinquapin oak (*Quercus muehlenbergii* Engelm.). The backbone is composed of sandstone, with sections of shallow bedrock remaining mostly open with scattered shortleaf pine (*Pinus echinata* Mill), lichen, moss, little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and big bluestem (*Andropogon gerardi* Vitman). The backbone supports oak-hickory woodlands in areas of deeper soil development. The slopes below the knobs and backbone are xeric oak-hickory woodlands with post oak (*Quercus stellata* Wangenh.), blackjack oak (*Quercus marilandica* Münchh.), northern red oak (*Quercus rubra*), shortleaf pine, black hickory (*Carya texana* Buckley), and mockernut hickory (*Carya tomentosa* Nutt.). The knobs and backbone exhibit no evidence of cutting or grazing, but the wooded slopes below have been cleared or logged in the past century. At Calico Rock, 15.1 km northwest of the site, the mean annual precipitation is 1212 mm and the mean monthly temperature ranges from − 5.1 to 32.5 °C (NCDC 2019).

Field methods

To assess fire history, we used a chainsaw in the summer and fall of 2018 to collect a total of 23 sections from remnant logs, stumps, and living shortleaf pine trees for fire scar analysis (Arno and Sneck 1977). The samples, along with GPS points for mapping purposes, were collected

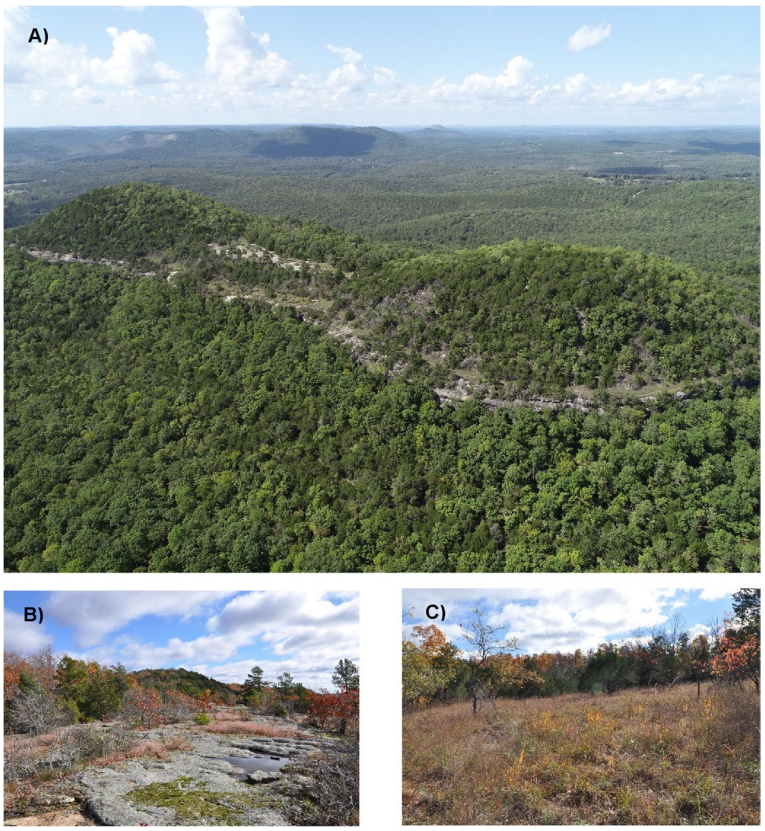


Fig. 1 **A** Drone photograph of the glade/barrens/woodland complex at Devil's Knob-Devil's Backbone Natural Area. Photo by Bryan Rupar/ANHC. **B** Acidic sandstone glade and barrens in the saddle between the two dolomitic knobs. Photo by ANHC. **C** Calcareous barrens. Photo by ANHC

from the slopes surrounding the knobs (Fig. 2). The area from which we collected samples was approximately 132 hectares and the most distant samples were 1.6 km apart. We collected increment cores from 14 live shortleaf pine trees to develop a crossdated twentieth-century ring-width chronology for overlap and comparison with older, cross section samples for which we did not have a bark date. To assess age structure in the glades and barrens, we established sampling plots during the spring of 2020 on the elevated knobs and backbone (from here forward, the knobs and connecting backbone will be referred to as the "glades and barrens") at the DKDB study site. The goal of our sampling was to characterize the temporal and spatial pattern of tree establishment and species composition in the glades and barrens. In ArcGIS (ESRI 2019), we generated 10 random sampling points within each of the two predominate soil series: the Ramsey series developed from sandstone parent material and the Moko series developed from limestone and dolomite parent material (SSURGO 2020). We navigated to the sampling points using GPS, marked the plot center, and established a 0.025-hectare circular plot. The three largest diameter trees in each plot were identified and we recorded their species, diameter at breast height (DBH), and distance and bearing to plot center. We collected 2 increment cores from each of these large trees. Cores were collected on opposite sides of the tree 15 cm from the ground and perpendicular to the slope. Due to rot, we were only able to collect a single core from 23 trees. We collected a total of 97 cores from 60 trees.

Laboratory methods

Cross sections and cores were dried, mounted, and surfaced with progressively finer grit sandpaper to reveal ring-width patterns and scarring (Orvis and Grissino-Mayer 2002). For the fire-scarred cross sections, we collected high-resolution image scans of the surface of each sample and ring widths were measured using the CooRecorder image analysis software (version 9.3.1) (Larsson 2018). Tree rings were visually crossdated and then dates were statistically verified using COFECHA software (Holmes 1983). Once the rings of an individual cross section were confidently dated, precise calendar years were assigned to fire scars within the dated rings. The seasonality of a fire was determined according to the scar position within the ring (Baisan and Swetnam 1990).

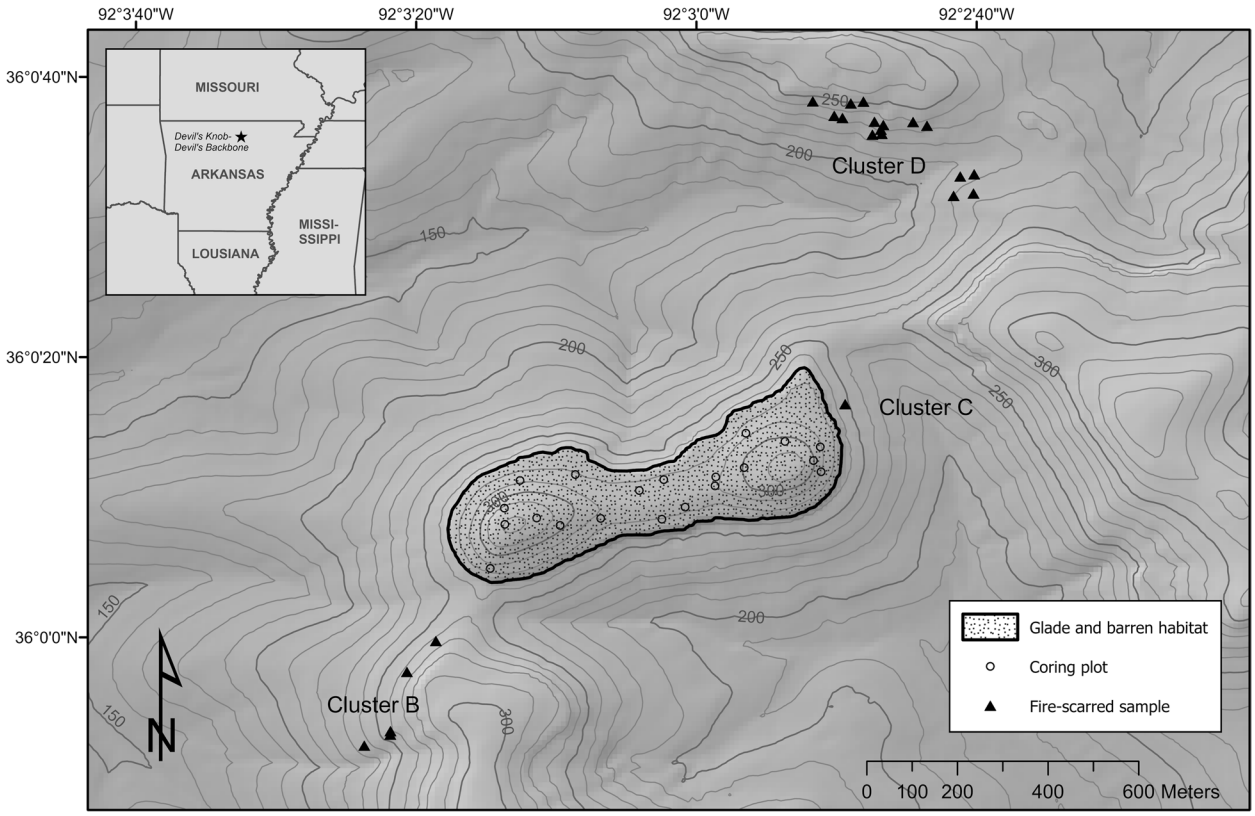


Fig. 2 Map of landscape at Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA, showing the location of fire-scarred trees sampled and the location of plots in the invaded glades and barrens where trees were cored

Dormant-season fires were assigned to the year of the ring formed after the scar (i.e., the year of the growing season following the dormant season when the scar was formed). For the cores obtained from the three trees sampled in each of the glade and barrens plots, we identified two groups of trees from the genus *Juniperus* (cedars, *J. virginiana* and *J. ashei*; $n=26$ trees) and *Quercus* (oaks, *Q. rubra*, *Q. muehlenbergii*, and *Q. alba* L.; $n=21$ trees) which had sufficient sample depth to crossdate. For these cores, we repeated the same dating procedure used for the cross sections. For the remaining cores, we conducted ring counts to determine coarse decadal estimates of establishment. Once the dating of the cores was finished, an establishment date was assigned based on the date of the pith. For trees that did not have a core that intersected the pith ($n=24$ trees), we used ring width and curvature of the earliest rings to estimate approximate establishment dates (Applequist 1958). The average number of years added to trees with a missing pith was 6.5.

Fire history analysis

We used FHAES software to record, graph, and analyze fire intervals (Brewer et al. 2016). To assess the frequency of fire at the site, we calculated a series of different fire interval metrics including the point, composite, and major fires mean fire interval (MFI). Major fires were fires that scarred greater than 25% of the recording samples in a given year. Recording samples were samples that had already recorded an initial scar and retained wood along the scarring surface that was sufficient to determine whether scarring occurred in the given year (Grissino-Mayer et al. 2004). We also calculated an area-wide fire interval to assess the frequency of fires that likely burned across the entirety of the sampled area (Aldrich et al. 2010). The DKDB study site included three clusters of fire-scarred cross sections that were separate from one another (clusters B, C, D, Fig. 2). An area-wide fire year was a year in which a fire scar was identified at both cluster B and cluster D. We chose not to include cluster C in the designation of area-wide fires, as this cluster contained only one scarred specimen and it was located about halfway between clusters B and D. Area-wide fires indicate years in which a fire burned at both the north and south ends of natural area, suggesting that it was a large fire that likely burned across much of the study area. Fire intervals were analyzed within the period of reliability, which was defined as the period after the first fire that was recorded on multiple cross- sections, calendar year

1793 at DKDB (Grissino-Mayer et al. 2004). We chose not to include the period of fire protection in the interval calculations because we were interested in accurately characterizing pre-fire protection fire intervals. We used superposed epoch analysis (SEA) to assess the influence of annual drought on fire occurrence (Swetnam and Baisan 1996). We tested both the composite and major fire years against the Cook et al. (1999) tree-ring reconstruction of Palmer Drought Severity Index (PDSI), gridpoint 202.

To assess temporal changes in fire frequency, we calculated composite MFIs for three separate land use periods: the Native American period (1793–1829), the Euro-American period (1830–1929), and the fire protection period (1930–2000). During the late 1700s, Cherokee peoples and other displaced tribes from the southeast began settling in the Ozark Region (Whayne 1995), with Native American populations peaking during the 1820s (Guyette et al. 2006) before these tribes migrated to Oklahoma at the end of the decade. Izard County, Arkansas, was established in 1825, and census records show steady increases in population during the decades from 1830 to 1910 as Euro-Americans arrived in the region (Shannon 2012, ADC 2020). We chose to define the fire protection period as starting in 1930, as this was the beginning of statewide fire prevention and suppression efforts (Strausberg and Hough 1997; Fowler and Konopik 2007). To test for differences between mean fire intervals for the different land use periods, we used a two-sample *t*-test, where data are normally distributed with unequal variance (Sokal and Rohlf 2003). We repeated the SEA analysis for the composite and major fires for each of the land use periods separately, to assess whether there were temporal changes in fire-climate relationships.

Analysis of tree establishment

We analyzed the influence of wildfire on tree establishment in the glades and barrens by plotting approximate tree establishment dates for comparison with the timing of past fire events in the surrounding woodland and forest and annual PDSI. Then we used multiple linear regression to assess the influence of the environmental site factors on the timing of post-fire protection cedar and oak tree invasion in the different plots (Kutner 2005). To quantify abiotic environmental site characteristics, we used the spatial analyst tool in ArcGIS to calculate elevation, slope, and amount of insolation from a 3-m digital elevation model for each of 10 plots in each soil type (ESRI 2019). The USDA Soil Survey for Izard County was used to identify soil series for each plot (SSURGO 2020). The independent variables that we assessed were soil series, elevation, slope, and amount of insolation. For dependent variables in the models, we used the age of trees that established after fire protection, as we were interested in the drivers of post-fire protection tree invasion. We removed the trees that were not successfully crossdated (5 oak trees) and then further subdivided the response variables into two categories: the oldest post-fire protection cedar tree in each plot ($n=10$) and the oldest post-fire protection oak tree in each plot ($n=9$). The goal of selecting this subset of trees was to identify plots with environmental conditions that facilitated early invasion by either cedar or oak trees. Three of the remaining red cedar trees required pith estimates with an average of 6.3 years added and three of the remaining oak trees required pith estimates with an average of 9.3 years added. We used the dredge function to evaluate all possible combinations of predictor variables and then applied the Akaike information criterion (AICc) to select the optimal model. Statistical analysis was conducted in the R software program version 4.4.1 using the "car" and "MuMIn" packages (Fox and Weisberg 2019; R Core Team 2024; Barton 2025).

Results

Fire history

We successfully crossdated 22 of 23 fire-scarred shortleaf pine samples collected at DKDB. Dated samples contained rings that spanned the dates from 1670 to 2018 and the samples contained 136 fire scars that recorded 65 separate fire years (Fig. 3). The earliest recorded fire year was in 1681, and the most recent scar was a 2016 dormant-season fire, which matches a prescribed fire conducted by the ANHC on December 1, 2015. During the period 1793–1929, the composite MFI was 2.6 years with a range of 1–15 years (Table 1). We identified seven area-wide fire years in 1860, 1873, 1889, 1895, 1910, 1960, and 2016. Excluding the fire protection period, the MFI for area-wide fires was 12.5 years with a range of 6–16 years. We determined the seasonality of 84.6% of the fire years, and the majority (96%) of fire years that were identified by season occurred in the dormant season (Table 2). The SEA analysis found no significant relationship between fire years and annual drought when assessing the entire fire record or during any of the individual land use periods (Supplemental Fig. 1).

Fire was most frequent during the Euro-American period, with a composite MFI of 2.0 years and a range of 1–5 years (Table 3). The Native American period had a MFI of 6.0 years and a range of 2–15 years. The fire protection period exhibited a longer MFI of 16.0 years with a range of 13–29 years. The point MFI for the Native American period is based on just four intervals from individual samples due to the relatively short period of analysis. Two late growing-season scars were identified during the Euro-American settlement period, but the majority

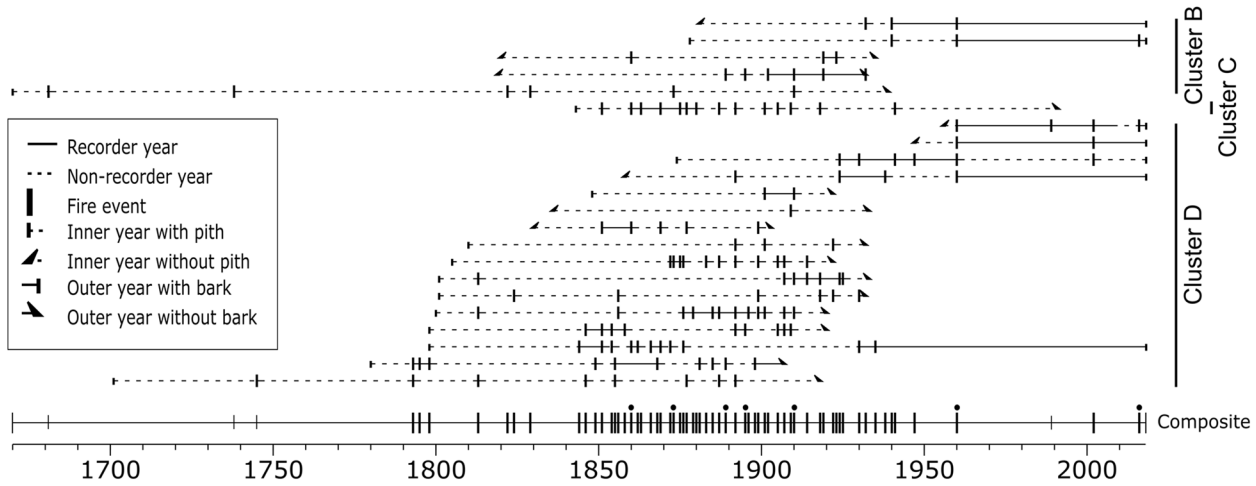


Fig. 3 Fire chronology for Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA. Horizontal lines indicate the time spanned by each tree/sample, with dashed lines indicating non-recording years and solid lines indicating recording years. Short vertical bars represent dated fire scars. The horizontal bar at the bottom of the chart represents the composite fire record, combining all fires that occurred at the site. On the composite fire record, thick longer bars represent major fires (scarred > 25% of recording years) and circles represent area-wide fire years

Table 1 Fire interval metrics from the start of the period of reliability until the period of fire protection (1793–1929) at Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA. *SD*, standard deviation

Fire interval type	Initial fire year	Mean fire interval (years)	Weibull median fire interval (years)	SD (years)	Lower exceedance interval (years)	Upper exceedance interval (years)	Range (years)	No. intervals
Point	1793	11.6	7.8	15	1.4	24.2	1–94	100
Composite	1793	2.6	2.7	2.8	0.6	5.2	1–15	56
Filtered composite	1793	2.6	2.2	2.8	0.5	5.2	1–15	56
Area-wide	1860	12.5	12.7	4.5	8.5	16.6	6–16	4

Table 2 Seasonality of fire years determined according to the position of scar within the annual growth ring at Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA

	Dormant season	Early season	Late season	Undetermined season	Total
Number of fire years	53	0	2	10	65
Percent of fire years	81.5	0	3.1	15.4	100

of scars across all land use periods were dormant-season scars. The fire protection period did not include enough intervals to calculate a filtered composite MFI.

Tree establishment in glades and barrens

We collected 97 cores from the 20 plots in the glades and barrens at DKDB. From these cores, we were able to determine establishment dates for 56 of the 60 cored trees. The remaining trees exhibited rot that prevented us from collecting a complete core and determining the establishment date of the tree. In the oak group, we crossdated 16 of 21 trees with a series intercorrelation of 0.64 and 12 of the 16 crossdated trees included at least one core with a pith. In the *Juniperus* group, we crossdated 26 of 26 trees with a series intercorrelation of 0.48 and 14 of the 26 crossdated trees included at least one core with a pith.

Tree establishment dates at DKDB indicate that much of the current tree cover in the glades and barrens recruited during the fire protection period (Fig. 4). A large pulse of establishment occurred following the last two major fires in 1941 and 1960, with the majority of trees that we cored establishing after 1940. Trees that established after 1940 accounted for 75% of the cored trees. The decade with the most establishment was the 1940s (19 trees, 35% of cored trees) immediately following a major fire recorded on the adjacent slope in

Table 3 Mean fire intervals across the different land use periods at Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA. Values with the same letter are significantly different based on *t*-test ($P < 0.05$). *MFI*, mean fire interval (years)

	Native American period (1793–1829)	Euro-American period (1830–1929)	Fire protection period (1930–2018)
Point MFI	8.0[a]*	8.5[a]	21.5[a]
Composite MFI	6.0	1.9[b]	8.6[b]
Filtered composite MFI	6.0	1.9	9.6

* Based on only four intervals

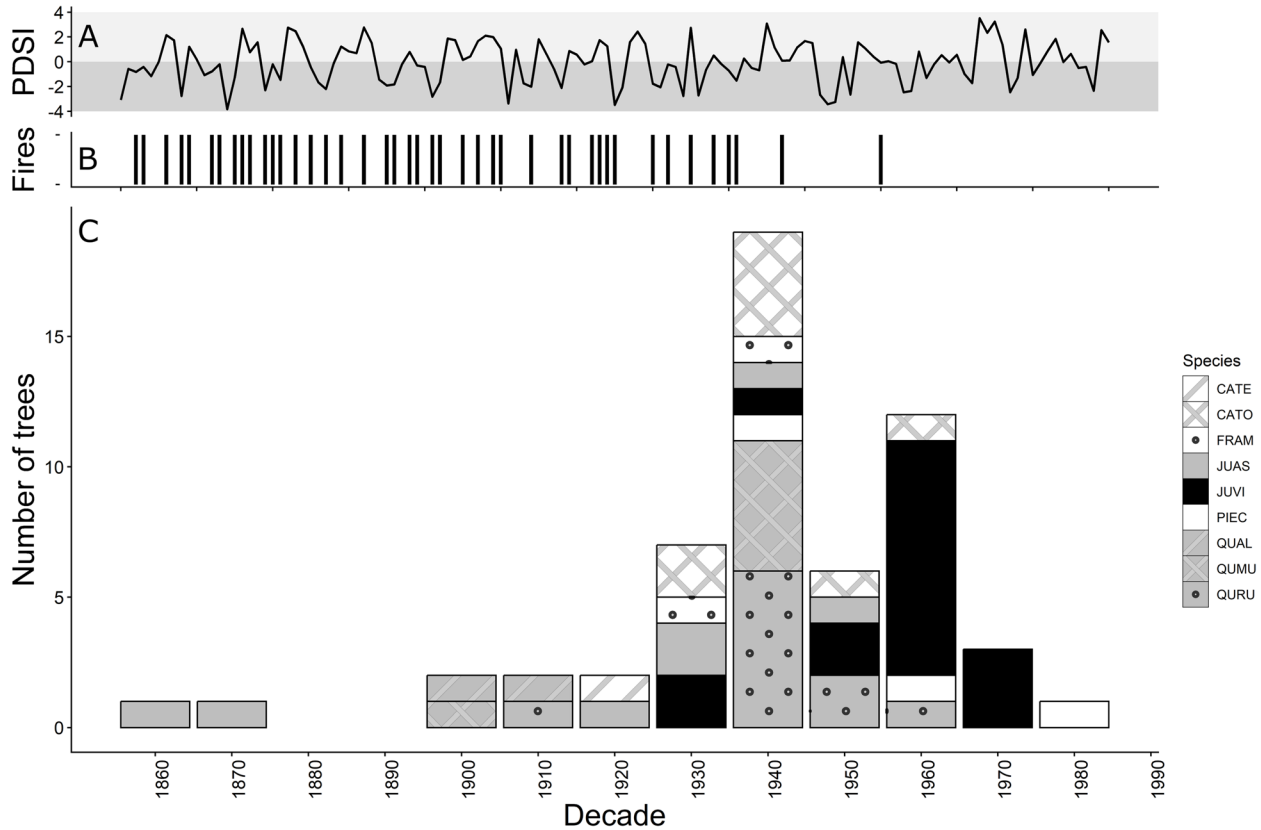


Fig. 4 Timing of woody invasion in glades and barrens at Devil's Knob-Devil's Backbone Natural Area, Arkansas, USA. **A** Annual Palmer Drought Severity Index for central Arkansas (Cook et al. 1999), **B** major fire years recorded on the slopes surrounding the glade/barrens complex, **C** decadal age structure of tree species cored in plots in the glades and barrens. Species abbreviations are as follows: JUAS = *Juniperus ashei*, JUVI = *Juniperus virginiana*, CATE = *Carya texana*, FRAM = *Fraxinus americana*, QURU = *Quercus rubra*, QUAL = *Quercus alba*, CATO = *Carya tomentosa*, QUMU = *Quercus muehlenbergii*, PIEC = *Pinus echinata*

1941. This period of rapid establishment was relatively dry (1940–1960, mean PDSI = −0.15) compared to an extended wet period later in the century (1970–2000, mean PDSI = 0.39). Half of the plots (4 Ramsey soil series; 6 Moko soil series) contained trees that predated fire protection. The estimated ages of the cored trees suggest that there has been a shift in species recruitment from *Q. alba* and *J. ashei* prior to fire protection to *F. americana*, *C. tomentosa*, *J. virginiana*, *Q. muehlenbergii*, *Q. rubra*, and *P. echinata*. Red cedar was particularly prevalent among the post-fire protection trees. The resprouting-capable hardwood species (e.g., *Quercus*, *Carya*, and *Fraxinus*) established rapidly following fire protection, compared to red cedar which is an obligate seeder and recruited most heavily two decades after the initial pulse of hardwood recruitment.

The analysis of post-fire protection tree establishment provided some insight into the nature of tree invasion

in the glades and barrens. Linear models did not identify any explanatory relationships for the age of oak trees in the glades and barrens. However, multiple linear regression identified amount of insolation as a significant predictor of red cedar age in the glades and barrens ($F_{1,8}=8.33$, $P=0.02$, adj. $R^2=0.45$). Amount of insolation had a significant negative relationship with age of post-fire protection red cedar, indicating that increased insolation delayed red cedar establishment.

Discussion

Fire frequency

Our fire history reconstruction demonstrates that fires burned frequently at DKDB during the nineteenth and early twentieth century, prior to a decline in fire frequency during the fire protection period in the late twentieth century. A composite MFI of 2.6 years is within the range of fire intervals reported from other fire history studies conducted in the Ozark Plateau. Previous fire history reconstructions at two sites within 40 km of DKDB found similarly frequent fire, with MFIs ranging from 1.6 to 2.9 years during the nineteenth to early twentieth century (Stambaugh and Guyette 2006, Engbring, Heitzman, and Spetich 2008). Frequent fire on the slopes surrounding the glades and barrens at DKDB would have fostered fire-tolerant shortleaf pine, post oak, and blackjack oak, with chinquapin oak dominating the areas with dolomitic parent material. In the Missouri Ozarks, prior to the arrival of Euro-Americans, fire return intervals of 2–5 years promoted highly fire-tolerant shortleaf pine, while slightly longer intervals facilitated the establishment of post oak and black oak (Abrams 1985; Batek et al. 1999, Stambaugh, Guyette, and Dey 2007). Short fire intervals would likely have limited the establishment and persistence of fire-intolerant hardwoods and red cedar outside of wetter, fire-protected topographic positions (Dey and Hartman 2005).

In the absence of fire-scarred material from the glades and barrens, we cannot directly estimate the frequency of fires that burned into the glade and barrens habitat. It makes sense that we did not find fire-scarred samples in the glades and barrens, as older shortleaf pines, the only local species that reliably preserve scars, were rare to absent from the glades and barrens. However, based on the fire record from the surrounding slopes combined with the pattern of tree establishment following fire cessation, we suggest that fires likely burned into the glades and barrens with some frequency as was found in Guyette and McGinnes' (1982) previous study of fire history in an Ozark Glade. The area-wide MFI of 12.5 years at DKDB demonstrates that at the very least, several of the historical fires were large and burned across much of the study area including the woodlands adjacent to the glades and barrens. The glades and barrens are somewhat protected by bluff lines and steep rocky slopes (ranging from 5 to 20 ft in height) which mostly encircle the glades and barrens at the site. These topographic barriers may have acted as a fire break and reduced fire frequency compared to the surrounding forests and woodlands. However, in addition to any fires ignited by lightning directly striking the glades and barrens, it seems likely based on fire behavior during prescribed fires on the site and on other topographically similar sites on the nearby Sylamore Ranger District of the Ozark National Forest (D.M. Zollner, Nature Conservancy, Little Rock, AR, USA, personal communication) that many fires burned up onto the glades and barrens via routes where the bluffs are absent or through embers and flames spread by updrafts. Similarly, based on fire behavior during prescribed fires on the site, fires that did burn into the glades and barrens may have been highly spatially variable in their effects. Edaphic restrictions on fuel accumulation (i.e., patches of bare rock and thin soils with sparse fuels) may have limited fire intensity and spread, particularly within the glade habitat. However, grassy fuels would have facilitated fire spread within the barrens and adjacent woodland habitats. Based on the contemporary woody invasion of this site (as discussed below), it seems clear that fire played an important role in shaping vegetation within the glade and barren habitat.

Fire seasonality and climate associations

Most of the scars at DKDB for which seasonality could be determined were dormant-season scars. This pattern aligns with results from previous studies in the Ozark Mountains and the broader eastern US (Guyette et al. 2006; McEwan et al. 2007; Flatley et al. 2013). It is not possible to determine the source of ignition (i.e., lightning or anthropogenic) from tree-ring analysis. However, the dominance of dormant-season scars in the fire record suggests that many ignitions were anthropogenic in origin. Dormant-season scars were likely recorded by fires burning between the months of October and March, which aligns with the traditional season of anthropogenic burning in the Southeast and Midwest (Fowler and Konopik 2007; McClain et al. 2021). In the contemporary record, the number of lightning fires in the Ozark Ecoregion exhibits two peaks: in March–April and in July–August (Short 2022), both of which would generally impart growing-season scars. Lightning fires can occur in any month of the year in this region though the size and intensity of these fires may be limited by seasonal weather and fuel moisture conditions or, in the case of lightning-producing thunderstorms, event-specific precipitation amounts. It is also possible that occasional late summer droughts caused trees to shut down growth in

August and September resulting in late summer fires, either lightning or anthropogenic, being recorded as dormant-season scars. Still, the lack of significant fire-climate associations found in the SEA analysis provides additional support for the conclusion that people were the primary source of ignitions. Indeed, a lack of association between climate and fire occurrence has been interpreted as an indicator of human influence on a fire regime (Drobyshev et al. 2004). One explanation for this is that people may have chosen to burn during periods of less extreme fire weather, rather than during the driest periods when fires may have been more intense and destructive (Schuler and McClain 2003).

Temporal change in fire frequency

Fire frequency varied between the different land use periods at DKDB (Table 2). The Native American period exhibited a composite MFI of 6.0 years. Fire history studies from the Ozarks that analyzed the late seventeenth through the eighteenth century found fire intervals ranging from 4.6 to 60 years, with most sites falling within the 10–20-year range (Guyette and Spetich 2003; Guyette et al. 2006; Stambaugh and Guyette 2006; Stambaugh et al. 2013). These studies have generally concluded that fire was less frequent in this region during this era due to limited human population density and associated ignitions. In the 1600s and 1700s, the Osage people used the Ozarks for seasonal hunting camps rather than permanent settlements, but seasonal hunting may have been accompanied by regular burning to drive game and increase carrying capacity of deer, elk, and bison (DuVal 2006; Jurney 2012). The pollen and charcoal record indicate that Osage occupancy coincided with increases in fire and the expansion of fire-adapted shortleaf pine despite overall wetter conditions (Nanavati and Grimm 2020). Limited fire-scarred sample depth at DKDB prior to the 1800s makes it difficult to draw strong conclusions about fire frequency in this earliest period. However, if fire was more frequent at DKDB than at other sites in the Ozarks, this may have been the result of its close proximity to the White River, a travel corridor that would have brought greater numbers of people and associated ignitions into the area (Stambaugh and Guyette 2006). The latter decades of this land use period were also a time when population in the region was increasing due to the arrival of the Cherokee and other Native peoples displaced from the southeastern US (Whayne 1995; Guyette et al. 2006). Still, the fire frequency at DKDB was highly variable during this period, with short intervals of 2 years followed by longer intervals of 15 years. Seven fire years were recorded during this roughly 40-year period, with three fires occurring in close succession from 1793 to 1798, followed by three more from 1822 to 1829. This was a period of conflict, temporary settlement, and migration compared to the subsequent Euro-American period in which permanent settlements and farmsteads were established nearby (Whayne 1995; Shannon 2012). It is possible that migrations of people during this period led to fluctuations in the frequency of human ignitions, producing periods of frequent fire followed by longer gaps in fire occurrence.

Fire was more frequent during the Euro-American period, likely due to increasing numbers of Euro-Americans arriving in the area (Shannon 2012). Euro-Americans used fire for a multitude of purposes including increasing forage for livestock and land clearing (Pyne 1982). In the Ozarks, Guyette et al. (2002) found a strong positive correlation between human population and fire frequency during an initial settlement phase, followed by declines in fire frequency during a later fuel fragmentation stage (1890–1940) and fire protection. We did not see a decline during this fuel fragmentation phase at our site. Relatively frequent fire continued at DKDB well into the mid-twentieth century. However, there was a decline in fire frequency during the later twentieth century fire protection period with a composite MFI of 16.0 years, which was on the lower end of fire protection intervals compared to other sites in the Ozark Mountains, with most ranging from 27.7 to 80 + years (Guyette and Spetich 2003; Guyette et al. 2006). The shorter fire intervals are partially due to scars produced by two prescribed fires that were conducted by the ANHC in 2001 and 2015. The majority of the fires during the fire protection period burned in the initial two decades, which matches with the mesophication theory that posits that fire exclusion leads to ongoing successional shifts in vegetation and fuels that decrease the probability of fire (Nowacki and Abrams 2008). The longer fire intervals after 1960s seem to support this conclusion.

Fire history and glade/barrens invasion

The timing of tree establishment combined with the fire history from the surrounding pine-oak forest and woodland at DKDB supports the hypothesis that past wildfires shaped vegetation in the glade and barrens complex and the decline of fire disturbance has been an important factor enabling woody invasion of these communities. Tree establishment in the glades and barrens was limited prior to the start of fire protection in the 1930s and no fire-sensitive red cedar predated the fire protection period. Aerial photographs taken in 1938, 1946, and 1949 show significant areas of open to shrubby barrens and cedar-free hardwood woodlands with two main areas of dense cedars, concentrated on the south- and southeast-facing slopes of the glades and barrens (NARA 2025). The two large pulses of establishment occurred as fire intervals

increased, with the last three fires occurring in 1941, 1947, and 1960, excluding recent prescribed fires starting in 2001. Fire intervals of four or more years are generally sufficient for the establishment of oak cohorts (Stambaugh et al. 2014). It is possible that land use changes also contributed to the shift in tree establishment. The initial site descriptions collected by the ANHC starting in 1976 note that there was no evidence of logging in the glades and barrens (Grimmett, Miller, and Davis 1976). However, livestock may have been grazed on the glades and barrens prior to that time. Studies have found that livestock grazing can remove understory competition and disrupt fire regimes, facilitating tree establishment in grassland habitats (Briggs et al. 2002; Nelson 2010). Thin, rocky soils are undoubtedly a prerequisite for the presence of these communities at DKDB and throughout the Ozarks. However, based on our data, fire appears to have played an important role in tipping the site towards open habitat and maintaining the glades and barrens in this state.

If climate fluctuations were an important factor in the twentieth century invasion of the glades and barrens, then we would expect wetter conditions to align with the pulses of establishment. The DKDB site is about 500 km east of the prairie-forest boundary in the Midwestern US, where lands further west receive insufficient precipitation to support tree growth. Therefore, prolonged periods of drought rather than excess moisture are most likely to limit tree establishment at our site. However, the decades of rapid tree establishment from 1940 to 1970 were drier than the decades preceding or following. Red cedar may benefit from canopy openings created by droughts (DeSantis et al. 2011; Hoff et al. 2018) and the years of 1953 and 1954 were exceptionally dry (ranked 15th and 19th driest of the last 500 years). This multi-year drought may have shifted establishment from oaks to red cedar. However, oak recruitment initiated prior to this drought and red cedar recruitment continued from the 1950s through the 1970s. Recruitment over multiple decades, which included significant periods of both drought and wetting, suggests that this was a longer-term shift in disturbance regime, rather than a short-term climatic fluctuation that facilitated woody invasion of the glades and barrens. Therefore, the evidence of frequent fire in the surrounding landscape, combined with the timing of tree establishment in the glade and barrens complex, provides strong evidence that fire was playing an important role in maintaining these open habitats.

Patterns of tree invasion following fire protection

The glades and barrens have been rapidly invaded by woody species during the last 80 years of fire protection with red cedar, oaks, and hickories dominating establishment. The rapid establishment of resprouting oaks and hickories following the last fire suggests that these trees were previously established in the glades and barrens, likely persisting as sprouts in a shrub form during the frequent fire period. Hardwoods may have continually resprouted in the glades and barrens during the frequent fire period but then grew into a closed canopy following the last fires. The establishment of oaks from sprouts that predated fire protection helps explain the absence of a clear relationship between oak tree age and the environmental site conditions (i.e., soil series, slope, elevation, and amount of insolation). The spatial pattern of past fires, rather than environmental site conditions, may have played an important role in the location of oak sprouts prior to fire protection. It is important to note that our age structure is not a random sample of all trees the glades and barrens, but a targeted sample of the three largest trees in each plot. A more complete sample of age structure, including all size classes, would potentially include a greater proportion of trees that established in recent decades and might also include different frequencies of species. For example, red cedar established more recently and might be better represented in younger age classes.

The delayed recruitment of red cedar, compared to oaks and hickories, matches patterns found at prairie-woodland transitions west of our site in Oklahoma (DeSantis et al. 2011; Stambaugh et al. 2014; Hoff et al. 2018). This later timing is logical considering that red cedar do not regenerate through sprouting (Anderson 2003), their seeds are subject to mortality from the heat produced by fires (Hahn and Orrock 2014), and they are not fire tolerant when younger (Anderson and Schwegman 1991). Ortmann et al. (1995) found that prescribed burning at approximately 8-year intervals excluded cedars from grasslands in Nebraska. Environmental site conditions did influence the timing and location of red cedar establishment. Red cedar establishment occurred earliest on sites with lower total insolation, suggesting that higher heat load and/or lower moisture availability may limit or delay red cedar establishment. Another potential explanation is that these sunnier spots had dense grass cover which helped resist cedar establishment. This aspect-driven pattern has been observed in previous studies of red cedar invasion in grasslands and is supported by the overall distribution of glades and barrens on south to southwest facing aspects in the Ozarks (Schmidt and Stubbendieck 1993; Ware 2002). The insolation pattern suggests that wetter and deeper-soiled sites within formerly more extensive glades and barrens are probably the most heavily invaded, the most degraded habitats, and the most threatened in terms of species conservation. These sites are also less likely to be recognized as

formerly open habitats, as they will have been invaded most rapidly following fire cessation and support trees that are older and larger.

The pattern of invasion that we found aligns with the Noss (2012) model in which multiple interacting factors (fire, drought, substrate, landform, grazing) can be responsible for inhibiting woody invasion. The removal of one factor, in this case fire disturbance, means that substrate and landform (soils, aspect) are the remaining controls on woody invasion. The wetter sites quickly shift from a treeless state to woody cover. The drier sites are invaded later, perhaps due to feedbacks such as increased shading from adjacent tree canopies and litter accumulation increasing moisture availability (Van Els et al. 2010). It stands to reason that under more frequent burning regimes—as during the Euro-American period at this site—that recurring fires would have excluded or reduced the density of trees across a broader range of substrates, landforms, and hydrologic regimes and that open habitats, particularly barrens and open woodlands, would expand to cover more area and a greater diversity of environmental conditions. A similar process of expansion of xeric grasslands and glades occurred in the Ozarks due to greater aridity during the mid-Holocene approximately 7500–4500 years BP (Delcourt et al. 1986; Denniston et al. 2000).

Management implications

The DKDB landscape was protected by the ANHC because it contains a mix of native open to semi-open ecosystems that support species and natural communities of conservation concern. However, these species and communities have declined due to past fire suppression, both on the site and across the broader landscape. This has led the ANHC to incorporate prescribed fire into management of the site, but more detailed information on fire history and past woody encroachment from the site and surrounding landscape is needed to inform management decisions. Our work indicates that this broader landscape experienced frequent fire in the past and that the more recent exclusion of fire has initiated substantial vegetation changes, particularly in the glade and barrens habitats. The continued reintroduction of fire to glades, barrens, and surrounding woodlands can help restore these natural communities by reducing tree density, reducing the litter layer, and increasing light at the ground surface (Stephen et al. 2024). Furthermore, restoration of the surrounding oak-hickory woodlands (i.e., applying fire prescriptions at the landscape scale) may be an important step in restoring the structure and function of the glades and barrens. Prescribed burns that include multiple ecological communities are more beneficial for embedded glades and barrens because they remove seed sources for red cedar invasion from surrounding woodlands and they create more diverse, patchy fire effects due to shifting fire behavior over longer burn windows (Miller et al. 2017; Maginel et al. 2019; Stephen et al. 2024). For example, prescribed burning in a glade and barrens complex and the surrounding oak-hickory forest and woodland led to the successful reintroduction and expansion of collared lizard populations in Missouri by facilitating the dispersal of lizards between glade openings and supporting the establishment of stable metapopulations (Brisson et al. 2003; Templeton et al. 2011). The return of regular fire to this landscape could benefit a range of species of plants, insects, birds, and reptiles associated with glades, barrens, and pine-oak woodlands (Jenkins and Jenkins 2006; Comer et al. 2011; Tyndall 2015).

However, for prescribed fire and other ecological restoration and management at DKDB to be most ecologically effective, several data gaps need to be acknowledged. First, the uncertainty around the frequency and character of historical fire within the glades and barrens precludes specific prescriptions for burn frequency based on historical reference conditions. Furthermore, the natural, edaphically driven variability of fuel is likely to create highly variable spatial patterns of fire behavior and effects. Therefore, we suggest an iterative approach where managers reintroduce fire, collect monitoring data, and shape prescriptions based on desired conditions that will promote target species diversity. One challenge to achieving these desired conditions is that larger diameter trees that have been growing in the glade and barrens complex for 60 plus years may be resistant to low-severity fires. Red cedar become more tolerant of fire as they increase in height and diameter (Anderson 2003). Maturing oaks and hickories are likely to be even more tolerant of fire. Third, dense red cedar cover could make it difficult to burn the glades and barrens at less than high severity due to the fuel structure created by the dense red cedar-oak woodland (Hoff et al. 2018). High-severity fire may be less of a concern since the goal is to remove trees (Twidwell et al. 2016). However, safety, liability, and implications for damaging non-woody vegetation and wildlife are all concerns with higher-severity fire. Therefore, large red cedars, oaks, and hickories may need to be thinned to reduce the cover of trees within the glades, barrens, and surrounding woodlands. Once these trees have been thinned and fuels have been reduced, allowing prescribed fires conducted in the surrounding woodlands to burn into the glades and barrens will likely facilitate more open glade and barrens habitat that support desired conservation values.

Conclusion

DKDB Natural Area is a site with high conservation value. It protects a relatively intact landscape that includes two distinct glade and barrens communities, cliff and talus communities, hardwood forest, oak-hickory woodlands, and small patches of shortleaf pine woodlands. The glades and barrens provide habitat for several species that are imperiled or critically imperiled regionally, including powdery cloak fern (*Argyrochosma dealbata* (Pursh) Windham), white sagebrush (*Artemisia ludoviciana* Nutt. ssp. *mexicana* (Willd. ex Spreng.) D.D. Keck), tassel flower (*Brickellia grandiflora* (Hook.) Nutt.), cedar sedge (*Carex planostachys* Kunze), flatrocks tickseed (*Coreopsis grandiflora* Hogg ex Sweet var. *saxicola* (Alexander) E.B. Smith), Nuttall's pleat-leaf (*Nemastylis nuttallii* Pickering ex R.C. Foster), and silvery aster (*Symphyotrichum sericeum* (Vent.) Nesom). We provide evidence that fire has played an important and long-term role in maintaining glade and barrens habitats that support these and other rare and endemic species. The reintroduction of fire through prescribed burning could play an important role in restoring these landscape components that are currently declining but were once prevalent across the Ozark Plateau.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00458-8.

Additional file 1: Supplemental Figure 1 Superposed epoch analysis results for different fire year categories at Devil's Knob-Devil's Backbone, Arkansas, USA. Sample size refers to the number of fire years analyzed. Years of analysis are 1793–1941 for entire record, 1793–1829 for Native American period, and 1830–1941 for Euro-American period. Solid lines indicate 95% confidence interval.

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Authors' contributions

WF conceptualized the research. WF, AR, and LB collected the data. AR and LB processed and dated the tree ring samples. WF completed the analysis and produced the figures. WF wrote the original draft. WF and TW reviewed and edited the manuscript.

Data availability

Data will be made available upon 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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