RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

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RESEARCH ARTICLE

Formation and ecology of oak shrubby layers during long-term oak savanna restoration

Scott R. Abella[1,2,3], Karen S. Menard[4], Timothy A. Schetter[4], LaRae A. Sprow[4], Timothy L. Walters[5], Lawrence G. Brewer[6], Kevin M. Berghel[1], Lindsay P. Chiquoine[1]

Woody plant encroachment can eliminate open-structured habitats and commonly triggers ecological restoration. However, the long-term dynamics and formation processes of encroaching woody layers are often unclear, including after initial restoration has reestablished open habitats, making sustainability of restoration gains in open habitats uncertain. To examine the multi-decade change and formation processes of encroaching oak shrubby layers in midwestern U.S. savannas and woodlands undergoing restoration, we measured: (1) oak shrubby layers (primarily *Quercus velutina*) for 24–34 years on 24 restoration sites receiving 2–17 prescribed fires, (2) demographics of 379 shrubby oak shoots, and (3) age structure to determine recruitment history of oak shoots. The oak shrubby layer did not form until the second or third decade of restoration management. It was maximized when sites had cumulatively received ≥4 fires, but none within 3 years, and overstories were open. Most (91%) small-diameter (<2.5 cm at 1.4 m) oak shoots were top-killed by fire if incurring ≥15% scorch, but 99% resprouted. Moreover, the greater the scorch, the faster resprouts subsequently grew. Repeated establishment of the shrubby layer occurred through synchronized, even-aged pulses the year after fires. Results suggest that the oak shrubby layer, and its resilience, expands decades into restoration management and represents a conundrum. Some oak regeneration must occur to maintain savanna-woodland structure, and depauperate oak regeneration threatens oak ecosystems in many regions. Yet for restoring savannas, continual restoration inputs were required to perpetually reduce encroachment by oak, and the inputs needed increased—not decreased—as restoration sites aged.

Key words: brushland, fire frequency, oak grubs, overstory-understory relationships, *Quercus velutina*, woodland, woody plant encroachment

Implications for Practice

- Once an oak shrubby layer forms decades into oak savanna restoration, low-severity fires at least every 3 years or potentially more severe disturbances must be used to arrest its development to avoid having open habitat restoration negated.
- Dormant-season fires need to keep occurring before oak stems attain fire-resistant sizes as small as 2.5 cm diameter at 1.4 m, and even for stems less than 2.5 cm, fires must scorch at least 15% of a stem to achieve top-kill.
- Developing additional treatments for limiting encroachment by the oak shrubby layer warrants consideration, as does pinpointing how long plant species of open savannas can maintain resilience (including in soil seed banks) to encroachment for determining the minimum management frequency required to maintain open-habitat restoration gains.

Introduction

Woody plant encroachment, the establishment or expansion of tall shrubs or trees in historically open-structured habitats such as savannas and woodlands, is among the most common triggers of ecological restoration (Anderson & Bowles 1999; Borghesio 2014; Ding & Eldridge 2024). Open-structured ecosystems include some of Earth's most biodiverse habitats and offer unique ecological functions (O'Connor et al. 2014; Pile Knapp et al. 2024). As woody plant encroachment advances, open-habitat quality and functions can degrade, eventually resulting in the replacement of open- with closed-canopy habitat (Ratajczak et al. 2012; Teleki et al. 2020).

Many uncertainties remain regarding the formation, ecology, and management of encroaching woody layers across the diversity of settings in which they occur globally (Ding & Eldridge 2024). This uncertainty pertains both to encroachment

Author contributions: all authors conceived and designed the research; LAS implemented prescribed fires; SRA, KSM, TAS, TLW, LGB collected field data; KMB, LPC conducted dendroecological analyses; SRA analyzed the data and wrote the manuscript; all authors reviewed and edited the manuscript.

[1]School of Life Sciences, University of Nevada Las Vegas, Las Vegas, NV 89154-4004, U.S.A.
[2]Natural Resource Conservation LLC, 1400 Colorado Street, Boulder City, NV 89005, U.S.A.
[3]Address correspondence to S. R. Abella, email scott.abella@unlv.edu
[4]Metroparks Toledo, 5100 West Central Avenue, Toledo, OH 43615, U.S.A.
[5]Haley & Aldrich, Inc., 6420 South Macadam Avenue, Portland, OR 97239, U.S.A.
[6]Center for Environmental Restoration, Northern Kentucky University, Highland Heights, KY 41099, U.S.A.

doi: 10.1111/rec.14386
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14386/suppinfo

as a process triggering initial ecological restoration of open habitats and as a process that may occur after initial restoration activities or during ongoing restoration management (Miller et al. 2017). For example, after initial restoration has removed woody plant encroachment, such as via cutting or fire to restore open habitats, the degree or time frame whereby woody layers may re-encroach is often uncertain (Haney et al. 2008; Taft 2020). The degree or timing of woody plant encroachment can depend on many factors, such as dynamics in canopy cover of mature trees, frequency or severity of disturbances including restoration activities (e.g. prescribed fires), and features of encroaching woody plants such as palatability to browsers or resprouting capability (Borghesio 2014; Vander Yacht et al. 2020). The rates at which woody layers encroach horizontally and grow vertically have been highly variable among studies (e.g. Dey & Hartman 2005; O'Connor et al. 2014; Knapp et al. 2017). It is often unclear whether woody plant encroachment forms via a discrete recruitment event producing even-aged structure or more gradually over time, producing uneven-aged structure (Hruska & Ebinger 1995). These uncertainties complicate restoration project planning, such as how frequently restoration management must occur to avoid having gains in open-habitat restoration negated by repeated woody plant encroachment (Taft 2020).

We examined woody plant encroachment during the restoration of oak (*Quercus*) savannas and woodlands in the midwestern United States. Here, over 99% of savannas and woodlands present in the 1800s were lost due to clearing for agriculture, pasture, or urban-suburban development and due to succession to forest primarily from lack of frequent fires that had been set by Native Americans for millennia (Nuzzo 1986; Pile Knapp et al. 2024). In our study area, after closed-canopy forests were restored back to open savanna-woodland habitats and restoration management entered the second through fourth decades post-restoration, the same oak species forming the overstory tree layer were the encroaching woody plants in the understory (Fig. 1). This creates a challenge for restoration because clearly opportunities for oak recruitment are required to sustain oak habitats, in savannas as well as in oak forests where pervasive oak regeneration failure is a concern (Abrams et al. 2022; Hutchinson et al. 2024). However, dense oak shrubby layers (from which individuals have the capability of attaining tree height) can undermine restoration gains in herbaceous plant diversity, pollinators, and open-habitat wildlife (Reinhardt et al. 2017; Grundel et al. 2020; Abella et al. 2023).

Our work first identified long-term temporal patterns in oak shrubby layers through multi-decade sampling at savanna-woodland restoration sites and then examined processes associated with shrubby layer formation, such as post-fire recruitment and growth of individual oak shoots. We examined four questions associated with the patterns and processes of oak shrubby layer formation: (1) When during the multi-decade course of open-habitat restoration management do oak shrubby layers form and persist? (2) What associations exist among changes in overstory tree layers, fire frequencies, and encroaching oak shrubby layers? (3) Is survival or growth of oak shoots after

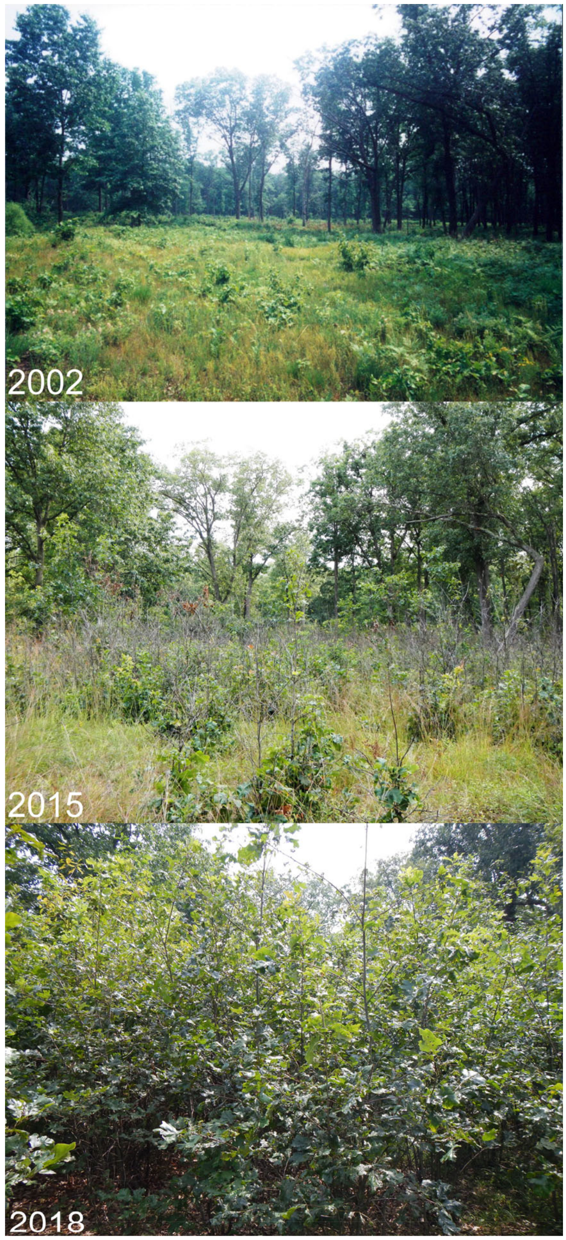

Figure 1. Repeat photos from the same location within an example plot showing the formation of an oak shrubby layer, Ohio, United States. This site was a mixed-species forest before initial restoration treatments (cutting non-oak trees and an initial prescribed fire) were completed by summer 1999 to reestablish oak savanna structure. The site was then burned six additional times between 2000 and 2021, for an average of one fire every 3.3 years, with the longest fire-free period being 7 years (2008–2015). The density of small ($\geq 1 < 10$ cm diameter at 1.4 m) *Quercus velutina* stems remained zero in all sampling years during the first 17 years of restoration. This is exemplified in the 2002 photo in which herbaceous plants (e.g. *Lupinus perennis*, *Tephrosia virginiana*, *Carex pensylvanica*, and *Pteridium aquilinum*) and small shrubs (e.g. *Rosa carolina* and *Vaccinium pallidum*) predominated 4 years into restoration. A well-developed oak shrubby layer is visible by 2015, when 160 *Q. velutina* stems per hectare occurred, despite a spring burn preceding summer sampling that year. By 2018, 2420 *Q. velutina* stems per hectare were present, and herbaceous plants were restricted to small openings between *Q. velutina* sprouts within the well-developed oak shrubby layer. Photos by S.R. Abella.

prescribed fires predictable from stem size and degree of scorch? (4) Are encroaching layers even- or uneven-aged (Table 1)?

Methods

Study Area

The study area was the 1797 ha Oak Openings Preserve (41°33′N, 83°51′W), administered by Metroparks Toledo, within the 45,000 ha Oak Openings region in northwestern Ohio, United States (Fig. S1; Schetter et al. 2013). Climate is temperate, with daily average temperature ranges of −8 to 0°C in January and 17–29°C in July and 86 cm/year of precipitation (34 cm in summer from May through August; 1955–2023 records, Toledo Airport station; National Oceanic and Atmospheric Administration, National Centers for Environmental Information, Asheville, NC, U.S.A.). The low-relief, sandy, Oak Openings region formed on sediments deposited along dynamic shorelines of Ice Age-era lakes larger than present-day Lake Erie, situated just northeast of the region. Analysis of U.S. General Land Office surveys, conducted from 1817 to 1832 and considered to represent pre-settlement reference conditions, revealed that vegetation was dominated by oak savanna (averaging 14 trees/ha ≥13 cm in diameter at 1.4 m stem height [hereafter, diameter at breast height [DBH]] of primarily black oak [*Quercus velutina*] and white oak [*Quercus alba*]) and oak woodland (90 trees/ha of the same oaks as savannas) on uplands bisected by low-lying prairie and floodplain forest wetlands (Brewer & Vankat 2004). Ground layers in the historical savannas and woodlands were described as containing a diversity of forbs, graminoids, and shrubs (Brewer & Vankat 2004), though the abundance of tree species seedlings or sprouts and their dynamics in these ground layers are not well documented. Comparable oak savannas in the Midwest were reported to have been burned by Native Americans nearly annually to at least once per decade (e.g. Chapman & Brewer 2008), with those in the Oak Openings expected to have burned with similar frequency (Brewer & Vankat 2004). Woodlands are thought to have burned less frequently than savannas and developed on leeward sides of water bodies or during periods of less frequent fire in locations that, if burned more frequently, could have been savannas (Brewer & Vankat 2004). In our study area, upland savannas and woodlands inhabited the same soil types, Udipsamments of the Ottokee and Oakville series. In the absence of fire through the 1900s, savannas and woodlands became closed-canopy oak forests, typically with less fire-tolerant trees (e.g. red maple [*Acer rubrum*]) comprising ascending sub-canopy layers (Brewer & Vankat 2004).

Restoration Activities and Data Collection

Questions 1 and 2: Long-Term Change in Oak Shrubby Layers and Associations With Overstories and Fires at 1998 and 1988 Oak Savanna-Woodland Restoration Sites. To address our first two questions regarding long-term dynamics of oak shrubby layers and associations with tree layers and fire frequencies, we collected data during a 24-year period at 23 savanna-woodland sites where restoration began in 1998 and during a 34-year period at the region's oldest savanna restoration site beginning in 1988 (Table 1). Before restoration in summer 1998 at the 1998 restoration sites, 23 plots (each 20 m × 25 m [0.05 ha]) were located throughout the preserve in portions prioritized for restoration on the basis of containing oak savanna or woodland in the early 1800s land survey (Brewer & Vankat 2004), being conducive to reintroducing fire (i.e. in the interior of the preserve away from surrounding land uses such as rural residences), and containing mature oak structure with trees approximately 50–100+ years old (sensu Leach & Givnish 1998). To utilize existing tree structure, locations with higher densities of mature oaks were targeted for woodland restoration while those with fewer oaks were targeted for savanna restoration. After pre-treatment data collection (described below) in summer 1998, non-oak trees (primarily red maple and black cherry [*Prunus serotina*]) too large

Table 1. Summary of study questions and associated data for examining long-term formation and recruitment processes of oak shrubby layers (consisting mainly of *Quercus velutina*) during oak savanna and woodland restoration, Ohio, United States. The figure column refers to the figure number in the paper or Figure S3. A map of each set of plots is in Figure S1.

Study questions and data	*Description*	*Data collection*	*Figures*
Questions 1 and 2: timing of shrubby layer formation and relationships with fire and overstory variables			
1998 restoration sites	Twenty-three plots (compared with eight plots in unmanaged oak forests added in 2002) where savanna or woodland restoration began in 1998 using tree cutting and prescribed fire	1998–2021	2, S3
1988 restoration site	Six plots, burned irregularly from 1988 to 2021, and hit by a tornado in 2010	1988–2021	3
Question 3: processes of post-fire recruitment and growth of oak shrubby stems			
379 tracked stems	Demographic tracking of post-fire fate and growth of oak stems on three oak savanna restoration sites initially burned in 2017, 2018, or 2019; with the 2019 site re-burned in 2020	2017–2021	4, 5
Question 4: age structure and recruitment timing of shrubby layers			
24 aged stems	Random selection of oak stems at 24 locations for dendroecological analysis	2018	6

(typically >10–15 cm DBH) to be top-killed by prescribed fires (Abella et al. 2021) were mechanically cut and removed. Sites (ranging in size from 1 to 5 ha) containing the plots then began to receive prescribed fires as early as autumn 1998 and continuing on an irregular schedule varying in frequency and season through time among plots (Table S1). Fires were dormant-season burns in spring (March–April) or autumn (November), included strip and head fires, and had behavior (e.g. flame lengths typically <1 m, with some localized torching such as up into the crowns of sub-canopy trees) typical of the dormant-season fires widely described in midwestern oak forests, savannas, and woodlands (e.g. Haney et al. 2008). Burn frequency and timing on a plot was a function of both logistical factors, contingent on suitable fire weather (e.g. wind direction and fuel moisture) in any given plot and availability of personnel, and ecological factors. Ecologically, the intention was to burn on an irregular, non-systematic schedule and to have at least three fires/decade in savannas and one to two fires/decade in woodlands. This intention was met in woodlands and partly met in savannas, as logistical constraints resulted in some plots receiving fewer than three fires/decade during some time periods.

In 2002, to provide a comparison of change in restoration plots with that in unmanaged sites, eight additional plots were randomly located in unburned, unmanaged oak forests (age 70+ years) throughout the preserve. Plots in unmanaged oak forest and those undergoing savanna or woodland restoration were interspersed across the landscape. The pairwise geographic distance between the 31 plots averaged 2.0 km, and the maximum extent between plots was 5.3 km (Fig. S1).

In summer, between June and September, we measured DBH for each stem ≥1 cm DBH for each tree species on each plot. We then divided stems into those ≥ 1 < 10 cm DBH, representing the sub-canopy layer, and those ≥10 cm DBH, representing larger trees (hereafter termed canopy trees). Once restoration plots began being burned, oaks comprised most or all stems ≥1 < 10 cm DBH on plots, and we focus on oaks in this layer (hereafter termed the oak shrubby layer) in all analyses (Fig. 1). Black oak typically comprised most (>90%) or all of the oak stems, with only small amounts of White oak or others (e.g. pin oak [*Quercus palustris*]), so we combined oak species. The sampling schedule of plots in the 1998–2021 study period is detailed in Table S1.

At the 1988 oak savanna restoration site, we augmented a published dataset that included an inventory of all trees (≥1 cm DBH) on six, 20 m × 25 m (0.05 ha) plots repeatedly measured between 1988 (before restoration) up to and including 2015 and detailed in Abella et al. (2018). This 40 ha site was black oak forest in 1988, began receiving prescribed fires in autumn 1988, and was hit by a tornado in 2010 that halved oak overstory tree (≥10 cm DBH) basal area (Abella et al. 2018). For the present study, we continued remeasuring all stems of tree species (≥1 cm DBH) in summer annually from 2018 to 2021, during which time plots continued to be burned with variable frequencies in autumn or spring or during the growing season (August) in 2020. In summary, plots were inventoried up to 17 times and burned 4–16 times during the 34-year period spanning 1988–2021 (Table S2).

Question 3: Oak Demography Plots Tracking Post-Fire Fate and Recruitment. To examine our third question, regarding processes of oak shrubby layer formation, we tracked the survival and growth of individual oak shoots in the shrubby layer after fires (Table 1). In each of three oak savanna restoration sites (ranging in size from 4 to 10 ha) with open black oak overstories (≤40 trees/ha ≥10 cm DBH) that contained oak shrubby layers, we randomly located a 10 m × 50 m (0.05 ha) plot to facilitate mapping and tracking of individual oak stems in the shrubby layer. In each plot, we mapped each oak stem ≥1 cm DBH to the nearest 0.1 m into an x, y coordinate system. Each plot then received one prescribed fire, in either April 2017, April 2018, or October 2019. At ignition times, temperatures ranged from 14 to 19°C, relative humidity from 32 to 46%, and winds from 8 to 14 km/hour. The burn prescription included strip and head fires with flame lengths mostly ≤2 m.

In August of the growing season immediately following fires (i.e. 4 months after April fires and 9 months after the October fire), for each mapped oak, we recorded: status (crown alive, crown dead but resprouting from the base of the stem, or completely dead with no live crown and no resprouting), DBH, height to the top of live crown for resprouts if present, percent (in 5% increments) of the stem scorched from ground level to a height of 1 m, and maximum height (m) of scorch up the stem. We also surveyed plots for any newly recruiting stems ≥1 cm DBH and mapped, recorded DBH, and measured the height of these recruits. Our focus was on the features of individual oak stems associated with their post-fire status and growth, and as results were qualitatively similar among the three plots, we combined individual oaks among plots into one dataset for analysis of first post-fire growing season change (Table S3). On the 2018 burn plot, we continued tracking status, growth (DBH and height), and recruitment of stems to 4 years post-fire (inventories in 2018, 2020, and 2021 following the spring 2018 fire). The October 2019 burned plot, inventoried in summer 2020, was re-burned in October 2020 and re-inventoried in August 2021 after the second fire.

Question 4: Dendroecological Sampling of Aboveground Age Structure. To examine the timing of recruitment of oak shoots and whether the oak shrubby layer was even- or uneven-aged (Question 4) at restoration sites, we analyzed age structures of oak shrubby layers (Table 1). We selected 24 locations with patches of the oak shrubby layer using random geographic coordinates from within a pool of the 26 areas containing the 1998 restoration plots and the demographic plots. At each location in September 2018, we recorded the height (to crown top) and DBH of the nearest black oak ≥1 < 10 cm DBH in the shrubby layer. Using a hand saw, we cut black oak stems as close to ground level as possible (within 2 cm) to obtain a 2-cm-thick cross-section from each of the 24 stems. We sanded cross-sections, cross-dated the rings using local climate records

(Fig. S2), and obtained records at the tree locations of prescribed fire occurrences (Metroparks Toledo, Toledo, OH, U.S.A.).

Statistical Analysis

To model spatial and temporal variation of the oak shrubby layer on the 1998 savanna-woodland restoration plots, with and without unmanaged oak forests included (Table 1), we used regression trees, a recursive partitioning technique accommodating mixtures of continuous, ordinal, and categorical variables (Breiman et al. 1984). With oak stems/ha (≥1 < 10 cm DBH) as the response variable, we input as potential explanatory variables the following: overstory density (trees/ha for trees ≥10 cm DBH) and basal area (m^2/ha) in total for all species and for only oak, the cumulative number of fires a plot had received, the time since the most recent fire (years; nominally assigned 20 years in 1998 for restoration plots to reflect no recent fire and assigned 20 years in 2002 for unmanaged oak forests), the number of fires within the previous 3 years, whether a fire had occurred since the previous growing season (yes, no as a categorical variable), and the sampling year (ranging from 1998 to 2021). We implemented regression trees in WEKA 3.8 using the RandomTree algorithm and five-fold cross-validation (Bouckaert et al. 2017).

To model the density of the oak shrubby layer for the 1988 restoration site, we used a regression tree with the same settings and explanatory variables (plus a categorical variable of before/after the 2010 tornado) as for the 1998 restoration sites. Unlike the geographically separated and spatially interspersed 1998 restoration sites, the 1988 plots were at a single geographically distinct site (Fig. S1). Thus, statistical inference for the 1988 plots should be viewed as applicable to this particular site (identified as the 1988 restoration site in Fig. S1 and Table 1) as a long-term (34-year) case study, rather than replicating across the landscape like the complementary 1998 restoration sites.

To analyze the oak shrubby layer demographic data (Tables 1 & S3), we used a classification tree (J48 algorithm, five-fold cross-validation in WEKA 3.8) to model individual oak stem crown status (alive or dead) in the first post-fire growing season based on DBH (cm), stem scorch (%) from ground level up to 1 m, and maximum height of scorch up the stem (m). For top-killed (i.e. dead crown) oaks that resprouted from the base of stems, we modeled resprout height growth (m) the first growing season post-fire using a regression tree with DBH, scorch %, and maximum scorch height input as explanatory variables. For oak stems repeatedly measured 1–4 years post-fire, we used repeated measures analysis of variance (with Tukey tests) in SAS 9.4 to separately analyze temporal change in mean DBH for oaks that were not or were top-killed but resprouted (resprout DBH was analyzed in this case). For oaks that were top-killed, we further analyzed temporal change in resprout height (m).

For the 24 oak stems in the dendroecological dataset, we assessed the relationship between aboveground stem age (years) and DBH and height using linear regressions in SAS 9.4 (Table 1).

Results

Questions 1 and 2: Multi-Decade Change in Oak Shrubby Layers and Associations With Overstories and Fires

Between 1998 and 2021, in oak savannas and woodlands undergoing restoration beginning in 1998 and including unmanaged oak forests, conditions promoting dense oak shrubby layers included low overstory tree basal area, restorations greater than 17 years old that had been repeatedly burned, and either no fire or at least one prescribed fire that stimulated oak resprouting within the previous 3 years (Fig. 2). The oak shrubby layer was maximized when plots had cumulatively received at least four fires, but none in the previous 3 years, and the year was after 2015. At the other extreme, there was no oak shrubby layer if plots were rarely burned and large tree (≥10 cm DBH) basal area exceeded 32 m^2/ha. Moderately dense (averaging 76–101 oak stems/ha that were ≥1 < 10 cm DBH) oak shrubby layers occurred if a site had received four or more prescribed fires and the year was 2015 or earlier (≤17 years since restoration

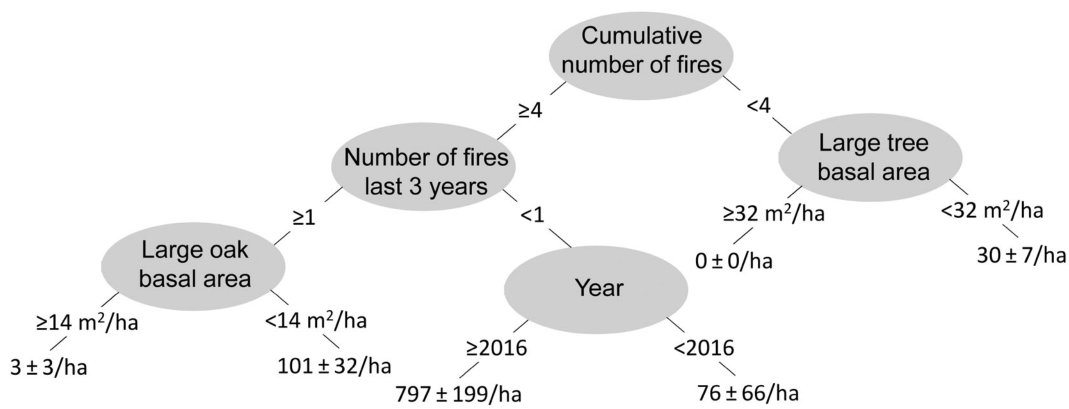

Figure 2. Regression tree estimating the density of the oak shrubby layer based on prescribed fire, large tree (≥10 cm diameter at 1.4 m), and time (within a 1998–2021 period) estimators for 31 plots spanning a gradient of restored oak savannas and woodlands and unmanaged forests, Ohio, United States. The terminal nodes represent the estimated average (±SEM) density of small oak stems (≥1 < 10 cm diameter at 1.4 m). Under cross-validation, the regression tree had a Pearson *r* of 0.66 and a relative absolute error of 66%. A regression tree including only savanna-woodland restoration plots is in Figure S3.

commenced), or, for sites burned within the previous 3 years, large oak basal area was less than 14 m^2/ha.

Excluding unmanaged oak forests and including only the 23 plots in oak savanna-woodlands undergoing restoration beginning in 1998, the densest oak shrubby layers appeared when sites had cumulatively received at least four prescribed fires, time since fire was at least 4 years, and large oak basal area was low (Fig. S3). Moderately dense oak shrubby layers (averaging 101 stems/ha) formed once sites had received at least four fires, time since fire was less than 4 years, and large oak basal area was low. The oak shrubby layer was minimal (<3 stems/ha), regardless of the number of cumulative fires or time since fire, if large tree or oak basal area was high (≥17 or 14 m^2/ha).

During 34 years of restoration from 1988 to 2021 at the 1988 restoration site, dynamics of the oak shrubby layer changed after a tornado hit the site in 2010 and halved large oak basal area (Fig. 3). Before the tornado, the oak shrubby layer was regulated by the number of fires occurring in the previous 3 years, with minimal oak shrubby layers if at least one fire had occurred within 3 years. After the tornado, dense oak shrubby layers formed and persisted, irrespective of the prescribed fires applied, where large-tree density was low.

Question 3: Post-Fire Survival, Recruitment, and Growth of Oak Shoots

On the demographic plots, DBH and the percent of stem scorch from ground level to a height of 1 m influenced crown survival of small oaks (≥1 < 10 cm DBH) the first growing season after prescribed fires (Fig. 4A). If 15% or less of the stem was scorched, almost all (93%) small oaks had their crowns survive. Conversely, almost all (91%) stems were top-killed if they were scorched over 15% and were ≤2.5 cm DBH. Of these 222 top-killed stems, however, 219 (99%) resprouted from the base. Only three stems (1%) were completely dead (i.e. no live crown and no resprouting) the first growing season post-fire. If DBH exceeded 2.5 cm, nearly all (96%) stems had their crowns survive fire even if over 15% of their stem was scorched.

For top-killed oaks that resprouted, the greater the scorch percentage and scorch height, the faster resprout height growth was during the first post-fire growing season (Fig. 4B). Stems with the highest percentage and height of scorch had resprouts averaging 109 cm tall the first growing season, while stems scorched the least averaged 73 cm tall.

Longer-term trends of oak resprouts indicated consistent diameter and height growth through the fourth post-fire growing season. For small oaks that had their crowns survive fire, their DBH increased by an average of 0.5 cm/year (Fig. 5A). For shoots with crowns that died after fire but resprouted, resprout DBH averaged 1.6 cm by 4 years post-fire, thus increasing 0.4 cm/year on average from a zero baseline the first post-fire year when no resprouts had a DBH of at least 1 cm (Fig. 5B). In height, resprouts grew 53 cm/year on average, attaining an average height of 213 cm by 4 years post-fire (Fig. 5C).

Complete mortality (i.e. dead crowns and no basal resprouting) of small oak shoots after fire was rare and was exceeded by new recruitment. On the 2018 once-burned demographic plot, only 2 of 74 (3%) post-fire, live-canopy oak shoots died between 2018 and 2021 (one to four growing seasons after fire), and only 2 of 32 (6%) resprouting individuals died. Along with three shoots already dead in the first growing season, this totaled seven shoots dying by 2021. However, 14 new shoots were recruited, resulting in a net gain of 7 shoots (140/ha net recruitment, or an increase from 2180 shoots/ha the first post-fire year to 2320/ha by the fourth post-fire year). Even on the twice-burned demographic plot, only 1 of 146 (0.7%) oak shoots died completely in the 2-year period (2020–2021) after the 2019 and 2020 fires.

Question 4: Age Structure and Recruitment Timing

Dendroecological analysis of shoot age at ground level supported the demographic data by revealing that 22 of 24 (92%) sample individuals originated in the first growing season after an autumn or spring prescribed fire. The remaining two shoots originated within two growing seasons after fires. There was thus a high degree of synchronization in recruitment through even-aged pulses of regeneration as sprouts or seedlings after fire. Relating shoot age to DBH in the dendroecological samples returned an estimated DBH increase of 0.4 cm/year, similar to

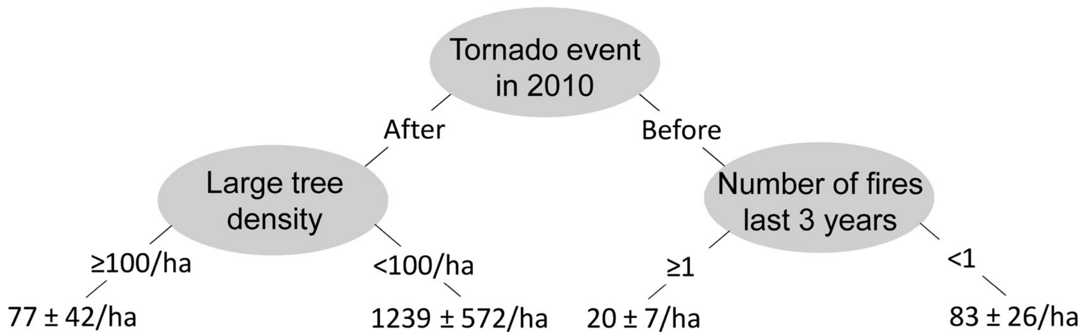

Figure 3. Regression tree estimating the density of the oak shrubby layer using prescribed fire, large tree (≥10 cm diameter at 1.4 m), and before/after tornado event estimators during 34 years (1988–2021) at the 1988 oak savanna restoration site, Ohio, United States. The terminal nodes represent the estimated average (±SEM) density of small oak stems (≥1 < 10 cm diameter at 1.4 m). Under cross-validation, the regression tree had a Pearson *r* of 0.55 and a relative absolute error of 63%.

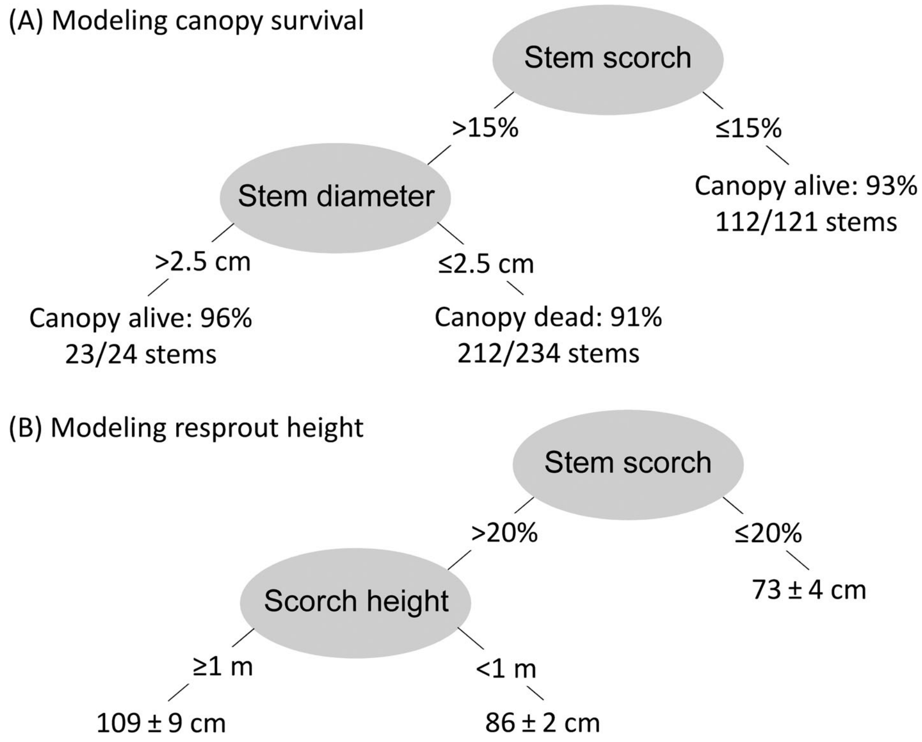

Figure 4. (A) Classification tree estimating crown status (canopy alive and dead) based on stem diameter (at a height of 1.4 m) and percent of the stem scorched from ground level to a height of 1 m for small oaks (≥1 < 10 cm diameter at 1.4 m) after prescribed fire in oak savanna, Ohio, United States. Under cross-validation, the classification tree correctly categorized 92% of instances and had a Kappa statistic of 0.82. (B) Regression tree estimating height growth of resprouting oaks during the first growing season after being top-killed by prescribed fire. The terminal nodes represent the estimated average (±SEM) height of oak resprouts. Under cross-validation, the regression tree had a Pearson *r* of 0.11 and a relative absolute error of 98%.

the 0.4–0.5 cm/year we measured non-destructively on the demographic plots (Fig. 6). Similarly, 10-year-old oak shoots were estimated to be 5 m tall, comparable to the 0.5 m/year height growth we measured for post-fire, resprouting oaks on the demographic plots.

Discussion

Formation of the Oak Shrubby Layer During Restoration

Our long-term and integrated research approaches helped identify the conditions in which oak shrubby layers formed. Oak shrubby layers only appeared on savanna-woodland restoration sites and were absent in oak forests. In fact, oaks that were ≥ 1 < 10 cm DBH were never recorded on any oak forest plot within the 20-year period (2002–2021) during which we monitored forest plots. Although seedling-size oaks (<1 cm DBH) were plentiful in oak forests (Abella et al. 2018*b*), no individuals advanced to at least 1 cm DBH. This is consistent with the oak regeneration failure widely reported in closed-canopy, long-undisturbed eastern North American forests with oak overstories but red maple and other non-oak species recruiting in sub-canopy layers (e.g. Lorimer et al. 1994; Dey & Hartman 2005; Hutchinson et al. 2024). Poor oak recruitment in such forests has been partly attributed to oak's only intermediate shade tolerance (enabling seedlings to occur but lacking the ability for height growth in shade) and non-competitiveness with other trees in shaded, minimally disturbed forests (Abrams et al. 2022).

In contrast, conditions in savanna restoration sites in our study were especially conducive to pervasive oak regeneration and formation of dense oak shrubby layers. Conditions in which the densest oak shrubby layers formed included overstory basal area less than 14 m^2/ha (<40% canopy cover; Abella et al. 2023), after a site had received ≥4 prescribed fires, into the second to third decade after restoration began, and if time since fire was ≥4 years. Moderately dense (approximately 100 stems/ha) oak shrubby layers could form via rapid oak height growth even if fires had occurred within 3 years, once sites had burned four or more times and overstory basal area was less than 14 m^2/ha. Although few other multi-decade studies of oak shrubby layer dynamics during the restoration of midwestern oak savannas exist for comparison, our finding that prescribed fires needed to occur at least as frequently as every 3 years to arrest oak shrubby layer development is within the range reported by prior studies. At least three fires/decade were required to prevent the development of dense oak shrubby layers in an Indiana oak savanna during a 20-year restoration management period (Haney et al. 2008), in a Minnesota savanna during a 32-year period (Peterson & Reich 2001), and in an Oklahoma savanna during a 26-year period (Masters & Waymire 2012). Typical prescribed fires used in oak savanna restoration are

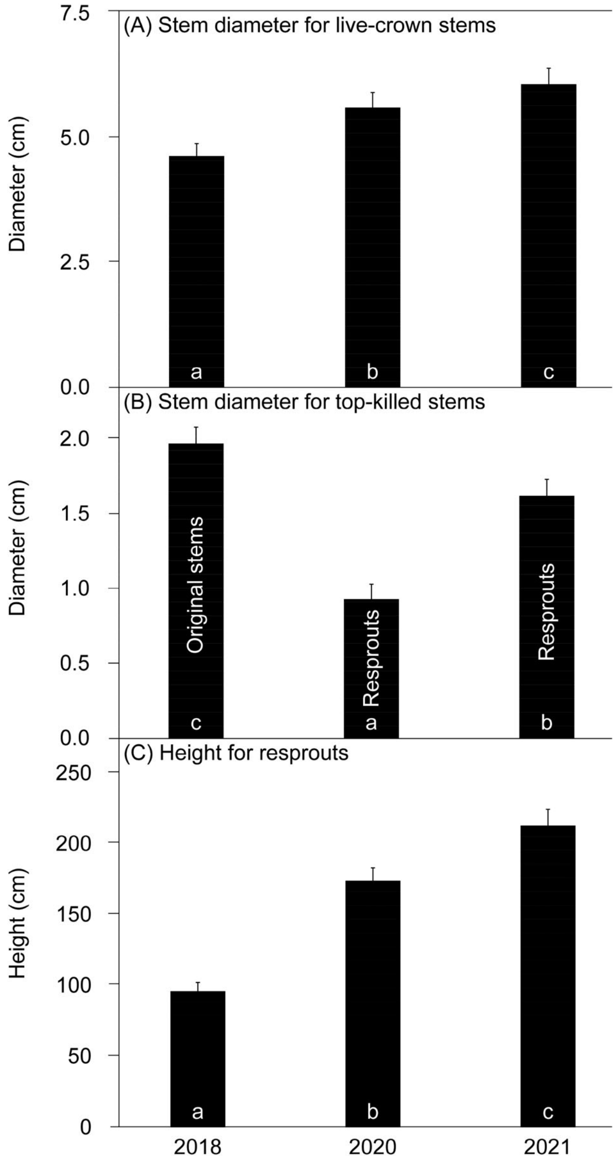

Figure 5. Change in stem diameter (at a height of 1.4 m) for oaks that (A) had their crowns survive and (B) were top-killed by an April 2018 prescribed fire and thereafter resprouted. The diameter in (B) in 2018 is for top-killed stems (none of the resprouts had diameters ≥1 cm at 1.4 m) and in 2020 and 2021 is for the resprouts originating from the top-killed individuals. Also for resprouts, (C) shows change in height, with 2018 representing their height during the first growing season after prescribed fire. For all graphs, bars are means and error bars stand for +1 SE. Within a graph, means without shared letters differ at p less than 0.05.

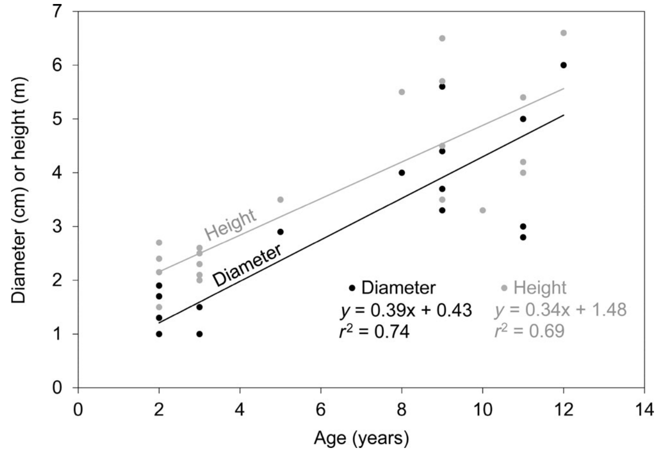

Figure 6. Relationship between shoot age (determined at ground level) and shoot diameter (at a height of 1.4 m) and height for 24 oak shoots in the oak shrubby layer of oak savannas undergoing restoration, Ohio, United States. For diameter, the standard error was 0.05 for the slope and 0.38 for the intercept. For height, the standard error was 0.05 for the slope and 0.37 for the intercept.

dormant-season, low-severity burns (Miller et al. 2017; Taft 2020). As suggested by Haney et al. (2008), it is possible that higher-severity burns could have more persistent effects on the shrubby layer such that fewer burns would be required. However, we found that more severe scorching was associated with faster oak resprout growth.

The demographic and dendroecological data suggested potential processes by which the oak shrubby layer formed under the open and frequently burned habitat conditions of restored savannas. Oaks in the shrubby layer arose from largely even-aged pulses of resprouting cohorts the growing season after fires. These resprouts could exceed 1 cm DBH within two to three growing seasons and rapidly grew in height 1 m/year. The greater the extent of stem scorching, the faster resprouts subsequently grew. It is unclear if this may be associated with direct stimulatory effects of fire or secondary effects, such as reduced competing vegetation, warming microclimates to extend growing seasons, increased soil nutrient availability, or a combination of factors (Cocking et al. 2014). Once resprouts attained a DBH as small as 2.5 cm, they became resistant to top kill by prescribed fires. Black oak, the primary species in the shrubby layer, can develop bark sufficiently thick to limit fire damage when stems attain diameters of only 2–3 cm (Cole et al. 1992; Dey & Hartman 2005). Owing to the continued accumulation of resprouts with repeated fires and their resistance to top kill after attaining 2.5 cm DBH, the oak shrubby layer in our study became more dense through post-fire recruitment and persistence processes as restoration sites matured and were repeatedly burned.

The oak shrubby layer appeared to consist of mostly or completely oak grubs, recognized by investigators in midwestern savannas as early as the early 1800s (e.g. Cottam 1949; Curtis 1959; Chapman & Brewer 2008). Oak grubs are shrub-like sprouts of oaks repeatedly top-killed by fires (Anderson & Bowles 1999; Peterson & Reich 2001). We aged stems at ground level in our dendroecological sampling, and the root systems could be much older (Dee et al. 2022). Naturalist J. Muir and other observers of frequently burned oak savannas in the 1800s in the Midwest suggested that oak grubs only 1 m tall had root systems similar in size to those of full-sized trees, commonly exceeded 100 years old, and had been top-killed but survived perhaps 50–100 fires (Cottam 1949; Curtis 1959). The fact that the oak shrubby layer did not fully appear in our study until multiple decades into restoration, after sites had been burned at least four times, suggests the possibility that the contemporary restoration sites were undergoing a process of oak grub accumulation and persistence described for some historical savannas.

Uncertainty in Consistency With Reference Conditions

To what extent the structure (e.g. extensiveness and density) of the oak shrubby layer on contemporary savanna restoration sites resembles historical savannas is uncertain and difficult to evaluate. Nuzzo (1986) categorized two basic types of oak savannas in the pre-Euro-American-settlement Midwest based on their understories: herbaceous-dominated or brushy savannas dominated by woody plants such as oak grubs. Nuzzo (1986) further noted that patches of each type could have been spatially or temporally interspersed within sites or landscapes. Other than this general understanding that oak shrubby areas occurred historically in some areas of the Midwest, brushy savannas are poorly understood with little information available on their extent, density, temporal dynamics (e.g. expanding or contracting with variation in fire regimes or drought), and relationships with environmental gradients (Grimm 1984; Brudvig & Asbjornsen 2009). In the Oak Openings region where our study occurred, land surveyors during 1817–1832 mentioned areas of no undergrowth (e.g. "land open oakland, no undergrowth") and areas apparently with oak shrubby layers. For example, surveyors described these as "understory little scrub oak, undergrowth thick scrub oak, land grassy prairie and brush oakland, and barrens land with scrubby oak" (compiled by Brewer & Vankat 2004). Surveyors also mentioned encountering trails of Native Americans, who were observed periodically igniting fires described as drivers of savanna physiognomy (Bourne 1820).

Although these observations suggest that oak shrubby layers occurred historically in parts of the landscape, at least four factors (loss of large animals, hydrologic changes, climatic changes, and differences in fire activity) that have changed since settlement could be promotive processes in oak shrubby layer extent and density. Before becoming extinct in Ohio by 1800, American bison (*Bison bison*) inhabited prairies-savannas in northwestern Ohio as "vast herds" described by early 1700s observers (Allen 1876). Although bison diets primarily include graminoids with only small portions of woody plants (Knapp et al. 1999), other activities of bison (e.g. trampling and horning behavior) could have reduced densities of woody plants as they do in contemporary prairies-savannas (Coppedge & Shaw 1997; Hess et al. 2014). Following the loss of these large herbivores, another major landscape change was the installation of extensive networks of drainage ditches in the 1800s and early 1900s to drain wet prairies and low-lying savannas (Tryon & Easterly 1975). Although it is uncertain to what extent this hydrological change influenced tree regeneration in the more upland habitats that were the focus of our study, increased depths and durations of flooding at the margins of upland-lowland sites can limit recruitment of flood-intolerant trees such as black oak (Guo et al. 1998).

Two of the climatic changes include wetter early summers (May–June) and rising atmospheric [CO_2], both potentially aiding tree growth (Davis et al. 2007; Maxwell et al. 2016). Based on the Palmer Drought Severity Index for northwestern Ohio from 1895 to 2021, early summers received increased precipitation in recent decades while droughts became infrequent. For example, exceptionally wet (index $\geq +2$) early summers occurred only once in 37 years from 1960 to 1996 but six times (every 4.2 years) from 1997 to 2021. Furthermore, 2008 and 2019 had the two wettest early summers in at least the last 127 years. Moderate–severe drought occurred every 4.1 years from 1931 to 1988 but only once (2012) in the last 33 years from 1989 to 2021. Moreover, consecutive years of early summer drought happened four times from 1931 to 1988 but never since. Most annual growth of black oak (dominating shrubby layers in our study) occurs in May–June and is positively correlated with precipitation then (LeBlanc & Stahle 2015). In fact, early summer climate has become so favorable for the growth of these trees in recent decades that Maxwell et al. (2016) described a "fading drought signal" whereby favorable climate nearly every year has reduced inter-annual variation in tree ring widths. Extending the climate record in Ohio back to the 1600s using tree rings, recent decades appear even more favorable for tree growth relative to the previous four centuries (Matheus & Maxwell 2018). The only drought year (2012) after 1988, for example, ranked only the 88th driest in the 332 years from 1680 to 2012 (Matheus & Maxwell 2018).

In addition to early summer precipitation likely benefiting early growing trees relative to warm-season herbaceous plants, trees may disproportionately benefit from elevated atmospheric [CO_2] (Long et al. 2004). In a Minnesota oak savanna, elevated [CO_2] increased oak seedling survival by $5\times$ and height growth by 50% (Davis et al. 2007). Elevated [CO_2] particularly benefited oak seedlings in the driest years (Davis et al. 2007). This suggests that elevated [CO_2] could blunt effects of even the now infrequent dry years, further making the current climate conducive to tree growth.

The fourth major factor that has changed since settlement is the nature of fires occurring on the landscape. Fires set by Native Americans in historical midwestern oak savannas were commonly described as sweeping across large landscapes for tens of kilometers, perhaps burning until reaching streams or other firebreaks (Gleason 1922; Grimm 1984). Given the small preserves, fragmentation (e.g. due to roads), and logistical constraints (e.g. smoke management for air quality) on the modern midwestern landscape, contemporary prescribed fires in restored savannas-woodlands are often small (less than tens to hundreds of hectares; Cole et al. 1992; Peterson & Reich 2001; Haney et al. 2008). In addition to modern prescribed fires potentially being timed to burn at lower intensity to be more controllable, the small size of modern fires could result in fires of lower severity than occurred historically (Nuzzo 1986). In noting a dearth of information on the effects of fire seasonality and severity in midwestern savannas, Meunier et al. (2021) suggested further research on how prescribed fires could be timed to interact with the physiology (e.g. carbohydrate storage) of encroaching woody plants to improve meeting open-habitat restoration objectives while minimizing negative effects on other species.

Habitat Quality Tradeoffs

Well before the likely outcome of the oak shrubby layer growing to forest to replace savanna-woodland in the absence of disturbance (Taft 2009; Masters & Waymire 2012; Reinhardt et al. 2017), habitat utilization by biota appears to rapidly change as the oak shrubby layer develops. For example, the biomass of the berry-producing, savanna-woodland shrubs *Gaylussacia* and *Vaccinium* was reduced by two-thirds on sites with high compared to low oak shrubby layer cover (Reiners 1967). Herbaceous plants and small shrubs of prairies-savannas declined sharply and had nearly disappeared once time since fire exceeded 3 years and the oak shrubby layer reached at least 1.4 m tall (Abella et al. 2023). For birds, some shrubby cover (e.g. up to 35%; Mabry 2013) may maximize species richness by enabling coexistence of birds primarily favoring herbaceous vegetation and those benefiting from greater woody cover (Chapman et al. 2004). However, Grundel and Pavlovic (2007) found that prairie-savanna birds declined sharply by just 3 years post-fire as shrubby layers matured. These observations suggest that biota typical of open savannas-woodlands disappear quickly as dense oak shrubby layers grow into thickets of small trees in the absence of disturbance or management (Taft 2009).

Restoration Management Applications

Formation of oak shrubby layers decades into oak savanna restoration presents uncertainties for restoration management because (1) it is unclear how closely the contemporary oak shrubby layers match reference conditions, (2) oak shrubby layers eventually formed on any open savanna site managed using prescribed fire and limited restoration of herbaceous-dominated savanna, (3) oaks in the shrubby layers can grow to small trees to form young forest within a decade to negate major investments in savanna restoration, and (4) oak shrubby layers may be difficult to manage in contemporary conditions potentially more conducive to tree growth than in the past. We offer three main approaches for managing the oak shrubby layer during oak savanna restoration.

First, new and mature (approximately two to three decades old) savanna restoration sites where the oak shrubby layer is allowed to transition to young forest could be rotated spatially within landscapes through time. For example, intensive tree clearing and burning could be used to temporarily restore savanna for a few decades, and then once the oak shrubby layer firmly establishes, the site could transition to forest for a period of decades before again being intensively restored to savanna. An advantage of this approach is that it could create high spatio-temporal variation in habitat structure, promoting landscape-scale floral and faunal diversity (Grundel & Pavlovic 2007; Abella et al. 2020*ab*; Grundel et al. 2020). Disadvantages are that many midwestern preserves where oak savanna restoration occurs may be too small to accommodate this spatio-temporal variation, it may be difficult for practitioners to regularly mobilize resources for the intensive, initial savanna restorations, and propagule sources for savanna plants may not persist through decades of closed-canopy forest occupancy (Reinhardt et al. 2017; Abella et al. 2020*a*).

Second, prescribed fires or mechanical treatments (e.g. mastication) applied to the oak shrubby layer at least as frequently as every 3–4 years appear capable of enabling the persistence of herbaceous understories and keeping savannas open indefinitely under prevailing conditions (Peterson & Reich 2001; Haney et al. 2008; Abella et al. 2023). An advantage of this approach is that it could represent maintenance management for sustaining the initial investment in savanna restoration. This could instead be a disadvantage whereby management resources would be required in perpetuity frequently, with a potential tradeoff of limiting how many new initial savanna restorations can occur.

Third, more aggressive treatments could be periodically attempted to reduce the development of the oak shrubby layer. Although all may require further examination for efficacy and tradeoffs, herbicide, severe fire, numerous cuttings in a growing season to deplete plant carbohydrate reserves, or uprooting intensive treatments could be periodically applied to oak grubs, potentially followed by periods of less-intensive maintenance management.

Acknowledgments

Metroparks Toledo funded this study via contract with Natural Resource Conservation LLC. J. Jaeger and many staff with Metroparks Toledo initially established and sampled the 1998 restoration plots. For help sampling the 1998 restoration plots in 2018, we thank Metroparks interns R. Dollard and J. Penkava, and in 2021, R. Mohamed and J. Cira. We also thank the coordinating editor and two anonymous reviewers for reviewing the manuscript.

LITERATURE CITED

Abella SR, Hodel JL, Schetter TA (2020*a*) Unusually high-quality soil seed banks in a midwestern U.S. oak savanna region: variation with land use history, habitat restoration, and soil properties. Restoration Ecology 28:1100–1112. https://doi.org/10.1111/rec.13164

Abella SR, Menard KS, Schetter TA, Sprow LA, Jaeger JF (2020*b*) Rapid and transient changes during 20 years of restoration management in savanna-woodland-prairie habitats threatened by woody plant encroachment. Plant Ecology 221:1201–1217. https://doi.org/10.1007/s11258-020-01075-4

Abella SR, Schetter TA, Jaeger JF, Brewer LG, Menard KS, Gallaher TD, Diver JJ, Sprow LA (2018) Resistance and resilience to natural disturbance during ecological restoration. Ecological Restoration 36:284–294. https://doi.org/10.3368/er.36.4.284

Abella SR, Sprow LA, Menard KS, Schetter TA, Brewer LG (2023) Changes in groundlayer communities with variation in trees, sapling layers, and fires during 34 years of oak savanna restoration. Natural Areas Journal 43: 243–252. https://doi.org/10.3375/0885-8608-43.4.243

Abella SR, Sprow LA, Schetter TA (2021) Delayed tree mortality after prescribed fires in mixed oak forests in northwestern Ohio. Forest Science 67:412–418. https://doi.org/10.1093/forsci/fxab022

Abrams MD, Nowacki GJ, Hanberry BB (2022) Oak forests and woodlands as indigenous landscapes in the eastern United States. Journal of the Torrey Botanical Society 149:101–121. https://doi.org/10.3159/torrey-d-21-00024.1

Allen JA (1876) The American bisons, living and extinct. Harvard University Press, Cambridge, United Kingdom

Anderson RC, Bowles ML (1999) Deep-soil savannas and barrens of the midwestern United States. Pages 155–170. In: Anderson RC, Fralish JS, Baskin JM (eds) Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York. https://doi.org/10.1017/CBO9780511574627.010

Borghesio L (2014) Can fire avoid massive and rapid habitat change in Italian heathlands? Journal for Nature Conservation 22:68–74. https://doi.org/10.1016/j.jnc.2013.09.002

Bouckaert RR, Frank E, Hall M, Kirkby R, Reutemann P, Seewald A, Scuse D (2017) Weka manual for version 3-8-2. Hamilton, New Zealand: University of Waikato.

Bourne A (1820) On the prairies and barrens of the West. American Journal of Science 2:30–34

Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) Classification and regression trees. Chapman and Hall, New York

Brewer LG, Vankat JL (2004) Description of the vegetation of the oak openings of northwestern Ohio at the time of Euro-American settlement. Ohio Journal of Science 104:76–85

Brudvig LA, Asbjornsen H (2009) The removal of woody encroachment restores biophysical gradients in midwestern oak savannas. Journal of Applied Ecology 46:231–240. https://doi.org/10.1111/j.1365-2664.2008.01590.x

Chapman KA, Brewer R (2008) Prairie and savanna in southern Lower Michigan: history, classification, ecology. Michigan Botanist 47:1–48

Chapman RN, Engle DM, Masters RE, Leslie DM (2004) Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. Ecoscience 11:55–63. https://doi.org/10.1080/11956860.2004.11682809

Cocking MI, Varner JM, Knapp EE (2014) Long-term effects of fire severity on oak-conifer dynamics in the southern cascades. Ecological Applications 24:94–107. https://doi.org/10.1890/13-0473.1

Cole KL, Klick KF, Pavlovic NB (1992) Fire temperature monitoring during experimental burns at Indiana Dunes National Lakeshore. Natural Areas Journal 12:177–183

Coppedge BR, Shaw JH (1997) Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189–196. https://doi.org/10.2307/2426665

Cottam G (1949) The phytosociology of an oak woods in southwestern Wisconsin. Ecology 30:271–287. https://doi.org/10.2307/1932609

Curtis JT (1959) The vegetation of Wisconsin. University of Wisconsin Press, Madison

Davis MA, Reich PB, Knoll MJB, Dooley L, Hundtoft M, Attleson I (2007) Elevated atmospheric CO_2: a nurse plant substitute for oak seedlings establishing in old fields. Global Change Biology 13:2308–2316. https://doi.org/10.1111/j.1365-2486.2007.01444.x

Dee JR, Stambaugh MC, Dey DC (2022) Age, growth, longevity, and post-fire/thinning response of chinkapin oak seedlings in a Kansas upland hardwood forest. Journal of the Torrey Botanical Society 149:122–134. https://doi.org/10.3159/torrey-d-21-00027.1

Dey DC, Hartman G (2005) Returning fire to Ozark Highland forest ecosystems: effects on advance regeneration. Forest Ecology and Management 217:37–53. https://doi.org/10.1016/j.foreco.2005.05.002

Ding J, Eldridge DJ (2024) Ecosystem service trade-offs resulting from woody plant removal vary with biome, encroachment stage and removal method. Journal of Applied Ecology 61:236–248. https://doi.org/10.1111/1365-2664.14551

Gleason HA (1922) The vegetational history of the Middle West. Annals of the American Association of Geographers 12:39–86. https://doi.org/10.2307/2560590

Grimm EC (1984) Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs 54:291–311. https://doi.org/10.2307/1942499

Grundel R, Dulin GS, Pavlovic NB (2020) Changes in conservation value from grasslands to savannas to forests: how a temperate canopy cover gradient affects butterfly community composition. PLoS One 15:e0234139. https://doi.org/10.1371/journal.pone.0234139

Grundel R, Pavlovic NB (2007) Response of bird species densities to habitat structure and fire history along a midwestern open-forest gradient. Condor 109:734–749. https://doi.org/10.1093/condor/109.4.734

Guo Y, Shelton MG, Lockhart BR (1998) Effects of flood duration and season on germination of black, cherrybark, northern red, and water oak acorns. New Forests 15:69–76. https://doi.org/10.1023/A:1006535619398

Haney A, Bowles M, Apfelbaum S, Lain E, Post T (2008) Gradient analysis of an eastern sand savanna's woody vegetation, and its long-term responses to restored fire processes. Forest Ecology and Management 256:1560–1571. https://doi.org/10.1016/j.foreco.2008.07.004

Hess AN, Hess RJ, Hess JLM, Paulan B, Hess JAM (2014) American bison influences on lepidopteran and wild blue lupine distribution in an oak savanna landscape. Journal of Insect Conservation 18:327–338. https://doi.org/10.1007/s10841-014-9640-x

Hruska MC, Ebinger JE (1995) Monitoring a savanna restoration in east-central Illinois. Transactions of the Illinois State Academy of Science 88:109–117

Hutchinson TF, Adams BT, Dickinson MB, Heckel M, Royo AA, Thomas-Van Gundy MA (2024) Sustaining eastern oak forests: synergistic effects of fire and topography on vegetation and fuels. Ecological Applications 34:e2948. https://doi.org/10.1002/eap.2948

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie. Bioscience 49:39–50. https://doi.org/10.2307/1313492

Knapp BO, Hullinger MA, Kabrick JM (2017) Effects of fire frequency on long-term development of an oak-hickory forest in Missouri, U.S.A. Forest Ecology and Management 387:19–29. https://doi.org/10.1016/j.foreco.2016.07.013

Leach MK, Givnish TJ (1998) Identifying highly restorable savanna remnants. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:119–127

LeBlanc DC, Stahle DW (2015) Radial growth responses of four oak species to climate in eastern and central North America. Canadian Journal of Forest Research 45:793–804. https://doi.org/10.1139/cjfr-2015-0020

Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. Annual Review of Plant Biology 55:591–628. https://doi.org/10.1146/annurev.arplant.55.031903.141610

Lorimer CG, Chapman JW, Lambert WD (1994) Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology 82:227–237. https://doi.org/10.2307/2261291

Mabry C (2013) Optimal shrub density for bird habitat in the midwestern United States. Ecological Restoration 31:63–68. https://doi.org/10.3368/er.31.1.63

Masters RE, Waymire JR (2012) Oak savanna restoration: oak response to fire and thinning through 28 years. Pages 69–91. In: Dey DC, Stambaugh MC, Clark SL, Schweitzer CJ (eds) Proceedings of the 4th Fire in Eastern Oak Forests Conference. General Technical Report NRS-P-102. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania

Matheus TJ, Maxwell JT (2018) Placing modern droughts in historical context in the Ohio Valley using tree-rings. Physical Geography 39:343–353. https://doi.org/10.1080/02723646.2018.1426166

Maxwell JT, Harley GL, Robeson SM (2016) On the declining relationship between tree growth and climate in the midwest United States: the fading drought signal. Climatic Change 138:127–142. https://doi.org/10.1007/s10584-016-1720-3

Meunier J, Holoubek NS, Johnson Y, Kuhman T, Strobel B (2021) Effects of fire seasonality and intensity on resprouting woody plants in prairie-forest communities. Restoration Ecology 29:e13451. https://doi.org/10.1111/rec.13451

Miller JED, Damschen EI, Ratajczak Z, Özdoğan M (2017) Holding the line: three decades of prescribed fires halt but do not reverse woody encroachment in grasslands. Landscape Ecology 32:2297–2310. https://doi.org/10.1007/s10980-017-0569-9

Nuzzo VA (1986) Extent and status of Midwest oak savanna: presettlement and 1985. Natural Areas Journal 6:6–36

O'Connor TG, Puttick JR, Hoffman MT (2014) Bush encroachment in southern Africa: changes and causes. African Journal of Range and Forage Science 31:67–88. https://doi.org/10.2989/10220119.2014.939996

Peterson DW, Reich PB (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914–927. https://doi.org/10.1890/1051-0761(2001)011[0914:PFIOSF]2.0.CO;2

Pile Knapp LS, Dey DC, Stambaugh MC, Thompson FR, Varner JM (2024) Managing forward while looking back: reopening closed forests to open woodlands and savannas. Fire Ecology 20:72. https://doi.org/10.1186/s42408-024-00312-9

Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across north American grasslands and savannas. Ecology 93: 697–703. https://doi.org/10.1890/11-1199.1

Reiners WA (1967) Relationship between vegetational strata in the pine barrens of central Long Island, New York. Bulletin of the Torrey Botanical Club 94:87–99. https://doi.org/10.2307/2483705

Reinhardt JR, Nagel LM, Swanston CW, Keough H (2017) Community-level impacts of management and disturbance in western Michigan oak savannas. American Midland Naturalist 177:112–125. https://doi.org/10.1674/0003-0031-177.1.112

Schetter TA, Walters TL, Root KV (2013) A multi-scale spatial analysis of native and exotic plant species richness within a mixed-disturbance oak savanna landscape. Environmental Management 52:581–594. https://doi.org/10.1007/s00267-013-0120-y

Taft JB (2009) Effects of overstory stand density and fire on ground layer vegetation in oak woodland and savanna habitats. Pages 21–39. In: Hutchinson TF (ed) Proceedings of the 3rd Fire in Eastern Oak Forests Conference. General Technical Report GTR-NRS-P-46. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newton Square, Pennsylvania

Taft JB (2020) Do early trends in oak barrens fire treatment predict later outcomes? Insights from three decades of vegetation monitoring. Fire Ecology 16:23. https://doi.org/10.1186/s42408-020-00083-z

Teleki B, Sonkoly J, Erdős L, Tóthmérész B, Prommer M, Török P (2020) High resistance of plant biodiversity to moderate native woody encroachment in loess steppe grassland fragments. Applied Vegetation Science 23:175–184. https://doi.org/10.1111/avsc.12474

Tryon CA, Easterly NW (1975) Plant communities of the Irwin prairie and adjacent wooded areas. Castanea 40:201–212

Vander Yacht AL, Keyser PD, Kwit C, Stambaugh MC, Clatterbuck WK (2020) Thresholds in woody and herbaceous component co-existence inform the restoration of a fire-dependent community. Applied Vegetation Science 23:159–174. https://doi.org/10.1111/avsc.12483

Supporting Information

The following information may be found in the online version of this article:

Table S1. Schedule of prescribed fires and sampling years for measuring development of oak shrubby layers in savanna-woodland restoration sites where restoration began in 1998, Ohio, United States.

Table S2. Summary of prescribed fire history, disturbance, and sampling years for measuring development of oak shrubby layers.

Table S3. Qualitatively similar results for fate of individual oak stems in the first post-fire year among 3 oak demographic plots.

Figure S1. Location of the Oak Openings region and the 1797 ha Oak Openings Preserve study area.

Figure S2. Palmer Drought Severity Index for May–June from 1895 to 2021 for the northwestern Ohio climatic division.

Figure S3. Regression tree estimating the density of the oak shrubby layer based on prescribed fire and large tree (≥10 cm diameter at 1.4 m) estimators through time for 23 plots in restored oak savannas and woodlands, Ohio, United States.

Coordinating Editor: Stuart Allison

Received: 17 June, 2024; First decision: 13 July, 2024; Revised 21 January 2025 and 14 January 2025; Accepted: 21 January, 2025

Table S1. Schedule of prescribed fires and sampling years (×) for measuring development of oak shrubby layers in savanna-woodland restoration sites where restoration began in 1998, Ohio, U.S.A. Spring and autumn fires were in the dormant season. The number of plots (out of 23 restoration plots) burned is in parentheses, with individual plots burned up to 11 times during the 24-year study period between 1998 and 2021. In 2002, an additional eight plots in unmanaged (i.e. no prescribed fires) oak forests were added to the study for comparison and were sampled in 2002, 2015, 2018, and 2021. Only years with sampling or fires are shown.

Year	Sampling	Fires (no. plots)
1998	×	Autumn (8)
1999	×	Spring (6), autumn (6)
2000	×	Spring (6)
2001		Spring (2), autumn (6)
2002	×	Autumn (5)
2003		Spring (2), autumn (11)
2004	×	Spring (6), autumn (2)
2005	×	Spring (12)
2006	×	Spring (9)
2007		Spring (7)
2008		Spring (6), autumn (4)
2009		Spring (2)
2012		Spring (3)
2013		Spring (2)
2014		Spring (1)
2015	×	Spring (15), autumn (4)
2016		Spring (2)
2018	×	
2019		Spring (6)
2020		Autumn (2)
2021	×	Spring (8)

Table S2. Summary of prescribed fire history, disturbance (notably a 2010 tornado that halved overstory tree density), and sampling years (×) for measuring development of oak shrubby layers in the 1988 restoration site where restoration management began in 1988 and continued for 34 years via prescribed fires, Ohio, U.S.A. Within the 1988-2021 study period, only years with sampling or events are shown. Spring and autumn fires were in the dormant season, and typically half of the six plots at the site were burned. The 2020 summer fire was in August, during the growing season.

Year	Sampling	Events
1988	×	Autumn fire
1989		Spring fire
1990		Spring fire
1991	×	
1993	×	Autumn fire
1994		Autumn fire
1997	×	Spring fire
1998	×	Autumn fire
1999	×	
2000	×	
2001		Autumn fire
2002	×	
2004	×	Autumn fire
2006	×	
2007	×	
2008		Spring fire
2010		Tornado
2012	×	Spring fire, autumn fire
2013		Spring fire
2015	×	Spring fire, autumn fire
2016		Autumn fire
2018	×	
2019	×	Spring fire, autumn fire
2020	×	Summer fire
2021	×	Spring fire

Table S3. Qualitatively similar results for fate of individual oak stems the first post-fire year among three, geographically separated, oak demographic plots as a basis for combining data among the plots for modeling crown survival of individual oak stems (mostly *Quercus velutina*) after prescribed fires, Ohio, U.S.A. Data in the table correspond with the left side division (stems with scorch > 15%, then subdivided into stems with diameters at 1.4 m [DBH] of > and ≤ 2.5 cm) of the regression tree in Figure 4A of the paper. As shown in the table, results were nearly identical among the three plots. If > 15% of a stem was scorched, all or nearly all oak stems with DBH > 2.5 cm had their crowns survive. Conversely, almost all crowns died on stems with DBH ≤ 2.5 cm.

	For stems with scorch > 15%	
	> 2.5 cm DBH	≤ 2.5 cm DBH
	— % of stems with live crowns —	
Plot 1	89	3
Plot 2	100	14
Plot 3	100	7

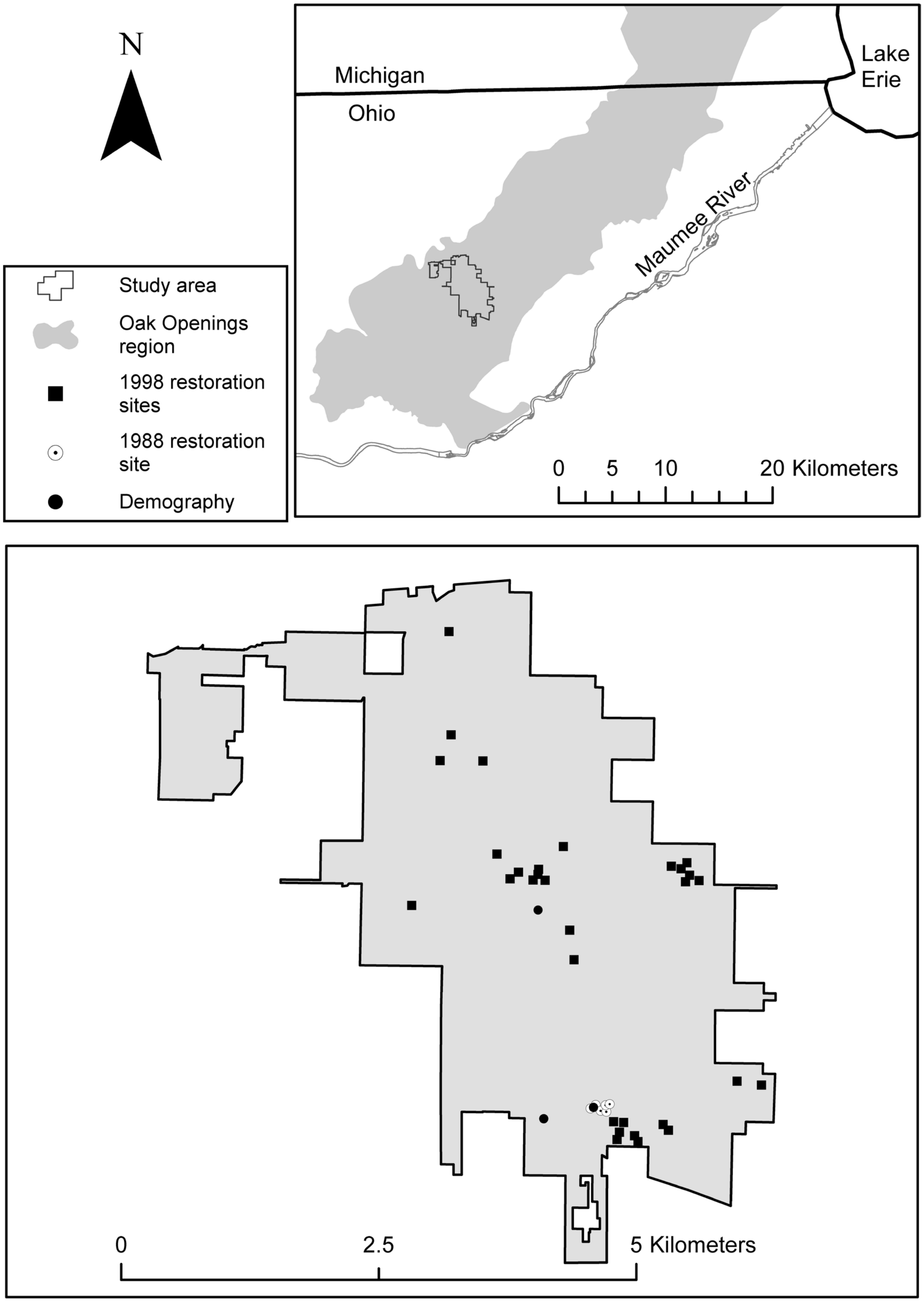

Figure S1. Location of the Oak Openings region and the 1,797-ha Oak Openings Preserve study area including the distribution of study plots, Ohio, U.S.A. Each point is a plot associated with each of the first three study questions summarized in Table 1 of the paper. Unmanaged oak forest plots (n = 8) are included with the 1998 restoration plots (n = 23) in the map.

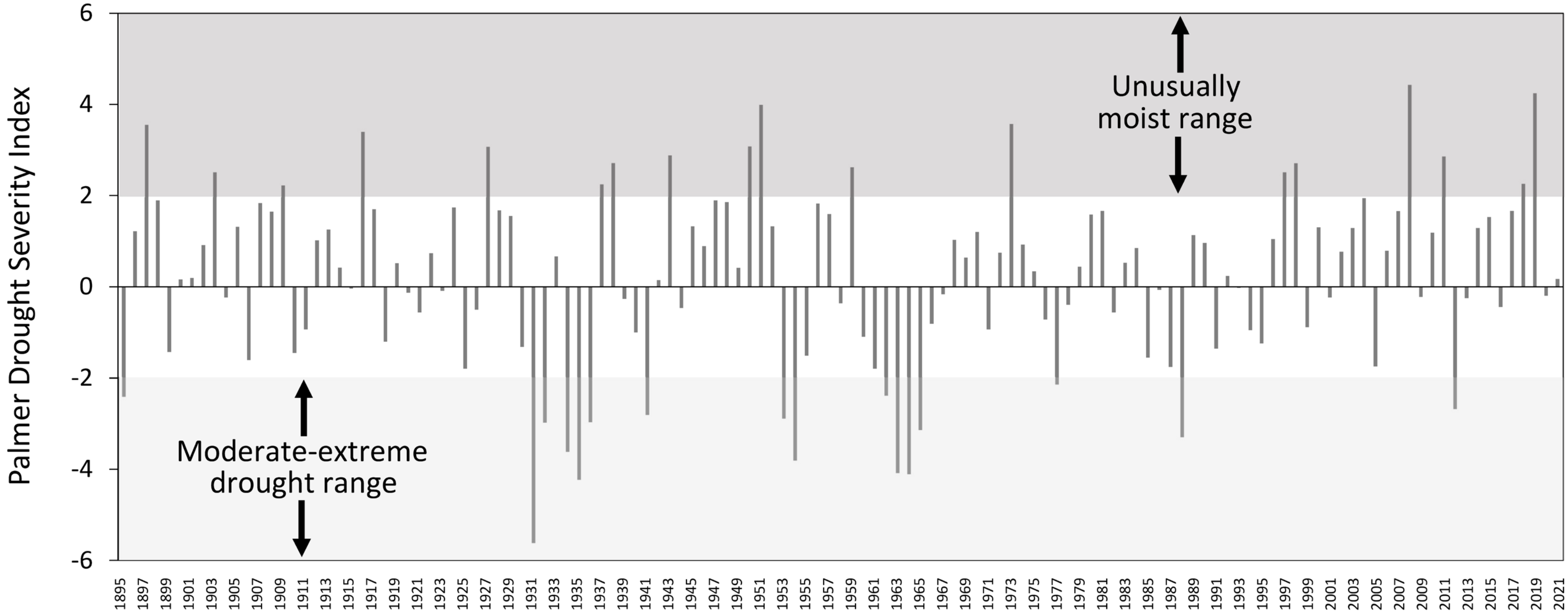

Figure S2. Palmer Drought Severity Index for May-June from 1895-2021 for the northwestern Ohio climatic division (National Centers for Environmental Information, Asheville, North Carolina, U.S.A.).

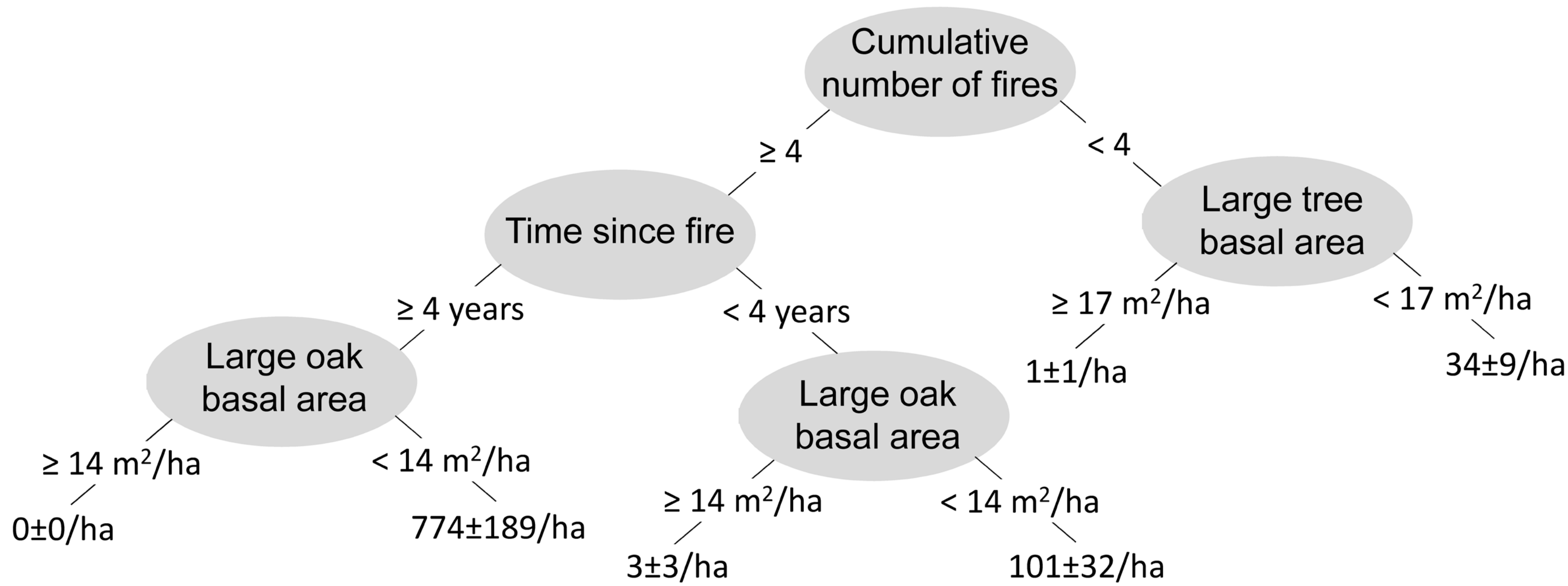

Figure S3. Regression tree estimating the density of the oak shrubby layer based on prescribed fire and large tree (≥ 10 cm diameter at 1.4 m) estimators through time for 23 plots in restored oak savannas and woodlands, Ohio, U.S.A. The terminal nodes represent the estimated average (± SEM) density of small oak stems (≥ 1 < 10 cm diameter at 1.4 m). Under cross-validation, the regression tree had a Pearson r of 0.52 and a relative absolute error of 77%.