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# Fire effects on plant communities in Ozark woodlands and glades

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## Abstract

**Background** Decades of fire suppression caused drastic changes to community structure and composition across ecosystems, including in Ozark woodlands in Missouri, USA. Reintroducing fire can restore ground flora by reducing midstory tree density, increasing ground layer light, and reducing leaf litter accumulation, but we lack a clear understanding of how these effects vary across time and space. We investigated the effects of repeated prescribed fire on ground flora species richness, floristic quality, abundance, community composition, and stand structure over 20 years in a landscape matrix of dry-mesic woodlands, dry woodlands, and glades using data collected from the Ozark National Scenic Riverways Fire Effects Monitoring program in the Current River Watershed in the Missouri Ozarks.

**Results** We found that fire plays a key role in driving community structure and dynamics across community types, although with varying levels of intensity. Herbaceous species richness, abundance, and floristic quality index increased across all community types, while mean coefficient of conservatism decreased. Abundance and floristic quality effects were stronger in drier sites. Community composition changed with successive burns, resulting in several indicator species for post burn treatments. The density of midstory trees declined across community types with repeated fire. The number of burns significantly affected overstory tree density overall, but overstory tree density only declined in dry woodlands and glades and not in dry-mesic woodlands.

**Conclusions** Our results suggest that landscape fire shapes plant community structure and dynamics. Specifically, these findings show that fire effects vary among community types and suggest that land managers should consider landscape heterogeneity in fire application for restoration. Separate community types imbedded in the same landscape may respond to fire differently. Understanding repeated fire effects over several decades across multiple community types is critical to informing fire-driven woodland restoration across landscape scales.

**Keywords** Community composition, Diameter distribution, Fire effects, Floristic quality, Ground flora, Oak woodlands, Ozarks, Prescribed fire, Species richness, Stand structure

## Resumen

**Antecedentes** Décadas de supresión de fuegos causaron drásticos cambios en la estructura y composición de comunidades vegetales de distintos ecosistemas, incluyendo los Bosques de Ozark en Missouri, EEUU. La reintroducción del fuego puede restaurar la flora del sotobosque mediante una reducción en la densidad de árboles del dosel medio, incrementando la luz que llega al suelo y reduciendo la acumulación de mantillo, aunque carecemos de un entendimiento claro sobre cómo esos efectos varían en el tiempo y en el espacio. Investigamos los efectos

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de quemas prescriptas repetidas sobre la riqueza de especies de sotobosque, en la calidad florística, abundancia, composición de la comunidad, y la estructura de los rodales por 20 años en una matriz de paisaje de bosques secos-mésicos, bosques secos, y claros de bosque, usando datos coleccionados por el programa de Monitoreo sobre efectos del fuego en la Ozark National Scenic Riverway, en la cuenca actual del rio en Ozark en Missouri.

**Resultados** Encontramos que el fuego juega un rol clave en la composición de la estructura y dinámica a través de diferentes tipos de comunidades, aunque con variados niveles de intensidad. La riqueza de especies de herbáceas, la abundancia, y el índice de la calidad florística se incrementó en todos los tipos de comunidades, mientras que el nivel de conservación decreció. Los efectos sobre la abundancia y la calidad florística fueron más fuertes en sitios secos. La composición de las comunidades fue cambiando con quemas sucesivas, lo que resultó en diferentes indicadores de las especies para los tratamientos en el post fuego. La densidad de los árboles del dosel medio fue declinando a través de los bosques secos y en claros de bosque, pero no en bosques mésicos.

**Conclusiones** Nuestros resultados sugieren que los fuegos en el paisaje modelan la estructura y dinámica de las comunidades vegetales. Específicamente, estos resultados muestran que los efectos del fuego varían entre diferentes tipos de comunidades y sugieren que los gestores de tierras deben considerar las heterogeneidades del paisaje en la aplicación del fuego para la restauración. Tipos de comunidades separadas pero ensambladas en un mismo paisaje pueden responder al fuego de manera diferente. Entender los efectos de fuegos repetidos por muchas décadas y a través de múltiples tipos de comunidades es crítico para informar sobre la restauración de bosques mediante el fuego a diferentes escalas.

## Background

Before European settlement, fire use by Native Americans was common on the landscape in oak ecosystems across eastern North America and determined plant structure and species composition (Guyette et al. 2002; Dey and Kabrick 2015; Varner et al. 2016). Oak ecosystems consist of forests, woodlands, savannas, and intermittent glades, and account for about half of Eastern North American forests (Smith et al. 2009; Dey and Kabrick 2015). These different community types imbedded together create a heterogeneous landscape which provides increased niches for wildlife diversity and can be particularly important for species of conservation concern that require open habitat (North American Bird Conservation Initiative 2000; Brisson et al. 2003). Across these ecosystems, fire suppresses woody competition and midstory growth, which promotes increased light at the ground level, supporting rich floral diversity (Arthur et al. 2012, 2015; Willson et al. 2018; Barefoot et al. 2019; Maginel et al. 2019). Fire suppression in more recent history largely drove oak woodland succession to forests across Eastern North America (Nowacki and Abrams 2008; Hanberry et al. 2014b; Varner et al. 2016). There are no known examples of low density, large diameter oak woodlands that have not experienced suppression to their historic fire regime in the present day (Hanberry et al. 2014a). The continuing conversion of woodlands to forests via fire suppression may have serious consequences for biodiversity (Nowacki and Abrams 2008; Hanberry et al. 2020).

The long history of fire in Eastern North American woodlands is confirmed by historical, cultural, and biological records such as tree ring fire scars and charcoal found in sediments and soils (Guyette et al. 2005; Hart and Buchanan 2012). The presence and density of Native American and later European settler populations played a dominant role as an ignition source in historical fire regimes (Batek et al. 1999; Guyette et al. 2002, 2005). Most fires in oak ecosystems likely occurred during the dormant season (Guyette et al. 2005). Historical fire regimes were likely site specific (Hart and Buchanan 2012), particularly in topographically rough areas, and varied in frequency over time due to changes in human population density (Guyette et al. 2002, 2005; Stambaugh and Guyette 2008). Based on fire-scarred trees, average fire frequency in the Current River Watershed within the Ozarks likely ranged from every 6.1 to 12.1 years from 1701 to 1820 depending on location in the watershed (Batek et al. 1999).

Post fire suppression, prescribed fire can be used as a tool to halt trends toward mesophication (i.e., process promoting shade tolerant species as defined by Nowacki and Abrams 2008; Alexander et al. 2021) and restore plant communities (Pyke et al. 2010; Brose et al. 2013; Dey and Kabrick 2015; Knapp et al. 2015; Varner et al. 2016). Woodland management utilizing fire often focuses on restoring or maintaining woody structure by reducing tree density and increasing light availability, which promotes germination, growth, and reproduction of native herbaceous species and increases ground flora richness and abundance (Lettow et al. 2014; Dey and Kabrick 2015; Knapp et al. 2015; Willson et al. 2018; Maginel et al. 2019). Prescribed fire also reduces litter depth, which is associated with greater floral diversity and abundance due to its effects on germination and establishment of understory species (Dey and Kabrick 2015; Willson et al. 2018; Barefoot et al. 2019). Studies conducted with timelines under 20 years show that fire alone can reduce midstory tree stem densities, but not basal area or tree density of overstory trees (Arthur et al. 2012; Lettow et al. 2014; Willson et al. 2018; Maginel et al. 2019). However, Knapp et al. (2015) found that 60 years of repeated fire resulted in reduced growth in basal area when compared with unburned plots. Additionally, variability in fire frequency with opportunity for fuel accumulation can assist in midstory tree thinning (Maginel et al. 2019).

Prescribed fire conducted as large landscape burns can provide additional benefits to the ground flora layer by increasing landscape heterogeneity. Here, we define landscape burns as incorporating multiple community types within a fire-managed unit. In landscape burns, fire behavior can change depending on topography, time of day and associated changes in relative humidity, amount of fuel accumulated, fuel moisture, and types of fuels distributed across the landscape, resulting in variable fire effects like intensity and severity (Pyke et al. 2010). Diverse fire effects across a topographically and biotically variable landscape diversifies local community types and may encourage different responses by species present (Nelson 2005; Maginel et al. 2019). For example, plant species richness can respond differently to fire by community type, increasing the most in drier sites and even decreasing in the wettest of sites (Maginel et al. 2019). Maintaining variability in fire effects to create a more heterogenous landscape can be an effective land management goal (Dey and Kabrick 2015).

Although work examining the impact of prescribed fire on hardwood woodland communities has increased over time, only a handful of studies have examined this over a longer timeline and at a landscape scale (Peterson and Reich 2001; Peterson et al. 2007; Maginel et al. 2019). This study examines the response of three community types—dry-mesic woodlands, dry woodlands, and glades—to 21 years of repeated prescribed fire. Due to a fire effects monitoring program initiated by Ozark National Scenic Riverways (ONSR), operated by the U.S. National Park Service, we have the opportunity to understand how these three community types have changed with repeated landscape burns. We investigate the impacts of repeated prescribed fire on these communities' stand structure and ground flora.

Regarding herbaceous ground flora, we determine how repeated prescribed fire impacts species richness, abundance, composition, and floristic quality across Ozark dry-mesic woodlands, dry woodlands, and glades. We hypothesize that repeated prescribed fire will increase ground flora abundance, species richness, and floristic quality overall with greatest impact in dry woodlands due to the most observed loss of herbaceous diversity by land managers at project initiation. Additionally, previous work suggests species richness increases more in drier sites (Maginel et al. 2019). Although glades are our driest sites, preburn observations suggested that even though they were heavily degraded from woody encroachment, the herbaceous ground layer had persisted through fire suppression more than in dry woodlands. Regarding stand structure and composition, we determine how repeated prescribed fire impacts native overstory and midstory tree density, basal area, and species diameter distributions across Ozark dry-mesic woodlands, dry woodlands, and glades. We hypothesize that repeated prescribed fire will reduce tree density in the midstory in all community types. Overstory tree density will begin to decrease in glades and dry woodlands due to more intense fire effects on these drier sites. Repeated fire will not affect basal area as larger trees will continue to grow even as smaller trees die. Repeated prescribed fire will result in more uniform diameter distributions of fire adapted species and a decline in mesic species, resulting in a shift in tree community composition most strongly observed in dry woodlands.

## Methods

### Study sites

All study sites were located within the Current River Watershed in the Current River Hills Subsection of the Ozark Highlands on the Salem Plateau, a highly dissected karst plain, in southern Missouri (Nigh and Schroeder 2002; Thornberry-Ehrlich 2016), on land owned by ONSR, the Missouri Department of Conservation, or by the L-A-D Foundation. Due to its rivers and tributaries, this region is a topographically varied landscape with low mountains, rolling hills, and valleys (Thornberry-Ehrlich 2016). The Salem Plateau contains upland elevations of 390 to 430 m above mean sea level with local relief between 30 and 65 m in the uplands and 60 to 155 m in other areas (Wilkerson 2003). Elevation within the Current River Watershed ranges from 85 to 460 m above mean sea level. The Current River Watershed is in the Ozark Soil Region, which has soils formed from cherty limestone or dolomite (Wilkerson 2003).

In the Missouri Ozarks, an estimated 65% of the historic landscape was open or closed woodlands and 19% was savanna with only 16% designated as forest (Hanberry et al. 2014a). Public Land Survey notes from the early 1800s and tree ring fire scar data indicate that in the Current River watershed, shortleaf pine (*Pinus echinata*) stands, oak savannas, and open woodlands containing xeric oak species like black oak (*Quercus velutina*), post oak (*Quercus stellata*), and blackjack oak (*Quercus marilandica)* were dominant species on the southwest side of the Current River. White oak (*Quercus alba*), scarlet oak (*Quercus coccinea*), and northern red oak (*Quercus rubra*) were more dominant northeast of the river. Hickories (*Carya* spp.) and more fire sensitive species like blackgum (*Nyssa sylvatica*), maples (*Acer* spp.), and eastern redcedar (*Juniperus virginiana*) were also more prevalent northeast of the river which is topographically more dissected. Differences in stand composition were likely driven by variability of fire frequency in addition to geographic features (Batek et al. 1999).

We established permanent plots at study sites in three community types in the Current River Watershed: dry-mesic woodlands, dry woodlands, and glades. Community types were delineated using several factors: associations with specific ecological land types (T. Nigh et al., Missouri Department of Conservation, Jefferson City, MO, USA, unpublished manual; Table S1), soil maps created for ONSR by Missouri Department of Natural Resources, and community type descriptions established in the ONSR Fire Effects monitoring plan. Dry-mesic woodland plots were established on sites with gentle to steep saddle, shoulder, backslope, or bench landforms (Meinert et al. 1997), generally on protected slopes and benches on Gasconade or Eminence-Potosi dolomite geologic formations. Aspects were predominantly north and east (315–135°). Soils were well drained and contained gravel and boulders of chert, dolomite, or sandstone at or near the surface. Canopy was open to closed at 60–100% cover, generally 70–100' tall. *Q. alba*, pignut hickory (*Carya glabra*), mockernut hickory (*Carya tomentosa*), *Q. rubra*, and *Q. velutina* were dominant canopy species. Herbaceous cover was typically at 20–80% ground cover and included high relative cover by *Hylodesmum nudiflorum* and *Amphicarpaea bracteata*.

Dry woodland plots were established on sites with flat or gentle to moderately steep summit, shoulder ridge, shoulder, and backslope landforms (Meinert et al. 1997), typically on exposed upper slopes and summits on Roubidoux sandstone or Upper Gasconade dolomite formations (but also found on exposed lower slopes on Lower Gasconade, Gunter sandstone, or Eminence-Potosi dolomite). Aspects were predominantly south and west (135–315°). Soils were rapidly draining with frequent occurrence of chert gravel or boulders at or near the surface. Canopy was open to closed at 60–90% cover, generally 50–75' tall. Dominant canopy species included *Q. velutina*, *Q. stellata*, *Q. coccinea*, *Q. alba*, *P. echinata*, and *Carya* species. Herbaceous cover was less than 20%. Characteristic species included *Pteridium aquilinum*, *Danthonia spicata*, *Desmodium*, *Hylodesmum*, and *Lespedeza* species.

Glade plots were established on sites with gentle to steep summit, backslope, and bench landforms (Meinert et al. 1997), typically on exposed sites on lower Gasconade dolomite but also on igneous rhyolite, Eminence-Potosi dolomite, or occasionally blufftops on Roubidoux sandstone. Aspects were predominantly south and west (135-315°). Soils consist of patches of bedrock and various sized boulders. Glades are dominated by the herbaceous layer and transition into woodland or forest at their edges. Plots often incorporated some of this transition area due to the limited size of many glades. Dominant species included *Schizachyrium scoparium*, *Sporobolus clandestinus*, *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Rudbeckia missouriensis*, and *Liatris* species.

Community types were mapped in planned fire-managed units (burn units), and plot location points were randomly generated for each community type across burn units (number of plots within each burn unit was determined randomly). Plots were then assessed in the field to ensure they contained the appropriate community types by confirming dominant canopy species (majority of canopy trees) and that the herbaceous layer matched descriptions. This was done visually by park ecologists and not by basal area or standardized tree density assessments. Plots were not included if they contained patches of vegetation not associated with that community type or were within 30 m of roads, trails, or streams. In both woodland communities, rock could not cover more than 20% of the ground. In glade communities, rock could not cover more than 35% of the ground. Because glades tend to be small, and plots generally encompassed transition zones, plots were rejected if they were less than 80% open glade or transitional woodland (no more than 20% non-transitional woodland community type).

Encroachment from eastern redcedar commonly occurs on fire-suppressed glades (Nelson 2005). Because eastern redcedar is resistant to fire once it reaches a large enough size, cedars were mechanically cleared from some glade plots. Dry and dry-mesic woodland plots received no mechanical tree removal. We did not exclude eastern redcedars from analyses, because early data exploration indicated that overall results would be the same with and without them, despite mechanical removal.

## Experimental setup and data collection

Ozark National Scenic Riverways established 14 dry-mesic plots, 21 dry woodland plots, and 27 glade plots (Fig. 1). Plots in dry-mesic and dry woodlands were 50 m × 20 m while plots in glades were 25 m × 10 m due to differences in overall size of these community types. We collected preburn data in each plot the growing season before the first burn occurred. We collected post

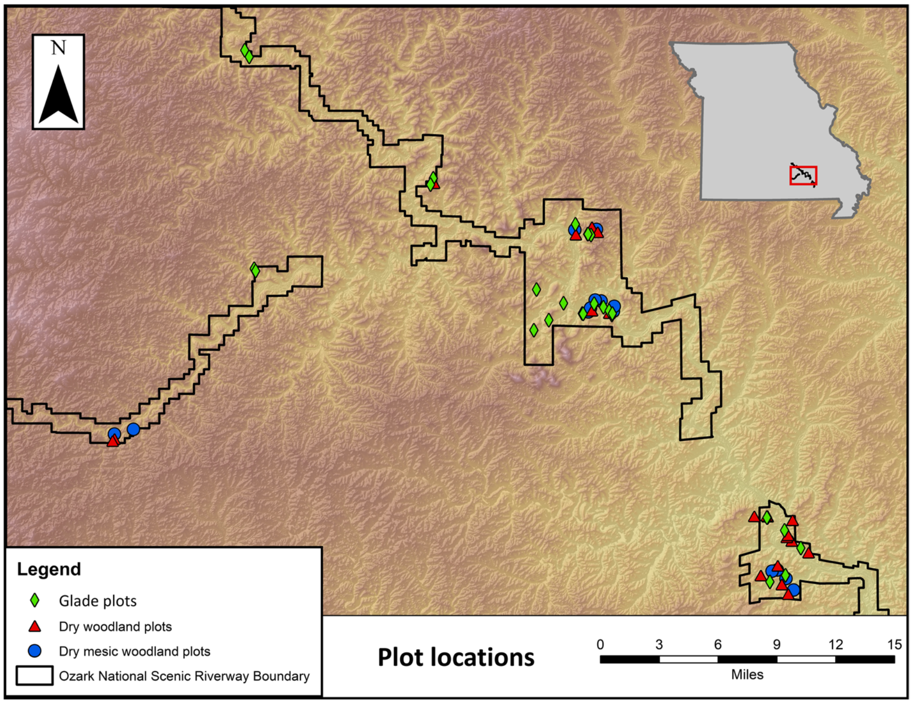


**Fig. 1** Study site and plot locations. Locations of Ozark National Scenic Riverways fire effects plots in Current River Watershed in Shannon and Carter Counties, Missouri. Data was collected from 1999 to 2021

burn data at each plot during the growing season after it received a prescribed fire treatment. We usually collected data within a 2-week window of the original preburn data collection date at each plot to prevent seasonal effects (Table S2). Throughout 22 years of monitoring, data collection occurred between May 20th and September 28th. Data collection began in 1999. This dataset has been analyzed through 2021. The number of plots was expanded throughout the study, with initial plots established in 1999 and additional plots established as late as 2015.

All prescribed burns occurred between February 15 and April 15, during the late dormant season to early growing season, which typically encouraged patchy, surface fires with flame lengths below 1 m. Most burns (over 80%) occurred in March. Over the course of data collection, some burn units were expanded or multiple units were consolidated into fewer, larger units. When accounting for all plots in their "preburn" unit, our data came from eighteen burn units that ranged in size from 29 to 744 hectares with a mean of 239.8 ± 232.5 (σ) hectares. By the end of this study period, there were thirteen burn units that ranged in size from 29 to 903 ha with a mean of 475.2 ± 314.2 (σ) ha. Units were scattered over a 33-km area throughout ONSR and adjacent land. Because burn units changed over the course of the study, so did the number of plots within each unit. When accounting for all plots in their "preburn" unit, there were two to six plots in each burn unit, with a mean of 3.4 ± 1.5 (σ) plots. When accounting for all plots in their year of final data collection, there were two to fifteen plots in each burn unit, with a mean of 4.4 ± 3.7 (σ) plots (Table S3). Because burning was not at the plot level, data was only recorded if 75% of the plot was sufficiently burned. Fifty-eight total prescribed burns occurred in this study between 1999 and 2021. Plots had a mean of 3.8 ± 1.6 (σ) years between burns.

### *Native herbaceous species richness, abundance, composition, and floristic quality*

To measure species richness, we placed 1 $m^2$ quadrats 10 m apart along two permanent transects in glade and dry-mesic woodland plots and along three permanent transects in dry woodland plots (Figure S1). Due to differences in preburn herbaceous density, we placed 5 quadrats in glade plots, 10 quadrats in dry-mesic woodland plots (located along outer two 50-m transects), and 15 quadrats in dry woodland plots (located along central and outer two 50-m transects). Within each quadrat, we identified the presence of each individual plant rooted inside to species, unless it did not have enough distinguishing characteristics, in which case, we identified it to the lowest taxonomic group we could achieve with confidence. We recorded each species once per quadrat. Species were identified using *Steyermark's Flora of Missouri*

(Yatskievych 1999, 2006, 2013) and subsequent species references utilize that taxonomy to maintain names utilized in the dataset. We calculated native herbaceous species richness as the unique number of native species summed across quadrats in each plot. For analysis, we excluded woody vines, shrubs, and trees. Three glade plots were dropped from our dataset for herbaceous species richness analysis due to conflicting protocols in their first year of monitoring.

To measure species abundance, we placed an intercept rod perpendicular to the ground at intercept points located at 0.3-m intervals along the same transects used for species richness. We recorded every plant under 2 m tall that intercepted the rod, identified to species, with only a single count per species per rod. In glade plots, we sampled one 30-m-long transect with 100 intercept points, and in dry-mesic and dry woodland plots, we sampled two 50-m transects, resulting in 332 intercept points in total. For analysis, we excluded woody vines, shrubs, and trees.

We determined floristic quality by using data from the species richness quadrats and calculating a floristic quality index (FQI) for each plot as defined by the mean coefficient of conservatism (mean C) multiplied by the square root of native species richness (Taft et al. 1997; Maginel et al. 2016). Values for coefficients of conservatism (C value) for each species came from Ladd and Thomas (2015). Nonnative species were assigned a C value of 0. Because species were not typically identified to variety in the dataset, for C value designation we chose the lowest C value out of the possible varieties to remain conservative, except in the case of *Sporobolus compositus var. compositus* which is a common variety in our study sites. We supplemented the FQI with separate indicator species analyses (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009; De Cáceres et al. 2010). This analysis determines which species have the highest associations within site types and is run via permutational statistics. Exotic species were not included in the indicator species analyses because they only represented 0.12% of occurrences in this dataset.

#### *Stand measurements*

We distinguished overstory trees as those with diameter at breast height (DBH) of 15 cm or greater. We tagged and mapped all overstory trees in all plots (250 $m^2$ in glade plots and 1000 $m^2$ in dry-mesic and dry woodland plots). We defined midstory trees as those with DBH between 2.5 and 14.9 cm. We recorded midstory trees in 250-$m^2$ subplots in all community types to standardize the area sampled. We recorded species, DBH and survival status (alive or dead) for all overstory and midstory trees. We converted stand structure data into measures of basal area and tree density per hectare for analyses.

#### *Slope and aspect*

We calculated average slope and aspect for each plot in our dataset using 10-m Digital Elevation Models (DEMs) from publicly available GIS data from USGS provided by the National Map Data Download and Visualization Services (U.S. Geological Survey 2019). We obtained slope and aspect values using ArcGIS ArcMAP (Esri Inc. 2021) from the four corners of glade plots and the four corners and the center point of woodland plots. We then averaged these points to obtain a mean slope for each plot. We categorized aspect values as "exposed" (136–315°) and protected (0–135° and 316–360°). We categorized any values that fell on ridges, which were not assigned an aspect value in the DEM, as "exposed." If all points in a plot fell into one category, we assigned that plot that same category of "exposed" or "protected." If a plot contained aspect values that fell into both "exposed" and "protected" categories, we assigned a third category called "border."

### Data analysis

We ran three types of models for our analyses, (1) generalized mixed effects models, (2) multivariate permutational ANOVAs, and (3) indicator species analyses. Given that each category of models had similar structure, we define the broad statistical modeling approach here, and then provide details on predictor and response variables below. For our generalized mixed effects models, we conducted all GLM statistical analyses (R Core Team 2022) using the glmmTMB package (Brooks et al. 2017). All models included plots as random intercepts nested within community types as random slopes. To account for repeated sampling over time, we incorporated an AR1 correlation structure (Brooks et al. 2017). Additionally, we followed a backwards selection approach, where if the interaction between fixed effects were not found to be significant, we dropped the interaction from the model to incorporate these as additive factors. We ran the multivariate permutational ANOVA analyses using the vegan package (Oksanen et al. 2022), and the indicator species analyses using the indicspecies package (De Cáceres and Legendre 2009). All analyses were run in R v. 4.3.1 (R Core Team 2022).

#### *Native herbaceous species richness, abundance, composition, and floristic quality*

To examine how the number of landscape burns influenced herbaceous ground flora richness and abundance, we ran two generalized linear mixed effects models, one with native herbaceous species richness as our dependent variable, modeled with a negative binomial distribution, and the other with the natural log of native herbaceous abundance as our dependent variable, modeled with a normal distribution. To examine how repeated prescribed fire affected FQI and mean C, we ran two separate generalized linear mixed effects models, one with FQI as the dependent variable and one with mean C as the dependent variable, both modeled with normal distributions. For all four models, we included number of burns and community type as interactive fixed effects and slope and aspect category (exposed, protected, or border) as additive fixed effects. To better understand mean C and FQI results, we further analyzed species richness by running models separately for species with C values 0–3 (labelled low C value species), species with C values 4–6 (labelled mid C value species), and species with C values 7–10 (labelled high C value species). For all three models, we used a negative binomial distribution for our dependent variables based on changes in data distribution once mean C was broken out into C value groups. We included number of burns and community type as interactive fixed effects, and slope and aspect category as additive fixed effects.

To examine changes in species composition across our plots, we analyzed how multivariate community composition, as measured through Jaccard (presence-absence) and Bray–Curtis (abundance-weighted) dissimilarity matrices, changed with burn number. We created species composition matrices for each plot in each year across the three community types by summing the occurrence of each species across all 1-m$^2$ quadrats along the transects within plots. Then, we standardized our matrices by presence/absence (Jaccard) or site totals across rows (Bray–Curtis). We ran permutational ANOVAs (PERMANOVAs) for each community type with the standardized species matrix as the response variable and burn number as the predictor variable with 10,000 permutations using the "adonis2" function (Oksanen et al. 2022). Finally, we followed up our multivariate exploration with an indicator species analysis using the species richness quadrat data (De Cáceres and Legendre 2009; De Cáceres et al. 2010). We analyzed each community type separately, as different community types are already known to have different species composition. We calculated abundance as the proportion of quadrats a species appeared in at each plot. We grouped data by number of prescribed burns to determine indicator species with increasing burns. We analyzed indicators for each individual burn number including preburn, as well as each combination of burn numbers. We conducted our indicator species analyses with 999 random permutations (De Cáceres and Legendre 2009). To simplify results, in our interpretation, we focused on indicator species early on in treatments (preburn, burn 1, and burn 2) and later in treatments (burns 4 and 5), but have indicated which species were indicators for a single burn number and which were indicators for combinations.

#### *Stand structure*

We analyzed midstory and overstory responses in two separate models for tree density, defined as trees per hectare, due to their different responses to fire. We explored how number of burns influenced tree density with midstory tree density as a dependent variable modeled with a negative binomial distribution, and overstory tree density as a dependent variable with a normal distribution. To determine how the number of burns affected overstory basal area, we ran a model with overstory basal area as our dependent variable with a normal distribution. For all models, fixed effects included the number of burns and community type as interactive factors and slope and aspect category as additive factors.

We also visually explored diameter distributions of trees in plots pre and post burning for both overstory and midstory trees. Trees were lumped into DBH increments of 2 cm. In preburn distributions, we only included plots that also had data for all five burns. For post burn distributions, we depicted plots after 5 burns. Diameter distributions were separated by community type, species groups (red oaks, white oaks, hickories, and other), as well as by oak species. We chose to review distributions for the more common oak species in each community type, but diameter distributions for all oak species in our dataset can be found in the supplement.

## Results

### Native herbaceous species richness, abundance, composition, and floristic quality

We found that native herbaceous species richness increased additively with increasing number of burns in all three community types ($p \leq 0.001$, Table 1). This effect varied by community type ($p = 0.001$) where dry woodlands increased by 122.6% from preburn to 5th burn, dry-mesic woodlands increased 78.6%, and glades increased 41.6% (Fig. 2A). Mean slope ($p = 0.223$) and plot aspect ($p = 0.277$) had no effect on species richness. The FQI increased across all three community types with repeated prescribed fire ($p \leq 0.001$, Table 1). This effect varied by community type ($p = 0.037$) with an interaction between number of burns and community type ($p = 0.050$). The strongest increase from preburn to fifth burn was in the dry woodlands (48.0% increase) followed by dry-mesic woodlands (28.9% increase) and glades (11.1% increase, Fig. 2B). Mean C decreased with repeated prescribed fire in all three community types, additively ($p \leq 0.001$, Table 1). This effect varied by community type ($p = 0.020$)

**Table 1** Native herbaceous species richness, FQI, and abundance ANOVA statistics

| Analysis | Variable | Df | $\chi^2_{df=1}$ | *p* value |
|---|---|---|---|---|
| Species richness | **Burn number** | 1 | 144.084 | **≤ 0.001** |
| | **Community type** | 2 | 13.501 | **= 0.001** |
| | Mean slope | 1 | 1.477 | = 0.223 |
| | Plot aspect | 2 | 2.410 | = 0.277 |
| FQI | **Burn number** | 1 | 87.054 | **≤ 0.001** |
| | **Community type** | 2 | 6.607 | **= 0.037** |
| | **Burn number: Community type** | 2 | 5.979 | **= 0.050** |
| | Mean slope | 1 | 0.976 | = 0.323 |
| | Plot aspect | 2 | 1.328 | = 0.515 |
| Mean C | **Burn number** | 1 | 30.556 | **≤ 0.001** |
| | **Community type** | 2 | 7.847 | **= 0.020** |
| | Mean slope | 1 | 0.183 | = 0.590 |
| | Plot aspect | 2 | 1.289 | = 0.536 |
| Abundance (natural log) | **Burn number** | 1 | 193.374 | **≤ 0.001** |
| | **Community type** | 2 | 108.261 | **≤ 0.001** |
| | **Burn number: Community type** | 2 | 34.646 | **≤ 0.001** |
| | Mean slope | 1 | 0.951 | = 0.329 |
| | Plot aspect | 2 | 3.279 | = 0.194 |

Multivariate permutational ANOVA statistics for herbaceous ground flora models of species richness, floristic quality index, mean C (coefficient of conservatism) and abundance at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021

with a 7.1% decrease in glades from preburn to 5th burn, a 5.2% decrease in dry woodlands, and a 3.4% decrease in dry-mesic woodlands (Fig. 2C). In total, we identified 439 native species. Twelve species in the richness data were nonnative species (0.16% of occurrences).

When we separated and analyzed species richness by low, mid, and high C values, low C value species increased additively with increasing number of burns by 120.9% in dry-mesic woodlands, 211.2% in dry woodlands, and 121.5% in glades ($p \leq 0.001$, Fig. 3A, Table 2). This effect varied by community type ($p \leq 0.001$). Low C value species richness increased slightly with higher mean slope ($p = 0.040$) and was marginally affected by aspect ($p = 0.090$) with a tendency for increased species richness on exposed sites (Figures S2 and S3). Mid C value species increased additively with increasing number of burns by 46.1% in dry-mesic woodlands, 89.1% in dry woodlands, and 24.3% in glades ($p \leq 0.001$, Fig. 3B, Table 2). This effect varied by community type ($p \leq 0.001$). High C value species did not change significantly with increasing burn number ($p = 0.727$, Fig. 3C, Table 2).

The natural log of native herbaceous abundance increased with increasing number of burns in all three community types ($p \leq 0.001$, Fig. 4, Table 1). Community type affected abundance response ($p \leq 0.001$) with an interactive effect between number of burns and community type ($p \leq 0.001$). The strongest increase in abundance occurred in the dry woodlands at 169.2% increase from preburn to 5th burn, followed by dry-mesic woodlands (43.0% increase) and glades (16.7% increase). Mean slope ($p = 0.329$) and aspect ($p = 0.194$) had no effect on abundance.

For our compositional analyses, we found that the number of burns had a significant impact on both Jaccard and Bray–Curtis dissimilarity across all three community types. The number of burns showed significant effects on community composition for both Jaccard dissimilarity (dry-mesic woodlands: $p = 0.005$; dry woodlands: $p \leq 0.001$; glades: $p \leq 0.001$, Table 3) and Bray–Curtis dissimilarity (dry-mesic woodlands: $p = 0.010$; dry woodlands: $p \leq 0.001$; glades: $p \leq 0.001$, Table 3). Additionally, the indicator species analysis revealed a lack of indicator species in preburn and early burn years whereas plots with 4 and 5 burns had several indicator species across community types (Tables 4, 5, and 6). *Erechtites hieraciifolia* was found as an indicator species in all community types for a combination of burn 1, burn 2, burn 3, burn 4, and burn 5. Indicator species varied in C value from 0 to 7.

### Stand structure

Overall, overstory tree density decreased with increasing burn number ($p \leq 0.001$, Table 7). Response varied by community type ($p = 0.018$) with an interactive effect between burn number and community type ($p = 0.003$). The strongest response was in the dry woodlands and

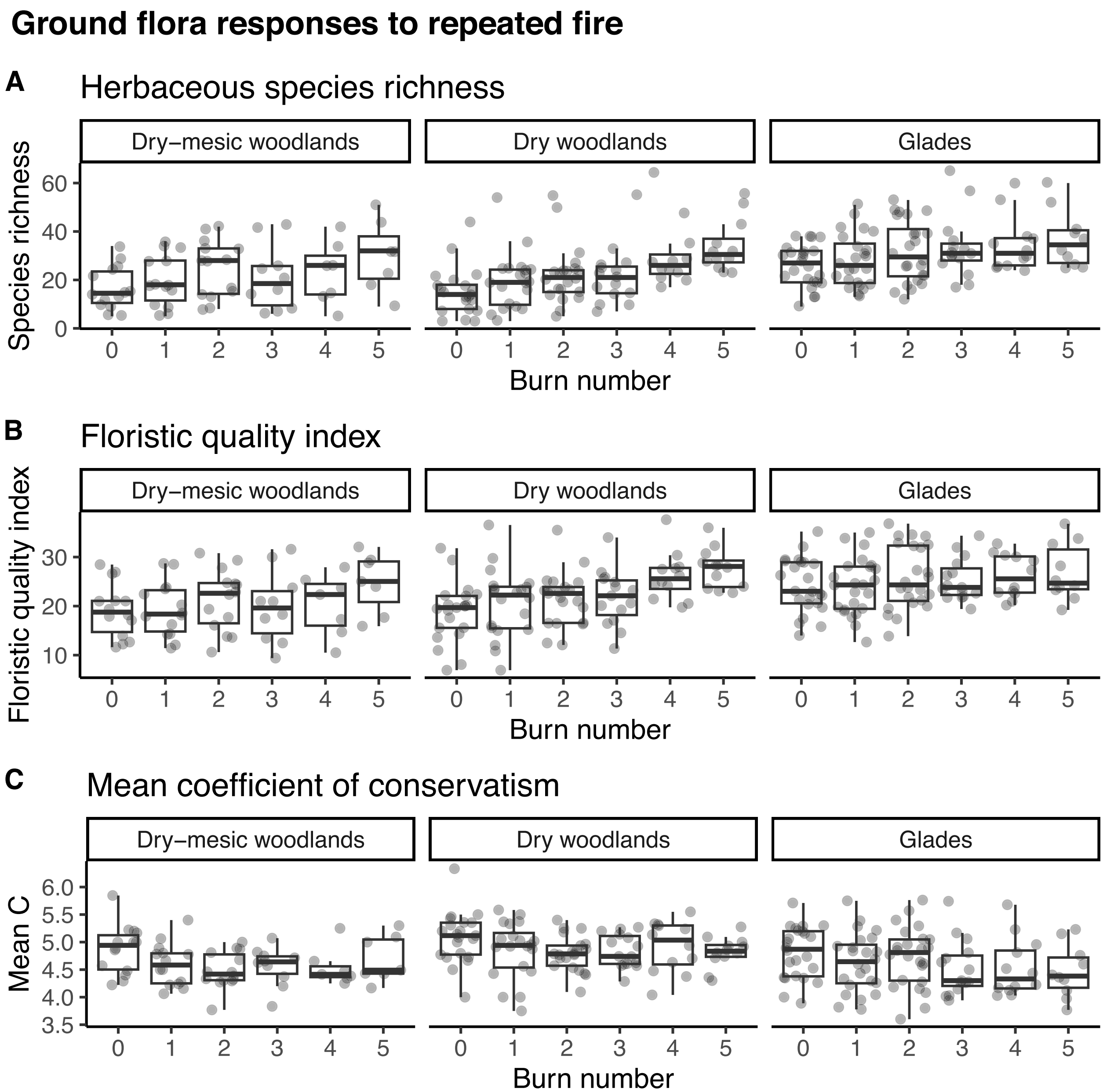


**Fig. 2** Ground flora responses to repeated fire. Ground flora response to repeated prescribed fire is represented via **A** native herbaceous species richness, **B** floristic quality index (FQI), and **C** mean coefficient of conservatism (mean C) in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. **A** Herbaceous species richness increased in all community types. **B** The FQI increased in all community types, with the strongest increase in dry woodlands. **C** Mean C decreased in all community types

glades which decreased by 22.8% and 23.4% from preburn to 5th burn, respectively (Fig. 5). Dry-mesic woodlands did not appear to have strong response with a 6.2% decrease. Mean slope ($p=0.967$) and aspect ($p=0.377$) did not have significant effects on overstory tree density. Midstory tree density decreased with burn number ($p\leq0.001$, Table 7). Midstory tree density decreased by 72.8% in dry woodlands, by 76.1% in dry-mesic woodlands, and by 75.4% in glades from preburn to 5th burn (Fig. 6). Response was not significant by additive community type ($p=0.097$, Figure S4). Aspect had no effect on midstory tree density ($p=0.225$). Overstory basal area increased over time with the number of burns ($p=0.004$, Table 7), and this effect varied by community type ($p\leq0.001$, Fig. 7). Dry-mesic woodlands increased 3.1% in basal area, dry woodlands increased 1.9% in basal

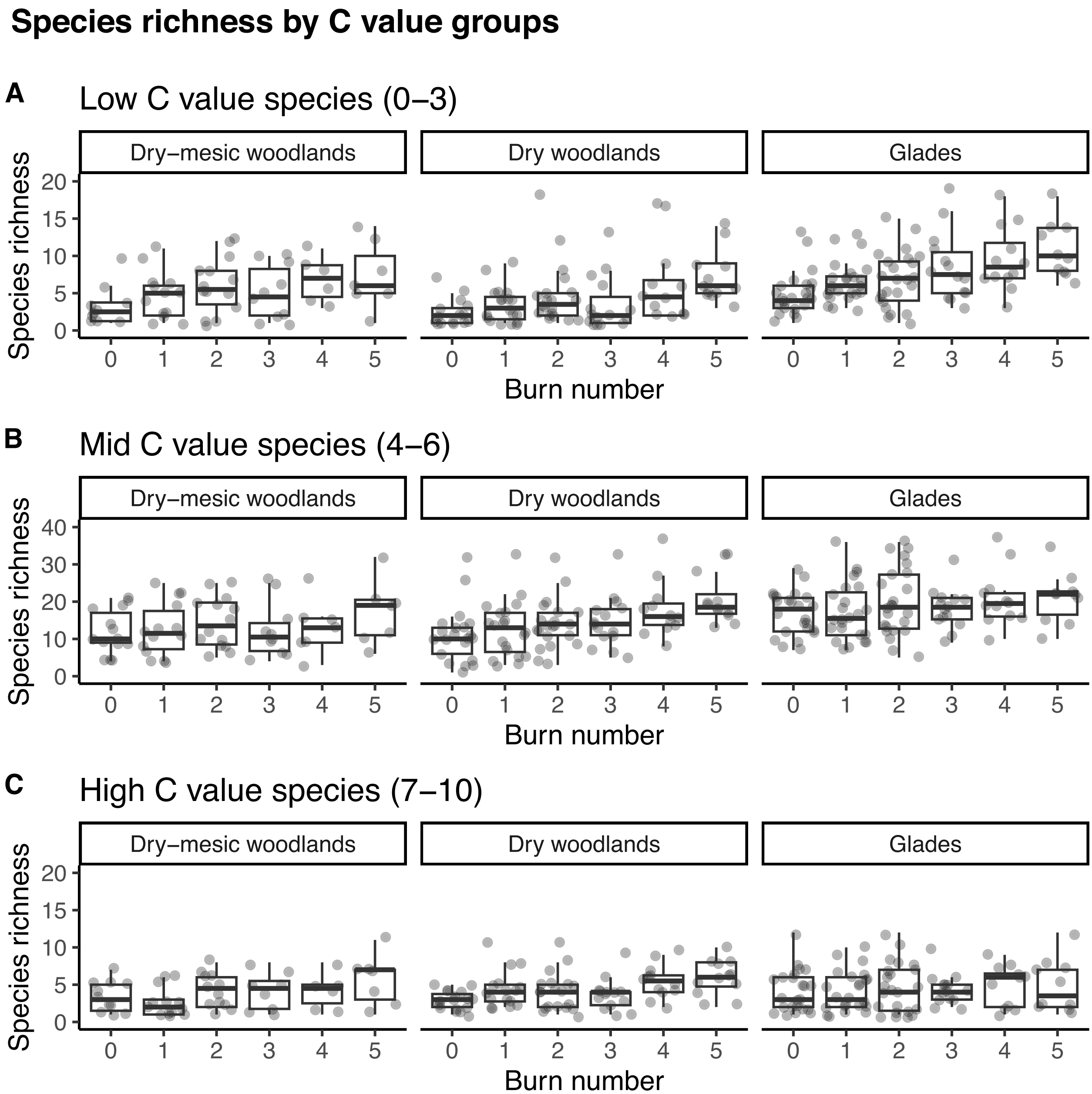


**Fig. 3** Species richness by C value groups. Species richness response to repeated prescribed fire is separated by coefficients of conservatism (C values): **A** species with C values 0–3 (low C value species), **B** species with C values 4–6 (mid C value species), and **C** species with C values 7–10 (high C value species) in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. Species richness only increased significantly for low C value and mid C value species

area, and glades decreased 3.3% from preburn to 5th burn. Mean slope ($p=0.357$) and aspect ($p=0.535$) had no significant effect on overstory basal area.

Diameter distributions generally declined in smaller diameter trees and shifted to uniform distributions post burn treatments when compared with preburn data across community types, species groups, and oak species. In dry-mesic woodlands, red oak and white oak groups declined in midstory size classes so much so that they are only present in few to single plots. *Q. alba* and *Q. rubra* declined in midstory densities but did not transition completely out of the midstory (Fig. 8). In dry woodlands, the white oak group remained in midstory size classes, but only in a handful of plots. Hickories and other species largely persist in the midstory as well as in the overstory, although in smaller numbers. *Q. alba*, *Q. coccinea*,

**Table 2** Mean C by low, mid, and high C-value species ANOVA statistics

| Analysis | Variable | Df | $\chi^2_{df=1}$ | *p* value |
|---|---|---|---|---|
| Mean C | **Burn number** | 1 | 30.556 | **≤ 0.001** |
| | **Community type** | 2 | 7.847 | **= 0.020** |
| | Mean slope | 1 | 0.183 | = 0.590 |
| | Plot aspect | 2 | 1.289 | = 0.536 |
| Low C value species | **Burn number** | 1 | 101.973 | **≤ 0.001** |
| | **Community type** | 2 | 24.656 | **≤ 0.001** |
| | **Mean slope** | 1 | 4.198 | **= 0.040** |
| | Plot aspect | 2 | 4.810 | = 0.090 |
| Mid C value species | **Burn number** | 1 | 76.044 | **≤ 0.001** |
| | **Community type** | 2 | 9.792 | **= 0.007** |
| | Mean slope | 1 | 2.166 | = 0.141 |
| | Plot aspect | 2 | 1.680 | = 0.432 |
| High C value species | Burn number | 1 | 0.122 | = 0.727 |
| | Community type | 2 | 0.144 | = 0.931 |
| | Mean slope | 1 | 0.089 | = 0.765 |
| | Plot aspect | 2 | 2.013 | = 0.366 |

Multivariate permutational ANOVA statistics for mean C (coefficient of conservatism) value models for low C value species richness (values 0–3), mid C value species richness (4–6), and high c value species richness (7–10) at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021

*Q. stellata*, and *Q. velutina* all declined in the midstory and became more uniform in their distribution in larger size classes with *Q. alba* maintaining limited presence in the midstory (Fig. 9). In glades, most trees were under 20 cm DBH. The largest trees in glades all belonged to the white oak group. *Q. marilandica*, *Q. muehlenbergii*, and *Q. stellata* were the most consistently present. All species declined in midstory size classes but were not eliminated (Fig. 10).

## Discussion

We found that in all three community types, herbaceous species richness and abundance increased with repeated landscape fire, which supports other studies in oak woodland ecosystems (Phillips and Waldrop 2008; Lettow et al. 2014; Knapp et al. 2015; Willson et al. 2018; Maginel et al. 2019). We also found that species abundance increased at a higher rate in the dry woodlands when compared to the dry-mesic woodlands, which differs slightly to other work that found species richness tends to increase more in drier sites and may even decline in wetter sites (Maginel et al. 2019). While we saw no effect from slope and aspect, studies found that more exposed sites typically increase more in species richness and abundance with fire (Elliott et al. 1999; Maginel et al. 2019). Slope

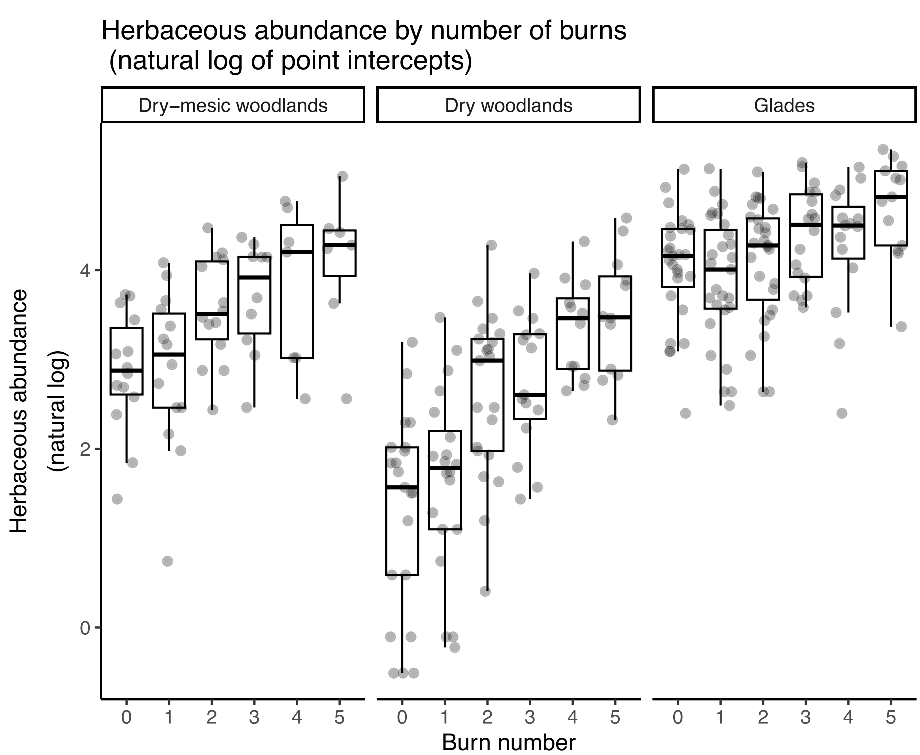


**Fig. 4** Natural log of herbaceous abundance by number of burns. Natural log of herbaceous abundance with increasing number of burns in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. The natural log of herbaceous species abundance increased in all community types and varied in response by community type with the greatest increase in dry woodlands

**Table 3** Native herbaceous composition analyses statistics

| Community type | | Jaccard dissimilarity | | | Bray–Curtis dissimilarity | | |
|---|---|---|---|---|---|---|---|
| | df | F | *p* | $R^2$ | F | *p* | $R^2$ |
| Dry-mesic woodlands | 1, 64 | 2.01 | **= 0.005** | 0.030 | 2.66 | **= 0.01** | 0.040 |
| Dry woodlands | 1, 99 | 4.10 | **≤ 0.001** | 0.040 | 5.01 | **≤ 0.001** | 0.048 |
| Glades | 1, 107 | 2.80 | **≤ 0.001** | 0.026 | 3.45 | **≤ 0.001** | 0.031 |

Jaccard and Bray–Curtis dissimilarity analyses for herbaceous ground flora communities at Ozark National Scenic Riverways from 1999 to 2021

**Table 4** Dry-mesic woodlands indicator species analysis

| **Early burn indicator species** | | | |
|---|---|---|---|
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| None | NA | NA | NA |
| **Later burn indicator species** | | | |
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| *Carex amphibola*[a] | 0.604 | $p = 0.007$ | 3 |
| *Cirsium altissimum*[a] | 0.495 | $p = 0.016$ | 4 |
| *Desmodium nuttallii*[a] | 0.478 | $p = 0.031$ | 7 |
| *Ageratina altissima* | 0.643 | $p = 0.017$ | 2 |
| *Sanicula odorata* | 0.600 | $p = 0.050$ | 2 |
| *Ceanothus americanus* | 0.557 | $p = 0.010$ | 7 |
| *Clitoria mariana* | 0.535 | $p = 0.017$ | 7 |
| *Oxalis dillenii* | 0.519 | $p = 0.010$ | 0 |

[a] indicator for Burn 5 alone

Dry-mesic woodlands indicator species analysis for herbaceous ground flora at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021. Early burn indicator species include species determined indicators for preburn, burn 1, burn 2, or a combination thereof. Later burn indicator species include species determined for burn 4, burn 5, or burns 4 and 5 combined. No indicator species were found for early burn groups (NA). $\sqrt{IndVal_{ind}}$ is the square root of the product of the probability that a site belongs to a group due to that species' presence and the probability of encountering species in sites that belong to a group. Defined groups are burn numbers and combinations of burn numbers

position can affect vegetative community type due to exposure, so any effects from slope and aspect may have been masked by our community types. Additionally, the increasing trend across number of burns for species richness (Fig. 2A) and abundance (Fig. 4) suggest that these community types have not yet stabilized and will continue to increase in richness and abundance with additional burns.

Herbaceous response to fire is likely due to the impact of fire on light availability and litter reduction. Increasing light availability due to canopy openness is an important driver in herbaceous diversity (Bowles et al. 2007; Scharenbroch et al. 2012; Lettow et al. 2014; Willson et al. 2018). Repeated burning likely has a cumulative effect by increasing light availability slowly with increased number of burns (Alexander et al. 2008). Reduction in litter depth as well as availability of exposed mineral soil after

**Table 5** Dry woodlands indicator species analysis

| **Early burn indicator species** | | | |
|---|---|---|---|
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| None | NA | NA | NA |
| **Later burn indicator species** | | | |
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| *Schizachyrium scoparium*[a] | 0.543 | $p = 0.007$ | 5 |
| *Strophostyles umbellata*[a] | 0.470 | $p = 0.003$ | 3 |
| *Bromus pubescens*[a] | 0.445 | $p = 0.004$ | 5 |
| *Aristida purpurascens*[a] | 0.408 | $p = 0.028$ | 5 |
| *Chaemaecrista fasciculata*[a] | 0.368 | $p = 0.032$ | 2 |
| *Veronicastrum virginicum*[b] | 0.408 | $p = 0.029$ | 7 |
| *Galactia regularis* | 0.700 | $p = 0.001$ | 6 |
| *Hieracium gronovii* | 0.642 | $p = 0.002$ | 4 |
| *Chamaecrista nictitans* | 0.604 | $p = 0.001$ | 2 |
| *Ageratina altissima* | 0.592 | $p = 0.001$ | 2 |
| *Solidago ulmifolia* | 0.588 | $p = 0.019$ | 4 |
| *Solidago hispida* | 0.516 | $p = 0.046$ | 6 |
| *Lespedeza frutescens* | 0.500 | $p = 0.005$ | 5 |
| *Euphorbia corollata* | 0.491 | $p = 0.038$ | 3 |
| *Apocynum cannabinum* | 0.489 | $p = 0.026$ | 3 |
| *Carex retroflexa* | 0.484 | $p = 0.013$ | 4 |
| *Carex cephalophora* | 0.453 | $p = 0.008$ | 5 |
| *Rubus enslenii* | 0.439 | $p = 0.031$ | 5 |

[a] indicator for burn 5 alone

[b] indicator for burn 4 alone

Dry woodlands indicator species analysis for herbaceous ground flora at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021. Early burn indicator species include species determined indicators for preburn, burn 1, burn 2, or a combination thereof. Later burn indicator species include species determined for burn 4, burn 5, or burns 4 and 5 combined. No indicator species were found for early burn groups (NA). $\sqrt{IndVal_{ind}}$ is the square root of the product of the probability that a site belongs to a group due to that species' presence and the probability of encountering species in sites that belong to a group. Defined groups are burn numbers and combinations of burn numbers

**Table 6** Glades indicator species analysis

| | | | |
|---|---|---|---|
| **Early burn indicator species** | | | |
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| None | NA | NA | NA |
| **Later burn indicator species** | | | |
| *Species* | $\sqrt{IndVal_{ind}}$ | *P value* | *Coefficient of conservatism* |
| *Conyza canadensis*[a] | 0.405 | $p=0.024$ | 0 |
| *Acalypha monococca* | 0.562 | $p=0.001$ | 3 |
| *Symphyotrichum oolentangiense* | 0.562 | $p=0.005$ | 7 |
| *Penstemon pallidus* | 0.533 | $p=0.003$ | 5 |
| *Panicum flexile* | 0.508 | $p=0.004$ | 3 |
| *Panicum dichotomum* | 0.471 | $p=0.012$ | 6 |
| *Aristida purpurascens* | 0.456 | $p=0.003$ | 5 |
| *Panicum commutatum* | 0.418 | $p=0.029$ | 7 |
| *Carex muhlenbergii* | 0.411 | $p=0.013$ | 5 |
| *Lespedeza frutescens* | 0.381 | $p=0.035$ | 5 |

[a] indicator for burn 5 alone

Glades indicator species analysis for herbaceous ground flora at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021. Early burn indicator species include species determined indicators for preburn, burn 1, burn 2, or a combination thereof. Later burn indicator species include species determined for burn 4, burn 5, or burns 4 and 5 combined. No indicator species were found for early burn groups (NA). $\sqrt{IndVal_{ind}}$ is the square root of the product of the probability that a site belongs to a group due to that species' presence and the probability of encountering species in sites that belong to a group. Defined groups are burn numbers and combinations of burn numbers

prescribed fire are also associated with increased species richness and abundance (Willson et al. 2018; Barefoot et al. 2019).

The FQI increased while mean C decreased with increasing number of burns, which suggests conflicting results as to changes in floristic quality. Other studies have found that FQI can be strongly correlated with species richness, whereas richness and mean C are sometimes negatively correlated, depending on site type and scale (Bowles and Jones 2006; Maginel et al. 2016). Although overall mean C decreased, when species richness is parsed out by C value groups, no group of species declines. The lack of increase in high C value species while low and mid C value species increase may be the main driver in the overall decline in mean C across community types. Additionally, more conservative species (high c value) may take a longer time to recover, possibly longer than this dataset reflects. Changes to mean C can affect FQI differently depending on level of species richness, with a more pronounced effect when species richness is higher (Maginel et al. 2016). Ruderal species assigned low C values generally are adapted to frequent disturbances that provide short opportunities for reproduction (Taft et al. 1997), like a sudden nutrient flush or open fuel bed provided by fire. Mean C and FQI were not calculated in years beyond the first season post burn, but certain ruderal species may decline in subsequent years between burns (Hutchinson et al. 2005).

Like other studies, we found a strong shift in both abundance-based and presence/absence-based composition of the ground flora communities in our three community types as the number of burns increased (Hutchinson et al. 2005; Phillips and Waldrop 2008; Willson et al. 2018; Barefoot et al. 2019; Reid et al. 2020). Our indicator species analysis identified several indicator species in all community types in later burn years. All

**Table 7** Stand density and basal area ANOVA statistics

| Analysis | Variable | Df | $\chi^2_{df=1}$ | *p* value |
|---|---|---|---|---|
| Overstory tree density | **Burn number** | 1 | 12.809 | **$\le 0.001$** |
| | **Community type** | 2 | 7.981 | **$=0.018$** |
| | **Burn number: Community type** | 2 | 11.773 | **$=0.003$** |
| | Mean slope | 1 | 0.002 | $=0.967$ |
| | Plot aspect | 2 | 1.953 | $=0.377$ |
| Midstory tree density | **Burn number** | 1 | 383.741 | **$\le 0.001$** |
| | Community type | 2 | 4.667 | $=0.097$ |
| | Mean slope | 1 | 2.824 | $=0.093$ |
| | Plot aspect | 2 | 2.979 | $=0.225$ |
| Overstory basal area | **Burn number** | 1 | 8.524 | **$=0.004$** |
| | **Community type** | 2 | 51.423 | **$\le 0.001$** |
| | Mean slope | 1 | 0.849 | $=0.357$ |
| | Plot aspect | 2 | 1.251 | $=0.535$ |

Multivariate permutational ANOVA statistics for stand structure models including overstory tree density (trees ha$^{-1}$), midstory tree density (trees ha$^{-1}$), and overstory basal area (ha$^{-1}$) at Ozark National Scenic Riverways, MO with data collected from 1999 to 2021

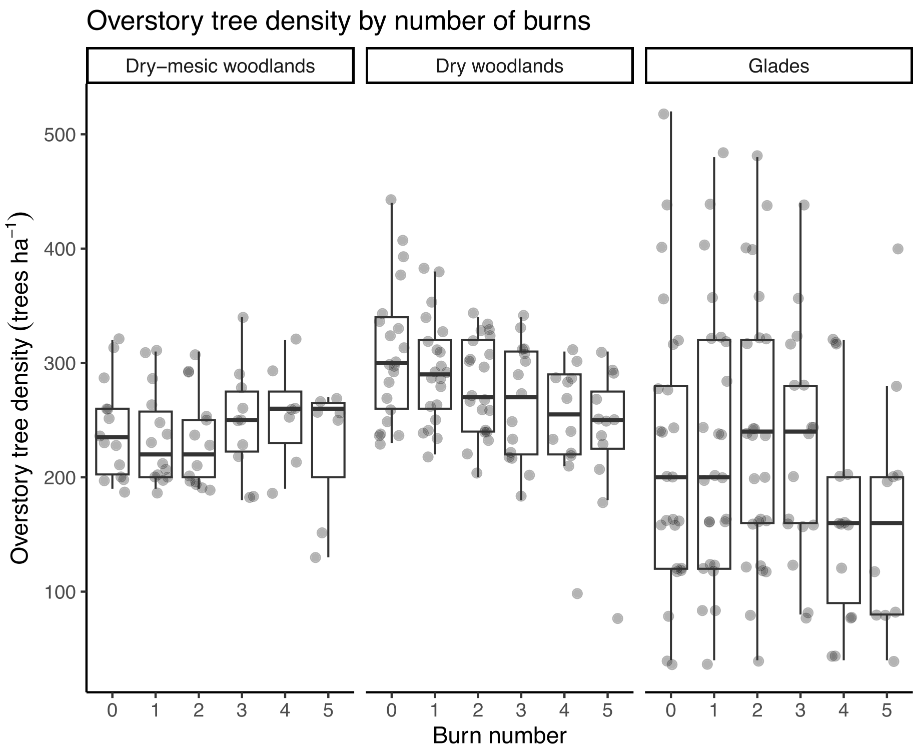


**Fig. 5** Overstory tree density by number of burns. Overstory (≥ 15 cm DBH) tree density (trees ha$^{-1}$) with increasing number of burns in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. Burn number affects the density of overstory trees but response varied by community type, with decreases in density seen in the dry woodlands and glades

habitats saw indicators representing low, mid, and high C values, suggesting that prescribed fire favors specific species rather than ruderal vs. conservative species, although mid C value species (generally considered matrix species) were more common indicators in dry woodlands and glades. The lack of preburn indicator species suggests limited succession to a new community type not adapted to fire. This corroborates other indicator species analyses in which few to no preburn indicator species were identified when compared to burn treatments (Barefoot et al. 2019; Maginel et al. 2019). Fire reintroduction drove communities back toward composition that was fire adapted, which suggests an intact seed bed. Anecdotally from ecologists working in our study site, vegetative perennial species known to prefer sunnier conditions persist without reproducing for many years in overgrown woodlands but bloom again once fire is reintroduced and more light reaches the ground layer. These species may assist in quickly repopulating the seed bank once conditions are favorable.

Annual forb *E. hieraciifolia* was an indicator species in all community types for all burn numbers except for preburn. This is consistent with other findings, in which *E. hieraciifolia* increased post burn and returned to preburn abundance in years without fire (Hutchinson et al. 2005), suggesting that some indicators may have fluctuations in abundance between burn years which was not captured in this dataset. Several of the species identified as indicator species in later burn years have also been identified as indicators of burn treatments in other studies, including *Ageratina altissima*, *Apocynum cannabinum*, *Cirsium altissimum*, *Ceonothus americanus*, *Chamaecrista fasciculata*, *Chamaecrista nictitans*, *Clitoria mariana*, *Carex cephalophora*, *Carex muehlenbergii*, *Desmodium nutallii*, *Euphorbia corollata*, *E. hieraciifolia*, *Galactia regularis*, *Lespedeza frutescens*, *Panicum commutatum*, *Panicum dichotomum*, *Solidago hispida*, *Sanicula odorata*, *Solidago ulmifolia*, and *Strophostyles umbellata* (Hutchinson et al. 2005; Willson et al. 2018; Barefoot et al. 2019; Maginel et al. 2019).

Overstory tree density declined with number of burns in dry woodlands and glades, but not in dry-mesic woodlands, while basal area increased in all three community types. The decline in overstory tree density differs from other findings (Arthur et al. 2012; Lettow et al. 2014; Willson et al. 2018; Maginel et al. 2019), although many studies do not track responses for over 20 years. Studies that look at density responses over longer time scales had variable results. A 32-year study in oak savanna and woodland stands in Minnesota found frequent fires (2–3

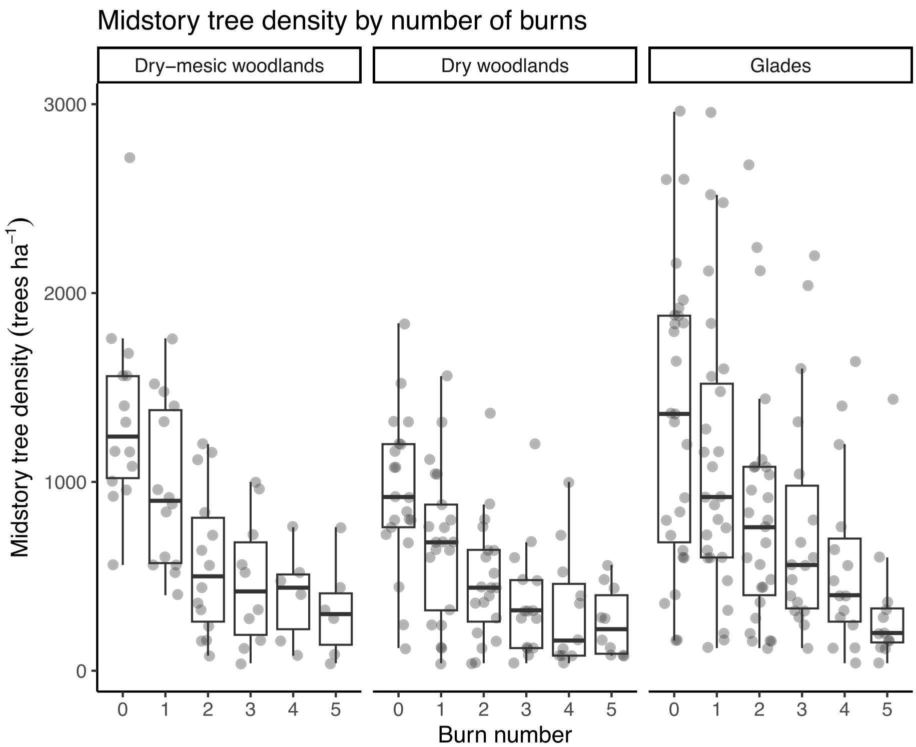


**Fig. 6** Midstory tree density by number of burns. Midstory (2.5–14.9 cm DBH) tree density (trees ha$^{-1}$) with increasing number of burns in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. Midstory tree density decreases with increasing number of burns

fires per decade) decreased overstory tree density and basal area (Peterson and Reich 2001); however, a 42-year study in oak barrens in Tennessee did not find significant reductions in overstory tree densities or basal area, although canopy cover was reduced (Stratton 2007). A 60-year study in a Missouri Ozark oak-hickory forest showed declines in overstory tree density, but this decline was not significantly different than the declines seen in control treatments. Conversely, basal area increased in burn treatments but did so less than in control plots (Knapp et al. 2015). Overstory basal area can increase at higher increments than unburned areas after fires (Anning and McCarthy 2013). We did not have a control to follow through time to which we can compare overstory tree density or basal area, so we cannot fully parse out our result from potential overstocking and competitive exclusion.

A stronger decline in overstory density may also be due to more intense fire effects in drier sites like the dry woodlands and glades. The interactive effect between burn number and community type suggests distinct response differences in the community types, with dry woodlands exhibiting the steepest decline in overstory tree density (Fig. 5). Although data was not collected on fire intensity at the plot level, ecologists working on this project noted that the dry woodland plots typically had the most complete burn coverage and tended to have higher charring on tree bark. Although glades are also very dry sites, they often seep moisture in the spring. Because most plots were burned in March, wet spring conditions could result in patchier burns through glade plots. Additionally, heavy shading from cedar and moist cedar duff on glades may have inhibited fire intensity before cedars were cleared from glades.

Declines in overstory tree density are generally considered important to woodland restoration, as it increases light exposure to the ground which benefits the herbaceous layer. Historical woodlands likely had 30–100% canopy cover (Hanberry et al. 2014a; Dey and Kabrick 2015), and many studies focused on woodland management look at mechanical thinning in combination with fire as a method to reduce overstory canopy cover more quickly (Willms et al. 2017; Willson et al. 2018; Barefoot et al. 2019). Our data suggests that over longer timescales, repeated fire may also thin overstory tree density on drier sites. Although there is regional variation, evidence suggests that thinning treatments and burning treatments do not necessarily have equivalent responses. For example, thinning treatments may be more likely to result in nonnative invasion in the herbaceous layer

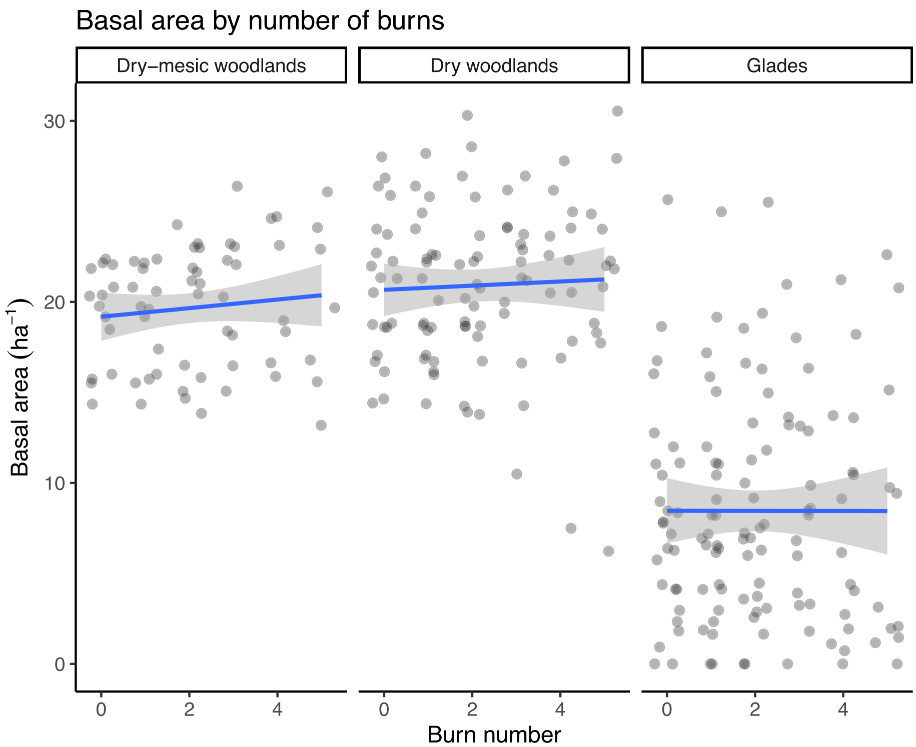


**Fig. 7** Basal area by number of burns. Overstory (≥ 15 cm DBH) basal area with increasing number of burns in dry-mesic woodlands, dry woodlands, and glades at Ozark National Scenic Riverways. Data was collected from 1999 to 2021. Overstory basal area generally increases with number of burns

(Schwilk et al. 2009; Willms et al. 2017). Future areas of study could compare long-term herbaceous compositional and floristic quality differences between fire alone and fire combined with thinning treatments at different canopy reduction rates to determine if ground flora communities respond differently to sudden versus gradual reopening of the canopy.

Our result that midstory tree density declines with increasing number of fires corroborates findings from several previous studies (Arthur et al. 2012; Brose et al. 2013; Lettow et al. 2014; Willson et al. 2018; Maginel et al. 2019). Reducing midstory tree density can increase light at the ground layer, which is considered a driver of increased oak recruitment (Arthur et al. 2012). Although slope and aspect were not significant, midstory densities treated with fire can be affected by landscape position (Arthur et al. 2015; Maginel et al. 2019). Although there is increased focus on reducing overstory tree density to increase light availability, historical evidence suggests that a closed canopy with little to no midstory may have been the prominent stand structure across the Ozarks and would still have allowed enough light to sustain a diverse herbaceous understory (Fralish and McArdle 2009; Hanberry et al. 2014a). In fact, some dry tree species can have lower specific leaf areas and less dense canopies that are more light-permeable than closely related forest tree species (Fralish 2004; Hoffmann et al. 2005; Ratnam et al. 2011). Therefore, overstory tree density may not be as critical to light availability as the midstory.

Diameter distributions indicated that red oaks and white oaks dropped out of midstory size classes substantially in the dry woodlands and dry-mesic woodlands, which may impede future recruitment of overstory trees. Numerous other studies have raised concerns over oak recruitment to the overstory in fire frequent regimes and typically suggest implementing periods of time that are fire-free to allow for smaller oaks to reach a size more suitable to surviving fires to ensure overstory recruitment (Dey and Fan 2009; Arthur et al. 2012; Knapp et al. 2015). However, given the longevity of oak species, fire free intervals would not need to be implemented frequently (Dey and Fan 2009).

Notably, although oak midstory trees declined in glades, glades retained more midstory oak trees than dry woodlands and dry-mesic woodlands. Glades are dominated by flashy grass fuels as opposed to leaf litter like in the woodlands. Flashier fuels typically burn faster, which decreases the residency time of fire which could in turn impact survival of smaller trees.

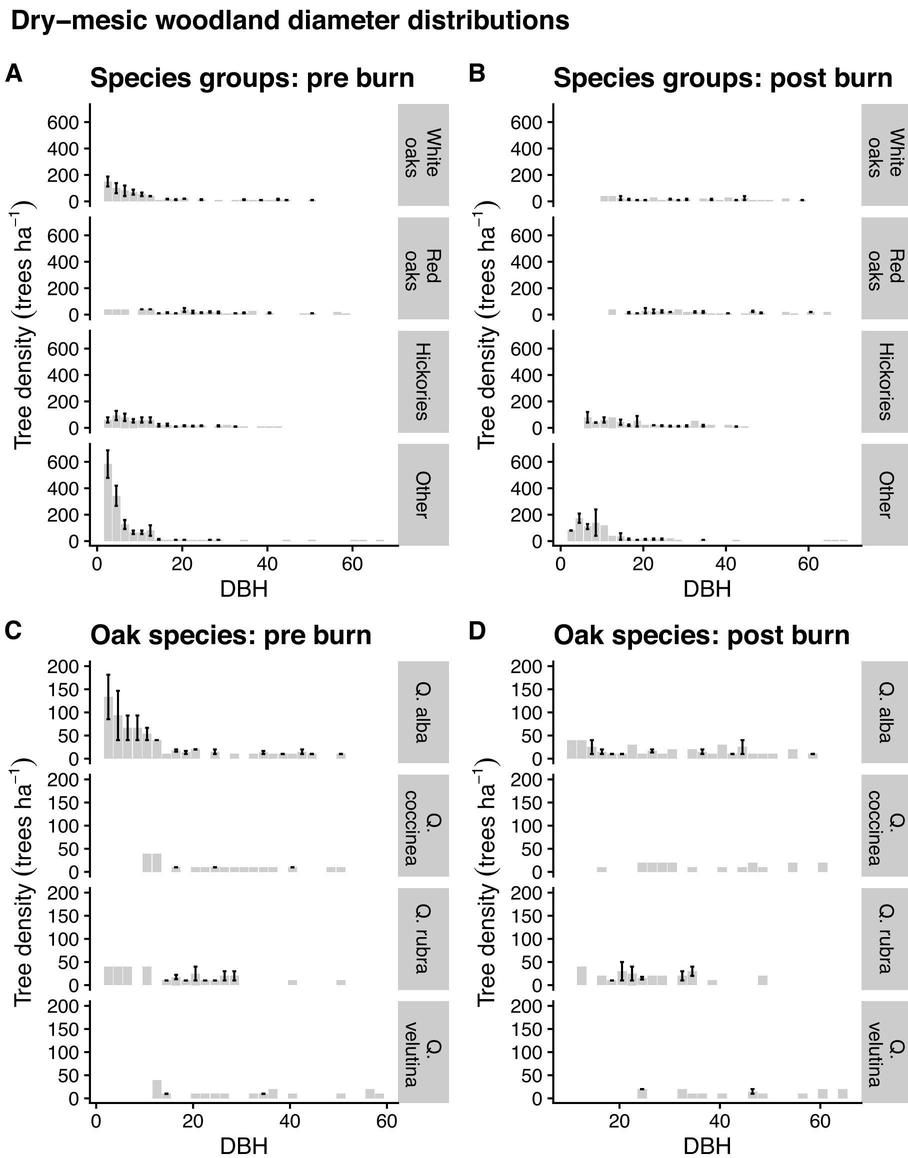


**Fig. 8** Dry-mesic woodland diameter distributions at Ozark National Scenic Riverways. Post burn data indicates data collected after 5 burns. A lack of error bar indicates that only one plot had trees in that species group for a given diameter at breast height (DBH). Data was collected from 1999 to 2021. **A** Pre burn species groups diameter distributions. **B** Post burn species groups diameter distributions. Smaller diameter trees declined in post burn treatments across all species groups, and distributions became more uniform in both red oaks and white oaks. **C** Pre burn oak species diameter distributions. **D** Post burn oak species diameter distributions. The dominant species was *Q. alba*, which declined in midstory trees but did not completely lose the midstory layer in post burn treatments

Decomposing litter loses mass faster when the carbon to nitrogen ratio is lower (Hector et al. 2000), suggesting that glades may have higher decomposition rates due to their dominant herbaceous flora as opposed to leaf litter and thus less fuel loading. Additionally, glades often have large amounts of exposed bedrock, which may act as fuel breaks particularly for small trees growing around bedrock. Even in dense grassland ecosystems, heterogeneity in vegetation may act as fuel breaks and impact fire effects (Mitchell et al. 2009). Because lower fuel accumulation can lessen fire severity (Stambaugh et al. 2006), less fuel loading coupled with bedrock fuel breaks on glades may result in a higher density of midstory oaks. Finally, because of shallow, dry soils, and harsher exposures, glades typically do not sustain many or large overstory trees (Fig. 10). However, smaller trees may in fact be quite old and may have developed thick bark to resist fire compared to similar

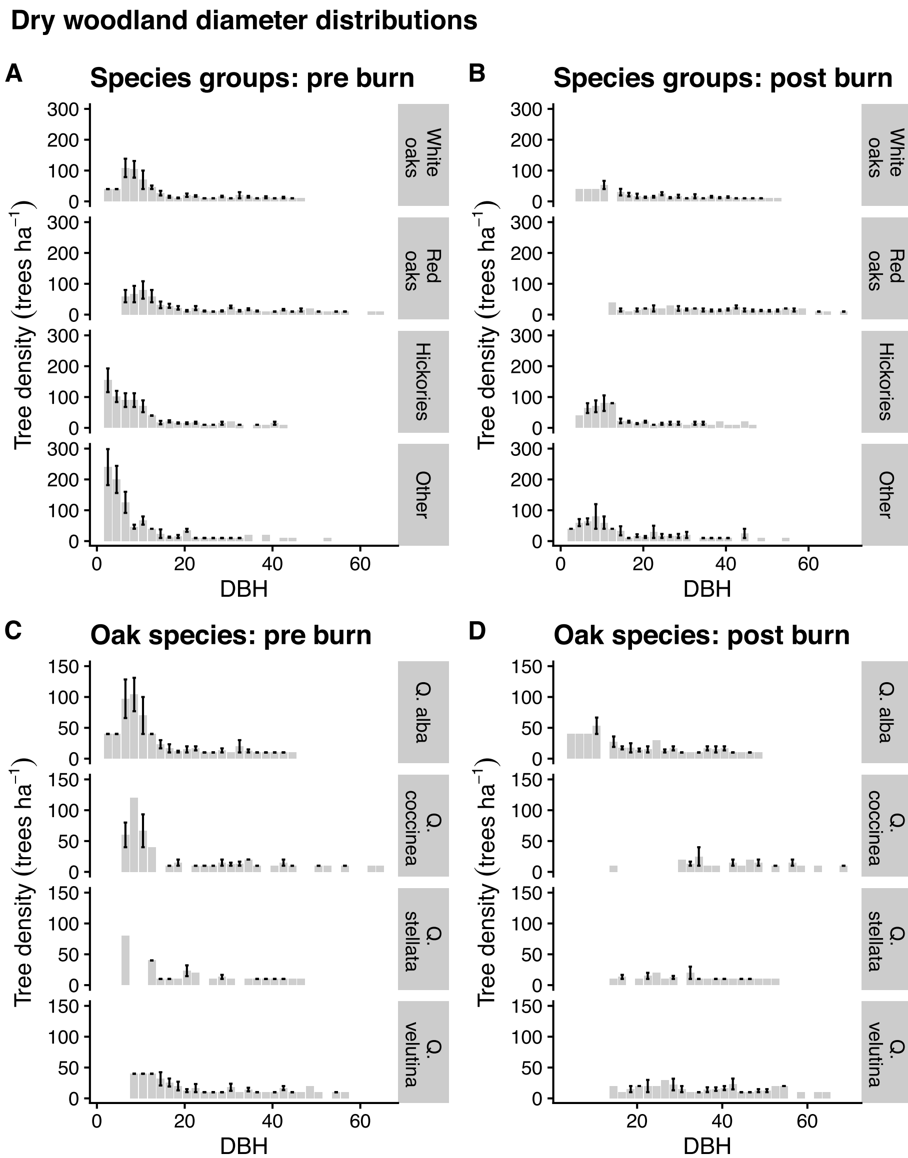


**Fig. 9** Dry woodland diameter distributions at Ozark National Scenic Riverways. Post burn data indicates data collected after 5 burns. A lack of error bar indicates that only one plot had trees in that species group for a given diameter at breast height (DBH). Data was collected from 1999 to 2021. **A** Pre burn species groups diameter distributions. **B** Post burn species groups diameter distributions. Smaller diameter trees declined in post burn treatments across all species groups, and distributions became more uniform in both red oaks and white oaks. White oaks remain in midstory. **C** Pre burn oak species diameter distributions. **D** Post burn oak species diameter distributions. *Q. alba*, *Q. coccinea*, and *Q. velutina* all see declines in lower diameter trees. All species but *Q. alba* appear to lose their midstory layer, and even for *Q. alba*, very few to only single plots contain midstory size trees

sized trees in nearby woodlands, thus allowing smaller trees to persist.

Diameter distributions by oak species corroborated that response to fire is often species-specific (Fan et al. 2012; Short et al. 2019). All three community types retained species from the red oak and white oak groups, although *Q. alba* appeared to have more tolerance of repeated fire in the midstory size classes than other oak species (Figs. 8, 9, and 10) in the dry woodlands and dry-mesic woodlands. Glades had representation from both white and red oak groups persisting in the midstory, with strong presence from *Q. marilandica* and *Q. stellata*, as well as some presence from *Q. muhlenbergii*. White oaks tolerate fire more favorably than red oaks (Fan et al. 2012).

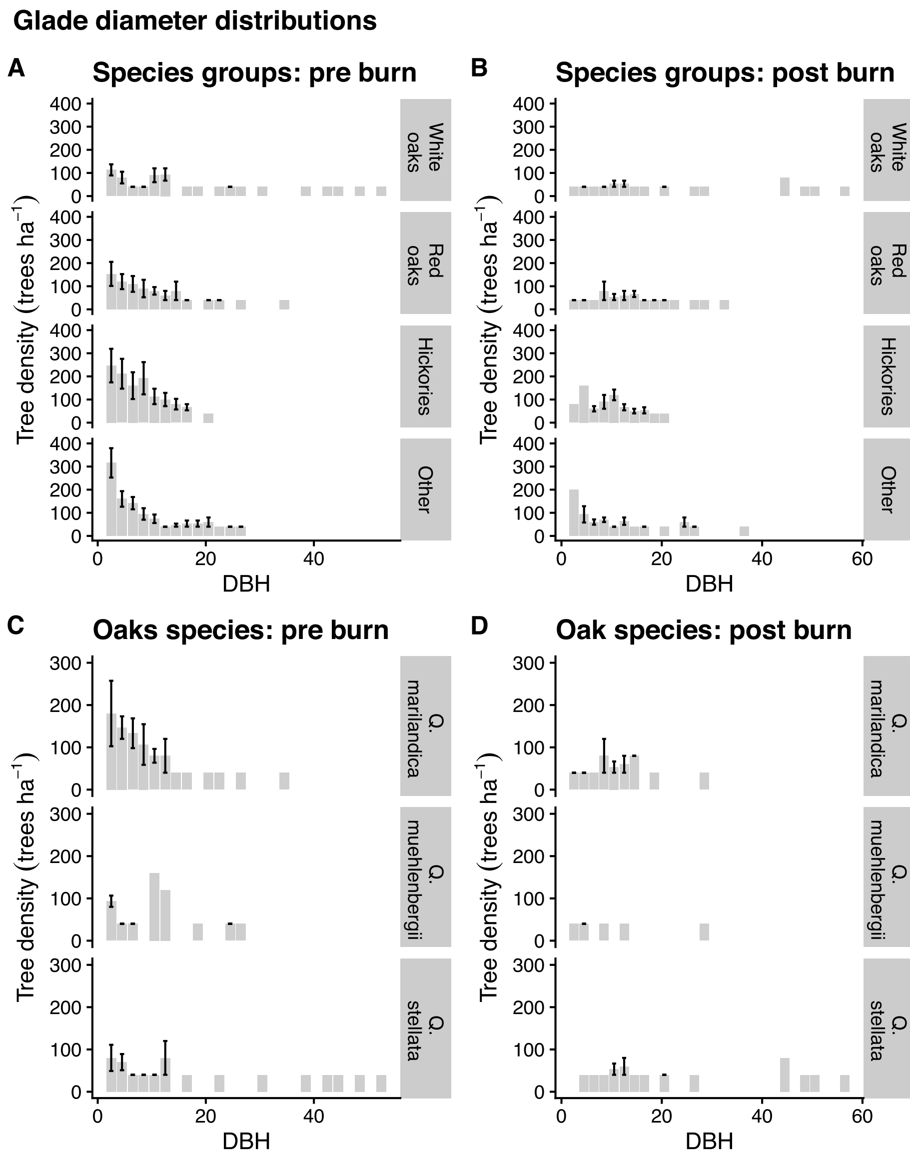


**Fig. 10** Glade diameter distributions at Ozark National Scenic Riverways. Post burn data indicates data collected after 5 burns. A lack of error bar indicates that only one plot had trees in that species group for a given diameter at breast height (DBH). Data was collected from 1999 to 2021. **A** Pre burn species groups diameter distributions. **B** Post burn species groups diameter distributions. Smaller diameter trees declined in post burn treatments across all species groups, and distributions became more uniform in both red oaks and white oaks. All species groups remain in midstory size classes. **C** Pre burn oak species diameter distributions. **D** Post burn oak species diameter distributions. All three major oak species in glades decline in midstory trees in post burn treatments

## Conclusions

Repeated landscape fire alone over longer timescales reduces midstory and overstory tree density in drier sites, thus increasing canopy openness for the herbaceous layer. Ground flora responds favorably in richness, abundance, and composition with increasing number of fires. However, our results vary by community type across the landscape, and natural resource managers should consider dominant communities and landscape heterogeneity in their management goals. Fire is typically applied by land managers at landscape scales, but community types will likely respond differently and may stabilize in their herbaceous layer at different rates.

### Abbreviations

| | |
|---|---|
| C value | Coefficient of conservatism |
| DBH | Diameter at breast height |
| FQI | Floristic Quality Index |
| Mean C | Mean coefficient of conservatism |
| ONSR | Ozark National Scenic Riverways |

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00299-3.

Supplementary Material 1.

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**Authors' contributions**
CAS conducted analyses, interpreted results, and led manuscript writing. DGD executed data collection by training and leading technicians. DGD interpreted data and management implications. JHL executed data collection and assisted with data cleaning. LLS guided and conducted data analyses and interpretation. All authors contributed to manuscript editing.

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CAS worked on this manuscript as part of her master's degree with the Division of Biological Sciences at the University of Missouri. CAS is now a natural resource ecologist with the Missouri Department of Natural Resources, focusing on natural resource management at state parks. DGD retired from his position as Fire Ecologist with Ozark National Scenic Riverways in April 2023. He worked in this role for 14 years as a part of a career dedicated to land management with several natural resource agencies in Missouri. JHL currently works as the Fire Ecologist at Ozark National Scenic Riverways and continues to train, guide, and lead in data collection for this long-term fire effects monitoring project in addition to her other ecologist duties. LLS in a professor and researcher at Michigan State University. Her research focuses on plant movement ecology, restoration ecology, invasion ecology, and quantitative methods.

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**Availability of data and materials**
The data that support the findings of this study are available from Ozark National Scenic Riverways, which is a part of the National Park Service. Data from ONSR were used under permit OZAR-2020-SCI—0002 and are not currently publicly available but may become so in the future. Data is available upon reasonable request and with permission of ONSR.

## 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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## Publisher's Note