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Savanna restoration on the Cumberland Plateau impacts whole-ecosystem carbon storage and increases biodiversity

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ABSTRACT

Across the central and eastern U.S., fire-maintained oak (*Quercus* spp.) and pine (*Pinus* spp.) savannas are transitioning to closed-canopy forests because of fire exclusion and land-use change, prompting restoration efforts using low-intensity prescribed fire. Although restoring and maintaining open ecosystems with fire can increase plant diversity and improve wildlife habitat, there are largely unknown consequences for overall ecosystem carbon (C) balance, especially in relation to fire regime (frequency/seasonality). We investigated ecosystem C and plant biodiversity response to 14 years of savanna restoration treatments (early vs. late growing season fire at 1-, 2-, or 3-year frequency) compared to an unmanaged, closed-canopy forest and early-successional old-field on the Cumberland Plateau in Tennessee, USA. Because of greater tree biomass, the closed-canopy forest stored 2–3 times more total C (226.6 Mg ha^{-1}) than the restored savanna (78.6–111.5 Mg ha^{-1}) and old-field (86.2 Mg ha^{-1}). However, the savanna stored as much or more C in protected (e.g., fine roots/mineral soils) and quickly recovering (e.g., understory vegetation) pools than the closed-canopy forest. Within the restored savanna, early growing season fires led to more total C (98.9 Mg ha^{-1}) than those conducted later in the growing season (86.3 Mg ha^{-1}), largely as a result of elevated fine root and mineral soil C. Plant diversity was greatest in the savanna regardless of fire regime. We documented a trade-off between total C storage and biodiversity in closed vs. open ecosystem states and increased C pools when burning earlier in the growing season. Overall, savanna restoration may increase plant biodiversity while promoting long-term C storage in protected and resilient pools.

1. Introduction

A large portion of the central and eastern U.S. historically comprised savannas and woodlands, defined by their bilayer structure with an overstory of mature, fire-tolerant (pyrophytic) oaks (e.g., *Quercus alba, Q. velutina, Q. stellata*) and pines (e.g., *Pinus palustris, P. echinata*), little to no midstory, and a flammable and diverse herbaceous forb and graminoid understory (Hanberry et al., 2018, 2020b; Pile Knapp et al., 2024). Frequent, low-intensity surface fire coupled with large-mammal herbivory ensured persistence of these ecosystems by limiting woody regeneration and enabling sufficient light to promote an understory dominated by shade-intolerant herbaceous plant species (Hanberry et al., 2020a; McEwan et al., 2011; Pile Knapp et al., 2024). Post-European colonization, loss of indigenous burning practices, and fire suppression policies resulted in forest densification and a transition to a more closed-canopy forest structure. These closed-canopy forests contain a dense midstory of shade-tolerant, often fire-sensitive species (i. e., mesophytes) whose crown, bark, and leaf litter traits reinforce low-flammability conditions and mesophyte proliferation at the expense of pyrophytic oaks and pines (Alexander et al., 2021; Nowacki and Abrams, 2008). Densification and mesophication of these forests has led to a drastic range contraction of oak and pine savannas across the region, which now exist only in small fragments (Barrioz et al., 2013; Lettow et al., 2014; Nuzzo, 2025). The diverse understory plant communities of savannas and woodlands contain species not found in other systems and are further ecologically important as they provide native pollinator and

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wildlife habitat and resources (Arthur et al., 2021; Brudvig and Asbjornsen, 2009; Harper et al., 2016). Thus, in response to ongoing transition of savannas and woodlands to closed-canopy forests, land managers throughout the region have begun to restore these ecosystems using a variety of management techniques, especially thinning to open the canopy while favoring pyrophytic species, followed by frequent, low-intensity prescribed fire of varying frequency and seasonality (Bones et al. *in press*; Brawn, 2006; Dey et al., 2017; Hutchinson et al., 2024, 2012; Vander Yacht et al., 2020). However, the implications of savanna and woodland restoration on above and belowground carbon (C) sequestration, and potential trade-offs with biodiversity, are largely unknown (Bradford and D'Amato, 2012), especially in the central and eastern U.S. Understanding the C consequences of such restoration is especially important given that managing forests for C sequestration is a global priority to help mitigate climate warming (Canadell and Raupach, 2008; Malmsheimer et al., 2008; Ontl et al., 2020).

Restoring savannas and woodlands will likely impact C dynamics by altering the quantity and distribution of C pools, as well as their vulnerability to loss. Because savannas and woodlands contain fewer trees than closed-canopy forests, and trees contain considerable C stocks, their restoration could decrease C sequestration potential simply by reducing tree biomass (Bradford and D'Amato, 2012; Malmsheimer et al., 2008). Increased understory vegetation biomass could offset some tree biomass loss, especially if it leads to more belowground C storage as a result of increased fine root biomass inputs and/or incorporation of fire-deposited ash and organic matter into mineral soils (Alcañiz et al., 2018). Storing more C in quickly-recovering understory vegetation (Clark et al., 2015) and protected belowground pools (Alcañiz et al., 2018; Davis et al., 2022) could also increase ecosystem C resistance to and resilience following disturbance. Decreasing C vulnerability to long-term loss is particularly important given increased wildfire risk in the eastern U.S. (Donovan et al., 2023; Gao et al., 2021), which is correlated with increased woody cover (i.e., woody infilling and encroachment) (Ivey et al., 2024). Under many conditions, particularly those targeted for prescribed fires, unmanaged, closed-canopy forests have low flammability because of the fire-suppressing fuel traits of encroaching mesophytic species (Alexander et al., 2021). However, these fuels become increasingly ignitable and susceptible to fire-driven loss because increased tree density, leaf litter buildup, and ladder fuels interact with climate conditions to increase the probability that wildland fires result in crown fires and tree mortality (Adams, 2013; Regelbrugge and Smith, 1994). Thus, restoration of woodlands and savannas may increase ecosystem C resilience by shifting C storage to pools that are relatively more protected and resilient and increasing resistance of the tree C pool through reduced stand density, even if unmanaged, closed-canopy forests store more total C because of greater tree biomass.

Although regular and relatively frequent prescribed fire is necessary to restore woodlands and savannas, the fire regime implemented varies depending on management objectives for biodiversity, and variations in fire frequency and/or seasonality may have implications for C storage. Fire frequency and/or seasonality may affect fire behavior (Bones et al. *in press*; Knapp et al., 2009; Knapp and Keeley, 2006; Turner et al., 2024), vegetation structure, growth, and biodiversity (Peterson and Reich, 2001; Robertson and Hmielowski, 2014; Turner et al., 2025, 2024; Vander Yacht et al., 2017), and soil dynamics (Coates et al., 2018; Czimczik et al., 2005), all of which impact ecosystem C. Decreased fire frequency should lead to increased time for C to recover during the fire-free interval. For example, Wright et al. (2021) reported total ecosystem C, soil C, and aboveground productivity decreased with increasing fire frequency in a longleaf pine woodland. Fire seasonality may influence C through decreased sapling growth and survival in the growing season compared to the dormant season because of greater plant physiological activity and decreased availability of belowground root reserves (Cain and Shelton, 2000; Robertson and Hmielowski, 2014). Seasonality may additionally influence C via a fire intensity effect. In the southeastern U.S., environmental conditions, on average, allow higher-intensity fire with greater burn coverage during the early portion of the growing season when leaf expansion is not yet complete, than during the latter portions of the growing season (Turner et al., 2024, Bones et al. *in press*). Higher-intensity fire tends to decrease soil C pools more than low-intensity fire due to increased organic matter combustion, structural changes, and leaching, among other factors (Alcañiz et al., 2018; Certini, 2005; Nave et al., 2011). However, this trend is largely driven by high-intensity wildfires, the effects are more pronounced on the soil organic layer than the mineral soil, and prescribed fire has been demonstrated to increase total soil carbon in multiple oak forest ecosystems, suggesting even higher-intensity prescribed fire may increase soil C under some circumstances (Fontúrbel et al., 2021; Scharenbroch et al., 2012; Taylor and Midgley, 2018). Overall, the influence of fire seasonality and frequency on C storage with open forest restoration remains unclear.

Given the motivation to restore imperiled oak- and pine-dominated woodlands and savannas, understanding restoration impacts on a variety of ecosystem services, such as C storage and biodiversity, is critically important. To explore the effects of savanna restoration on C, diversity, and potential trade-offs between these ecosystem services, we investigated a long-term mixed oak-pine savanna restoration effort on the Cumberland Plateau in White County, TN, and compared it to a nearby unmanaged closed-canopy forest and an old-field, which is another common open ecosystem state that may differ in C storage and biodiversity from restored savannas because of different land-use history and management. We addressed the following questions: 1) How does C pool distribution differ among a restored savanna and nearby unmanaged closed-canopy forest and old-field? 2) What are the effects of savanna restoration techniques, including fire frequency and seasonality, on ecosystem C storage? 3) Are there ecosystem carbon-diversity trade-offs among savannas, old-fields, and closed-canopy forests? We predicted greater total C in the unmanaged, closed-canopy forests compared to the old-field or restored savanna, but anticipated more quickly-recovering and protected C and more herbaceous biodiversity in the savanna and to a lesser extent in the old-field. We additionally predicted more C in the less-frequently burned savanna and savanna burned during the early growing season. Our study contributes to a holistic understanding of the response of multiple ecosystem services to open oak and pine savanna restoration, and how such restoration may influence the ability of these systems to continue to provide these services in the context of increased disturbance risk associated with global change.

2. Methods

2.1. Study site and experimental design

We conducted our study at the Bridgestone-Firestone Centennial Wilderness Wildlife Management Area (BSFS), which is owned by the Tennessee Wildlife Resources Agency (TWRA) on the Cumberland Plateau in White County, Tennessee, USA (35°52'34.9"N 85°15'13.5"W). Specifically, we conducted our study at the Bridgestone/Firestone Fire Demonstration Area and the adjacent Farm Unit of BSFS, encompassing approximately 280 ha dominated by early-successional forbs and grasses with sparse shrub/tree cover. The area had been dedicated as a Quail Focal Area and was managed by TWRA specifically for northern bobwhite (*Colinus virginianus*). The Fire Demonstration Area covered 54 ha with soils comprising Lonewood loam Typic Hapludults and Ramsey-Lily complex Typic Hapludlts/Lithic Dystrudepts (Soil Survey Staff, 2025). Mean annual temperature from 2006 to 2020 was 14.7 °C, and mean annual precipitation was 151.5 cm (Sparta Wastewater Plant, White County, TN) (Palecki et al., 2021).

In 2011, the Fire Demonstration Area (called the Demonstration Area hereafter) was established by TWRA and the University of Tennessee as an oak-shortleaf pine savanna restoration experiment to investigate the effects of fire frequency and seasonality on vegetation composition, structure, and biodiversity and wildlife response. Prior to the experiment, the Demonstration Area was a loblolly pine (*Pinus taeda*) stand, which was cleared in 1997. The TWRA purchased the property in 1998, and the area where the loblolly pine stand occurred was allowed to regenerate naturally. The area was burned twice during the dormant season from 2002 to 2008 prior to the establishment of the Demonstration Area. By 2011, the Demonstration Area was dominated by black needlegrass (*Piptochaetium avenaceum*), poverty oat grass (*Danthonia spicata*), *Rubus* spp., and goldenrod (*Solidago* spp.), with a developing sparse overstory of white oak (*Q. alba*), post oak (*Q. stellata*), shortleaf pine (*Pinus echinata*), and mockernut hickory (*Carya tomentosa*). The Demonstration Area was sectioned into 6 treatment units, each between 6.5 and 13.8 ha. Each treatment unit was randomly assigned a combination of fire-return interval (1, 2, or 3 years) and burn season (early- or late-growing season). Thus, our savanna treatments were 1-year interval late growing season ("1-Late"), 2-year interval late growing season ("2-Late"), 3-year interval late growing season ("3-Late"), 1-year interval early growing season ("1-Early"), 2-year interval early growing season ("2-Early"), and 3-year interval early growing season ("3-Early") (Fig. 1). We compared the effects of burning during the early and latter portions of the growing season because previous work has suggested burning at different times of the growing season may influence the rate of woody resprouting and herbaceous layer composition, but not all studies agree (Howe, 1995, Sparks et al., 1998, Gruchy et al., 2009, Knapp et al., 2009, Robertson and Hmielowski, 2014).

We also included two additional units outside of the Demonstration Area in our study (Fig. 1). We included a mixed pine-hardwood closed-canopy forest (44–54 m^2 ha^{-1} basal area) to the south of the Demonstration Area that had not received any management ("Closed") but had similar overstory composition to the restored savanna. The dominant overstory was shortleaf pine with scattered post oak, hickory (*Carya* spp.), and yellow poplar (*Liriodendron tulipifera*). The midstory was dominated by red maple (*Acer rubrum*) and black cherry (*Prunus serotina*). We also included a previously abandoned agricultural field located to the west of the Demonstration Area ("old-field"). The old-field in the previous 40 years had been planted to various vegetable crops and later planted to tall fescue (*Lolium arundinaceum*) and orchardgrass (*Dactylis glomerata*). The nonnative grasses were terminated from 2014 to 2018 to transition from a nonnative plant community to one dominated by native plant species arising from the existing seedbank or dormant rhizomes. The old-field was burned in the late dormant season on average every three years since the early 2000s, and disking and spot-spraying was conducted occasionally to control nonnative species, such as johnsongrass (*Sorghum halepense*) and sericea lespedeza (*Lespedeza cuneata*).

We conducted carbon sampling and vegetation surveys in all treatments of the Demonstration Area, the closed-canopy forest, and the old-field. We note that although we had replicate plots (3) in all treatments, there was no treatment-level replication in this study. Given the homogenous pre-treatment land-use conditions and proximity of all treatments, the chances that treatment-level effects are driven by factors other than fire treatment are minimized. However, our investigation represents a case study, and we therefore caution against broad extrapolation of our results.

2.2. Prescribed burns

We conducted early growing season (EGS) fire treatments mid- to late-April through early May and late growing season (LGS) fire treatments mid-late September through October, with the end of October defining the end of the growing season in this area. We implemented the first LGS fire treatment in 2011 and the first EGS fire treatment in 2012. Burn day weather included average temperatures of 12–27 °C, relative humidity 25–50 %, and in-stand wind speed 4–13 km/hour. We chose these conditions to meet our objectives of maintaining a low-intensity fire hot enough to top-kill woody saplings and shrubs, consume leaf litter, and maximize burn coverage, but not damage overstory trees. We primarily used backing fires to best consume fine fuels; however, we used flanking and strip-heading fires if needed to achieve desired fire intensity.

In 2023, we used UX-100 HOBO dataloggers and 12-inch Type K thermocouples (Onset Computer Corporation, Bourne, MA, USA; hereafter, "temperature loggers") to record maximum fire temperature and residence times at five fixed sampling points within each of the six units in the Demonstration Area (30 total sampling points). The temperature loggers recorded temperature from 0 to 900 ℃ every second during the burn, which was used to determine maximum temperature and residency time above 60 ℃.

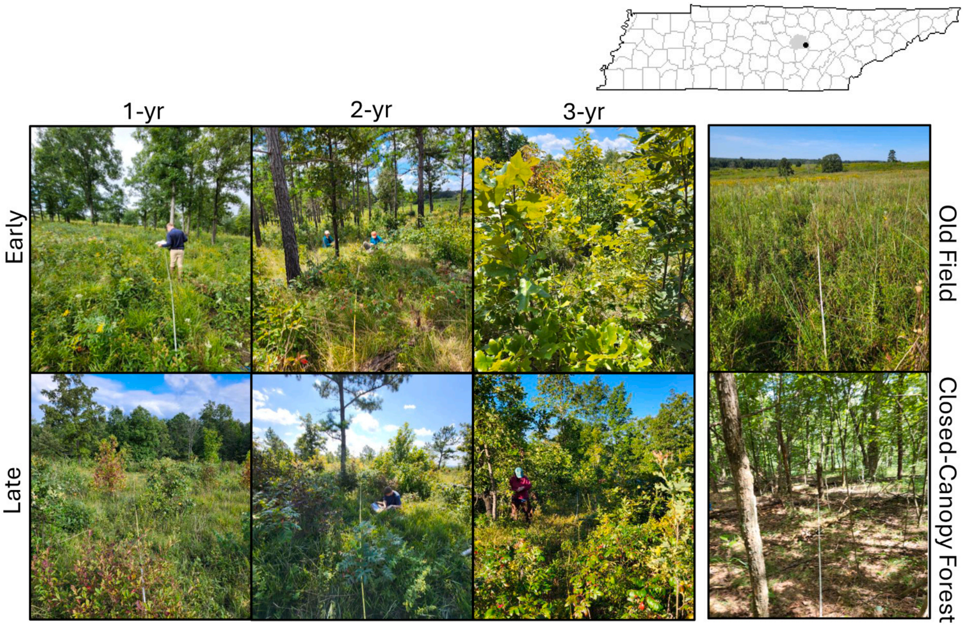

Fig. 1. ***Study site treatments***: Top shows a map of the state of Tennessee, with White County in grey and a black point representing the location of the study area. Photos are representative of each of our sampled treatments (1-, 2-, or 3-year fire frequency; early growing season or late growing season fire; an adjacent old-field; an adjacent closed-canopy forest).

2.3. Whole ecosystem carbon storage

To quantify C pools, we established three 15-m fixed-radius plots in each of the eight treatments. Plot centers were randomly selected within treatments and located ~ 100 m from each other and ≥ 50 m from the edge of a treatment unit. Three transects were extended from plot center in the north (0°), southeast (135°), and southwest (225°) directions, and we sampled live and dead (i.e., snags) trees, understory or groundlayer vegetation, downed woody debris, leaf litter, the soil organic layer (SOL), mineral soil, and fine/small coarse root C pools within each plot. All C sampling occurred in August 2023 to capture peak growing season biomass. Thus, time since fire for all EGS fire treatments (4, 16, and 28 months for 1-year, 2-year, and 3-year fire return intervals, respectively) was seven months less than time since fire for LGS treatments (11, 23, and 25 months for 1-year, 2-year, and 3-year fire return intervals, respectively).

2.3.1. Overstory

We estimated C stored in live and standing dead trees by conducting tree inventories in each plot. We identified trees to species and measured diameter at breast height (DBH; ~ 1.3 m aboveground) of live and dead overstory (≥ 20 cm), midstory (10.1–19.9 cm), and sapling (0.1–10 cm) trees within a 15, 10, or 5-m radius, respectively, around the plot center using a DBH tape or calipers. We identified dead trees to genus when we could not identify to species level and to hardwood or softwood if we could not identify genus. We used the "allodb" package (Gonzalez-Akre et al., 2022) in R to estimate aboveground biomass from DBH and geographical coordinates, which we converted to C pools (Mg ha^{-1}) using % C values from the FIA DataMart database based on C concentrations from Doraisami et al. (2022).

2.3.2. Understory vegetation

We harvested three understory/groundlayer vegetation samples per plot. We placed a 0.5-m x 0.5-m (0.25-m^2) quadrat 1 m to the right of the 9-m mark of each transect. If the quadrat intercepted a large tree, we moved the quadrat away from plot center to avoid obstruction. Within each quadrat, we clipped all rooted (i.e., not litter) alive and dead biomass (including only woody stems < DBH height) at ground level and placed it in a labeled paper bag. Upon returning to the lab, we dried vegetation at 60 °C for 48 h or to a constant weight. We converted understory vegetation biomass to Mg ha^{-1} and then converted biomass to C pool using 50 % C (Johnson et al., 2017).

2.3.3. Downed woody debris

We measured fine (FWD) and coarse woody debris (CWD) C pools using the Brown's Planar Intercept Method along each of the three plot transect lines (Brown, 1974). Beginning at the 2-m mark of each transect, we tallied wood pieces of different sizes and timelags (number of hours for each size class to respond to a certain level of change in relative humidity (Brown, 1974) in a nested approach, with smaller pieces tallied along a shorter distance than larger pieces. Size class diameters included 0–0.6 cm (1-hour), 0.6–2.5 cm (10-hr), 2.5–7.6 cm (100-hr), > 7.6 cm (1,000-hr). We measured the two smallest classes from 2 m to 4 m, the 100-hr class from 2 m to 7 m, and 1000-hr class from 2 m to 15 m. We measured the diameter of 1000-hr fuels (CWD) where logs crossed the transect, assigned a decay class between 1 and 5 (Lutes et al., 2006), and identified logs to species or genus when possible. We calculated woody biomass by converting the number of intersections tallied to mass using Brown's formulas (Brown, 1974). We estimated specific gravity (SG) for the 1-, 10-, and 100-hour timelag fuel classes based on Anderson (1978) for southern and southeast forest types as follows: 1- and 10-hour, 0.70; 100-hour, 0.58. For CWD, we used specific gravity, decay constants, and dead wood % C values from FIA DataMart, primarily from Miles and Smith (2009) and Woodall et al. (2019). When CWD pieces were not identifiable because of charring or decay, we used species-weighted SG, decay constants, and % C values, weighted based on species overstory contribution to plot basal area.

2.3.4. Leaf litter and organic soil

We collected three litter and SOL samples per plot. We defined litter as slightly decomposed plant material that was still recognizable and the SOL as the layer between the leaf litter and the top of mineral soil. We placed a 25-cm x 25-cm quadrat to the right of the 10-m mark of each transect, recorded four litter depths (one at each corner of the quadrat), gently clipped around the quadrat's edges, and then collected litter. In the lab, we removed any non-litter material from the sample and then dried the sample at 60 °C for 48 h to a constant weight. We collected SOL at the 9-m mark to the left of each transect. We used a soil knife and clippers to harvest the SOL in a ~10-cm x 10-cm area, and we placed the collection in a labeled plastic bag. We measured and recorded the length and width of the collection and the depth at each of the four corners. We removed any non-decomposed organic material, including vegetation or woody debris, during lab processing. We picked live and dead roots out of the SOL sample and dried them at 60 °C for ~ 48 h prior to weighing. We also removed rocks (≥ 2 mm diameter) from the sample, then placed the sample in a graduated cylinder, and recorded volume displacement. We then dried the SOL sample at 60 °C for 48 h, removed it from the oven, allowed it to return to room temperature, and weighed it. We ground an ~ 5 g sub-sample, placed it in a vial, and sent it to a U.S. Forest Service Laboratory in Research Triangle Park, NC, USA where the samples were oven-dried at 65 °C for 24 h, allowed to cool thoroughly, and analyzed for % C using a Flash EA1112 Carbon/Nitrogen Analyzer (CE Elantech, Inc., Lakewood, NJ, USA). Three certified standards and a blank were used in each sample set to check the accuracy of the sample values. We calculated SOL pools using bulk density (the dry weight of organic soil divided by the sample volume excluding rocks), organic soil depth, and % C. We calculated leaf litter C pools from bulk density, litter depth, and average litter % C measured in oak savannas as part of a separate study (Shrestha et al. unpublished data) (44.7 %).

2.3.5. Mineral soil and roots

We collected three mineral soil cores per plot, one along each of the three transects at the 9-m mark. We first removed litter and the SOL to expose mineral soil, then extracted a 30-cm core that we sectioned into three 10-cm depth increments. If we encountered an obstruction (e.g., rocks, coarse roots) before 30 cm, we attempted to re-core in a nearby location. If two re-coring attempts failed, we recorded the maximum depth reached. We placed each core section in labeled plastic bags, and upon return to the lab, stored them in a freezer at −20°C until processed. When ready to be processed, we allowed samples to thaw by air-drying for ~ 2 days; samples were then sequentially sieved through a 2-mm then a 1-mm sieve. We separated fine roots, rinsed and dried them for 48 h at 60 °C, and then weighed them. We did not distinguish among belowground vegetative structures, thus rhizomes < 2 mm diameter would fall into the category we called "fine roots." We removed rocks (≥ 2 mm diameter), placed them in a graduated cylinder, and recorded volume displacement. We then dried the processed mineral soil sample at 105 °C and weighed it. We ground a subsample of ~ 5 g and sent it to the Forest Service Laboratory for % C and % nitrogen (N) analysis (details above). Mineral soil samples were analyzed for % N in addition to % C to allow us to further investigate potential factors influencing mineral soil C pools. We used soil bulk density (dry weight of soil/sample volume excluding rocks) and % C to calculate or extrapolate (when obstructions prevented coring to desired depth) C pools to 30 cm depth (Mg ha^{-1}).

We collected three soil monoliths per plot, one per transect, to determine small coarse root (> 2 mm) C pools. We did not distinguish among belowground vegetative structures, thus coarse roots, rhizomes, and geoxyles were grouped into our "coarse root" carbon pool. We note that we do not have a complete assessment of coarse root C pools because we did not excavate/investigate coarse roots associated with individual trees, thus only coarse roots present in harvested monoliths were included in C pool estimations. In addition, much of the coarse root-like material harvested in areas with few trees was likely rhizomes. Monolith size was 20-cm length x 20-cm width x 30-cm depth, but varied slightly in the case of an obstruction such as a large rock. We placed monoliths in labeled plastic bags, and measured and recorded the final length, width, and depth at each corner of the harvested area. We picked all live and dead coarse roots (> 2 mm diameter) from the soil in the lab, rinsed them, dried them at 60 °C for 48 h or to a constant weight, and then recorded dry weight. For both fine and coarse roots, we used 45.6 % C, the average value of eight root samples that were analyzed for % C from this site, along with root bulk density and depth to calculate C pools (Mg ha^{-1}).

2.4. Plant biodiversity

To determine plant biodiversity, we conducted vegetation surveys between August and October 2024. Within the Demonstration Area, at each of the 30 (five per each of the six units) fixed sampling points used for the fire behavior loggers, we placed line-point intercept transects that intersected the fixed sampling point and extended east-west across the entire treatment unit. At each 10-m mark, we identified to species and recorded any plant that crossed above or below the transect, resulting in a total of 91–171 sampling points, depending on the size of the unit. If we could not identify a plant to species, we identified it to genus. In the closed-canopy forest and old-field, we surveyed along three 60-m transects placed east-west and centered on each of the C plots. At every 2-m mark, we documented every plant as mentioned above. Our sampling resulted in 90 points surveyed in the closed-canopy forest and old-field units.

2.5. Statistical analysis

For comparisons of individual, total, slowly-recovering (trees, snags, CWD, SOL), and quickly-recovering/belowground (fine woody debris, vegetation, fine and coarse roots, mineral soil) C pools among all treatments, we used linear models of C pools as a function of treatment. We used the “performance” R package (Lüdecke et al., 2021) to assess model diagnostics and used transformations if necessary to conform to assumptions. We used the “emmeans” package for post-hoc treatment pairwise comparisons with a Tukey p-value adjustment for multiple comparisons (Lenth, 2023). We additionally analyzed C pools as a function of fire frequency and fire season just within the Demonstration Area using similar methods.

To explore factors that may be driving mineral soil C across treatments, we analyzed mineral soil bulk density, % C, and % N (N cycling is tightly linked to C cycling) as a function of treatment using linear mixed effects models conducted using the “lme4” and “lmerTest” R packages (Bates et al., 2015, Kuznetsova et al., 2017), and used transformations if necessary to fulfill statistical assumptions. We used the “emmeans” package for post-hoc treatment pairwise comparisons with a Tukey p-value adjustment for multiple comparisons (Lenth, 2023). We additionally compared maximum temperature and time above 60 °C between EGS and LGS treatments using linear mixed effects models, however we did not investigate the effect of fire frequency on fire behavior because of insufficient temperature logger data for all frequencies.

We used the “iNEXT” R package to estimate diversity indices (Chao et al., 2014; Hsieh et al., 2016). We found the estimated sample coverage at double the minimum treatment sample size ($n = 63$, sample coverage $= 0.904$ at $n = 126$), and used the “estimateD” function to compute species richness and 95 % confidence intervals at that sample coverage for each ecosystem type (savanna, old-field, closed forest) and treatment (Chao and Jost, 2012). We used the “ChaoShannon” and “ChaoSimpson” functions to estimate asymptotic Shannon and Simpson diversity, respectively, and associated 95 % confidence intervals based on Chao et al. (2014). We only present differences among ecosystem types because we did not detect differences among savanna treatments, and because a more detailed study of understory vegetation communities as a function of treatment is ongoing. Shannon diversity is the exponential of Shannon entropy, and Simpson diversity is the inverse of Simpson’s index. Richness weights all species equally and is therefore highly influenced by rare species, whereas Shannon diversity weights species relative to their abundance, and Simpson diversity discounts all but the dominant species (Chao et al., 2014). Diversities were considered different if 95 % confidence intervals were non-overlapping. All analyses were conducted using R statistical software version 4.3.1 (R Core Team, 2023).

3. Results

Total C pools varied among units ($F = 49.4$, $p < 0.001$) (Fig. 2A), driven by > 2-fold more C stored in closed-canopy forests (226.6 Mg ha^{-1}) compared to all other treatments. About 65 % of the C stored in closed-canopy forests was ‘slowly-recovering’ (147.9 Mg ha^{-1}; Fig. 2B), including trees, CWD, and SOL (Table 1; Fig. S1), whereas 3–20 % of C stored in the savanna treatments was in this category. Quickly-recovering and protected C pools ranged from 72.9 Mg ha^{-1} in 3-Late to 106.1 Mg ha^{-1} in 3-Early, with the closed-canopy forest falling in the middle toward the low end (78.6 Mg ha^{-1}) (Fig. 2C).

Carbon pools in the restored savanna differed from the closed-canopy forest and the old-field in both quantity, location, and proportional contribution to total C. Individual C pools contributing most to the greater total C in closed-canopy forests compared to the other two ecosystem types were trees, the SOL, and to a lesser extent, FWD (Table 1, Fig. S1). Trees represented on average 7 % of total C in the savanna treatments, compared to 58 % in the closed-canopy forest. In contrast, understory vegetation C was greatest in the old-field (4.3 Mg ha^{-1}) and least in the closed-canopy forest (0.2 Mg ha^{-1}). CWD and coarse roots were similar among units, whereas leaf litter C was greater in the closed-canopy forest than some savanna units. Fine root C was least in the old-field (1.6 Mg ha^{-1}), with closed-canopy forest fine root C pools (4.3 Mg ha^{-1}) falling in the middle of the range of restored savanna fine root values (2.6 Mg ha^{-1} in 1-Late to 5.5 Mg ha^{-1} in 2-Early). Both the greatest and least mineral soil C values were in savanna treatments, ranging from ~ 64 Mg ha^{-1} in 3-Late and 1-Early (~ 70 % of total C) to 86.5 Mg ha^{-1} in 3-Early (~ 78 % of total C), with closed-canopy forest (65.9 Mg ha^{-1}, ~30 % of total C) and old-field (78.0 Mg ha^{-1}, 90 % of total C) values closer to the low and high end of the range, respectively (Table 1, Fig. S1).

Within the Demonstration Area, total C, litter, SOL, fine root, and mineral soil C responded to treatment (Fig. 3, Table S1). Late growing season (LGS) treatments contained on average ~15 % less total C than EGS (86.3 Mg C ha^{-1} and 98.9 Mg C ha^{-1} respectively, $p < 0.05$), and this trend was driven largely by 2- and 3-year fire-return intervals (Fig. 3A). LGS treatments contained more litter and SOL C than EGS units (Fig. 3B, C), driven by units with more frequent fire for litter. Three-year fire-return intervals resulted in more litter C than either 1- or 2-year fire-return intervals, reflecting longer time since fire and therefore litter accumulation in 3-year units (Fig. 3B). Fire season influenced fine-root C pools: EGS treatments had greater fine-root C than LGS treatments ($p < 0.005$; Fig. 3D). For mineral soil C pools, EGS units trended higher than LGS units, driven by units with less frequent fire (Fig. 3E).

Mineral soil % C and bulk density varied among treatments (Fig. S2), particularly within the first 10-cm of mineral soil depth (Fig. 4). Less frequent fire-return intervals in EGS treatments trended toward higher % C, with the 3-year EGS units having the highest value (5.13 %), the 2-year LGS units demonstrating the lowest % C value (3.24 %), and the closed-canopy forest demonstrating the broadest C fraction range (Fig. 4A). The 2-year LGS unit had the highest bulk density, which was greater than closed-canopy forest bulk density (Fig. 4B). The old-field had the highest mean % N (0.29), whereas LGS fire units trended lower (0.18–0.2) (Fig. 4C). As depth increased, bulk density increased, C

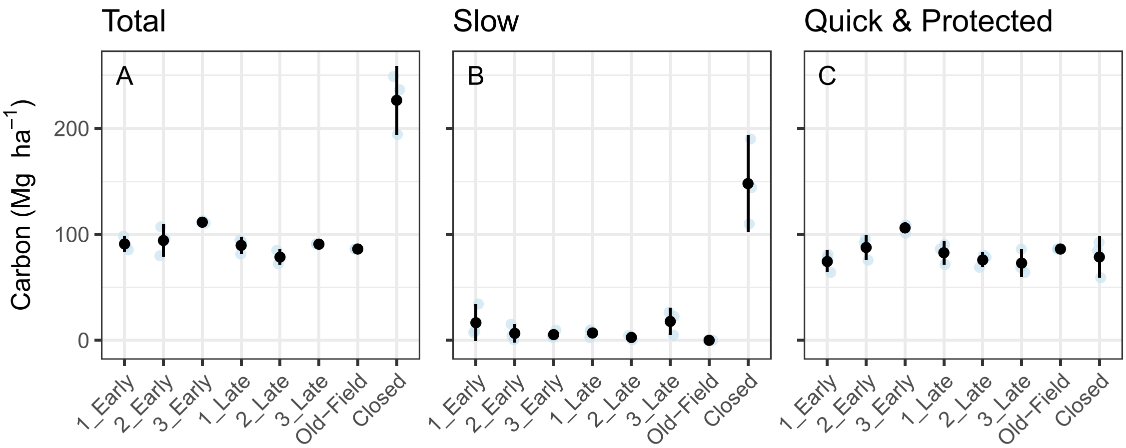

Fig. 2. ***Total C and C binned by recovery timeframe as a function of treatment.*** Total C (A), slowly-recovering C (B) which includes trees, coarse woody debris, and the soil organic layer, and quickly-recovering and protected C (C) which includes understory vegetation, leaf litter, fine woody debris, and belowground carbon (coarse and fine roots and mineral soil), by treatment (1-, 2-, or 3-year fire-return interval and early- or late growing-season fire in the restored savanna, closed = adjacent unmanaged, closed-canopy forests, old-field = adjacent, early-successional old-field). Individual plot values are blue points, mean treatment values are black points, and treatment 95 % confidence intervals are black lines.

Table 1

Mean and standard deviation (SD) (Mg C ha^{-1}) of individual carbon pools, summed slowly recovering pools (i.e., Slow) (trees, CWD (coarse woody debris), and SOL (soil organic layer)), and summed quickly-recovering and protected belowground (Quick+BG) pools (FWD (fine woody debris), understory, litter, roots, mineral soil) in each of the eight treatments (1-, 2-, or 3-year fire-return interval and early or late growing season fire in the restored savanna, closed = adjacent, unmanaged closed-canopy forests, old-field = adjacent, early-successional old-field). ANOVA F-values and p-values shown with p-values bolded when $p \leq 0.05$ and italicized when $p \leq 0.1$. Non-overlapping superscript letters represent significant pairwise differences at $p \leq 0.1$.

	Mean (Mg C ha^{-1}) (SD)									
	1-Early	2-Early	3-Early	1-Late	2-Late	3-Late	Old-field	Closed	F-value	p-value
Tree	14.8^{b}	4.9^{b}	5.2^{b}	0.6^{b}	1.4^{b}	12.2^{b}	0.0^{b}	132.8^{a}	21.9	**< 0.001**
	(13.9)	(5.4)	(3.6)	(1.0)	(1.7)	(12.6)	(0.0)	(36.7)		
CWD	0.3	0.4	0.4	0.0	0.0	0.0	0.0	1.3	0.8	0.568
	(0.6)	(0.7)	(0.7)	(0.0)	(0.0)	(0.0)	(0.0)	(2.3)		
FWD	0.0^{bc}	0.5^{bc}	0.2^{bc}	1.6^{ab}	0.0^{c}	0.6^{bc}	0.0^{c}	3.2^{a}	7.9	**< 0.001**
	(0.0)	(0.4)	(0.1)	(1.9)	(0.0)	(0.2)	(0.0)	(1.5)		
Understory	2.6^{ab}	1.6^{b}	2.7^{ab}	2.0^{ab}	1.7^{b}	1.6^{b}	4.3^{a}	0.2^{c}	8.3	**< 0.001**
	(1.6)	(0.2)	(0.8)	(0.4)	(0.9)	(0.5)	(1.2)	(0.1)		
Litter	0.2^{b}	0.4^{b}	1.2^{ab}	0.9^{ab}	0.9^{ab}	1.2^{ab}	0.9^{ab}	1.7^{a}	3.4	**0.021**
	(0.2)	(0.1)	(0.3)	(0.6)	(0.5)	(0.2)	(0.5)	(0.8)		
SOL	1.5^{bc}	1.3^{bc}	0.3^{bc}	6.4^{ab}	1.3^{bc}	5.7^{ab}	0.0^{c}	13.9^{a}	6.3	**0.001**
	(1.8)	(1.6)	(0.2)	(3.3)	(2.3)	(5.2)	(0.0)	(6.7)		
Coarse root	4.1	1.5	10.3	5.0	3.4	1.8	1.3	3.5	1.9	0.135
	(3.1)	(1.3)	(8.2)	(3.6)	(1.8)	(1.0)	(0.5)	(3.3)		
Fine root	3.7^{abc}	5.5^{a}	5.1^{a}	2.6^{bc}	3.0^{abc}	4.0^{abc}	1.6^{c}	4.3^{ab}	5.6	**0.002**
	(0.3)	(1.2)	(0.8)	(0.5)	(0.9)	(1.7)	(0.5)	(1.0)		
Mineral soil	63.9	78.0	86.5	70.7	66.9	63.7	78.0	65.9	2.2	*0.095*
	(6.1)	(8.8)	(10.1)	(11.7)	(5.6)	(9.9)	(0.8)	(16.6)		
Slow	16.6^{b}	6.6^{b}	5.4^{b}	7.0^{b}	2.7^{b}	17.8^{b}	0.0^{b}	147.9^{a}	28.8	**< 0.001**
	(15.3)	(7.7)	(3.6)	(3.8)	(2.1)	(11.4)	(0.0)	(40.2)		
Quick+BG	74.4^{b}	87.6^{ab}	106.1^{a}	82.7^{ab}	75.8^{b}	72.9^{b}	86.2^{ab}	78.6^{b}	3.5	**0.018**
	(9.1)	(10.6)	(4.4)	(9.9)	(6.2)	(11.7)	(0.1)	(17.5)		
Total	91.0^{bc}	94.2^{bc}	111.5^{b}	89.6^{bc}	78.6^{c}	90.7^{bc}	86.2^{bc}	226.6^{a}	49.4	**< 0.001**
	(6.6)	(13.7)	(1.2)	(7.3)	(6.3)	(0.4)	(0.04)	(28.7)		

fraction decreased, and differences among units decreased (Fig. S2).

Maximum temperature (°C) and fire residency times (seconds above 60 °C) trended higher in EGS than in LGS units ($p = 0.057$ and $p = 0.053$, respectively) (Fig. S3, S4). In addition, all EGS fires, but not all LGS fires, reached 60 °C.

Diversity was higher in the restored savannas than either the old-field or the closed-canopy forest for all metrics (Fig. 5A-C), whereas the old-field and closed-canopy forest were similar in all diversity metrics. All estimated savanna diversity levels were about two times higher than those of the closed-canopy forest.

4. Discussion

Our study contributes to a holistic understanding of the combined response of ecosystem C and plant biodiversity to oak/pine savanna restoration in the southeastern U.S. Although savanna restoration reduced total C storage, the proportional distribution of C pools that are relatively more protected from disturbance (e.g., mineral soils and fine roots) or that recover quickly (e.g., understory vegetation) increased, as did groundcover plant biodiversity. Fires conducted during the EGS appeared to enhance this stable C storage. Thus, as wildfire and other disturbance (e.g. hurricanes, tornadoes) probability increases, so does the importance of savanna and woodland restoration and maintenance

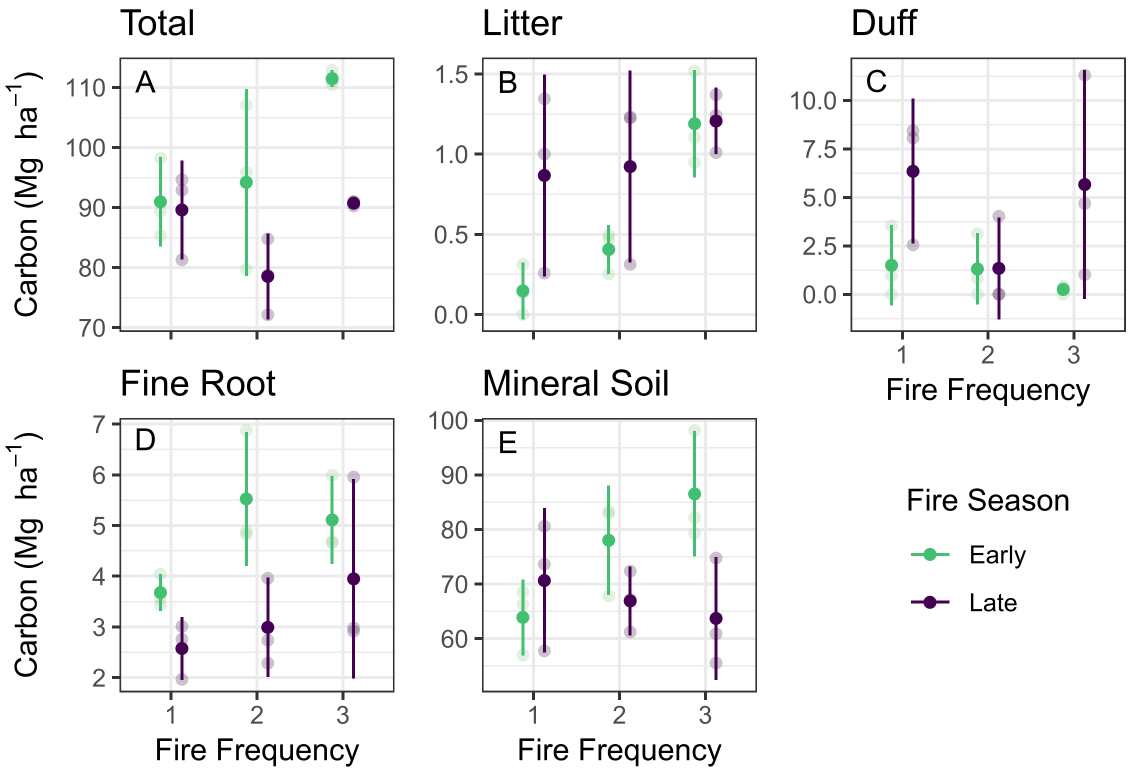

Fig. 3. ***Savanna fire regime effects***: Effects of fire frequency (1-, 2-, and 3-year) and season (early vs. late) on carbon pools that were affected by either fire frequency or fire season, including (A) total C, (B) leaf litter, (C) duff, (D) fine roots, and (E) mineral soils. Translucent points represent plot values, filled in points represent treatment-level means, and bars represent treatment 95 % confidence intervals.

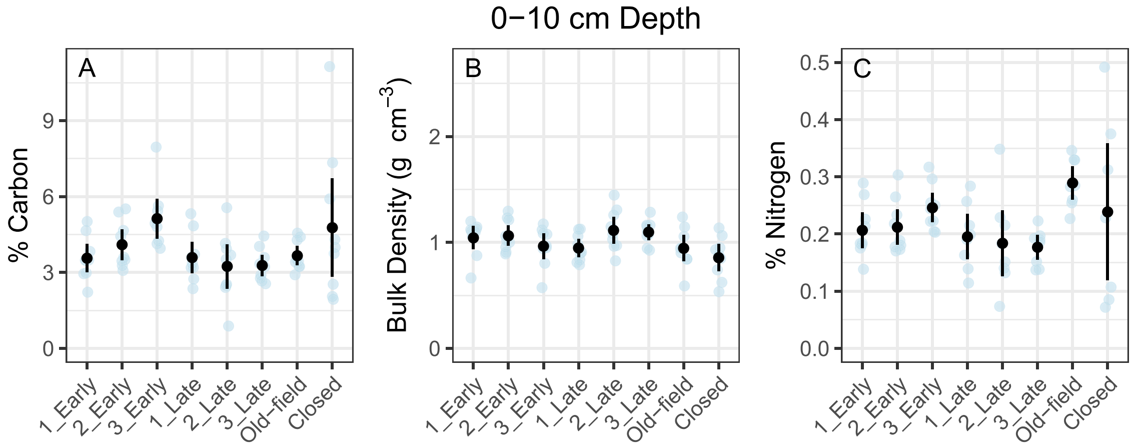

Fig. 4. ***Mineral soil characteristics as a function of treatment***: Percent carbon (A), bulk density (g/cm^3; B), and % N (C) for each treatment (1-, 2-, or 3-year fire-return interval, early or late growing-season fire) within the 0–10 cm mineral soil depth range. Individual samples are blue points, mean treatment values are black points, and treatment 95 % confidence intervals are black lines.

for biodiversity and C resilience.

Although greater tree biomass and a relatively thick SOL led to greater total C pools in the unmanaged, closed-canopy forest compared to the restored savanna and old-field, resilience and resistance of these C pools to disturbance is likely low. Greater overstory and midstory tree density in the closed-canopy forest likely increases C vulnerability to loss, as greater tree density and cover often correlate with increased susceptibility to disturbance (Bottero et al., 2017; Bradford and Bell, 2017), especially wildfires (Ivey et al., 2024), which are increasing in frequency and extent across the central and eastern U.S. (Donovan et al., 2023). Development of a relatively thick, undisturbed SOL also contributed to greater C storage in the closed-canopy forest, but this pool is also at high risk of loss with wildfire (Alcañiz et al., 2018; Certini, 2005; González-Pérez et al., 2004; Lavoie et al., 2010; Nave et al., 2011). SOL smoldering during fire can also increase tree mortality, and thereby C loss, because of fine root consumption and decreased sap flux and coarse root carbohydrates (Susaeta et al., 2022; Varner et al., 2016, 2007). Ultimately, restoring savannas will generate an initial C loss through tree removal (Dey et al., 2017), but post-restoration C pools should exhibit greater stability (Hanberry et al., 2018), especially as slow-growing, fire-tolerant species with relatively dense wood such as post oak (*Q. stellata*) and white oak (*Q. alba*) (Doraisami et al., 2022) mature in the overstory and develop large belowground C pools in coarse roots (Zhou et al., 2022).

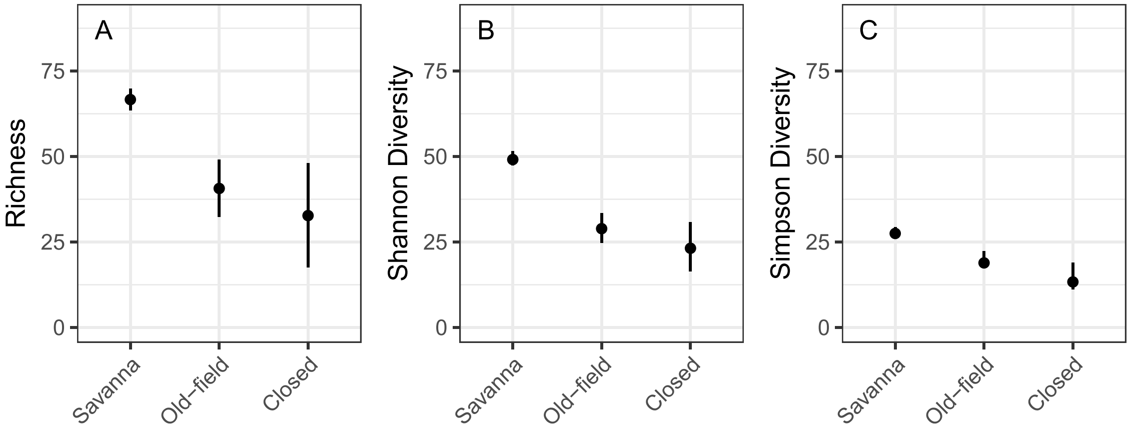

Fig. 5. ***Ecosystem type biodiversity effects:*** Estimated diversity metrics (points) and 95 % confidence intervals (lines) for each of the 3 ecosystem types, including (A) richness estimated based on the sample coverage (.904) at twice the minimum unit sample size and asymptotic extrapolated metrics of (B) Shannon diversity and (C) Simpson diversity.

More understory or groundlayer vegetation biomass in the restored savanna treatments and old-field compared to the closed-canopy forest reflects management leading to increased light levels in these open ecosystems, but more groundlayer biomass did not always equate to greater fine root biomass. Opening the canopy increases available light, and consequently, herbaceous understory vegetation cover (Brewer, 2016; Hanberry et al., 2020b; Vander Yacht et al., 2020), whereas regular burning maintains the herbaceous layer by preventing woody encroachment from outcompeting the herbaceous species (Hutchinson et al., 2012; Nanney et al., 2018; Peterson and Reich, 2001). In the old-field, current management, including regular fire, mechanical soil disturbance, and spot-spray herbicide applications, promoted herbaceous plant cover with scattered shrubs and an open structure at ground-level, which are desirable characteristics when managing habitat for northern bobwhite (Gruchy and Harper, 2014; Powell et al., 2022). Elevated soil % N in the old-field probably was a result of prior use as an agricultural field and likely led to increased aboveground biomass (Feng et al., 2023). Conversely, the old-field had the lowest fine root biomass, possibly because elevated soil N levels can reduce root biomass due to decreased root allocation in nutrient-rich soils (Dress and Boerner, 2001; Feng et al., 2023). Also, the old-field groundlayer was dominated by early-successional forbs due to land use legacy and subsequent soil disturbance (disking) implemented to enhance northern bobwhite habitat (Gruchy and Harper, 2014), and high forb cover at the expense of graminoids, combined with overall lower functional diversity, likely reduced belowground biomass (Fornara and Tilman, 2008). Fine root C was similar in savanna treatments and the closed-canopy forest, despite savannas having substantially greater understory vegetation biomass. At a broad scale, tree fine root biomass strongly correlates with basal area (Finér et al., 2011). Consequently, the greater basal area and dense midstory in the closed-canopy forest certainly contributed to the relative similarity of the fine root C pool between savannas and closed-canopy forest, likely by increasing tree fine root biomass while decreasing understory vegetation fine root biomass. Furthermore, although we sampled roots to 30-cm depth, we may not have detected all fine roots, especially in fire-treated areas, as burning can impact fine root biomass at deeper depths (60 – 90 cm) (Kitchen et al., 2009). Thus, although fine root C was least in the old-field and similar among all other units, deeper sampling is recommended to verify these results.

Within the restored savanna treatments, fire regime (frequency and seasonality) influenced several C pools because of differential effects on vegetation composition, structure, and biomass, and their interactions with fire timing and intensity. We expected less frequent burning to lead to more total C, as a longer interval between fires allows more time for recovery and less regular stress to woody stems (Robertson and Hmielowski, 2014), but that occurred only in the EGS treatment, where a 3-year return interval stored more C than 1- or 2-year. The frequency effect in the EGS treatments seems largely attributed to mineral soil C (discussed below), and although we observed that sapling density increased with less frequent fire, similar to Peterson et al. (2007), sapling trends did not influence our total tree C pool. In the EGS treatments, lower average relative humidity and fuel moisture and higher wind speeds led to higher fire temperatures than in LGS treatments, similar to previous fire-seasonality research in the region (Bones et al. *in press*; Turner et al., 2024). Early growing season burning increased fine root C pools, likely driven by increased C4 perennial grass coverage, which store more fine root C than other herbaceous functional groups (Mahaney et al., 2008). Greater fine root biomass in EGS treatments may also have resulted from a post-fire increase in herbaceous fine root growth to capitalize on increased nutrient and soil space availability (Li et al., 2025), which was enabled in EGS treatments where fire was, on average, more intense and more likely to top-kill small saplings. Greater relative early season rainfall events may also increase soil moisture and buffering capacity against direct heat damage to roots in EGS fires (Cerdà and Robichaus, 2009).

The savanna treatment trend of increasing mineral soil C with less-frequent fire in EGS but not LGS units likely stemmed from a combination of changes in belowground biomass and post-fire C inputs. Belowground biomass contributes disproportionally more than aboveground biomass to soil organic C (Berhongaray et al., 2019; Lu et al., 2023), so increased fine root biomass was likely a factor leading to increased mineral soil C in certain EGS treatments. Post-fire ash and pyrogenic C inputs can increase mineral soil C (Alcañiz et al., 2018; Certini, 2005), and this effect may have been strongest with less-frequent EGS fire because of the combination of increased fuel buildup and greater fire intensity relative to the more-frequent and LGS treatments. Increased particulate organic material inputs to the forest floor from repeated fire, followed by early season rain events that leach dissolved C into the soil profile (Michalzik and Martin, 2013), may have also contributed to increased mineral soil C pools in the EGS treatment. As with root biomass, mineral soil carbon effects may be occurring at depths below 30 cm, thus deeper soil sampling for a more complete soil carbon picture is an important next step. Although our observed trends should be interpreted as context-specific, and the longevity/stability of mineral soil C is influenced by many factors, an increase in stable mineral soil C, including black C, is an important strategy for increasing long-term C stocks, highlighting the importance of continued investigations of prescribed fire effects on mineral soil C pools over time (Rumpel et al., 2012). In particular, more detailed investigation of how vegetation structure and fire influence carbon form and longevity would provide necessary information for a deeper understanding of long-term

C storage potential of open ecosystems.

Greater plant diversity in the restored savanna than the old-field and closed-canopy forest reflects a combination of a light- and fire-stimulated seedbank as well as lack of prior soil disturbance. Increased available sunlight and relatively frequent prescribed fire stimulates germination of the seedbank and spread of plant species via root systems or seed (Estill and Cruzan, 2001; GeFellers et al., 2020; Glasgow and Matlack, 2007; Leach and Givnish, 1999). In addition, the savanna units pooled together provide pyrodiversity resulting from treatment differences as well as heterogeneous burn coverage. Although the old-field had the greatest understory vegetation C pool and the greatest abundance of early-successional forbs, the diversity values were lowest and more comparable to the closed-canopy forest. This trajectory was likely a result of the legacy effects of past management, which included a long history of soil disturbance, planting nonnative species, and herbicide applications. To our knowledge (and that of TWRA), the area where the Demonstration Area was established had not been cropped or planted in nonnative herbaceous plants prior to being planted to loblolly pine. Although unmanaged loblolly pine stands are notoriously scarce in understory diversity, the seedbank and dormant rhizomes persist and can respond once overstory trees are removed and litter consumed by burning (Bones et al. *in press*; Cohen et al., 2004; Nanney et al., 2018). Overall, savanna restoration resulted in at least twice as much ground-layer plant diversity as the other ecosystem types, emphasizing the important role of restoration to promote a diverse groundcover forb and grass layer, which provides habitat for northern bobwhite, declining grassland birds such as Henslow's sparrow (*Centronyx henslowii*), the Tennessee state-threatened northern pine snake (*Pituophis melanoleaucus*), and many other wildlife species (Harper et al., 2021). Taken together, the carbon and biodiversity results demonstrate a clear tradeoff, with savannas supporting high biodiversity but less total C than closed forests. This tradeoff, and the extent to which it is driven by carbon pools that are relatively less protected, suggest open forest ecosystems should not be ruled out when considering climate mitigation goals, and better future understanding of risk of loss of all carbon pools under various climate scenarios could help us understand where these systems may fit into reaching carbon storage and biodiversity conservation goals.

Although the trends demonstrated in our study should encourage future hypothesis testing, we note some limitations to be considered when interpreting our results. Importantly, we did not have treatment-level replication of combinations of fire frequency and season within the savanna restoration experiment. Therefore, we advise caution in extrapolating results broadly to other systems, as site-specific factors may be playing a role. Additionally, although we documented trends among savanna treatments, closed-canopy forest, and the old-field, lack of replication limited our ability to detect interactive effects of fire season and frequency, which remains an important question in open ecosystem restoration. Landscape level variability in edaphic factors may influence carbon dynamics (Jackson et al., 2017), thus similar studies in other regions are required to determine whether these treatment-level results may be meaningful in alternative geographic contexts. Finally, we conducted a one-time carbon sampling to estimate carbon pools and did not measure flux processes or changes in carbon stocks over time. Thus, we lack complete information on the effects of open ecosystem restoration on carbon balance, and we encourage investigation of temporal carbon dynamics as an important next step.

Our results indicated a strong trade-off between total C storage and plant biodiversity, with unmanaged, closed-canopy forests storing large quantities of C relative to a restored savanna but containing significantly less understory plant diversity. We also demonstrated that in addition to providing greater levels of plant species diversity, the savanna we studied stored as much or more C as unmanaged forests in pools that are likely to remain stable over time with continued savanna management, such as mineral soil, fine root, and understory vegetation C, even in the face of increasingly frequent and extreme disturbance. Finally, our study suggests that early compared to late growing season prescribed fire may maximize these stable C pools. Our findings suggest the importance of restoring and maintaining savannas and ecosystem diversity at the landscape scale to maximize multiple ecosystem services and mitigate risk in the context of global change.

CRediT authorship contribution statement

Nathan Wilhite: Writing – review & editing, Project administration, Methodology. **Maya M. Lapp:** Writing – review & editing, Methodology, Data curation. **Craig A. Harper:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition. **Heather D. Alexander:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Milton Tamara:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123489.

References

Adams, M.A., 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. For. Ecol. Manag 294, 250–261. https://doi.org/10.1016/j.foreco.2012.11.039.

Alcañiz, M., Outeiro, L., Francos, M., Úbeda, X., 2018. Effects of prescribed fires on soil properties: a review. Sci. Total Environ. 613–614, 944–957. https://doi.org/10.1016/j.scitotenv.2017.09.144.

Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J., Varner, J.M., 2021. Mesophication of Oak Landscapes: evidence, knowledge gaps, and future research. BioScience 71, 531–542. https://doi.org/10.1093/biosci/biaa169.

Anderson, H.E., 1978. Graphic aids for field calculation of dead, down forest fuels, 45. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Arthur, M.A., Varner, J.M., Lafon, C.W., Alexander, H.D., Dey, D.C., Harper, C.A., Horn, S.P., Hutchinson, T.F., Keyser, T.L., Lashley, M.A., Moorman, C.E., Schweitzer, C.J., 2021. Fire ecology and management in eastern broadleaf and appalachian forests. In: Greenberg, C.H., Collins, B. (Eds.), Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems, Managing Forest Ecosystems. Springer International Publishing, Cham, pp. 105–147. https://doi.org/10.1007/978-3-030-73267-7_4.

Barrioz, S., Keyser, P., Buckley, D., Buehler, D., Harper, C., 2013. Vegetation and Avian response to Oak Savanna restoration in the Mid-South USA. Am. Midl. Nat. 169, 194–213. https://doi.org/10.1674/0003-0031-169.1.194.

Bates, D., Bolker, B.M., Mächler, M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Soft 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Berhongaray, G., Cotrufo, F.M., Janssens, I.A., Ceulemans, R., 2019. Below-ground carbon inputs contribute more than above-ground inputs to soil carbon accrual in a bioenergy poplar plantation. Plant Soil 434, 363–378. https://doi.org/10.1007/s11104-018-3850-z.

Bones, J.T., Marshall, S.G., Turner, M.A., Lapp, M.M., Gulsby, W.D., Willcox, E.V., & Harper, C.A. Vegetation response varies by season of burning in pine woodlands across the southeastern US. *Fire ecology, in press*.

Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614. https://doi.org/10.1111/1365-2664.12847.

Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Front. Ecol. Environ. 15, 11–17. https://doi.org/10.1002/fee.1445.

Bradford, J.B., D'Amato, A.W., 2012. Recognizing trade-offs in multi-objective land management. Front. Ecol. Environ. 10, 210–216. https://doi.org/10.1890/110031.

Brawn, J.D., 2006. Effects of restoring Oak Savannas on bird communities and populations. Conserv. Biol. 20, 460–469. https://doi.org/10.1111/j.1523-1739.2006.00310.x.

Brewer, J.S., 2016. Natural canopy damage and the ecological restoration of fire-indicative groundcover vegetation in an Oak-Pine Forest. Fire Ecol. 12, 105–126. https://doi.org/10.4996/fireecology.1202105.

Brown, J., 1974. Handbook for Inventorying Downed Woody Material (USDA Forest Service General Technical Report No. INT-16).

Brudvig, L.A., Asbjornsen, H., 2009. The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas. J. Appl. Ecol. 46, 231–240. https://doi.org/10.1111/j.1365-2664.2008.01590.x.

Cain, M.D., Shelton, M.G., 2000. Survival and growth of Pinus echinata and Quercus seedlings in response to simulated summer and winter prescribed burns. Can. J. For. Res. 30 (11), 1830–1836.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320, 1456–1457. https://doi.org/10.1126/science.1155458.

Cerdà, A., Robichaus, P.R. (Eds.), 2009. Fire effects on soils and restoration strategies, 1st edition. ed, Land reconstruction and management series. Science Publishers, Enfield, NH Jersey Plymouth. ⟨https://doi.org/10.1201/9781439843338⟩.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547. https://doi.org/10.1890/11-1952.1.

Clark, K.L., Skowronski, N., Gallagher, M., 2015. Fire management and carbon sequestration in pine barren forests. J. Sustain. For. 34, 125–146. https://doi.org/10.1080/10549811.2014.973607.

Coates, T.A., Hagan, D.L., Aust, W.M., Johnson, A., Keen, J.C., Chow, A.T., Dozier, J.H., 2018. Mineral soil chemical properties as influenced by long-term use of prescribed fire with differing frequencies in a Southeastern Coastal Plain Pine Forest. Forests 9, 739. https://doi.org/10.3390/f9120739.

Cohen, S., Braham, R., Sanchez, F., 2004. Seed bank viability in disturbed longleaf pine sites. Restor. Ecol. 12, 503–515. https://doi.org/10.1111/j.1061-2971.2004.00382.x.

Czimczik, C.I., Schmidt, M.W.I., Schulze, E.D., 2005. Effects of increasing fire frequency on black carbon and organic matter in Podzols of Siberian Scots pine forests. Eur. J. Soil Sci. 56, 417–428. https://doi.org/10.1111/j.1365-2389.2004.00665.x.

Davis, T.S., Meddens, A.J.H., Stevens-Rumann, C.S., Jansen, V.S., Sibold, J.S., Battaglia, M.A., 2022. Monitoring resistance and resilience using carbon trajectories: analysis of forest management–disturbance interactions. Ecol. Appl. 32, e2704. https://doi.org/10.1002/eap.2704.

Dey, D.C., Kabrick, J.M., Schweitzer, C.J., 2017. Silviculture to restore Oak Savannas and woodlands. J. For. 115, 202–211. https://doi.org/10.5849/jof.15-152.

Donovan, V.M., Crandall, R., Fill, J., Wonkka, C.L., 2023. Increasing large wildfire in the Eastern United States. Geophys. Res. Lett. 50, e2023GL107051. https://doi.org/10.1029/2023GL107051.

Doraisami, M., Kish, R., Paroshy, N.J., Domke, G.M., Thomas, S.C., Martin, A.R., 2022. A global database of woody tissue carbon concentrations. Sci. Data 9, 284. https://doi.org/10.1038/s41597-022-01396-1.

Dress, W.J., Boerner, R.E., 2001. Root dynamics of southern Ohio oak-hickory forests: influences of prescribed fire and landscape position. Can. J. For. Res. 31, 644–653. https://doi.org/10.1139/x00-196.

Estill, J.C., Cruzan, M.B., 2001. Phytogeography of rare plant species endemic to the Southeastern United States. Castanea 66 (1-2), 3–23.

Feng, H., Guo, J., Peng, C., Kneeshaw, D., Roberge, G., Pan, C., Ma, X., Zhou, D., Wang, W., 2023. Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: a global meta-analysis. Glob. Change Biol. 29, 3970–3989. https://doi.org/10.1111/gcb.16731.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011. Factors causing variation in fine root biomass in forest ecosystems. For. Ecol. Manag 261, 265–277. https://doi.org/10.1016/j.foreco.2010.10.016.

Fontúrbel, T., Carrera, N., Vega, J.A., Fernández, C., 2021. The effect of repeated prescribed burning on soil properties: a review. Forests 12, 767. https://doi.org/10.3390/f12060767.

Fornara, D.A., Tilman, D., 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. J. Ecol. 96, 314–322. https://doi.org/10.1111/j.1365-2745.2007.01345.x.

Gao, P., Terando, A.J., Kupfer, J.A., Morgan Varner, J., Stambaugh, M.C., Lei, T.L., Kevin Hiers, J., 2021. Robust projections of future fire probability for the conterminous United States. Sci. Total Environ. 789, 147872. https://doi.org/10.1016/j.scitotenv.2021.147872.

GeFellers, J.W., Buehler, D.A., Moorman, C.E., Zobel, J.M., Harper, C.A., 2020. Seeding is not always necessary to restore native early successional plant communities. Restor. Ecol. 28, 1485–1494. https://doi.org/10.1111/rec.13249.

Glasgow, L.S., Matlack, G.R., 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. For. Ecol. Manag 238, 54–64. https://doi.org/10.1016/j.foreco.2006.08.344.

Gonzalez-Akre, E., Piponiot, C., Lepore, M., Herrmann, V., Lutz, J.A., Baltzer, J.L., Dick, C.W., Gilbert, G.S., He, F., Heym, M., Huerta, A.I., Jansen, P.A., Johnson, D.J., Knapp, N., Král, K., Lin, D., Malhi, Y., McMahon, S.M., Myers, J.A., Orwig, D., Rodríguez-Hernández, D.I., Russo, S.E., Shue, J., Wang, X., Wolf, A., Yang, T., Davies, S.J., Anderson-Teixeira, K.J., 2022. *allodb*: An R package for biomass estimation at globally distributed extratropical forest plots. Methods Ecol. Evol. 13, 330–338. https://doi.org/10.1111/2041-210x.13756.

González-Pérez, J.A., González-Vila, F.J., Almendros, G., Knicker, H., 2004. The effect of fire on soil organic matter—a review. Environ. Int. 30, 855–870. https://doi.org/10.1016/j.envint.2004.02.003.

Gruchy, J.P., Harper, C.A., 2014. Effects of management practices on northern bobwhite habitat. J. Southeast. Assoc. Fish. Wildl. Agencies 1, 133–141.

Gruchy, J.P., Harper, C.A., Gray, M.J., 2009. Methods for controlling woody invasion into CRP fields in Tennessee. Natl. Quail Symp Proc. 6 (1), 315–321.

Hanberry, B.B., Abrams, M.D., Arthur, M.A., Varner, J.M., 2020a. Reviewing fire, climate, deer, and foundation species as drivers of historically open oak and pine forests and transition to closed forests. Front. For. Glob. Change 3, 56. https://doi.org/10.3389/ffgc.2020.00056.

Hanberry, B.B., Bragg, D.C., Alexander, H.D., 2020b. Open forest ecosystems: an excluded state. For. Ecol. Manag 472, 118256. https://doi.org/10.1016/j.foreco.2020.118256.

Hanberry, B.B., Bragg, D.C., Hutchinson, T.F., 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. Ecosphere 9, e02431. https://doi.org/10.1002/ecs2.2431.

Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the central hardwoods and Appalachian Regions, USA. Fire Ecol. 12, 127–159. https://doi.org/10.4996/fireecology.1202127.

Harper, C.A., Gefellers, J.W., Buehler, D.A., Moorman, C.E., Zobel, J.M., 2021. Plant community response and implications for wildlife following control of a nonnative perennial grass. Wildl. Soc. Bull. 45, 618–629. https://doi.org/10.1002/wsb.1232.

Howe, H.F., 1995. Succession and fire season in experimental prairie plantings. Ecology 76, 1917–1925. https://doi.org/10.2307/1940723.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Hutchinson, T.F., Adams, B.T., Dickinson, M.B., Heckel, M., Royo, A.A., Thomas-Van Gundy, M.A., 2024. Sustaining eastern oak forests: synergistic effects of fire and topography on vegetation and fuels. Ecol. Appl. 34, e2948. https://doi.org/10.1002/eap.2948.

Hutchinson, T.F., Yaussy, D.A., Long, R.P., Rebbeck, J., Sutherland, E.K., 2012. Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. For. Ecol. Manag 286, 87–100. https://doi.org/10.1016/j.foreco.2012.08.036.

Ivey, M.A., Wonkka, C.L., Weidig, N.C., Donovan, V.M., 2024. Woody cover fuels large wildfire risk in the Eastern US. Geophys. Res. Lett. 51, e2024GL110586. https://doi.org/10.1029/2024GL110586.

Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Piñeiro, G., 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. Annu. Rev. Ecol. Syst. 48 (1), 419–445. https://doi.org/10.1146/annurev-ecolsys-112414-054234.

Johnson, K.D., Domke, G.M., Russell, M.B., Walters, B., Hom, J., Peduzzi, A., Birdsey, R., Dolan, K., Huang, W., 2017. Estimating aboveground live understory vegetation carbon in the United States. Environ. Res. Lett. 12, 125010. https://doi.org/10.1088/1748-9326/aa8fdb.

Kitchen, D.J., Blair, J.M., Callaham, M.A., 2009. Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie. Plant Soil 323, 235–247. https://doi.org/10.1007/s11104-009-9931-2.

Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers (No. PSW-GTR-224). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA. ⟨https://doi.org/10.2737/PSW-GTR-224⟩.

Knapp, E.E., Keeley, J.E., 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. Int. J. Wildland Fire 15, 37. https://doi.org/10.1071/WF04068.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Soft 82 (13), 1–26. https://doi.org/10.18637/jss.v082.i13.

Lavoie, M., Starr, G., Mack, M.C., Martin, T.A., Gholz, H.L., 2010. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. Nat. Areas J. 30, 82–94. https://doi.org/10.3375/043.030.0109.

Leach, M.K., Givnish, T.J., 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. Ecol. Monogr. 69, 353–374. https://doi.org/10.1890/0012-9615(1999)069[0353:gitcsa]2.0.co;2.

Lenth R. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.8, <⟨https://CRAN.R-project.org/package=emmeans⟩>.

Lettow, M.C., Brudvig, L.A., Bahlai, C.A., Landis, D.A., 2014. Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. For. Ecol. Manag 329, 89–98. https://doi.org/10.1016/j.foreco.2014.06.019.

Li, F., Gu, J., Zhao, B., Jinhua, G., Sun, L., 2025. The short-term effects of prescribed burning on the root biomass and soil carbon dynamics of larch plantations. Forests 16, 143. https://doi.org/10.3390/f16010143.

Lu, X., Gilliam, F.S., Yue, X., Wang, B., Kuang, Y., 2023. Shifts in above- versus below-ground carbon gains to terrestrial ecosystems carbon sinks under excess nitrogen inputs. Glob. Biogeochem. Cycles 37, e2022GB007638. https://doi.org/10.1029/2022GB007638.

Lüdecke, et al., 2021. Performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6 (60), 3139. https://doi.org/10.21105/joss.03139.

Lutes, D.C., Keane, R.E., Caratti, J.F., Key, C.H., Benson, N.C., Sutherland, S., Gangi, L.J., 2006. FIREMON: Fire effects monitoring and inventory system (No. RMRS-GTR-164). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. ⟨https://doi.org/10.2737/RMRS-GTR-164⟩.

Mahaney, W.M., Smemo, K.A., Gross, K.L., 2008. Impacts of C4 grass introductions on soil carbon and nitrogen cycling in C3-dominated successional systems. Oecologia 157, 295–305. https://doi.org/10.1007/s00442-008-1063-5.

Malmsheimer, R.W., Heffernan, P., Brink, S., Crandall, D., Deneke, F., Galik, C., Gee, E., Helms, J.A., McClure, N., Mortimer, M., Ruddell, S., Smith, M., Stewart, J., 2008. Forest management solutions for mitigating climate change in the United States. J. For. 106, 115–117. https://doi.org/10.1093/jof/106.3.115.

McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34, 244–256. https://doi.org/10.1111/j.1600-0587.2010.06390.x.

Michalzik, B., Martin, S., 2013. Effects of experimental duff fires on C, N and P fluxes into the mineral soil at a coniferous and broadleaf forest site. Geoderma 197–198, 169–176. https://doi.org/10.1016/j.geoderma.2013.01.010.

Miles, P.D., Smith, W.Brad, 2009. Specific gravity and other properties of wood and bark for 156 tree species found in North America (No. NRS-RN-38). U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. ⟨https://doi.org/10.2737/NRS-RN-38⟩.

Nanney, J.S., Harper, C.A., Buehler, D.A., Bates, G.E., 2018. Nutritional carrying capacity for cervids following disturbance in hardwood forests. J. Wildl. Manag 82, 1219–1228. https://doi.org/10.1002/jwmg.21473.

Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2011. Fire effects on temperate forest soil C and N storage. Ecol. Appl. 21, 1189–1201. https://doi.org/10.1890/10-0660.1.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the Eastern United States. BioScience 58, 123–138. https://doi.org/10.1641/B580207.

Nuzzo, V.A., 2025. Extent and status of midwest oak savanna: presettlement and 1985. Nat. Areas J. 6 (2), 6–36.

Ontl, T.A., Janowiak, M.K., Swanston, C.W., Daley, J., Handler, S., Cornett, M., Hagenbuch, S., Handrick, C., Mccarthy, L., Patch, N., 2020. Forest management for carbon sequestration and climate adaptation. J. For. 118, 86–101. https://doi.org/10.1093/jofore/fvz062.

Palecki, M., Durre, I., Applequist, S., Arguez, A., Lawrimore, J. 2021: U.S. Climate Normals 2020: U.S. Annual Climate Normals (2006-2020). NOAA National Centers for Environmental Information.

Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savannah: fire frequency effects on stand structure and dynamics. Ecol. Appl. 11, 914–927. https://doi.org/10.1890/1051-0761(2001)011[0914:PFIOSF]2.0.CO;2.

Peterson, D.W., Reich, P.B., Wrage, K.J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. J. Veg. Sci. 18 (1), 3–12. https://doi.org/10.1111/j.1654-1103.2007.tb02510.x.

Pile Knapp, L.S., Dey, D.C., Stambaugh, M.C., Thompson, F.R., Varner, J.M., 2024. Managing forward while looking back: reopening closed forests to open woodlands and savannas. Fire Ecol. 20, 72. https://doi.org/10.1186/s42408-024-00312-9.

Powell, B.L., Buehler, D.A., Moorman, C.E., Zobel, J.M., Harper, C.A., 2022. Vegetation structure and food availability following disturbance in recently restored early successional plant communities. Wildl. Soc. Bull. 46, e1372. https://doi.org/10.1002/wsb.1372.

R Core Team (2023). R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <⟨https://www.R-project.org/⟩>.

Regelbrugge, J.C., Smith, D.W., 1994. Postfire tree mortality in relation to wildfire severity in mixed oak forests in the blue ridge of Virginia. North. J. Appl. For. 11, 90–97. https://doi.org/10.1093/njaf/11.3.90.

Robertson, K.M., Hmielowski, T.L., 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174, 765–776. https://doi.org/10.1007/s00442-013-2823-4.

Rumpel, C., Chabbi, A., Marschner, B., 2012. Carbon storage and sequestration in subsoil horizons: knowledge, gaps and potentials. In: Lal, R., Lorenz, K., Hüttl, R.F., Schneider, B.U., Von Braun, J. (Eds.), Recarbonization of the Biosphere. Springer Netherlands, Dordrecht, pp. 445–464. https://doi.org/10.1007/978-94-007-4159-1_20.

Scharenbroch, B.C., Nix, B., Jacobs, K.A., Bowles, M.L., 2012. Two decades of low-severity prescribed fire increases soil nutrient availability in a Midwestern, USA oak (Quercus) forest. Geoderma 183–184, 80–91. https://doi.org/10.1016/j.geoderma.2012.03.010.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: ⟨http://websoilsurvey.sc.egov.usda.gov/⟩.

Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W., Bukenhofer, G.A., 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. J. Veg. Sci. 9 (1), 133–142.

Susaeta, A., Fill, J., Crandall, R., Varner, J.M., 2022. Hidden costs of fire exclusion in longleaf pine forests linked to duff and carbon management. J. For. 120, 504–512. https://doi.org/10.1093/jofore/fvac009.

Taylor, Q.A., Midgley, M.G., 2018. Prescription side effects: Long-term, high-frequency controlled burning enhances nitrogen availability in an Illinois oak-dominated forest. For. Ecol. Manag 411, 82–89. https://doi.org/10.1016/j.foreco.2017.12.041.

Turner, M.A., Bones, J.T., Marshall, S.G., Harper, C.A., 2024. Canopy reduction and fire seasonality effects on deer and Turkey habitat in upland hardwoods. For. Ecol. Manag 553, 121657. https://doi.org/10.1016/j.foreco.2023.121657.

Turner, M.A., Bones, J.T., Marshall, S.G., Harper, C.A., 2025. Effect of growing season fire timing on oak regeneration. Fire Ecol. 21. https://doi.org/10.1186/s42408-025-00350-x.

Vander Yacht, A.L., Barrioz, S.A., Keyser, P.D., Harper, C.A., Buckley, D.S., Buehler, D.A., Applegate, R.D., 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For. Ecol. Manag 390, 187–202. https://doi.org/10.1016/j.foreco.2017.01.029.

Vander Yacht, A.L., Keyser, P.D., Barrioz, S.A., Kwit, C., Stambaugh, M.C., Clatterbuck, W.K., Jacobs, R., 2020. Litter to glitter: promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. Fire Ecol. 16, 17. https://doi.org/10.1186/s42408-020-00072-2.

Varner, J.M., Hiers, J.K., Ottmar, R.D., Gordon, D.R., Putz, F.E., Wade, D.D., 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can. J. For. Res. 37, 1349–1358. https://doi.org/10.1139/X06-315.

Varner, J.M., Kane, J.M., Hiers, J.K., Kreye, J.K., Veldman, J.W., 2016. Suites of fire-adapted traits of Oaks in the Southeastern USA: multiple strategies for persistence. Fire Ecol. 12, 48–64. https://doi.org/10.4996/fireecology.1202048.

Woodall, C.W., Monleon, V.J., Fraver, S., Russell, M.B., Hatfield, M.H., Campbell, J.L., Domke, G.M., 2019. The downed and dead wood inventory of forests in the United States. Sci. Data 6, 180303. https://doi.org/10.1038/sdata.2018.303.

Wright, J., DeLaMater, D., Simha, A., Ury, E., Ficken, C., 2021. Changes in prescribed fire frequency alter ecosystem carbon dynamics. Ecosystems 24, 640–651. https://doi.org/10.1007/s10021-020-00540-5.

Zhou, Y., Singh, J., Butnor, J.R., Coetsee, C., Boucher, P.B., Case, M.F., Hockridge, E.G., Davies, A.B., Staver, A.C., 2022. Limited increases in savanna carbon stocks over decades of fire suppression. Nature 606 (7901), 445–449. https://doi.org/10.1038/s41586-022-04438-1.