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Simulated fire regimes favor oak and pine but affect carbon stocks in mixed oak forests in Pennsylvania, U.S.A.

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ABSTRACT

Changes in fire regimes can alter patterns of species dominance and forest carbon stocks by amplifying or diminishing fire vegetation feedbacks. The combined influence of 19th century forest harvesting followed by 20th century fire exclusion has caused a shift in species composition in fire adapted mixed oak forests toward fire sensitive shade tolerant hardwoods that reduce flammability of surface fuels. Prescribed fire is a tool with potential to restore fire adapted oak forests with a history of fire exclusion, but outcomes from the practice of prescribed burning are unclear due to a paucity of studies that apply prescribed fire over multi decadal periods. Here we use simulation modeling to investigate how variation in fire frequencies and period of burning influence simulated dominance of oak, pine, and other hardwoods and forest carbon stocks in Pennsylvania mixed oak forests. Single burns had little effect on basal area (BA) or species composition while more frequent burning increased pine BA, especially when pine was initially abundant. Simulated fire regimes with fire intervals of 10–20 years applied for multiple decades maintained high oak BA and reduced fire sensitive hardwoods. Average BA at the end the 60-year simulation period was inversely related to fire frequency and live carbon stocks decreased with more frequent burning. Simulated fire effects suggest implementation of prescribed fire regimes over periods of decades may be a feasible strategy to maintain or increase oak and pine dominance where management objectives are compatible with fire use. Moreover, several simulated fire regimes seem capable of maintaining BA of fire adapted species and maintaining or increasing overall live C stocks providing a range of management options for maintaining oak and pine, and live carbon stocks using prescribed fire.

1. Introduction

Fire is a key disturbance process in temperate forest ecosystems that renews limiting resources, generates spatial and temporal heterogeneity in vegetation and fuels and contributes to maintenance of species diversity (Bond and Keeley, 2005; Turner, 2010). The effects of fire on forest structure and dynamics are diverse and tied to both short term variation in species response to individual fire characteristics (i.e. fire intensity) (Ryan and Reinhardt, 1988), and longer term variation in fire regimes driven by climate and human activity (Nowacki and Abrams, 2008; Taylor et al., 2016; Stambaugh et al., 2018). Changes in fire regimes (e.g. seasonal timing, return interval, extent, severity) can alter patterns of species dominance in fire adapted forests and generate new fire vegetation feedbacks that may amplify (Brose, 2014; Lauvaux et al., 2016) or diminish (Nowacki and Abrams, 2008; Hanberry, 2013) future fire effects on forest structure, and forest ecosystem services (Martin et al.2015; Johnstone et al., 2016; Seidl et al., 2016; Hurteau et al., 2019). Fire regime change effects on vegetation and fuels can persist for decades, or even centuries, and may shift forest conditions to a new ecosystem state with reduced fire resilience and diminished ecosystem services (Adams, 2013). Reintroducing fire into forests with highly altered fire regimes is one of several approaches that can be used to restore, maintain, and confer resilience to fire adapted forests (Brose et al., 2001; Nowacki and Abrams, 2008; North et al., 2015) though it is not without risks, and can impair ecosystem services such as carbon storage (Varner et al., 2005; Ryan et al., 2013; Brockerhoff et al., 2017).

Forests in the US offset 12–19% of annual US carbon dioxide emissions and much of the offset is attributed to forest biomass increase in the eastern US (EPA, 2015; USGCRP, 2018). Prescribed fire increases both direct emissions through combustion and indirect emissions through decomposition of fire killed trees, although in some cases increased C uptake from surviving trees can offset these emissions

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(Williams et al., 2016). Identifying trade-offs between forest C storage and introduction of prescribed fire regimes in mixed oak forests is important given the role of eastern U.S. forests in mitigating anthropogenic carbon dioxide emissions (Williams et al., 2016). Prescribed burning has not been shown to negatively impact forest C uptake (Chiang et al., 2008, Swanteson-Franz et al., 2018), and long term management can increase and maintain forest C stability (Earles et al., 2014, Harris et al., 2019).

Fire regimes in mixed oak forests in the mid-Atlantic region of the United States (US) have changed dramatically since postglacial forest composition stabilized about 4000 years ago (Delcourt and Delcourt, 1997; Willard et al., 2005; Menking et al., 2012). Fire scar records spanning four centuries show that fire regimes in Pennsylvania forests were driven mainly by humans. The fire scar records show a sequence of anthropogenic fire regimes with longer fire return intervals (5–20 years) with Native American influenced fire regimes, and then shorter fire return intervals (3–10 years) after Native American depopulation and Euro-American settlement and expansion beginning in the mid-18th century (Abrams, 1992; Stambaugh et al., 2018). These pre-20th century fire interval estimates were derived mainly from fire scarred pines growing on very dry sites embedded in an oak forest matrix and may overestimate fire frequency in oak dominated forests on more mesic sites. In the late 19th and early 20th century, mixed oak forests were dramatically altered by industrial scale clearcut logging, and slash driven high severity fires (Abrams, 1992; Brose et al., 2001). Fires have been infrequent since the 1930s when a policy of excluding fire was implemented (Brose et al., 2001; Stambaugh et al., 2018). Oaks responded vigorously to the disturbed conditions after logging and oaks are now canopy dominants in many Appalachian forests (Abrams, 1992; McEwan et al., 2007). Dendroecological studies and comparisons with early colonial land surveys suggest that with the onset of fire suppression conditions for oak regeneration have declined and oaks have been replaced by a suite of fire sensitive shade tolerant hardwoods, particularly maple (*Acer* spp.) (Abrams, 1998, Hutchinson et al., 2008; Nowacki and Abrams, 2008; Thompson et al., 2013). This forest compositional shift has been termed “mesosphication” and describes a positive feedback between the increasing abundance of fire sensitive species and cooler, more mesic, and shaded understory conditions with less flammable surface fuel beds that further limit oak regeneration and regeneration of other fire adapted species (Nowacki and Abrams, 2008; Kreye et al., 2013, 2018; Dickinson et al., 2016; Dyer and Hutchinson, 2019; Knott et al., 2019). Fire dependent pines (*Pinus* spp.) including pitch pine (*P. rigida* Mill.) and Table Mountain pine (*Pinus pungens* Lamb), and fire adapted eastern white pine (*Pinus strobus* L.) often co-occur with oak depending on site conditions and they exhibit a range of traits that are adaptive to fire. Table Mountain pine and pitch pine can survive low severity fire due to thick bark, and they also regenerate after high severity crown damaging fire through epicormic and basal sprouting and release of seed from serotinous cones (Zobel, 1969; Lafon et al., 2017). Eastern white pine is fire resistant and can survive low severity surface fire due to thick bark when mature (Wendel and Smith, 1990; Jackson et al., 1999). Changes in forest composition and surface fuel flammability due to fire suppression and mesophication has raised concerns about future dominance by oak, whether fire can be used to restore fire adapted species, and how reintroduced fire may affect forest ecosystem services (Welch et al., 2000; Brose et al., 2013; Dey, 2014; Vose and Elliott, 2016; Lafon et al., 2017; Kreye et al., 2018).

Prescribed fire is often used to restore fire to fire adapted forests with a history of fire exclusion, but public acceptance and use of prescribed burning by management agencies varies within the US (Ryan et al., 2013). In Pennsylvania, legal barriers constrained prescribed fire use until 2009 when the Prescribed Burning Practices Act was passed (Pennsylvania House Bill 262). Since passage of the act, there has been a twentyfold increase in the number of burns and a tenfold increase in area burned by prescribed fire, with nearly 7300 ha burned in 2017, mainly on state managed lands (NIFC, 2018). Empirical studies of prescribed fire effects in eastern oak forests show mixed success in promoting oak, especially with single or several short interval low intensity burns in mature forests applied over short periods (i.e., over <1 to 9 years, Brose et al., 2006; Hutchinson et al., 2005, 2012; Brose et al., 2013; Dey, 2014; Keyser et al., 2017; Dems et al., 2021). Outcomes from implementation of a *prescribed fire regime* remain unknown due to a paucity of longterm studies. Application of a fire regime would include variation in the frequency, seasonality, extent and severity of fire which are parameters used to describe a fire regime (Agee 1993).

An exception is a study of applying prescribed fire for six decades in a Missouri Ozark oak-hickory forest (Knapp et al., 2015, 2017). Burning at four year intervals over six decades reduced overstory density and canopy cover and favored white (*Quercus alba*) and post (*Q. stellata*) oak, over scarlet (*Q. coccinea*), Spanish (*Q. falcata*), and black (*Q. velutina*) oak, and hickories (*Carya* spp.) compared to annual burning or no fire. Tree regeneration was infrequent with a four year fire interval suggesting canopy recruitment may be linked to longer fire free periods (Loftis, 1990; Knapp et al., 2015, 2017). Similarly, prescribed fire kills most eastern white pine seedlings and saplings while pole sized trees with thicker bark survive fire suggesting recruitment may be tied to longer fire free intervals (Blankenship and Arthur, 1999). Investigation of multidecadal effects of applying prescribed fire regimes with different fire intervals are needed to improve our understanding of the potential use of prescribed fire to maintain or restore oaks and pine in mixed oak forests, and to determine how prescribed fire may influence key ecosystem services (Varner et al., 2016).

Here we use simulation modeling to investigate how application of different prescribed fire regimes over multidecadal periods affects species dominance and forest carbon stocks in Pennsylvania mixed oak forests. Specifically, we use simulations to test the hypotheses that future dominance by fire adapted oak and pine will be greatest in forests with: 1) higher initial dominance of oak and pine; 2) when prescribed fire is applied over longer periods of 30–60 years; and 3) when forests are burned at intermediate fire frequencies of 5–20 years. We also expect prescribed fires to alter the magnitude of live and dead above ground C pools with live C stocks being regulated by fire frequency and burning period. Our study advances understanding of the potential outcomes of reintroducing prescribed fire regimes into fire adapted oak-pine forests after a long period of fire exclusion, and how prescribed fire use may affect ecosystem services as measured by C stocks (Williams et al., 2016; Hurteau et al., 2019).

2. Methods

2.1. Study area

Our study focused on mixed-oak forests in the Ridge and Valley physiographic province in eastern and central Pennsylvania. This area is characterized by folded Paleozoic era sedimentary rocks and a series of sandstone ridges and intervening shale and carbonate valleys. Soil properties including texture, drainage and nutrient content are linked to underlying bedrock and parent material (Ciolkosz et al., 1990). Elevation ranges from 130 to 770 m and mean annual temperature ranges from 8 to 13 °C depending on elevation. Annual average annual precipitation is ca. 1130 mm and is evenly distributed throughout the year. Forests are typically second growth and developed after a period of intense harvesting in the 19th century and early 20th century (Abrams, 1992; Brose et al., 2001). Forest stands 81–120 years old comprise 65% of the forest cover in the region (Reed and Kaye, 2020). Forests are dominated by oaks including chestnut oak (*Quercus montana* Willd.), northern red oak (*Q. rubra* L.), white oak (*Q. alba L.*), scarlet oak (*Q. coccinea* Münchh.) and black oak (*Q. velutina* Lam.) and oaks comprise > 60% of the forest biomass in the region (Reed and Kaye, 2020). Other common species include red maple (*A. rubrum* L.), black gum (*Nyssa sylvatica* Marsh.), sassafras (*Sassafras albidum* (Nutt.) Nees), and black cherry (*Prunus serotina* Ehrh.).

2.2. Oak forest data

We used forest inventory data collected by Bureau of Forestry in the Pennsylvania Department of Conservation of Natural Resources and the Pennsylvania Game Commission (PGC) to identify forest characteristics for our simulation study. Inventory plots are distributed across Pennsylvania and provide data on forest growth, forest volume and structure, forest mortality, and forest change on state lands. Inventory data were collected in 800 m^2 plots using a nested plot design to sample trees, saplings, and seedlings. We extracted inventory plots ($n = 1623$) that were classified as oak, or oak-pine forest or woodlands for this study. Data for each plot included plot identification, species, diameter at breast height (DBH), height, status (live, dead), damage for all trees (stems > 2.54 cm DBH), and counts of tree seedling by height class. We grouped plots into stands, which have a 3000 tree record limit (Dixon, 2002), that included approximately equal numbers of plots, yielding 54 stands. These stands were then classified for our analysis into forest types based on the proportional basal area (BA) of oaks (*Quercus* spp.), pines (*Pinus* spp.), and other species (Table 1). We selected 10 stands from this group to simulate forest response to different fire regimes. For widespread forest types we used up to three stands for simulations that represented low, intermediate or high BA proportions for pine, oak, or other species in that forest type (Table 1).

2.3. Simulation modeling

We simulated forest response to prescribed fire regimes for 60 years using the USDA Forest Vegetation Simulator (FVS). FVS is an individual tree, distance independent growth and yield model that simulates forest vegetation change to natural disturbance or other management scenarios (Dixon, 2002). FVS has been used frequently to evaluate the effects of different management practices, including prescribed and wildland fire, on forest structure and live and dead forest C stocks (e.g. Finney et al., 2007, Hurteau and North, 2009; Buma et al., 2013; Gunn et al., 2020) and FVS is parameterized for forests in different geographical regions. We used the Northeastern Variant (NE) of FVS for this study (Dixon and Keyser, 2008). FVS has multiple extensions and we used the Fire and Fuels Extension (FFE) to simulate changes in BA and forest C stocks caused by simulated fire regimes (Rebain, 2010). FVS is deterministic and does not provide information on the range of possible outcomes for a stand but relies instead on well-defined user specified initial conditions and allows for further calibration of the equations simulating forest processes, such as regeneration and tree mortality. We derived initial conditions for our forest types using the stands we identified from the state inventory data (Table 1).

Both background and post-fire tree regeneration were incorporated into simulations. Simulations of forest growth in the NE variant of FVS automatically incorporate regeneration of hardwood species from stump and root sprouts and allow for user specified regeneration from seed (Dixon and Keyser, 2008). Background regeneration was scheduled every decade whenever a stand was not burned, based on approaches used by Fulé et al. (2004), Cheek et al. (2012), and Schwenk et al. (2012). However, for decades in which a stand was burned we used post-burn regeneration parameters rather than background regeneration as described below. Regeneration from seed for simulations was specified using seedling height frequency distributions from the forest inventory data, and seedling height survival rates based on values in Keane et al. (2001) and Vickers et al. (2019) (Table S1). Post-fire regeneration from seed represented a separate class of regeneration and empirical data on post-fire regeneration in mid-Atlantic oak forests are sparse. To estimate post-fire regeneration we used pre- and one year post-fire data from 75 plots in oak forests burned by the PGC, and the George Washington and Jefferson National Forest, and Shenandoah National Park that are in Virginia (Personal communication Lane Gibbons, Shenandoah National Park; Brian Stone Pennsylvania Game Commission; Lindsey Curtin George Washington and Jefferson National Forest). These plot data were used to calculate the percentage change between tree regeneration densities in unburned and post-fire stands that we used to parameterize post-fire tree regeneration (Table S2). For seedlings of species present post-fire that were not present pre-fire, we calculated a seedling density relative to species' pre-burn BA and used this value to estimate post-fire regeneration. If a particular species was not present in the stand, then no post-burn regeneration was specified for that species. To be consistent with observed post-burn regeneration, post-burn regeneration events were scheduled for one year post-fire. A sensitivity analysis of post-fire seedling regeneration showed adjusting regeneration density (±5–20%) of key species had little impact on simulated outcomes. Adjustments of ±20% resulted in at most a 2% difference in total stand BA, and 4–15% difference in total stand density across simulations, relative to simulated BA and density from tree regeneration values that we used. One explanation for the relatively low sensitivity of the model to changes in post-fire regeneration density is that eventual recruitment into the tree size class depends on stand conditions (i.e. stand density and BA). The sensitivity analysis suggests that our model results are robust to minor adjustments in post-fire tree regeneration densities.

2.4. Prescribed fire regimes

We simulated seven prescribed fire regimes using FFE-FVS to evaluate the influence of initial conditions, fire frequency (intervals), and duration of burning on oak and pine abundance, and C stocks. Fire regimes tested included unburned, single burn, and burns at intervals of 5, 10, and 20 years over either a 30-year or 60-year period (duration) in each stand. We replicated each fire regime three times to incorporate stochastic variation in projected stand conditions using randomly selected radial growth rates provided by FVS (Dixon, 2002). Fires were scheduled before spring green-up, the most common period for prescribed burning in the region (personal communication Scott Bearer, Pennsylvania Game Commission). Weather conditions during simulated prescribed fires were drawn from burn plans and consultation with fire managers. For our burns, temperature and wind speed at 6 m (20 feet) were set to 18.3 °C (65 °F) and ~13 km hr^{-1} (8 mph), respectively, and fuel moisture was classified as dry (1 h 8%; 10 h 8%; 100 h 10%; 1000 h 15%; duff 50%; live 110%) (Rebain, 2010). We chose dry fuel moistures because fires that are intense enough to kill midstory and a limited number of overstory trees may be particularly successful at increasing the competitiveness of oaks, due to the positive effect of canopy gaps and light availability on oak regeneration (Hutchinson et al., 2012; Iverson et al., 2017). Conversely, even repeated low-intensity fires may be insufficient to promote oak competitiveness if they are not accompanied by a disturbance to create canopy gaps (Alexander et al., 2008; Hutchinson et al., 2005; Iverson et al., 2008).

Initial fuel models (i.e. Scott and Burgan, 2005) for each stand were identified in consultation with prescribed fire managers and are based

Table 1
Forest types, number of stands developed from initial forest inventory data, number of stands simulated, and number of plots within each simulated stand.

Forest type	BA specification	Total number of stands	Number of simulated stands	Number of plots in the simulated stands
Oak-dominant	Oaks ≥ 70%	4	3	71
Mixed-oak	Oaks 50–69%; Pines < 10%	43	3	123
Oak-pine	Oaks 50–69%; Pines 10–49%	1	1	39
Mixed-species	Oaks < 50%; Pines < 50%	6	3	64

on observed fire effects from fuel models used to plan outcomes from prescribed fire. Fuel models (and weights) were as follows: Moderate Load Broadleaf Litter (TL6) (80%) and Low Load Humid Climate Timber-Shrub (SH4) (20%) for mixed-oak, Moderate Load Conifer Litter (TL3) (100%) for mixed species and TL6 (70%) and SH4 (30%) for oak-pine (Scott and Burgan, 2005). Canopy fuel variables were calculated by FFE from tree lists using default values for each species (Rebain, 2010). Automatic fuel model selection was invoked in FFE after a fire based on projected stand conditions (Rebain, 2010).

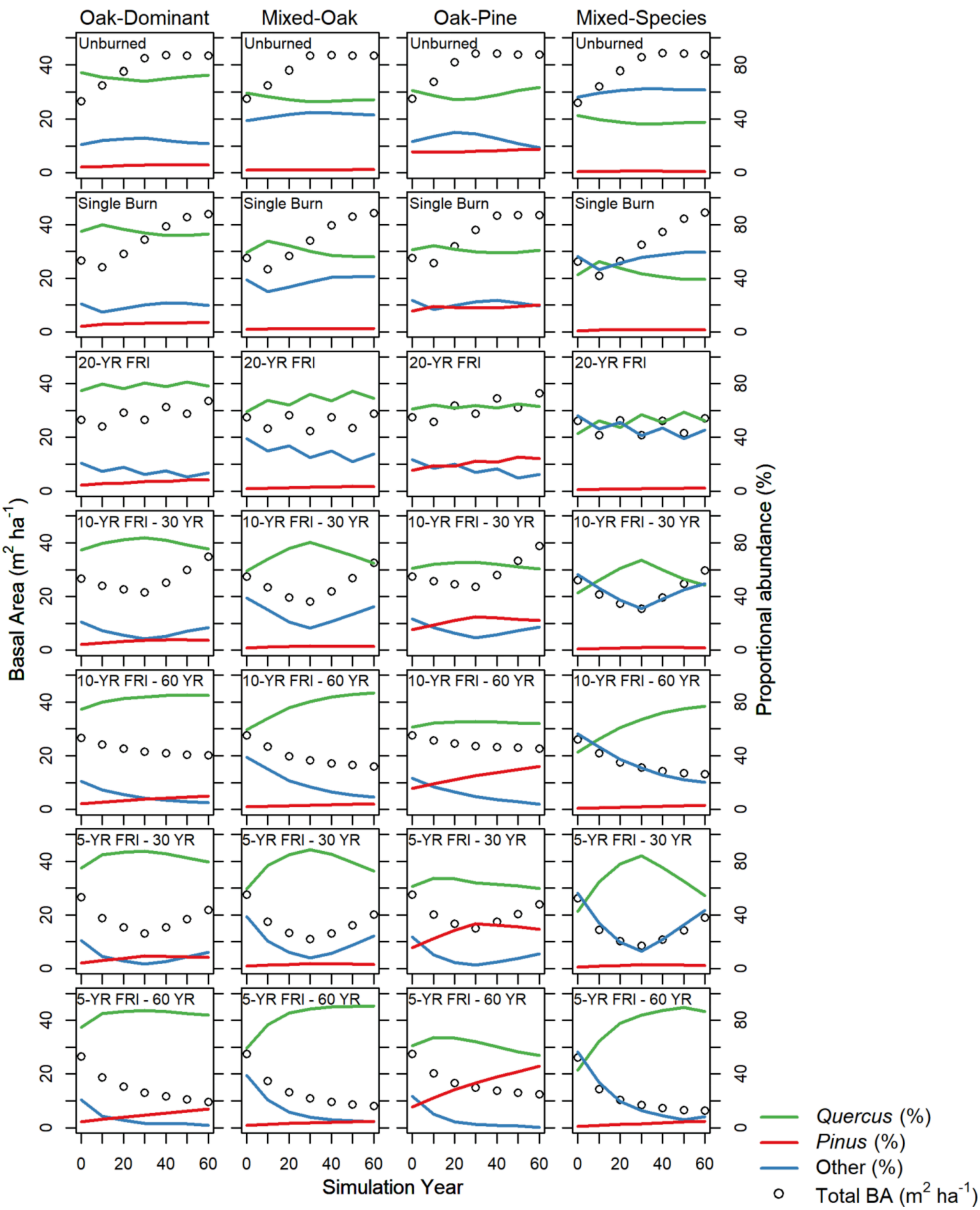

Fig. 1. Proportional abundance (BA) of oak (*Quercus*), pine (*Pinus*), and all other species ("Other") to simulated fire regimes in Pennsylvania mixed oak forests. Fire regimes were unburned, burned once, and burned at intervals of 5, 10, and 20 years for a 30 or 60 year period.

2.5. Simulated forest response

To assess forest change over time for each fire regime we calculated stand composition (%) of pines, oaks, and other species based on BA, and aboveground C stocks at 10 year time steps using default FVS logic. Aboveground C stocks were calculated using stand tree lists and FFE allometric equations based on tree diameter for each tree species and C pools were divided in four categories, which we refer to collectively as "C stocks": live trees, standing dead trees, downed woody material, and litter and duff. We did not include C in understory vegetation because FFE simply assigns the same nominal value for herbs and shrubs to all stands (0.7 Mg ha^{-1}, Rebain, 2010), and we did not consider belowground C. We used default tree species mortality values in FFE in the simulations, except for pitch pine. Tree mortality for pitch pine was reduced to 20% of the default value to more accurately reflect pitch pine mortality from fire (Gallagher, 2017). Tree mortality from fire in FFE is calculated using percentage of crown scorch and bark thickness, and species specific multipliers are used to determine bark thickness in the Northeast variant of FFE (Rebain, 2010). In addition, the FFE model adjusts mortality as follows: all hardwoods < 2.5 cm DBH and all maples < 10.2 cm DBH die when hit by the flaming front, and mortality is reduced by 50% for oaks and 20% for other hardwoods when burning occurs before green up as was the case in our simulations. We also calculated the proportional abundance (BA and density) of the top four species at each time step and report these values for year 30 and 60 of the simulations.

3. Results

3.1. Structural and compositional responses to fire regimes

At the start of the simulations, oaks were initially dominant in the oak-dominant, mixed-oak, and oak-pine forest types, and without fire, oaks still comprised 54–73% of basal area (BA) at year 60 (Fig. 1). Oaks were not initially dominant in the mixed-species type, and without burning they declined slightly by the end of the simulation. The first simulated fire in each forest type was of low intensity, with flame lengths averaging 0.1 m in the mixed-species type and 0.3 m for each of the other forest types. Flame lengths more than doubled between the first and second fire for all forest types and simulated fire regimes, and mean flame lengths averaged 0.9–1.1 m in years 40–50.

Temporal trends in BA of oak, pine, and other species for single burns were similar to unburned patterns, except early in the simulation period when there was a small increase in oak and pine and a decrease in other species. This initial shift had little longterm effect on BA proportions or average BA for these species groups by year 60.

Burning more than once and over longer periods led to larger changes in forest BA and species dominance. The magnitude of change varied with fire return interval, duration of the fire regime, and initial stand conditions (Fig. 1). With a 20-year fire interval, oak dominance increased modestly across forest types. Burning at shorter 5 and 10-year fire intervals over 60 years strongly increased the proportion of oak and caused a decline in hardwoods such as red maple (Table S3) with larger oak increases for the 5-year interval, except in the oak-pine forest type. In the oak-pine type, burning at 5-year intervals caused pine to reach nearly 50% of stand BA by year 60. In the other forest types, burning with 5-year intervals more than doubled proportional BA of pine, though pine still comprised only 10–15% of stand BA by year 60. For scenarios in which burning ceased after 30 years, fire-driven shifts in species composition began to reverse themselves although oak and pine dominance were still higher by year 60 in these scenarios compared to the unburned scenario.

3.2. Carbon stocks and emissions from fire

Projected aboveground C stocks were influenced by fire return interval and period of burning (30 vs. 60 years). When forests were not burned or burned once, forests were a C sink with C stocks nearly doubling across all forest types due primarily to increases in live tree C stocks but also to increases in dead wood C and litter and duff (Fig. 2). With a 20 year fire interval increases in C were small for the first 30 years but increased by 14–65% over initial pre-burn values to become a C sink at year 60. Burning at 10 year intervals for 30 years caused modest declines in C stocks over the first 30 years, but C stocks increased by 19–65% over initial values by year 60. With a 10 year fire return interval for 60 years, live C in the oak-pine and oak-dominant types increased marginally but mixed oak and mixed-species forests became a C source with C values 21% and 27% below initial stock values, respectively, after 60 years. Burns at 5 year return intervals caused all forest types to become a C source with a steady decline in C stocks, and C stocks were only able to recover to initial values for the oak-pine type with cessation of burning at 30 years. All burning scenarios resulted in lower C stocks than the unburned scenario at year 60: 9–14% lower for the single burn, 32–47% lower for 20 year intervals, 31–46% and 53–72% lower for 10 year intervals over 30 and 60 years respectively, and 56–66% and 73–86% lower for 5 year intervals over 30 and 60 years respectively.

4. Discussion

Forest dominance (BA) by oaks (*Quercus* spp.) in the mid-Atlantic region reflects a legacy of chronic anthropogenic disturbance, first as repeated understory burning by Native Americans, and then logging and severe fire associated with Euro-American land clearing, and mining particularly in the 19th century (Abrams, 1992; Brose et al., 2001; Stambaugh et al., 2018). Currently, second growth mixed oak forests dominate the region, with fire having been virtually eliminated since the early decades of the 20th century due to a policy of fire suppression. Exclusion of fire coupled with forest succession shifted forest composition towards shade tolerant fire sensitive mesophytic hardwood species that reduce litter flammability, and reinforce conditions that favor mesophytic species (Nowacki and Abrams, 2008; Kreye et al., 2018). Our simulation experiments indicate that prescribed fires have the potential to restore species composition towards precolonial values and reduce the abundance of mesophytic species in mixed-oak and oak-pine forests in the mid-Atlantic region. Prescribed fire effects varied with the fire regime applied (i.e. return interval, duration of regime, and initial forest dominants), and not all outcomes may be desirable from a forest management or ecosystem services perspective. The simulations also suggest that without prescribed fire oaks would remain dominant (BA) in the overstory of most oak forest types over the 60-year simulation period. This contrasts with the potential decline of overstory oak dominance from persistently low oak recruitment in eastern oak forests over the last 50–100 years, except on the most xeric sites (Abrams, 2005). Initial stand conditions and/or species growth and mortality parameters in FVS may have contributed to the relatively modest trends in modeled mesophication compared to trends inferred from empirical studies (e.g. Abrams and Nowacki, 1992; Signell et al., 2005).

Across our simulations the second fire had at least double the flame lengths of the initial fire, which in the FFE model was due to fallen trees providing more surface fuel. This effect was noted by Iverson et al. (2008), who studied the effects of thinning and repeated fire on mixed-oak stands in Ohio. They found that an initial prescribed fire directly after thinning caused little consumption of 100 and 1000-hour fuels. However, a second fire four years later caused flame lengths of 1 m of more due to drier conditions and surface fuels having cured (Iverson et al., 2008). This more intense fire created limited canopy gaps and helped to increase the relative abundance of oak regeneration and also killed larger diameter trees (Hutchinson et al., 2012; Iverson et al., 2008). Fire-generated mortality in our stands, on average, was high (90%) in the smallest diameter class (<13 cm DBH), intermediate (34%) in mid-sized trees (13–25.4 cm DBH), and some larger trees (>25.4 cm

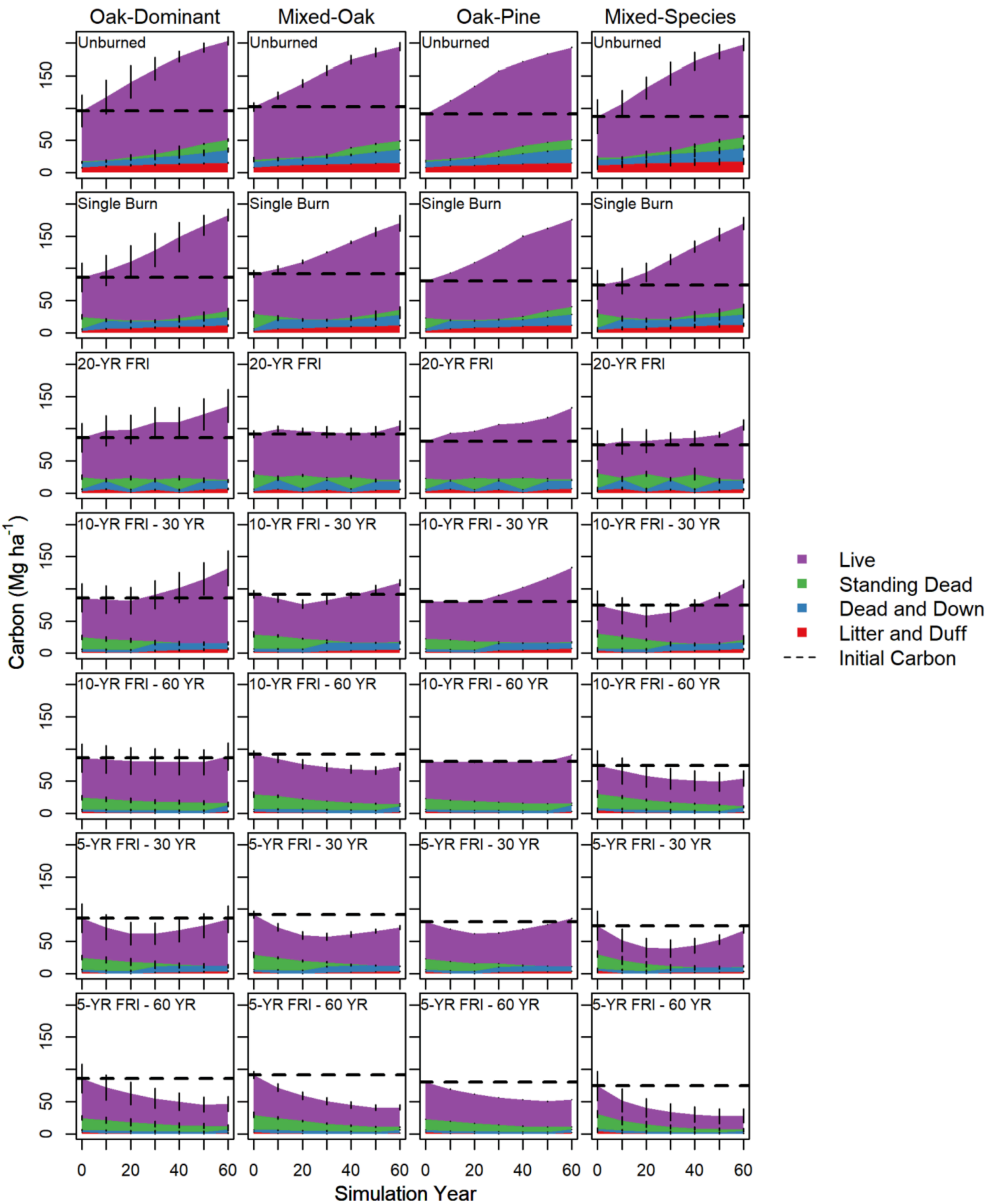

Fig. 2. Aboveground C stocks at 10-year intervals for simulated fire regimes in Pennsylvania mixed oak forests divided into live trees, standing dead trees, downed woody material, and litter and duff. Bars represent SD of each category. Fire regimes were unburned, burned once, and burned at intervals of 5, 10, and 20 years for a 30 or 60 year period.

DBH) were also killed (9%) opening the forest canopy. Although many studies of prescribed fire in mature oak forests have reported minimal overstory tree mortality (Brose et al., 2014), a low to moderate degree of overstory mortality has been observed in some studies (Hutchinson et al., 2012; Iverson et al., 2008; Loucks et al., 2008; Waldrop et al., 2008) suggesting that our modeled tree mortality is not unreasonable particularly given the fuel moistures used in our analysis. The dry fuel moistures that we used in our simulations likely benefited oak by leading to more intense fire, but we acknowledge that burning under dry conditions is not always a viable option for managers and suggest that the effects of fuel moisture and fire seasonality on simulated forest changes would be an excellent topic for future research. We also did not evaluate the effects of repeated fires in short succession (e.g., annual fire for three years), and suggest that these effects be evaluated in future simulation modeling studies because multiple fires is a much-discussed management strategy (Brose et al., 2014).

Forest composition and structure can influence competitive relationships and the response of oaks, pines and mesophytic hardwoods to prescribed fire (Brose et al., 2013; Hutchinson et al., 2012). In our relatively xeric oak dominant, and oak-pine forest types, oaks remained dominant (BA) even without burning, and single burns had little effect on BA of pines or other hardwoods. Burning at shorter intervals promoted pine establishment, especially when pine was relatively abundant in a forest at the onset of simulations. The increase in pine with simulated prescribed fire is consistent with empirical observations on the short and long term patterns of pine establishment and regeneration post-fire (Blankenship and Arthur, 1999; Welch et al., 2000; Stambaugh et al., 2019).

Mixed-oak and mixed-species forests types exhibited a pattern of declining oak when unburned or burned once compared to the other forest types. Our simulations suggest that continuous burning over a sixty year period at intermediate intervals (i.e. 20 years) increases oak relative to other hardwoods and maintained C stocks similar to initial conditions by the end of the simulation period. Shorter burn intervals further increased the proportion of oaks, but C stock declined to half or less of an unburned or single burned forest. These findings suggest that inclusion of both short and long fire free intervals over a 60 year period of burning would promote oak regeneration and recruitment of oak into the canopy. Dendroecological studies of historical fire frequency and oak and pine recruitment also suggest that variation in fire intervals was important for maintaining dominance for fire adapted species, because fire-free intervals allowed trees to grow into fire-resistant size classes (Abrams et al., 1995; Shumway et al., 2001; McEwan et al., 2007). In contrast, burning annually, or every 4 years, over a 60 year period in a Missouri oak-hickory forest prevented oak recruitment into the canopy (Knapp et al., 2015, 2017). Canopy recruitment in other forest types with a frequent fire regime, such as yellow pine dominated forests in the western US, has also been linked to longer fire free periods (Brown and Wu, 2005). Our simulation results, combined with this prior work on tree recruitment, suggests that burning every 5 years is too frequent to maintain carbon storage and tree recruitment, but that burning at 10–20 year intervals may strike a balance between favoring oak and pine while still promoting tree recruitment and carbon storage. Moreover, if fire alone is used as the disturbance, it may require multiple burns at shorter intervals, followed by a fire-free intervals before applying fire as a maintenance tool.

Simulated prescribed fire regimes shifted dominance patterns of fire adapted and shade tolerant tree species. With no burning or just single fires species composition remained fairly stable in each forest type. On the other hand, simulated prescribed fire regimes increased or maintained oak dominance depending on the fire return interval and initial stand composition. Fire dependent pitch pine increased under regimes with the shortest fire intervals when it was initially present. Field measurements of fire effects from single or multiple prescribed fires implemented over a decade have shown limited success in promoting oak recruitment into the canopy, and management guidelines based on these studies emphasize prescribed fire use in combination with additional silvicultural treatments and a longer fire free period to promote oak recruitment (Hutchinson et al., 2005, 2012, Alexander et al., 2008, Fan et al., 2012, Arthur et al., 2015, Keyser et al., 2017). Our simulation results, however, suggest that a long term (>30 years) program of prescribed burning with a range of fire intervals could be a feasible strategy for restoring or maintaining mixed-oak forests and oak-pine forests where management objectives are compatible with fire use (Hutchinson et al., 2005, 2012; Knapp et al., 2015, 2017).

Prescribed fire and other forest treatments such as thinning influence stand structure, which largely determines the size of tree C stocks (Boerner et al., 2008; Hurteau et al., 2016). Thus, C tradeoffs associated with implementing different prescribed fire regimes hinge on their cumulative effect on forest structure and composition, and direct and indirect emissions through combustion and decomposition of fire killed trees. In our simulations, aboveground C stocks were highest when forests were unburned, as tree BA increased and surface fuels accumulated. Single burns had minimal influence on C stocks by the end of our 60 year simulation period and C stocks were close (<10%) to those in unburned forests. This simulation result is consistent with measured shorter term C-stock responses to single prescribed burns in a range of US temperate forests, including eastern oak-hickory forests where live C stocks recovered to pre-fire values after <5 years because fire related tree mortality was concentrated in small diameter stems (<10 cm DBH) (Chiang et al., 2008). As prescribed fire was simulated in our forests, C stocks declined, indirect emissions increased, and BA declined with some variation among forest types. Oak-pine forests that have proportionally more fire adapted pines and oaks, and fewer mesophytic hardwoods, experienced lower live C-stock declines than other oak forests. Only one experimental study we are aware of in temperate forests has tracked response of C-pools to different fire regimes (Bennett et al., 2014). This study found the same relationship we found in our simulation studies, higher frequency of burning resulted in larger decreases in live C stocks (Bennett et al., 2014). Dead C stocks were also lower in the forests with applied fire regimes than in unburned forest reflecting consumption of woody surface fuels that resulted in fire related C emissions (Aponte et al., 2014). There are no comparable studies for oak forests in the eastern US. The overall trends in C stocks in our simulations of different prescribed fire regimes are consistent with modeling studies and the limited empirical work on C pool responses to prescribed fires in temperate forests (Chiang et al., 2008, Boerner et al., 2008; Hurteau and North, 2009; Bennett et al., 2014; Aponte et al., 2014). Our study extends these results to a 60 year period, and also indicates a potential management tradeoff between sequestering C and increasing or restoring pine to mixed oak and oak-pine forests using prescribed fire regimes. Our simulations also indicate that fire regimes that reduce mesophytic species, increase oak, and maintain BA over the 60 year simulation period can also maintain relatively high C stocks. Moreover, burning is not just a source of C to the atmosphere, pyrogenic C from incomplete combustion can sequester C on site for centuries (Santín et al., 2016).

4.1. Limitations in the modeling approach

Our modeling approach has several limitations. First, tree regeneration is a key process that influences stand structure and forest development and it includes establishment from both sprouting and true seedlings (Grime, 2006). We used a simplified approach to parameterizing tree regeneration from seed that did not account for variation in survivorship over time. Moreover, post-fire regeneration inputs were estimated from a limited number of fires and plots in Ridge and Valley oak forests. The FVS partial establishment model also does not include conifer sprouting of pitch pine, which can happen after fire (Little and Garrett, 1990), and which could lead to underestimation of the regeneration response of pitch pine in our simulations. Second, FFE-FVS uses a mortality model developed by Ryan and Reinhardt (1988) that uses tree diameter, bark thickness and crown scorch to estimate tree mortality without any additional models for the tree species in our study. The NE variant of FVS does include species specific bark thickness parameters that would generate variation in species mortality based on tree mortality. Moreover, mortality for small diameter trees for burns with leaf-off conditions before spring green up is adjusted upwards for red maple and downward for oaks and other hardwoods in FFE (Rebain, 2010) which could influence forest characteristics over the simulations period. Third, live C estimates did not include any variation in site that could influence tree form characteristics and estimates of live tree biomass

(Smith et al., 2017, Reed and Kaye, 2020). Growth calibration with site conditions could improve model estimates of C stocks (MacLean et al., 2014), though variation in stand structure or disturbance history could mask contributions by forest types. Fourth, the FFE automatic fuel model selection logic for the NE variant of FVS is limited, and fuel models and weights are selected based on loading projected for each simulation cycle, and live herb and shrub fuels are modeled very crudely (Rebain, 2010). More refined fuel models could influence simulated fire behavior and fire effects and impact the modeled response of forest structure and C dynamics to prescribed fire.

Although the fuel moistures that we used represent realistic springtime, dormant-season conditions, they did produce substantial woody fuel consumption. For example, at the 15% moisture value that we used for 1000-hour fuels, consumption of 1000-hour fuels is 35 to >90% depending on size class in FFE (Rebain, 2010). By contrast, the relatively few studies that have examined consumption of coarse woody fuels from prescribed fires in oak stands have found small and non-significant decreases in 1000-hour fuels (often <10% although sometimes >30%) (Arthur et al., 2017; Kolaks et al., 2004; Loucks et al., 2008), although Kolaks et al. (2004) speculated that 1000-hour fuel moistures of <15% could produce high fuel consumption. FFE also assumed 100% litter consumption from fire, and duff consumption was 65% based on the 50% moisture value that we used. Complete or near-complete litter consumption from prescribed fire is not unusual in oak forests, although our duff consumption values are higher than those reported in the literature (Kolaks et al., 2004; Loucks et al., 2008). In summary, our simulations produced greater C losses from surface fuels than has been reported from prescribed fires that were conducted under higher fuel moistures than in our simulations. However, our simulated averaged flame lengths of 0.1–0.3 m for the first fire and 0.9–1.1 m in years 40–50 are in line with the range observed in past studies in oak forests (Iverson et al., 2008; Kolaks et al., 2004; Loucks et al., 2008; Waldrop et al., 2010), suggesting that our simulated fire intensities are not unrealistic. We chose to focus on differences among forest types in our simulations, but future work considering different fuel moisture and weather scenarios would be valuable.

4.2. Management implications

Historical studies of mixed-oak and oak-pine forest fire regimes suggest that fires burned regularly at intervals of 5–20 years before the onset of fire exclusion, and that these fires helped maintain oak and controlled establishment of more mesophytic tree species (Nowacki and Abrams, 2008; Holzmueller et al., 2009; Stambaugh et al., 2018). Experimental and observational studies on prescribed fire use over 10–20 years, however, suggest limited success of using repeat burns to encourage oak, and additional silvicultural techniques in combination with fire have been recommended to ensure oak dominance (Hutchinson et al., 2005, 2012, Alexander et al., 2008, Brose, 2008; Fan et al., 2012, Arthur et al., 2015, Keyser et al., 2017). Our simulation results suggest implementation of a prescribed *fire regime* over longer periods (60 years) has potential to maintain and or shift dominance towards oak and increase the abundance of fire-adapted pines in drier oak forests without other management intervention. Return intervals tested in this experiment were evenly spaced throughout the simulation period; additional strategies that consider varied fire return intervals should be explored in managing for desired regeneration and forest structure in future simulation studies. Moreover, several fire regimes appear capable of maintaining initial C stocks and maintaining or increasing oak and pine. This provides flexibility to managers who seek to use prescribed fire to maintain and restore oak forests while maintaining C stocks or other ecosystems services. Long term experimental studies that apply a range of fire regimes are needed to evaluate simulation studies and guide management of oak forests using prescribed fire.

CRediT authorship contribution statement

Anthony Zhao: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **Alan H. Taylor:** Conceptualization, Methodology, Supervision, Writing - review & editing, Funding acquisition. **Erica A.H. Smithwick:** Writing - review & editing, Funding acquisition, Project administration. **Margot Kaye:** Writing - review & editing, Funding acquisition. **Lucas B. Harris:** Formal analysis, Data curation, Writing - review & editing.

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. Supplementary material

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References

Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42, 346–353.
Abrams, M.D., 1998. The red maple paradox. Bioscience 48, 355–364.
Abrams, M.D., 2005. Prescribing fire in eastern oak forests: Is time running out? North. J. Appl. For. 22, 190–196. https://doi.org/10.1093/njaf/22.3.190.
Abrams, M.D., Nowacki, G.J., 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bull. Torrey Bot. Club 19–28.
Abrams, M.D., Orwig, D.A., Demeo, T.E., 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. J. Ecol. 83, 123–133.
Adams, M.A., 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. For. Ecol. Manage. 294, 250–261.
Alexander, H.D., Arthur, M.A., Loftis, L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manage. 256, 1021–1030.
Aponte, C., Tolhurst, K.G., Bennett, L.T., 2014. Repeated prescribed fires decrease stocks and change attributes of coarse woody debris in a temperate eucalypt forest. Ecol. Appl. 24, 976–989.
Arthur, M.A., Blankenship, B.A., Schörgendorfer, A., Alexander, H.D., 2017. Alterations to the fuel bed after single and repeated prescribed fires in an Appalachian hardwood forest. For. Ecol. Manage. 403, 126–136. https://doi.org/10.1016/j.foreco.2017.08.011.
Arthur, M.A., Blankenship, B.A., Schorgendorfer, A., Loftis, D.L., Alexander, H.D., 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. For. Ecol. Manage. 340, 46–61.
Bennett, L.T., Aponte, C., Baker, T.G., Tolhurst, K.G., 2014. Evaluating long-term effects of prescribed fire regimes on carbon stocks in a temperate eucalypt forest. For. Ecol. Manage. 328, 219–228.
Blankenship, B.A., Arthur, M.A., 1999. Prescribed fire affects eastern white pine recruitment and survival on eastern Kentucky ridgetops. South. J. Appl. For. 23, 144–150.
Boerner, R.E., Huang, J., Hart, S.C., 2008. Fire, thinning, and the carbon economy: effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate. For. Ecol. Manage. 255, 3081–3097.
Bond, W.J., Keeley, J.E., 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394.
Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D.,

2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers. Conserv. 26, 3005–3035.
Brose, P.H., 2014. Development of prescribed fire as a silvicultural tool for the upland oak forests of the eastern United States. J. Forest. 112, 525–533.
Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? Forest Sci. 59, 322–334.
Brose, P.H., Dey, D.C., Waldrop, T.A., 2014. The Fire – Oak Literature of Eastern North America: Synthesis and Guidelines. USDA Forest Service Northern Research Station General Technical Report NRS-135, Newtown Square, PA, USA.
Brose, P., 2008. Prescribing regeneration treatments for mixed oak forests in the mid-Atlantic region, vol. 33. US Department of Agriculture, Forest Service, Northern Research Station.
Brose, P.H., Schuler, T.M., Ward, J.S., 2006. Responses of oak and other hardwood regeneration to prescribed fire: What we know as of 2005. In: Dickinson, M.B. (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 123–135.
Brose, P., Schuler, T., Van Lear, D., Berst, J., 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J. Forest. 99, 30–35.
Brown, P.M., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86, 3030–3038.
Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., Johnstone, J.F., 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience 63, 866–876.
Cheek, J.W., Biondi, R., Sibold, J.S., Tausch, R., 2012. Fuel analysis and potential fire behavior in mixed conifer woodlands of the Great Basin, Nevada, USA. Phys. Geogr. 33, 205–228.
Chiang, J.M., McEwan, R.W., Yaussy, D.A., Brown, K.J., 2008. The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net primary production of overstory trees in an oak-hickory ecosystem in southern Ohio. For. Ecol. Manage. 255, 1584–1594.
Ciolkosz, E.J., Carter, B.J., Hoover, M.T., Cronce, R.C., Waltman, W.J., Dobos, R.R., 1990. Genesis of soils and landscapes in the Ridge and Valley province of central Pennsylvania. Geomorphology 3, 245–261.
Delcourt, H.R., Delcourt, P.A., 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conserv. Biol. 11, 1010–1014.
Dems, C.L., Taylor, A.H., Smithwick, E.A., Kreye, J.K., Kaye, M.W., 2021. Prescribed fire alters structure and composition of a mid-Atlantic oak forest up to eight years after burning. Fire Ecol. 17, 1–13.
Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. Forest Sci. 60, 926–942.
Dickinson, M.B., Hutchinson, T.F., Dietenberger, M., Matt, F., Peters, M.P., 2016. Litter species composition and topographic effects on fuels and modeled fire behavior in an oak-hickory forest in the Eastern USA. PLoS ONE 11, e0159997.
Dixon, G.E., 2002. Essential FVS: A user's guide to the Forest Vegetation Simulator. Internal Rep. U.S. Department of Agriculture, Forest Service, Forest Management Service Center, Fort Collins, CO. 226p. (Revised: January, 2020).
Dixon, G. E., Keyser, C.E., 2008. Northeast (NE) variant overview - Forest Vegetation Simulator. Internal Rep. U.S. Department of Agriculture, Forest Service, Forest Management Service Center, Fort Collins, CO. 55p. (Revised: January, 2020).
Dyer, J.M., Hutchinson, T.F., 2019. Topography and soils-based mapping reveals fine-scale compositional shifts over two centuries within a central Appalachian landscape. For. Ecol. Manage. 433, 33–42.
Earles, J.M., North, M.P., Hurteau, M.D., 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol. Appl. 24, 732–740.
EPA, 2015. Inventory of U.S. Greenhouse Gas Emissons and Sinks: 1990–2013. United States Environmental Protection Agency, Washington, DC.
Fan, Z., Ma, Z., Dey, D.C., Roberts, S.D., 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri. For. Ecol. Manage. 266, 160–169.
Finney, M.A., Seli, R.C., McHugh, C.W., Ager, A.A., Bahro, B., Agee, J.K., 2007. Simulation of long-term landscape-level fuel treatment effects on large wildfires. Int. J. Wildland Fire 16, 712–727.
Fulé, P.Z., Crouse, J.E., Cocke, A.E., Moore, M.M., Covington, W.W., 2004. Changes in canopy fuels and potential fire behavior 1880–2040: Grand Canyon, Arizona. Ecol. Model. 175, 231–248.
Gallagher, M.R., 2017. Monitoring fire effects in the New Jersey Pine Barrens with burn severity indices. Diss. Rutgers, The State University of New Jersey - School of Graduate Studies.
Grime, J.P., 2006. Plant strategies, vegetation processes, and ecosystem properties. John Wiley and Sons.
Gunn, J.S., Ducey, M.J., Buchholz, T., Belair, E.P., 2020. Forest Carbon Resilience of Eastern Spruce Budworm (*Choristoneura fumiferana*) Salvage Harvesting in the Northeastern United States. Front. For. Glob. Change 3, 14.
Hanberry, B.B., 2013. Changing eastern broadleaf, southern mixed, and northern mixed forest ecosystems of the eastern United States. For. Ecol. Manage. 306, 171–178.
Harris, L.B., Scholl, A.E., Young, A.B., Estes, B.L., Taylor, A.H., 2019. Spatial and temporal dynamics of 20th century carbon storage and emissions after wildfire in an old-growth forest landscape. For. Ecol. Manage. 449, 117461.
Holzmueller, E.J., Jose, S., Jenkins, M.A., 2009. The response of understory species composition, diversity, and seedling regeneration to repeated burning in Southern Appalachian oak-hickory forests. Natural Areas J. 29, 255–262.
Hurteau, M., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Front. Ecol. Environ. 7, 409–414.
Hurteau, M.D., Liang, S., Martin, K.L., North, M.P., Koch, G.W., Hungate, B.A., 2016. Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. Ecol. Appl. 26, 382–391.
Hurteau, M.D., North, M.P., Koch, G.W., Hungate, B.A., 2019. Opinion: Managing for disturbance stabilizes forest carbon. Proc. Natl. Acad. Sci. 116, 10193–10195.
Hutchinson, T.F., Long, R.P., Ford, R.D., Sutherland, E.K., 2008. Fire history and the establishment of oaks and maples in second-growth forests. Can. J. For. Res. 38, 1184–1198.
Hutchinson, T.F., Long, R.P., Rebbeck, J., Sutherland, E.K., Yaussy, D.A., 2012. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can. J. For. Res. 42, 303–314.
Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.
Iverson, L.R., Hutchinson, T.F., Peters, M.P., Yaussy, D.A., 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: Influence of light and moisture. Ecosphere 8. https://doi.org/10.1002/ecs2.1642.
Iverson, L.R., Hutchinson, T.F., Prasad, A.M., Peters, M.P., 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. For. Ecol. Manage. 255, 3035–3050. https://doi.org/10.1016/j.foreco.2007.09.088.
Jackson, J.F., Adams, D.C., Jackson, U.B., 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. Am. Nat. 153, 614–632.
Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., Schoennagel, T., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14, 369–378.
Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree mortality in gap models: application to climate change. Clim. Change 51, 509–540.
Keyser, T.L., Arthur, M., Loftis, D.L., 2017. Repeated burning alters the structure and composition of hardwood regeneration in oak-dominated forests of eastern Kentucky, USA. For. Ecol. Manage. 393, 1–11.
Knapp, B.O., Hullinger, M.A., Kabrick, J.M., 2017. Effects of fire frequency on long-term development of an oak-hickory forest in Missouri, U.S.A. For. Ecol. Manage. 387, 19–29.
Knapp, B.O., Stephan, K., Hubbart, J.A., 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. For. Ecol. Manage. 344, 95–109.
Knott, J.A., Desprez, J.M., Oswalt, C.M., Fei, S., 2019. Shifts in forest composition in the eastern United States. For. Ecol. Manage. 433, 176–183.
Kolaks, J.J., Cutter, B.E., Loewenstein, E.F., Grabner, K.W., Hartman, G., Kabrich, J.M., 2004. The effect of thinning and prescribed fire on fuel loading in the Central Hardwood Region of Missouri, in: Yaussy, D.A., Hix, D.M., Long, R.P., Goebel, P.C. (Eds.), Proceedings of the 14th Central Hardwood Forest Conference. USDA Forest Service Northern Research Station GTR-NE-316, Wooster, Ohio, USA, pp. 168–178.
Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl. 23, 1976–1986.
Kreye, J.K., Varner, J.M., Hamby, G.W., Kane, J.M., 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. Ecosphere 9, e02078.
Lafon, C. W., Naito, A.T., Grissino-Mayer, H.D., Horn, S.P., Waldrop, T.A., 2017. Fire history of the Appalachian region: a review and synthesis. Gen. Tech. Rep. SRS-219. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 97.
Lauvaux, C.A., Skinner, C.N., Taylor, A.H., 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. Forest Ecology and Management.
Little, S., Garrett, P.W., 1990. Pinus rigida Mill. pitch pine. In: Burns, Russell M., Honkala, Barbara H., (technical coordinators). Silvics of North America. Volume 1. Conifers. Agricultural Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 456–462.
Loftis, D.L., 1990. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. Forest Sci. 36, 908–916.
Loucks, E., Arthur, M.A., Lyons, J.E., Loftis, D.L., 2008. Characterization of fuel before and after a single prescribed fire in an Appalachian hardwood forest. South. J. Appl. For. 32, 80–88. https://doi.org/10.1093/sjaf/32.2.80.
MacLean, R.G., Ducey, M.J., Hoover, C.M., 2014. A comparison of carbon stock estimates and projections for the northeastern United States. Forest Sci. 60, 206–213.
Martin, K.L., Hurteau, M.D., Hungate, B.A., Koch, G.W., North, M.P., 2015. Carbon tradeoffs of restoration and provision of endangered species habitat in a fire-maintained forest. Ecosystems 18, 76–88.
McEwan, R.W., Hutchinson, T.F., Long, R.P., Ford, D.R., McCarthy, B.C., 2007. Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America. J. Veg. Sci. 18, 655–664.
Menking, K.M., Peteet, D.M., Anderson, R.Y., 2012. Late-glacial and Holocene vegetation and climate variability, including major droughts, in the Sky Lakes region of southeastern New York State. Palaeogeogr. Palaeoclimatol. Palaeoecol. 353, 45–59.
NIFC 2018 National Interagency Fire Center Year End Fire Statistics.
North, M.P., Stephens, S.L., Collins, B.M., Agee, J.K., Aplet, G., Franklin, J.F., Fule, P.Z., 2015. Reform forest fire management. Science 349, 1280–1281.
Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.
Rebain, S.A., 2010. The Fire and Fuels Extension to the Forest Vegetation Simulator: Updated model documentation. Internal Rep. U.S. Department of Agriculture, Forest

Service, Forest Management Service Center, Fort Collins, CO. 403p. (Revised: March 23, 2015).
Reed, W.P., Kaye, M.W., 2020. Bedrock type drives forest carbon storage and uptake across the mid-Atlantic Appalachian Ridge and Valley, USA. For. Ecol. Manage. 460, 117881.
Ryan, K.C., Reinhardt, E.D., 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. 18, 1291–1297.
Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15–e24.
Santín, C., Doerr, S.H., Kane, E.S., Masiello, C.A., Ohlson, M., de la Rosa, J.M., Preston, C. M., Dittmar, T., 2016. Towards a global assessment of pyrogenic carbon from vegetation fires. Glob. Change Biol. 22, 76–91.
Shumway, D.L., Abrams, M.D., Ruffner, C.M., 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA. Can. J. For. Res. 31, 1437–1443.
Schwenk, W.S., Donovan, T.M., Keeton, W.S., Nunery, J.S., 2012. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. Ecol. Appl. 22, 1612–1627.
Scott, J.H., Burgan, R.E., 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Gen. Tech. Rep. RMRS-GTR-153. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 72.
Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129.
Signell, S.A., Abrams, M.D., Hovis, J.C., Henry, S.W., 2005. Impact of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. For. Ecol. Manage. 218, 146–158.
Smith, L.A., Eissenstat, D.M., Kaye, M.W., 2017. Variability in aboveground carbon driven by slope aspect and curvature in an eastern deciduous forest, USA. Can. J. For. Res. 47, 149–158.
Stambaugh, M.C., Marschall, J.M., Abadir, E.R., Jones, B.C., Brose, P.H., Dey, D.C., Guyette, R.P., 2018. Wave of fire: an anthropogenic signal in historical fire regimes across central Pennsylvania, USA. Ecosphere 9, e02222.
Stambaugh, M.C., Marschall, J.M., Abadir, E.R., Jones, B.C., Brose, P.H., Dey, D.C., Guyette, R.P., 2019. Successful hard pine regeneration and survival through repeated burning: an applied historical ecology approach. For. Ecol. Manage. 437, 246–252.
Swanteson-Franz, R.J., Krofcheck, D.J., Hurteau, M.D., 2018. Quantifying forest carbon dynamics as a function of tree species composition and management under projected climate. Ecosphere 9, e02191.
Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S.L., 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. Proc. Natl. Acad. Sci. 113, 13684–13689.
Thompson, J.R., Carpenter, D.N., Cogbill, C.V., Foster, D.R., 2013. Four Centuries of Change in Northeastern United States Forests. PLoS ONE 8, e72540.
Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849.
USGCRP, 2018. Risks, and Adaptation in the United States: The Fourth National Climate Assessment, vol. II. US Global Change Research Program.
Varner III, J.M., Gordon, D.R., Putz, F.E., Hiers, J.K., 2005. Restoring fire to long-unburned Pinus palustris ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restor. Ecol. 13, 536–544.
Varner, J.M., Arthur, M.A., Clark, S.L., Dey, D.C., Hart, J.L., Schweitzer, C.J., 2016. Fire in eastern North American oak ecosystems: filling the gaps. Fire Ecology 12, 1–6.
Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Saunders, M.R., Shifley, S. R., Kabrick, J.M., Dey, D.C., Larsen, D.R., Westfall, J.A., 2019. Using a tree seedling mortality budget as an indicator of landscape-scale forest regeneration security. Ecol. Ind. 96, 718–727.
Vose, J.M., Elliott, K.J., 2016. Oak, fire, and global change in the eastern USA: What might the future hold? Fire Ecol. 12, 160–179.
Waldrop, T., Phillips, R.A., Simon, D.A., 2010. Fuels and predicted fire behavior in the southern Appalachian Mountains after fire and fire surrogate treatments. Forest Sci. 56, 32–45. https://doi.org/10.1093/forestscience/56.1.32.
Waldrop, T.A., Yaussy, D.A., Phillips, R.J., Hutchinson, T.A., Brudnak, L., Boerner, R.E.J., 2008. Fuel reduction treatments affect stand structure of hardwood forests in Western North Carolina and Southern Ohio, USA. For. Ecol. Manage. 255, 3117–3129. https://doi.org/10.1016/j.foreco.2007.11.010.
Welch, N.T., Waldrop, T.A., Buckner, E.R., 2000. Response of southern Appalachian table mountain pine (*Pinus pungens*) and pitch pine (*P. rigida*) stands to prescribed burning. For. Ecol. Manage. 136, 185–197.
Wendel, G.W., Smith, H. Clay, 1990. Pinus strobus L. eastern white pine. In: Burns, Russell M., Honkala, Barbara H., (technical coordinators). Silvics of North America. Volume 1. Conifers. Agricultural Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 476–488.
Willard, D.A., Bernhardt, C.E., Korejwo, D.A., Meyers, S.R., 2005. Impact of millennial-scale Holocene climate variability on eastern North American terrestrial ecosystems: pollen-based climatic reconstruction. Global Planet. Change 47, 17–35.
Williams, C.A., Gu, H., MacLean, R., Masek, J.G., Collatz, G.J., 2016. Disturbance and the carbon balance of US forests: A quantitative review of impacts from harvests, fires, insects, and droughts. Global Planet. Change 143, 66–80.
Zobel, D.B., 1969. Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. Ecol. Monogr. 39, 302–333.