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Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pineland

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Abstract. Forests have a prominent role in carbon sequestration and storage. Climate change and anthropogenic forcing have altered the dominant characteristics of some forested ecosystems through changes to their disturbance regimes, particularly fire. Ecosystems that historically burned frequently, like pinelands in the southeastern United States, risk changes in their structure and function when the fire regime they require is altered. Although the carbon storage potential in an unburned southeastern U.S. forest would be larger, this scenario is unrealistic due to the likelihood of wildfire. Additionally, fire exclusion can have negative consequences on these forests health, biodiversity, and species endemism. There is a need, specifically for the southeast, to estimate carbon and species dynamics based on the differences between various fire regimes, and particularly the differences between prescribed fire and wildfire. These are important factors to consider given that prescribed fire is a common tool used in the southeast, and wildfires are ever more present. Field data from an experimental *Pinus palustris* (longleaf pine) forest of southwest Georgia were used to parametrize the forest landscape model LANDIS-II. The model simulated how carbon and species dynamics differ under a fire exclusion, a prescribed fire, and multiple wildfire scenarios. All scenarios except fire exclusion resulted in net emissions to the atmosphere, but prescribed fire produced the least carbon emissions from fire and maintained the most stable aboveground biomass compared to wildfire scenarios. Removing fire for approximately a century was necessary to obtain an average stand-level biomass greater than that of prescribed fire and net emissions less than that of prescribed fire. The prescribed fire scenario produced a longleaf pine-dominated forest, the exclusion scenario converted to predominantly oak species *Quercus virginiana* (live oak), *Q. stellata* (post oak), and *Q. margaretta* (sand post oak), while scenarios with intermediate wildfire regimes supported a mix of other fire-facilitator hardwoods and pine species, such as *Q. incana* (bluejack oak) and *Pinus elliotti* (slash pine). Overall, this study supports prescribed fire regimes in southeastern U.S. pinelands to both minimize carbon emissions and preserve native biodiversity.

Key words: carbon sequestration; deciduous oaks; ecosystem modeling; fire emission; Ichauway; Landscape Disturbance and Succession II; longleaf pine; prescribed fire; savanna; wildfire.

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Introduction

Forests impact the global carbon balance by sequestering ~30% of annual anthropogenic carbon dioxide emissions and storing ~45% of terrestrial carbon (Canadell et al. 2007, Bonan 2008). Their ability to continue to sequester carbon and remain a sink depends on a variety of factors such as current ecosystem state, land-use history, climate change, disturbance regimes, and other interacting processes that frequently are interconnected (Denslow 1980, Emanuel et al. 1985, Prentice and Fung 1990, Bachelet et al. 2001, Hurtt et al. 2002, Bonan 2008, Xu et al. 2009, Dale et al. 2011, Pan et al. 2011, Millar and Stephenson 2015). These interactions and their impact on future forest distribution, stability, and carbon sequestration potential are important research topics for scientists, resource managers, and policy makers.

The global process of wildland fire (Bond and Keeley 2005, Bowman et al. 2009) and climate–fire interactions (Kang et al. 2006, Goetz et al. 2012, Liu et al. 2014) are particularly critical uncertainties as emission and sequestration feedbacks are complex and multi-scalar (Hurteau and North 2009, Wiedinmyer and Hurteau 2010). Methods to reduce wildfire intensity and spread, such as prescribed fire and forest thinning, compete against the goal of carbon sequestration (Hurteau et al. 2008, Loudermilk et al. 2014). This is certainly important in low-intensity surface fire regimes (Mitchell et al. 2009, Hurteau and Brooks 2011) for estimating carbon and species dynamics through time. These are difficult to estimate because when burn intervals are short (1- to 3-yr return time), post-fire understory and midstory re-growth and regeneration are quick (Starr et al. 2015), and overstory survival is high (Glitzenstein et al. 1995), though long-term implications exist if fire return intervals increase to within a decade or more (Hartnett and Krofta 1989, Kirkman et al. 2004, Slack et al. 2016). The longleaf pine (*Pinus palustris*) ecosystem of the southeastern coastal plain of the United States is an archetype of a forest with a frequent surface fire regime (Mitchell et al. 2009). Frequent burning creates a varied herbaceous vegetation community with savanna ecosystem properties (Veldman et al. 2015). Through the continued use of frequent prescribed fire, this endangered ecosystem with many endemic flora and fauna (Hardin and White 1989, Walker 1993, Kirkman et al. 2016) has the potential to remain a global hotspot of diversity, maintain resilience to future droughts, and minimize large carbon emission pulses that can occur with wildfire (Hurteau and North 2009, Gonzalez-Benecke et al. 2015, Starr et al. 2015).

There is a need to quantify carbon and species dynamics in longleaf pine forests and the feedbacks due to altered fire frequency and alternative stable states, namely transitions from longleaf pine to hardwood-dominated stands when fire is excluded (Provencher et al. 2001, Varner et al. 2007, Kirkman et al. 2016). The differences in carbon allocation and emissions between prescribed fire and wildfires are also important factors to consider given that prescribed fire is a common tool used in the southeast, and wildfire risk is increasing (Bachelet et al. 2001, Mitchell et al. 2014, Krofcheck et al. 2017, Schoennagel et al. 2017). Only a few studies have measured and/or modeled carbon dynamics within longleaf pine stands. Field studies generally support the conclusion that frequent fire maintains above- and belowground carbon levels through time, where the effects of prescribed fire on (mainly understory plant) carbon levels are short-lived and are replenished quickly after each surface fire (Mitchell et al. 1999, Starr et al. 2015, Kirkman et al. 2016). Outcalt and Wade (2004) measured mortality in southern pine forests after a wildfire based on time since prescribed fire and found a regular prescribed fire regime reduced mortality in both natural and planted pine stands. Whelan et al. (2013) showed that ecosystem physiology returns to pre-fire levels within 30–60 d following prescribed fire at three sites with varying soil water-holding capacity. Similar studies used eddy flux towers to model and estimate carbon flux between mesic and xeric longleaf sites before and after a prescribed fire and found distinct changes in gross primary production but that ecosystem physiological activity was statistically similar to pre-fire conditions within 30 d (Starr et al. 2015). In a longleaf and slash pine forest that had not burned in six years, Lavoie et al. (2010) found that understory carbon pools took three years to recover to pre-fire levels. Similar results are also found in modeling studies. Gonzalez-Benecke et al. (2015) found that the main difference in aboveground carbon stocks between simulations of longleaf pine plantations was in reductions in forest floor carbon due to prescribed burning. Using forest landscape model simulations, Martin et al. (2015) found that prescribed fire with thinning increased longleaf pine habitat necessary for the red-cockaded woodpecker but stored 22% less total ecosystem carbon than an unburned and unthinned site. Swanteson-Franz et al. (2018) ran a study at the same site and found the potential to increase total carbon storage with prescribed fire, but only if subsequent planting accompanied the burn. There is, however, no known study that examines the difference in carbon and species dynamics in longleaf pine stands across different fire regimes at the landscape scale.

In this study, we explored the interactions between fire regime scenarios and ecosystem carbon and species dynamics using a forest landscape model applied to stands within an extensive longleaf pine experimental forest in southwest Georgia, United States. We used the Landscape Disturbance and Succession II model (LANDIS-II, v6.2.1; Scheller et al. 2007) to project the response of pine and hardwood species to different fire regimes, namely (1) fire exclusion, (2) prescribed fire at two-year return intervals, and (3) wildfire at 20-, 50-, and 100-yr return intervals. The impact of each scenario was evaluated by the effects on (1) total live aboveground biomass (AGB), (2) net ecosystem carbon balance (NECB), (3) carbon emissions from fire, and (4) species composition as estimated by relative landscape-level AGB.

Methods

Study area

The Joseph W. Jones Ecological Research Center (JWJERC) at Ichauway is a 115 km^2 (11,736 ha) research and conservation site located in the Coastal Plain of southwestern Georgia, United States (31°13′ N, 84°29′ W; Fig. 1; Mitchell et al. 1999, Goebel et al. 2001). It is situated within the Dougherty Plain physiographic region (Hodler and Schretter 1986) in the Gulf Coastal Plain Province described by Walker and Coleman (1987) of the Lower Coastal Plain and Flatwoods (LCPF) section (Plains and Wiregrass Plains subsections) described by McNab et al. (2007). The area is a karst landscape with flat, weakly dissected alluvial deposits over Ocala Limestone and is characteristic of the LCPF section, and elevation ranges from 23 m to 91 m above sea level (Hodler and Schretter 1986). The soils are fine to moderately fine-textured loamy or clayey subsoils, and drainage classes range from excessively to poorly drained (Goebel et al. 2001). The climate is characterized as humid subtropical (Christensen 2013) and consists of long, hot summers with mean daily temperatures ranging from 21°C to 34°C and short, cool winters with mean daily temperatures ranging from 5°C to 17°C (Lynch et al. 1986,

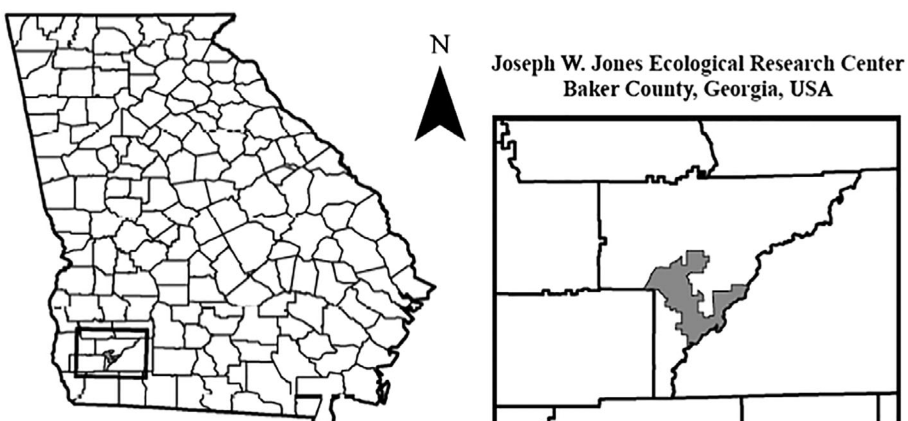

Fig. 1. Map of Georgia and its counties with the location of the Joseph W. Jones Ecological Research Center (JWJERC) at Ichauway highlighted.

Goebel et al. 1998). The average annual precipitation of 131 cm is evenly distributed throughout the year (Goebel et al. 1998).

Ichauway is composed of a diverse range of ecological communities: prominent longleaf pine forests, slash pine forests, old field loblolly pine stands, mixed pine–hardwood forests, riparian hardwood forests, isolated depressional wetlands, agricultural fields, shrub–scrub uplands, human cultural zones, rivers, and creeks (Goebel et al. 2001). Species commonly found in the forests include longleaf pine, loblolly pine (*P. taeda*), shortleaf pine (*P. echinata*), slash pine (*P. elliotti*), live oak (*Quercus virginiana*), laurel oak (*Q. laurifolia*), water oak (*Q. nigra*), southern red oak (*Q. falcata*), and post oak (*Q. stellate*; Mitchell et al. 1999, Kirkman et al. 2001). Open longleaf pine forest covers 6000 ha, with wiregrass (*Aristida beyrichiana* or *A. stricta*) an understory component on approximately 4000 ha (Goebel et al. 2001, Kirkman et al. 2001). Longleaf pine ecosystems at Ichauway, including longleaf–wiregrass ecosystems, span the range of soil moisture conditions found in the LCPF Province (Mitchell et al. 1999, Wilson et al. 1999). For the past 80 yr, frequent prescribed fire every two to four years has been used to decrease competing vegetation (i.e., hardwoods) and reduce litter in the fire-maintained longleaf pine–wiregrass forest. We focused our study area to 1267 ha within the JWJERC where longleaf pine ecosystems are the dominant forest community under a range of environmental conditions and long-term monitoring plots were available. The study area was an extensive site of 2nd growth longleaf pine, with predominantly 80- to 100-yr-old trees in the overstory. Dormant season prescribed burns have been applied at a frequency of one to three years for at least 80 yr. Previously, the area was predominantly used for agriculture. The understory was primarily composed of wiregrass, many forb and prairie grass species, as well as inter-dispersed hardwood shrubs (e.g., *Diospyros* spp., *Prunus* spp, *Quercus* spp., and *Sassafras albidum*). Hardwoods are generally maintained at shrub size with frequent fire, but mature hardwoods make up a minor component of the overstory as well.

Simulation modeling framework

For this study, we used the Landscape Disturbance and Succession II model (LANDIS-II, v6.2.1; Scheller et al. 2007), which integrates various ecosystem processes and disturbances that interact at the landscape scale and over longer time periods. LANDIS-II uses a gridded landscape where each cell contains species-age cohorts of woody species whose growth and succession are governed by a species competitive ability, dispersal, and reproduction. It has been successfully implemented for understanding ecosystem dynamics, succession, insects, fire, wind, dispersal, harvesting, fuel treatment effectiveness, and climate change research (Sturtevant et al. 2004, 2009, Scheller et al. 2011*b*, Syphard et al. 2011, Xu et al. 2012, Loudermilk et al. 2013, 2014, 2017).

LANDIS-II was the chosen forest landscape model not only for its wide range of capabilities that enabled the simulations, but also because it had already been parameterized and validated at nearby Fort Benning in Southwest GA (Martin et al. 2015, Swanteson-Franz et al. 2018). The initial vegetation communities (see the *Model Inputs* section) at Ichauway differed slightly from Fort Benning so values from the literature and available databases, including the NECN succession guide, were used to complete the parameterization (Botkin et al. 1972, Pastor and Post 1986, Burns and Honkala 1990, Sutherland et al. 2000, Bachelet et al. 2001, Wimberly 2004, Hendricks et al. 2006, Scheller et al. 2011*a*, *b*, 2012, Samuelson et al. 2014). Key parameters can be found in Appendix S1: Tables S1–S5, and all model inputs and processing scripts can be found on the dedicated GitHub LANDIS-II repository, https://github.com/LANDIS-II-Foundation, under Project-JonesEcologicalResearchCenter-2019.

Within LANDIS-II, we used the Net Ecosystem Carbon and Nitrogen (NECN) Succession extension (v4.2; Scheller et al. 2011*a*) and the Biomass Harvest extension (v3.1.6; Gustafson et al. 2000). The NECN extension implements succession with above- and belowground carbon and nitrogen and simulates the regeneration and growth of vegetation based on age, competition for resources (water, nitrogen, light), and disturbance. Vegetation growth and response to disturbance are determined by unique species attributes (e.g., shade tolerance). Dead biomass (woody and leaf litter) and soil organic carbon (SOC) are also tracked over time. Biomass Harvest simulates the removal of aboveground live leaf and woody biomass of designated species and ages within selected areas. The Biomass Harvest extension was used to simulate all fire regimes. LANDIS-II has dedicated fire extensions (He and Mladenoff 1999, Sturtevant et al. 2009) that simulate fire ignition and spread as stochastic processes. Prescribed fires are, however, only currently being simulated within the Biomass Harvest extension (Martin et al. 2015, Hurteau 2017, Krofcheck et al. 2017, Swanteson-Franz et al. 2018). We focused on how the carbon balance of the forest was altered by a wildland fire at various successional stages if a wildfire occurred so the Biomass Harvest extension was used for both wildfires and prescribed fire that provided comparisons within the same modeling framework. Specific features of LANDIS-II are described in more detail in the *Model Scenarios* section.

Model inputs

*Ecoregions.—*Ecoregions are sections of the study area with similar climate and soils which have homogeneous species establishment and ecosystem process rates. As climate is similar across the study area, ecoregion definitions were purely based on soil characteristics so they are essentially soil types. To create ecoregions, soils were grouped by soil series (sand, loamy sand, fine sandy loam) and drainage (e.g., poorly drained, well drained, and excessively drained), with consideration to spatial configuration. Soil data were obtained from the National Resources Conservation Service Soil Survey Geographic database (NRCS SSURGO) and nine ecoregions designated.

*Climate.—*The Climate Library (v1.0; Lucash and Scheller 2015) accompanying the NECN Succession extension was used to implement climate in the model simulations. Temperature and precipitation climate data were obtained from the Georgia Automated Environmental Monitoring Network (GAEMN). The daily summary of minimum temperature, maximum temperature, and precipitation was acquired for 16 yr (1 January 2000–31 December 2015). Monthly values were calculated for model inputs (average minimum temperature [C], average maximum temperature [C], and total precipitation [mm/month]). To smooth any irregularities that might have arisen from an anomalous year in regard to climate, the 16 yr of monthly data was averaged to form a representative yearly climate for the region that was applied for the duration of the simulation. The same climate data were used for all ecoregions because of the small landscape size.

*Initial vegetation communities.—*Initial vegetation communities were created with data supplied by the JWJERC. The land base at Ichauway, and the smaller study area for this research, is comprised of longleaf pine woodland with extensive long-term monitoring (LTM) plots. For longleaf pine plantations, time series satellite images determined the establishment year of corresponding raster cells. For non-plantation areas, 120 0.1-ha LTM plots provided species composition and DBH measurements of trees greater than 10 cm were used to estimate ages from diameter–age equations or regressions for the twelve most prominent species. The species are defined by individual characteristics (Appendix S1: Tables S1 and S2) and also a plant functional type (PFT) group (Appendix S1: Table S3) to reduce some calculations performed by LANDIS-II when species traits are similar. The PFT groups were pine and hardwood. The pine PFT contained the species longleaf pine, slash pine, and pond cypress (*Taxodium ascendens).* The hardwood PFT consisted of eight oak species, southern red, laurel (*Q. hemisphaerica*), bluejack (*Q. incana*), turkey (*Q. laevis*), sand post (*Q. margaretta*), water, post, live, and also swamp tupelo (*Nysa biflora*). Aerial photography and ground truthing from the JWJERC produced a map of land cover, separated into eight classes, that the LTM plots were grouped by. The initial communities associated with LTM plots were created by assigning a species-age cohort to each raster cell by randomly selecting a LTM plot within the corresponding land cover class. Non-forest land cover classes were excluded from model simulations. The percentage of total AGB for each species at the start of the simulation is shown in Table 1.

Model scenarios

Five different fire frequency scenarios were used: continuous fire exclusion, prescribed fire with a 2-yr return interval, and three wildfire scenarios (20-, 50-, and 100-yr return intervals). All scenarios were run for 300 yr at a yearly time

Table 1. The percentage of total AGB for each species at the start of the simulation.

Species	Percentage of total AGB
Longleaf pine	57
Live Oak	16
Laurel Oak	7
Slash Pine	5
Southern Red Oak	4
Water Oak	3
Turkey Oak	2
Post Oak	2
Swamp Tupelo	1
Pond Cypress	1
Sand Post Oak	<1
Bluejack Oak	<1

Note: AGB is aboveground biomass.

step and 1-ha spatial resolution. Under the fire exclusion scenario, the ecosystem and vegetation grew without external disturbance from the initialized state. For the prescribed fire scenario, the entire landscape burned every two years—the mean fire return interval for management at Ichauway—with a species-dependent percentage of all cohorts, regardless of age, removed such that the proportion of longleaf to hardwoods AGB approximated the values presented in Loudermilk et al. (2011). Removal by age, where older trees had a higher chance of survival, was considered but required continuous changes to the removal percentages to achieve the desired proportion of hardwoods to longleaf. The lack of justification for continuously changing how species were removed if the same effect was being applied resulted in the decision to remove by percentage. With consistent prescribed fire, hardwoods occupied ~5% of the total landscape vs. ~8% in Loudermilk et al. (2011), who simulated a slightly longer fire return interval (~2.85 yr) and demonstrated a decline in percentage of hardwoods as the return interval was lowered. The AGB of the mature longleaf pine stand of ~190 Mg/ha is similar to Gonzalez-Benecke et al. (2015) who reported ~230 Mg/ha in an unthinned, burned longleaf pine stand with a 3-yr fire return interval.

Removing fire for as little as two decades causes the community type to transition to a hardwood-dominated stand (Hartnett and Krofta 1989, Varner et al. 2005) and when fires do occur, they can cause high mortality, with overstory mortality rates up to 100% (Outcalt and Wade 2004, Varner et al. 2007) mainly caused by consumption of the duff and ingrown fine roots (Varner et al. 2007, Varner et al. 2009, O'Brien et al. 2010). Stand-replacing fires in this ecosystem have been recorded at as low as a 6-yr fire return interval (Outcalt and Wade 2004), and 91% mortality of the overstory was found when fire was suppressed for 45 yr (Varner et al. 2007). Although environmental conditions can influence mortality rates, this ecosystem can experience a stand-replacing fire if suppression occurs for only a few years. As such, all wildfires were simulated as a stand-replacing fire. Also, we set a conservative lower boundary for wildfire frequency at a 20-yr interval. We chose 50- and 100-yr intervals to represent other forest successional stages at the time of wildfire. In reality, a small percentage of overstory conifer and hardwood trees could survive such a wildfire depending on fuel moisture conditions; younger cone-bearing pines might survive to provide a seed source, and smaller hardwoods (understory and midstory trees) could re-sprout after a fire (Rebertus et al. 1989). To simplify these effects, we created a surrogate approach by simulating survival of the youngest cohorts (ages 1–3) so that it was not necessary to re-seed or re-sprout the domain. All other age classes were removed during a wildfire which was simulated in a single time step for the entire domain. Species interactions functioned the same way in all scenarios with the Harvest extension as a proxy for fire-altering species abundance when implemented at the specified interval. Fuel consumption measurements taken by Ottmar et al. (2016) at Ichauway and similar southeastern forests, which were 30% for woody AGB and 77% for litter, were the prescribed fire scenario consumption values. For wildfire scenarios, 81% of woody AGB (Regelbrugge and Smith 1994) and 100% of litter (Reinhardt et al. 1997) were consumed. Though the Biomass Harvest extension allowed the simulation of deterministic fire events instead of stochastic ones, several model components (establishment, reproduction, resprouting) were stochastic, so each scenario was replicated five times to capture variability. The relatively low number of five runs was chosen because the use of the Biomass Harvest extension removes almost all of the stochastic variability in the system. Deterministic fire events dominate stochastic physiological processes in driving long-term ecosystem carbon dynamics.

Model validation

Additional model validation was performed by comparing model-predicted net ecosystem exchange (NEE) with three flux towers at Ichauway. Starting with the initial communities generated by the parameterization, five explicit years of climate data (January 2009–December 2013) was run to correspond with the available flux data measurements provided by the JWJERC. As the JWJERC has a fire return interval of two years, the prescribed fire scenario was used for the comparison. Yearly model-predicted and actual values were -15 gC·m^{-2}·yr^{-1} and -20 gC·m^{-2}·yr^{-1}, respectively.

Results

Aboveground biomass

The average AGB ranged from ~35 Mg/ha with the 20-yr wildfire return to ~250 Mg/ha in the fire exclusion scenario (Fig. 2). Suppression before a wildfire needs to last on the order of 100 yr for average AGB to be higher than the prescribed fire scenario (~190 Mg/ha vs. ~195 Mg/ha) for sites used in this study. A 50-yr return simulated an average AGB of ~130 Mg/ha. The total average was affected by the initial conditions, but it took ~40 yr following wildfire for AGB to exceed that of prescribed fire. The prescribed fire scenario also experienced a slight drop in AGB at the start of the simulation as a large portion of hardwoods in the LTM plots were killed by the reintroduction of fire (Fig. 3A).

Net ecosystem carbon balance

Yearly model output of net ecosystem productivity (NEP), which does not account for biomass removed by fire (through the Biomass Harvest extension), fluctuated from being a carbon sink in years without fire to a source when a fire occurred, which persisted for several years following fire (Fig. 4). Taken cumulatively, all scenarios were projected to result in a carbon sink (Fig. 5A). After a fire, a decrease in cumulative NEP is seen for a few years (Fig. 5A), but the site quickly returns to a carbon sink (Figs. 4, 5A).

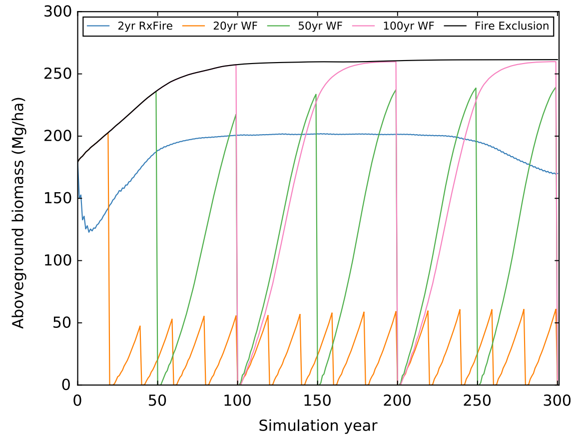

Fig. 2. Model-predicted aboveground biomass with respect to simulation year for the five fire frequency scenarios: prescribed fire (RxFire) every 2 yr, wildfire (WF) at 20-, 50-, and 100-yr return intervals, and fire exclusion.

The 50-yr return scenario projects the most carbon sequestration as it has more time to mature than the 20-yr scenario, but does not plateau and become carbon neutral like the 100-yr scenario. This dynamic caused the 50-yr scenario to lose the greatest amount of biomass to fire (Fig. 5B). NECB was found by combining the model output of NEP with the loss of biomass from fire (Fig. 5C). At the end of the simulation, the forest is projected to be a carbon sink only under complete fire exclusion. Though the species composition was still changing 100 yr after a wildfire, the ecosystem has reached maximum total AGB (Fig. 2) and there was an equal change in NEP after each 100-yr wildfire (Fig. 4). The drop in NECB after a wildfire is greater than the sequestration before fire in all wildfire scenarios so cumulative NECB for wildfires always trends toward net emissions (Fig. 5C).

Species distribution

The objective of this study was based on estimating carbon balance but as the model is constructed to allow for research into individual species dynamics if desired, we provide some preliminary results here. The initial graphs used to report these trends can be found on the GitHub repository. The prescribed fire regimes produced a longleaf-dominated ecosystem (Fig. 3A) with a small amount of all hardwood species. Longleaf

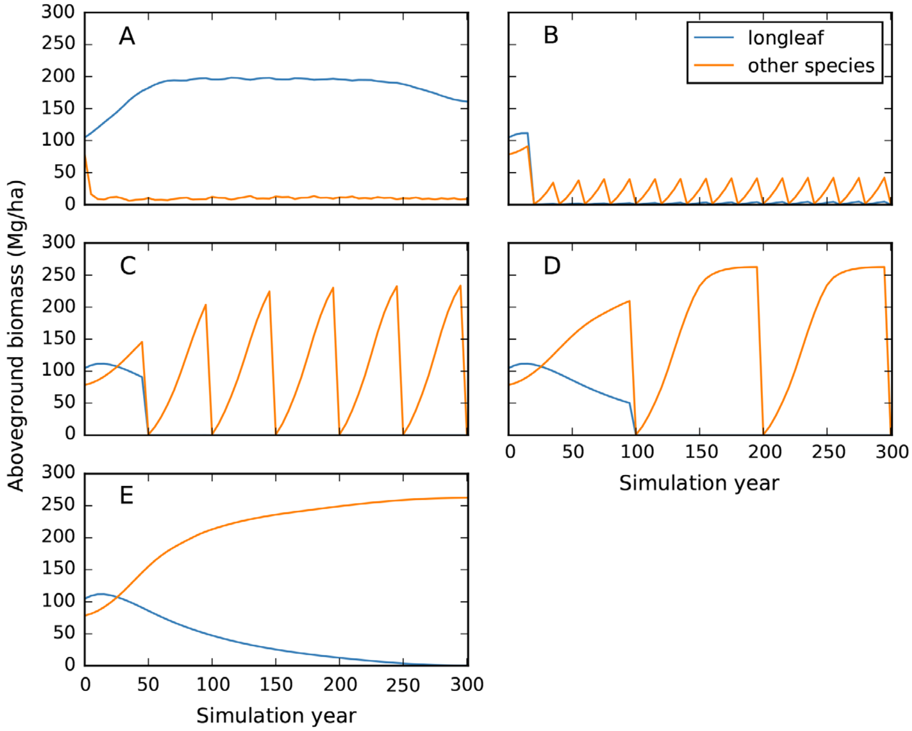

Fig. 3. Longleaf vs. all other species AGB for the five fire scenarios. The prescribed fire regime (A) resulted in a longleaf-dominated forest and stabilized AGB. Wildfire regimes of 20-, 50-, and 100-y (B–D) return intervals caused AGB to fluctuate and dominant species depended on successional response. Fire exclusion (E) stabilized AGB but converted to a hardwood forest.

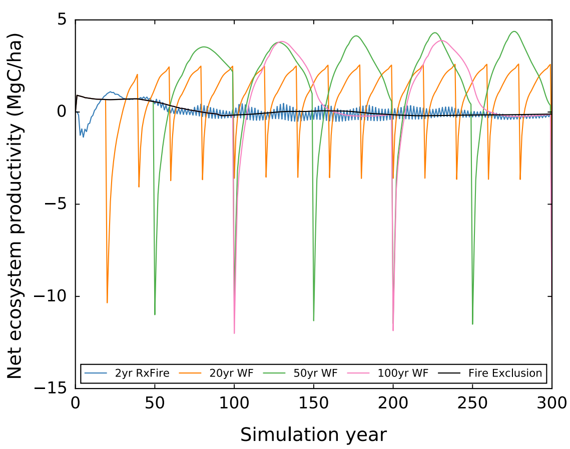

Fig. 4. Yearly model-predicted NEP for each scenario. This does not account for biomass removed through fire to produce NECB.

is outcompeted in the system unless prescribed fire is applied, which presented as abrupt disappearance following wildfire (Fig. 3B–D) but as a gradual decline in fire exclusion scenarios (Fig. 3E). The wildfire regimes illustrated successional trajectories between fires, where hardwoods dominate when fire is removed from the system for even short periods (two or more decades). Twenty years after a wildfire, the primary contributors to total AGB are slash pine and bluejack oak. At 50 yr since wildfire, bluejack oak was the dominant species and remained so at 100 yr but was decreasing in percentage of total AGB as live and post oak began to dominate. At 100 yr since wildfire, longleaf and slash pine, swamp tupelo, and pond cypress have been outcompeted by the hardwoods and are almost nonexistent. Under fire exclusion, an oak-dominated ecosystem (Fig. 3E) emerged with the highest proportion of biomass coming from live oak, post oak, and sand post oak.

Discussion

We used the forest landscape model LANDIS-II to estimate the effects of fire frequency on

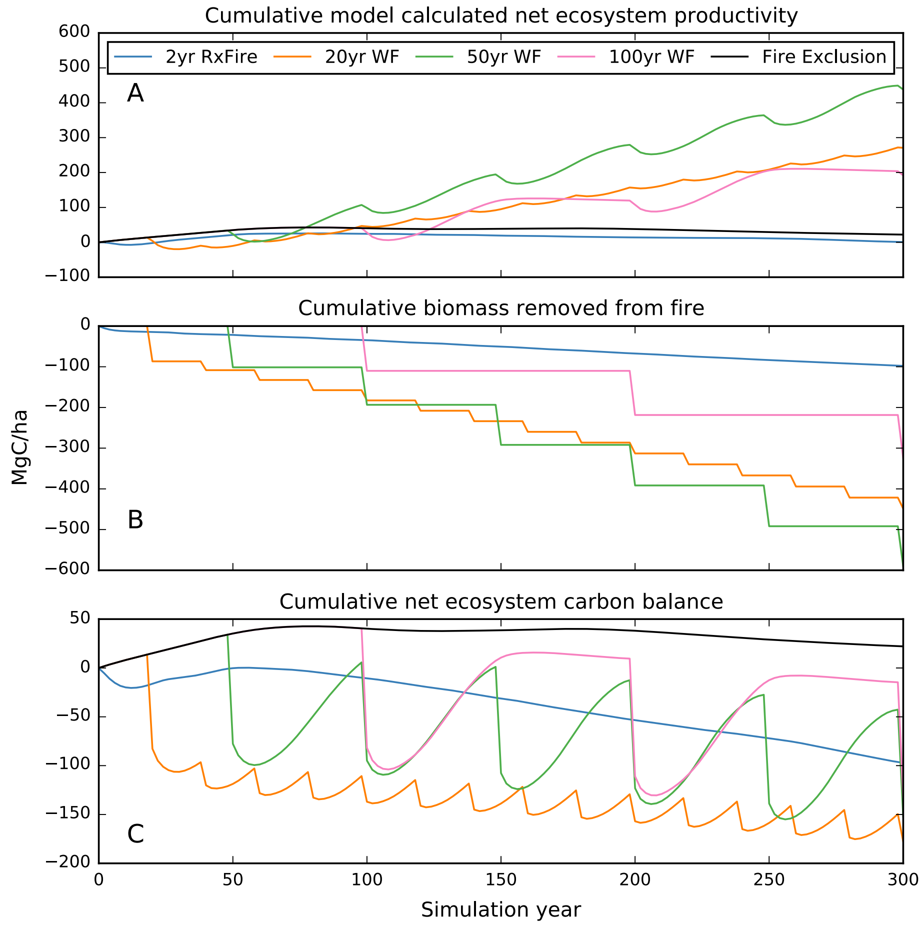

Fig. 5. Cumulative model-predicted NEP (not including carbon biomass removed from fire) (A), cumulative carbon removed from fire (B), and their combination, resulting in cumulative NECB (C) for the five fire frequency scenarios. Carbon is represented as the mean landscape density (Mg C/ha) across the landscape at each time step.

aboveground carbon and species dynamics in a southeastern U.S. pine forest to understand differences associated with prescribed fire, wildfire, and fire exclusion. We found that overall emissions from prescribed fire are less than those from periodic wildfires, unless fire is excluded for a century or more (Fig. 5). In fact, when wildfires occurred on relatively short (20 and 50 yr) intervals they emitted cumulatively more carbon than prescribed fire (Fig. 5). The 20- and 50-yr wildfire scenarios emitted ~200 MgC/ha over the duration of the simulation versus ~100 MgC/ha for the prescribed fire scenario. The 100-yr wildfire scenario emitted ~150 MgC/ha with a ~120 MgC/ha drop at the end of the simulation. A similar drop would occur at any fire return intervals greater than 100 yr, as the forest is carbon neutral (Fig. 5A) after 100 yr since the last fire. As such, one would need to suppress fire on the order of centuries to see a forest emit less carbon than it would under regular prescribed fire, which in this case was applied 50 times per century (Fig. 5C).

The forest reached maximum growth potential (Fig. 2) and remained a carbon sink (Fig. 5C) only with complete fire exclusion where faster-growing hardwoods became the dominant species as longleaf recruitment ceased and its overstory slowly died off (Fig. 3E). However, this scenario is unrealistic given the likelihood of fires in the southeastern United States and future projections of climate–fire interactions (Liu et al.

2014, Prestemon et al. 2016). Furthermore, the exclusion of fire from longleaf ecosystems would cause a major reduction in biological diversity. With prescribed fire, longleaf pine illustrated its positive response to frequent fire that stabilized AGB (Fig. 2) and kept competitive hardwoods in the understory or midstory (Fig. 3). The loss of AGB in the prescribed fire scenario around simulation year ~250 is from age-related mortality. As a second-growth forest, the older longleaf trees were of a relatively similar age at initialization, and this impacted age-related morality in the model, decreasing total AGB when a large portion of the similarly aged overstory died. However, if this simulation continued past 300 yr, these values would rebound to the established high values (~195 Mg/ha) as the age-related perturbation is overcome as new longleaf pine trees achieve overstory stature (data not shown). Without prescribed fire, hardwoods began to dominate (Fig. 3) and subsequent wildfires induced large emission pulses (Fig. 4) and drastically decreased ecosystem stability. Wildfire regimes caused AGB (Fig. 2) and species composition (Fig. 3) to become highly variable as large-scale overstory death occurred when a fire came through and AGB ultimately became landscape detrital carbon (snags, downed logs).

The reported values depend on initial conditions of species distribution and chosen removal techniques as a surrogate for fire, but the potential carbon and ecosystem benefits of a prescribed fire regime in a southeastern U.S. pine forest are independent of these choices. The amount of AGB consumed by fire and the amount converted to detrital carbon were strong determinants of NECB and were based off of literature values, but the same trend of prescribed fire emitting less carbon than wildfires existed regardless of the proportions chosen (graphs not shown). The biomass removal method as a surrogate for fire is supported by studies of high-intensity fire causing high mortality (mainly by forest floor consumption) and that longleaf pine ecosystems have the potential for a high-intensity fire under the right environmental conditions in as little as 20 yr (Hartnett and Krofta 1989, Outcalt and Wade 2004, Varner et al. 2007). The southeastern United States has the highest density of wildfire occurrence in the United States (Balch et al. 2017) with increased fire potential (Liu et al. 2013) and severity (Barbero et al. 2015) from climate change (Wear and Greis 2013), so it is likely a wildfire that leads to high mortality will occur within the span of a century. The results are realistic based on known species life history traits and successional response to a varying fire regime.

Improved model representation of the time scale of carbon cost could better predict empirical values. The majority of biomass was immediately removed from the system when a wildfire occurred, but the empirical values associated with the tradeoffs between the short-term carbon cost of prescribed fire and the long-term carbon cost of decomposition are unknown, but of interest, in these ecosystems. New decomposition strategies as well as the incorporation of recalcitrant carbon to more accurately represent NECB through time could be useful. In fact, the dynamics of recalcitrant forms of pyrogenic organic material (Masiello 2004) is a major source of uncertainty with relevance for this system. For example, charcoal and soot are produced by every fire whether prescribed or not, and can last for thousands of years in sediments (Singh et al. 2012). Estimates of the proportion of burned biomass converted into recalcitrant forms of carbon range widely, from 0.12% to 9.5% (Forbes et al. 2006) influencing the ecosystem carbon balance significantly. If some amount of soil carbon remained as recalcitrant carbon, then this would reduce the slope of the cumulative NECB for prescribed fire (Fig. 5C), and the system would be closer to carbon neutral. Additionally, the presence of charred material in soils has a large impact on biogeochemistry and increases ecosystem productivity (Biederman and Harpole 2013).

The interaction between time since fire, fuels, and fire energy release is an area of interest for future research. A severe fire can send a forest on an alternative trajectory essentially changing the initial conditions after the fire (Beisner et al. 2003). This is particularly true when introducing low-intensity surface fires into long-unburned stands where duff consumption is directly related to overstory tree mortality and subsequent growth of surviving trees. This is important for longleaf pine (Varner et al. 2007, Morgan Varner et al. 2009, O'Brien et al. 2010) as well as western U.S. pines (Ryan and Frandsen 1991, Swezy and Agee 1991). Effects from altered ecosystem state on the characterization of available fuels may be a useful avenue of research, particularly when evergreen hardwoods alter the litter composition to impede fire ignition and spread (Kane et al. 2008). This effect may be reduced by the effects from future climate or the potential for prolonged drought that may negatively impact growth and survival of more mesic and evergreen species and promote drier fuels.

The tradeoffs between carbon sequestration, fire, and ecosystem type are a multifaceted societal issue. Prescribed fire in the southeastern United States is engrained in southern culture, and fire use has occurred for millennia with indigenous peoples (Jackson et al. 2018, McIntyre et al. 2018*a*, *b*). These frequently burned ecosystems are also global hotspots for biodiversity and species endemism, and many need conservation efforts to maintain frequent low-intensity surface fires (Lashley et al. 2014). Furthermore, suppression techniques have been estimated to cost 20–50 times more than prescribed fire applications in a given area (Butry et al. 2001, North et al. 2012), notwithstanding the risk of complete change in ecosystem state with the onset of subsequent wildfires. These tradeoffs can be seen where recovery from logging and ongoing fire exclusion are responsible for much of the South's carbon sink (Caspersen et al. 2000, Houghton 2003, Dangal et al. 2014) but at a loss of unique ecosystem types. Balancing the demand to maximize carbon sequestration while managing wildfire and smoke risk and other social tradeoffs becomes more difficult, yet critical, in predicted future climate (Liu et al. 2014) and wildfire regimes (Mitchell et al. 2014).

Maintaining an intact longleaf pine overstory by using frequent fire is critical to ensuring ecosystem stability through time. Of the southern pine species, longleaf pine is the most resistant to frequent surface fires, prolonged drought, disease, insects, and hurricane damage, particularly while prescribed fire regimes are in place (Wahlenberg 1946). This is notwithstanding the preservation of many endemic flora and fauna (Kirkman et al. 2001). This study highlights the vulnerability of emissions due to high severity wildfires at multiple frequencies in southeastern U.S. forests and supports the application of frequent prescribed burning to mitigate long-term carbon emissions and maintain ecosystem stability. Future work could also incorporate additional environmental components such as projected climate change, disturbances from additional sources such as pests and windthrow, environmental adaptations, and the use of multiple models that produce a range of results. Although LANDIS-II is one of the most comprehensive models currently available that provides above- and belowground carbon accounting and ecosystem flux affected by disturbances, all at the landscape level, other alternatives exist. LANDIS-II and LANDIS-PRO were found to have slightly different times to maximum potential AGB (Xiao et al. 2017) which would alter the length of the suppression period needed before prescribed fire is not carbon beneficial with respect to emissions from a potential future wildfire. Climate change can alter disturbance rates (Dolan et al. 2017), create environmental conditions that favor different dominant species (Flanagan et al. 2016), and alter prescribed fire activities by limiting prescription windows (Mitchell et al. 2014). These scenarios present many avenues for future research on the complex relationships between longleaf pine, hardwoods, and fire frequency.

Conclusions

This study of fire-dependent longleaf pine woodlands in the southeastern United States provides projections of changes in ecosystem carbon dynamics, fire emissions, and species distribution based on a range of fire frequencies. There are four major conclusions from our model simulations: (1) There are large potential changes to total aboveground biomass in response to fire frequency, where ongoing prescribed fire maintains the most stable aboveground biomass and an intact longleaf pine ecosystem; (2) although removing fire entirely illustrated a carbon sink, this takes close to a century to achieve and wildfire exclusion in perpetuity is unrealistic in these fire-prone landscapes; (3) dependent on the prescribed fire and wildfire fire frequency and effects on ecosystem state, the southeastern United States will likely become a source of carbon emissions; and (4) the continuation of a prescribed fire regime would minimize fire emissions through time and maintain a stable ecosystem that serves as a global hotspot for biodiversity and species endemism.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2772/full