

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

STEVEN A. FLANAGAN,^{1,†} SMRITI BHOTIKA,^{2,3} CHRISTIE HAWLEY,² GREGORY STARR^{1D},⁴ SUSANNE WIESNER,⁴ J. KEVIN HIERS,¹ JOSEPH J. O'BRIEN,² SCOTT GOODRICK,² MAC A. CALLAHAM JR.,² ROBERT M. SCHELLER,⁵ KIER D. KLEPZIG,⁶ R. SCOTT TAYLOR,⁶ AND E. LOUISE LOUDERMILK²

¹Wildland Fire Science Program, Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, Florida 32312 USA

²Center for Forest Disturbance Science, Southern Research Center, U.S. Forest Service, 320 Green Street, Athens, Georgia 30602 USA

³AAAS, 1200 New York Avenue, NW, Washington, D.C. 20005 USA

⁴Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487 USA

⁵Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina 27695 USA

⁶Joseph W. Jones Ecological Research Center, 3988 Jones Center Dr., Newton, Georgia 39870 USA

Citation: Flanagan, S. A., S. Bhotika, C. Hawley, G. Starr, S. Wiesner, J. K. Hiers, J. J. O'Brien, S. Goodrick, M. A. Callahan Jr., R. M. Scheller, K. D. Klepzig, R. S. Taylor, and E. L. Loudermilk. 2019. Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pineland. *Ecosphere* 10(6):e02772. 10.1002/ecs2.2772

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.

Received 16 April 2019; **accepted** 25 April 2019. Corresponding Editor: David M. Bell.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** sflanagan@talltimbers.org

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 km² (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,

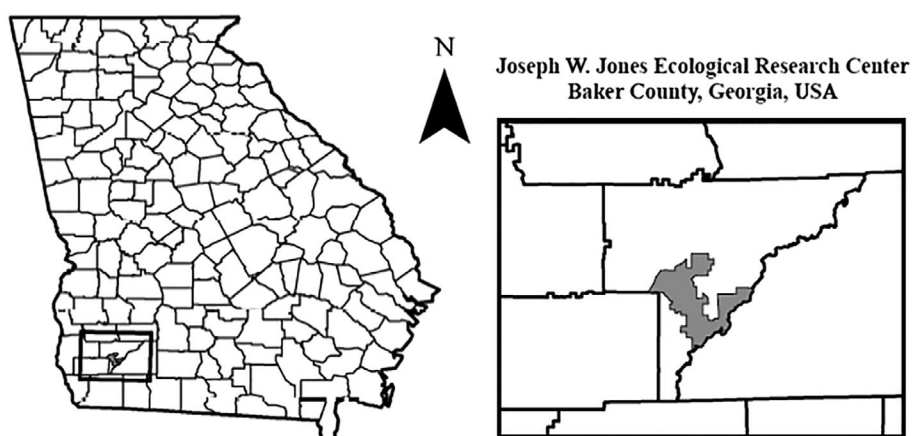


Fig. 1. Map of Georgia and its counties with the location of the Joseph W. Jones Ecological Research Center (JWJERC) at Ichauway highlighted.

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. elliotii*), live oak (*Quercus virginiana*), laurel oak (*Q. laurifolia*), water oak (*Q. nigra*), southern red oak (*Q. falcata*), and post oak (*Q. stellata*; 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. 2011b, 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. 2011a, 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. 2011a) 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 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 mid-story 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 $-15 \text{ gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and $-20 \text{ gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively.

RESULTS

Aboveground biomass

The average AGB ranged from $\sim 35 \text{ Mg/ha}$ with the 20-yr wildfire return to $\sim 250 \text{ Mg/ha}$ 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 ($\sim 190 \text{ Mg/ha}$ vs. $\sim 195 \text{ Mg/ha}$) for sites used in this study. A 50-yr return simulated an average AGB of $\sim 130 \text{ Mg/ha}$. 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).

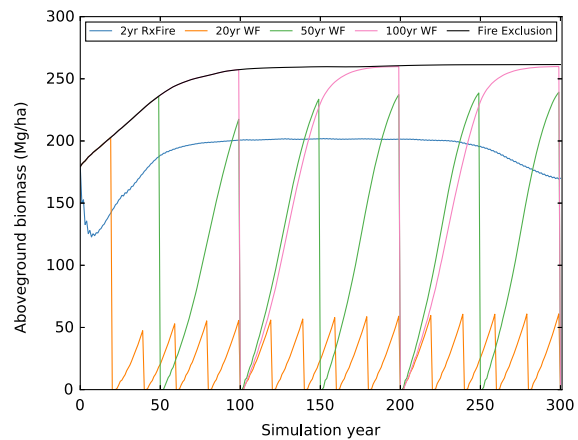


Fig. 2. Model-predicted aboveground biomass with respect to simulation year for the five fire frequency scenarios: prescribed fire (RxFire) every 2 yr, wildfire (WF) at 20-, 50-, and 100-yr return intervals, and fire exclusion.

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

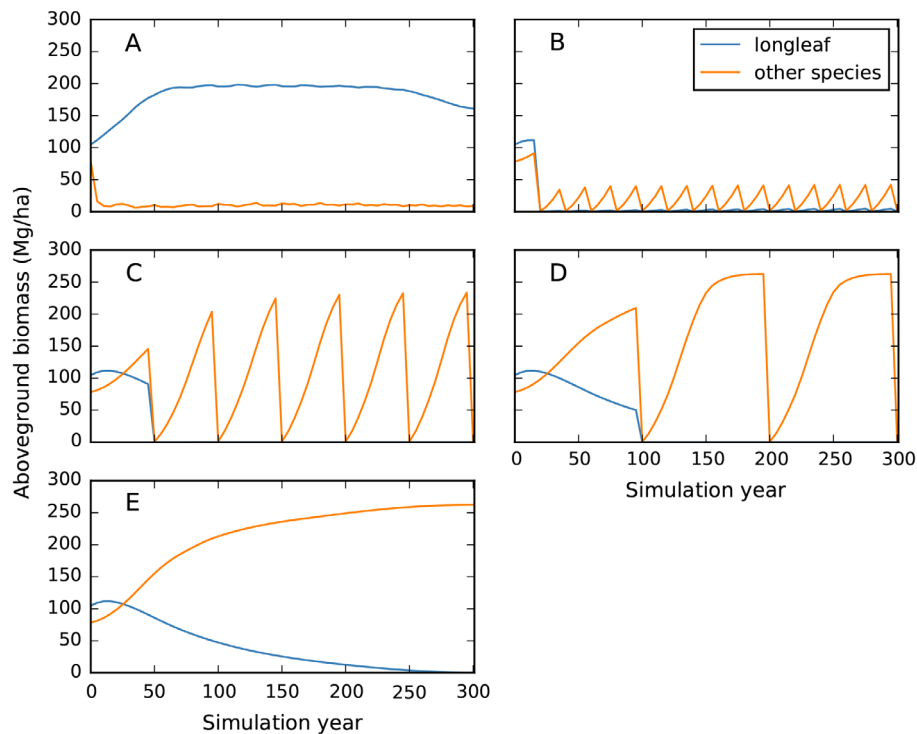


Fig. 3. Longleaf vs. all other species AGB for the five fire scenarios. The prescribed fire regime (A) resulted in a longleaf-dominated forest and stabilized AGB. Wildfire regimes of 20-, 50-, and 100-y (B–D) return intervals caused AGB to fluctuate and dominant species depended on successional response.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

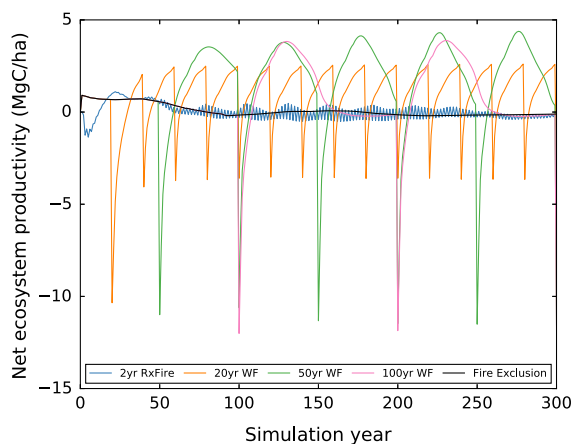


Fig. 4. Yearly model-predicted NEP for each scenario. This does not account for biomass removed through fire to produce NECB.

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

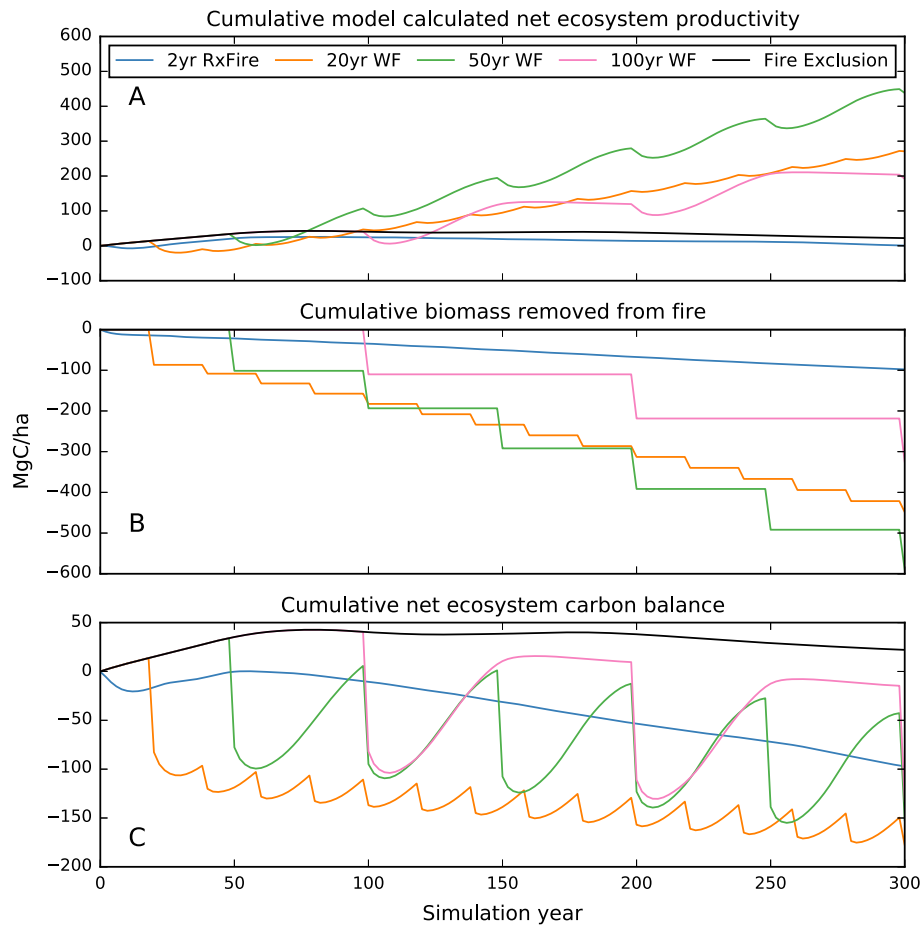


Fig. 5. Cumulative model-predicted NEP (not including carbon biomass removed from fire) (A), cumulative carbon removed from fire (B), and their combination, resulting in cumulative NECB (C) for the five fire frequency scenarios. Carbon is represented as the mean landscape density (Mg C/ha) across the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

ACKNOWLEDGMENTS

This research was funded by the US Department of Defense Environmental Security Technology Certification Program (#RC-201467, 201736) and the Strategic Environmental Research and Development Program (#RC-2243). This work was also supported by the US Department of Agriculture Forest Service National Fire Plan. We acknowledge the US Department of Agriculture Forest Service, Southern Research Station, and the Center for Forest Disturbance Science, Athens, GA, for their support. We thank the Joseph W. Jones Ecological Research Center at Ichauway, Newton, GA, for their support and data needs for this project, with a special thanks to the former Director, Dr. Lindsay Boring.

LITERATURE CITED

- Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drake. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4:164–185.
- Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences* 114:2946–2951.
- Barbero, R., J. T. Abatzoglou, N. K. Larkin, C. A. Kolden, and B. Stocks. 2015. Climate change presents increased potential for very large fires in the contiguous United States. *International Journal of Wildland Fire* 24:892–899.
- Beisner, B., D. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.
- Biederman, L. A., and W. S. Harpole. 2013. Biochar and its effects on plant productivity and nutrient cycling: a meta-analysis. *GCB Bioenergy* 5:202–214.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. *TRENDS in Ecology and Evolution* 20:387–394.
- Botkin, D., J. Jamak, and J. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849–872.
- Bowman, D. M. J. S., et al. 2009. Fire in the earth system. *Science* 324:481–484.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America*. Volume 1 and 2. Agriculture Handbook. U. S. Department of Agriculture, Forest Service, Washington, D. C., USA.
- Butry, D. T., E. D. Mercer, J. P. Prestemon, J. M. Pye, and T. P. Holmes. 2001. What is the price of catastrophic wildfire? *Journal of Forestry* 99: 9–17.
- Canadell, J. G., C. Le Quéré, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America* 104:18866–18870.
- Caspersen, J. P., S. W. Pacala, J. C. Jenkins, G. C. Hurtt, P. R. Moorcroft, and R. A. Birdsey. 2000. Contributions of land-use history to carbon accumulation in U.S. Forests. *Science* 290:1148–1151.
- Christensen, N. L. 2013. History landscape change and ecological. *Journal of Forest History* 33:116–125.
- Dale, V. H., et al. 2011. Climate change and forest disturbances. *BioScience* 51:723–734.
- Dangal, S. R. S., B. S. Felzer, and M. D. Hurteau. 2014. Effects of agriculture and timber harvest on carbon sequestration in the eastern US forests. *Journal of Geophysical Research: Biogeosciences* 119:35–54.
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18–21.
- Dolan, K. A., G. C. Hurtt, S. A. Flanagan, J. P. Fisk, R. Sahajpal, C. Huang, Y. Le Page, R. Dubayah, and J. G. Masek. 2017. Disturbance distance: quantifying forests’ vulnerability to disturbance under current and future conditions. *Environmental Research Letters* 12:114015.
- Emanuel, W. R., H. H. Shugart, and M. P. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7:29–43.
- Flanagan, S., G. Hurtt, J. Fisk, R. Sahajpal, M. Hansen, K. Dolan, J. Sullivan, and M. Zhao. 2016. Potential vegetation and carbon redistribution in northern North America from climate change. *Climate* 4:2.
- Forbes, M. S., R. J. Raison, and J. O. Skjemstad. 2006. Formation, transformation and transport of black carbon (charcoal) in terrestrial and aquatic ecosystems. *Science of the Total Environment* 370:190–206.
- Georgia Automated Environmental Monitoring Network. 2015. GAEMN historical data. Joseph W. Jones Ecological Research Center, Newton, Georgia, USA. <http://www.georgiaweather.net/index.php?content=gp&site=NEWTON>
- Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. *Ecological Monographs* 65:441–476.

- Goebel, P. C., B. J. Palik, L. K. Kirkman, M. B. Drew, L. West, D. C. Pederson, S. Journal, T. Botanical, and N. J. Mar. 2001. Forest ecosystems of a lower gulf coastal plain landscape: multifactor classification and analysis forest ecosystems of a lower gulf coastal plain landscape. *Journal of the Torrey Botanical Society* 128:47–75.
- Goebel, P. C., B. J. Palik, L. K. Kirkman, and L. West. 1998. Field guide: landscape ecosystem types of Ichauway. Technical Report 97-1. Joseph W. Jones Ecological Research Center at Ichauway, Newton, Georgia, USA.
- Goetz, S. J., et al. 2012. Observations and assessment of forest carbon dynamics following disturbance in North America. *Journal of Geophysical Research: Biogeosciences* 117:G02022.
- Gonzalez-Benecke, C. A., L. J. Samuelson, T. A. Martin, W. P. Cropper, K. H. Johnsen, T. A. Stokes, J. R. Butnor, and P. H. Anderson. 2015. Modeling the effects of forest management on in situ and ex situ longleaf pine forest carbon stocks. *Forest Ecology and Management* 355:24–36.
- Gustafson, E. J., S. R. Shifley, D. J. Mladenoff, K. K. Nimerfro, and H. S. He. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 30:32–43.
- Hardin, E. D., and D. L. White. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. *Natural Areas Journal* 9:234–245.
- Hartnett, D. C., and D. M. Krofta. 1989. 55 years of post-fire succession in a southern mixed hardwood forest. *Bulletin of the Torrey Botanical Club* 116:107–113.
- He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest- landscape fire disturbance and succession. *Ecology* 80:81–99.
- Hendricks, J., R. Hendrick, C. Wilson, R. Mitchell, S. Pecot, and D. Gou. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* 94:40–57.
- Hodler, T. W., and H. A. Schretter. 1986. *Atlas of Georgia*. Institute of Community and Area Development, Athens, Georgia, USA.
- Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus, Series B: Chemical and Physical Meteorology* 55:378–390.
- Hurteau, M. D. 2017. Quantifying the carbon balance of forest restoration and wildfire under projected climate in the fire-prone southwestern US. *PLOS ONE* 12:e0169275.
- Hurteau, M. D., and M. L. Brooks. 2011. Short- and long-term effects of fire on carbon in US dry temperate forest systems. *BioScience* 61:139–146.
- Hurteau, M. D., G. W. Koch, and B. A. Hungate. 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. *Frontiers in Ecology and the Environment* 6:493–498.
- Hurteau, M., and M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Frontiers in Ecology and the Environment* 7:409–414.
- Hurt, G. C., S. W. Pacala, P. R. Moorcroft, J. Caspersen, E. Shevliakova, R. A. Houghton, and B. Moore. 2002. Projecting the future of the U.S. carbon sink. *Proceedings of the National Academy of Sciences* 99:1389–1394.
- Jackson, S. T., J. M. Varner, and M. C. Stambaugh. 2018. Biogeography: an interweave of climate, fire, and humans. Pages 17–38 in L. K. Kirkman and S. B. Jack, editors. *Ecological restoration and management of longleaf pine forests*. CRC Press, Boca Raton, Florida, USA.
- Kane, J. M., J. M. Varner, and J. K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impiders. *Forest Ecology and Management* 256:2039–2045.
- Kang, S., J. S. Kimball, and S. W. Running. 2006. Simulating effects of fire disturbance and climate change on boreal forest productivity and evapotranspiration. *Science of the Total Environment* 362:85–102.
- Kirkman, L. K., L. M. Giencke, R. S. Taylor, L. R. Borning, C. L. Staudhammer, and R. J. Mitchell. 2016. Productivity and species richness in longleaf pine woodlands: resource-disturbance influences across an edaphic gradient. *Ecology* 97:2259–2271.
- Kirkman, L. K., P. C. Goebel, B. J. Palik, and L. T. West. 2004. Predicting plant species diversity in a longleaf pine landscape. *Ecoscience* 11:80–93.
- Kirkman, L. K., R. J. Mitchell, R. C. Helton, M. B. Drew, and J. W. Jones. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88:2119–2128.
- Krofcheck, D. J., M. D. Hurteau, R. M. Scheller, and E. L. Loudermilk. 2017. Restoring surface fire stabilizes forest carbon under extreme fire weather in the Sierra Nevada. *Ecosphere* 8:e01663.
- Lashley, M. A., M. Colter Chitwood, A. Prince, M. B. Elfelt, E. L. Kilburg, C. S. Deperno, and C. E. Moorman. 2014. Subtle effects of a managed fire regime: a case study in the longleaf pine ecosystem. *Ecological Indicators* 38:212–217.
- Lavoie, M., G. Starr, M. C. Mack, T. A. Martin, and H. L. Gholz. 2010. Effects of a prescribed fire on

- understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. *Natural Areas Journal* 30:82–92.
- Liu, Y., S. Goodrick, and W. Heilman. 2014. Wildland fire emissions, carbon, and climate: wildfire-climate interactions. *Forest Ecology and Management* 317:80–96.
- Liu, Y., S. L. Goodrick, and J. A. Stanturf. 2013. Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management* 294:120–135.
- Loudermilk, E. L., W. P. Cropper, R. J. Mitchell, and H. Lee. 2011. Longleaf pine (*Pinus palustris*) and hardwood dynamics in a fire-maintained ecosystem: a simulation approach. *Ecological Modelling* 222: 2733–2750.
- Loudermilk, E. L., R. M. Scheller, P. J. Weisberg, and A. Kretchun. 2017. Bending the carbon curve: fire management for carbon resilience under climate change. *Landscape Ecology* 32:1461–1472.
- Loudermilk, E. L., R. M. Scheller, P. J. Weisberg, J. Yang, T. E. Dilts, S. L. Karam, and C. Skinner. 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interactions. *Global Change Biology* 19:3502–3515.
- Loudermilk, E. L., A. Stanton, R. M. Scheller, T. E. Dilts, P. J. Weisberg, C. Skinner, and J. Yang. 2014. Effectiveness of fuel treatments for mitigating wildfire risk and sequestering forest carbon: a case study in the Lake Tahoe Basin. *Forest Ecology and Management* 323:114–125.
- Lucash, M. S., and R. M. Scheller. 2015. LANDIS-II climate library v1.0 user guide. Portland State University, Portland, Oregon, USA.
- Lynch, J. M., A. K. Gholson Jr., and W. W. Baker. 1986. Natural features of Ichauway Plantation, Georgia. The Nature Conservancy, Southeast Regional Office, Chapel Hill, North Carolina, USA.
- Martin, K. L., M. D. Hurteau, B. A. Hungate, G. W. Koch, and M. P. North. 2015. Carbon tradeoffs of restoration and provision of endangered species habitat in a fire-maintained forest. *Ecosystems* 18:76–88.
- Masiello, C. A. 2004. New directions in black carbon organic geochemistry. *Marine Chemistry* 92:201–213.
- McIntyre, K., B. B. McCall, and D. N. Wear. 2018a. The social and economic drivers of the southeastern forest landscape. Pages 39–67 in L. K. Kirkman and S. B. Jack, editors. *Ecological restoration and management of longleaf pine forests*. CRC Press, Boca Raton, Florida, USA.
- McIntyre, R. K., S. B. Jack, and L. K. Kirkman. 2018b. The fire forest of the past and present. Pages 3–17 in L. K. Kirkman and S. B. Jack, editors. *Ecological restoration and management of longleaf pine forests*. CRC Press, Boca Raton, Florida, USA.
- McNab, W., D. Cleland, J. A. Feeouf, J. E. Keys Jr., G. Nowacki, and C. Carpenter. 2007. Description of ecological subregions: sections of the conterminous United States. Report WO-76B. United States Department of Agriculture, Forest Service, Washington, D. C., USA.
- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826.
- Mitchell, R. J., J. K. Hiers, J. O'Brien, and G. Starr. 2009. Ecological forestry in the southeast: understanding the ecology of fuels. *Journal of Forestry* 107:391–397.
- Mitchell, R. J., L. K. Kirkman, S. D. Pecot, C. A. Wilson, B. J. Palik, and L. R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine – wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research* 29:743–751.
- Mitchell, R. J., Y. Liu, J. J. O'Brien, K. J. Elliott, G. Starr, C. F. Miniati, J. K. Hiers, and J. W. Jones. 2014. Future climate and fire interactions in the southeastern region of the United States. *Forest Ecology and Management* 327:316–326.
- Morgan Varner, J., F. E. Putz, J. J. O'Brien, J. Kevin Hiers, R. J. Mitchell, and D. R. Gordon. 2009. Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management* 258:2467–2474.
- North, M., B. M. Collins, and S. Stephens. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *Journal of Forestry* 110:392–401.
- O'Brien, J. J., J. K. Hiers, R. J. Mitchell, J. M. Varner III, and K. Mordecai. 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *Fire Ecology* 6:1–12.
- Ottmar, R. D., A. T. Hudak, S. J. Prichard, C. S. Wright, J. C. Restaino, M. C. Kennedy, and R. E. Vihnanek. 2016. Pre-fire and post-fire surface fuel and cover measurements collected in the south-eastern United States for model evaluation and development – RxCADRE 2008, 2011 and 2012. *International Journal of Wildland Fire* 25:10–24.
- Outcalt, K. W., and D. D. Wade. 2004. Fuels management reduces tree mortality from wildfires in southeastern United States. *Southern Journal of Applied Forestry* 28:28–34.
- Pan, Y., et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.

- Pastor, J., and W. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2:3–27.
- Prentice, K. C., and I. Y. Fung. 1990. The sensitivity of terrestrial carbon storage to climate change. *Nature* 346:48–51.
- Prestemon, J. P., U. Shankar, A. Xiu, K. Talgo, D. Yang, E. Dixon, D. Mckenzie, and K. L. Abt. 2016. Projecting wildfire area burned in the south-eastern United States. *International Journal of Wildland Fire* 25:715–729.
- Provencher, L., B. J. Herring, D. R. Gordon, H. L. Rodgers, K. E. M. Galley, G. W. Tanner, J. L. Hardesty, and L. A. Brennan. 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. *Restoration Ecology* 9:13–27.
- Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. *Ecology* 70:60–70.
- Regelbrugge, J. C., and D. W. Smith. 1994. Postfire tree mortality in relation to wildfire severity in mixed oak forests in the blue ridge of Virginia. *Northern Journal of Applied Forestry* 11:90–97.
- Reinhardt, E. D., R. E. Keane, and J. K. Brown. 1997. First Order Fire Effects Model: FOFEM 4.0, User's Guide.
- Ryan, K., and W. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* laws. *International Journal of Wildland Fire* 1:107–118.
- Samuelson, L. J., T. A. Stokes, J. R. Butnor, J. H. Johnson, C. A. Gonzalez-Benecke, P. Anderson, J. Jackson, L. Ferrari, T. A. Martin, and W. P. Cropper Jr. 2014. Ecosystem carbon stocks in *Pinus palustris* forests. *Canadian Journal of Forest Research* 44:476–486.
- Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201:409–419.
- Scheller, R. M., D. Hua, P. V. Bolstad, R. A. Birdsey, and D. J. Mladenoff. 2011a. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling* 222:144–153.
- Scheller, R. M., S. Van Tuyl, K. L. Clark, J. Hom, and I. La Puma. 2011b. Carbon sequestration in the New Jersey pine barrens under different scenarios of fire management. *Ecosystems* 14:987–1004.
- Scheller, R. M., A. M. Kretchun, S. V. Tuyl, K. L. Clark, M. S. Lucash, and J. Hom. 2012. Divergent carbon dynamics under climate change in forests with diverse soils, tree species, and land use histories. *Ecosphere* 3:art110.
- Schoennagel, T., et al. 2017. Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences of the United States of America* 114:4582–4590.
- Singh, N., S. Abiven, M. S. Torn, and M. W. I. Schmidt. 2012. Fire-derived organic carbon in soil turns over on a centennial scale. *Biogeosciences* 9:2847–2857.
- Slack, A. W., N. E. Zeibig-Kichas, J. M. Kane, and J. M. Varner. 2016. Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. *Forest Ecology and Management* 364:130–138.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database. Available online at <https://sdmdataaccess.sc.egov.usda.gov>
- Starr, G., C. L. Staudhammer, H. W. Loescher, R. Mitchell, A. Whelan, J. K. Hiers, and J. J. O'Brien. 2015. Time series analysis of forest carbon dynamics: recovery of *Pinus palustris* physiology following a prescribed fire. *New Forests* 46:63–90.
- Sturtevant, B. R., E. J. Gustafson, W. Li, and H. S. He. 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. *Ecological Modelling* 180:153–174.
- Sturtevant, B. R., R. M. Scheller, B. R. Miranda, D. Shinneman, and A. Syphard. 2009. Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. *Ecological Modelling* 220:3380–3393.
- Sutherland, E. K., B. J. Hale, and D. M. Hix. 2000. Defining species guilds in the Central Hardwood Forest, USA. *Plant Ecology* 147:1–19.
- Swanteson-Franz, R. J., D. J. Krofcheck, and M. D. Hurteau. 2018. Quantifying forest carbon dynamics as a function of tree species composition and management under projected climate. *Ecosphere* 9:e02191.
- Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21:626–634.
- Syphard, A. D., R. M. Scheller, B. C. Ward, W. D. Spencer, and J. R. Strittholt. 2011. Simulating landscape-scale effects of fuels treatments in the Sierra Nevada, California, USA. *International Journal of Wildland Fire* 20:364–383.
- Varner, J. M., D. R. Gordon, F. E. Putz, and J. Kevin Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and

- consequences for long-unburned ecosystems. *Restoration Ecology* 13:536–544.
- Varner, J. M., J. K. Hiers, R. D. Ottmar, D. R. Gordon, F. E. Putz, and D. D. Wade. 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. *Canadian Journal of Forest Research* 37:1349–1358.
- Varner, J. M., F. E. Putz, J. J. O'Brien, J. K. Hiers, R. J. Mitchell, and D. R. Gordon. 2009. Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management* 258:2467–2474.
- Veldman, J. W., et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13:154–162.
- Wahlenberg, W. G. 1946. Longleaf Pine: its use, ecology, regeneration, protection, growth, and management. *Quarterly Review of Biology* 22:73–74.
- Walker, J. 1993. Rare vascular plant taxa associated with the longleaf pine ecosystems: patterns in taxonomy and ecology. *Proceedings of the Tall Timbers Fire Ecology Conference* 18:105–125.
- Walker, H. J., and J. M. Coleman. 1987. Atlantic and Gulf Coastal province. Pages 51–110 in W. L. Graf, editor. *Geomorphic systems of North America*. Spec. Vol. No. 2. Geological Society of America, Boulder, Colorado, USA.
- Wear, D. N., and J. G. Greis. 2013. The southern forest futures project: technical report. Gen. Tech. Rep. SRS-GTR-178. USDA-Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Whelan, A., R. Mitchell, C. Staudhammer, and G. Starr. 2013. Cyclic occurrence of fire and its role in carbon dynamics along an edaphic moisture gradient in longleaf pine ecosystems. *PLOS ONE* 8:e54045.
- Wiedinmyer, C., and M. D. Hurteau. 2010. Prescribed fire as a means of reducing forest carbon emissions in the western United States. *Environmental Science and Technology* 44:1926–1932.
- Wilson, C. A., R. J. Mitchell, J. J. Hendricks, and L. R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine — wiregrass savannas. II. Nitrogen dynamics. *Canadian Journal of Forest Research* 29:752–760.
- Wimberly, M. C. 2004. Fire and forest landscapes in the Georgia Piedmont: an assessment of spatial modeling assumptions. *Ecological Modelling* 180:41–56.
- Xiao, J., Y. Liang, H. S. He, J. R. Thompson, W. J. Wang, J. S. Fraser, and Z. Wu. 2017. The formulations of site-scale processes affect landscape-scale forest change predictions: a comparison between LANDIS PRO and LANDIS-II forest landscape models. *Landscape Ecology* 32:1347–1363.
- Xu, C., G. Z. Gertner, and R. M. Scheller. 2009. Uncertainties in the response of a forest landscape to global climatic change. *Global Change Biology* 15:116–131.
- Xu, C., G. Z. Gertner, R. M. Scheller, C. Xu, G. Z. Gertner, and R. M. Scheller. 2012. Importance of colonization and competition in forest landscape response to global climatic change. *Climatic Change* 110:53–83.

SUPPORTING INFORMATION

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