

The effects of management on long-term carbon stability in a southeastern U.S. forest matrix under extreme fire weather

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Abstract. How fire interacts with an ecosystem is driven by forest structure, fuel bed heterogeneity, topography, and weather. The juxtaposition of two distinct vegetation types with divergent properties can further influence the effects of fire on an ecosystem. In the southeastern United States, pine flatwoods and hardwood–cypress swamps are distinct ecosystems that can be geographically intermixed as a function of elevation, affecting how fires move across the landscape. We sought to understand the consequence of extreme fire weather on landscape wildfire severity and biomass accumulation taking into consideration the spatial configuration of the two ecosystems and fuels reduction management strategies. We used a spatially explicit growth and succession model at the landscape scale to simulate a suite of management activities employed at the Osceola National Forest (Florida, USA), which are aimed at mitigating severe wildfire, maintaining ecosystem function, and producing wood fiber. We found that with extreme fire weather, hardwood–cypress swamps were more available to burn because of drier and hotter conditions, increasing the risk of high-severity fire in the adjacent pine flatwoods. This reduced landscape aboveground biomass stability relative to contemporary fire weather, with an end-of-simulation range from 59.2 to 69.2 Mg C/ha. When we incorporated targeted mechanical thinning and prescribed burning into the simulations under extreme fire weather, the landscape showed higher aboveground biomass stability, with an end-of-simulation range of 70.9–72.8 Mg C/ha. We found that targeting mechanical thinning treatments to the interface of the hardwood–cypress swamps and maintaining the pine flatwoods with prescribed burning constrained the spread of high-severity wildfire at the landscape scale. These results highlight the importance of understanding how changes to fire weather severity may alter fire regimes and consequently carbon stability of these highly interspersed yet functionally dissimilar ecosystems.

Key words: extreme fire weather; fuels management; hardwood–cypress swamps; pine flatwoods; treatment placement; wildfire.

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INTRODUCTION

Forests provide a suite of ecosystem services, including climate regulation through the uptake of carbon (C) from the atmosphere, the provision of which can be impacted by disturbances such

as fire. Ongoing climatic change is increasing the frequency of extreme weather events, including those that can alter fire behavior and drive increases in area burned (Differbaugh et al. 2005, Collins 2014, Terando et al. 2016). Forest management has the potential to alter the

influence of changing climate and disturbance regimes on forest C dynamics (Dangal et al. 2014, Swanteson-Franz et al. 2018), but effectively allocating different management strategies across the landscape requires an understanding of how they will modify the influence of disturbance events (Krofcheck et al. 2018).

The juxtaposition of one vegetation type with another can alter disturbance regimes through controls on microclimate, fuel accumulation, or fire spread between these vegetation types. For example, in the sky islands of the southwestern United States, fire can move from drier, low elevation forests into mesic, high elevation forests, resulting in higher elevation forests in these systems experiencing more frequent fire than might occur in a different topographic setting (O'Connor et al. 2014). Similarly, propagation of wildfires in lowland grass savannas drives upslope impacts to mesic forests types in Hawaii (Cordell et al. 2016).

This juxtaposition is also true in the southeastern United States, where slight topographic variability (2–5 m change in elevation) often results in a patchwork of pine flatwoods, hardwood–cypress swamps, and others (Kirkman et al. 1999) all governed by fire. Much of the pine flatwoods (Abrahamson and Hartnett 1990) was historically dominated by longleaf pine (*Pinus palustris*) that experienced frequent surface fires on the order of once every 1–5 yr and can be intermixed with slash pine (*Pinus elliottii*) flatwoods on hydric soils (Glitzenstein et al. 1995, Stambaugh et al. 2011, White and Harley 2016). Hardwood–cypress swamps (Ewel 1990) burn far less frequently because of the high-water table, variable hydroperiods, and high fuel moisture characteristics that limit the frequency with which ignitions lead to fires (Kirkman et al. 2000). When they do burn however, fire effects in these hardwood–cypress swamp systems tend to be more severe than in the neighboring pine forests (Kirkman et al. 2000, Martin and Kirkman 2009).

The fire regime in longleaf pine ecosystems is well documented in terms of historic frequency (Frost 2007, Stambaugh et al. 2011, Rother et al. 2018), fire behavior (O'Brien et al. 2016), effects on biodiversity (Kirkman et al. 2004, 2013), and productivity (Mitchell et al. 1999, Wright et al. 2013, Powell et al. 2008). Frequent prescribed burning is the most important management tool

for maintaining form and function in these ecosystems. These fires are typically low intensity, surface fires that spread through pine litter, grasses, forbs, and shrubs (Hiers et al. 2009, Mitchell et al. 2009) and are critical to maintain one of the most diverse understory plant communities in the world (Walker and Peet 1984, Sorrie and Weakley 2001, Kirkman et al. 2004). Wildfires on the other hand occur less frequently and with lower intensity in a well-managed longleaf pine forest (Outcalt and Wade 2004, Addington et al. 2015).

Within the soil gradient of longleaf pine, pine flatwoods are the most mesic and most productive in terms of biodiversity, growth rates, and fuel accumulation (Abrahamson and Hartnett 1990, Kirkman et al. 2001). This level of productivity allows for the highest fire frequency of any longleaf pine habitat, with the fire return interval as short as 1 yr, and the potential for high wildfire severity when prescribed fire is removed for even short periods (<10 yr). Hardwood–cypress swamp ecosystems in the southeast represent a hotspot of diversity (Sharitz 2003, Martin and Kirkman 2009), but with highly variable fire regimes. In the modern landscape, accumulations of organic soils and resulting fire behavior in hardwood–cypress swamp fuels often restrict the burn window to milder conditions particularly when water levels are high (Wendel et al. 1962, Frandsen 1997). During drought conditions, they typically sustain fire through smoldering combustion of the deep (now dry) organic layer, exacerbating fire behavior and severity. Smoldering fuels challenge restoration efforts of wetland fire regimes through prescribed fire (Reardon et al. 2007, Watts and Kobziar 2013). Furthermore, the conditions that preclude prescribed fire in these systems are the same that predispose hardwood–cypress swamps to large, high-severity fire. Consumption of the organic peats and soils characteristic of these wetland systems can result in substantive C loss in these otherwise rather recalcitrant soils (Watts 2013), notwithstanding the potential for high overstory mortality.

Landscapes that contain this mosaic of pine flatwoods and embedded hardwood–cypress swamps produce the most extreme fire behavior potential in the eastern United States (Hough and Albin 1978, Wade et al. 1989), including

large wildfires (e.g., West Mims 2017, 61,900 ha; Honey Prairie 2011, 166,300 ha; Georgia-Florida Bay Complex 2007, 239,000 ha; Impassable Bay Fire 2004, 17,400 ha). When the hardwood–cypress swamps are available to burn, and fire propagates into the pine flatwoods with an understory dominated by saw palmetto and gallberry (*Ilex glabra* (L.) Gray) shrubs, the rate of spread is typically high and flame lengths are moderate (Scott and Burgan 2005). These variations in fuel types are among the most widespread and dynamic wildland fire fuel types in North America (Wade et al. 1989) and create unique patterns of burn severity within and between vegetation types (Malone et al. 2011).

Increases in weather events that result in extreme fire behavior and the concurrent increased flammability of the wetland forests pose economic risks, and rapid increases in the wildland urban interface (Radeloff et al. 2018) create significant societal risk. Nearly 5.2 million ha of pine plantations (Wear and Greis 2002) are responsible for roughly 82% of all softwood, pulpwood, and roundwood production in the United States. In 2013, 78% of all U.S. pulpwood was grown in southern forests (Howard and Jones 2016), characterized by predominantly longleaf and loblolly pine stands intermixed with patches of wetland forest. Climate-driven increases in wetland forest flammability could facilitate the propagation of severe fire events through southeastern U.S. pine production forests.

We sought to quantify how landscape carbon dynamics would respond to both contemporary and extreme fire weather conditions and the potential mitigating effects of management. Further, we considered the potential of both weather and management to cause shifts in fire frequency, severity, and propagation into and out of the pine flatwoods and hardwood–cypress swamp mosaic of the Osceola National Forest (ONF) in north-central Florida, USA. We designed a simulation experiment using the LANDIS-II model to quantify the aboveground biomass and wildfire severity dynamics of a suite of management activities aimed at mitigating severe wildfire, maintaining ecosystem function, and facilitating wood fiber production, all in the context of more frequent extreme fire weather events. We hypothesized that (1) 90th percentile and greater

fire weather conditions would reduce the stability of forest C stocks because an increased proportion of the landscape would experience severe fire; (2) optimized placement of treatments to reduce fire severity would stabilize forest C stocks by mitigating the high-severity wildfire risk associated with the juxtaposition of wetland forests and upland pine forests; and (3) additional low-volume harvest for wood fiber production would result in little additional increase in C stability over the treatments targeted at reducing high-severity fire and would further reduce forest C stocks.

METHODS

We used landscape scale simulations to investigate the relationship between vegetation growth and succession, fuels management, and wildfire severity across a roughly 90,000-ha region encompassing the ONF in north Florida (Fig. 1), that is part of a Collaborative Forest Landscape Restoration Project (CFLRP, Schultz et al. 2012). With a mean elevation of approximately 40 m, the ONF is composed of a mixture of low-lying wetland forests and upland pine flatwood forests, with little topographic relief (<10 m) separating the two forest types. This strong dichotomy of drier upland sites and predominantly saturated wetland sites creates discrete edaphic heterogeneity throughout the landscape that dictates the aboveground vegetation structure and influences fire regimes (Wade et al. 1980).

The ONF is a flatwoods forest type dominated by a mosaic of natural stands of slash (*P. Elliottii* Engelm.) and longleaf pine (*P. palustris* Mill.), mixed with slash pine plantations. Embedded throughout the area are wet depressional wetlands dominated by hardwood-pond cypress (*Taxodium distichum* var. *nutans* [Ait] Sweet), swamp blackgum (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.), and loblolly bay (*Gordonia lasianthus* [L.] Ellis) (Outcalt and Wade 2004). Hardwood–cypress swamps are primarily a dense mixture of *Liquidambar styraciflua*, *Magnolia virginiana*, *Gordonia lasianthus*, *Acer rubrum*, *N. sylvatica* var. *biflora*, *T. distichum*, and *Taxodium ascendens*. A complete list of vegetative characteristics can be found in Glitzenstein et al. (2003).

The ONF has been managed with periodic prescribed burning for the previous 40 yr, using

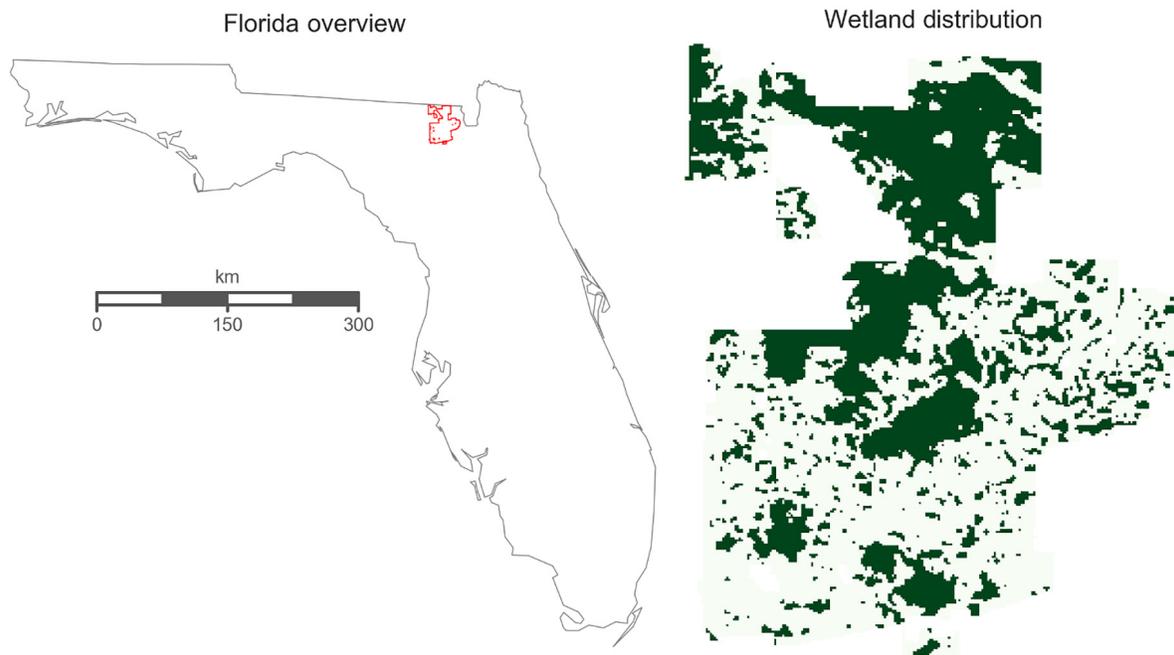


Fig. 1. Study area showing the Osceola National Forest in northeastern Florida. The distribution of hardwood–cypress swamps (dark green) and pine flatwoods (mint) that make up the forest is shown on the right.

predominantly dormant season burns with occasional growing season burning during the most recent 20 yr (Outcalt and Wade 2004). The pine flatwoods have a history of wood harvest in both naturally regenerated stands and pine plantations. The hardwood–cypress swamps experience infrequent fire that is correlated with drought and a decrease in the water table. Soil moisture plays a significant role in the probability that organic soils in hardwood–cypress swamps ignite (Frandsen 1997) and drought makes these systems more available to burn.

Model description and parameterization

We used LANDIS-II (v6.2), a spatially explicit and cohort-based succession and disturbance model (Scheller et al. 2007) that allows for species and age-specific interactions resulting from wildfire, prescribed fire, and succession. We simulated carbon dynamics using the Net Ecosystem Carbon and Nitrogen (NECN) extension (v4.0), which is based on the CENTURY model and simulates above and belowground pools and fluxes of carbon and nitrogen (Parton et al. 1993, Scheller et al. 2011). We used the Dynamic Fuels and Fire extension (v2.1) to simulate wildfire and fuels

interactions (Sturtevant et al. 2009) and the Biomass Harvest extension (v3.0) to simulate management and harvesting (Gustafson et al. 2000). We modeled the landscape on a 150-m grid, resulting in 40,780 actively simulated 2.25-ha pixels.

Net Ecosystem Carbon and Nitrogen, the Dynamic Fuels and Fire, and Biomass Harvest extensions each require the creation of distinct thematic raster inputs to simplify calculations across the landscape. LANDIS-II requires the delineation of climatically and edaphically distinct zones referred to by the model as ecoregions (hereafter referred to as model regions), each of which are assigned soil characteristics and climate drivers to govern vegetation growth and succession. Given the lack of topographic variability across the Osceola, we let the edaphic variability govern model region delineation. We used a geospatial layer of wetland areas (Provided by the USFS Osceola National Forest) to delineate the wetland model regions and allocated the remainder of the vegetated landscape to upland model regions. We then used a method similar to Krofcheck et al. (2017) to assign the soil characteristics to each model region using GSSURGO data (<https://gdg.sc.egov.usda.gov/>).

The Dynamic Fuels and Fire extension assigns a fuels class to each grid cell based on the species, age, and total biomass present, at every time step. We parameterized the different fuels classifications based on overstory vegetation and the influence of management and fire on the distribution of biomass. This creates an explicit link between disturbance, management, and fuels characterization in the model. During each time step, fire ignitions are attempted across the landscape in a stochastic manner, and the occurrence of a fire is a function of the fuel conditions at the ignition location and a draw from the fire weather distribution. The maximum potential fire size is determined by a draw from the fire size distribution, and the simulated fire size is a function of weather and fuels conditions in adjacent grid cells (Sturtevant et al. 2009). The Dynamic Fire model requires the creation of fire regions, which allow area specific parameterization of fire size distributions, number of ignitions, fire probability, and seasonal variability in surface fuel moisture content. We defined the fire regions using the same edaphic characteristics that defined the model regions. We used 17 yr of wildfire data recorded by the ONF to parameterize the fire size distribution and number of fires per year following Krofcheck et al. (2017). The mean and variance of wildfire size were used to generate a lognormal distribution, and the distribution was consistent across fire regions. Our parameterization of the landscape did not include the road network that is present on the ONF and roads can limit fire spread. However, the influence of roads on fire size is implicit in the empirical fire size data. When wildfire occurs, the model determines the fire severity as a function of the effects on the tree cohorts within a grid cell. The severity classification system ranges from 1 to 5, with class 1 and 2 being surface fire, class 3 being primarily surface fire with some torching, class 4 has increased overstory mortality, and class 5 is complete overstory mortality. Overstory mortality is governed by the fraction of the crown that is killed by the fire.

The Biomass Harvest extension requires that the landscape be divided into management units to simulate the spatial and temporal distribution of management activities. We divided the landscape based on wetland and upland model regions and a third class that included upland

forest within 300 m of wetland locations. This allowed us to simulate management activities targeted at modifying wildfire behavior when burning from wetland to upland forest.

Generation of initial communities

LANDIS-II requires an initial community layer that is comprised of age cohorts of species for each grid cell on the landscape. We used USFS Forest Inventory Analysis (FIA) data stratified by upland and wetland forest model regions to create species and age distributions for the landscape. We then used spatial data of stand age and recent harvests provided by the ONF to inform the stand ages for each grid cell. The species assignment for each upland grid cell was then a probabilistic function of stand age, and the species abundance described by the FIA plots. The resulting upland forest demographics were constrained to capture past management activities that resulted in primarily single- or two-aged stands. The wetland forest model region cells were populated entirely using FIA data and time since disturbance. As a result, the initial communities layer reflected the distribution of species and biomass represented in the FIA data. The presence of slash pine plantations was not well represented in the FIA data, and we did not artificially impose slash pine plantations on the initial communities layer because the ONF planning effort is focused on uneven-aged, fire-maintained structure in the pine flatwoods.

Climate inputs

We drove vegetation dynamics with historical Daymet daily surface weather over a 1-km grid for the period 1980–2015, acquired via the USGS Geo Data Portal (<http://cida.usgs.gov/gdp/>; Thornton et al. 2012). We computed weighted area grid statistics for the Osceola using the export service in the data portal. The NECN extension then converted these data to monthly means. At each annual time-step, the model randomly drew from the entire distribution to provide monthly climate data for simulating vegetation growth and reproduction. We chose to use the same climate inputs for both model regions, given their similar elevations and relatively small spatial extent. The Dynamic Fire and Fuels extension requires a separate weather input to drive fuels and fire behavior. We used local

RAWS stations to produce distributions of temperature, relative humidity, and precipitation from which we built the required fire weather inputs for the simulation (Krofcheck et al. 2017). We generated two distributions of fire weather: contemporary and extreme. We used the entire 15 yr of RAWS data for the contemporary fire weather inputs. We used the 90th percentile subset of that data to produce the extreme fire weather inputs (Fig. 2).

Model scenario description

We developed three management scenarios: no-management, targeted, and targeted with harvest. The scenarios were based on discussions with ONF managers about the objectives for the CFLRP planning process. The targeted scenario involved thinning approximately 10% of the biomass, followed by prescribed burning within the 300 m buffers surrounding hardwood–cypress swamps. The remaining pine flatwoods were treated with prescribed fire using a 5-yr return interval. Thinning and the initial prescribed fire were completed in the buffer areas within the first ten years. The targeted with harvest scenario included the same prescription as the targeted scenario, plus the addition of harvesting 50% of the biomass of cohorts 30 yr and older in the pine flatwoods. The harvest prescription was applied at a rate of 2% of the pine flatwood area per year. No-management prescriptions were applied to the hardwood–cypress swamps. Treatment

implementation rates are presented in Table 1. We ran simulations across the Osceola of each of these management prescriptions with wildfire events driven by either contemporary or extreme fire weather inputs, resulting in six model scenarios.

We ran 30 replicate 100-yr simulations for each of the six model scenarios, using the stochastic nature of vegetation growth and succession, wildfire ignition and propagation, and treatment interactions to investigate the range of carbon and fire severity outcomes for each scenario. We quantified aboveground carbon (AGC, Mg C/ha) both spatially and temporally, including changes in AGC resulting from management and

Table 1. Management prescriptions used in the scenarios where fuels reduction and biomass harvest were applied.

Prescription	Targeted		Targeted with harvest	
	Wetland forest buffer	Upland forest	Wetland forest buffer	Upland forest
Prescribed fire (ha/yr)	6094.6	4831.6	6094.6	4831.6
Thinning (ha/yr)	6094.6	–	6094.6	–
Harvest (ha/yr)	–	–	–	483.16

Notes: All thinning treatments were conducted over a 5-yr period, and not repeated for the duration of the simulations. Prescribed fire rates resulted in a 5-yr return interval across the treated areas. Hardwood–cypress swamps were not treated. En dash indicates that no thinning or harvest occurred in that forest type.

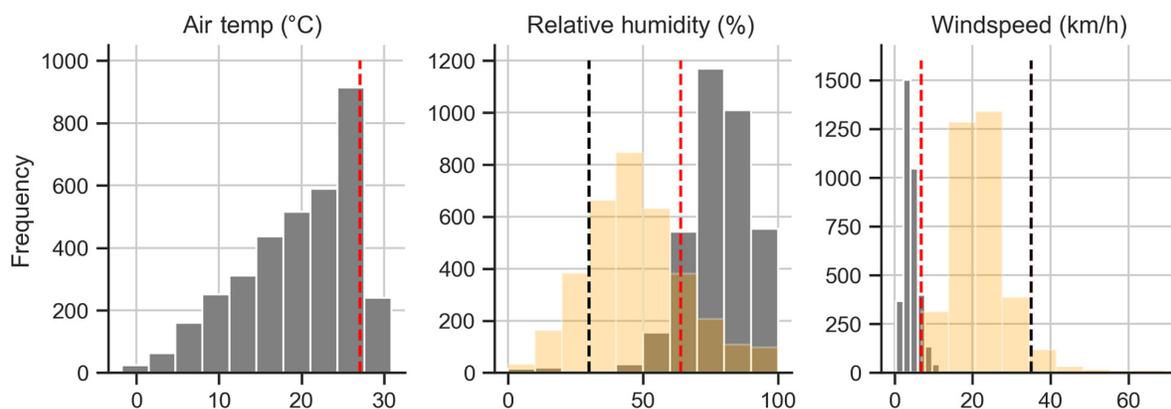


Fig. 2. Contemporary (gray) and extreme (orange) fire weather distributions used to drive wildfire in the model simulations. The 90th percentile of the contemporary data (red line) is shown along with the measured conditions during a notable high-severity wildfire that took place on March 24, 1956 (black line, the Impassible Bay fire). Temperature data for the Impassible Bay fire were unavailable.

wildfire. We also quantified the influence of management activities on wildfire severity spatially. We used the Kolmogorov–Simonov test for comparing distributions and used analysis of variance and Tukey’s honestly significant difference for mean separation following Bartlett’s test for homoscedasticity. For comparisons where data were heteroscedastic, we employed Kruskal–Wallis tests with post hoc Dunn’s comparisons. We used a threshold of $P < 0.01$ to determine statistically significant difference. We conducted all model parameterization and output analyses, as well as figure generation using Python (Python Software Foundation, version 2.7. <http://www.python.org>).

RESULTS

Under contemporary fire weather conditions, we found no significant differences in mean wildfire severity between both treatment scenarios and the no-management scenario (Fig. 3a, c, e). Additionally, there were no significant differences in either wildfire severity or variance in wildfire severity between the targeted and targeted with harvest scenarios. However, the mean annual cumulative area burned from wildfire decreased with treatment when compared to no-management under both contemporary and extreme fire weather (Fig. 4), and the largest wildfires were less frequent in all treatment scenarios when compared to no-management under extreme fire weather.

While extreme fire weather conditions significantly increased landscape scale mean wildfire severity in all scenarios ($P < 0.001$, Fig. 3), treatment reduced mean fire severity significantly (targeted scenario reduced mean fire severity by 21.7%, $P < 0.001$, and targeted with harvest reduced mean fire severity by 18.4% $P < 0.001$). The variance of mean wildfire severity was significantly reduced by both the targeted ($P < 0.001$, 38% reduction) and targeted with harvest ($P < 0.001$, 34% reduction) scenarios, relative to no-management.

Spatially, the reduction in mean fire severity under extreme fire weather was largest in the pine flatwoods where wildfires intersected mechanical thinning and prescribed fire treatments (Fig. 5). A reduction in mean wildfire size in the flatwoods due to treatment resulted in

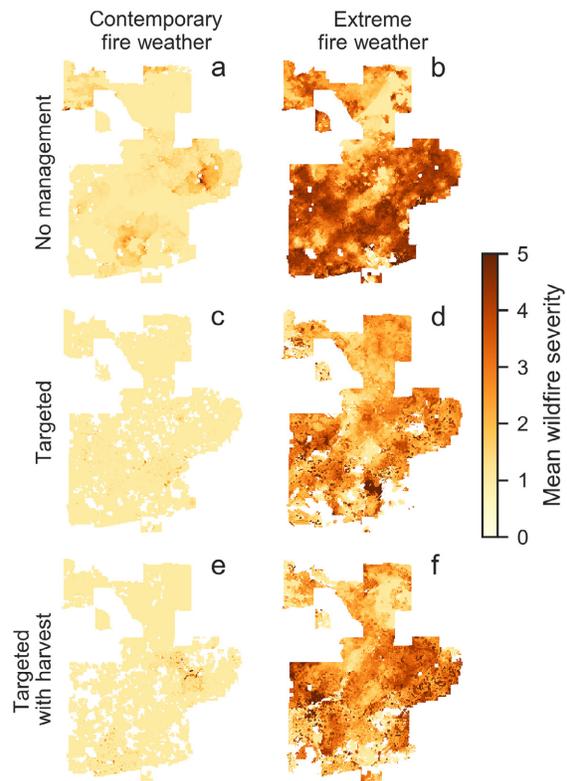


Fig. 3. Mean wildfire severity for both contemporary fire weather (left column) and extreme fire weather (right column) simulations. No-management (a, b), targeted (c, d), and targeted with harvest (e, f) are shown from top to bottom.

fewer fires ignited in pine flatwoods spreading into hardwood–cypress swamps. Consequently, the hardwood–cypress swamps experienced less frequent fire, yet had an increase in mean fire severity relative to no-management, driven by increased fuel accumulation.

Aboveground carbon dynamics showed little difference across all scenarios under contemporary fire weather (Fig. 6a, c, e). Carbon accumulation at the end of simulation under no-management had a range of 67.1–69.7 Mg C/ha, with a mean AGC of 68.8 Mg C/ha. The targeted scenario AGC ranged from 71.0 to 72.8 Mg C/ha, with a mean of 72.0 Mg C/ha, and the targeted with harvest scenario ranged from 70.7 to 73.0 Mg C/ha with a mean of 72.0 Mg C/ha.

Under extreme fire weather, treatment scenarios had higher means and smaller ranges of AGC accumulation than no-management (Fig. 6b, d,

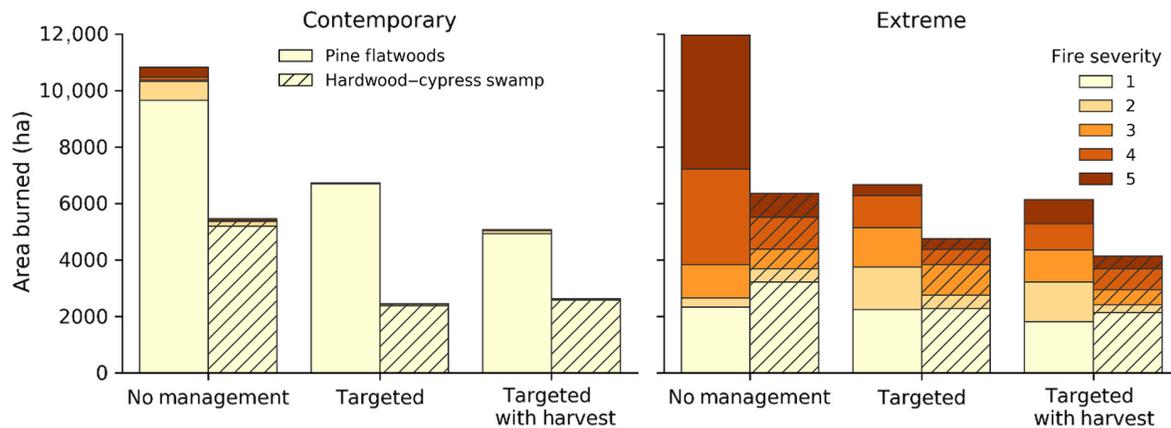


Fig. 4. Mean area burned over the 100 yr of simulation, binned by fire severity. Fire severity ranges from low (1) to high (5) for both pine flatwoods (no hashes) and hardwood–cypress swamps (hashes) under both contemporary (left) and extreme (right) fire weather.

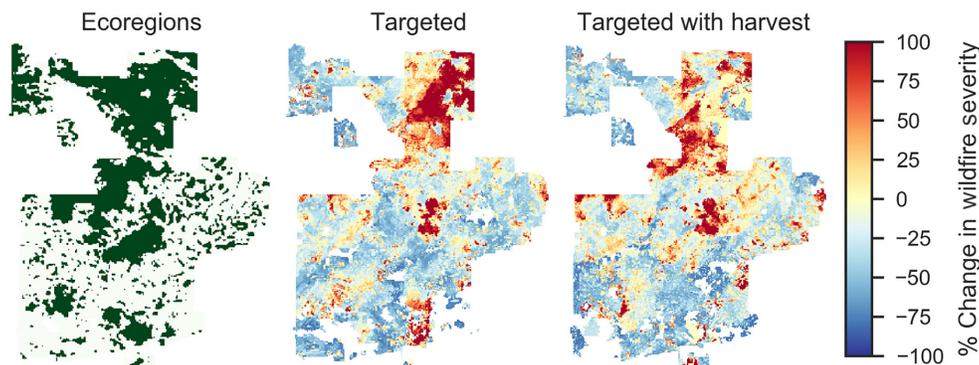


Fig. 5. Percent change in mean wildfire severity between no-management and treatment scenarios under extreme fire weather conditions. Negative values indicate that fire severity was lower relative to the no-management scenario, whereas positive values indicate that fire severity was higher relative to the no-management scenario. Distribution of hardwood–cypress swamps (dark green) and pine flatwoods (mint) are shown for context.

f). While maximum AGC did not vary between scenarios, large and severe wildfires early in the no-management scenario decreased the mean and minimum of AGC compared to the treatment scenarios. No-management ranged from 59.2 to 69.2 Mg C/ha with a mean of 66.3 Mg C/ha, targeted ranged from 70.9 to 72.8 Mg C/ha with a mean of 71.9 Mg C/ha, and the targeted with harvest scenario ranged from 70.7 to 72.9 with a mean of 71.9 Mg C/ha.

These ecosystem differences in AGC were largely driven by changes in biomass accumulation in the upland forests, with both treatment scenarios showing significant increases in biomass accumulation on the scale of the landscape

relative to the no-management scenario (targeted: 6.0% mean increase; targeted with harvest: 7.3% mean increase, $P < 0.001$ in both cases). Despite the increases in wetland area mean wildfire severity with treatment (Figs. 4, 5), those regions showed little change in biomass accumulation (Fig. 7). The regions of the largest increase in biomass accumulation bordered or had close proximity to wetland forested regions.

DISCUSSION

The contemporary structure and fire regime of the pine flatwoods of the ONF are a product of the significant management influence associated

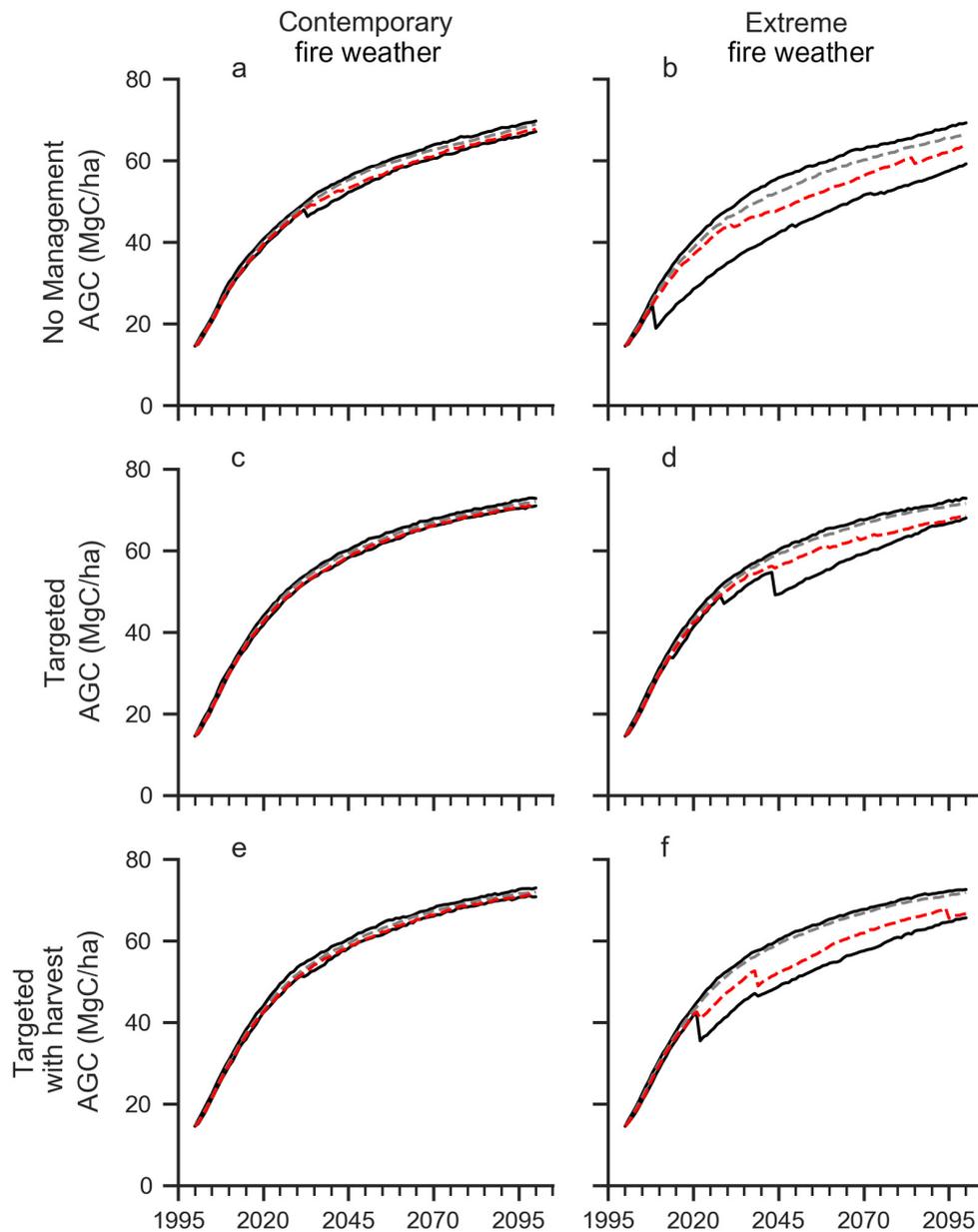


Fig. 6. Aboveground carbon (AGC) for both contemporary (left) and extreme (right) fire weather scenarios. Treatments are shown by row: no-management (a, b), targeted treatment (c, d), and targeted treatment with harvest (e, f). Each subplot shows the absolute minimum and maximum (black lines), mean (gray dashed), and lowest 95th percentile (red dashed) of AGC for each year across 30 replicate simulations.

with longleaf pine restoration, fire management, and wood harvest. Like many similar landscapes in the region, the Osceola is composed of a patchwork of both managed pine flatwoods and hardwood-cypress swamps, which are relatively unmanaged. With the abrupt change in

vegetation type when moving from upland to wetland forest, there is a commensurate change in fuels composition. The pine flatwoods, shaped by frequent-fire, are characterized by relatively low surface fuel loads when compared to the infrequent-fire hardwood-cypress swamps,

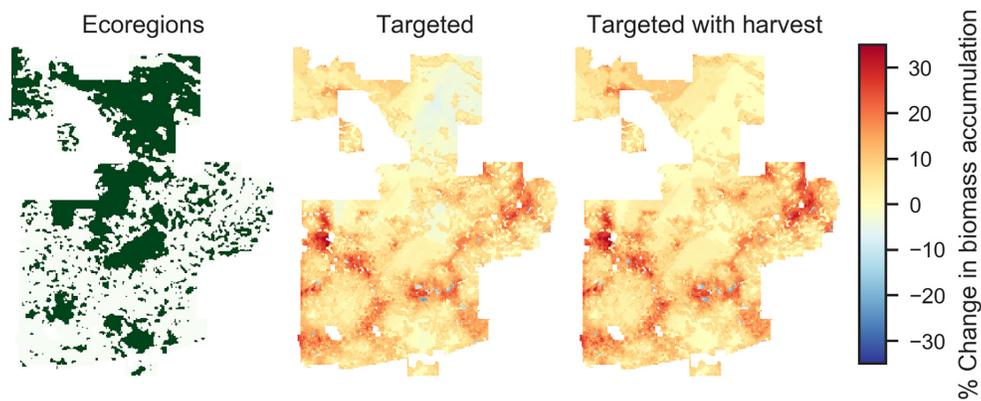


Fig. 7. Percent change in accumulated aboveground carbon between no-management and treatment scenarios under extreme fire weather conditions. Negative values indicate that biomass was lower relative to the no-management scenario, whereas positive values indicate that biomass was higher relative to the no-management scenario. Distribution of hardwood–cypress swamps (dark green) and pine flatwoods (mint) is shown for context.

which are typically less susceptible to fire due to long hydroperiods. However, during prolonged hot and dry periods, the wetland forests become highly flammable, capable of supporting large, high-severity crown fires and consumption of the deep organic layer (Ewel 1990, Hungerford et al. 1995, Picotte and Robertson 2011).

Given that large, high-severity fires homogenize the structure of these ecosystems, the provision of ecosystem services is contingent on building resilience to the most severe wildfires. In our simulations, the targeted treatment of pine flatwoods adjacent to hardwood–cypress swamps increased forest structure and fuels heterogeneity, creating a buffer of discontinuous tree canopy adjacent to hardwood–cypress swamps. This targeted treatment strategy effectively reduced both the size of the largest wildfires and the total area burned from wildfires in our simulations, indicating support for our hypothesis that optimized treatment placement would stabilize C stocks (Figs. 4, 5). The mechanism for these changes across the landscape was a combination of reduced fire severity as wildfires burned from swamps into flatwoods and the decrease in likelihood that ignitions in the pine flatwoods spread far enough to interact with hardwood–cypress swamps. The regular application of prescribed fire throughout the pine flatwoods created a mosaic of discontinuous surface fuels, which limited fire spread. The culmination of the stochastic combination of these

outcomes was an overall decrease in mean wild-fire severity in the upland forests, resulting in more stable AGC accumulation, indicating support for our hypothesis that 90th percentile and greater fire weather would reduce C stock stability (Fig. 6). The carbon stock stability was fairly consistent between the targeted and targeted with harvest scenarios because there was little difference in the proportion of the landscape burned by high-severity fire (Fig. 4). However, the AGC range for the targeted with harvest scenario was greater than the targeted scenario, indicating that the additional harvest could result in a reduction of AGC, depending on the interaction with wildfire. These results suggest partial support for our hypothesis that additional low-volume harvest would reduce C stocks over the targeted scenario. However, there is no support for additional harvest adding stability to the C stock.

The stability of the AGC stock provided by the targeted treatment scenario was contingent on both the initial thinning of the swamp-adjacent pine flatwoods and the continued application of prescribed fire to pine flatwoods to control fuel loads and maintain ecosystem structure and function. This fire regime, with a legacy that predates European settlement (Frost 2007, Jackson et al. 2017), reduced the prevalence of vegetation structure and fuels conditions that can produce large, severe wildfires, a fire regime that has been largely interrupted across the southeastern

United States with aggressive fire suppression. In contrast to the frequent-fire systems in the southwestern United States, southeastern pine ecosystems lack the combination of dry conditions and complex terrain that can produce mixed-severity fire regimes (Pederson et al. 2008, Collins and Stephens 2010), making the resilience to large, high-severity wildfires in the southeast more a function of forest structural heterogeneity than topography.

Maintaining heterogeneity within these forests and across these landscapes also provides habitat for federally listed faunal species, such as the red-cockaded woodpecker (RCW; USFWS 2003), gopher tortoise, and eastern indigo snake, notwithstanding the diversity of groundcover communities (Glitzenstein et al. 2003). The provision of RCW habitat is well aligned with the need to maintain frequent fire on the landscape (Hiers et al. 2016) as well as increase stand-age heterogeneity in order to increase resilience to wildfire and maintain foraging and breeding habitat (Dickinson 2014, Bigelow et al. 2018).

Climate projections for this region suggest an increase in the frequency of hot and dry periods that could increase the frequency with which wetland forests burn (Liu et al. 2014). Recent historic droughts and fires in the southeastern United States echo the climate–fire interactions that are also impacting the western United States (Bigelow et al. 2018). Furthermore, increases in the frequency of extreme fire weather events could reduce the window of time in which prescribed fire can be safely applied to the landscape (Mitchell et al. 2014), further stressing the importance of early action in an effort to increase carbon stock stability and build adaptive capacity into these fire-prone systems (Krofcheck et al. 2018).

Our simulation environment did not take into account the influence of future climate on vegetation growth and succession, carbon stock and flux changes, or the cascading implications of increasing fire weather severity with changes in climate. In the southeastern United States, the projected increase in soil moisture deficit (Liu et al. 2014) stands to reduce AGC storage in the long term, as competition for water increases and disturbance regimes shift in intensity. However, actively managing conifer biomass has near-term carbon costs, yet in the long term can yield reductions in competition resulting in increased

carbon accumulation of the remaining vegetation (Loudermilk et al. 2014, 2017, Hurteau et al. 2016). These trajectories are ultimately governed by the direction and rate of the progression of disturbance frequency and intensity, management efficacy, and the integrated carbon costs associated with management (Krofcheck et al. 2018, Swanteson-Franz et al. 2018).

Further, the belowground dynamics in the carbon-rich soils of wetland forests can potentially release large amounts of sequestered carbon in the form of CH₄ with increases in temperature and changes in soil moisture, resulting in significant feedbacks to climate (Zhang et al. 2017). This is a process not described by LANDIS-II or any of its extensions. During prolonged hot and dry conditions, the fuels in the wetland forests burn with high severity and can smolder for significant periods of time. Ultimately, prolonged fires in these areas can consume kilograms of recalcitrant C per square meter (Turetsky et al. 2011). Forest management for fuels reduction in areas surrounding carbon-rich wetland ecosystems therefore may also serve to safeguard large, and otherwise recalcitrant, carbon pools by reducing the likelihood of fire spread into the wetland systems. This consequence of increased high-severity fire in wetland ecosystems represents another large yet poorly described source of uncertainty in our modeling environment.

These upland–wetland forested systems represent a unique management challenge, given the patchwork of fuel loads, fire regimes, and subsequent fire risk. The potential for increased frequency of conditions making hardwood–cypress swamps available to burn with ongoing climate change stands to destabilize the carbon stocks of even the managed pine flatwoods by increasing the risk of high-severity wildfires propagating from the swamps. Our results suggest that the targeted application of fuels management around the wetland adjacent upland forests can build adaptive capacity into the system in the context of more frequent and extreme wildfires and help protect the provision of ecosystem services against a more fire-prone future.

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