Ecosystems (2015) 18: 76–88
DOI: 10.1007/s10021-014-9813-1

ECOSYSTEMS

Carbon Tradeoffs of Restoration and Provision of Endangered Species Habitat in a Fire-Maintained Forest

Katherine L. Martin,[1,2]* Matthew D. Hurteau,[1] Bruce A. Hungate,[3] George W. Koch,[3] and Malcolm P. North[4]

[1]*Department of Ecosystem Science & Management, The Pennsylvania State University, 306 Forest Resources Building, University Park, Pennsylvania 16802, USA;* [2]*Present address: Center for Integrated Forest Science, Southern Research Station, USDA Forest Service, 3041 Cornwallis Rd, Research Triangle Park, North Carolina 27709, USA;* [3]*Center for Ecosystem Science and Society and Department of Biology, Northern Arizona University, 617 Beaver St, PO Box 5640, Flagstaff, Arizona 86011, USA;* [4]*Pacific Southwest Research Station, USDA Forest Service, 1731 Research Park Dr., Davis, California 95618, USA*

Abstract

Forests are a significant part of the global carbon cycle and are increasingly viewed as tools for mitigating climate change. Natural disturbances, such as fire, can reduce carbon storage. However, many forests and dependent species evolved with frequent fire as an integral ecosystem process. We used a landscape forest simulation model to evaluate the effects of endangered species habitat management on carbon sequestration. We compared unmanaged forests (control) to forests managed with prescribed burning and prescribed burning combined with thinning. Management treatments followed guidelines of the recovery plan for the endangered red-cockaded woodpecker (RCW), which requires low-density longleaf pine (*Pinus palustris*) forest. The unmanaged treatment provided the greatest carbon storage, but at the cost of lost RCW habitat. Thinning and burning treatments expanded RCW habitat by increasing the dominance of longleaf pine and reducing forest density, but stored 22% less total ecosystem carbon compared to the control. Our results demonstrate that continued carbon sequestration and the provision of RCW habitat are not incompatible goals, although there is a tradeoff between habitat extent and total ecosystem carbon across the landscape. Management for RCW habitat might also increase ecosystem resilience, as longleaf pine is tolerant of fire and drought, and resistant to pests. Restoring fire-adapted forests requires a reduction in carbon. However, the size of the reduction, the effects on sequestration rates, and the co-benefits from other ecosystem services should be evaluated in the context of the specific forest community targeted for restoration.

Key words: carbon sequestration; climate change; ecosystem services; endangered species; fire; longleaf pine; *Pinus palustris*; prescribed burning; red-cockaded woodpecker.

Introduction

Globally forests absorb 30% of annual anthropogenic carbon dioxide (CO_2) emissions and store 45% of terrestrial carbon (C) (Canadell and others 2007; Bonan 2008). Maintaining the strength of this sink is important for near-term climate change

Received 22 May 2014; accepted 2 September 2014;
published online 16 October 2014
Electronic supplementary material: The online version of this article (doi:10.1007/s10021-014-9813-1) contains supplementary material, which is available to authorized users.

Author Contributions KLM performed research and analyzed the data; MDH, BAH, GWK, and MPN conceived of and designed the study; KLM, MDH, BAH, GWK, and MPN wrote the paper.
**Corresponding author; e-mail:* katie_martin@ncsu.edu

mitigation (Pacala and Socolow 2004; Canadell and Raupach 2008). In the eastern US, recovery from logging, land-use change during the early twentieth century, and on-going fire exclusion are responsible for much of the region's forest C sink (Caspersen and others 2000; Houghton 2003; Dangal and others 2014), in part because young forests sequester C rapidly (Pregitzer and Euskirchen 2004; Pan and others 2011).

Although fire exclusion has contributed to greater C density (Caspersen and others 2000; Houghton 2003; Pan and others 2011), frequent fire is an integral ecosystem process in many forests that supports other ecosystem services, including biodiversity (Nowacki and Abrams 2008; Hurteau and Brooks 2011). In longleaf pine (*Pinus palustris*) forests, fire return intervals of approximately 2–4 years create open-canopy forests that support high plant and wildlife biodiversity (Lemon 1949; Kirkman and others 2004). In the absence of fire, fire-sensitive hardwood species create an increasingly dense understory that excludes much of the biodiversity that depends on open forests, including up to 40 plant species per square meter and the unique wildlife that depend on this habitat (Walker and Peet 1984; Glitzenstein and others 1995). Currently, longleaf pine only occupies approximately three percent of its historical range across the southeastern Coastal Plain of the United States. Although fire exclusion is a contributing factor, much of the region was converted to agriculture and plantation forests of faster growing pine species after the original longleaf pine forest was logged (Glitzenstein and others 1995; Landers and others 1995). The loss of fire-maintained longleaf pine forest led to the decline of associated species including the federally endangered red-cockaded woodpecker (RCW; *Picoides borealis*). RCWs require mature forests with open understories for foraging and trees, preferably longleaf pine, at least 60 years old for nesting (Engstrom and Sanders 1997; Mitchell and others 2009). The species recovery plan recommends RCW habitat management for low-density stands with treatments to maintain large, old pine trees, open mid and understories, dispersed areas of regeneration, and prescribed burning on a 1–3 years rotation to promote the dominance of diverse herbaceous ground cover (USFWS 2003).

Although restoration of fire-maintained habitat for legally protected species such as the RCW is mandated, the associated effects on forest C dynamics are not well understood. We evaluated the effects of RCW habitat management, including thinning and prescribed fire, on forest C dynamics to quantify its potential tradeoffs with species conservation. Using the landscape at Ft. Benning, GA, we simulated forest C dynamics for three scenarios, designed to estimate the impacts of a range of management options: (1) control (no management), (2) prescribed burning (maintain open understories in existing RCW habitat), and (3) thinning coupled with prescribed burning (increase RCW habitat). We evaluated the impact of each scenario on C dynamics and RCW habitat availability using (1) C sequestration in terms of total ecosystem C and net ecosystem carbon balance (NECB) and (2) landscape changes in forest composition (longleaf pine dominance).

Methods

Study Area

Ft. Benning is a 73,533 ha military installation on the Georgia-Alabama border in the Sandhills ecological region and is defined as a core population site in the RCW species recovery plan (Dilustro and others 2002; USFWS 2003). The installation includes upland forest dominated by longleaf pine, mixed pines (longleaf, loblolly *Pinus taeda* and shortleaf *P. echinata*), mixed pine-hardwoods with species including *Quercus falcata*, *Q. marilandica*, *Q. laevis*, *Carya tomentosa*, and plantations of longleaf pine and loblolly pine (Figure 1). The hardwood species are native, fire-sensitive (relative to longleaf pine) typically dispersed throughout longleaf pine-dominated forest that become abundant in the absence of fire. Across the landscape, Ft. Benning forest inventory data indicate stands range in age from less than 10 to greater than 100 years old, with 53% of stands currently less than 60 years old. Soils across the upland portion of the landscape, the focus of this study, are predominately loamy sands or sandy loams (NRCS 2013). National Climatic Data Center (NCDC) datasets collected for this study recorded an average maximum temperature of 33°C in July, minimum temperature of 2°C in January and mean annual precipitation of 119 cm.

Field Methods

We collected vegetation, soil, and surface fuels data at upland sites across Ft. Benning to represent a range of stand ages and compositions to parameterize a landscape simulation model. Sampling sites were selected based on RCW habitat classification, advice from natural resource managers and military training operation schedules. Sampling was designed to capture the range of longleaf stand

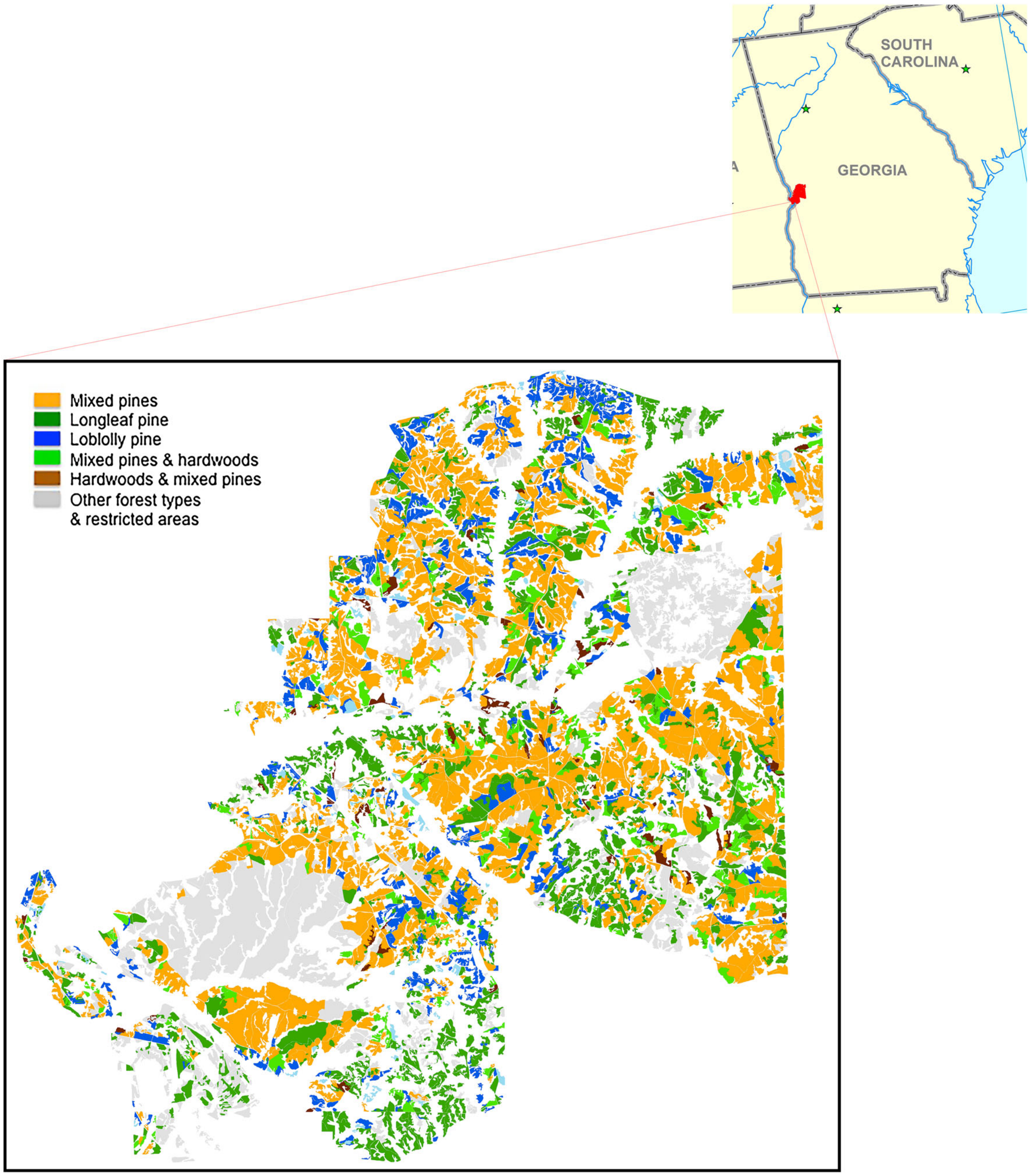

Figure 1. Map of Ft. Benning location and forest types.

conditions from newly established plantations to mature natural forest. A total of 223 plots were established, with 63 in younger stands (≤10 years old, restoration sites that are future RCW habitat), 88 in maturing stands (30–60 years, foraging habitat), and 72 in older stands (≥60 years, roosting habitat). Stands 10–30 years old had limited availability for sampling. Trees at least 50 cm diameter at breast height (DBH) were sampled in 1/5 ha (25.2 m radius) plots, whereas nested circular subplots (1/10 ha; 1/50 ha) were used to measure smaller diameter trees that occur with greater frequency (≥30 cm DBH and ≥5 cm DBH, respectively). Tree-specific measurements included species identification, DBH, height, height to live crown and status (live or dead). Regeneration was tallied by height class within a 2-m radius of plot center, and surface fuels (litter and duff) and coarse woody debris were measured along three 15 m modified Brown's fuels transects (Brown 1974). A subsample of plots was selected to capture the range of stand conditions for sampling soil C.

Replicate soil samples (4–7 per stand) were collected at 0–15 and 15–30 cm depths from four stands 10–85 years old, and then shipped to the Colorado Plateau Stable Isotope Lab (http://www.isotope.nau.edu) for processing. Soils were oven-dried and ground to a fine powder using a ball mill. Sub-samples were weighed into tin capsules and analyzed by Dumas combustion on a CE Elantech elemental analyzer coupled to an isotope-ratio mass spectrometer (Thermofinnigan Delta Advantage) to quantify total C.

Simulation Model Description

The effects of forest management treatments on forest C stocks, NECB, and forest composition were simulated using the LANDIS-II forest landscape succession and disturbance model (Scheller and others 2007). NECB is the balance between C gains from net primary productivity (NPP) and losses from heterotrophic respiration (R), leaching and disturbance (Chapin and Matson 2011). In LANDIS-II, the landscape is represented as a grid of pixels that is populated with initial forest communities. LANDIS-II does not simulate individual trees; rather, species in communities are represented as biomass in age classes, and each community can include multiple age classes of different species. Forest growth and disturbance impacts are based on species' life history parameters, including growth rate, dispersal distance, and tolerance of shade and fire. Within and across communities, age cohorts grow, compete, reproduce, and interact through spatial processes including dispersal and disturbances that spread across cells.

We used the LANDIS-II Century succession extension to simulate both above- and below-ground C pools (Scheller and others 2011a). The Century extension was developed from the CENTURY soil model (Metherell and others 1993; Parton and others 1993; Parton 1996), which has been widely applied across ecosystems to simulate both above- and below-ground growth, mortality, decomposition, and nutrient dynamics. Ecosystem dynamics and transfers of C between pools are determined by climate, soil properties, and the species-specific chemistry (lignin, C:N ratios) of wood, leaves, litter, and roots. In addition to growth and respiration, soil properties and climate are used to determine species-specific establishment probabilities (Scheller and others 2011a, b).

Forest management treatments were simulated using the Dynamic Fire and Leaf Biomass Harvest extensions. The Dynamic Fire extension models fire behavior based on fuel types and climate data using methodology similar to the Canadian Forest Fire Behavior Prediction System (Van Wagner and others 1992; Sturtevant and others 2009). Fuel types were assigned to each pixel using the Dynamic Biomass Fuels extension, where simulated fuel loading is determined by the species composition and biomass in each cell (Sturtevant and others 2009). The Leaf Biomass Harvest extension can simulate multiple harvest prescriptions in overlapping periods, and prescriptions can encompass a range of methodologies for site selection and species cohort removal (Gustafson and others 2000).

Model Parameterization

LANDIS-II was parameterized using the field data, spatially explicit forest inventory data provided by resource managers at the installation, and values from the literature. We divided the landscape into four ecoregions based on the predominant soil textures: loamy sand, sandy loam, sandy clay loam, and loam, which were identified using the NRCS SSURGO dataset (NRCS 2013). Active artillery range areas that were not accessible for research were excluded from analysis, as were riparian and floodplain areas because our objective was to examine upland portions of the landscape managed for RCWs. Topography and climate were assumed to be similar across the relatively flat landscape.

We divided the landscape into 4 ha pixels so that each pixel represented approximately half of an average sized management unit, which was 9 ha. Based on field data, we selected ten species that accounted for greater than 96% of the basal area in our sample plots (Supplementary Table S1–S3). Although not abundant in our field plots that are burned regularly, red maple (*Acer rubrum*) was also included because it is a prolific, shade-tolerant species that becomes more common with fire exclusion (Nowacki and Abrams 2008). Cells of similar forest types were then assigned initial communities with combinations of species and age cohorts selected to represent the distribution of forest conditions in our field data and the spatial inventory data. The spatially explicit inventory data provided information on stand composition, tree ages, and management history.

The Century succession extension requires parameters for climate, soil, and species to simulate forest growth (Supplemental Tables S4–S5). We used 51 years (1962–2012) of weather data from the Columbus, GA weather station (station ID GHCND: USW00093842) available from the National Climate Data Center. Soil parameters were determined using the SSURGO database (NRCS

2013) and field collected soil samples. Soil C values were divided into three (fast, passive, and slow) pools following methodology outlined in the CENTURY model documentation (Metherell and others 1993). Following Loudermilk and others (2013), soil organic matter decay rate parameters were calibrated so that at the first simulation time step following spin-up (where the forest communities are grown until they reach the parameterized ages) the soil C fell within the range of sampled values. Soil C values and accumulation rates following spin-up were also compared with values reported in the literature for similar forest and soil types (Post and others 1982; Schiffman and Johnson 1989; Birdsey 1992; Parton and others 1993; Schimel and others 1994; Smith and others 1997; Richter and others 1999; Wilson and others 1999; Markewitz and others 2002; Hooker and Compton 2003; Li and others 2012; Samuelson and others 2012; Samuelson and Whitaker 2012). Species and functional groups were parameterized with values from the literature, including available databases and the CENTURY user guide (Post and others 1982; Pastor and Post 1986; Metherell and others 1993; Mitchell and others 1999; Wilson and others 1999; Kirkman and others 2001; Samuelson and others 2012; Samuelson and Whitaker 2012; Whelan and others 2013).

We parameterized the Dynamic Fire extension to estimate the effects of prescribed fires typical of longleaf pine ecosystem management, which are ignited under conditions that favor low-severity, surface fires of predetermined sizes (Supplementary Tables S6–S7). The Dynamic Fire extension randomly selects cells to test for ignition, which is determined by an ignition probability parameter. To reflect the planned nature of prescribed burning, ignition probabilities were set to 1.0 and the average fire size was parameterized as 7 ha because low-severity, prescribed fires include small areas within a stand that remain unburned. Fires were parameterized to occur primarily during the spring under high fuel moisture conditions, which is a typical management prescription for RCW habitat maintenance (USFWS 2003). Fires ignited were ignited in a stochastic manner, but the number of fires was parameterized so that approximately one-third of the landscape was burned each year, representing the three-year fire return interval typical of management at Ft. Benning, and within the RCW recovery recommendations. Following the example of Scheller and others (2011b), fuel parameters were adjusted from the Canadian Forest Fire Behavior Prediction System (Van Wagner and others 1992), based on comparisons to fire spread rates in Scott and Burgan (2005), field measurements of fuels, and the extensive longleaf pine fire ecology literature (Lemon 1949; Glitzenstein and others 1995; Mitchell and others 1999; Kirkman and others 2001; Varner and others 2005). Parameters were tested and considered to be representative of prescribed burning based on the resulting fire severity and mortality across the fire regions over the course of the simulation. For example, we parameterized the fire conditions to prevent the complete removal of biomass from a cell, as this is atypical of a prescribed fire in the longleaf pine ecosystem.

The Leaf Biomass Harvest extension was used to develop harvest prescriptions representing a spectrum of management intensity for different forest types. The landscape was divided into five harvest management units based on RCW habitat requirements: longleaf and mixed pine stands at least 60 years old (RCW roosting habitat), longleaf and mixed pine stands 30–60 years old (foraging habitat), younger (< 30 years old) longleaf and mixed pine stands, mixed hardwood-pine (requiring restoration to develop as RCW habitat), and loblolly pine (requiring conversion to longleaf for optimal RCW habitat). Prescriptions are outlined in Table 1 and include thinning of pines, removal of hardwoods and, in some cases, planting longleaf pine to improve RCW habitat, as outlined in the recovery plan (USFWS 2003). Harvests occur across a user-defined portion of the landscape at each time step, but individual pixels are selected randomly and harvested if they meet implementation criteria. Following harvest prescriptions, fuel types were adjusted to reflect increased canopy base height for the following three fire cycles. We parameterized the Dynamic Fire extension to cause partial mortality of the youngest age cohorts of fire-tolerant pines (longleaf and shortleaf), reflecting the ecology of the species. However, because the Dynamic Fire extension cannot simulate partial cohort mortality, burning a newly planted stand where all cohorts were young would have resulted in complete removal of biomass, which is not a practice implemented in this managed landscape. Therefore, we excluded newly planted seedlings from fire for the first ten years to prevent 100% mortality by assigning a temporary fuel type where fire ignitions did not occur.

Model Validation

To assess the accuracy of model estimates, we compared LANDIS-II forest biomass estimates to field data. We calculated the biomass of maturing

Table 1. Harvest Prescriptions Implemented in the Thin and Burn Treatment

Harvest prescription	Description	Implementation
Thin	Hardwoods: all removed Lobolly pine removals: all ≤60 years old, 75% >60 years old Shortleaf pine removals: 10% ≤10 years old, 5% 11–20 years old Longleaf pine removals: 25% ≤10 years old, 20% 11–60 years old	Approximately every 30 years in all stands, from the beginning of the simulation in longleaf pine and mixed pine stands and beginning in 30 years after a restore or convert prescription
Restore	Hardwoods: all removed Lobolly pine removals, all ≤60 years old, 75% >60 years old Shortleaf and longleaf pine removals: 20% ≤0 years, 10% 11–30 years, 5% 31–60 years Longleaf pine planted	Applied once in stands with significant hardwood component
Convert	Hardwoods: all removed Loblolly pine: all ≤60 years old removed Longleaf pine planted	Applied once to loblolly pine plantations

Prescriptions were designed based on RCW habitat requirements and recommendations from the species recovery plan. Implementation to the timing of prescriptions includes adjustments made based on forest type.

and older longleaf-dominated, mixed species, multi-age stands from field measurements using allometric equations from Jenkins and others (2003). In each stand, 3–5 plots were randomly selected to create a mean stand-scale biomass value that incorporated the variability due to disturbance. We then ran simulations initiated with young longleaf pine-dominated communities (10 years old) and extracted biomass estimates from cells when the simulated ages were equivalent to the measured stand ages for comparison with the field-derived biomass estimates. The field data used for validation included stands representing an age range from 38–86 years old. Each modeled estimate was the mean value of 100 simulation replicates. Simulation estimates included fire, because the field data were collected in stands maintained with prescribed burning on an approximately 3-year rotation. Soil types were held constant across comparisons, although a lack of empirical data for older stands on loamy soils precluded comparisons for this soil type, which is restricted to 3% of the landscape.

Biological and Environmental Factors

Prior to simulating the complex landscape with multiple species and age combinations across soil types, two simulations were run to separate the influence of species and soil properties on C dynamics: loblolly pine only and longleaf pine only scenarios. Loblolly pine has been the preferred plantation species in the southeastern US because it exhibits faster initial growth rates (Mitchell and others 1999). Comparisons between loblolly-only and longleaf-only runs were used to determine the effect of different species productivity on C sequestration. These simulations, where the landscapes were composed of a single-age cohort of the same species, also allowed us to quantify the effects of soil texture, which is an important driver of moisture availability and in turn, productivity (Mitchell and others 1999; Kirkman and others 2001; Kirkman and others 2004; Ford and others 2012). To eliminate the influence of land-use history on growth, each scenario began with an initial community consisting of a single 1-year old cohort of the respective species, and growth was simulated for 100 years and replicated 100 times to account for stochastic processes in the model. LANDIS-II randomly selects climate conditions at each time step based on the average and standard deviation of monthly inputs. For this study, we used over 50 years of climate records to advance understanding of the C dynamics associated with RCW habitat management.

Forest Management

Using the initial communities layer developed with forest inventory data, we tested the effects of RCW habitat management on forest C dynamics and forest composition using three treatments (control, burn, and thin and burn) to address our research questions. The control was used for comparison of the C dynamics of an unmanaged forest, but would not provide RCW habitat. We adapted treatments from management guidelines that are defined in terms of basal area and diameter distributions for use in LANDIS-II, where prescriptions are defined by the removal of biomass from age cohorts. Prescribed burning alone was simulated because it might be sufficient to sustain existing RCW habitat by maintaining the open understory by reducing fire-sensitive species. The 3-year fire return interval we selected is typical of longleaf pine management and implemented at Ft. Benning (Kirkman and others 2001; Samuelson and others 2014). When hardwoods become abundant, thinning is often used prior to the reintroduction of fire to reduce severity and pine mortality, as well as to reduce overstory density (Varner and others 2005). The thin and burn treatment simulated the conversion of mixed pine-hardwood areas to longleaf pine-dominated RCW habitat by removing hardwoods and reducing pine density, particularly younger cohorts. In the thin and burn treatments, the largest loblolly pine trees were retained because they will occasionally be used by RCWs, but smaller loblolly pine trees were removed because they do not provide habitat and are not very fire-tolerant. Our selected treatments were designed to provide comparisons on the landscape scale over the long term, and necessarily did not include the full suite of tools and adaptations necessary to manage forests at the stand scale. All simulations were run for 100 years and replicated 100 times to capture stochastic model behavior and compare the temporal changes in C dynamics between treatments as the majority of the landscape developed toward an old-growth forest.

Results

Model Validation

Field data used for comparison were from older stands with varying site histories, and the specific simulated grid cells used for validation were randomly sampled from the population of grid cells occupied by young stands for which growth was simulated with stochastic climate and fire. Our simulated biomass estimates were consistent with calculations from field measurements, with a root mean square error (RMSE) of 1,365.1 g m^{-2}, 24.2% of the mean (Figure 2). There was variation in both the field and modeled data, but discrepancies between the two demonstrate a lack of model bias (−3.4%) toward over- or under-prediction.

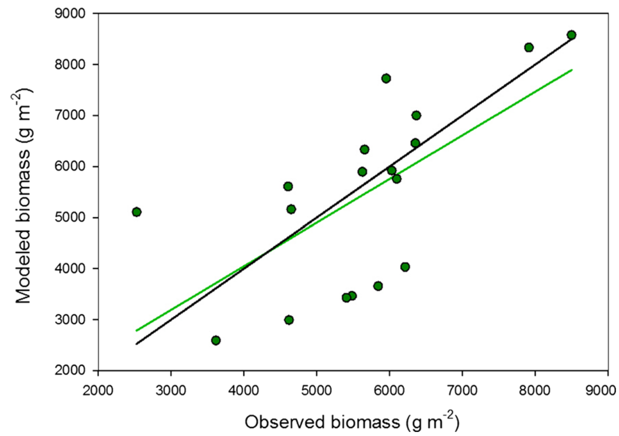

Figure 2. Comparison of modeled forest biomass and forest biomass calculated from data collected in a longleaf pine-dominated, multi-species, multi-age forest community of the same age and soil type. The *green line* represents a linear regression of modeled against observed (n = 18, adjusted R^2 = 0.39, P = 0.004). The *gray line* represents 1:1 agreement.

Biological and Environmental Factors

The single-species simulations demonstrated the effects of species-specific growth strategy and soil texture on productivity. Longleaf pine's specific growth and dispersal parameters led to slower C accumulation. However, sustained productivity resulted in a higher NECB in the longleaf scenario relative to loblolly in the latter half of the simulation period (Figure 3), decreasing the difference in C storage over time (Figure 4). In both species, lower productivity on more xeric, loamy sands led to lower C stocks than on more mesic, loamy soils (Table 2). Although soil type affected the productivity of both species, differences across soil types were lower for longleaf pine, which is more drought tolerant than loblolly pine (Kush and others 2004).

Effects of Forest Management

All treatments gained C over time, but at different rates. In the control treatment, a maximum NECB of approximately 200 g C m^{-2} y^{-1} occurred in the first two decades and then declined until the end of the simulation (Figure 5a). NECB in the burn treatment followed a similar pattern, peaking at a maximum rate about 13% higher than the control (Figure 5b). Relative to the other treatments, the thin and burn had the most variable NECB, but maintained higher rates over a longer time span (Figure 5c). Approximately 10 years into the simulation, NECB was signifi-

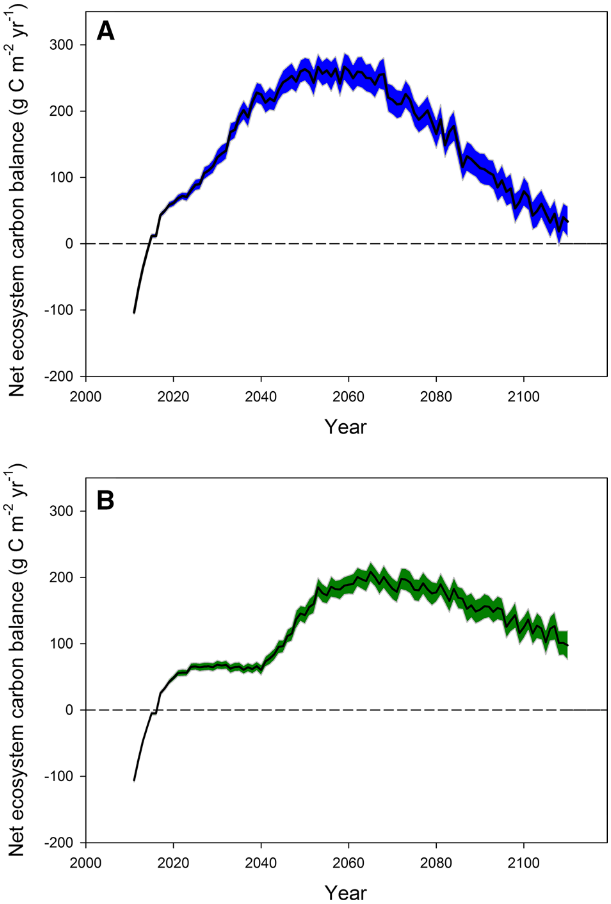

Figure 3. Net Ecosystem Carbon Balance (NECB) of simulated forest development over 100 years. Simulations began with a single one-year-old age cohort of one pine species. *Lines* represent the mean and shading the 95% confidence interval of estimates from 100 simulation replicates for **A** loblolly pine only, **B** longleaf pine only.

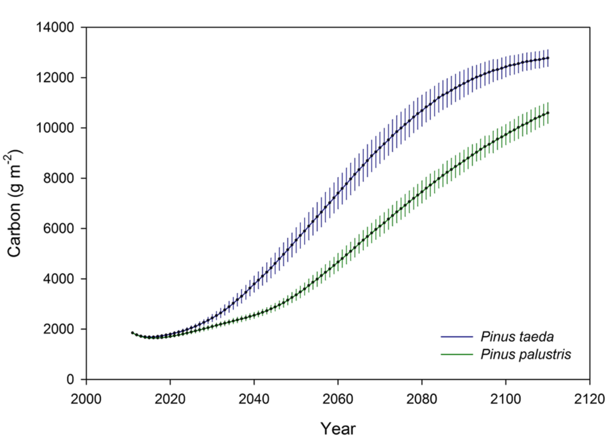

Figure 4. Carbon accumulation in simulations that began with a single one-year-old age cohort of one pine species. Values represent the mean (SD) above- and below-ground carbon from 100 simulation replicates. *Blue* is loblolly pine only, and *green* is longleaf pine only.

cantly lower in the thin and burn as harvesting occurred and loblolly plantations were converted to longleaf, but the landscape remained a C sink. At year 50, when the control and burn were both accumulating approximately 100 g C m^{-2} y^{-1}, NECB in the thin and burn was 170 g C m^{-2} y^{-1}. At the end of the 100-year simulation, C accumulation rates in the thin and burn were double the burn and triple the control simulations. Total ecosystem C declined with increasing treatment intensity (Figure 6). When C stocks approached an asymptote at the end of the simulation period in both the control and burn, the treatments differed by approximately 14%. C stocks in the thin and burn treatment did not reach an asymptote, but were approximately 10% less than the burn treatment and 22% less than the control simulation in the last 5 years of the simulation.

Although increasing management intensity decreased total ecosystem C, it increased the portion of the landscape dominated by longleaf pine and thus potential RCW habitat. Without management, less than 5% of the landscape was at least greater than 50% longleaf pine after 100 years (Figure 7a). By implementing prescribed burning every 3 years, the landscape in the burn simulation was almost entirely pine species, with nearly a quarter of the landscape dominated by longleaf pine (Figure 7b). The addition of thinning treatments increased RCW habitat availability even further as 91% of the landscape was at least 50% longleaf pine (Figure 7c).

Discussion

Management and restoration of longleaf pine ecosystems using prescribed burning and thinning creates tradeoffs between priorities for species conservation and C sequestration. Past conversion of longleaf pine forest to loblolly pine plantations occurred in part because of the faster growth rate of loblolly pine. Our single-species simulations demonstrate that although longleaf pine has a slower growth rate, NECB is sustained at a higher rate than loblolly pine (Figure 3), and our results for total ecosystem C suggest that the difference between longleaf and loblolly pine may diminish with age (Figure 4). Results from the single-species simulation provide insight into the C tradeoffs between managing for wood fiber production (loblolly pine) and RCW habitat (longleaf pine).

Longleaf pine has one of the most frequent fire return intervals of any forest, and in its absence, the landscape transitions to a higher density forest increasingly dominated by hardwood species

Table 2. Carbon Accumulation Across Soil Types in Single-Species Simulations

	2036	2061	2086	2010
Loblolly pine only				
Loamy sand	2,326 (356)	6,111 (937)	10,033 (992)	11,645 (539)
Sandy loam	3,983 (454)	8,826 (1129)	12,764 (1085)	14,477 (646)
Loam	5,620 (636)	11,104 (1028)	15,307 (909)	17,515 (644)
Sandy clay loam	2,833 (451)	7,959 (1132)	11,673 (625)	12,132 (374)
Longleaf pine only				
Loamy sand	1,772 (168)	3,791 (554)	7,155 (729)	9,800 (687)
Sandy loam	3,148 (178)	5,686 (617)	9,307 (684)	11,743 (620)
Loam	4,466 (292)	7,877 (606)	11,190 (642)	13,389 (712)
Sandy clay loam	2,019 (247)	4,772 (502)	8,167 (742)	10,312 (742)

Simulations began with a single one-year-old age cohort of one pine species. Years represent simulation years beginning in 2011. Values are mean g C m^{-2} (SD) from 100 replicates.

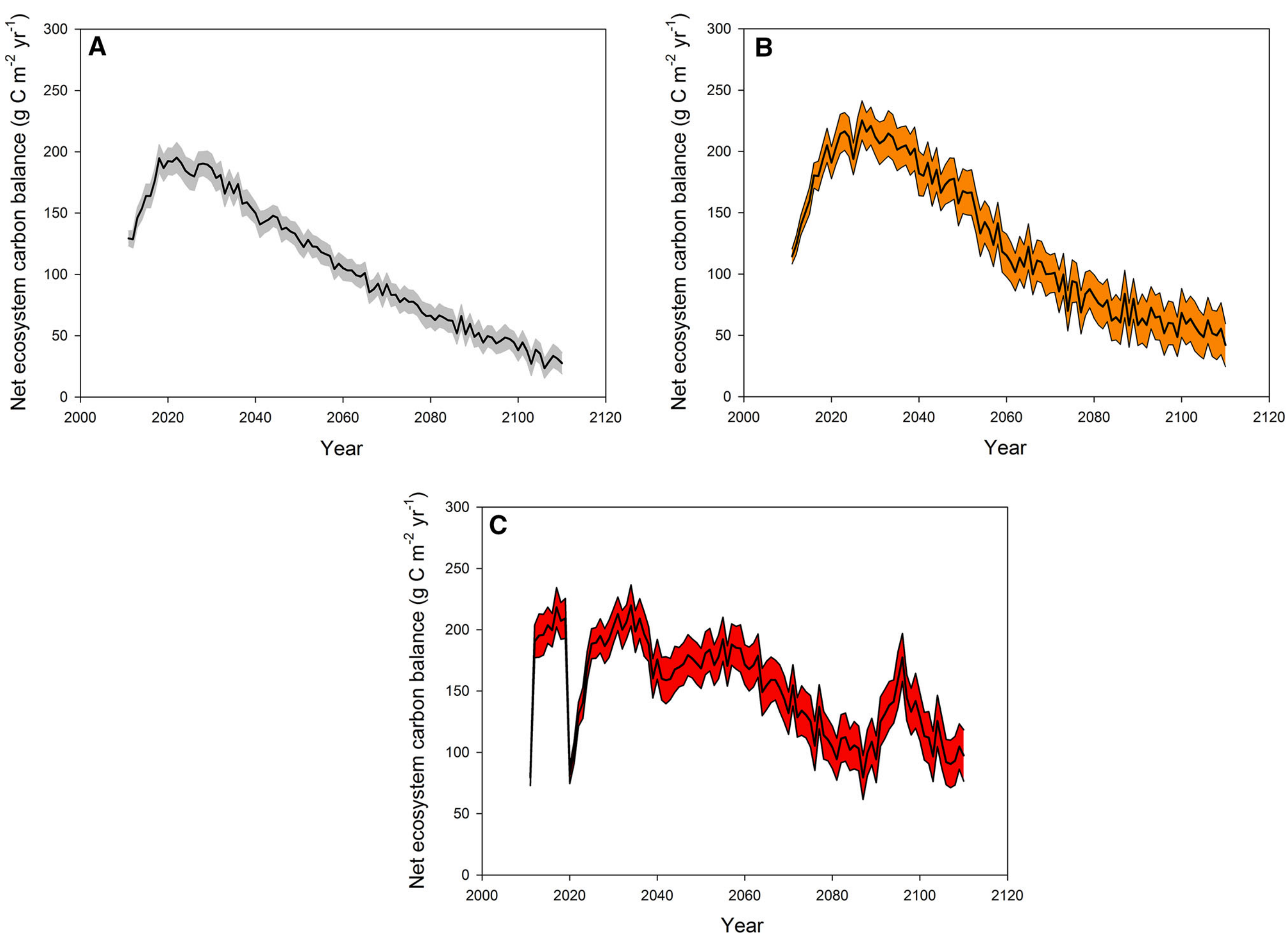

Figure 5. Net Ecosystem Carbon Balance (NECB) of simulated forest management treatments over 100 years. *Lines* represent the mean and shading the 95% confidence interval of estimates from 100 simulation replicates for **A** control treatment: no management, **B** burn: prescribed burning approximately every 3 years to maintain an open understory for RCW habitat, and **C** thin and burn: thinning approximately every 30 years and prescribed burning every 3 years to maintain and expand RCW habitat.

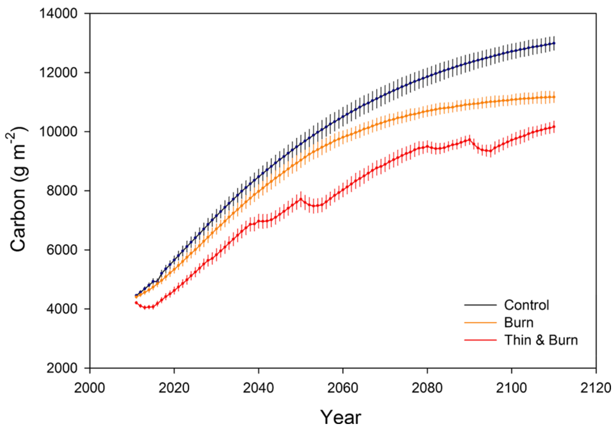

Figure 6. Carbon accumulation across simulated forest management treatments over 100 years. Values represent the mean (SD) above- and below-ground carbon from 100 simulation replicates. *Dark blue lines* indicate control (no management), *orange* are burn only (applied every 3 years to maintain an open understory for RCW habitat), and *red thin* and burn treatments (thinning approximately every 30 years and prescribed burning every 3 years to maintain and expand RCW habitat).

(Gilliam and Platt 1999). Our study suggests fire-suppressed forests sequester more C, but this increase in C density comes at the expense of biodiversity. The fire-maintained low-density forests necessary for RCW habitat also harbor high plant species richness and abundant and unique wildlife species, including the gopher tortoise (*Gopherus polyphemus*), which is a species of concern throughout most of its range. Restoring and maintaining low-density longleaf forests that support biodiversity causes regular C emissions, but managed forest sustained positive NECB over extended time periods.

The spatial and temporal scale of our study adds greater understanding to longleaf C dynamics. Our study indicates Ft. Benning is likely to remain a C sink, even when regular prescribed fire is coupled with restoration thinning. Studies conducted at the stand scale over shorter time scales suggest that longleaf pine forests are potential C sources, particularly when restoration treatments are applied (Samuelson and Whitaker 2012; Remucal and others 2013; Whelan and others 2013). However, an assessment of C stocks across Ft. Benning indicated C continues to accumulate as forests age, even when managed with regular fire (Samuelson and others 2014). In our simulation study, stand-scale C dynamics were affected by climate, soil texture, and moisture availability, which are important drivers of productivity in the longleaf ecosystem (Mitchell and others 1999). Thinning and burning also affected C dynamics at the stand scale. However, at the landscape scale, stands that were temporary C sources were offset by those that were sinks, resulting in continued C accumulation even when prescribed fire on a three-year return interval was coupled with restoration thinning. Across the region, variations in patterns of land use and land-use change exert an even larger effect on sequestration rates than the differences in management intensity identified in this study (Zhao and others 2010).

The C costs of longleaf pine restoration directed at RCW habitat recovery appear to be lower than those incurred with restoration treatments to reduce fuels and mitigate wildfire severity in western forests (Hurteau and Brooks 2011; Hurteau and others 2011; Restaino and Peterson 2013). For example, thinning often removes a significant portion of the live tree C in ponderosa pine (*Pinus ponderosa*) forests (Hurteau and others 2011). In a mixed-conifer forest in California, the significant removals of C caused by fuels treatments were followed by only modest C gains over the 100-year simulation study (Hurteau and North 2009). In comparison, our longleaf-dominated landscape continued to gain significant C across treatments. This is likely attributable to species and climate factors, as longleaf pine is adapted to very frequent (2–4 years) fire and is less water limited in the humid Southeast (Mitchell and others 1999). Further, a large portion of our landscape was smaller trees and younger forest with high growth rates (Pregitzer and Euskirchen 2004), where the C cost of restoration might be lower than in old-growth forests (Hurteau and North 2009; Hurteau and others 2011).

Forest C sequestration is an important tool to mitigate climate change. High density forests, including plantations, might maximize forest C sequestration while also providing valuable timber resources (Onaindia and others 2013). However, natural and lower-density forests provide more benefits to biodiversity and environmental quality, including water resources. For example, across a diverse Spanish landscape, natural forests had higher biodiversity and increased water quality and yield compared to plantations (Onaindia and others 2013). Water yield was also higher in low-density, fire-maintained pine (*Pinus elliottii*) forests maintained for biodiversity in Florida (McLaughlin and others 2013). In the southeastern U.S., longleaf pine is considered a biodiversity hotspot, and restoration is a conservation priority even where RCWs are no longer present (Landers and others 1995; Kirkman and others 2001; Mitchell and others 2009).

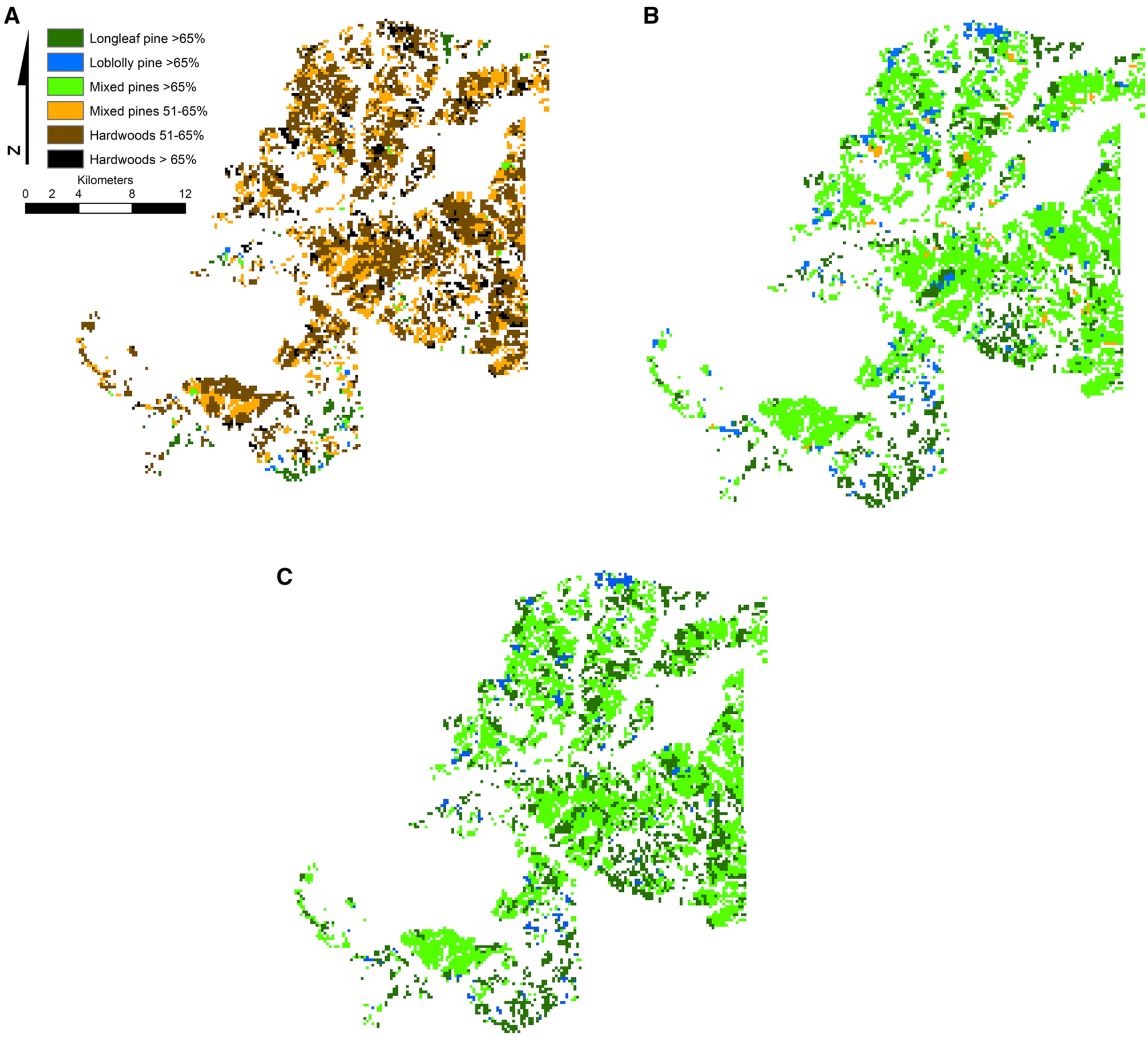

Figure 7. Map of forest types across the landscape after 100 years. Dominance of pines species and southern hardwoods represents the average of 100 simulation replicates for **A** control (no management), **B** burn (applied every 3 years to maintain an open understory for RCW habitat), and **C** thin and burn treatments (thinning approximately every 30 years and prescribed burning every 3 years to maintain and expand RCW habitat).

Beyond benefits to biodiversity, including endangered species, restoration of frequent-fire forests can enhance forest resilience to wildfire by reducing fuel loads (Hurteau and Brooks 2011). Regular fire also increases the dominance of species that evolved to be disturbance tolerant, and thus more resilient (Earles and others 2014). With an extensive taproot, longleaf pine is tolerant of drought and hurricanes (Johnsen and others 2009; Samuelson and others 2014), and it is also resistant to the southern pine beetle *Dendroctonus frontalis* infestations that affect other southern pines (Kush and others 2004). Due to its disturbance tolerance and long lifespan, longleaf pines are thought to accumulate C past 400 years in age (West and others 1993). Therefore, longleaf pine is more likely to provide resilient, long-term C benefits when compared to associated species. These benefits are important to consider when evaluating the C tradeoffs associated with the provision of RCW habitat. Across ecosystems, particularly those that evolved with frequent fire, ecosystem service benefits of restoration should be evaluated together with C storage tradeoffs as part of land management decision-making.

ACKNOWLEDGEMENTS

Funding for this research was provided by the US Department of Defense's Strategic Environmental Research Development Program (SERDP). We thank the Ft. Benning field crew for assistance with data collection and James Parker and Rob Addington for providing data and facilitating access to field locations. We are grateful for the constructive feedback from anonymous reviewers.

REFERENCES

Birdsey RA. 1992. Carbon storage and accumulation in United States forest ecosystems. Washington, DC: US Department of Agriculture, Forest Service.

Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–9.

Brown JK. 1974. Handbook for inventorying downed woody material. General Technical Report INT-16. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Canadell JG, Le Quéré C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Conway TJ, Gillett NP, Houghton RA, Marland G. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proc Natl Acad Sci USA 104:18866–70.

Canadell JG, Raupach MR. 2008. Managing forests for climate change mitigation. Science 320:1456–7.

Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA. 2000. Contributions of land-use history to carbon accumulation in U.S. Forests. Science 290:1148–51.

Chapin FS, Matson PPA. 2011. Principles of terrestrial ecosystem ecology. New York: Springer.

Dangal SRS, Felzer BS, Hurteau MD. 2014. Effects of agriculture and timber harvest on carbon sequestration in the eastern US forests. J Geophys Res. doi:10.1002/2013JG002409.

Dilustro JJ, Collins BS, Duncan LK, Sharitz RR. 2002. Soil texture, land-use intensity, and vegetation of Fort Benning upland forest sites. J Torrey Bot Soc 129:289–97.

Earles M, North M, Hurteau M. 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol Appl 24:732–40.

Engstrom RT, Sanders FJ. 1997. Red-cockaded Woodpecker foraging ecology in an old-growth longleaf pine forest. Wilson Bull 109:203–17.

Ford CR, McGee J, Scandellari F, Hobbie EA, Mitchell RJ. 2012. Long- and short-term precipitation effects on soil CO_2 efflux and total belowground carbon allocation. Agric For Meteorol 156:54–64.

Gilliam FS, Platt WJ. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. Plant Ecol 140:15–26.

Glitzenstein JS, Platt WJ, Streng DR. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol Monogr 65:441–76.

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30:32–43.

Hooker TD, Compton JE. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecol Appl 13:299–313.

Houghton RA. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus B 55:378–90.

Hurteau M, North M. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Front Ecol Environ 7:409–14.

Hurteau MD, Brooks ML. 2011. Short- and long-term effects of fire on carbon in us dry temperate forest systems. Bioscience 61:139–46.

Hurteau MD, Hungate BA, Koch GW, North MP, Smith GR. 2013. Aligning ecology and markets in the forest carbon cycle. Front Ecol Environ 11:37–42.

Hurteau MD, Stoddard MT, Fule PZ. 2011. The carbon costs of mitigating high-severity wildfire in southwestern ponderosa pine. Glob Change Biol 17:1516–21.

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. 2003. National-scale biomass estimators for United States tree species. For Sci 49:12–35.

Johnsen KH, Butnor JR, Kush JS, Schmidtling RC, Nelson CD. 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. South J Appl For 33:178–81.

Kirkman LK, Coffey KL, Mitchell RJ, Moser EB. 2004. Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna. J Ecol 92:409–21.

Kirkman LK, Mitchell RJ, Helton RC, Drew MB. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. Am J Bot 88:2119–28.

Kush JS, Meldahl RS, McMahon CK, Boyer WD. 2004. Longleaf pine: a sustainable approach for increasing terrestrial carbon in the southern United States. Environ Manage 33:S139–47.

Landers JL, Vanlear DH, Boyer WD. 1995. The longleaf pine forests of the Southeast—requiem or renaissance. J For 93:39–44.

Lemon PC. 1949. Successional responses of herbs in the longleaf-slash pine forest after fire. Ecology 30:135–45.

Li DJ, Niu SL, Luo YQ. 2012. Global patterns of the dynamics of soil carbon and nitrogen stocks following afforestation: a meta-analysis. New Phytol 195:172–81.

Markewitz D, Sartori F, Craft C. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. Ecol Appl 12:1276–85.

Metherell AK, Harding LA, Cole CV, Parton WJ. 1993. CENTURY soil organic matter model environment technical documentation. Agroecosystem Version 4.0. Fort Collins, CO: USDA-ARS.

Mitchell R, Engstrom T, Sharitz RR, De Steven D, Hiers K, Cooper R, Kirkman LK. 2009. Old forests and endangered woodpeckers: old-growth in the southern coastal plain. Nat Areas J 29:301–10.

Mitchell RJ, Kirkman LK, Pecot SD, Wilson CA, Palik BJ, Boring LR. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. I. Aboveground net primary productivity. Can J For Res 29:743–51.

Nowacki GJ, Abrams MD. 2008. The demise of fire and ''Mesophication'' of forests in the eastern United States. Bioscience 58:123–38.

NRCS. 2013. Web Soil Survey. United States Department of Agriculture Natural Resources Conservation Service. Available online at http://websoilsurvey.nrcs.usda.gov. Accessed 1 July 2013.

Onaindia M, Fernández de Manuel B, Madariaga I, Rodríguez-Loinaz G. 2013. Co-benefits and trade-offs between biodiversity, carbon storage and water flow regulation. For Ecol Manage 289:1–9.

Pacala S, Socolow R. 2004. Stabilization wedges: solving the climate problem for the next 50 years with current technologies. Science 305:968–72.

Pan Y, Chen JM, Birdsey R, McCullough K, He L, Deng F. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–32.

Parton WJ. 1996. The CENTURY model. In: Powlson D, Smith P, Smith J, Eds. Evaluation of soil organic matter models. Berlin: Springer. p 283–91.

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut JC, Seastedt T, Moya EG, Kamnalrut A, Kinyamario JI. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem Cycles 7:785–809.

Pastor J, Post WM. 1986. Influence of climate, soil-moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3–27.

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG. 1982. Soil carbon pools and world life zones. Nature 298:156–9.

Pregitzer KS, Euskirchen ES. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob Change Biol 10:2052–77.

Remucal JM, McGee JD, Fehrenbacher MM, Best C, Mitchell RJ. 2013. Application of the climate action reserve's forest project protocol to a longleaf pine forest under restoration management. J For 111:59–66.

Restaino JC, Peterson DL. 2013. Wildfire and fuel treatment effects on forest carbon dynamics in the western United States. For Ecol Manage 303:46–60.

Richter DD, Markewitz D, Trumbore SE, Wells CG. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400:56–8.

Samuelson LJ, Stokes TA, Butnor JR, Johnsen KH, Gonzalez-Benecke CA, Anderson P, Jackson J, Ferrari L, Martin TA, Cropper Jr WP. 2014. Ecosystem carbon stocks in *Pinus palustris* forests. Can J For Res (in press).

Samuelson LJ, Stokes TA, Johnsen KH. 2012. Ecophysiological comparison of 50-year-old longleaf pine, slash pine and loblolly pine. For Ecol Manage 274:108–15.

Samuelson LJ, Whitaker WB. 2012. Relationships between soil CO_2 efflux and forest structure in 50-year-old longleaf pine. For Sci 58:472–84.

Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, Mladenoff DJ. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Model 201:409–19.

Scheller RM, Hua D, Bolstad PV, Birdsey RA, Mladenoff DJ. 2011a. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. Ecol Model 222:144–53.

Scheller RM, Van Tuyl S, Clark KL, Hom J, La Puma I. 2011b. Carbon sequestration in the new jersey pine barrens under different scenarios of fire management. Ecosystems 14:987–1004.

Schiffman PM, Johnson WC. 1989. Phytomass and detrital carbon storage during forest regrowth in the southeastern United States Piedmont. Can J For Res 19:69–78.

Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem Cycles 8:279–93.

Scott JH, Burgan RE. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. The Bark Beetles, Fuels, and Fire Bibliography: 66.

Smith P, Smith JU, Powlson DS, McGill WB, Arah JRM, Chertov OG, Coleman K, Franko U, Frolking S, Jenkinson DS, Jensen LS, Kelly RH, Klein-Gunnewiek H, Komarov AS, Li C, Molina JAE, Mueller T, Parton WJ, Thornley JHM, Whitmore AP. 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81:153–225.

Sturtevant BR, Scheller RM, Miranda BR, Shinneman D, Syphard A. 2009. Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. Ecol Model 220:3380–93.

USFWS. 2003. Recovery plan for the red-cockaded woodpecker (*Picoides borealis*): second revision. Atlanta, GA: United States Fish and Wildlife Service. p 296.

Van Wagner CE, Stocks BJ, Lawson BD, Alexander ME, Lynham TJ, McAlpine RS. 1992. Development and structure of the Canadian forest fire behavior prediction system. Ottawa, ON: Fire Danger Group, Forestry Canada.

Varner JM, Gordon DR, Putz E, Hiers JK. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restor Ecol 13:536–44.

Walker J, Peet RK. 1984. Composition and species-diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55:163–79.

West DC, Doyle TW, Tharp ML, Beauchamp JJ, Platt WJ, Downing DJ. 1993. Recent growth increases in old-growth longleaf pine. Can J For Res 23:846–53.

Whelan A, Mitchell R, Staudhammer C, Starr G. 2013. Cyclic occurrence of fire and its role in carbon dynamics along an edaphic moisture gradient in longleaf pine ecosystems. PLoS One 8(1):e54045.

Wilson CA, Mitchell RJ, Hendricks JJ, Boring LR. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. II. Nitrogen dynamics. Can J For Res 29:752–60.

Zhao SQ, Liu SG, Li ZP, Sohl TL. 2010. Federal land management, carbon sequestration, and climate change in the southeastern us: A case study with Fort Benning. Environ Sci Technol 44:992–7.