Frequently burned loblolly–shortleaf pine forest in the southeastern United States lacks the stability of longleaf pine forest

GEORGE MATUSICK,† STEPHEN J. HUDSON, CALEB Z. GARRETT, LISA J. SAMUELSON, JAMES D. KENT, ROBERT N. ADDINGTON, AND JAMES M. PARKER

1School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Drive, Alabama 36849 USA
2Directorate of Public Works, Natural Resources Management Branch, IWBE-PWE-N, Fort Benning, Georgia 31905 USA
3The Nature Conservancy, Colorado Field Office, 2424 Spruce Street, Boulder, Colorado 80302 USA

Citation: Matusick, G., S. J. Hudson, C. Z. Garrett, L. J. Samuelson, J. D. Kent, R. N. Addington, and J. M. Parker. 2020. Frequently burned loblolly–shortleaf pine forest in the southeastern United States lacks the stability of longleaf pine forest. Ecosphere 11(2):e03055. 10.1002/ecs2.3055

Abstract. In recent decades, conservation objectives have driven changes to the management of some pine forests in the southeastern United States. Forest thinning and frequent burning of old-field and plantation pine forests have resulted in an open loblolly–shortleaf pine forest community which resembles the original longleaf pine forest. It is, however, unclear how the structure, composition, and function of the loblolly–shortleaf forest compare to natural longleaf pine forest, and whether it represents an alternative stable state, or simply a transitional state. Understanding the stability of open loblolly–shortleaf pine forest is critical, particularly because several threatened and endangered species are now reliant on it for habitat. The structure and composition of loblolly–shortleaf forest and natural longleaf pine forest were compared using data from permanent forest plots at Fort Benning, Georgia, USA. To assess the stability of the loblolly–shortleaf pine forest and determine whether it is an alternative stable or transitional state, the LANDIS-II forest landscape simulation model was used to simulate changes in forest type cover under no disturbance, and a frequent-fire regime at Fort Benning. Under both management scenarios, nearly all loblolly–shortleaf pine forest converted to mixed hardwood forest over the course of the simulation, with most conversion occurring within 60 yr. In contrast, longleaf pine forest cover increased under frequent fire. Several important structural and compositional differences may have contributed to the instability of loblolly–shortleaf pine forest compared to longleaf pine forest. These include, among other factors, higher densities of resprouting hardwood trees and shrubs in loblolly–shortleaf pine forest, including sweetgum, a resilient broadleaf species capable of transforming ecosystem structure. These results highlight the instability of the open loblolly–shortleaf pine forest community and confirm that is a transitional state, destined for mixed hardwood forest in the coming decades under either no disturbance or frequent fire alone. Future forest planning should consider an active transition from the loblolly–shortleaf pine forest in the coming decades if open pine forest is to be conserved for wildlife and conservation objectives.

Key words: alternative stable state; ecosystem function; ecosystem stability; forest community; frequent-fire; LANDIS-II; loblolly pine; longleaf pine; prescribed fire; shortleaf pine; sustainability; transitional state.

Received 10 September 2019; revised 10 December 2019; accepted 19 December 2019; final version received 15 January 2020. Corresponding Editor: Charles Canham.

Copyright © 2020 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: g.matusick24@gmail.com
INTRODUCTION

Many forests transition between different states after disturbance, following a predictable pathway toward their climax state. When disturbance or environmental parameters change, communities may shift to an alternative stable state (Beisner et al. 2003), arresting the typical successional pathway. The transition of forest ecosystems to alternative stable states may occur due to anthropogenic disturbance (Kitzberger et al. 2016) or may result from a unique sequence of natural disturbances (Jasinski and Payette 2005). Determining whether a community represents an alternative stable state or a transitional state is critical for predicting ecosystem trajectory and development (Jasinski and Payette 2005). Understanding this distinction is particularly important as humans manipulate ecosystems with increasing intensity.

The upland forests of the Atlantic and Gulf Coastal Plain region in the southeastern United States have undergone substantial changes since European settlement. The once-dominant longleaf pine (Pinus palustris Mill.) ecosystem that stretched from southern Virginia to eastern Texas was nearly completely removed as a result of exploitive harvest, conversion to agriculture and intensively managed pine plantations, altered fire regimes, and urbanization (Van Lear et al. 2005). Longleaf pine forests and woodlands generally do not follow predictable successional pathways toward a climax condition, as is seen in many other forests. Rather, frequent, low-intensity surface fires maintain the ecosystem in a perpetual state of early succession, where single, small group, and occasional larger-scale tree mortality events drive turnover and regeneration on sub-stand scales (Platt and Rathbun 1993). When longleaf pine communities are removed, and the natural disturbance regime is disrupted, the reforestation process takes a predictable successional pathway to mixed hardwood forest and generally does not lead back to longleaf pine dominance (Hartnett and Krofta 1989).

Old-field succession in the southeastern United States is among the most well-studied successional pathways in ecology (Christensen and Peet 1981). Early successional pine species, including loblolly (Pinus taeda L.) and shortleaf pine (Pinus echinata Mill.), are among the first tree species to pioneer cutover and abandoned agricultural sites (Bormann 1953). These pine species, which were represented in low proportions in the native longleaf pine ecosystem (Shultz 1997), dominate the canopy structure in the first stages of secondary forest succession. In the absence of disturbance, the pine-dominated canopy gives way to mixed hardwood forest (Oosting 1942, Quarterman and Keever 1962, Hartnett and Krofta 1989, Shultz 1997). Similarly, intensively managed loblolly and slash pine (Pinus elliottii Engelm.) plantations, which replaced much of the original longleaf pine forest, if never harvested or disturbed, revert to closed-canopy mixed hardwood forests. Through widespread removal of longleaf pine and arresting of the periodic maintenance fires which sustained it, a region-wide mesophication has occurred since European arrival (Kreye et al. 2013), which transformed the predominant longleaf pine forest ecosystem across the region to one destined for mixed hardwood forest (Nowacki and Abrams 2008).

In recent decades, there has been a concerted effort to restore the native longleaf pine ecosystem throughout its original range, and the frequent-fire regimes that maintain it (Van Lear et al. 2005). Frequent fires facilitate an open forest structure, with overstory canopy gaps, minimal midstory strata development, and a dense herbaceous ground layer. Several important threatened and endangered species rely on open pine forest structure, including the federally endangered red-cockaded woodpecker (Leuconotopicus borealis Viellot; James et al. 2001). The coastal plain region is considered one of 36 global biodiversity hot spots due to its species richness and endemism, and threat of continued biodiversity loss (Noss et al. 2015). The naturally open, species-diverse structure of longleaf forest contrasts strongly with the dense, closed nature of forests that have resulted from abandonment of agriculture (Bragg and Heitzman 2009, Brudvig and Damschen 2011) and intensively managed pine plantations (Hedman et al. 2000).

Successful restoration of the longleaf pine ecosystem is contingent on the conversion of forest types dominated by off-site pine species (e.g., loblolly pine, slash pine, and shortleaf pine), originating from agricultural abandonment or intensively managed plantations (Knapp et al.
2011), while at the same time conserving threatened and endangered species (Van Lear et al. 2005). On most public lands and many private lands throughout the southeastern United States, forest management has focused on thinning hardwoods and midstory pines through prescribed fire, and mechanical and chemical treatments to reach ecological objectives and bridge restoration to longleaf pine forest (Kirkman et al. 2007, Greene et al. 2019). The result of these restorative steps in the upper coastal plain region is a loblolly–shortleaf pine forest community that resembles the longleaf pine forest, including dominant overstory pines, open midstory, and herbaceous understory (Fig. 1). It is unclear, however, in what ways this community differs with respect to forest structure and composition from native longleaf pine forest. More importantly, it is uncertain whether this forest represents an alternate stable state or a transitional state remaining destined for hardwood forest. Elsewhere, it has been shown that altering fire regimes can transition pyrophobic forests to pyrophytic communities, resulting in alternative forest states (Beckage and Ellingwood 2008, Kitzberger et al. 2016). The fate of the loblolly–shortleaf pine forest is particularly important given that many species, including multiple threatened and federally endangered species, have become reliant on the services it provides (Wood et al. 2008, Greene et al. 2019). Here, the objective is to compare the structure, composition, and function of an open loblolly–shortleaf pine forest to the natural longleaf pine forest in the region. Through the use of an ecological forest landscape model (LANDIS-II), we also aim to determine whether the open loblolly–shortleaf pine forest represents an alternative stable state or a transitional state destined for hardwood forest. Combined, these objectives are intended to improve our understanding of potential successional trajectories to inform future management.

**METHODS**

**Study area**

Fort Benning is a 73,652-ha United States Army installation straddling the Georgia–Alabama state line in the southeastern United States, with most of the installation area occurring in west-central Georgia (Fig. 2). The regional climate of Fort Benning is humid subtropical, with 1188 mm of annual precipitation, mean high temperature of 24.5°C, and low temperature of 12.8°C. Fort Benning is among four military installations occurring in the upper coastal plain (fall line region) of the southeastern United States, which spans from Alabama to Virginia. The fall line designates the convergence of the Piedmont and Coastal Plain ecoregions, and is characterized by complex mixing of topography, soils, and vegetation communities. Soils on Fort Benning, and characteristic of the fall line, range from deep sandhills representing the remnants of prehistoric sand dunes to loam hills and rich alluvial flats surrounding the Chattahoochee River. The complex mixing of soils has helped to create a diverse assemblage of native plants and plant communities in the region, contributing to the recently recognized global biodiversity hot spot (Noss et al. 2015).

![Fig. 1. Longleaf pine forest (a) and loblolly–shortleaf pine forest (b) on Fort Benning, Georgia, USA.](image-url)
The upland forest at Fort Benning is currently composed of a mixture of mature (31–100 yr of age) loblolly and loblolly–shortleaf pine forest, and longleaf pine forest ranging from newly established stands to old (100+ yr) remnants (Fig. 3). The longleaf pine forest and loblolly–shortleaf pine forest communities are spatially interspersed across the landscape, making them ideally suited for comparison. The range in forest types and ages on Fort Benning are representative of many federal, state, and private lands in the East Gulf Coastal Plain and sea–island sections of the Coastal Plain Physiographic Province and are a product of changing land-use patterns since European arrival. These include widespread clearing for agriculture by the early 1900s (Frost 2009), land abandonment from agriculture following acquisition by the government, management for timber and pulp through the late 1980s, and longleaf pine forest restoration and conservation efforts since the early 1990s.

**Plot network**

Forest structure and composition were assessed using data from a network of permanent forest monitoring plots distributed throughout the managed upland pine forest on Fort Benning as part of their ecological monitoring program. Forest monitoring plots were established between 2010 and 2014 in order to quantify the current forest condition and monitor changes in response to natural and forest
management-related disturbance. Plots were stratified based on forest type and dominant soil texture to establish proportional representation in the monitoring plot sample. While marginally more loblolly–shortleaf pine forest occurs on finer texture soils (Table 1), the two forest types occupy a similar range of soil conditions, which would be predicted by the fact that they are interspersed in close proximity throughout the study area. Due to repeated and frequent disturbance in the form of tree thinning and fire (both wildfire and prescribed fire; Addington et al. 2015a), and the associated vegetation changes that result, monitoring plots are measured during the second full growing season following disturbance. For most plots, the baseline condition was the year the plot was established. However, a subset of plots was either not established in the second full growing season following disturbance, was disturbed annually for a period of time following establishment, or had a gap in measurements due to another factor. In these cases, the baseline measurement condition is not identical to the establishment year. Therefore, baseline measurements used for this analysis were made between 2010 and 2017, with most plot measurements (~88%) occurring between 2011 and 2015. A total of 189 loblolly–shortleaf pine forest and 68 longleaf pine forest plots were used for analyses.

**Plot structure and variables**

Permanent forest monitoring plots at Fort Benning have a nested plot structure. The overstory trees, defined as all trees equal to or >10.1 cm diameter at breast height (DBH; ~4"), were tracked individually with permanent tree tags and unique identifiers in a 30 × 30-m² plot-oriented north–south and east–west (Appendix S1: Fig. S1). Primary overstory tree variables used in the analysis included DBH, height, and age. Tree DBH was measured on each tree, while tree height and age were assessed on three representative dominant or co-dominant pine trees per plot. Where plots included multiple overstory pine species, two representative trees were selected for each species, resulting in four or six representative trees per plot. Tree heights were estimated using a clinometer (Nikon Forestry Pro Laser Rangefinder). Tree cores were extracted at DBH and at an aspect parallel to the slope contour, where applicable. Plant area index (PAI), a measure of the projected plant area per unit ground area including both leaves and woody material, was estimated using a Digital Plant Canopy Imager (CI 100, CID, Vancouver, Washington, USA) by taking hemispherical photographs from 1 m above the ground at five points within each plot. The measurement was

---

Table 1. Proportion of forest monitoring plots distributed across six surface soil textures used in the analysis for longleaf pine and loblolly–shortleaf pine forest communities at Fort Benning, Georgia, USA.

| Surface soil texture | Longleaf pine forest (%) | Loblolly–shortleaf pine forest (%) |
|----------------------|--------------------------|-----------------------------------|
| Fine sandy loam      | 0                        | 2                                 |
| Loamy coarse sand    | 6                        | 5                                 |
| Loamy sand           | 67                       | 52                                |
| Sand                 | 3                        | 2                                 |
| Sandy clay loam      | 16                       | 22                                |
| Sandy loam           | 7                        | 16                                |

---

**Fig. 3.** Age class structure of the upland forest types at Fort Benning, Georgia, from forest-wide stand inventory data (described in more detail below). Mixed Pine-Longleaf is forest where longleaf pine occurs between 25% and 70% and is mixed with either loblolly pine or shortleaf pine.
taken suspended from the ground (1 m) in an effort to exclude ground layer, understory vegetation. Measurement locations included at plot center and 14.1 m from plot center at 45°, 135°, 225°, and 315° aspects (Appendix S1: Fig. S1).

Four 10 × 10 m subplots were nested within the main plot to assess midstory trees and shrubs, which are defined as any woody stems <10.1 cm DBH and equal to or >1 m in height. In each subplot, all midstory stems were tallied by functional group or indicator species to determine woody midstory density (Table 2). In subplot 1 (northwest subplot), all woody stems between 0.9 and 10.1 cm were measured at the species level to establish complete diameter distributions.

Understory vegetation groundcover was assessed within 16, 1 × 1 m nested microplots. The understory stratum was defined as any vegetation <1 m height. Groundcover of each functional group and indicator species (Table 3) was estimated using Carolina Vegetation Survey ground cover classes, including trace (1), 0–1% (2), 1–2% (3), 2–5% (4), 5–10% (5), 10–25% (6), 25–50% (7), 50–75% (8), 75–95% (9), and 95–100% (10; Lee et al. 1998).

**Statistical analysis**

A general linear model approach (GLM procedure, SAS version 9.4, Cary, North Carolina, USA) was used to examine forest structural and compositional variables measured from monitoring plots. Prior to analysis, homogeneity of variance and normality assumptions was checked using residual and Q–Q plots, respectively. Independent variables related to tree and shrub densities as well as PAI were log-transformed to satisfy model assumptions. Since understory functional group cover classes represent a proportion of ground covered, they were logit transformed prior to analysis based on recommendations by Warton and Hui (2011). Each measured stem was categorized into 10 cm diameter classes to produce diameter distributions for each forest type. To examine differences in diameter classes between forest type, nonparametric Mann-Whitney U tests were used.

**Simulation model**

The LANDIS-II forest landscape model version 6.0 was used to estimate the stability of longleaf

---

**Table 2. Categories used for grouping midstory tree and shrub species on ecological monitoring plots at Fort Benning, Georgia.**

| Functional groups and species       | Primary species |
|-------------------------------------|-----------------|
| Xeric hardwoods                     | Quercus laevis, Q. incana, Q. marilandica, Q. margaretta |
| Upland hardwoods                    | Q. falcata, Q. rubra, Q. alba, Q. stellata, Carya species |
| Transitional hardwoods              | Q. nigra, Q. phellos, Q. laurifolia, Q. hemisphaerica |
| Other hardwoods                     | Cornus florida, Diospyros virginiana, Nyssa sylvatica, Prunus species |
| Shrubs                              | Crataegus species, Vaccinium species, Rubus species, etc. |
| Sweetgum                            | Liquidambar styraciflua |
| Lobolly pine                        | Pinus taeda |
| Shortleaf pine                      | P. echinata |
| Slash pine                          | P. elliottii |
| Longleaf pine                       | P. palustris |

**Table 3. Functional groups and indicator species used for assessing understory groundcover on ecological monitoring plots at Fort Benning, Georgia.**

| Groundcover functional groups and species | Primary species |
|-------------------------------------------|-----------------|
| Total herbaceous                          | All herbaceous vegetation |
| Total woody                               | All woody vegetation |
| Bunchgrass                                | Andropogon spp., Schizachyrium scoparium, etc. |
| Non-bunch-forming graminoid               | Panicum spp., Carex spp., Arundinaria gigantea, etc. |
| Leguminous forb                           | Desmodium spp., Galactia spp., Lespedeza spp., etc. |
| Non-leguminous forb                       | Aster spp., Asclepias spp., Circium spp., etc. |
| Fern                                      | Pteridium aquilinum, Polystichum acrostichodes, etc. |
| Woody vine                                | Smilax spp., Campsis radicans, Vitis spp. |
| Pine tree                                 | Pinus taeda, P. echinata, P. palustris, P. elliottii |
| Hardwood tree                             | Quercus spp., Carya spp., Liquidambar styraciflua, etc. |
| Shrub                                     | Crataegus spp., Vaccinium spp., Rubus spp., Ilex glabra, etc. |
| Bracken fern                              | Pteridium aquilinum |
| Longleaf pine                             | Pinus palustris |
| Sweetgum                                  | Liquidambar styraciflua |
| Water oak                                 | Quercus nigra |
| Other oaks                                | Quercus species |
| Gallberry                                 | Ilex glabra |
| Blackberry                                | Rubus species |
| Blueberry                                 | Vaccinium species |
pine and loblolly–shortleaf pine forest types under multiple management scenarios over 200 yr from 2017 to 2217. LANDIS-II is a spatially explicit ecological model, which simulates forest dynamics by incorporating landscape (seed dispersal, disturbance) and stand-level (succession, growth, mortality) processes, along with species-specific attributes (Scheller et al. 2007). The upland forest areas of Fort Benning were divided into 2-ha grid cells or sites (12,987 total sites). This size cell was used since it represents 25% of the average stand size (~8 ha) at Fort Benning. The upland forest of Fort Benning was simulated under two management scenarios, including with and without fire disturbance. Each management scenario was replicated twenty times, and outputs were extracted in 10-yr time-steps. LANDIS-II has been used previously on Fort Benning to successfully investigate changes to forest carbon as it relates to forest restoration (Martin et al. 2015) and climate change (Swanteson-Franz et al. 2018). Here, our aim was to investigate forest community changes with and without realistic future management regimes.

**Model inputs**

The LANDIS-II model runs through a series of model extensions, including one of five extensions to model succession. Here, we used the biomass succession extension version 3.2, which calculates how tree cohorts reproduce, age, die, and change in biomass (g/m²) over-time (Scheller et al. 2007). Fort Benning was divided into six ecoregions, representing the predominant surface soil textures determined by the SSURGO dataset and represented by the ecological monitoring plots (Appendix S1: Fig. S2). Using stand-level forest inventory data, collected within the last 10 yr (accessed February 2017), each grid cell was assigned to one of 119 forest communities (i.e., initial communities). To determine the communities, Fort Benning’s extensive stand-level inventory was used. Each of Fort Benning’s forest stands is categorized into a series of forest types (Fig. 3), based on the composition of overstory (≥25.4 cm DBH). Communities were stratified by forest type and overstory age, and nested within ecoregions. Only communities that occurred on a minimum of 100 acres were considered, and the 119 resulting communities represented >98% of the upland forest area. The initial community input file includes the age cohort for each tree species included in the community. Age cohorts were in 10-yr increments. A list of basic plant traits was required to run LANDIS-II, including tree longevity, maturity, shade and fire tolerance, and seed dispersal parameters, among others (Appendix S1: Table S1). A variety of sources were used to inform these traits and others required for the biomass succession extension, including published studies (Samuelson et al. 2001, Jokela et al. 2004), as well as data from permanent ecological monitoring plots.

**Experimental design**

To examine the future forest dynamics between native longleaf pine forest and the loblolly–shortleaf pine forest, we modeled the Fort Benning environment under two fire management scenarios: with fire and without fire. As mentioned previously, periodic, low-intensity surface fires are necessary to maintain longleaf pine forest. However, loblolly pine is more intolerant of fire, and the loblolly–shortleaf pine forest is thought to result from a period of fire suppression (Williams 1998). Forest restoration efforts have focused heavily on treating all upland pine forests at Fort Benning with frequent prescribed fire to maintain the open midstory canopy condition. The control or no-burn treatment simply simulated forest changes in the absence of disturbance.

To simulate the burn treatment in LANDIS-II, the Dynamic Fire System extension (Sturtevant et al. 2009) was used in conjunction with the Dynamic Biomass Fuels extension. The Dynamic Biomass Fuels extension uses cohort biomass, along with cohort age and mortality, to classify the fuels for every site in the model environment. The Dynamic Fire System extension uses fuel information from the sites as one input to determine fire occurrence, and the size of the fire event. In addition to critical estimates of fuel type and load, the extension utilizes historical weather data to estimate wind speed and direction, and fuel moisture (Appendix S1: Table S2). The Dynamic Fire System was designed to simulate wildfire, which does occur on Fort Benning as a result of military munitions. However, prescribed fire is the primary type of fire disturbance on the Fort Benning landscape. So, multiple adjustments to the extension were
required to mimic the effects of prescribed fire as closely as possible. We aimed to treat between 30% and 50% of the upland forest landscape each year with fire, since the current fire regime aims for fire return intervals of 2–3 yr. To accomplish this, we simulated two active fire ecoregions, with slightly different parameters (Appendix S1: Fig. S3). These fire regimes (fire ecoregions) included areas of the installation that are more difficult to treat with prescribed fire due to their proximity to boundaries and interaction with military training (Fire regime 2), having a lower fire frequency compared to the remainder of the installation area. In order to replicate prescribed fire effects on vegetation, most fires were set to occur during the spring season (85%) when most fire is applied at Fort Benning and throughout the southeastern United States (Appendix S1: Table S3). A smaller proportion of simulated fires were set to occur during the summer (13%) and fall (2%), under dry fuel conditions and different fire weather to simulate wildfire, which occur at approximately the rates expressed here.

**Forest classification**

The forest type for each site was classified following each simulation using the Biomass Output extension version 3.0 (Scheller et al. 2007), which was used to extract total biomass by species. Next, the total biomass of pine tree, hardwood tree, and total tree species were derived for each site. The proportion of hardwood trees and each of the pine tree species (loblolly, longleaf, shortleaf, and slash pines) were derived by dividing the total biomass of each group (hardwood trees) and species by the total biomass for the site. Finally, each site was classified into forest types (matching the input forest types from inventory data), using a set of criteria based on biomass (Table 4). Using this method, each site was assigned one forest type at each 10-yr time-step during the simulation.

**Model validation**

To estimate the accuracy of the biomass succession model, we compared biomass estimates derived from field-collected data to modeled sites. Only longleaf pine forest sites were used for validation for two reasons. First, nearly all of the young (<20 yr old) forest at Fort Benning is planted longleaf pine. Young forest is necessary to estimate future forest biomass under modeled scenarios. Second, longleaf pine stands at Fort Benning have been used to develop accurate biomass regressions for longleaf pine (Samuelson et al. 2014), whereas estimates of biomass from other tree species rely on generalized regional regression equations. We determined the population of ecological monitoring plots that occurred in longleaf-dominated forest stands and contained a longleaf pine-dominated overstory. From the population of plots, we randomly selected 20 for use in the validation. Each of the stratified soil textures was represented in the sample, and plot ages ranged from 44 to 120 yr old. For each plot, we estimated the total aboveground biomass of the trees using regression equations outlined in Samuelson et al. (2014) for longleaf pine and Jenkins et al. (2004) for all other species. Next, we selected the population of young longleaf pine plantations (age 10) from each of the represented soil textures in the model environment. Sites were selected randomly from the population to correspond with each of the 20 field sites. The selected sites were modeled to their respective ages that correspond to their validation field sites using the burn-only scenario, since the validation field sites have been managed under a frequent-fire regime for the recent past. Total biomass was compared between modeled site and their corresponding field sites to validate biomass estimates.

### Table 4. Predominant upland forest types at Fort Benning, Georgia, and their definition for classification following LANDIS-II model simulations.

| Forest type            | Definition                                      |
|------------------------|-------------------------------------------------|
| Hardwood              | Hardwood biomass ≥ 69.5%                        |
| Hardwood-pine         | Hardwood biomass 49.5–69.5%                     |
| Pine-hardwood         | Hardwood biomass 29.5–49.5%                     |
| Shortleaf pine        | Hardwood biomass < 29.5% and pine species biomass > 49.5% |
| Slash pine            | Hardwood biomass < 29.5% and pine species biomass > 49.5% |
| Loblolly pine         | Hardwood biomass < 29.5% and pine species biomass > 49.5% |
| Longleaf pine         | Hardwood biomass < 29.5% and pine species biomass > 49.5% |
| Mixed pine-longleaf   | Hardwood biomass < 29.5% and longleaf pine biomass 29.5–49.5% |
| loblolly–shortleaf pine | Hardwood biomass < 29.5% and loblolly and shortleaf pine biomass 29.5–70.5% |
RESULTS

Baseline forest structure

Loblolly pine dominated the loblolly–shortleaf pine forest sites (mean 10.3 m²/ha ± 0.4), with shortleaf pine representing ~15% of the total pine basal area (mean 2.0 m²/ha, ±0.2). Longleaf pine forest was dominated by longleaf pine (14.0 m²/ha, ±0.4), with shortleaf (0.1 m²/ha) and loblolly pine (1.4 m²/ha) rarely co-occurring with longleaf in the overstory. The overstory of loblolly–shortleaf pine forest was significantly younger than longleaf pine forest on average (53 vs. 83 yr, F = 100.19, P < 0.0001). While the total tree basal area and tree density (trees ≥ 10 cm DBH) were similar between forest types (basal area 14.9 vs. 15.7 m²/ha, F = 1.00, P = 0.3171; tree density 231 vs. 176 trees/ac, F = 2.70, P = 0.1015), the plant area index was 25% higher in loblolly–shortleaf pine forest (1.15 vs. 0.86, F = 8.30, P = 0.0054). Loblolly–shortleaf pine forest had higher densities of pines in smaller size classes (e.g., 10–20, 20–30, 30–40 cm DBH), whereas longleaf pine forest had significantly more trees in larger size classes (e.g., 40–50, 50–60, 60+ cm DBH; Fig. 4). Loblolly–shortleaf pine forest has significantly more hardwood trees (40 vs. 8 trees/ha; F = 20.11, P < 0.0001), higher hardwood tree basal area (F = 13.84, P = 0.0002), and lower pine tree basal area (F = 7.42, P = 0.0069) in the overstory than longleaf pine forest (Fig. 5).

In the midstory, loblolly–shortleaf pine forest had significantly higher densities of shrub species (1429 vs. 514 stems/ha, F = 34.40, P < 0.0001), variable oak species (Quercus nigra and Quercus hemisphaerica; 313 vs. 82 stems/ha, F = 38.86, P < 0.0001), and sweetgum (Liquidambar styraciflua; 1198 vs. 165 stems/ha, F = 79.09, P < 0.0001), while longleaf pine forests had higher densities of xeric hardwood tree species (81 vs. 144 stems/ha, F = 7.88, P = 0.0054) including blackjack (Quercus marilandica), bluejack (Quercus incana), and turkey (Quercus laevis) oaks. Loblolly–shortleaf pine forest had naturally higher densities of loblolly (68 vs. 4 stems/ha; F = 12.15, P = 0.0006) and shortleaf pines (52 vs. 1 stems/ha; F = 14.58, P = 0.0002); however, there was no significant difference in midstory longleaf pine trees between forest types (31 vs. 46 stems/ha; F = 0.82, P = 0.3675).

The understory of loblolly–shortleaf pine forest had higher woody groundcover, including greater pine tree, hardwood tree, and shrub cover compared to longleaf pine forest (Table 5). Differences between the forest types in groundcover of herbaceous functional groups were also

Fig. 4. Mean pine tree densities by diameter class in loblolly–shortleaf and longleaf pine forests at Fort Benning, Georgia. Error bars represent the standard error of the mean. Double asterisks denote significant difference at alpha = 0.05, and single asterisks denote significant difference at alpha = 0.1 from Kruskal-Wallis test.

Fig. 5. Mean hardwood and pine tree basal area in loblolly–shortleaf and longleaf pine forest at Fort Benning, Georgia. Error bars represent the standard error of the mean. Both hardwood and pine tree basal areas were significantly different at alpha = 0.05 between forest types.
observed, including greater cover of non-bunchgrass-forming graminoids and less fern (mostly *Pteridium aquilinum* (L.) Kuhn) cover compared to longleaf pine forest. More specifically, loblolly–shortleaf pine forest had greater cover of sweetgum and water oak, two key woody indicator tree species, while longleaf pine forest had higher longleaf pine and *Vaccinium* (blueberry) species cover (Table 5).

**Model simulation**

Model validation confirmed a significant positive association between observed and modeled biomass data in longleaf pine forest (*T*-value = 5.03, *P* < 0.0001, *r*² = 0.58; Fig. 6). The burn scenario resulted in an average 12,506 ha (±21 ha) burned annually (48% of total), a mean of 123 spring burns averaging 86 ha (±0.1 ha), and totaling 10,624 ha (±20.8 ha; Appendix S1: Fig. S4).

At the year 2217 under the no-burn scenario, nearly all of the upland forest at Fort Benning had transitioned to hardwood-dominated forest (Fig. 7). Under the burn scenario, forest types that are dominated by loblolly and shortleaf pine convert to hardwood forest, while forest types with longleaf pine present in 2017 were dominated by longleaf pine in 2217 (Fig. 8). Under the no-burn scenario, pine-dominated forest at the beginning of the simulation quickly converted to pine-hardwood, before ultimately converting to hardwood forest (Fig. 9a). Repeated prescribed burning was capable of maintaining or increasing longleaf pine forest.

### Table 5. Mean understory groundcover (%) of plant functional groups and indicator species in loblolly–shortleaf and longleaf pine forest plots at Fort Benning, Georgia.

| Groundcover variable | Loblolly–shortleaf pine forest | Longleaf pine forest | *F*-value | *P*-value |
|----------------------|--------------------------------|----------------------|-----------|-----------|
| Total herbaceous     | 42 (1)                          | 40 (2)               | 0.22      | 0.6392    |
| Total woody          | 31 (1)                          | 25 (2)               | 8.47      | 0.0039    |
| Bunchgrass           | 18 (1)                          | 17 (2)               | 0.09      | 0.7585    |
| Non-bunch-forming graminoid | 5 (0)           | 4 (1)               | 5.73      | 0.0174    |
| Non-leguminous forb  | 14 (1)                          | 12 (1)               | 0.14      | 0.7062    |
| Leguminous forb      | 5 (0)                           | 6 (1)                | 2.07      | 0.1514    |
| Fern                 | 1 (0)                           | 4 (1)                | 16.21     | <0.0001   |
| Woody vine           | 2 (0)                           | 2 (0)                | 1.69      | 0.1951    |
| Pine tree            | 1 (0)                           | 0                    | 6.38      | 0.0121    |
| Hardwood tree        | 15 (1)                          | 10 (2)               | 13.37     | 0.0003    |
| Shrub                | 15 (1)                          | 14 (1)               | 2.82      | 0.0942    |
| Bracken fern         | 1 (0)                           | 4 (1)                | 17.66     | <0.0001   |
| Longleaf pine        | 0                               | 0                    | 4.8       | 0.0294    |
| Sweetgum             | 6 (1)                           | 1 (1)                | 19.52     | <0.0001   |
| Water oak            | 1 (0)                           | 0                    | 19.52     | <0.0001   |
| Other oaks           | 5 (1)                           | 3 (1)                | 0.09      | 0.7691    |
| Gallberry            | 1 (0)                           | 2 (1)                | 0.07      | 0.7859    |
| Blackberry           | 5 (1)                           | 3 (1)                | 0.06      | 0.8075    |
| Blueberry            | 5 (0)                           | 5 (1)                | 10.8      | 0.0012    |

*Notes:* Standard error is reported in parentheses. *F*- and *P*-values represent results from general linear model following logit transformation.

---

Fig. 6. Linear relationship between biomass measured on permanent monitoring plots and biomass predicted from the LANDIS-II simulation at Fort Benning, Georgia.
throughout the simulation period, while all forest dominated by loblolly and shortleaf pine converted to hardwood forest within the first ~80 yr (Fig. 9b).

**DISCUSSION**

The study results provided no evidence that the open loblolly–shortleaf pine forest represents an alternative stable state in the southeastern United States. Our field study and modeling experiment combine to illustrate both structural similarities, and significant composition and functional differences between the loblolly–shortleaf pine forest and longleaf pine forest. While our results confirm the stability of longleaf pine forest with frequent, low-intensity burning, loblolly–shortleaf pine forest is unstable over moderate (60-yr) timescales. This forest community, prevalent throughout the southeastern United States, likely represents a transitional state between abandoned agricultural land and hardwood forest, not unlike undisturbed forest originating from abandoned agriculture (Oosting 1942).

The open loblolly–shortleaf pine forest has many structural attributes in common with natural longleaf pine forest but differs in several critical compositional attributes that likely contribute to its instability. The prevalence of shrubs and hardwood trees in the midstory of loblolly–shortleaf pine forest contrasts strongly with that of natural longleaf pine forest. The dominance of resilient, resprouting shrub and hardwood tree

**Fig. 7.** Chord diagram and bar chart illustrating forest type changes on Fort Benning after 200 yr of no burning during LANDIS-II simulation. The chord width represents area of forest type change. The color of the chord and the thin white line depict the destination forest type. The bar chart indicates the initial (2017) and final (2217) areas occupied by each forest type.
species in these strata can transform fuel beds from pine-dominated to those dominated by fire-suppressive fuels of broadleaf plants (e.g., sweetgum leaves and twigs; Addington et al. 2012). Higher hardwood tree and shrub cover can lead to a positive feedback cycle of lower fire severities, higher hardwood tree and shrub survival, continued growth and proliferation of tree and shrub stems, and continued suppression of fire effects (Thaxton and Platt 2006, Loudermilk et al. 2011, Kreye et al. 2013). Not only the density of shrub and hardwood species but also the composition of these species contributes to fire feedbacks and represents a critical distinction between loblolly–shortleaf pine and longleaf pine forest. Specifically, field data confirm loblolly–shortleaf pine forest is dominated by fire-suppressive shrub and hardwood tree species, while the hardwood trees and shrubs in longleaf pine forest are largely fire facilitators, producing foliage that will burn readily under many conditions (Kane et al. 2008). Additionally, high competition from hardwood tree regeneration in loblolly–shortleaf pine forest facilitates colonization of canopy gaps created from overstory tree loss, and loss of pine-dominance over-time (Knapp et al. 2014), especially on fine-textured soils at Fort Benning, where higher site productivity facilitates rapid regrowth of hardwood vegetation (Addington et al. 2015b). Finally, young loblolly pine regeneration, which is common in the understory of the loblolly–shortleaf pine forest, is intolerant of fire for the first few years (Shultz 1997, Williams 1998). For example, treatment with prescribed fire 2 yr following regeneration harvest killed over 70% of loblolly pine
seedlings (>10 cm in height) at Fort Benning (Knapp et al. 2011). Shortleaf pine seedlings and saplings are more tolerant of fire, due to their ability to resprout at a young age, and anecdotal results from repeated measurements show shortleaf pine to be the primary pine recruiting to the midstory in loblolly–shortleaf pine forest. Results from monitoring plots clearly show the presence of both loblolly and shortleaf pine trees in the midstory stratum in spite of frequent fire. However, the observed pine tree densities are severely outmatched by the hardwood trees and shrubs (~100 vs. ~3000 stems/ha). The combination of high competition from persistent, fire-suppressive hardwood tree and shrub species, and the susceptibility of young loblolly to fire is critical compositional attributes of loblolly–shortleaf pine forest that undermine its stability and sustainability under either no disturbance or frequent surface fires.

Additional interactions between dominant species traits and fire likely contribute to differences in modeled results between loblolly–shortleaf pine and longleaf pine forest. While longleaf pine needles have lower energy content than both loblolly and shortleaf pine foliage (Reid and Robertson 2012), fuel beds dominated by longleaf pine needles have a higher flammability compared to loblolly–shortleaf pine fuel beds for at least three reasons (Pausas et al. 2017). First, longleaf pine trees produce higher needle loads compared to loblolly and shortleaf pine under comparable tree densities (Reid and Robertson 2012), which may be explained by higher rates of needle retention in loblolly and shortleaf pine (2–3 yr) compared to longleaf pine (1–2 yr; Landers 1991). Second, longleaf pine needles have between two and three times higher densities of resin canals (Landers 1991) and produce higher rates of resin flow (Hodges et al. 1977) compared to loblolly and shortleaf pine. Pine resin is extremely flammable and is a well-known fire stimulant, contributing to fuel flammability (Romero et al. 2019). Third, longleaf pine needles are ~75% longer than loblolly and ~200% longer than shortleaf pine needles (Landers 1991). Long needles may contribute to higher fuel connectivity, facilitating fire spread across fuel beds at fine scales. Collectively, these differences in species traits interact with fire in different ways that contribute to forest functioning and stability under repeated burning.
While the objective of our study was to examine the stability of the forest communities under a practical burn-only scenario that could be employed forest-wide, the use of alternative management scenarios may affect the stability of the loblolly–shortleaf pine forest. For example, mechanical or chemical control of competing hardwood vegetation is often used to restore or maintain open pine forests (Brockway and Outcalt 2000, Guldin 2019). Used in conjunction with burning, these treatments have been shown to maintain the pine-dominated stands for several decades (Shelton and Cain 2000, Cain and Shelton 2002, Liechty and Hooper 2016). However, the use of these treatments to sustain the community over the long-term remains unclear, and repeated treatment with chemical is likely necessary to control and eradicate resilient hardwood and shrub species (Freeman and Jose 2009). Such intensive management intervention is commonly only feasible on small landholdings or in certain critical spots of large landholdings. Additionally, the intensive management scenarios are unsuitable for examining community stability and potential for an alternative ecosystem state, which explains why we did not examine their effects here. The use of alternative management regimes, including the repeated use of mechanical, chemical, and fire, to control competing hardwood vegetation and accommodate the sustainable production of overstory trees over multiple generations requires comprehensive examination.

The overstory composition and location of the loblolly–shortleaf pine community in the region may also affect future forest trajectory under frequent fire alone. Shortleaf pine, in decline throughout its range, naturally dominated and regulated certain frequent-fire communities in the southeastern and mid-Atlantic regions of the United States (Clewell 2013, Anderson et al. 2016, Guldin 2019). For example, in the Interior Highlands region of Arkansas and Oklahoma, shortleaf pine dominates a pine savanna community, regulated by frequent fire, which is largely analogous to longleaf pine savannas on the coastal plain (Hedrick et al. 2007, Guldin 2019). In contrast, the community described in this study is loblolly pine dominated. While shortleaf pine is present in each stratum, loblolly pine regulates the light environment and litter–fire–groundcover interactions. Therefore, the findings from this study may not be representative of communities where shortleaf pine is present in higher proportions, dominates the overstory, or is present with less aggressive interfering hardwood vegetation.

The clear instability and decline in longleaf pine forest under no disturbance highlight the importance of frequent fire for the maintenance of longleaf pine forest (Van Lear et al. 2005). A similar, recent modeling experiment utilizing LANDIS-II showed an identical rapid (<50 yr) decline in longleaf pine and increase in hardwood dominance in the absence of fire (Flanagan et al. 2019). Frequent fire is not only critical to the maintenance of longleaf pine forest, but also critical to its proliferation over-time (Brockway et al. 2006). Our results suggest that the area covered by longleaf pine forest increases under frequent fire, with the greatest transition occurring in forest with some longleaf pine presence but dominated by loblolly and shortleaf pine at the start of the simulation (Mixed Pine-Longleaf forest type). Evidence from monitoring plots confirms the presence of longleaf pine in both the understory and midstory of the loblolly–shortleaf pine forest, at some level. However, our modeling results illustrate that where longleaf pine was absent from the overstory at the start of the simulation (loblolly pine, mixed pine, and hardwood forest types), no significant conversion to longleaf pine forest occurred under frequent fire. These results are supported by the fact that colonization of new areas in the absence of seed trees is rare, due in part to the fact that longleaf pine seeds are heavy and fall within 20 m of the parent tree (Croker and Boyer 1975). Collectively, these findings highlight the fact that frequent fire is necessary for the maintenance and expansion of longleaf pine forest, and fire facilitates a transition to longleaf pine dominance in areas where overstory longleaf pine is present.

Precise future forest planning is necessary in many areas of the southeastern United States to maintain open pine forests, given the apparent instability of the open loblolly–shortleaf pine forest combined with its importance to conservation of multiple threatened and endangered species. Results presented here using Fort Benning as a case study, including several important changes to the forest composition in the coming decades,
suggest several steps could be taken to maximize the conservation of threatened and endangered species habitats. Continued treatment with frequent fire may increase the longevity of loblolly–shortleaf pine forest, compared to restricting disturbance. Additionally, adjusting of fire frequency and fire intensity, important factors affecting hardwood tree encroachment (Waldrup et al. 1992, Robertson and Hmielowski 2014, Reilly et al. 2017), may need to occur where sufficient pine fuels are present on fine-textured soils to avoid natural conversion (Addington et al. 2015b). While it was not tested here, periodic treatment with herbicides is very likely to help with prolonging the dominance of loblolly–shortleaf pine forest in some areas by excluding competing hardwood vegetation and promoting herbaceous plants (Addington et al. 2012). The conversion of loblolly–shortleaf pine to longleaf pine forest is necessary where minimal overstory longleaf pine trees currently exist. Modeling results highlight the importance of establishing overstory longleaf pine trees, and continued treatment with frequent fire to maintain and increase the open pine forest communities at Fort Benning. In open loblolly–shortleaf pine forest where longleaf pine does not currently exist, forest planning should consider establishment of longleaf pine, and continued suppression of hardwood trees and shrubs prior to the expected decline of the loblolly–shortleaf pine canopy. Several studies on Fort Benning and elsewhere have shown multiple methods are effective at converting a mature pine canopy to longleaf pine while maintaining the services of an open pine canopy, including underplanting (Knapp et al. 2011) and patch cutting (Kirkman et al. 2007, Knapp et al. 2011).

CONCLUSIONS

The open loblolly–shortleaf pine forest should be considered a transitional forest state and not an alternative stable state (Beisner et al. 2003). Therefore, it will be critical to identify areas with limited longleaf pine overstory and establish it over the next 20 yr to provide the greatest potential for maintaining pine dominance where open loblolly–shortleaf pine forest currently exists. Our results suggest that in the absence of a planned transition from loblolly–shortleaf pine forest to longleaf pine forest, many upland sites are poised to become hardwood-dominated in the coming decades, potentially sacrificing important forest management and conservation objectives.

ACKNOWLEDGMENTS

This research was funded by an Intergovernmental Support Agreement between Fort Benning and Auburn University, Alabama (BENNING-IGSA-16-00). We thank the Nature Conservancy in Georgia who established many of the permanent forest plots used in the study, and the current and former staff of the Natural Resources Management Branch at Fort Benning who contributed to the collection of forest-wide datasets necessary to perform the study. A special thanks to Stephen Kerlin, Mark Byrd, Darrell Odom, and Thomas Hutcherson for their critical field observations and thoughtful ideas, which led to the study. Finally, we thank the contribution of two anonymous reviewers.

LITERATURE CITED

Addington, R. N., T. A. Greene, M. L. Elmore, C. E. Prior, and W. C. Harrison. 2012. Influence of herbicide site preparation on longleaf pine ecosystem development and fire management. Southern Journal of Applied Forestry 36:173–180.

Addington, R. N., S. J. Hudson, J. K. Hiers, M. D. Hurdteau, T. F. Hutcherson, G. Matusick, and J. M. Parker. 2015a. Relationships among wildfire, prescribed fire, and drought in a fire-prone landscape in the south-eastern United States. International Journal of Wildland Fire 41:778–783.

Addington, R. N., B. O. Knapp, G. G. Sorrell, M. L. Elmore, G. W. Wang, and J. L. Walker. 2015b. Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration. Forest Ecology and Management 354:130–138.

Anderson, M., L. Hayes, P. D. Keyser, C. M. Lituma, R. D. Sutter, and D. Zollner. 2016. Shortleaf Pine Restoration Plan: restoring an American forest legacy. Shortleaf Pine Initiative. http://shortleafpine.net/shortleaf-pine-initiative/shortleaf-pine-restoration-plan

Beckage, B., and C. Ellingwood. 2008. Fire feedbacks with vegetation and alternative stable states. Complex Systems 18:159–173.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and Environment 1:376–382.

Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in the early old-field
succession in the Piedmont of North Carolina. Ecological Monographs 23:339–358.

Bragg, D. C., and E. Heitzman. 2009. Composition, structure, and dynamics of a mature, unmanaged, pine-dominated old-field stand in southeastern Arkansas. Southeastern Naturalist 8:445–470.

Brockway, D. G., and K. W. Outcalt. 2000. Restoring longleaf pine wiregrass ecosystems: Hexazinone application enhances effects of prescribed fire. Forest Ecology and Management 137:121–138.

Brockway, D. G., K. W. Outcalt, and W. D. Boyer. 2006. Longleaf pine regeneration ecology and methods. Pages 95–134 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem. Springer, New York, New York, USA.

Brudvig, L. A., and E. I. Damschen. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34:257–266.

Cain, M. D., and M. G. Shelton. 2002. Does prescribed burning have a place in regenerating uneven-aged loblolly-shortleaf pine stands? Southern Journal of Applied Forestry 26:117–123.

Christensen, N. L., and R. K. Peet. 1981. Secondary forest succession on the North Carolina Piedmont. Page 230–244 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession. Springer-Verlag, New York, New York, USA.

Flanagan, S. A., et al. 2019. Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pine forest. Ecosphere 10:e02772.

Freeman, J. E., and S. Jose. 2009. The role of herbicide in savanna restoration: effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. Forest Ecology and Management 257:978–986.

Frost, C. C. 2009. Historic fire regimes and presettlement vegetation of Fort Benning, Georgia. Report prepared for Department of Public Works Environmental Management Division, Land Management Branch, Fort Benning, Georgia, USA.

Greene, R. E., R. B. Iglay, K. O. Evans, T. B. Wigley, and D. A. Miller. 2019. Estimating capacity of managed pine forests in the southeastern U.S. to provide open pine woodland condition and gopher tortoise habitat. Forest Ecology and Management 432:200–208.

Guldin, J. M. 2019. Restoration of native fire-adapted southern pine-dominated forest ecosystems: diversifying the tools in the silvicultural toolbox. Forest Science 65:508–518.

Hartnett, D. C., and D. M. Krofta. 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. Bulletin of the Torrey Botanical Club 116:107–113.

Hedman, C. W., S. L. Grace, and S. E. King. 2000. Vegetation composition and structure of southern coastal plain forests: an ecological comparison. Forest Ecology and Management 134:233–247.

Hedrick, L. D., G. A. Bukenhofer, W. G. Montague, W. F. Pel, and J. Guldin. 2007. Shortleaf pine-bluestem restoration in the Ouachita National Forest. In J. M. Kabrick, D. C. Dey, and D. Gwazw, editors. Shortleaf Pine Restoration and Ecology in the Ozarks: Proceedings of a Symposium. General Technical Report NRS-P-15. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.

Hodges, J. D., W. W. Elam, and W. F. Watson. 1977. Physical properties of the oleoresin system of the four major southern pines. Canadian Journal of Forest Research 7:520–525.

James, F. C., C. A. Hess, B. C. Kicklighter, and R. A. Thum. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecological Applications 11:854–870.

Jasinski, J. P. P., and S. Payette. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecological Monographs 75:561–583.

Jenkins, J. C., D. C. Choynacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive database of diameter-based biomass regression for North American tree species. General Technical Report NE-319. USDA Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, USA.

Jokela, E. J., P. M. Dougherty, and T. A. Martin. 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. Forest Ecology and Management 192:117–130.

Kane, J. M., J. M. Varner, and J. K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. Forest Ecology and Management 256:2039–2045.

Kirkman, L. K., R. J. Mitchell, M. J. Kaeser, S. D. Pecot, and K. L. Coffey. 2007. The perpetual forest: using undesirable species to bridge restoration. Journal of Applied Ecology 44:604–614.
Kreye, J. K., J. M. Varner, J. K. Hiers, and J. Mola. 2013. Fire-vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. New Zealand Journal of Botany 54:247–272.

Knapp, B. O., J. L. Walker, G. G. Wang, H. Hu, and R. N. Addington. 2014. Effects of overstory retention, herbicides, and fertilization on sub-canopy vegetation structure and functional group composition in loblolly pine forests restored to longleaf pine. Forest Ecology and Management 320:149–160.

Knapp, B. O., G. G. Wang, H. Hu, J. L. Walker, and C. Tennant. 2011. Restoring longleaf pine (Pinus palustris Mill.) in loblolly pine (Pinus taeda L.) stands: effects of restoration treatments on natural loblolly pine regeneration. Forest Ecology and Management 262:1157–1167.

Kreye, J. K., J. M. Varner, J. K. Hiers, and J. Mola. 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecological Applications 23:1976–1986.

Landers, L. L. 1991. Disturbance influences on pine traits in the southeastern United States. Pages 61–98 in Proceedings of the Tall Timbers Fire Ecology Conference, No. 18, High Intensity Fire in Wildlands: Management Challenges and Options. Tall Timbers Research Station, Tallahassee, Florida, USA.

Lee, M. T., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274.

Liechty, H. O., and J. J. Hooper. 2016. Long-term effect of periodic fire on nutrient pools and soil chemistry in loblolly-shortleaf pine stands managed with single-tree selection. Forest Ecology and Management 380:252–260.

Loudermilk, E. L., W. P. Cropper Jr, 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.

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.

Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Diversity and Distributions 21:236–244.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “Mesophication” of forests in the eastern United States. BioScience 58:123–138.

Oosting, H. J. 1942. An ecological analysis of the plant communities of the Piedmont, North Carolina. American Midland Naturalist 28:1–126.

Pausas, J. G., J. E. Keeley, and D. W. Schwilk. 2017. Flammability as an ecological and evolutionary driver. Journal of Ecology 105:289–297.

Platt, W. J., and S. L. Rathburn. 1993. Dynamics of old-growth longleaf pine population. Pages 275–297 in S. M. Hermann, editor. Proceedings of the Tall Timbers Fire Ecology Conference, No. 18, The Longleaf Pine Ecosystem: Ecology, Restoration and Management. Tall Timbers Research Station, Tallahassee, Florida, USA.

Quartermann, E., and C. Keever. 1962. Southern mixed hardwood forest: climax in the southeastern Coastal Plain, U.S.A. Ecological Monographs 32:167–185.

Reid, A. M., and K. M. Robertson. 2012. Energy content of common fuels in upland pine savannas of the south-eastern US and their application to fire behavior modelling. International Journal of Wildland Fire 21:591–595.

Reilly, M. J., K. Outcalt, J. J. O’Brien, and S. Wade. 2017. Effects of repeated growing season prescribed fire on the structure and composition of pine-hardwood forests in the southeastern Piedmont, USA. Forests 8:8.

Robertson, K. M., and T. L. Hmielowski. 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174:765–776.

Romero, B., C. Fernandez, C. Lecareux, E. Ormeño, and A. Ganteaume. 2019. How terpene content affects fuel flammability of wildland-urban interface vegetation. International Journal of Wildland Fire 28:614–627.

Samuelson, L., T. Stokes, J. R. Butnor, K. 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.

Samuelson, L., T. Stokes, T. Cooksey, and P. McLemore III. 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. Tree Physiology 21:369–376.

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.
Shelton, M. G., and M. D. Cain. 2000. Regenerating uneven-aged stands of loblolly and shortleaf pines: the current state of knowledge. Forest Ecology and Management 129:177–193.

Shultz, R. P. 1997. Loblolly pine: the ecology and culture of loblolly pine (Pinus taeda L.). Agricultural Handbook 713. USDA Forest Service, Washington, D.C., USA.

Sturtevant, B. R., R. M. Scheller, B. R. Miranda, D. Shinneman, and A. Syphard. 2009. Simulating dynamics and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. Ecological Modeling 220:3380–3393.

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 change. Ecosphere 9:e02191.

Thaxton, J. M., and W. J. Platt. 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87:1331–1337.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management 211:150–165.

Waldrup, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. Forest Ecology and Management 47:195–210.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Williams, R. A. 1998. Effects of fire on shortleaf and loblolly pine reproduction and its potential use in shortleaf/oak/hickory ecosystem restoration. Pages 321–325 in T. A. Waldrup, editor. Proceedings of the ninth biennial southern silvicultural research conference. General Technical Report SRS-20. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Wood, D. R., F. J. Vilella, and L. W. Burger Jr. 2008. Red-cockaded woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest. The Wilson Journal of Ornithology 120:793–800.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3055/full