Overstory-derived surface fuels mediate plant species diversity in frequently burned longleaf pine forests

Jane E. Dell,[1],† Lora A. Richards,[1] Joseph J. O'Brien,[2] E. Louise Loudermilk,[2] Andrew T. Hudak,[3] Scott M. Pokswinski,[4] Benjamin C. Bright,[3] J. Kevin Hiers,[4] Brett W. Williams,[5] and Lee A. Dyer[1]

[1]*Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, 1664 N. Virginia Street, Reno, Nevada 89557 USA*
[2]*Center for Forest Disturbance Science, Southern Research Center, U.S. Forest Service, 320 Green Street, Athens, Georgia 30602 USA*
[3]*Forestry Sciences Laboratory, Rocky Mountain Research Station, U.S. Forest Service, 1221 South Main Street, Moscow, Idaho 83843 USA*
[4]*Wildland Fire Science Program, Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, Florida 32312 USA*
[5]*Air Force Wildland Fire Center, Eglin AFB, 107 FL-85, Niceville, Florida 32578 USA*

Abstract. Frequently burned low-latitude coniferous forests maintain a high-diversity understory. Longleaf pine (*Pinus palustris* Mill.) forests and woodlands have exceptionally high diversity at fine scales and very frequent fire return intervals (1–3 yr). Furthermore, the positive association between high-frequency, low-intensity surface fires and high species richness in longleaf pine ecosystems is well documented but poorly understood. Recent studies have demonstrated additional linkages between specific fuel assemblages and fire intensity at small spatial scales. In this study, we build upon both patterns by using long-term datasets to examine the relationship between fire and specific fuel types, and how the combination of these two elements contributes to ground cover species diversity. We used 11 yr of monitoring data from longleaf pine forests at Eglin Air Force Base, Florida (USA), to parameterize a structural equation model that examines causal relationships between fuels and fire history on ground cover plant diversity. Overstory-derived fuels, including pine needle litter, pine cones, and other 10 and 100-h woody fuels, had the greatest positive impact on diversity in relatively open-canopied, frequently burned reference stands. A second model examined surface fuel components originating from the forest overstory as characterized by airborne light detection and ranging and found that pine needle litter was positively associated with canopy density. Our parameter estimates for causal relationships between easily measured variables and plant diversity will allow for the development of management models at the stand scale while being informed by fuels measured at the plot scale.

† **E-mail:** jane.dell@nevada.unr.edu

Introduction

Frequently burned coniferous forests often share a similar forest structure globally, with a monospecific overstory of pine, a sparse midstory, and a high-diversity understory. These forests are widely distributed around the lower latitudes of the Northern Hemisphere and constitute a global conservation concern (Veldman et al. 2015). Longleaf pine (*Pinus palustris* Mill.) forests represent an archetype of these systems and are dependent on very frequent fires for maintenance of biodiversity and ecosystem function (Glitzenstein et al. 2003, Kirkman et al. 2004, O'Brien et al. 2008,

Mitchell et al. 2009). For any terrestrial ecosystem, fire can be a catalyst of community interactions via attenuating competition between plant species, allowing for seedling establishment by reducing surface fuels, and adding nutrients to the soil (Kirkman et al. 2001, 2004, Mitchell et al. 2006, 2009). Fires burning in longleaf pine forests are typically high-frequency, low-intensity disturbances that predominately run through surface fuels and understory shrubs with little effect on the canopy. These frequent fires are the major force driving the high levels of ground cover plant diversity found in longleaf pine stands, with up to 50 species/m^2 (Walker and Peet 1984, Kirkman et al. 2001, 2004, Palmquist et al. 2015).

Today, longleaf pine forests occupy a fraction of their historic range. Deforestation, logging, and development have reduced forested areas, and decades of fire exclusion policy and practice have given a competitive advantage to faster-growing tree species that thrive in the absence of fire. Combined, these events have resulted in extensive habitat degradation and reductions in biodiversity (Noss et al. 1995, Frost 2006, Mitchell et al. 2006). Conservation of longleaf pine ecosystems is also important because these forests possess high levels of endemism and are located within a proposed global hotspot of biodiversity (Noss et al. 2015). While effective management via prescribed burning or low-intensity wildfire is critical for continued health of the longleaf pine ecosystem, mechanistic models of the role of fire in maintaining diversity need considerable development. Variation in fire intensity within burned areas has been found to be an important driver of plant community function and structure, including high ground cover diversity and horizontal or vertical distribution of plant and debris layers within a forest or forest structure (Hiers et al. 2009, Wiggers et al. 2013, Loudermilk et al. 2016, O'Brien et al. 2016a). One possible source leading to variation in local-scale fire intensities is the variation in distributions of surface fuels, or fuels found near the forest floor (O'Brien et al. 2016a). These fuels are derived from the overstory, midstory, and understory. This variation in fuel sources and effects on fire intensities is a critical part of the ecology of fuels concept (Mitchell et al. 2009), which focuses on cycles of impacts of forest structure and vegetative composition on fuel heterogeneity, which in turn affects fire behavior and community responses to fire, including changes in plant diversity and long-term forest structure.

Heterogeneity in fuels across the landscape directly affects fire intensities in these surface fire regimes. Woody fuels, such as pine cones and branches, are spatially associated with pine tree distribution and temporally associated with changing canopy cover (tree mortality, growth) and episodic cone production cycles (Boyer 1998). These dense fuels burn for extended periods with up to 12 times more energy release than finer fuels (grasses, forbs, shrubs) and vary at scales <0.25 m^2 (Fonda and Varner 2004, Mitchell et al. 2009, O'Brien et al. 2016a). Understory-derived fuels such as shrubs and deciduous oaks comprise a significant portion of the litter on the forest floor, and volatile shrubs and other fine fuels, such as pine needle litter, grasses, forbs, and legumes, are important for carrying fire across the landscape. Using the spatially explicit wildland fuel cell concept, Loudermilk et al. (2012) empirically linked fine-scale variation in fuel as the driver of heterogeneity in fire behavior and fine-scale fire intensity. We know that fire is the critical element in maintaining biodiversity in longleaf pine forests (Kirkman et al. 2004); thus, understanding the causal mechanisms linking plant community composition to fuel type and understanding the contribution of various fuel types to fire effects are major goals for ecology (Thaxton and Platt 2006, Mitchell et al. 2009, Gagnon et al. 2010).

The issue is that different fuels burn simultaneously, making it difficult through retrospective assessments alone to disentangle each fuel type's contribution to the ecological consequences of fire. New empirical methods utilizing infrared thermography can capture in-fire, spatially resolved, radiative heat flux and relate these patterns to fire effects (O'Brien et al. 2016a, b). While these data are informative at fine scales, they need to be linked to coarser-scale patterns in forest structure in order to investigate the impacts of forest management on different scales of diversity (Hiers et al. 2003). Structural equation modeling (SEM) is a statistical approach that allows the testing of hypothesized causal relationships among complex associations of variables (Grace et al. 2015, Shipley 2016). It is especially useful for testing proposed causal linkages between fine-scale

fuel measurements and landscape-scale patterns of forest structure. For example, the use of active remote sensing, specifically airborne light detection and ranging (LiDAR), can provide detailed information on forest structure at the landscape scale and can be used to test hypotheses about how such forest structure affects diversity at smaller scales.

In this study, we created SEMs to examine associations between fire, fuels, and plant species richness at fine scales (<1 m^2) in frequently burned longleaf pine forests of northwest Florida and then assessed whether LiDAR maps of forest structure over a landscape (100s of km^2) could predict relevant patterns of fuel types driving patterns of diversity. We initially tested for associations among the number of fires and the distribution of six common litter fuel types. We hypothesized that spatiotemporally variable distribution of these common fuel types drives heterogeneous fire behavior. We also examined associations between each fuel type and associated ground cover diversity. From this, we modeled the indirect effects of fire on ground cover diversity mediated by fuel type. Finally, at a coarser scale, we investigated and modeled how forest structure predicts each fuel type (Hudak et al. 2016a, b). Combined, we were able to test causal relationships responsible for maintaining high levels of plant diversity in longleaf pine ecosystems based on fuel types and forest structures that are common in other forests with similar structure and burn frequency.

The statistical modeling was guided by two primary objectives: first, to model the effects of burning different fuel types on variation in ground cover plant diversity in reference stands, and second, to evaluate the ability to up-scale patterns of fuel, fire, and diversity to a management context through linkages to overstory forest structure as characterized by airborne LiDAR data and the field measurements of the fuel bed. While many fire modeling applications consider litter as a uniform component of surface fuels for increased ease of simulation (Keane 2015), separating out the specific types of litter can be highly informative when assessing fuel type contributions to fire effects. We used 11 yr of vegetative monitoring data (collected by the Natural Resources Branch, Eglin Air Force Base [EAFB], Hiers et al. 2007) from forested longleaf pine stands to parameterize

a SEM comprising hypothesized relationships between fire history, plant diversity, and ground measured surface fuel variables, represented by commonly occurring types of litter: woody fuels, oaks and shrubs, forbs, grasses, saw palmettos, and longleaf pine needles (Table 1). In an effort to better create a foundation upon which to understand the ecology of fuels, we focused our efforts on regularly burned reference stands. A second SEM was then created to assess LiDAR as an effective indicator of the origin of these fuel components within these reference plots (Table 1).

As a secondary objective relevant to both the generality and context dependency of our findings, we tested for differences in modeled effect size between vegetative community types and stand quality. To examine litter effects in the two predominant community types, we extended our main model by running the SEM separately through plots located in sandhills and flatwoods. In a second comparison, we examined how effect sizes vary along a gradient of stand quality represented by increased fire return intervals (FRI) found in sandhill plots located within reference, restoration, and plantation stands.

MATERIALS AND METHODS

Study area

All data were collected at EAFB located in the Gulf Coastal Plain of the Florida panhandle, USA. Eglin Air Force Base is over 180,000 ha in size, is home to over half of the remaining stands of old-growth longleaf pine, and is actively managed by frequent prescribed fire (Holliday 2001, Varner et al. 2005, Hiers et al. 2007). The climate is typified by hot, humid summers with frequent thunderstorms and lightning strikes, mild winters, mean annual temperature of 18.3°C, and annual precipitation of 1580 mm (Provencher et al. 2001). The area has relatively little topography (0–100 m a.s.l.) and is dominated by well-drained Lakeland series soils.

Xeric sandhills and mesic flatwoods are the dominant vegetative communities found at EAFB. Longleaf pine is a foundation species and is typically monodominant in the overstory with a relatively open canopy throughout the site. The sandhills are also comprised of shrubby hardwoods species such as turkey oak (*Quercus laevis*), blackjack oak (*Quercus incana*), and persimmon

Table 1. (A) Names and descriptions of variables in the SEMs with associated hypotheses and (B) LiDAR metrics collected during 2006 and 2008.

Variable	Descriptor	Range	Associated assumptions/hypotheses	Citations to support hypotheses
(A)				
Longleaf pine litter	Detection of longleaf pine needle litter found along fuel transect	0.22–0.58 kg/m^2	The burning of pine needles will be positively associated with diversity by acting as continuous, highly flammable fuel source conducive for fire spread	Loudermilk et al. (2012)
Woody fuels	Detection of 10 and 100-h fuels (including pine cones) found along fuel transect	0.04–0.29 kg/m^2	Pine cones will have longer residence burn times creating open spaces on forest floor for seedling establishment, which will increase diversity	Mitchell et al. (2009), Loudermilk et al. (2012)
Shrub and oak leaf litter	Detection of litter from shrub and oak species: *Ilex* spp., *Quercus laevis*, *Quercus minima*, *Smilax* spp., *Gaylussacia* spp., *Vaccinium* spp.	0.06–0.45 kg/m^2	Volatile shrubs will increase diversity by providing increased fuel flammability for more complete burns. Oak leaves will increase diversity by acting as a continuous, highly flammable surface fuel	Ellair and Platt (2013), Hiers et al. (2014)
Forb litter	Detection of forb-contributed litter found along fuel transect	0.01–0.13 kg/m^2	Forbs will contribute to fuel bed depth providing surface-level fuels, which will moderately increase diversity	Kirkman et al. (2001)
Grass litter	Detection of litter from all graminoid species	0–0.27 kg/m^2	Grass litter will increase diversity by providing another source of continuous fine fuels	Loudermilk et al. (2012)
Saw palmetto litter	Detection of litter from *Serenoa repens*	0–0.09 kg/m^2	Saw palmetto is highly flammable and will provide added fire intensities and increase diversity with post-fire soil nutrient input	Shafer and Mack (2010)
Number of fires	Number of prescribed fires conducted from 1995 to 2012	3–11 fires (FRI: 1.2–4.3 yr)	Frequent fire will have negative associations with fuels as they are consumed by burning	Mitchell et al. (2009)
Ground cover diversity	Mean species richness of ground cover vegetation (<1.37 m in height)	49–84 species in 400-m^2 subplots	Response variable in all SEMs	Walker and Peet (1984), Kirkman et al. (2001, 2004), Palmquist et al. (2015)
(B)				
Overstory density	LiDAR: % vegetation located above heights of 5 m	11.1–36.5%	Overstory LiDAR will indicate canopy-derived fuels	Hudak et al. (2016*a, b*)
Understory density	LiDAR: % vegetation located between heights of 0.5 and 1.37 m	0.3–17.4%	Understory LiDAR will indicate the amount of shrub and oak litter fuels	Hudak et al. (2016*a, b*)
Surface density	LiDAR: % vegetation located between heights of 0 and 0.5 m	52.1–81.3%	Surface-level LiDAR will indicate fuels on or near the forest floor	Hudak et al. (2016*a, b*)

Notes: EAFB, Eglin Air Force Base; FRI, fire return intervals; LiDAR, light detection and ranging; SEM, structural equation model. (A) Model variables represent monitoring data collected over the years 2001–2102 by Jackson Guard, EAFB, FL. (B) Data ranges are for plots located within longleaf pine reference stands.

(*Diospyros virginiana*); however, these species are generally absent from the flatwoods. Most of the hardwoods are in a shrub state, as they are continuously top-killed by fire. The ground cover vegetation contains most plant species and is dominated by several grasses, such as wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), as well as dwarf huckleberry (*Gaylussacia dumosa*), evergreen blueberry (*Vaccinium darrowii*), runner oak (*Quercus minima*), saw palmetto (*Serenoa repens*), and gallberry (*Ilex glabra*).

Eglin Air Force Base contains a diverse array of longleaf pine forests including reference

stands representing high-quality habitat with relatively open understories, stands undergoing the process of ecological restoration via chemical and mechanical treatments toward reference conditions, and plantations of longleaf pine. Current EAFB natural resource policies of increasing fire frequency for red-cockaded woodpecker (*Picoides borealis*) management began in 1995. Reference plots in the dataset experienced fire nearly every other year, from at least the mid-1990s through the time of data collection with variation in FRI of 1.6–6 yr, while restoration and plantation plots had a broader range of FRI of 2.1–18 yr.

Monitoring data

The EAFB Natural Resources Branch monitoring program began collecting fuel and vegetation data in 201, one-hectare plots randomly located across the base in 2001. All plots in the program were sampled one year following management activities including fire, herbicide treatments, and timber harvest to determine the effects on plant communities. With the regular application of fire occurring every 15–24 months, plots were revisited and resampled on two to five occasions between the years 2001 and 2012. Each plot visit included the measurement of understory species richness in four 10×10 m subplots nested within each monitoring plot, as well as collection of fuels data. During each sampling event, fuels were measured every 10 m along two 50-m point-intercept transects and averaged for each plot. Woody fuels were counted when they intercepted transects by time lag classes (Brown 1974), with intact pine cones and 2.54–7.62 cm diameter branches recorded as 100-h fuels and broken cones and branches 0.635–2.54 cm in diameter designated as 10-h fuels. Total litter depth was measured at each intercept, litter type determined from original form, and then tallied by individual litter class including longleaf pine needles, grasses, saw palmetto, oaks, shrubs, and forbs. The depth of the combined fermentation (Oe) and humus (Oa) layers, also known as duff, was recorded along transects. Live fuels for these same vegetation classes were also recorded with shrubs and oaks being classified into volatile and non-volatile categories. At the time of fuel measurement, grass litter was closely associated with live fuels as bunch grass represents a combination of some percentage of live fuels and litter.

Additionally, a tally was taken along transects of intercept with bare ground. Historical records were used to determine fire frequency over the last 40 yr. Additional details about the EAFB monitoring protocol can be found in Hiers et al. (2007).

In this study, we analyzed a subset of plots that were sampled between 2001 and 2012 in the EAFB monitoring dataset including those located within reference stands (35 plots: 26 sandhill and 9 flatwoods), monitoring plots within sandhill restoration stands (67 plots), and plots located within sandhill plantation stands (30 plots). Because individual plots were sampled numerous times over the 11 yr, measured fuel variables and species richness were averaged across time for each plot prior to analyses. While live fuels are an important consideration in terms of fuel continuity and fire intensity, they are consumed quickly when burned, resulting in brief residence times and little effect on plant mortality (Wenk et al. 2011, Gagnon et al. 2015, Fill et al. 2016). Therefore, we focused our analyses exclusively on dead and downed surface fuels. Furthermore, oak litter, which included both deciduous and evergreen species, was combined with shrub litter prior to analyses. For ease of interpretation (Table 1), fuels were converted into mass per area (kg/m^2) measurements with woody fuels following conversions outlined in Brown (1974) and litter loadings as described in Prichard et al. (2013).

LiDAR data

Airborne LiDAR uses high-frequency laser pulses to measure distances between the LiDAR sensor and underlying vegetation and terrain. When flown over a forest, LiDAR characterizes the forest structure as a three-dimensional cloud of points. These points resemble the spatial configuration of forest vegetation within the canopy, understory, and near the ground surface (Hudak et al. 2009). Light detection and ranging processing for forest management often entails reducing the three-dimensional data of canopy elements to metrics of canopy height and density that can serve as informative inputs into predictive models (Hudak et al. 2016*a*). By calculating these metrics within defined monitoring plot areas, the LiDAR metrics can serve as predictor variables to the observational data collected at finer spatial scales.

Table 2. Light detection and ranging (LiDAR) canopy density metrics.

Metric name	Height of LiDAR returns (m)	Measurement
d1	≥0 and <0.5	Surface vegetation
d2	≥0.5 and <1.37	Understory
d3	≥1.37 and <5	Midstory
d4	≥5 and <30	Overstory

Light detection and ranging data covering EAFB were downloaded from a public repository (http://www.nwfwmdLiDAR.com/); data were collected in 2006–2008 at mean return densities ranging from 0.5 to 2.9 points/m^2. Returns were classified as ground or nonground and normalized to height above ground using the "lasground" tool of the LAStools software program (Isenburg 2015). The "lascanopy" tool was then used to generate canopy density metrics within four vertical strata (Table 2) calculated at two levels: (1) within the discrete plot footprints where monitoring data were collected in the field (i.e., model level) and (2) within contiguous 30 × 30 m grid cells across the entirety of EAFB (i.e., map level). The calculated density metrics for the overstory, midstory, understory, and surface strata were then used as predictor variables in a SEM investigating the vertical canopy strata of origin for the plot measured litter categories described above. In addition, EAFB managers maintain a geodatabase of fire history that includes the fire boundary, date of burn, and fuel type for each fire that has occurred at EAFB since 1972. We summarized this geodatabase to produce a GIS layer that consisted of a 30 × 30 m raster of the number of fire occurrences between 1995 and 2012 (Fig. 1). Additional details regarding LiDAR processing and analysis are available in Hudak et al. (2016a).

Structural equation model formulation

The first SEMs were formulated to test hypothesized causal relationships between fire, fuels, and ground cover plant species diversity (Table 1A). Ubiquitous fuel types found in longleaf pine forests may contribute to ground cover diversity when consumed by fire; these fuel types include woody fuels (10 and 100-h time lag fuels, which includes both weathered and recently fallen pine cones) and litter (longleaf pine needles, shrub and oak, grass, forb, and saw palmetto). A second approach focused on the hypothesis that remotely sensed LiDAR metrics predict how forest layers (overstory, midstory, understory, and surface vegetation) contribute to the different fuel types examined in the first path analysis (Table 1B).

For all path models, all variables were standardized and transformed to meet assumptions of normality, and models were run using the lavaan package in R (Rosseel 2012, R Development Core Team 2015). All models were specified based on our predictions (Table 1), estimated by maximum likelihood, and tests of model fit
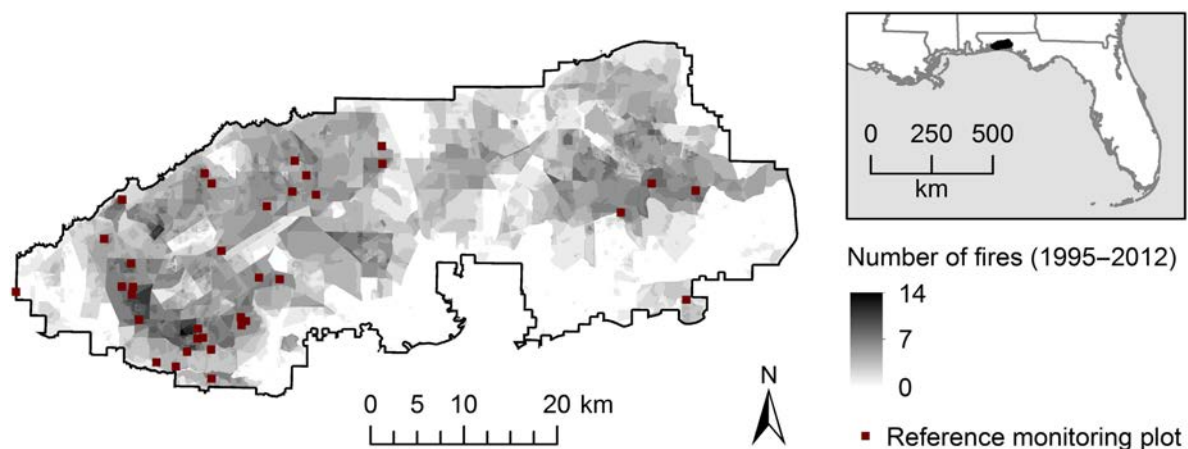

Fig. 1. Map of research locations at Eglin Air Force Base (EAFB) in northwestern Florida, USA. Shaded areas correspond to the number of fires occurring at EAFB during the 1995–2012 period, and red dots indicate the location of reference monitoring plots within EAFB.

followed guidelines outlined in Shipley (2016). Model fit indices including chi-square and Akaike information criterion (AIC) were used to determine the specific model that best fit the data after removal of non-significant associations, with *P*-values of >0.05 considered to indicate a good model fit. Direct effects were estimated directly using standardized path coefficients, while indirect effects of fire through each fuel type were simply the products of direct effects for each pathway from fire to diversity.

The SEM was run separately for flatwoods and sandhills reference plots to test differences in fuel contributions based on the two main vegetative community types found at EAFB. Additionally, the same SEM approach was utilized for different sandhill forest stand types: reference sites, restoration sites, and longleaf pine plantations to represent a gradient in forest quality. Because vegetation structure and composition are tightly linked with frequency of fire in longleaf systems, the gradient was based on lower number of fires and longer FRI. Over the 18-yr period of fires at EAFB used in the models, the mean FRI was 3.19, 5.89, and 7.87 yr in the reference stands, restoration sites, and plantations, respectively.

RESULTS

Fuel-diversity model

Fuel type had varied effects on species richness following fire in reference plots. Insignificant pathways with negligible effect on diversity included both shrub and oak litter, and forb litter, which were removed from the final model to improve model fit (full model: AIC = 649; reduced model: AIC = 407), yielding a parsimonious model that was a good fit to the data (Fig. 2; $\chi^2 = 5.5$; df = 7; $P = 0.60$). As hypothesized (Table 1), regular burning had negative effects on all litter types: longleaf pine litter (standardized path coefficient [spc] = −0.23; slope [β = −1.8]), grass litter (spc = −0.01; β = −0.03), saw palmetto litter (spc = −0.11; β = −0.13), and woody fuels (spc = −0.12; β = −0.96). Additionally, all fuel types were significantly and negatively (i.e., in their consumption) associated with ground cover plant species diversity (Table 3, Fig. 2). Specifically, saw palmetto litter had a significant negative effect on diversity (spc = −0.15, β = −0.68) followed by woody fuels (spc = −0.44, β = −0.31),

grass litter (spc = −0.37, β = −0.31), and longleaf pine litter (spc = −0.39, β = −0.25).

Overall, the indirect effects of fire on species richness, based on the products of measured direct effects from fire, through fuel type, to diversity, were positive for all fuel types (Table 3). The burning of overstory-derived fuels had the greatest positive effects on ground cover diversity with longleaf pine needle litter producing the largest indirect effect (spc = 0.09; β = 1.2) as well as pine cones and other woody fuels (spc = 0.05; β = 0.74). Saw palmetto litter also exerted a positive effect on species richness (spc = 0.02; β = 0.22; Table 3). The burning of grass litter provided little contribution to ground cover diversity (spc = 0.004; β = 0.03). Summing these individual contributions together results in a clear mechanism for the well-documented positive association between fires and ground cover diversity in longleaf pine systems and is indicated by the significant indirect effect (spc = 0.16, β = 2.2) as shown in the black dashed line in Fig. 2.

LiDAR model

In longleaf pine ecosystems, fuels are contributed from different forest layers, including the overstory (trees above 5 m), understory (plants 0.5–1.37 m height), and surface vegetation (0–0.5 m). Since reference stands do not typically have a well-developed midstory, this component of the forest canopy was excluded from the model. In reference stands, LiDAR density measurements were effective in representing most fuel types based on correlations with forest structure ($\chi^2 = 3.98$; df = 12; $P = 0.98$, Fig. 3). Overstory density was a strong predictor of pine needle litter (spc = 0.36; β = 0.77), and understory density predicted shrub and oak litter (spc = 0.20; β = 0.74). Overstory LiDAR was not an effective indicator of woody fuels (spc = −0.18; β = −0.36). The double-headed arrows indicate unestimated relationships, including a positive correlation between near-surface LiDAR (0–0.5 m) and forb litter (spc = 0.25; β = 0.36), a weaker association with saw palmetto litter (spc = 0.28; β = 0.07), and even less with grass litter (spc = 0.02; β = 0.03).

Forest community type

In a separate SEM, we compared fuel contributions in flatwood and sandhill reference plots (Fig. 4). Pine needles provided the greatest
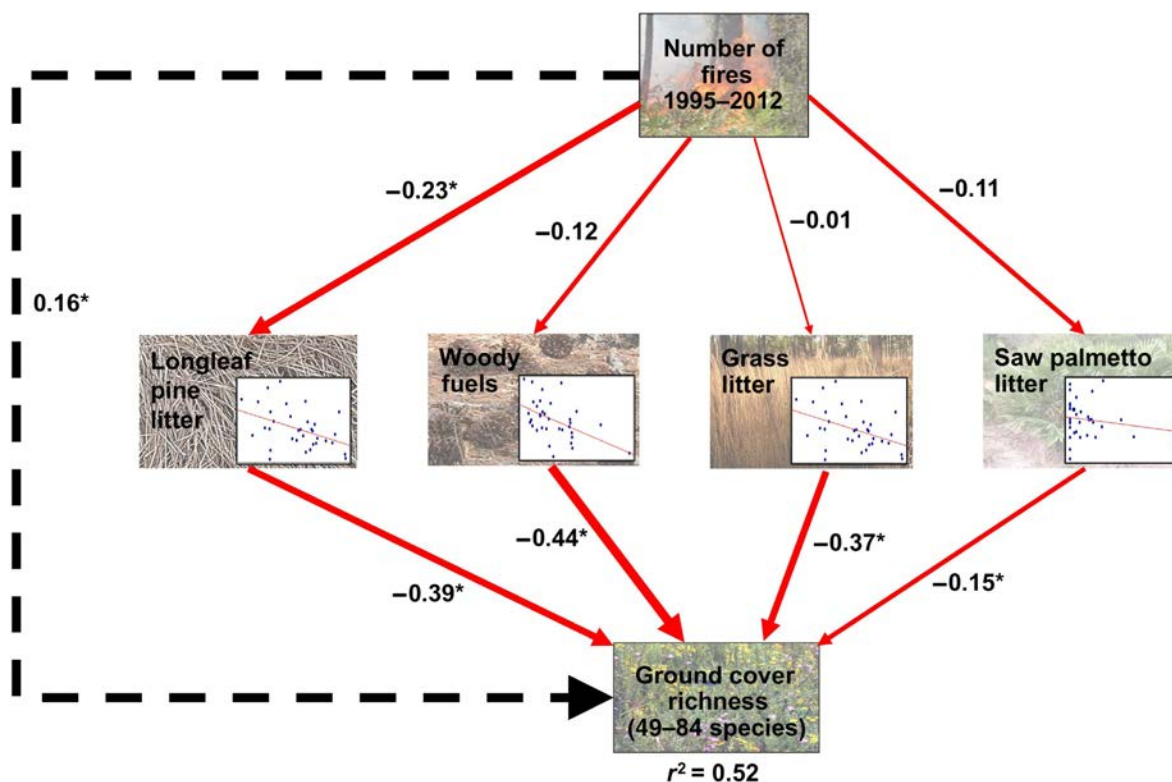
Fig. 2. Structural equation model including hypothesized causal relationships between the burning of individual fuel categories and plant diversity in longleaf pine reference stands. In fire-dependent ecosystems such as the longleaf pine forest, greater numbers of fires have positive effects on ground cover species richness. This relationship is mediated by the composition and consumption of different surface fuel types, including longleaf pine litter, pine cones, and other 10 and 100-h woody fuels, grass litter, and saw palmetto litter. Numbers next to lines are the standardized path coefficients. Line thickness corresponds to strength of path coefficient, and asterisks denote statistical significance ($P < 0.05$). Black dashed line represents total indirect effects of fire on diversity as indicated in Table 3. The model is a good fit to the data ($\chi^2 = 5.2$; df = 7; $P = 0.64$) as indicated by P-values larger than 0.05. Insets within fuel types are partial correlation plots of the paths between individual fuel types and species richness while accounting for the effects of all other fuel types.

Table 3. Indirect effects of fire on diversity for each fuel type.

Fuel	Fire effect on fuel	Fuel effect on diversity	Indirect effect (spc)	Indirect effect (S)
Longleaf pine litter	−0.23*	−0.39*	0.09	1.17
Woody fuels	−0.12	−0.44*	0.05	0.74
Grass litter	−0.01	−0.37*	0.004	0.03
Saw palmetto litter	−0.11	−0.15	0.02	0.22
Total Effects of Fire on Diversity			0.16*	2.16

Notes: Total effects are calculated as the sum of the product of individual standardized path coefficients (spc). Significant pathways are denoted with asterisk. Effect size in terms of species richness (S) is also shown as indicated by calculated slope (β) from fuel-diversity structural equation model.
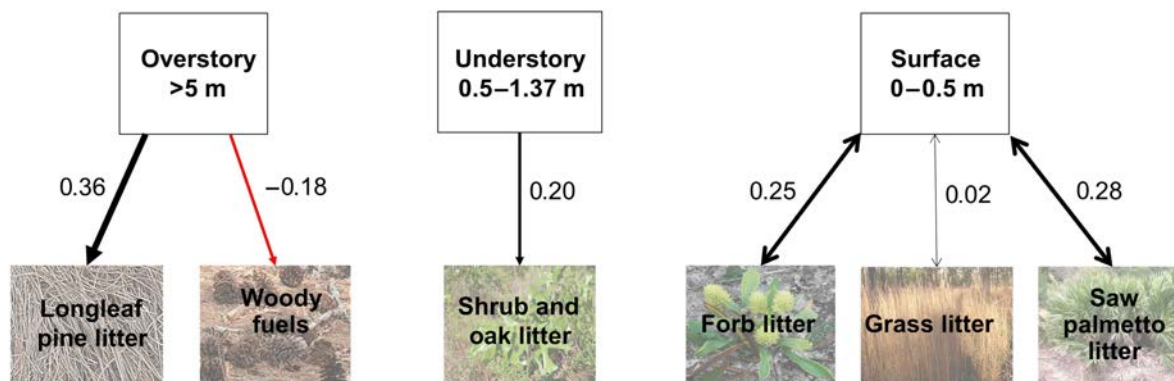
Fig. 3. Structural equation model illustrating light detection and ranging (LiDAR) detection of forest layers as predictors of each individual fuel category in longleaf pine reference stands. LiDAR data measured at various canopy heights (m) in the forest overstory, understory, and surface returns are hypothesized to predict various surface fuels that commonly occur within longleaf pine forests. Positive correlations are shown in black and negative correlations in red. Numbers next to lines are the standardized path coefficients. Line thickness corresponds to strength of path coefficient, and asterisks denote statistical significance ($P < 0.05$). Surface fuels originating from surface returns are modeled as covariates, indicated by double-headed arrows. The hypothesized model provides a good fit to the data ($\chi^2 = 3.98$; df = 12; $P = 0.98$).

positive contribution to diversity in sandhills with 0.34 kg/m^2 fuel loads resulting in a larger increase in diversity (spc = 0.09; β = 1.3) compared to flatwoods (spc = 0.03; β = 0.50). However, in flatwoods, the burning of 0.16 kg/m^2 of woody fuels resulted in a larger increase in diversity (spc = 0.16; β = 1.94) with a smaller increase in sandhills (spc = 0.04; β = 0.59). There was little
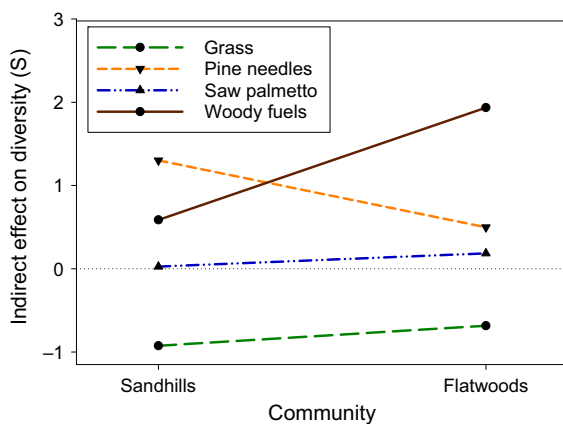

Fig. 4. Effect of different fuel types on diversity in each plant community. Indirect effect or combined effect of burning each fuel type on ground cover diversity, measured here as species richness (S) for reference sandhill and flatwood plant communities.

difference in direction of the contribution of saw palmetto and grass litter between the sandhills and flatwoods; however, the magnitude of indirect effect on ground cover diversity increases for each fuel type in the flatwoods (Fig. 4). Fuel loading of 0.02 kg/m^2 of saw palmetto litter had little effect in sandhills (spc = 0.002; β = 0.03) but a slight diversity increase in flatwoods (spc = 0.12; β = 0.18). Finally, grass exerted negative influences in sandhills (spc = −0.06; β = −0.925) and flatwoods (spc = −0.06; β = −0.69).

Stand quality

Finally, we ran the SEM for differing longleaf forest types located exclusively within intact sandhill communities. The model included reference sites, plots in the midst of restoration, and plots located within plantation stands to represent a gradient of stand quality based on fewer total burns and increased FRI. Approximately 0.30 kg/m^2 loading of pine needles had a positive effect on diversity in reference (spc = 0.09; β = 1.3) and restoration plots (spc = 0.05; β = 0.73), and negligible negative effect in plantations (spc = −0.001; β = −0.007). Similarly, woody fuels had a positive effect in reference stands (spc = 0.04; β = 0.59) and negative effect in restoration plots (spc = −0.007; β = −0.11).

However, woody fuels were the only fuel type to have a positive effect on diversity in plantations (spc = 0.09; β = 2.0). Additionally, there was a positive correlation between woody fuel loading and FRI with 0.08 kg/m^2 in reference sites increasing to 0.22 kg/m^2 in plantations. With a small contribution in terms of fuel loading (0.02 kg/m^2), saw palmetto had a positive influence on diversity in sandhill reference plots (spc = 0.002; β = 0.03), a negligible effect in restoration plots (spc = −0.05; β = −0.003), and was associated with declines in diversity in plantations (spc = −0.04; β = −0.82). Finally, a 0.08 kg/m^2 loading of grass litter had little effect in restoration plots (spc = 0.001; β = 0.007) and negative effects in reference plots (spc = −0.06; β = −0.93) and plantations (spc = −0.03; β = −0.62; Fig. 5).

Discussion

Our results that overstory-derived fuels help maintain plant diversity in longleaf pine forests are not surprising, but it is important to recognize that these effects are dependent on fuel types, which in turn are affected by the forest structure. These results should be generalizable
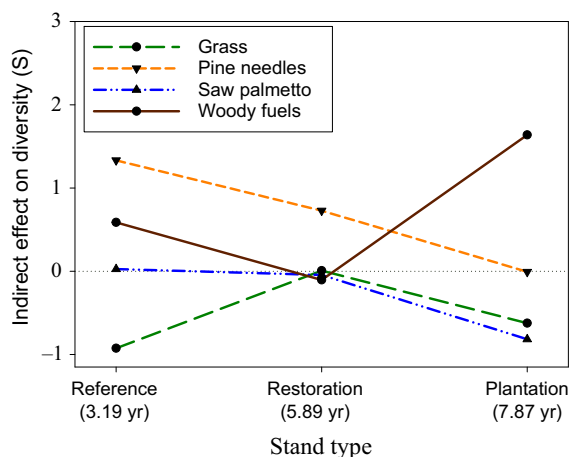

Fig. 5. Effect of the burning of each fuel type along a gradient of ecosystem quality. Indirect effects are calculated as the combined effect of burning each fuel type as it relates to ground cover diversity, measured here as species richness (S). Gradient of ecosystem quality in reference, restoration, and plantation sandhill stands is based on longer periods between burning. Numbers in parentheses next to each stand type refer to mean fire return interval.

to other coniferous forests based on the variety of systems we examined, including flatwood and sandhill communities, and a reasonable gradient of stand quality experiencing variable total burns and FRI. Similarly, the predictive power of LiDAR data for detecting these positive effects of fuels on diversity is likely to be similar in other forested systems and clearly demonstrates the indirect effects of basic forest structure characteristics on overall plant diversity.

Overstory-derived fuels

This study documented a positive influence of overstory on diversity in EAFB's characteristically open stands with canopy openness remaining similar across reference (51.5%), restoration (42.4%), and plantation stands (50.9%; Fig. 5; Battaglia et al. 2003, Hiers et al. 2007). In stands with few historical fires and which were undergoing restoration by tree removal, Platt et al. (2006) suggested that a dense overstory of longleaf pine hindered ground cover plant species diversity due to light limitation. In the stands we studied, light limitation was unlikely a factor. This was demonstrated by Hiers et al. (2007), where forest floor development, not canopy light interception, was the main driver of the loss in plant biodiversity. This occurs when forests remain unburned. We found that the overstory-derived fuels in stands maintained by frequent fire provided a significant contribution to species richness, particularly in flatwoods. We also found that longleaf pine litter exerted the greatest positive influence on ground cover richness in reference plots, where a mean fuel loading of 0.34 kg/m^2 added a mean of 1.2 plant species with each additional fire (Table 3, Fig. 2).

Overstory-derived fuels, mainly longleaf pine needles and cones on the forest floor, are a critical component of longleaf pine fire ecology (Hiers et al. 2009, Mitchell et al. 2009, Loudermilk et al. 2012, O'Brien et al. 2016a). Pine needles facilitate fire by supplying a continuous and highly combustible fuel bed (Rebertus et al. 1989, Hiers et al. 2009, Loudermilk et al. 2012). Ellair and Platt (2013) found that pine litter acted synergistically with other fuels to increase fire intensity, resulting in longer heating duration of understory vegetation and increased consumption of hardwood litter. Additionally, variation in the amount of pine litter had significant impact

on fire behavior and fire effects, which in turn alters forest structure by determining the prevalence of midstory hardwood species, such as the turkey oak (*Quercus laevis*; Hiers et al. 2009, Ellair and Platt 2013).

We found that woody fuels, which include small branches and pine cones derived from the longleaf canopy, significantly promoted ground cover diversity when burned, adding a mean 0.74 species in reference stands at loadings of 0.1 kg/m^2 (Table 3, Fig. 2). Woody debris burns at high intensity, releasing 12 times the radiative energy as fine fuels (O'Brien et al. 2016*a*), and has significantly longer residence times (Fonda and Varner 2004, Loudermilk et al. 2012, 2014). These hotspots of fire intensity can influence understory mortality as plants near woody debris have been found to be three times as likely to die from increased energy release from burning woody fuels (O'Brien et al. 2016*a*). These patches of increased mortality likely result in open areas of bare mineral soil for seedling establishment of both herbaceous species and longleaf pine resulting in increased variation in recruitment patterns post-fire (O'Brien et al. 2008, Wiggers et al. 2013).

When fire is removed from the landscape, litter and woody fuels accumulate on the forest floor contributing to an O horizon, decomposing to fermentation (Oe) and humus (Oa) layers, which is also described as duff or forest floor (Varner et al. 2005, Kreye et al. 2017). Hiers et al. (2007) showed that understory health is inversely linked with the amount of duff that has accumulated in the absence of fire in longleaf pine. Consistent with that study, we found that species richness was indirectly reduced with elevated litter in plantations, resulting from longer FRI (Fig. 5). This was not the case, however, with the consumption of woody fuels. Pine cones and woody fuels, especially during dry conditions, increase the probability of duff ignition and consumption (Kreye et al. 2017). When fire is reintroduced, the increased fire intensity and radiative energy released by woody fuels (Kreye et al. 2013, O'Brien et al. 2016*a*), coupled with longer residence times (Fonda and Varner 2004, Loudermilk et al. 2012), will result in the consumption of duff and exposure of bare mineral soil for seedling establishment (O'Brien et al. 2008, Hiers et al. 2009, Wiggers et al. 2013). Therefore, woody fuels consumption may be a

key process in maintaining diversity in forested stands characterized by more extended FRI (Fig. 5). Additionally, the positive effects on vegetative diversity resulting from burning woody debris, such as pine cones, may be significantly greater following longleaf pine masting events when individual trees may produce >100 cones (Mitchell et al. 2009, Brockway 2015). This potentially high contribution to diversity by woody debris consumption in flatwoods (Fig. 4) and pine plantations (Fig. 5) warrants further investigations into issues such as the fire radiative heat flux necessary to create open space in shrubby flatwoods or the consumption of duff in pine plantations (Varner et al. 2005).

Detrital fuels

Although oak litter often has been assumed to be associated with decreased plant diversity (Provencher et al. 2001, Thaxton and Platt 2006), oak litter did not appear to be associated with lower levels of diversity in this study. This may be due to the inclusive nature of this litter category which incorporated oaks with variable flammability. Pyrophytic oaks such as turkey oak (*Q. laevis*) are characterized by the production of flammable leaf litter, which burns with similar characteristics to longleaf pine needles (Kane et al. 2008, Varner et al. 2015). In contrast, fire-avoiding oak species such as live oak (*Quercus virginiana*) produce non-flammable litter, which prevents fire from reaching the plant (Varner et al. 2016). Removal of deciduous oaks in xeric sandhill habitat has often been the inappropriate target of intense management, but recent evidence suggests that they are benign at worst, and can actually add to conservation value of stands (Hiers et al. 2014). Our study confirms that xeric oaks native to sandhill habitat at Eglin have little influence on patterns of understory diversity. Moreover, data now suggest that deciduous oaks facilitate longleaf pine regeneration on xeric sites (Loudermilk et al. 2016). Additional insights may be gained if these flammable guilds were separated in future analyses.

Graminoids are a common feature of longleaf pine plant communities (Holliday 2001, Kirkman et al. 2001), yet we found that variation in grass litter had negligible influence on ground cover diversity in reference and restoration stands (Fig. 5). Furthermore, grass litter had an intermediate

negative effect in pine plantations (Fig. 5). In the absence of fire, grass litter can accumulate, limiting light resources and competitively excluding lower stature plants (Walker and Peet 1984). Grasses do play a role in fire ecology by contributing an abundant fine fuel source that dries out quickly, is highly ignitable, and combusts rapidly, thus promoting fire spread (Fill et al. 2016, Simpson et al. 2016). Grasses have also been shown to have similar peak heat flux to pine litter when burned, although residence times are shorter (Loudermilk et al. 2014, Fill et al. 2016). Therefore, grasses represent a self-perpetuating fuel load that also limits hardwood growth and reduces post-fire competition (Ripley et al. 2015, Simpson et al. 2016). The small effect size in our models suggests that the positive association that exists between grass and ground cover plant species diversity may be more likely due to subtle factors, such as pine needles that are caught and suspended on bunch grasses, contributing to aeration and continuity of the fuel bed (Loudermilk et al. 2014).

Saw palmetto litter had a small, positive effect on diversity in reference stands and flatwoods, and a negligible effect in restoration stands and sandhills (Figs. 4, 5). Although the effect was minimal, this litter may be an important source of depleted soil nutrients such as nitrogen (N) and phosphorus (P) to plants. While unmeasured and outside the scope of this study, nutrient input post-fire is highly variable (Lavoie et al. 2014) and has been shown to stimulate the growth of understory species (Certini 2005).

Relevance to management

Understanding how forest structure interacts with fire management to conserve biodiversity is critical for conservation in pine–grassland ecosystems (Mitchell et al. 2006, O'Brien et al. 2008). This study shows that plant diversity is linked to variation in fire intensity from canopy-derived overstory fuels. While it is documented that fire intensity is linked to heterogeneous fuels at fine spatial scales (Mitchell et al. 2009), it is important to also understand the role of forest structure, which is the most common attribute targeted by conservation managers. The focus of management for specific forest structure alone without understanding mechanisms has led to negative conservation outcomes (Hiers et al. 2014). This study provides a mechanistic link

and documents specific patterns between the burning of canopy-derived fuels and high levels of ground cover diversity commonly found in high-quality, frequently burned longleaf pine forests. Such patterns allow managers to discern the critical elements of forest structure, fuels, and subsequent fire behavior that drive biodiversity conservation in managed forests.

In light of changing climate and future uncertainty, long-term monitoring data are critical for understanding how ecosystems change in response to management (Jackson and Hobbs 2009, Hiers et al. 2016). As demonstrated here, long-term monitoring programs are critical in identifying and quantifying these changes; however, high-quality monitoring often requires substantive labor and financial inputs that cannot be sustained. Therefore, using remote sensing metrics to link to observed fuels data can contribute to more cost-effective management models conducted at broader scales or fill breaks in monitoring data acquisition. Our results from the LiDAR SEM demonstrate specific linkages and contributions of fuels from various vertical canopy strata within the forest structure using landscape-scale LiDAR data and plot-scale ground observations (Fig. 3).

While our fuel-diversity model (Fig. 2) explained over half of the variance in plant species richness, there are other factors that contribute to the fire–fuel–diversity relationship. Incorporating empirical fire intensity data could give increased insight to these models, by adding causal linkages between fuel types and heat flux. Improvements in the capture of empirical fire intensity data (O'Brien et al. 2016*a*, *b*) are providing important insights into explicit contributions of fuels to fire behavior and can help understand dose-dependent mortality (Sparks et al. 2017). Our analysis was also limited to common litter types and down woody debris. Other fuel variables, such as the structure and composition of live fuels and respective moisture content or fuel complexes (i.e., fuel cells), could also contribute to ground cover diversity through modification of the combustion environment, especially if measured immediately pre-ignition.

Conclusion

Feedbacks from fuels differentially affecting fire behavior and intensity leading to post-fire

community dynamics and forest structure at multiple scales are a critical principle of fire ecology (Mitchell et al. 2009). The path models in this study illustrated distinct forest structure and fuel attributes that drive biodiversity patterns at both plot and landscape scales. This study represents a new way of exploiting long-term monitoring datasets collected at the stand level by linking fuel characteristics and plant diversity. Our results reinforce the concept of the ecology of fuels where studies initially focused on the fine-scale linkages (Mitchell et al. 2009, Wiggers et al. 2013, O'Brien et al. 2016*a*, *b*), where this study expands this work to incorporate landscape structure and processes. This relationship is part of a more general property of disturbance in natural systems; as disturbances impact ecosystems at regular intervals, there should be predictable associations between vegetation in disturbed patches, fire (or other disturbance) intensity, and fuel composition. While neutral theory and empirical results still provide challenges to the utility of the intermediate disturbance hypothesis (Hubbell et al. 1999), it is clear that moderate disturbances, such as surface fires, contribute to biodiversity via complex pathways. Further investigations examining hypotheses focused on post-fire establishment and community composition will continue to be relevant to major biodiversity theories, such as the neutral theory of biodiversity (Hubbell 2001) or the continuum hypothesis (Gravel et al. 2006).

ACKNOWLEDGMENTS

LITERATURE CITED

Battaglia, M. A., R. J. Mitchell, P. P. Mou, and S. D. Pecot. 2003. Light transmittance estimates in a longleaf pine woodland. Forest Science 49:752–762.

Boyer, W. D. 1998. Long-term changes in flowering and cone production by longleaf pine. GTR-SRS 20. Southern Research Station, USDA Forest Service, Clemson, South Carolina, USA.

Brockway, D. G. 2015. Longleaf pine cone prospects. Southern Research Station, USDA Forest Service, Auburn, Alabama, USA.

Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service, Ogden, Utah, USA.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143:1–10.

Ellair, D. P., and W. J. Platt. 2013. Fuel composition influences fire characteristics and understorey hardwoods in pine savanna. Journal of Ecology 101:92–201.

Fill, J. M., B. M. Moule, J. M. Varner, and T. A. Mousseau. 2016. Flammability of the keystone savanna bunchgrass *Aristida stricta*. Plant Ecology 217:331–342.

Fonda, R. W., and J. M. Varner. 2004. Burning characteristics of cones from eight pine species. Northwest Science 78:322–333.

Frost, C. C. 2006. History and future of the longleaf pine ecosystem. Pages 9–48 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York, USA.

Gagnon, P. R., H. A. Passmore, W. J. Platt, J. A. Myers, C. E. T. Paine, and K. E. Harms. 2010. Does pyrogenicity protect burning plants? Ecology 91: 3481–3486.

Gagnon, P. R., H. A. Passmore, M. Slocum, J. A. Myers, K. E. Harms, W. J. Platt, and C. E. T. Paine. 2015. Fuels and fire influence vegetation via above and belowground pathways in a high-diversity plant community. Journal of Ecology 103:1009–1019.

Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal 23:22–37.

Grace, J. B., S. M. Scheiner, and D. R. Schoolmaster Jr. 2015. Structural equation modeling: building and evaluating causal models. Pages 168–199 *in* G. A. Fox, S. Negrete-Yankelevich, and V. J. Sosa, editors. Ecological statistics: from principles to applications. Oxford University Press, Oxford, UK.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9:399–409.

Hiers, J. K., S. T. Jackson, R. J. Hobbs, E. S. Bernhardt, and L. E. Valentine. 2016. The precision problem in conservation and restoration. Trends in Ecology and Evolution 31:820–830.

Hiers, J. K., S. C. Laine, J. J. Bachant, J. H. Furman, W. W. Greene, and V. Compton. 2003. Simple

spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Conservation Biology 17:1571–1578.

Hiers, J., J. O'Brien, R. Mitchell, J. Grego, and E. Loudermilk. 2009. The wildland fuel cell concept: an approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. International Journal of Wildland Fire 18:315–325.

Hiers, J. K., J. J. O'Brien, R. E. Will, and R. J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecological Applications 17:806–814.

Hiers, J. K., J. R. Walters, R. J. Mitchell, J. M. Varner, L. M. Conner, L. A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. Journal of Wildlife Management 78:383–393.

Holliday, P. P. 2001. Going, going. . .Saving the longleaf pine ecosystem before it's gone. Pages 54–62 *in* The fire forest: longleaf pine-wiregrass ecosystem. Georgia Wildlife Press, Covington, Georgia, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-cap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557.

Hudak, A., B. Bright, S. Pokswinski, E. Loudermilk, J. O'Brien, B. Hornsby, C. Klauberg Silva, and C. Silva. 2016a. Mapping forest structure and composition from low-density LiDAR for informed forest, fuel, and fire management at Eglin Air Force Base, Florida, USA. Canadian Journal of Remote Sensing 42:411–427.

Hudak, A., M. Dickinson, B. Bright, R. Kremens, E. Loudermilk, J. O'Brien, B. Hornsby, and R. Ottmar. 2016b. Measurements relating fire radiative energy density and surface fuel consumption – RxCADRE 2011 and 2012. International Journal of Wildland Fire 25:25–37.

Hudak, A. T., J. S. Evans, and A. M. S. Smith. 2009. LiDAR utility for natural resource managers. Remote Sensing 1:934–951.

Isenburg, M. 2015. LAStools: efficient tools for LiDAR processing, version 150304. http://lastools.org

Jackson, S. T., and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. Science 325:567–569.

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.

Keane, R. E. 2015. Wildland fuel fundamentals and applications. Springer International Publishing, Cham, Switzerland.

Kirkman, L. K., P. C. Goebel, B. J. Palik, and L. T. West. 2004. Predicting plant species diversity in a longleaf pine landscape. Ecoscience 11:80–93.

Kirkman, L. K., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. American Journal of Botany 88:2119–2128.

Kreye, J. K., J. M. Varner, C. J. Dugaw, J. Cao, J. Szecsei, and E. A. Engber. 2013. Pine cones facilitate ignition of forest floor duff. Canadian Journal of Forest Research 43:512–516.

Kreye, J. K., J. M. Varner, C. J. Dugaw, E. A. Engber, and L. N. Quinn-Davidson. 2017. Patterns of duff ignition and smoldering beneath old *Pinus palustris*: influence of tree proximity, moisture content, and ignition vectors. Forest Science 63:165–172.

Lavoie, M., M. C. Mack, J. K. Hiers, S. Pokswinski, A. Barnett, and L. Provencher. 2014. Effects of restoration techniques on soil carbon and nitrogen dynamics in Florida longleaf pine (*Pinus palustris*) sandhill forests. Forests 5:498–517.

Loudermilk, E., G. Achtemeier, J. O'Brien, J. Hiers, and B. Hornsby. 2014. High-resolution observations of combustion in heterogeneous surface fuels. International Journal of Wildland Fire 23:1016–1026.

Loudermilk, E. L., J. K. Hiers, S. Pokswinski, J. J. O'Brien, A. Barnett, and R. J. Mitchell. 2016. The path back: Oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7:e01361.

Loudermilk, E. L., J. J. O'Brien, R. J. Mitchell, W. P. Cropper, J. K. Hiers, S. Grunwald, J. Grego, and J. C. Fernandez-Diaz. 2012. Linking complex forest fuel structure and fire behaviour at fine scales. International Journal of Wildland Fire 21:882–893.

Mitchell, R. J., J. K. Hiers, J. J. O'Brien, S. B. Jack, and R. T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the south-eastern United States. Canadian Journal of Forest Research 36:2724–2736.

Mitchell, R. J., J. K. Hiers, J. O'Brien, and G. Starr. 2009. Ecological forestry in the southeast: understanding the ecology of fuels. Journal of Forestry 107:391–397.

Noss, R. F., E. T. LaRoe, and J. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. United States Fish and Wildlife Service, Moscow, Idaho, USA.

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.

O'Brien, J. J., J. K. Hiers, M. A. Callaham Jr., R. J. Mitchell, and S. Jack. 2008. Interactions among overstory structure, seedling life history traits and fire in frequently burned neotropical pine forests. Ambio 37:542–547.

O'Brien, J. J., E. L. Loudermilk, J. K. Hiers, S. Pokswinski, B. Hornsby, A. Hudak, D. Strother, E. Rowell, and B. C. Bright. 2016a. Canopy derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (Pinus palustris) sandhill in Northwest, FL, USA. Canadian Journal of Remote Sensing 42:489–500.

O'Brien, J. J., E. L. Loudermilk, B. Hornsby, A. T. Hudak, B. C. Bright, M. B. Dickinson, J. K. Hiers, C. Teske, and R. D. Ottmar. 2016b. High-resolution infrared thermography for capturing wildland fire behavior—RxCADRE 2012. International Journal of Wildland Fire 25:62–75.

Palmquist, K. A., R. K. Peet, and S. R. Mitchell. 2015. Scale-dependent responses of longleaf pine vegetation to fire frequency and environmental context across two decades. Journal of Ecology 103:998–1008.

Platt, W. J., S. M. Carr, M. Reilly, and J. Fahr. 2006. Pine savanna overstorey influences on ground-cover biodiversity. Applied Vegetation Science 9:37–50.

Prichard, S. J., D. V. Sandberg, R. D. Ottmar, E. Eberhardt, A. Andreu, P. Eagle, and K. Swedin. 2013. Fuel characteristic classification system. GTR-PNW 88. Pacific Northwest Research Station, USDA Forest Service, Portland, Oregon, USA.

Provencher, L., B. J. Herring, D. R. Gordon, H. L. Rodgers, K. E. Galley, G. W. Tanner, J. L. Hardesty, and L. A. Brennan. 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology 9:13–27.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology 70:60–70.

Ripley, B., V. Visser, P. A. Christin, S. Archibald, T. Martin, and C. Osborne. 2015. Fire ecology of C_3 and C_4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. Ecology 96:2679–2691.

Rosseel, Y. 2012. Lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Shafer, J. L., and M. C. Mack. 2010. Short-term effects of fire on soil and plant nutrients in palmetto flatwoods. Plant and Soil 334:433–447.

Shipley, B. 2016. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R. Cambridge University Press, New York, New York, USA.

Simpson, K. J., B. S. Ripley, P. Christin, C. M. Belcher, C. E. R. Lehmann, G. H. Thomas, C. P. Osborne, and H. Cornelissen. 2016. Determinants of flammability in savanna grass species. Journal of Ecology 104:138–148.

Sparks, A. M., A. M. S. Smith, A. F. Talhelm, C. A. Kolden, K. M. Yedinak, and D. M. Johnson. 2017. Impacts of fire radiative flux on mature Pinus ponderosa growth and vulnerability to secondary mortality agents. International Journal of Wildland Fire 26:95–106.

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.

Varner, J. M., D. R. Gordon, F. E. Putz, and J. K. Hiers. 2005. Restoring fire to long-unburned Pinus palustris ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restoration Ecology 13:536–544.

Varner, J. M., J. M. Kane, E. M. Banwell, and J. K. Kreye. 2015. Flammability of litter from southeastern trees: a preliminary assessment. GTR-SRS 203. Southern Research Station, USDA Forest Service, Asheville, North Carolina, USA.

Varner, M. J., J. M. Kane, J. K. Hiers, J. K. Kreye, and J. W. Veldman. 2016. Suites of fire-adapted traits of oaks in the southeastern USA: multiple strategies for persistence. Fire Ecology 12:48–64.

Veldman, R. G., et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment 13: 154–162.

Walker, J., and R. K. Peet. 1984. Composition and species diversity of pine–wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55:163–179.

Wenk, E. S., G. G. Wang, and J. L. Walker. 2011. Within-stand variation in understorey vegetation affects fire behaviour in longleaf pine xeric sandhills. International Journal of Wildland Fire 20:866–875.

Wiggers, M. S., L. K. Kirkman, R. S. Boyd, and J. K. Hiers. 2013. Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. Forest Ecology and Management 310:54–63.