Sánchez-López *et al. Fire Ecology* (2026) 22:9
https://doi.org/10.1186/s42408-025-00425-9

Fire Ecology

CASE STUDY

Open Access

Is this duff? Long-term prescribed burning effects on litter and duff in pine flatwoods of the southeastern US

N. Sánchez-López[1,2*], A. T. Hudak[2], M. K. Taylor[3,4], M. A. Callaham Jr.[3] and Joseph J. O'Brien[3]

Abstract

Background Mapping surface and ground fuels is key to supporting wildland fire research and management. Fuel loading, structure, distribution, and continuity, along with other factors, strongly influence fire spread and consumption. It is, therefore, essential to understand drivers of fuel accumulation such as the aboveground tree inputs from abscission, dispersion, decomposition, disturbances, and management practices (e.g., prescribed fire), particularly in fire-dependent forest ecosystems such as longleaf flatwoods savannas of the southeastern US. In 2022, we collected and measured litter load, duff load, and duff depth before and after prescribed burning in 72 field plots at pine flatwoods at Osceola National Forest, in northern Florida, where a long-term experiment on fire return intervals (FRI; 1, 2, 4 years and unburned controls) has been running since 1958. We assessed how FRI, proximity to trees, wind direction, and structural attributes such as stand basal area and density influenced the distribution and accumulation of litter and duff.

Results Overall, litter and duff were highly variable across FRI and before and after prescribed fire. Litter load, duff load, and duff depth all increased with longer FRIs and higher basal area. Consistent prescribed fire significantly increased duff bulk density—defined as the ratio of duff load to duff depth—compared to the long-unburned plots. Proximity to the tree bole was a significant factor explaining duff distribution within unburned plots, while both duff and litter were evenly distributed across the four cardinal directions.

Conclusions The FRI of the prescribed burning drove the inter-stand-level accumulation of duff and litter while aboveground tree biomass influenced intra-stand distribution. Consistent prescribed fire resulted in more compacted duff layers, an effect that warrants consideration in carbon assessment in fire-maintained forest ecosystems. This study advances our understanding of litter and duff accumulation dynamics in southern pine flatwoods under frequent prescribed fire management; however, comparison with data from other study sites is essential to corroborate these trends.

Keywords Forest floor, Organic horizon, Fuel accumulation, Fuel consumption, Fire return interval, Surface fuel, Ground fuel

Resumen

Antecedentes El mapeo de los combustibles muertos de superficie es clave para la investigación de incendios y la gestión forestal. La carga, estructura, distribución y continuidad de estos combustibles, junto con otros factores,

---

*Correspondence:
N. Sánchez-López
sanchezlnuria.fuo@uniovi.es
Full list of author information is available at the end of the article

influyen altamente en la propagación del fuego y la combustión de la vegetación. Por lo tanto, es esencial entender los factores que determinan su acumulación, como la biomasa arbórea resultante de procesos de abscisión, dispersión y descomposición, así como de perturbaciones forestales y prácticas de manejo (p.ej., quemas prescritas), especialmente en sistemas forestales dependientes del fuego como las sabanas de pino longleaf del sudeste de los Estados Unidos. En 2022 se recogió y midió la carga de hojarasca, la carga del mantillo (es decir, la materia orgánica en descomposición) y la profundidad del lecho de este mantillo, antes y después de realizar quemas prescritas. La toma de muestras se llevó a cabo en 72 parcelas de campo en sabanas de pino longleaf del Bosque Nacional de Osceola, en el norte de Florida, donde se desarrolla desde 1958 un experimento para evaluar el efecto del intervalo de retorno de las quemas prescritas (FRI, de sus siglas en inglés), con tratamientos cada 1, 2, 4 años, además de un tratamiento control sin quemar. En este estudio determinamos cómo el FRI, la proximidad a los árboles, la dirección del viento, y atributos estructurales de la masa forestal tales como el área basal y la densidad de árboles, influyen en la distribución y acumulación de la hojarasca y del mantillo.

Resultados En general, la hojarasca y el mantillo fueron altamente variables en las parcelas con diferentes FRI, tanto antes como después de las quemas prescritas. La carga de acículas, del resto de los componentes finos de la hojarasca, la del mantillo y la profundidad del mantillo aumentaron con períodos de retorno más largos y con mayores valores de área basales de la masa forestal. Las quemas prescritas incrementaron significativamente la densidad aparente del mantillo–definida como la relación entre carga del mantillo sobre la profundidad del mismo– en comparación con las parcelas no quemadas. La proximidad a los troncos de los árboles también fue un factor significativo para explicar la distribución del mantillo dentro de las parcelas no quemadas mientras que la hojarasca y el mantillo estaban igualmente distribuidos a lo largo de las cuatro direcciones de los puntos cardinales.

Conclusiones Las quemas prescritas y el FRI determinaron la acumulación de la carga de combustible de hojarasca y mantillo entre las distintas unidades de gestión, mientras que la biomasa arbórea influyó en la distribución dentro de cada una de estas unidades. Las quemas prescritas resultaron en capas del mantillo más compactas, un efecto que debe considerarse en la evaluación del carbono en ecosistemas gestionados con quemas prescritas. Este estudio avanza en el conocimiento de la dinámica de la acumulación de la hojarasca y del mantillo forestal en sabanas del sudeste de los Estados Unidos dominadas por pino longleaf que se gestionan con quemas prescritas. No obstante, la comparación con datos de otras zonas de estudio es esencial para corroborar estas tendencias.

Introduction

Longleaf pine (*Pinus palustris* Mill) flatwoods of the southeastern US are fire-dependent ecosystems in which forest floor fuel loading, dominated by litter and duff, is a major driver of fire spread and fuel consumption, with significant implications for fire effects (Agee and Skinner 2005; Hiers et al. 2009). Litter is the undecomposed fine organic material consisting of dead leaves and pine needles and other fine vegetative tissue such as bark flakes, buds, and non-woody twigs. "Duff" is a term applied by forest managers and wildland fire practitioners to describe that component of the forest floor beneath the litter that consists of partially and highly decomposed organic material. The continuity and depth of forest floor fuels, under certain dry conditions, strongly influences fire spread and consumption, and it may combust in long-term smoldering fires, producing elevated particulate emissions (Glenn et al. 2024) and causing considerable tree mortality and soil heating (Varner et al. 2005; O'Brien et al. 2010; Kreye et al. 2020).

Maps of litter and duff loading and depth across broad scales are key inputs to spatially explicit fire behavior models to support forest managers and fire practitioners in decision-making. However, these fuels are highly heterogenous at fine scales, making it difficult to quantify at high spatial resolutions. Litter and duff loading and its distribution on the forest floor are driven by aboveground tree biomass influenced itself by tree size, age, species, and stand density, as well as events that drive litterfall dispersion, such as prevailing wind direction and ecosystem processes such as decomposition or fires that remove fuels from the forest floor (Grace and Platt 1995; Robertson et al. 2019; Mugnani et al. 2019; Sánchez-López et al. 2023; McDanold et al. 2023). The extent to which these factors influence the accumulation process is still poorly described in many ecosystems.

Longleaf pine flatwoods are an extensive ecosystem in the Lower Coastal Plain of the US and are characterized by low, flat topography with poorly drained sandy soils (Abrahamson and Hartnett 1990). In the absence of fire, these soils develop thick organic duff layers. Litter and duff accumulate particularly near stems where more litter material drops from trees and decomposes over time. Prescribed fire partially consumes litter and duff on the forest floor. The level of consumption depends, among other factors, on the type, distribution, and amount of fuel and the environmental conditions circumscribed in the fire prescription. In this regard, field data and long-term studies can provide valuable information to further calibrate and validate models, test assumptions, and reduce uncertainties in predictions.

A fire experiment was established in 1958 by the USFS Macon Georgia Forest Fire Laboratory in the Osceola National Forest, in northeastern Florida (McKee 1982; Ross et al. 2024). The study has maintained regular prescribed fire treatments at three intervals along with a fire exclusion treatment. This experiment aimed to address the effect of prescribed burning on fuel accumulation under different fire return intervals (FRI). Currently, it constitutes one of the world's longest-running studies on FRI, offering a unique opportunity to address the effects of fire exclusion and consistent burning in longleaf pine ecosystems. In 2022, i.e., 64 years after the beginning of the experiment, we collected field samples of litter and duff before and after prescribed burning. Our goal was to better understand how FRI along with additional factors such as stand-level aboveground tree biomass, the proximity to individual trees, and prevailing wind directions influenced the spatial distribution of litter and duff. Additionally, we measured pre- and post-fire fuel loads, such that we could assess spatial consumption patterns resulting from prescribed fire.

Methods

Study site

The long-term study area is at the Olustee Experimental Forest (30.2372, −82.4109) located in the Osceola National Forest in the Lower Coastal Plain in northeastern Florida (McKee 1982). The experimental site consists of twenty-four ~0.85 ha plots arranged in a 4×6 grid, with six replicates of four fire treatments assigned via a randomized block design, blocked by latitude (north to south). Ongoing treatments consist of 1-yr burns, 2-yr burns, 4-yr burns, and fire exclusion (Fig. 1). Controlled dormant-season burns—defined as burning between first frost and spring green-up to minimize pine overstory scorch—began in 1958 after an initial whole-site burn. The original design included a 6-yr interval instead of annual burns; however, starting in 1963, the original 6-yr burn interval plots were converted to annual burns to mitigate control difficulties experienced with the 6-yr treatment. There was a pause in 1970–1971; however, treatments resumed in 1972 using consistent prescriptions and ignition protocols. Plots are ignited using strip head firing and are separated by annually maintained plowlines (mechanically created firebreaks). In 1985, an unplanned ignition burned a small area on the edge of a single control (unburned) plot, but that burned area was not sampled for this study.

The area is primarily classified as a Southern longleaf flatwood, characterized by low, flat topography. Soils are Spodosols characterized by poor drainage, acidity, sandy texture, and nutrient deficiency. At the time of establishment, the entire study site was a homogenous naturally recruited stand. The understory conditions and fire history were not recorded at that time; however, the overstory tree community was almost entirely longleaf pine with a few scattered slash pine (*Pinus elliottii* Engelm); these dominant and codominant trees in the experimental area were about 45 years old and had an average diameter at breast height of 28 cm and heights of 20 m (Sackett 1975). The understory varies by treatment, but burned plots are characterized by the lack of midstory and a surface layer dominated by various densities of saw palmetto (*Serenoa repens* [Bartr.] Small) and diverse herbaceous vegetation. In the unburned plots, a hardwood midstory has developed (Glitzenstein et al. 2003).

Prescribed fire treatments

The experimental area was burned in February and March of 2022, by hand ignition between 10:00 and 14:30 (Table S1). Overall, the prescription parameters for the prescribed fires in the area establish having 4% or more moisture on 10-h fuels (downed woody material of 0.6-2.5 cm), air temperature lower than 32.2 °C, relative humidity higher than 15%, 20' (~6.1 m) wind speed lower than 30 mph (<48 km h^{-1}), less than 60 days since the last rain, and probability of ignition of less than 95%. The weather conditions during the burn periods were within the established prescription window (Supplementary material Table S2). Units were ignited with strip head fires separated by approximately 10 m with two igniters using drip torches filled with a 50-50 gasoline-diesel mix. Fire behavior increased in intensity with longer FRI (O'Brien unpublished data) and was considered consistent with prior treatments observed by the Osceola National Forest fire operations staff. Burns in individual plots were complete in approximately 30 min (Fig. 2).

Field data collection

Tree inventory and surface fuel (duff and litter) data were collected within the 24 research units and distributed across 72 sample plots (Callaham et al. 2025). Three live longleaf pine trees per research unit were randomly selected as sample plot foci, labeled with a metal tag, and geolocated using a Trimble Geo7x GPS (Fig. 1C).

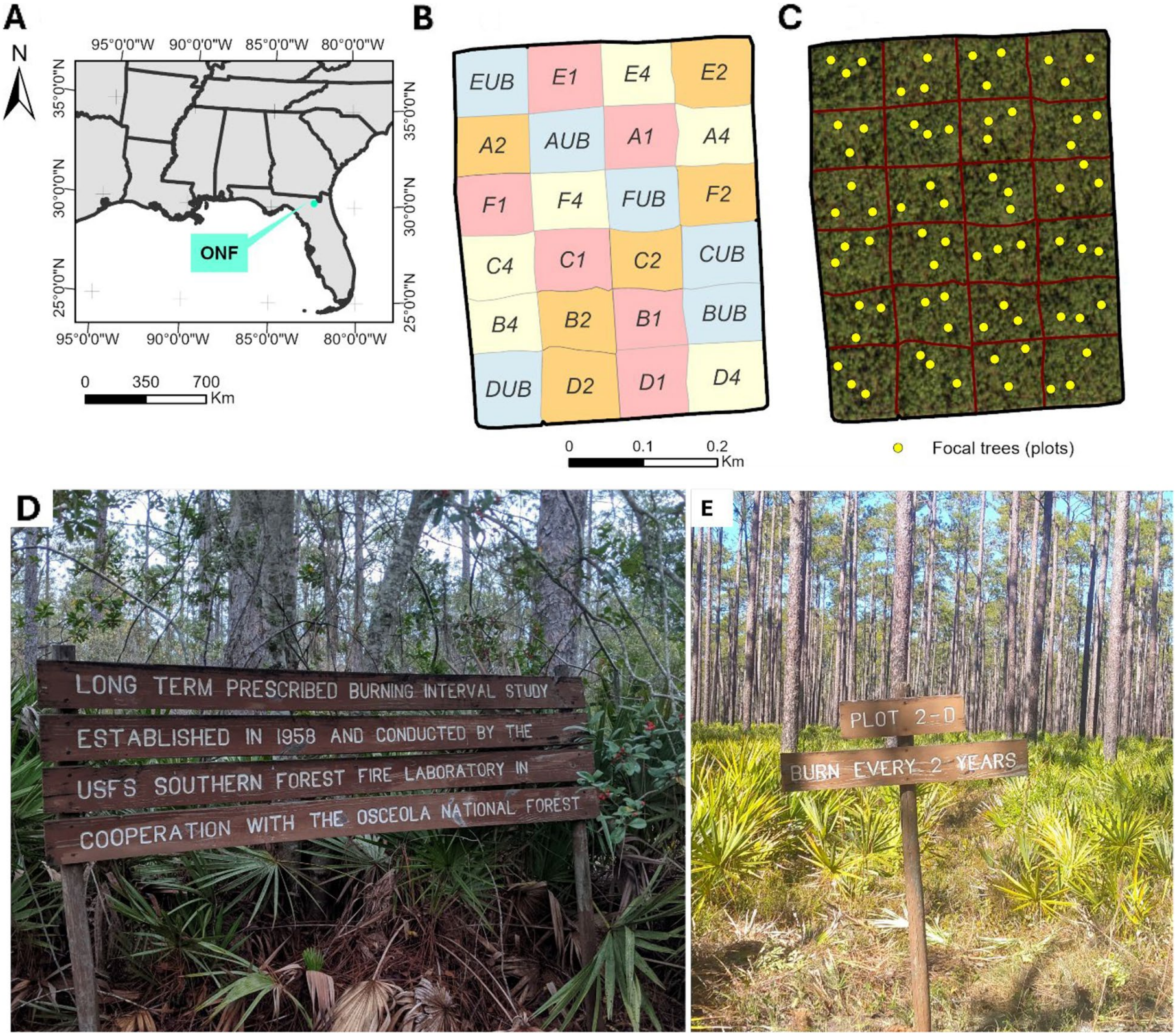

Fig. 1 Location of the Olustee Experimental Forest study in the Osceola National Forest (ONF) in northeastern Florida in the US (**A**). Randomized experimental research units at ONF with their corresponding fire return interval (**B**). Each treatment has six replicates (A, B, C, D, E, F) consisting of burns every 1, 2, or 4 years, or remaining unburned (UB) since 1958. Location of the focal trees sampled during the field campaign (**C**). Informative panel of the long-term study in prescribed fire set at Osceola National Forest in 1958 (**D**). Plot 2D, burned every 2 years at Osceola National Forest (**E**). Background image in **C** is from the Esri World Imagery basemap (Esri 2024), and the experimental research unit boundaries (plowlines) are overlaid

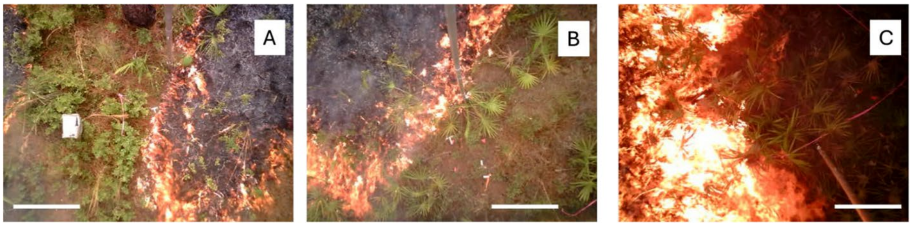

Fig. 2 Nadir view of representative fire behavior in 1 yr (**A**), 2 yr (**B**), and 4 yr (**C**) during the prescribed fire treatments. White bar represents 1 m

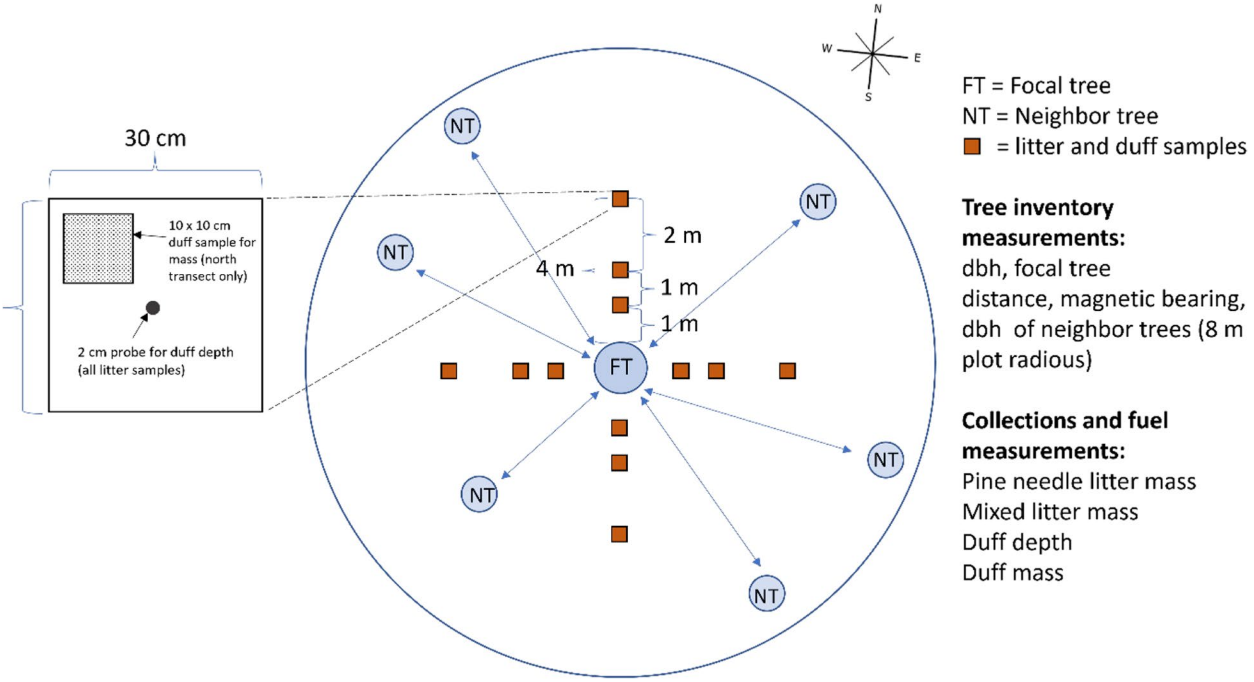

Fig. 3 Sampling design for collecting litter, duff, and tree inventory data at the Olustee Experimental Forest in Osceola National Forest in 2022. The transect directions are represented for the pre-fire data collection

The selected focal trees were separated by at least 16 m. Measurements in all units were collected before the prescribed fire campaign was conducted in February 2022, and post-fire measurements were collected on the burned units in April 2022, i.e., 1 or 2 months after the prescribed fire was conducted.

At each plot, duff and litter were systematically sampled along four transects radiating from the focal tree bole (Fig. 3). The transects during the pre-fire sampling were located at 0°, 90°, 180°, and 270°, and during the post-fire sampling were located at 45°, 135°, 225°, and 315°. The compass was not adjusted for magnetic declination, so these true coordinates were shifted counterclockwise by 6.20° W (NOAA 2025). For litter, square plots (30 × 30 cm) were located at 1, 2, and 4 m distances from the focal tree bole. A duff depth measurement (mm) near the 30 × 30 cm plot center was taken using a standard 2 cm diameter soil probe (Fig. 4A). Duff mass was also collected but only along the north transect using a stainless-steel cutter (10 cm × 10 cm; Fig. 4B), by pushing the sampler through the duff layer and into the mineral soil.

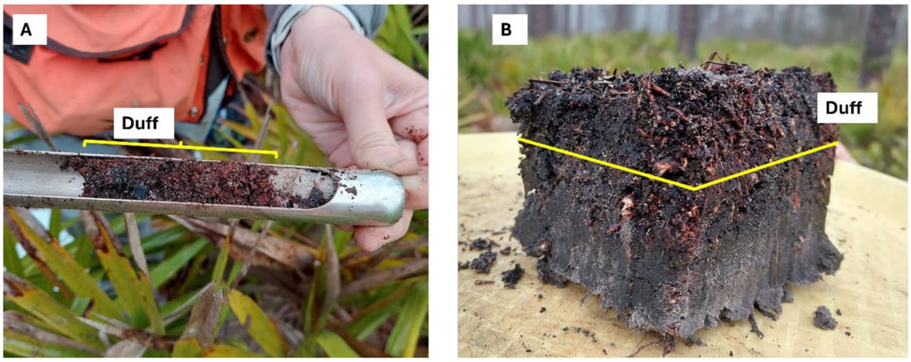

Fig. 4 Detail of duff depth measured with the 2 cm diameter soil probe (**A**) and detail of a duff sample collected with the 10 × 10 cm duff cutter (**B**). The yellow line represents the sharp separation between duff and the mineral soil. Note that a few stray mineral particles are visible on the surface of the sample in the image in **B**. This results from particles from previous samples adhering to the sampling tool. Care was taken to brush the particles away before collecting the duff sample

Separation of the litter layer from the duff layer was accomplished by the same team of individuals for all samples. Litter was identified using primarily visual cues (color, particle size, decomposition state), and sampling consisted of collecting all material on the surface that was undecomposed, recognizable as recently deposited plant material, and easily removed without digging. The boundary between litter and duff was defined as the point beneath which the organic material was in a state of partial decomposition and being held in place by fungal hyphae and/or fine roots. The separation of duff and mineral soil was performed using visual, tactile, and even auditory cues, as the duff material is organic, and the mineral components of soil are predominantly sand. A blade was pushed into the sample above and below the boundary until the available cues indicated where the boundary designation should be. The boundary has a characteristic look, feel, and sound when mineral particles are contacted with the blade. The boundary between mineral and duff layers in the soils at Osceola is generally distinct (with some undulations), with the duff being perched on the mineral horizons. In some cases, the boundary is strikingly distinct (as in Fig. 4A), whereas in other cases, the mineral horizons are stained with charcoal and soot, and the visual distinction is more difficult, but identifying the boundary is possible and repeatable with care and reliance on the other available cues (Fig. 4B).

Duff and litter samples were separately bagged and taken to the lab. In short, for each FRI, 216 measurements were taken for litter load and duff depth, and 54 for duff load. No post-fire measurements were made in the unburned units. In the lab, pine needles were sorted from the rest of the miscellaneous litter material that included bark flakes, buds, twigs, etc. Henceforth, we refer to this category as mixed litter. Litter and duff samples were oven dried at 65 °C and weighed. Litter and duff loads (kg m^{-2}) were calculated for each sample as the ratio of the mass (kg) and the sampled area (0.09 m^2 for litter and 0.01 m^2 for duff). Additionally, the duff bulk density (kg m^{-3}) was calculated as the ratio between duff load (kg m^{-2}) and duff depth (m). Notably, while in proximity, the duff depth measurements were not co-located with the duff mass samples (Fig. 3). There were three measurements (one pre-fire and two post-fire) where the duff depth measured with the 2 cm soil probe in the center of the clip plot was nil, but there was some duff mass in the sample collected with the duff cutter, and one measurement post-fire where duff mass was nil. We omitted these observations to report statistics of duff bulk density.

Tree inventory data were collected during the pre-fire data collection. Diameter at breast height (dbh, measured at 1.37 m height) was recorded for live trees (dbh $\geq$ 10 cm) and saplings (dbh $<$ 10 cm and height $>$ 1.37 m) within 8 m from the focal tree at the plot center (Fig. 3). The distance and magnetic bearing from the focal tree to the neighbor tree in the plot were also recorded for stem mapping. Longleaf pine was the dominant species in all inventoried plots, being the only species tallied in the burned units. In the unburned plots, 81.8% of tallied trees were longleaf pines, 16.9% were deciduous trees, and the remainder residual percentage corresponded to *Ilex* sp. Most deciduous trees were *Quercus* spp., but identification was not always possible because the sampling was conducted during leaf-off conditions. Saplings were 4.6% of all tallies, and 81% of them were on the unburned units. Plot-level basal area and stem density were calculated for each field plot, resulting in 18 observations per FRI ($n = 72$). Trees and saplings were both included to estimate tree density and basal area.

Statistical analysis

We assessed the effect of FRI treatment (1 yr, 2 yr, 4 yr, and unburned) on the fuel attributes of samples collected pre-fire (i.e., pine needle and mixed litter loads, duff loads, duff depth, duff bulk density) and tree structure characteristics derived from the tree inventory data (i.e., plot-level tree density and basal area). Differences in fuel loads given the collection time may reflect consumption rates during the prescribed fire. Therefore, we also checked if there were significant differences in fuels between the two collection times (pre- and post-fire), comparing the pre- and post-fire fuel attributes across the three burned treatments (1 yr, 2 yr, 4 yr). Similarly, we compared the fuels at different distances from the tree bole (i.e., 1 m, 2 m, or 4 m), and transect direction, which may reflect the influence of predominant wind direction effects. For all cases, we first used one-way ANOVA and the Shapiro-Wilk test to assess the normality of the residuals. If the residuals were normally distributed (p value $>$ 0.05) and ANOVA indicated significant differences, we proceeded with Tukey's HSD test for post hoc comparisons. If the residuals were not normally distributed, as occurred in most cases, we performed the Kruskal-Wallis test and the Dunn's test for pairwise comparisons as non-parametric alternatives to ANOVA.

We additionally compared the two plot-level forest attributes (tree density and basal area) with the average of

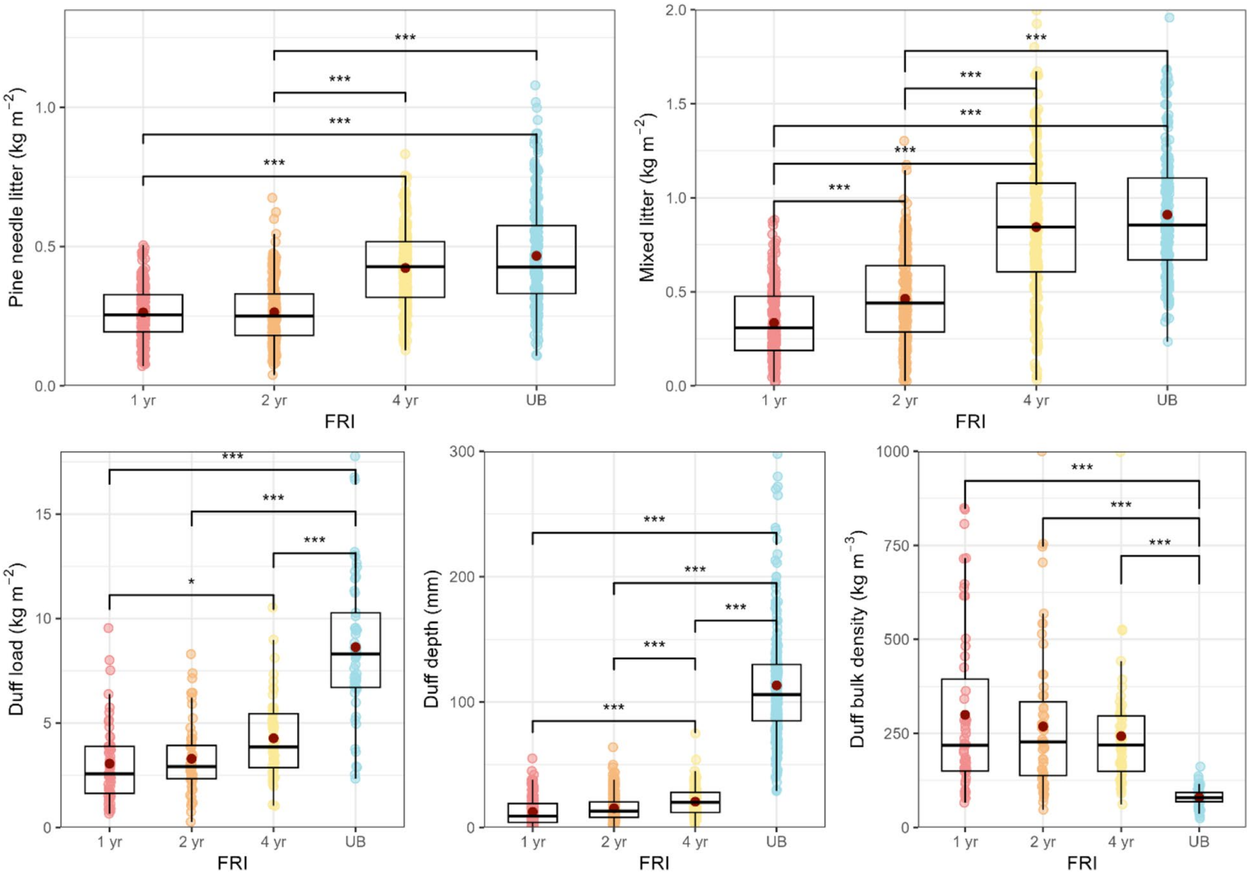

Fig. 5 Boxplot of the pine needle litter load, mixed litter load, duff load, duff depth, and duff bulk density measured pre-fire in the long-term experiment consisting of three fire return intervals (FRI: 1 yr, 2 yr, 4 yr) and unburned (UB) treatments. Boxes represent the interquartile range (25th–75th percentiles) with the median as the central line, and the whiskers extend to the most extreme values within 1.5 times the interquartile range. The red dot indicates the mean value. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) in fuel attributes based on post hoc pairwise comparisons as determined by Dunn's test. For visualization purposes, data points beyond the y-axis range label are not displayed

Table 1 Pine needle litter load, mixed litter load, duff load, duff depth, and duff bulk density (BD) measured pre- and post-fire at Osceola National Forest (ONF) experimental burns in 2022. Statistics are reported per fire return interval (FRI: 1 yr, 2 yr, 4 yr) and unburned (UB) treatments based on the 216 measurements taken for litter load and duff depth, and 54 for duff load. No post-fire measurements were made in the unburned units. Values are presented as mean ± standard deviation (coefficient of variation %)

FRI		Pine needles (kg m^{-2})	Mixed litter (kg m^{-2})	Duff load (kg m^{-2})	Duff depth (mm)	Duff BD (kg m^{-3})
1 yr	Pre-fire	0.26 ± 0.09 (35.7)	0.33 ± 0.19 (56.0)	3.05 ± 1.91 (62.6)	12 ± 10 (83.7)	378.6 ± 413.5 (109.2)
	Post-fire	0.05 ± 0.04 (80.5)	0.30 ± 0.20 (65.6)	2.79 ± 1.31 (46.8)	14 ± 9 (65.3)	243.1 ± 182.8 (75.2)
2 yr	Pre-fire	0.26 ± 0.11 (42.3)	0.46 ± 0.24 (52.0)	3.29 ± 1.71 (52.2)	15 ± 11 (70.0)	318.9 ± 328.4 (103.0)
	Post-fire	0.09 ± 0.07 (70.3)	0.25 ± 0.19 (73.4)	3.70 ± 1.99 (53.8)	17 ± 9 (57.0)	232.7 ± 100.8 (43.3)
4 yr	Pre-fire	0.42 ± 0.14 (33.2)	0.84 ± 0.37 (44.3)	4.27 ± 1.93 (45.3)	21 ± 11 (51.2)	258.6 ± 187.3 (72.4)
	Post-fire	0.14 ± 0.09 (66.3)	0.38 ± 0.26 (68.4)	4.38 ± 2.21 (50.5)	21 ± 10 (46.9)	221.2 ± 128.0 (57.9)
UB	Pre-fire	0.47 ± 0.19 (40.1)	0.93 ± 0.39 (41.4)	8.89 ± 3.94 (44.4)	113 ± 47 (41.5)	79.9 ± 26.5 (33.2)

the plot-level surface fuels collected pre-fire. To achieve this, we calculated the average of litter and duff load, duff depth, and duff bulk density as the average of the measurements made at each focal tree that defined each plot ($n = 72$). We first calculated Spearman's rank correlation. Regression analysis was performed to assess the

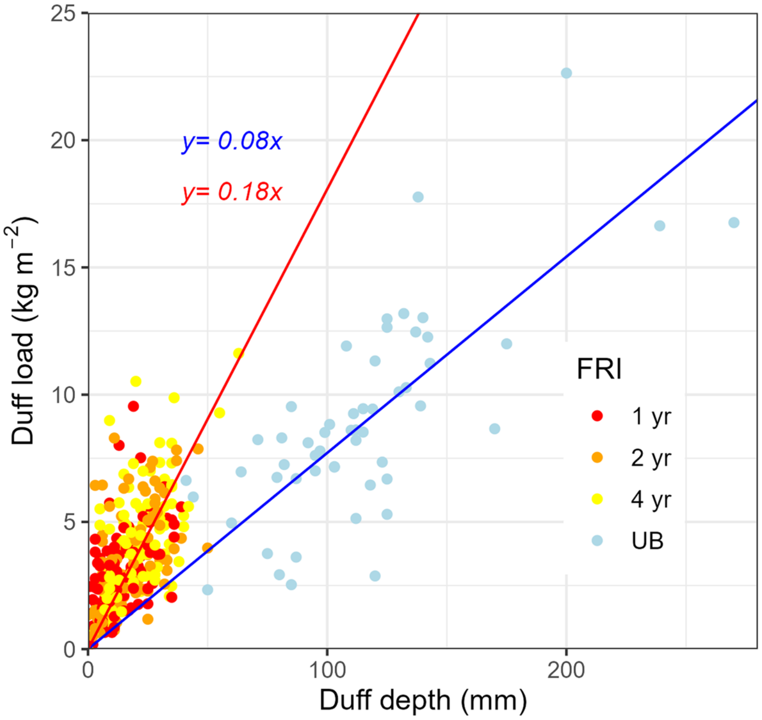

Fig. 6 Duff load versus duff depth of the field samples collected in 2022 in the long-term experiment consisting of three fire return intervals (FRI) and an unburned (UB) treatment. The dark blue line represents the linear regression forcing the intercept to zero using only the data collected in the unburned treatment pre-fire ($y = \beta_1 x$). The red line represents the linear regression forcing the intercept to zero using the data collected in the 1-, 2-, and 4-yr FRI treatments collected pre- and post-fire

independent effect of basal area or tree density with time since fire (Eq. 1). Unburned plots were assigned 64 years since fire given the time of the data collection (2022) and the beginning of the experiment (1958) to consider FRI as a continuous variable.

$$\text{Fuel variable} = \beta_0 + \beta_1 \text{FRI} + \beta_2 \text{Tree variable} \quad (1)$$

where the fuel variable is the plot-level average of the pine needle litter load (kg m^{-2}), mixed litter load (kg m^{-2}), duff load (kg m^{-2}), duff depth (mm), or duff bulk density (kg m^{-3}); FRI is the fire return interval; and the tree variable is either the plot-level basal area (m^2 ha^{-1}) or tree density (tree ha^{-1}).

Results

Effects of FRI on fuel loads

Prescribed burning treatment at different FRI was a significant factor explaining accumulated litter and duff loads (Fig. 5). Overall, fuel loads in the unburned plots were higher in comparison to the three FRI treatments (Table 1). In the burned plots, pre-fire average pine needle was 0.32 kg m^{-2}, mixed litter was 0.55 kg m^{-2}, duff depth was 16 mm, duff load was 3.54 kg m^{-2}, and duff bulk density was 318.7 kg m^{-3}. In the unburned plots, average pine needle and mixed litter loads were 0.47 and 0.93 kg m^{-2}, duff depth was 113 mm, duff load was 8.89 kg m^{-2}, and duff bulk density was 79.9 kg m^{-3}. Pine needle and mixed litter loads were significantly higher in the 4-yr FRI and unburned treatments than in the 1- and 2-yr FRI treatments (Table 1, Fig. 5). No significant difference was observed between the 4-yr FRI and unburned treatments for either the pine needle litter load or the mixed litter load (Fig. 5), and across treatments, standard deviation tended to increase with FRI. Mean and standard deviations of duff load and duff depth were higher in the unburned plots compared to the three FRI treatments, but the coefficient of variation was lower. Overall, unburned plots depicted the highest standard deviation compared to the burned units, except for duff bulk density that showed the opposite trend. Coefficient of variation was often higher for burned units, highlighting higher relative variability within these units (Table 1). Non-significant differences in duff bulk density were found between the 1-yr, 2-yr, and 4-yr FRI treatments, which indicates that the relationship between duff load and depth is similar for the burned systems but significantly different for the unburned treatment (Fig. 5).

Frequent prescribed fire strongly influenced duff bulk density. Plots regularly burned had significantly higher

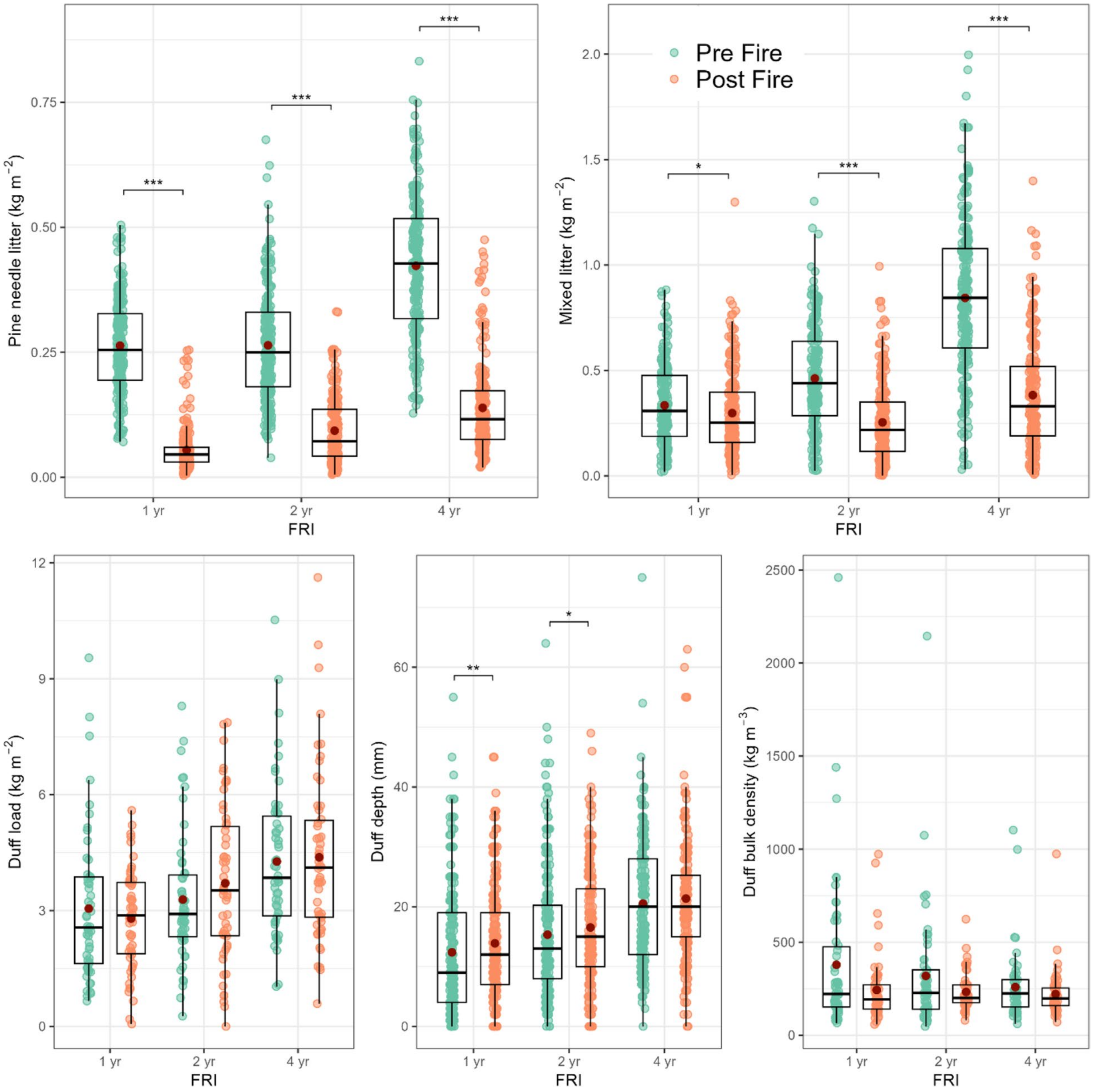

Fig. 7 Boxplots of the pine needle litter load, mixed litter load, duff load, duff depth, and duff bulk density of the samples collected pre- and post-fire in the long-term experiment consisting of three fire return intervals (FRI: 1 yr, 2 yr, 4 yr) treatments. Boxes represent the interquartile range (25th–75th percentiles) with the median as the central line, and the whiskers extend to the most extreme values within 1.5 times the interquartile range. The red dot indicates the mean value. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$) in the fuel attributes for post hoc pairwise comparisons as determined by Dunn's test pre- and post-fire

duff bulk densities compared to the plots located on the unburned units (Fig. 5). The relationship between duff load and duff depth (that defines bulk density) showed a different linear slope between the burned and unburned treatments, i.e., for a given depth, duff load on the burned plots would be nearly double that on the unburned plots (Fig. 6).

Fuel consumption during prescribed fire

As expected, litter loads were significantly higher before than after prescribed fire (Fig. 7). Nevertheless, the difference in mixed litter load pre- and post-fire was less significant for the 1-yr treatment, which could indicate less fuel consumption during the prescribed fire, perhaps due to less fuel continuity. These distinct patterns were reflected in litter composition: pre-fire, pine needle litter represented 41% of the total litter, while post-fire pine needle only represented 26% of the total litter on average. Overall, across all FRIs, duff loads were relatively similar before and after fire treatment even though the average loads post-fire (3.63 kg m^{-2}) were higher than pre-fire (3.54 kg m^{-2}). This pattern was also observed in duff depth, averaging 16 mm pre-fire and 17 mm post-fire. Overall, average pre-fire bulk density from 1 to 4 yr since fire was higher (318.7 kg m^{-3}) than post-fire bulk density (232.2 kg m^{-3}), but no significant differences were observed for the FRIs. The standard deviation of duff bulk density was larger pre-fire (sd = 325.2 kg m^{-3}) compared to post-fire (sd = 140.9 kg m^{-3}). The coefficient of variation was lower for pre-fire pine needle load and mixed litter load compared to the post-fire observations; it was relatively similar for duff loads pre- and post-fire, particularly for the 2- and 4-yr FRI; and it was higher for duff depth and bulk density pre- than post-fire (Table 1).

Tree bole proximity and wind effect on fuel loads

Pine needles on the forest floor were evenly distributed from 1 to 4 m from the tree bole (Fig. 8, first row), implying that under a tree crown, there was not significant spatial dependence in needle deposition. In contrast, the category composed of mixed litter was slightly higher on the pre-fire samples near the tree bole even though significant differences were not observed, except for the 2-yr FRI (Fig. 8, second row). However, post-fire loads of mixed litter showed a significant difference between the samples collected at 1 m from the tree bole and the ones collected at 2 and 4 m from the tree bole.

On the other hand, there were significant differences in duff load and duff depth in the unburned plots at different distances from the tree bole, precisely between 1 and 4 m from the focal tree. The difference was more significant with the duff loads compared to the depths. However, there was not much difference in the other three FRI treatments pre-fire or post-fire (Fig. 8, third and fourth row). No significant difference given the distance from the tree bole in duff bulk density was observed (Fig. 8, fifth row).

Higher presence of litter and/or duff loads in one of the transect directions could indicate anisotropic influence of the prevailing wind on litter deposition, accumulation, and resulting duff formation through time. In this regard, no significant difference was observed in fuel loads relative to sample transect directions, except for two cases with mixed litter (Supplementary Fig. S1). Overall, this suggested that wind was likely not a driving factor of litter or duff accumulation in these stands.

Basal area and tree density relationship to FRI and surface fuel loads

Average plot-level basal area was 25 m^2 ha^{-1} and tree density was 318 trees ha^{-1}. Mean basal area and tree density were higher in the unburned and 1-yr FRI plots than in the 2-yr and 4-yr FRI plots (Fig. 9, Table S2). Prescribed burning influenced tree density: it was significantly higher in the unburned plots compared to the burned units (Fig. 9).

Pine needles displayed a moderate Spearman's rank correlation with both basal area ($\rho = 0.40$) and tree density ($\rho = 0.44$). Mixed litter had a low correlation with basal area ($\rho = 0.23$) and tree density ($\rho = 0.35$). Duff load and depth also had low correlations with basal area ($\rho = 0.32$ and $\rho = 0.33$ respectively) and moderate correlations with tree density ($\rho = 0.44$ and $\rho = 0.43$ respectively). Duff bulk density had a low and modest negative correlation with basal area ($\rho = -0.19$) and tree density ($\rho = -0.31$).

Regression analysis showed that, in addition to FRI, basal area had a significant positive effect on litter and duff loads (Table 2). The influence was more significant for pine needles than for mixed litter. Tree density did not significantly influence mixed litter load. Both basal area and tree density had a positive significant effect on duff load and duff depth but not on duff bulk density. The residuals of the linear models were not always normally distributed, as shown by the Shapiro-Wilk normality test.

Discussion

Long-term FRI experiments such as the one at the Olustee Experimental Forest at Osceola National Forest provide excellent opportunities to evaluate the effect of FRI on accumulated litter and duff loads. This study was designed to address the influence of consistent prescribed burning, aboveground tree biomass, and wind direction on the distribution and accumulation of litter and duff.

(See figure on next page.)

Fig. 8 Boxplots of pre- and post-fire pine needle litter load, mixed litter load, duff load, duff depth, and duff bulk density of the samples collected in the three fire return interval (FRI: 1 yr, 2 yr, 4 yr) and an unburned (UB) treatment units at 1, 2, and 4 m from the tree bole. Boxes represent the interquartile range (25th–75th percentiles) with the median as the central line, and the whiskers extend to the most extreme values within 1.5 times the interquartile range. The red dot indicates the mean value. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$) for post hoc pairwise comparisons as determined by Dunn's test given the distance from the tree bole for a given FRI. For visualization purposes, data points beyond the y-axis label range are not displayed

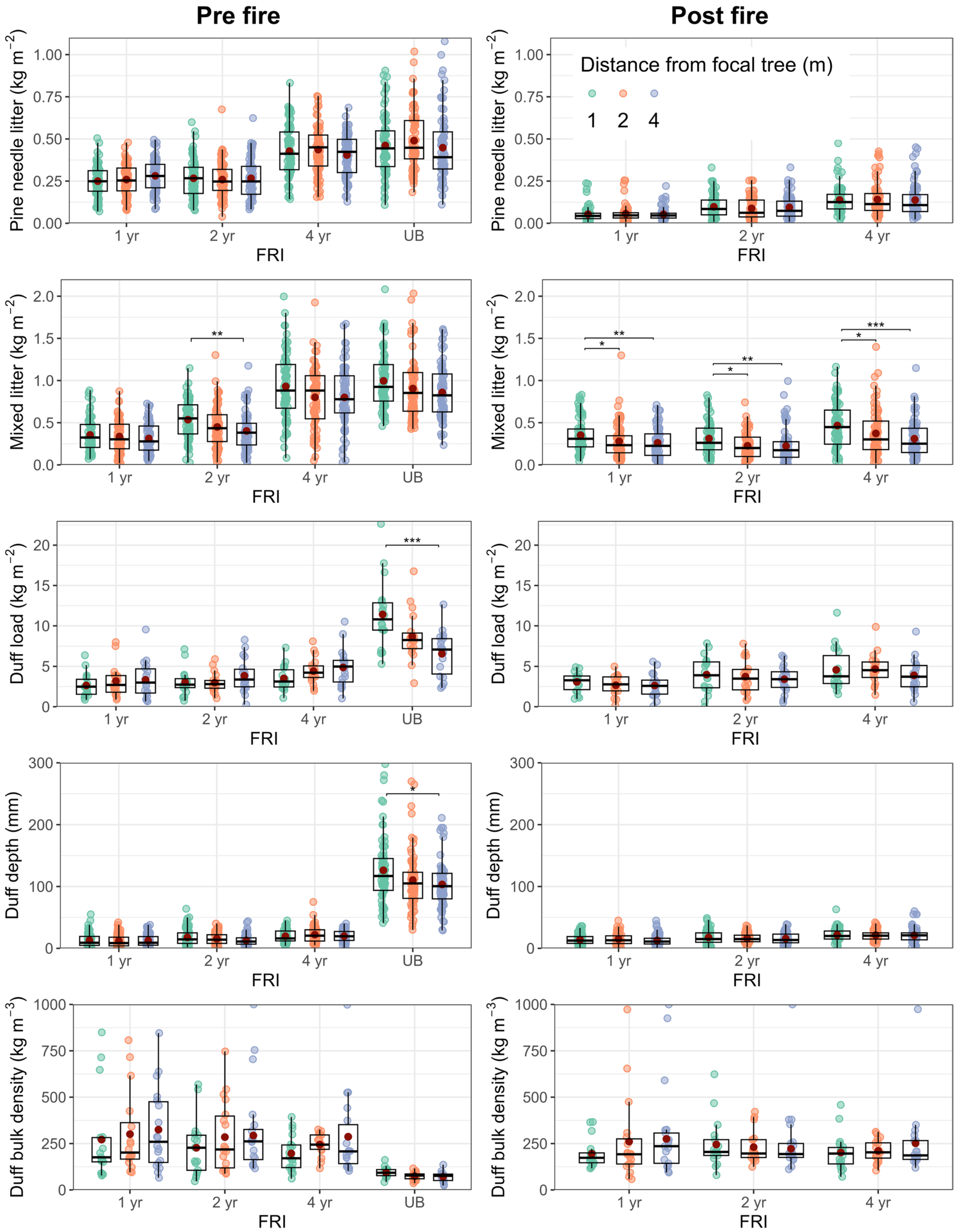

Fig. 8 (See legend on previous page.)

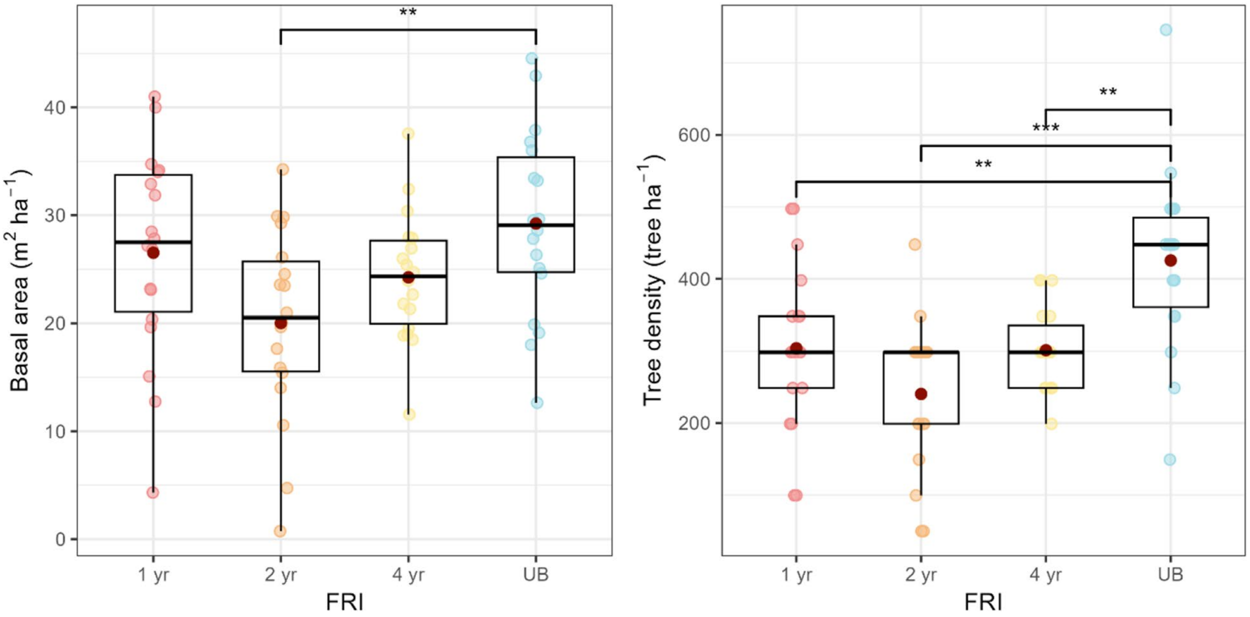

Fig. 9 Boxplots of plot-level basal area and tree density derived from the tree inventory data measured in the long-term experiment consisting of three fire return intervals (FRI: 1 yr, 2 yr, 4 yr) and unburned (UB) treatments. Boxes represent the interquartile range (25th–75th percentiles) with the median as the central line, and the whiskers extend to the most extreme values within 1.5 times the interquartile range. The red dot indicates the mean value. Asterisks indicate significance (**$p < 0.01$, ***$p < 0.001$) in the attributes based on post hoc pairwise comparisons as determined by HSD Tukey test

Table 2 Statistics of the regression model (Eq. 1) for the effect of fire return interval (FRI) and basal area (BA) or tree density (TD) on pine needle litter load, mixed litter load, duff load, duff depth, and duff bulk density (BD) using the pre-fire collected samples at the plot-level. The unburned treatment was assigned FRI of 64 to reflect the time since the last fire. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Dependent variable	Tree variable	Intercept	β_1	β_2	*F* value	Adj. R^2	*p* value	*p* value Shapiro-Wilk
Pine needle litter (kg m^{-2})	BA	0.046	0.070***	0.0053***	70.6	0.66	<2.2E−16	0.52
	TD	0.12***	0.068***	0.00020*	43.47	0.54	6.08E−13	1.00
Mixed litter (kg m^{-2})	BA	−0.024	0.21***	0.0056*	65.95	0.65	<2.2E−16	0.92
	TD	0.036	0.21***	0.00030	62.13	0.63	3.70E−16	0.85
Duff load (kg m^{-2})	BA	−1.78*	1.74***	0.092***	47.17	0.57	1.23E−13	0.12
	TD	−1.14	1.57***	0.0066**	44.82	0.55	3.35E−13	0.0060
Duff depth (mm)	BA	−63.93***	29.25***	1.25***	66.49	0.65	<2.2E−16	0.46
	TD	−56.52***	26.78***	0.094**	65.49	0.65	<2.2E−16	0.52
Duff BD (kg m^{-3})	BA	537.00***	−93.67***	−1.74	8.72	0.18	4.2E−04	2.61E−10
	TD	499.96***	−95.61***	−0.0049	8.51	0.17	5.00E−04	3.22E−10

In short, both FRI and tree aboveground attributes (basal area and tree density) had a significant influence on accumulated litter and duff loads (Fig. 5, Table 2), with longer FRIs and higher basal area leading to higher fuel loads. In contrast, duff bulk density was significantly higher on the burned units. For a given depth, duff load would be nearly twice as high in the burned plots compared to the unburned plots (Fig. 6), indicating a higher compaction of the duff layer. Litter loads significantly decreased after prescribed fire treatment, but had no effect on duff loads (Fig. 7). Proximity to the tree bole was relevant to explaining duff distribution within the unburned plots (Fig. 8), and litter and duff were evenly distributed in the four cardinal directions (Fig. S1), so it is likely that there was not a predominant wind direction that influenced the distribution of these fuels on the forest floor, nor was there any topographic slope. The sampling design neglected to consider the role of understory palmetto and shrubs patchily distributed across all the research units, which might influence mixed litter and duff loads.

Litter and duff loading, duff depth, and duff bulk density were highly variable, perhaps the most distinctive characteristic of our dataset. The high variability between the pre- and post-fire loading of both pine needle and mixed litter (Table 1) was likely due to burned and unburned patches created during the most recent prescribed fire but also during past prescribed fires, which may have influenced the continuity of the litter layer and fire spread. This might be particularly relevant in the 1-yr FRI, which is characterized by a short accumulation period that prevents the formation of a continuous litter layer. The average loading of pine needles, for instance, was similar between the 1- and 2-yr FRI (0.26 kg m^{-2}). We hypothesize that patchy fuel consumption may extend across multiple burning cycles and might produce conditions closer to a 2-yr cycle in this case. In addition to pre- and post-fire variability, the fuels also varied within and across FRI, revealing heterogeneity even under similar conditions of prescribed burning. These observations highlight the complex feedback between fire, fuels, and the drivers of the fuel accumulation process such as deposition and belowground dynamics, which in turn relates to aboveground biomass and stand structure, and decomposition.

Litter consumption likely increased proportionally to the amount of fuel available for burning. Before prescribed fire, litter loads were significantly lower in the 1- and 2-yr burned treatments compared to the 4-yr and UB treatments. After prescribed fire, litter loads were significantly lower across all three FRI treatments compared to the pre-fire levels. The pattern of consumption seemed dissimilar around the tree bole because, proportionally, more mixed litter was observed post-fire at 1 m from the tree bole than at 2 and 4 m (Fig. 8); notably, no significant difference in pre-fire mixed litter loads was observed due to distance from the tree bole, except for the 2-yr FRI. We speculate that near the tree bole, bark tissue was the dominant vegetative tissue of the mixed litter, while further from the bole, smaller particles such as reproductive buds or small twigs were in higher proportion. Other factors, including differences in structure and chemical composition that influence flammability, may also have contributed. For instance, small twigs are generally more flammable than bark because of their smaller particle size and higher surface-area-to-volume ratio (Brown 1970), and they also differ in chemical composition (Grootemaat et al. 2017). Another potential explanation for this observation is that 2 months elapsed between the prescribed fire and post-fire sampling. This could have led to more litter deposition (especially bark) from scorched trees or natural seasonal litterfall in closer proximity to the tree boles.

Duff loads were significantly higher near the tree bole on the unburned plots where both root biomass and the deposition of litter materials such as bark flakes were more abundant than further from the tree bole. Duff formation is driven by the decomposition of litter and downed woody debris, but it is also driven by the decomposition of belowground biomass, particularly the turnover of fine roots, that are known to significantly contribute to soil carbon accumulation (Ma et al. 2022). While this might be a subtle effect in the short term, when sustained over decades of fire exclusion, it appears to have contributed to the steeper gradient in accumulated duff with decreasing distance from the tree bole. We originally hypothesized that pine needle loading was higher near the tree bole because of higher canopy cover. However, we only evaluated distances from the tree bole ranging from 1 to 4 m, which is a relatively short distance given the radius of tree crowns for mature longleaf pine forests of similar characteristics, which often exceed 5 m (Sánchez-López et al. 2023). Indeed, we did not observe any significant difference in pre-fire pine needle loading when comparing samples collected at 1, 2, and 4 m from the focal tree bole (Fig. 8, first row). Therefore, we attribute the higher duff loading near the tree bole to belowground activity and the mixed litter decomposition, which showed some subtle differences given the distance from the tree bole (Fig. 8, second row).

Duff bulk density was considerably higher in burned plots than in unburned plots, highlighting the strong influence of consistent burning on this trait. There was a larger standard deviation in the duff bulk density of the pre-fire condition, with post-fire bulk density variation tending to be lower (Table 1, Fig. 7). However, there were no significant differences between pre- and post-fire conditions, suggesting that the bulk density was consistent across treatments. We speculate that after decades of consistent prescribed burning, partially burned litter and duff might be more compacted, i.e., structurally and chemically different from the decomposing debris on the unburned plots. In the absence of fire, the duff layer could be more porous and retain more water. Fire, on the other hand, might consume the more aerated and drier components of the surface fuels, assuming that a vertical gradient of increasing fuel moisture is present. Over time, this results in a more compacted duff layer, including a substantial mineral component that will limit burning, and the composition might be also different, with more humus, i.e., higher packing. Duff bulk densities in the unburned treatments (~79.9 kg m^{-3}) were close to values reported in other studies, but the bulk densities of the burned treatments were considerably higher on average (~275.7 kg m^{-3}, including pre- and post-fire samples). Ottmar and Andreu (2007), for instance, reported duff bulk densities ranging from 40.3 to 97.3 kg m^{-3} for loblolly and slash pine forests, and the majority of these forests were likely not prescribed burned in the years preceding field data collection (Ottmar, personal communication), and Prichard et al. (2025) reported ~31 kg m^{-3} duff bulk density averages for samples collected within 10 cm of a tree bole in southeastern flatwoods. These flatwoods were burned within the last 6 years prior to the data collection, but the fire history influencing the soil dynamics of each site of this former study was not reported. Our results suggest that bulk densities and duff mass/depth relationships need to be calibrated under different FRI management scenarios before deriving estimates of biomass. This might have important implications for evaluating carbon sequestration and emissions in fire-maintained forest ecosystems. We also suggest (without knowing the carbon concentrations) that the amount of carbon stored in frequently burned systems may be higher than what is normally assumed based on the duff depths, and the distribution might be highly affected by consumption patterns during the prescribed fires. However, further research and comparison with data from sites with a long history of prescribed fire management are needed as some external factors might also be at play. For instance, the soil properties of the Spodosols of the study site might alter its capacity to store carbon under frequent fire regimes. Another potential issue is that duff sampling involves identifying two boundaries: the litter and duff boundary and the duff and mineral soil boundary, which could lead to greater variability if the measurement protocols or experience of the field crews differ. In this context, this effect is likely small because the structural gradient in unburned plots often makes the duff layer more difficult to identify compared to burned plots.

In general, our analysis suggests that the number of samples collected might not have been sufficient to fully characterize duff consumption. The average duff loads following prescribed fire were measured to be higher than pre-fire for the 2- and 4-yr FRI (Table 1, Fig. 7), highlighting the inherently high fine-scale variability in forest floor fuels, particularly harder-to-measure duff (Hiers et al. 2009; Kreye et al. 2014). Our observations could be explained if charred, newly deposited fine litter material—difficult otherwise to separate from litter—was included in the duff samples during the post-fire data collection, or because the pre- and post-fire samples were not co-located because they were destructive samples. The use of pins to measure the difference in pre- and post-fire litter and duff depths might be a more precise method to measure consumption at a specific location. However, the difference between pre- and post-fire duff loads was too small to draw any conclusions regarding duff consumption, which was expected to be low. During prescription windows, the upper duff layer, corresponding to the Oe fermentation layer, is moister compared to the litter (Oi) layer which results in lower duff consumption rates (Varner et al. 2007, 2009). The complexity of assessing duff consumption has been highlighted in previous studies. Prichard et al. (2017) did not find robust relationships between consumption and pre-fire biomass loads using data from 60 sites in US southern pine forests, whereas Kreye et al. (2014) observed large fine-scale heterogeneity in duff characteristics, concluding, with which we agree, that aggregation across stands or units might obscure this variability. In this regard, the development of spatially explicit models to represent duff variability should be a research priority.

Fire exclusion led to higher tree density, which was observed mostly in the mid- and understory, but it did not have a strong influence on basal area as the average was only significantly different between the unburned and the 2-yr treatment (Fig. 9). Ross et al. (2024) indicated that fire frequency at this same study site mostly affected the understory. Aboveground biomass drove intra-stand variability in surface fuel loads, i.e., within each burned unit, both basal area and tree density helped to explain the distribution of litter, particularly pine needles, and duff loads (Table 2).

Conclusion

Understanding the distribution of litter and duff under different prescribed fire management scenarios is key to informing forest and fire managers, and modelers in assessing processes such as fire behavior and carbon sequestration. This information is also key to forecasting future trends and predicting the effects of different management scenarios. This study, made possible through more than six decades of consistent prescribed burning at Osceola National Forest, advances our understanding of litter and duff accumulation dynamics in southern pine flatwoods of the US, and provides valuable empirical information on the variability of litter load, duff load, duff depth, and duff bulk density under different FRIs. Our analyses suggest that FRI is an inter-stand-level driver of surface fuel accumulation while aboveground biomass is an intra-stand-level driver. This dataset also reveals that frequent low-intensity fires contribute to the development of smaller and more compact duff layers which should be carefully considered in carbon assessments in similar fire-maintained forest ecosystems. High heterogeneity and complex interactions between fire, fuels, and ecological factors drive surface and ground fuel accumulation processes. Further investigations and comparisons to datasets from other study sites are warranted. They will be essential to corroborate these long-term trends and assess mid-term dynamics, broadening our understanding of litter and duff accumulation over space and time.

Abbreviations

FRI	Fire return interval
ONF	Osceola National Forest
US	United States
yr	Year
GPS	Global positioning system
dbh	Diameter at breast height
BD	Bulk density
BA	Basal area
TD	Tree density
UB	Unburned

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00425-9.

Supplementary Material 1.

Acknowledgements

The authors are grateful for the assistance of Gregg Chapman, Steve Flanagan, Joe Paki, and Bayan Sheko in the described work and to the forest managers at the Osceola National Forest for maintaining the fire treatments for the long-term study. We thank the two anonymous reviewers for their constructive comments, which contributed to refining and improving the manuscript.

Authors' contributions

Conceptualization: N.S.L., A.T.H., M.A.C., M.K.T.; methodology: N.S.L., A.T.H., M.A.C., M.K.T.; resources: N.S.L., A.T.H., M.A.C., M.K.T., J.J.O.; data curation: N.S.L., M.K.T.; formal analysis: N.S.L.; software: N.S.L.; investigation: N.S.L.; original draft preparation: N.S.L., A.T.H; writing—review and editing: N.S.L., A.T.H., M.A.C., M.K.T., J.J.O.; visualization: N.S.L., M.A.C., J.J.O.; funding acquisition: A.T.H.

Funding

Funding was provided by the Department of Defense (DOD) Strategic Environmental Research and Development Program (SERDP) award RC20-1346 to the US Forest Service Rocky Mountain Research Station and a sub-award through International Joint Venture agreement 25-IJ-11221633-017 to the University of Oviedo Foundation (APR-24-056). This research was supported by the US Department of Agriculture, Forest Service, Rocky Mountain Research Station and the Southern Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US government determination or policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Data availability

The field data here described is publicly available in the Wildland Fire Science Initiative (WFSI) data portal (wfsi-data.org) in the data product of Callaham et al. (2025).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

ATH and NSL are associate editors of the journal, and are guest editors of the special issue 3D Fuels: characterizing the structure and composition of wildland fuels in three dimensions. The authors declare no other competing interests.

Author details

[1]Institute of Natural Resources and Spatial Planning (INDUROT), University of Oviedo, 33600 Mieres, Asturias, Spain. [2]Forestry Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 1221 S Main Street, Moscow, ID, USA. [3]Disturbance and Prescribed Fire Science Laboratory, Southern Research Station, USDA Forest Service, 320 Green St, Athens, GA, USA. [4]Center for Geospatial Analytics, North Carolina State University, 2800 Faucette Dr, Raleigh, NC, USA.

Received: 26 May 2025 Accepted: 15 October 2025

References

Abrahamson WG, Hartnett DC (1990) Pine flatwoods and dry prairies. In: Ecosystems of Florida

Agee, J.K., and C.N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211 (1–2): 83–96.

Brown, J.K. 1970. Ratios of surface area to volume for common fine fuels. *Forest Science* 16 (1): 101–105.

Callaham MA, Taylor MK, Sánchez-López N, Hudak AT, Bright B (2025) Tree inventory and field measurements of litter and duff collected at Osceola National Forest in 2022. https://doi.org/10.60594/W4XW2V

Esri, Maxar, Earthstar Geographics, and the GIS User Community (2024) World imagery [basemap]

Glenn, C. K., O. El Hajj, Z. McQueen, R. P. Poland, R. Penland, E. T. Roberts, J. H. Choi, B. Bai, N. Shin, A. Anosike, K. V. Kumar, M. I. Abdurrahman, P. Liu, I. J. Amster, G. D. Smith, S. Flanagan, M. A. Callaham, E. L. Loudermilk, J. J. O'Brien, and R. Saleh. 2024. Brown carbon emissions from biomass burning under simulated wildfire and prescribed-fire conditions. *ACS EST Air* 1 (9): 1124–1136. https://doi.org/10.1021/acsestair.4c00089.

Glitzenstein JS, Streng DR, Wade DD (2003) Fire frequency effects on longleaf pine (Pinus palustris P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal 23 (1): 22–37 2003

Grace, S. L., and W. J. Platt. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology*. https://doi.org/10.2307/2261152.

Grootemaat, S., I. J. Wright, P. M. van Bodegom, J. H. C. Cornelissen, and V. Shaw. 2017. Bark traits, decomposition and flammability of Australian forest trees. *Australian Journal of Botany* 65 (4): 327–338. https://doi.org/10.1071/BT16258.

Hiers, J. K., J. J. O'Brien, R. J. Mitchell, J. M. Grego, and E. L. 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 (3): 315–325. https://doi.org/10.1071/WF08084.

Kreye, J. K., J. M. Varner, and C. J. Dugaw. 2014. Spatial and temporal variability of forest floor duff characteristics in long-unburned *Pinus palustris* forests. *Canadian Journal of Forest Research* 44 (12): 1477–1486. https://doi.org/10.1139/cjfr-2014-0223.

Kreye, J. K., J. M. Varner, and L. N. Kobziar. 2020. Long-duration soil heating resulting from forest floor duff smoldering in longleaf pine ecosystems. *Forest Science* 66 (3): 291–303. https://doi.org/10.1093/forsci/fxz089.

Ma, W., S. Tang, Z. Dengzeng, D. Zhang, T. Zhang, and X. Ma. 2022. Root exudates contribute to belowground ecosystem hotspots: a review. *Frontiers in Microbiology* 13 : 937940.

McDanold, J. S., R. R. Linn, A. K. Jonko, A. L. Atchley, S. L. Goodrick, J. K. Hiers, C. M. Hoffman, E. L. Loudermilk, J. J. O'Brien, R. A. Parsons, C. H. Sieg, and J. A. Oliveto. 2023. DUET - Distribution of Understory using Elliptical Transport: a mechanistic model of leaf litter and herbaceous spatial distribution based on tree canopy structure. *Ecological Modelling* 483 : 110425. https://doi.org/10.1016/j.ecolmodel.2023.110425.

McKee WH (1982) Changes in soil fertility following prescribed burning on coastal plain pine sites. US Department of Agriculture, Southeastern Forest Experiment Station

Mugnani, M. P., K. M. Robertson, D. L. Miller, and W. J. Platt. 2019. Longleaf pine patch dynamics influence ground-layer vegetation in old-growth pine savanna. *Forests* 10 (5): 389. https://doi.org/10.3390/f10050389.

NOAA (2025) NCEI geomagnetic calculators. In: Magnetic field calculation. https://www.ngdc.noaa.gov/geomag/calculators/magcalc.shtml#ushistoric. Accessed 12 Feb 2025

O'Brien, J. J., J. Kevin Hiers, R. J. Mitchell, J. M. Varner, and K. Mordecai. 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *Fire Ecology* 6 (2): 1–12. https://doi.org/10.4996/fireecology.0602001.

Ottmar R, Andreu A (2007) Litter and duff bulk densities in the southern United States. Final report, JFSP project :04–2

Prichard SJ, Nemens D, Kennedy MC, et al. 2025. Forest floor properties in pine forests of the southeasternand western United States. *fire ecol.* 21, 85. https://doi.org/10.1186/s42408-025-00429-5.

Prichard, S. J., M. C. Kennedy, C. S. Wright, J. B. Cronan, and R. D. Ottmar. 2017. Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the United States. *Forest Ecology and Management* 405:328–338. https://doi.org/10.1016/j.foreco.2017.09.025.

Robertson, K. M., W. J. Platt, and C. E. Faires. 2019. Patchy fires promote regeneration of longleaf pine (*Pinus palustris* Mill.) in pine savannas. *Forests* 10 (5) : 367. https://doi.org/10.3390/f10050367.

Ross, C. W., E. L. Loudermilk, J. J. O'Brien, S. A. Flanagan, J. McDaniel, D. P. Aubrey, T. Lowe, J. K. Hiers, and N. S. Skowronski. 2024. Lidar-derived estimates of forest structure in response to fire frequency. *Fire Ecology* 20 (1) : 44. https://doi.org/10.1186/s42408-024-00279-7.

Sackett, S. S. 1975. Scheduling prescribed burns for hazard reduction in the southeast. *Journal of Forestry* 73 (3): 143–147.

Sánchez-López, N., A. T. Hudak, L. Boschetti, C. A. Silva, K. Robertson, E. L. Loudermilk, B. C. Bright, M. A. Callaham, and M. K. Taylor. 2023. A spatially explicit model of tree leaf litter accumulation in fire maintained longleaf pine forests of the southeastern US. *Ecological Modelling* 481 : 110369. https://doi.org/10.1016/j.ecolmodel.2023.110369.

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 (3): 536–544.

Varner, J. M., J. K. Hiers, R. D. Ottmar, D. R. Gordon, F. E. Putz, and D. D. Wade. 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. *Canadian Journal of Forest Research* 37 (8): 1349–1358. https://doi.org/10.1139/X06-315.

Varner, J. M., F. E. Putz, J. J. O'Brien, J. K. Hiers, R. J. Mitchell, and D. R. Gordon. 2009. Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management* 258 (11): 2467–2474.

Publisher's Note