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Variations in stand structure, composition, and fuelbeds drive prescribed fire behavior during mountain longleaf pine restoration

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A B S T R A C T

Across the central and eastern U.S., frequent-fire (~ 1–5 year interval) dependent savannas, woodlands, and forests have experienced widespread ecological state shifts due to decades of fire exclusion. Without fire, mesophytes (i.e., shade-tolerant, often fire-sensitive and/or opportunistic tree species) are encroaching in the midstory, creating shady, moist understories with low flammability and reduced biodiversity through a process known as "mesophication." Although prescribed fire is commonly used to reverse mesophication and restore fire-dependent ecosystems, fire behavior during restoration remains difficult to predict because variations in stand structure and composition and associated fuels interact to influence flammability. To better understand the mesophication mechanisms influencing fire behavior and to identify key predictors of fire behavior for the benefit of land managers, we assessed how metrics that describe fire intensity (maximum temperature, rate of spread, and residence time) and severity (fuel consumption) relate to pre-fire stand and leaf litter composition and structure. We focused on the restoration of remnant mountain longleaf pine (*Pinus palustris* Mill. (LLP)) stands during the dormant prescribed fire season in the Georgia Piedmont region, USA. Using Bayesian path analysis, we compared the effects of either stand or leaf litter composition and structure on fire behavior. Lower stand basal area and higher relative importance of pine and pyrophytic hardwoods (e.g., upland *Quercus* spp.) and associated leaf litter types were expected to increase fire intensity. Results showed that stand composition and structure significantly influenced fire behavior, but not because of their influence on litter structure (load and bulk density). Rather, leaf litter composition may better explain fire behavior than leaf litter structure. Results also suggest that simple measures of stand composition and structure alone can be used to predict fire behavior, providing a potentially useful tool for assessing restoration potential of fire-dependent ecosystems under threat of mesophication.

1. Introduction

Fire exclusion across the central and eastern U.S. is facilitating an ecosystem state change from historically open forests dominated by pyrophytic pines (*Pinus* spp. L.) and oaks (*Quercus* spp. L.) in the overstory to closed-canopy forests with dense midstories of shade-tolerant, often fire-intolerant species (i.e., mesophytes). While open forests include little midstory and a biodiverse herbaceous understory with highly-flammable fuels, closed-canopy forests have virtually no understory and fire-suppressing leaf litter fuelbeds (Babl et al., 2020; Hanberry et al., 2020; Nowacki and Abrams, 2008; Wade et al., 2000). Once established, mesophytes introduce self-reinforcing conditions of low light, moisture-retaining fuels and reduced fuel loads which render fire increasingly less likely and less intense through a process known as mesophication (Alexander et al., 2021; Nowacki and Abrams, 2008). Although prescribed fire is commonly used to maintain remnants and restore degraded fire-dependent open forests, our ability to predict fire behavior in these systems remains limited, likely due to variations in forest composition and structure that interact to influence fuelbed dynamics and forest flammability. Thus, effectively managing fire-dependent ecosystems in the region requires a better understanding of the mechanisms by which shifts in stand composition and structure

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(SCS) and fuelbed characteristics contribute to fire behavior.

Among the primary drivers of fire behavior, including topography, weather, and fuel (Rothermel, 1983), fuel is the one most influenced by changes in SCS and most directly manipulated in restoration (Bale, 2009). Leaf litter fuels are especially important in closed-canopy stands targeted for restoration, as they are more continuous in cover than downed wood and live understory vegetation (Arthur et al., 2015; Cabrera et al., 2023). Depending on both chemical and morphological traits, leaf litter can either promote or inhibit fire ignition and spread (Varner et al., 2015). For example, needles from longleaf pine (LLP; *Pinus palustris* Mill.) and other fire-dependent pine species contain flammable terpenes (Whelan et al., 2021; Ormeño et al., 2009) and decompose slowly (Hendricks et al., 2002; Melillo and Aber, 1982). The low-density structure of litter dominated by needles as opposed to broad-leaf litter, facilitates litter drying, which supports fire (Kreye et al., 2013a, 2013). Compared to mesophytic hardwood litter (e.g., *Acer rubrum* L., *Nyssa sylvatica* Marshall), pyrophytic hardwood litter (e.g., *Q. falcata* Michx., *Q. marilandica* Muenchh.) decomposes more slowly in part due to greater lignin: nitrogen ratios (Melillo and Aber, 1982,) and lower moisture holding capacity; thus leading to litter accumulation (Alexander and Arthur, 2014, Dickinson et al., 2016, Babl-Plauche et al., 2022). Pyrophytic hardwood litter also curls when dried, creating relatively deep and low-density litter with high surface area: volume ratios (Alexander et al., 2021; Babl-Plauche et al., 2022; McDaniel et al., 2021). Like pine needles, these traits promote drying and provide compaction resistance (McDaniel et al., 2021; Kreye et al., 2013a, 2013). In contrast, mesophytic leaf litter lies flat creating a shallow high–density fuel bed that traps moisture, and reduces airflow, suppressing fire (Babl et al., 2020; McDaniel et al., 2021). The faster decomposition of mesophyte litter reduces the amount of fuel in the litter layer and may decrease the amount of duff (i.e., fuel layer comprised of partially decomposed leaf litter and fine roots), which retains moisture longer than leaf litter (Babl-Plauche et al., 2022). In the case of longleaf pine, duff from slowly decomposing needles can build up around tree boles and smolder, killing even mature fire-adapted trees with thick bark (Varner et al., 2007). Because leaf litter dynamics are complex and fire is used as a tool to manage fire-dependent forest ecosystems under threat of mesophication, an increased understanding of how shifts in SCS influence fire behavior is critical to improve restoration and management outcomes.

Fire behavior in response to management activities is often a key component of restoration success. For example, fire temperature, rate of spread (RoS), and residence time during fire restoration efforts largely determine post-fire stand compositional and structural shifts due to mortality of targeted mesophytic species and regeneration of desired pyrophytic species (Glitzenstein et al., 1995, Bigelow and Whelan, 2019, Hutchinson et al., 2024). Fire temperature must be sufficient to partially consume the litter and duff layers for fire-dependent species such as LLP to germinate and to control competition from mesophytic species (Regelbrugge and Smith, 1994; Bigelow and Whelan, 2019); however, excessive fire intensity can damage soil structure and alter the microbiome which has implications for erosion, carbon storage, nutrient cycling, and ultimately plant community recovery (Nelson et al., 2022). Fires that pass too quickly (i.e.,fast RoS) may not kill undesired species, but a long residence time can damage the seed bank and even established, fire-adapted vegetation (Gagnon et al., 2015; Varner et al., 2007). Fire residence time is a good predictor of soil temperatures, and an increase in both are negatively related to post-fire vegetation regeneration (Gagnon et al., 2015). Thus, linking forest structure and composition to fire behavior is critical for assessing restoration success.

As fire is increasingly applied as a management tool, managers would benefit from the ability to predict relative fire behavior of stands targeted for restoration based on easily measurable stand qualities such as basal area and composition, in addition to commonly used weather data. To address this need, we use the understudied mountain (montane) longleaf pine ecoregion of Northwest Georgia, U.S.A., a high priority conservation area (High Priority Species and Habitat Summary Data, 2015), to assess how fire behavior metrics that describe fire intensity (maximum temperature, RoS, and residence time) and severity (fuel consumption) relate to pre-fire SCS and leaf litter structure (i.e., bulk density and load), in the restoration of forests experiencing mesophication.

Based on our initial analyses and prior literature regarding the importance of leaf litter flammability characteristics (reviewed above), we also assessed how the same fire behavior metrics relate to pre-fire litter composition and whether associated changes in the fuelbed's litter structure are important in predicting fire behavior. Leaf litter composition may provide another way for managers to predict fire behavior based on proportions of litter types within grab samples. We aimed to: 1) identify how shifts in forest SCS influence litter structure characteristics and fire behavior in mixed longleaf pine-hardwood forests, 2) determine if SCS alone can be used as a proxy (i.e., "proxy effect"; Fig. 1, path 1) to explain fire behavior, or if litter structural characteristics must be considered as mediating variables (i.e., “litter-mediated effect”, Fig. 1, path 1a), and in a similar inquiry 3) determine if leaf litter composition alone can be used as a proxy to explain fire behavior (Fig. 1, path 2), or if litter structural characteristics must be considered as mediating variables (Fig. 1, path 2a).

We hypothesized that because SCS are thought to be highly related to litter characteristics (Babl-Plauche et al., 2022; Dickenson et al., 2016), SCS can be used as a proxy to explain relative fire behavior without considering litter structure as a mediating variable. Specifically, we predicted that relative decreases in stand basal area and increases in the relative importance of pyrophytic pine and hardwoods (e.g., upland oaks) would increase fire RoS, residence time over a temperature threshold of 50 °C, and fuel consumption. We also expected that leaf litter composition alone could serve as a proxy to explain fire behavior without considering litter structure, due to litter chemical and morphological traits described above that impact flammability (de Magalhaes and Schwilk, 2012). We predicted that relative increases in pyrophytic pine and hardwood leaf litter and decreases in mesophytic leaf litter would increase fire intensity and severity. We used path analysis to compare how much variation in fire behavior was explained by the “proxy” vs. “litter-mediated” effects while also accounting for weather. This investigation will help restoration practitioners identify key factors that explain fire behavior to improve management.

2. Methods

2.1. Study site

This study examined mixed-species forest sites targeted for mountain LLP restoration within the Sheffield Wildlife Management Area (WMA) in Paulding County, Georgia, U.S.A. (34.020484, −84.904417) (Fig. 2). Sheffield WMA is a topographically dynamic forested area at the northwestern edge of the Piedmont ecoregion with narrow ridges and valleys ranging in elevation from 226 to 399 m. During the study year average monthly temperature ranged from 5 to 26 °C, and average monthly precipitation was 5–16 cm (National Centers for Environmental Information, https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/county/time-series). Soils are predominantly sandy loams of the Tallapoosa-Fruithurst complex (25–60 percent slopes) and Fruithurst-Braswell complex (6–15 percent slopes) (Natural Resources Conservation Service, Web Soil Survey, https://websoilsurvey.nrcs.usda.gov/). The forest contains remnant patches of approximately 70-year-old LLP trees among a larger mosaic of mixed pine and hardwood forest. As a result of fire exclusion through the latter half of the 20th century, LLP regeneration is generally low, and mesophytic hardwood species like blackgum (*Nyssa sylvatica* Marsh.) and red maple (*Acer rubrum* L.) now dominate the midstory and understory, preventing a herbaceous understory from developing. Co-dominant species in the overstory include loblolly pine (*Pinus taeda* L.), shortleaf pine

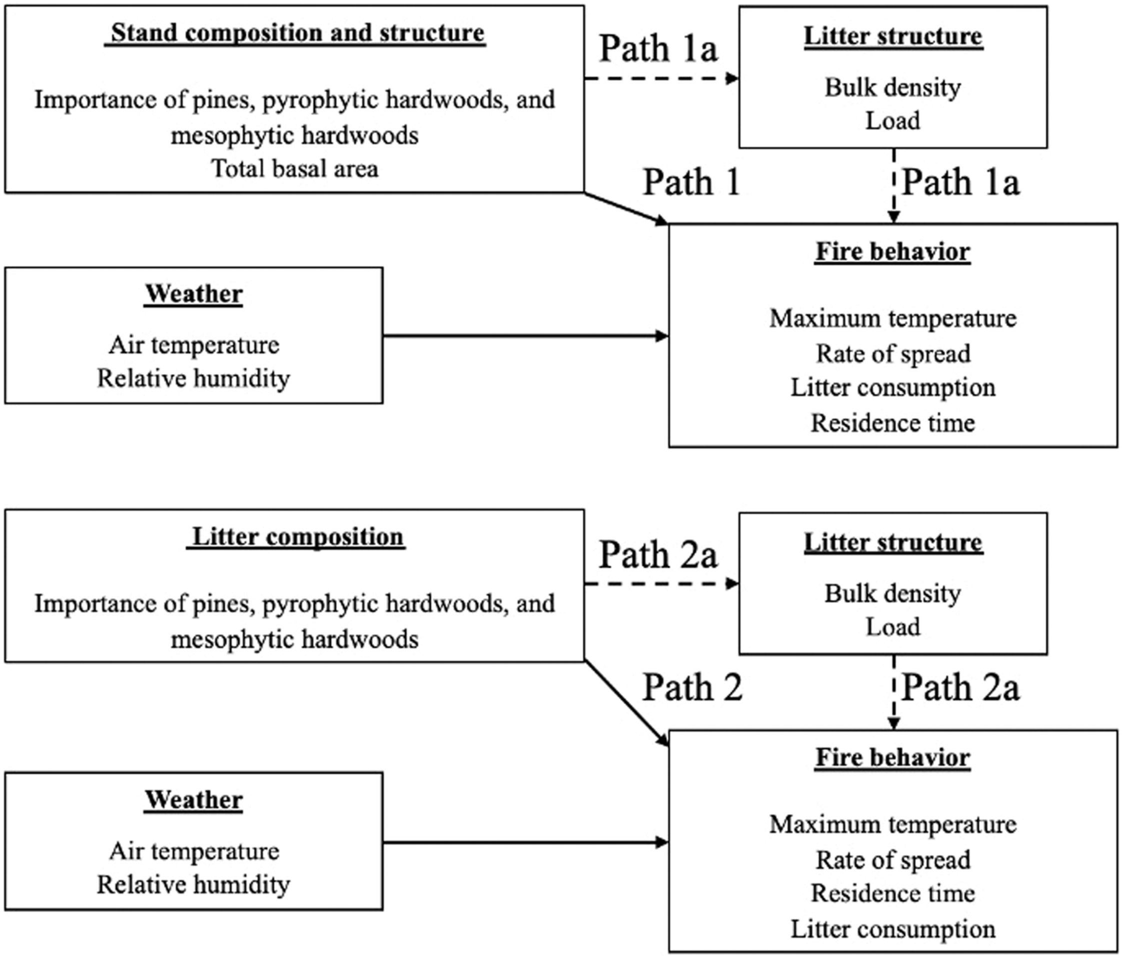

Fig. 1. Conceptual diagrams showing pathways for how either stand composition and structure or leaf litter composition might predict fire behavior acting as a proxy effect (solid arrows, Paths 1 and 2) or alternatively as a mediated effect i.e. through alteration of leaf litter structure (dashed arrows, Paths 1a and 2a). Weather is also included as an independent effect on fire behavior.

Fig. 2. Example restoration stages of mountain longleaf pine stands experiencing mesophication in Paulding County GA, USA. A. Closed canopy, mesophytic hardwood dominated sample plot "B" before prescribed burn. Photographed 8 February 2022 at 10:17 am. B. Open canopy, pine and pyrophytic hardwood dominated sample plot "G" before prescribed burn. Photographed 3 March 2022 at 8:32 am.

(*P. echinata*), Virginia pine (*P. virginiana*), Northern red oak (*Q. rubra*), Southern red oak (*Q. falcata* Michx.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Münch), black oak (*Q. velutina* Lam.), blackjack oak (*Q. marilandica* Münch.), chestnut oak (*Q. montana* Willd.), post oak (*Q. stellata*), and hickories (*Carya* spp.). Other species present include tulip-poplar (*Liriodendron tulipifera* L.), sourwood (*Oxydendrum arboreum* (L.) DC.), flowering dogwood (*Cornus florida* L.), and American beech (*Fagus grandifolia* Ehrh.). Since 2008, dormant season prescribed fire has been re-introduced to much of the WMA at 2–5-year intervals (B. Womack, personal communication, March 7, 2023.)

2.2. Study design

Within WMA units scheduled for prescribed burns in 2022, we established 20-m diameter fixed-radius sampling plots (Supp. Figure S2) to capture a gradient of SCS representing different restoration stages characterized by stand basal area (BA) and the ratio of pine to hardwood importance value (IV). Two plots were created in each of the five planned burn units (10 plots total), all of which were unburned since at least 2019. The intent of this study was not to describe fire behavior at the landscape scale, but rather to analyze fuels and fire across a restoration gradient. Plots were on slopes between 5 and 22 percent with aspects ranging from 100 to 260 degrees. All plots were located on upper slope positions ranging from 238 to 325 m in elevation (Table 1).

2.3. Stand and fuel characteristics

To examine the influence of SCS on fire behavior within each plot, we measured diameter at breast height (DBH; 1.37-m aboveground) for all trees that were rooted inside the plot and were at least 3-m tall. We calculated plot BA by summing the basal area of all individuals in the

Table 1
Topography, stand composition and structure, pre-burn litter composition and structure, burn timing, and during-burn weather conditions at sample plots (A-J) in Sheffield Wildlife Management Area, Paulding County GA, USA that experienced prescribed fire in Feb-Mar, 2022. IV = importance value. Numbers in parentheses are within-plot standard deviation.

		A	B	C	D	E	F	G	H	I	J
Topography	Aspect (°)	180	165	220	175	100	260	190	205	165	230
	Slope (%)	20	5	14	13	15	11	13	21	8	22
	Elevation (m)	321	300	314	325	238	315	317	310	299	296
Stand Composition and Structure	Pine IV:Hardwood IV ratio	0.7	0.1	1.4	0.1	1.0	0.6	2.3	2.2	1.2	0.5
	Pine IV	84.4	22.3	71.8	18.1	98.1	78.4	140.2	137.9	111.0	67.4
	Pyrophytic hardwood IV	101.2	52.5	18.7	78.0	24.1	100.9	45.6	62.1	47.7	83.5
	Mesophytic hardwood IV	14.4	125.1	34.4	48.2	77.8	20.7	14.2	0.0	41.3	49.1
	Basal area (m^2 ha^{-1})	34.7	29.2	32.7	36.8	11.9	23.4	19.2	22.7	19.7	41.0
	Canopy openness (%)	12.5	3.1	16.6	7.3	75.9	18.7	67.6	28.1	26.0	1.0
Litter Composition and Structure	Pine (kg m^{-2})	0.2 (0.1)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0.1 (0.0)	0.1 (0.0)	0.4 (0.3)	0.5 (0.1)	0.3 (0.2)	0.1 (0.0)
	Pyrophytic hardwood (kg m^{-2})	0.2 (0.1)	0.2 (0.1)	0.3 (0.1)	0.3 (0.2)	0.1 (0.0)	0.3 (0.1)	0.2 (0.2)	0.2 (0.2)	0.1 (0.2)	0.2 (0.0)
	Mesophytic hardwood (kg m^{-2})	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)
	Leaf litter load (kg m^{-2})	0.6 (0.2)	0.6 (0.1)	0.6 (0.2)	0.5 (0.1)	0.2 (0.1)	0.4 (0.1)	0.6 (0.2)	0.8 (0.3)	0.6 (0.2)	0.4 (0.0)
	Bulk density (kg m^{-3})	12.3 (5.7)	9.6 (1.8)	7.0 (2.2)	7.5 (1.8)	8.0 (2.4)	4.3 (0.9)	6.9 (4.1)	8.3 (4.0)	7.6 (2.9)	5.3 (0.9)
	Duff depth (cm)	2.1 (1.5)	1.6 (0.8)	1.6 (0.8)	2.1 (0.8)	1.1 (0.8)	2.1 (1.1)	1.1 (0.6)	3.1 (1.8)	2.2 (1.6)	1.5 (1.1)
	Leaf litter depth (cm)	5.8 (3.1)	6.3 (1.9)	8.2 (1.3)	7.2 (1.5)	3.3 (1.9)	10.1 (2.5)	10.0 (5.0)	9.9 (2.9)	7.7 (2.8)	7.3 (1.9)
Timing	Date of burn	8-Feb−22		9-Feb−22		2-Mar−22		3-Mar−22		4-Mar−22	
	Time of fire at plot	3 pm	2 pm	5 pm	1 pm	1 pm	2 pm	2 pm	1 pm	11 am	1 pm
Weather	Air temperature (°C)	12.2	11.7	16.1	15.6	23.3	24.4	26.1	25	20.6	23.9
	Relative humidity (%)	30	30	23	26	20	16	13	16	34	29
	Midflame windspeed (km h^{-1})	1.4	2.3	2.6	1.7	1.4	2.0	2.0	2.0	2.0	2.0
	10-hr Fuel moisture (%)	7.5	8.0	7.2	10.0	8.1	6.9	6.6	7.9	9.8	7.9

plot and determined the relative importance values (IV) for each functional group, i.e., pine, pyrophytic hardwood, and mesophytic hardwood by summing the relative density and relative dominance (BA) of each functional group. Hardwood species were classified as pyrophytic or mesophytic according to Nowacki and Abrams (2015) and Thomas-Van Gundy and Nowacki (2013). We also measured canopy openness by averaging the openness in each quadrant of the circular plot using a spherical densiometer. Understory stems < 3-m tall were not measured due to low abundance and the relatively small amount of fine fuel they contribute.

Pre-burn, we measured leaf litter and duff depth and harvested leaf litter to examine the relationships between SCS and litter structure, as well as the influence of litter structure on fire behavior within each plot. Pre-burn measurements were conducted within six weeks prior to the burn date and after leaf fall. Leaf litter and duff depth were measured separately using a ruler at four locations within eight 30-cm x 30-cm quadrats placed near the 3, 6, 12, and 15-m locations along two perpendicularly-intersecting transects (Fig. S3 in supplemental information). Leaf litter depth was measured from the top of the leaf litter to the top of the duff (partially decomposed Oe soil horizon). After removing the leaf litter, duff depth was measured from the top of the duff to the top of the fully decomposed Oa soil horizon. We harvested leaf litter from each quadrat by cutting around the quadrat with clippers and placing all contents above the duff horizon in a pre-labeled paper bag. To determine the influence of litter composition on fire behavior, leaf litter was sorted by functional group (pine, pyrophytic hardwood, mesophytic hardwood) after first removing reproductive structures, twigs, and bark, and oven dried at 60 °C to a constant weight. The dry mass of leaf litter was used to calculate mean leaf litter load and bulk density (dry mass/volume of sampling quadrat [900-cm^2 x litter depth]) and to determine the litter composition by mass of each functional group for each plot (Table 1). Post-burn, we measured leaf litter and duff depth following the same pre-burn methods within six weeks after fire and subtracted post-burn depths from pre-burn depths to calculate mean percent fuel consumption for each fuel layer. We offset measurement locations from pre- and post-burn sampling periods to ensure there were no disturbance impacts from the pre-burn harvesting on the post-burn measurements. We infrequently observed small amounts of *Andropogon* spp., *Smilax* spp., *Vaccinium* spp., *Vitis* spp., *Rubus* spp., and *Polystichum* spp., in the ground layer vegetation, but because of their heterogeneity and low abundance, we did not consider these as important fuels influencing fire behavior in this study. Downed woody debris can also be important to fire behavior (Willis et al., 2024). However, woody debris was less abundant and continuous compared to leaf litter, and coarse woody debris (> 7.62 cm diameter) was rare within sample plots. Therefore, we focused on leaf litter as it is the most spatially continuous fuel in our study area.

2.4. Prescribed burns

Dormant season prescribed burns were conducted by the Georgia Department of Natural Resources and The Nature Conservancy between February 8 and March 4, 2022. For each burn unit, drip torches were used to ignite backing fires along the unit perimeter, followed by interior ignition of ridge tops or valley bottoms depending on fuel type, fuelbed condition, weather, and topography. Each burn unit was ignited at approximately 10 a.m., and sample plots were generally burned during the early afternoon (Table 1). Average windspeed, air temperature, relative humidity, and 10-hr fuel moisture during each burn was acquired from the nearest remote automated weather station (RAWS; https://raws.dri.edu/cgi-bin/rawMAIN.pl?laGDAL) in Dallas, GA (34-km away at similar elevation to sample plots). Windspeed collected by RAWS at 6-m was converted to mid-flame windspeed (2-m) by using the conversion factor of 0.4 (Rothermel, 1983). RAWS data are not linked to plot characteristics but can account for how weather variables influence fire behavior temporally. The lowest average air temperature at time of burn was 11.7 °C and the highest was 26.1 °C with a mean of 19.9 ± 5.5 °C. Relative humidity ranged from 13 to 34 percent with a mean of 24 ± 7 percent. Average midflame windspeeds were weak (National Weather Service, n.d.) and varied little between burns (2.0 ± 0.4 km h^{-1}) so it was not used in further analysis. The lowest fuel moisture at time of burn was 7 percent and the highest was 10 percent with a mean of 8 ± 1 percent.

In this study, we use the term fire behavior to encompass fire intensity metrics (maximum temperature, RoS, and residence time over 50 °C) and fuel consumption, a metric of fire severity. While fire behavior has often been described by RoS, fire-line intensity, flame length, and flame height (Northwest Fire Science Consortium, 2018), the metrics we chose better relate to ecosystem responses to fire, rather than fire suppression and safety (Keeley, 2009). To measure fire behavior within each plot, we buried an enclosed CR1000 datalogger connected to two enclosed Am16/32 multiplexers (Campbell Scientific, Logan UT, USA), in the center of each sample plot within two hours prior to each burn. Multiplexers and central datalogger were each connected to two 0.81 mm diameter, high temperature inconel overbraided silica fiber insulated k-type thermocouples (Omega Engineering Inc., Norwalk CT, USA) installed ~1 cm above the litter layer. The thermocouples were connected by 3-m long cables, positioned to capture temperature responses in the upper, middle, and lower slope portions of the plot (Supp. Figure S3). Thermocouples measured temperature every two seconds, facilitating measurements of mean maximum temperature, mean RoS, and mean residence time over 50 °C (Table 3). Mean maximum fire temperature is the average of the maximum temperature from each thermocouple in a sample plot. Mean RoS was calculated as the distance between a thermocouple pair divided by the amount of time between the thermocouples in the pair reaching 50 °C, averaged across all thermocouple pairs that captured the dominant direction of fire spread in a plot. Mean residence time was calculated by averaging the amount of time each thermocouple in a sample plot remained over 50 °C. We chose 50 °C because thermocouple data showed this temperature to be the point at which temperatures consistently rose until maximum temperature, thereby reducing noise from measurements where the thermocouple warmed but likely did not have contact with the flame.

2.5. Analysis

We used path analysis to investigate hypothesized causal relationships (pathways) between either SCS or litter composition and litter structure, weather, and fire behavior (Fig. 1). Due to limited sample size (10 plots), we tested multiple smaller models (8 SCS models and 8 leaf litter composition models) rather than a single holistic model where all proxy and litter-mediated effects could be quantified simultaneously (Gagnon et al., 2015). SCS models described proxy and litter-mediated effects from SCS to litter structure to fire behavior (Fig. 1, path 1 and 1a, respectively), while litter composition models describe proxy and litter-mediated effects from litter composition to litter structure to fire behavior (Fig. 1, path 2 and 2a, respectively). All path models included a pathway between weather variables and fire behavior. Because air temperature and relative humidity influence fuel moisture (Rothermel, 1983), we also fit variants of models with fuel moisture instead of air temperature and relative humidity for comparison (not shown). Table S6 in supplementary information shows that models based on weather parameters or fuel moisture had similar fits. Models examined the proxy effect from SCS (or leaf litter composition) to fire behavior as well as the mediated path acting through litter structural characteristics to fire behavior to determine how much of the influence of SCS (or leaf litter composition) is mediated by litter structural characteristics. Total effects were also calculated as the mathematical product of the proxy and mediated effects.

Prior to modeling, all variables were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965), and redundant variables were identified using Pearson's product-moment correlation (Freedman et al., 2007). Percent canopy openness was highly correlated with basal area ($r = -0.84$, $df = 8$, $p = 0.002$) and therefore removed from further analysis. Mean percent leaf litter consumption varied minimally across plots (99.3 ± 1.5 percent) so only duff consumption, i.e., change in mean duff depth was used for analysis. Midflame windspeed also varied little across plots (2.0 ± 0.4 km h^{-1}) and was removed from further analysis.

To reduce model complexity, we conducted a principal component analysis (PCA) on each of four datasets; SCS, leaf litter composition, weather, and fire behavior (Fig. S1 and Table S2 in supplemental information), using the "prcomp" function in R (R Core Team, 2022). Each dataset was scaled and centered prior to conducting the PCA. The first two principal components (PC) from each PCA were used as variables in the path analysis models (Fig. S2), and the important PC loadings were used to interpret these variables and the relationships among them. PC loadings were considered important if they explained at least one variable worth of information, calculated by $\sqrt{\frac{1}{\#\ of\ PCs}}$ (Legendre and Legendre, 2012). For all modelled fire parameters except residence time, a positive value indicates an increase, and negative values indicate a decrease (Table S1). Because increased residence time was associated with lower scores on the PCA axis (axis PC2 in Fig. S1), its interpretation is the reverse, i.e. negative values indicate an increase in residence time while positive values indicates a decrease.

We fit each model using Bayesian estimation with the Stan method of Markov chain Monte Carlo (MCMC) sampling from the "blavaan" R package (v0.4.3; Merkle et al., 2021). Every model was fitted with three MCMC chains of 1000 burn-in and sampling iterations each. Relatively weak priors were used, i.e., the relationship between model variables was determined to be either (a) positive or (b) negative as informed by literature a priori (Table S1). We considered a relationship statistically significant if the posterior credibility interval did not include zero (Table S3 and S4). Though Bayesian analysis does not rely on large sample size as much as the frequentist approach, a sensitivity analysis of model estimates (Table S7) revealed that results were sensitive to priors which could be a consequence of small sample size (Depaoli and van de Schoot, 2017) and we acknowledge this limitation of the study (Lee and Song, 2004).

Each model was unique but shared certain relationships with several models. For example, the effect of increased mesophytic hardwood importance and decreased pyrophytic hardwood importance on leaf litter load was included in two models. The first model examined how the shift ultimately affects RoS and duff consumption and the second

Table 2
Mean and median importance values (IV) of functional groups and the most important tree species that were present in at least half of all sampling plots. Northern red, black, and scarlet oak were grouped due to their similar appearances. SD = standard deviation. IQR = interquartile range.

Functional group	Common name	Scientific name	Mean (SD) IV	Median (IQR) IV
Pines			83.0 (41.6)	81.4 (39.3)
	Longleaf pine	*Pinus palustris*	40.3 (46.9)	17.1 (53.7)
	Shortleaf pine	*P. echinata*	30.4 (33.6)	17.6 (48.0)
	Loblolly pine	*P. taeda*	10.9 (16.0)	1.8 (17.1)
Pyrophytic hardwoods			61.4 (29.1)	57.3 (36.0)
	Northern red/ black/scarlet oak	*Quercus rubra/ velutina/coccinea*	21.4 (25.0)	9.5 (43.1)
	Southern red oak	*Q. falcata*	21.3 (21.1)	15.1 (25.3)
	Blackjack oak	*Q. marilandica*	17.7 (20.0)	8.3 (22.2)
	White oak	*Q. alba*	9.9 (12.1)	7.8 (13.9)
Mesophytic hardwoods			42.5 (36.6)	37.8 (32.9)
	Black gum	*Nyssa sylvatica*	16.9 (22.8)	10.7 (11.7)
	Sourwood	*Oxydendrum arboreum*	12.4 (21.2)	4.2 (13.8)
	Red maple	*Acer rubrum*	11.8 (11.8)	11.6 (20.6)

Table 3
Mean fire behavior and effects measurements from sample plots (A-J). Maximum fire temperature is the average of the maximum temperature from each thermocouple in the sample plot. Mean residence time was calculated by averaging the amount of time each thermocouple in a sample plot remained > 50 °C. Mean rate of spread was calculated as the distance between a thermocouple pair divided by the amount of time between the thermocouples in the pair reaching 50 °C, averaged across all thermocouple pairs that captured the dominant direction of fire spread in a plot. Negative consumption values indicate an increase in fuel after fire. Numbers in parentheses are within plot standard deviation.

	A	B	C	D	E	F	G	H	I	J
Max. temperature (°C)	N/A	N/A	N/A	N/A	162.4 (118.4)	474.2 (69.0)	457.8 (74.1)	465.4 (112.2)	373.7 (87.5)	403.3 (59.2)
Residence time (min)	4.1 (1.5)	3.1 (1.4)	4.8 (1.3)	3.8 (1.4)	3 (0.8)	5.7 (1.5)	11.7 (2.3)	7.8 (0.8)	9.7 (1.4)	8.2 (1.4)
Rate of spread (m/min)	0.9 (0.7)	0.6 (0.5)	2.9 (2.4)	0.7 (0.4)	0.1[a]	1.3 (0.5)	0.6 (0.3)	2.1 (2.1)	0.3 (0.1)	1.2 (0.4)
Leaf litter consumption (%)	100.0	100.0	100.0	100.0	95.4	99.5	98.1	100.0	100.0	100.0
Duff consumption (%)	28.5	−33.0	41.8	18.2	27.5	60.8	3.0	63.4	14.9	−5.6

[a] Thermocouples were not able to capture accurate rate of spread at sample plot E due to the flame front failing to propagate across the plot. Mean rate of spread was estimated to be 0.10 m min^{-1} based on visual observations of a creeping flame front prior to extinguishment.

Table 4
Mean effect sizes for proxy, litter-mediated, and total effects of stand composition and structure, as well as mean effects of litter structural characteristics, and weather on fire behavior. Each effect size is the average of results from all models that included that same pathway. Numbers in parentheses are between-model standard deviation. The number of asterisks indicates the number of models in which the effect was statistically significant. All effects were estimated in two models, except weather was estimated in four. Fire rate of spread is RoS. Dashes indicate a relationship that was not modeled or the same identity.

	Leaf litter load	Bulk density	RoS and duff consumption	Residence time
Proxy effect				
Increased pine importance and decreased stand basal area	–	–	0.26 (0.02)	−0.3 (0.03)
Increased mesophytic hardwood importance relative to pyrophytic hardwood importance	–	–	−0.45 (0.07)*	0.36 (0.07)*
Litter-mediated effect				
Increased pine importance and decreased stand basal area	0.28 (0.00)	−0.24 (0.01)	0.11 (0.02)	−0.09 (0.03)
Increased mesophytic hardwood importance relative to pyrophytic hardwood importance	−0.38 (0.01)	0.07 (0.00)	−0.1 (0.07)	0.09 (0.07)
Litter structure				
Leaf litter load	–	–	0.44 (0.02)	−0.41 (0.01)
Bulk density	–	–	−0.45 (0.05)*	0.3 (0.06)
Total effect				
Increased pine importance and decreased stand basal area	–	–	0.37 (0.01)	−0.44 (0.05)*
Increased mesophytic hardwood importance relative to pyrophytic hardwood importance	–	–	−0.54 (0.00)**	0.45 (0.01)
Weather				
Increased air temperature and decreased relative humidity	–	–	0.38 (0.01)	−0.38 (0.04)

Table 5
Mean effect sizes for proxy, litter-mediated, and total effects of leaf litter composition, as well as mean effects of litter structural characteristics, and weather on fire behaviors. Each effect size is the average of results from all models that included that same pathway. Numbers in parenthesis are between model standard deviation. The number of asterisks indicates the number of models in which the effect was statistically significant. All effects were estimated in two models, except weather was estimated in four. Dashes indicate a relationship that was not modeled or the same identity.

	Leaf litter load	Bulk density	RoS and duff consumption	Residence time
Proxy effect				
Increase in mesophytic hardwood litter and decrease in pine litter	–	–	−0.27 (0.02)	0.41 (0.02)*
Increase in pyrophytic hardwood litter	–	–	0.65 (0.10)**	−0.40 (0.07)
Litter-mediated effect				
Increase in mesophytic hardwood litter and decrease in pine litter	−0.33 (0.00)	0.27 (0.03)	−0.15 (0.01)	0.10 (0.04)
Increase in pyrophytic hardwood litter	0.63 (0.01) **	−0.22 (0.00)	0.16 (0.05)	−0.16 (0.08)
Litter Structure				
Leaf litter load	–	–	0.39 (0.06)	−0.38 (0.01)
Bulk density	–	–	−0.48 (0.03)*	0.32 (0.05)
Total effect				
Increase in mesophytic hardwood litter and decrease in pine litter	–	–	−0.42 (0.02)	0.51 (0.15)**
Increase in pyrophytic hardwood litter	–	–	0.8 (0.10)**	−0.60 (0.01)*
Weather				
Increased air temperature and decreased relative humidity	–	–	0.42 (0.03)*	−0.29 (0.06)

Note: Residence time represents a principal component (PC) on which residence time increases with lower PC values. Therefore, a negative effect for residence time is interpreted as an increase in residence time.
Figure captions

model showed how the shift ultimately affects residence time. We averaged the repeated effect results to compare mean effect sizes (Tables 4 and 5).

3. Results

3.1. How shifts in stand composition and structure influence litter structure and fire

Overall trends, while not always significant, showed that greater leaf litter loads, lower bulk density, and greater fire intensity were related to more open pine and pyrophytic hardwood dominated stands compared to closed mesophytic hardwood stands. The influence of SCS on litter structure was weak although trends were in the direction we expected. Increased pine importance and decreased basal area weakly increased leaf litter load ($\mu = 0.28 \pm 0.00$) and weakly decreased litter bulk density ($\mu = -0.24 \pm 0.01$) (Table 4). Leaf litter load decreased with greater mesophytic hardwood importance relative to pyrophytic hardwoods ($\mu = -0.38 \pm 0.01$), but bulk density was not affected ($\mu = 0.07 \pm 0.00$). Proxy relationships between SCS and fire behavior, while not always significant, were stronger. Increased pine importance and lower stand basal area weakly increased RoS and duff consumption ($\mu = 0.26 \pm 0.02$) and residence time ($\mu = -0.3 \pm 0.03$). Increased importance of mesophytic hardwoods relative to pyrophytic hardwoods led to significantly slower RoS and less duff consumption ($\mu = -0.45 \pm 0.07$) and significantly shorter residence times ($\mu = 0.36 \pm 0.07$).

3.2. How shifts in leaf litter composition influence litter structure and fire

Similar to the increased mesophyte importance in stand composition, increased contribution of mesophytic leaf litter to the fuelbed tended to reduce leaf litter fuel load and fire intensity compared to pine and pyrophytic hardwood leaf litter, though not all modelled relationships were significant. Greater proportions of mesophytic leaf litter and smaller proportions of pine litter tended to lower leaf litter fuel loads ($\mu = -0.33 \pm 0.00$) and increase bulk density ($\mu = 0.27 \pm 0.03$). More pyrophytic hardwood litter significantly increased leaf litter fuel loads ($\mu = 0.63 \pm 0.01$) and tended to decrease litter bulk density ($\mu = -0.22 \pm 0.00$). Increased contribution of mesophytic hardwood leaf litter to the fuelbed, and smaller proportions of pine litter, also tended to reduce RoS and duff consumption ($\mu = -0.27 \pm 0.02$) and significantly reduced residence time ($\mu = 0.41 \pm 0.02$) while increases in pyrophytic hardwood litter significantly increased RoS and duff consumption ($\mu = 0.65 \pm 0.10$) and tended to increase residence time ($\mu = -0.40 \pm 0.07$).

3.3. Comparing proxy and litter-mediated effects on fire

We hypothesized that SCS alone can explain fire behavior and found that the mean proxy effects of SCS on fire behavior (Fig. 1, path 1) were consistently stronger than the litter-mediated effects ($\mu = |0.34| \pm 0.07$ and $\mu = |0.10| \pm 0.01$ respectively). Furthermore, the proxy effects of increased mesophytic hardwood importance on RoS and duff consumption ($\mu = -0.45 \pm 0.07$) and residence time ($\mu = 0.36 \pm 0.07$) were statistically significant but no litter-mediated effects of SCS on fire behavior were statistically significant.

We also hypothesized that leaf litter composition alone (proxy effect) can explain fire behavior (Fig. 1, path 2). Leaf litter composition alone had stronger effects on fire behavior than the litter-mediated effects of composition acting through leaf litter load and bulk density (path 2a in Fig. 2) ($\mu = |0.43| \pm 0.14$ and $\mu = |0.14| \pm 0.03$ respectively). The proxy effect of increased mesophytic hardwood litter on residence time ($\mu = 0.41 \pm 0.02$) and the proxy effect of increased pyrophytic hardwood litter on RoS and duff consumption ($\mu = 0.65 \pm 0.10$) were statistically significant but no litter-mediated effects of leaf litter composition on fire behavior were statistically significant. Warmer, drier weather positively affected fire intensity but was only statistically significant in one leaf litter composition model where RoS and duff consumption significantly increased ($\mu = 0.42 \pm 0.03$).

3.4. How shifts in litter structure influence fire

As expected, fire intensity tended to increase with greater leaf litter loads and lower litter bulk density though not all modelled relationships were significant (Tables 4 and 5). For example, in models using SCS (Table 4) as leaf litter load increased, RoS and duff consumption tended to increase ($\mu = 0.44 \pm 0.02$), as well as residence time ($\mu = -0.41 \pm 0.01$). Conversely, as bulk density increased, RoS and duff consumption significantly decreased ($\mu = -0.45 \pm 0.05$) and residence time tended to decrease as well ($\mu = 0.3 \pm 0.06$). Fuel composition models summarized in Table 5 show similar results.

4. Discussion

4.1. How shifts in stand composition and structure influence litter structure

Contrary to expectations, the relationships between SCS and litter structural characteristics thought to influence fire behavior were weak and not statistically significant. Although leaf litter load tended to decrease with greater mesophyte importance (as compared to pyrophytic hardwoods) the relationship was not significant, and bulk density was not affected (Table 4). Several studies have shown that mesophytic leaf litter decomposes faster than pyrophytic oaks and pines (Babl-Plauche et al., 2022; Alexander and Arthur, 2014; Melillo and Aber, 1982) and often has flatter, thinner leaf morphology (Babl et al., 2020; McDaniel et al., 2021), traits associated with higher fuelbed bulk density (Babl et al., 2020). The timing of our sampling relative to leaf fall may have weakened the link between stand composition and fuelbed characteristics. Because mesophyte leaf litter decomposes rapidly, and our sampling occurred ~ 3 months following leaf fall, mesophyte litter contribution to the fuelbed at the time of collection may have been relatively low compared to what it would have been if we sampled soon after leaf fall, minimizing its effect on bulk density. For example, in upland oak forests of north-central Kentucky, red maple litter lost ~40 % of biomass only three months after falling in early to mid-winter (November – December) (Babl-Plauche et al., 2022). Notably, the most mesophyte-dominated plot (B, Table 1) also had the greatest mesophyte litter proportion of all plots, but mesophyte litter only comprised 24 % of the fuelbed, supporting the possibility of significant mass loss before collection. These results agree with Babl-Plauche et al., 2022 and Dickinson et al., (2016) that mesophytes could suppress fire by reducing leaf litter loads. Alternatively, mesophyte litter impact on bulk density may decrease when fuelbeds are comprised of several species. In previous lab and field-based flammability trials, mesophyte leaf litter did not significantly impact flammability in fuelbeds mixed with pyrophytic oak leaf litter until mesophyte litter comprised two thirds of the fuelbed (Kreye et al., 2018, McDaniel et al., 2021). In addition, non-additive effects have been reported for mixed species fuelbeds where the most flammable species determined the flammability of the fuelbed (de Magalhaes and Schwilk, 2012; Ellair and Platt, 2013). This non-additive effect could also apply to bulk density where a threshold amount of pyrophytic litter could help maintain adequate aeration in the fuelbed, despite the mesophytic component.

Similarly, bulk density and leaf litter load were not significantly influenced by pine importance and stand basal area. It is possible that the effects of variation in bulk density were partially masked by differing fuel moisture conditions during bulk density measurements for each plot. Based on our observations during collection, conditions of greater fuel moisture may deflate the fuelbed while dryer conditions may allow the fuelbed to fully expand. It is unclear why leaf litter load was not more related to SCS. Though SCS did not relate well to litter structure, increased mesophyte importance significantly reduced all fire intensity metrics.

4.2. How shifts in litter structure influence fire

Despite only weak relationships between SCS and litter structure, fire intensity was promoted by greater leaf litter load and reduced bulk density as predicted. Increasing bulk density led to a statistically significant reduction in RoS and duff consumption, likely because dense fuelbeds allow less airflow to support fire (Kauf et al., 2019; Scarff and Westoby, 2006). Although not statistically significant, greater leaf litter loads had positive relationships with RoS, duff consumption, and residence time in agreeance with results from experimental manipulations of leaf litter load and moisture (Graham and McCarthy, 2006; Kreye et al., 2013; Gagnon et al., 2015).

4.3. Comparing proxy and litter-mediated effects of stand composition and structure on fire

We hypothesized that fire behavior can be explained by the proxy effect of SCS alone. In support of this idea, we found that the proxy effect of SCS had more influence on fire behavior as compared to its litter-mediated effects, apparently as a result of the weak relationships between SCS and litter structure. As discussed in Section 4.1, questions remain about how SCS influences the fuelbed, but leaf litter load and bulk density may not be the best characteristics to consider. The relatively weak litter-mediated effect of SCS on fire behavior may be explained if other unexamined fuelbed components are important. We focused on leaf litter as it was the most continuously distributed fuel in the study plots. However, other canopy-derived fuels not measured in our study, such as downed woody debris (DWD) and pinecones, may have influenced our findings. For example, 1-hr fuels (DWD $\leq$ 0.64-cm diameter) behave similarly to leaf litter fuels i.e., they respond rapidly to atmospheric moisture changes and influence rate of fire spread (Rothermel, 1983). We did not observe pinecones in concentrated amounts, but they could represent a significant contribution to fire behavior (Mitchell et al., 2009, Willis et al., 2024) as they have been shown to smolder for long durations (Fonda and Varner, 2005). Finally, stemflow, i.e., the precipitation that travels down tree boles, has been shown to be much greater for mesophytic hardwoods than pyrophytic oaks. The resulting greater concentration of water at the base of mesophytes may contribute to their ability to inhibit fire (Alexander & Arthur, 2010, Scavotto et al., 2024) and could explain the significant proxy effects on fire behavior. Stronger conclusions are precluded by the difficulties in distinguishing the influences of vegetation and fuels from those of variables that influence fire behavior independently of vegetation and fuels, i.e., interactions between fire and topography, wind direction, and fuel moisture under field conditions. Future studies may avoid this by utilizing experimental burn plots if possible, i.e., sample plots where fire is uniformly initiated under specific conditions (timing, direction, etc.), as opposed to plots being burned as part of a larger burn unit.

4.4. How shifts in leaf litter composition influence litter structure

Leaf litter composition results were consistent with the pattern observed with stand composition. Although relationships were generally not significant, as fuelbeds shifted from greater pine and pyrophytic hardwood litter proportions to greater mesophytic hardwood litter proportions, load tended to decrease, bulk density tended to increase, and fire behavior lost intensity (Table 5). Only the relationship between increasing pyrophytic hardwood litter and increasing litter load was significant, a result in alignment with studies showing that upland oak litter (the dominant pyrophytic hardwoods in our study) decomposes more slowly than oak-pine mixes (Li et al., 2009). The presence of pyrophytic hardwoods in montane longleaf pine forests is likely important in maintaining fuel continuity, and spatial models of litter accumulation (Sánchez-López et al., 2023) could help quantify their contributions.

4.5. Comparing proxy and litter-mediated effects of leaf litter composition on fire

We hypothesized that leaf litter composition alone could explain fire behavior. Consistent with this hypothesis (and like our findings regarding the influence of SCS), we found that leaf litter composition had more influence on fire behavior compared to the litter-mediated effects of composition on litter structure, i.e. effects that included litter bulk density and load. The lack of statistically significant litter-mediated effects further indicates that while leaf litter load and bulk density have influence over fire behavior, they may not be the most useful variables for explaining relative fire behavior in relation to SCS. We suggest that specific litter flammability traits of different functional groups (e.g. moisture holding capacity, curling) may better explain the relationship between SCS and fire behavior. The relative importance of leaf litter load, structure, and flammability traits of different species or functional groups is contentious. Some work shows that leaf litter flammability controls fire behavior regardless of fuel structure (de Magalhaes and Schwilk, 2012) while others show that aerated fuel structure determines heat release regardless of litter flammability traits (Scarff and Westoby, 2006). Our in-situ analysis provides some support for both mechanisms. Bulk density significantly reduced RoS and duff consumption, but leaf litter load and bulk density did not significantly mediate the effects of leaf litter composition on fire behavior. However, in-situ analysis precludes controlling for either leaf litter structure, composition or other fuelbed characteristics, which is likely necessary to reach a decisive conclusion.

Our study has several limitations that deserve mention. Our sample and plot sizes were relatively small due to logistical constraints associated with sampling within designated burn units under tight burn windows and installing and removing thermocouples within limited timeframes prior to and after fires. Although our plots were embedded within larger burned units, rather than being ignited independently, fire behavior patterns within plots could have been heterogeneous due to small-scale variations in topography or other conditions that go beyond the fuel and stand conditions explored in this study. Sampling small plots also may not fully capture fire behavior variability due to leaf litter fuels if these fuels were near downed coarse woody debris, tip-up mounds, canopy gaps, or other features that influence leaf litter fuel traits beyond loads and structure or if fuels from trees not associated with the plot impacted fuel traits. Our design could be improved upon in future studies by increasing replication, expanding plot size, and measuring tree attributes of individuals both within the plot and immediately adjacent to the plot within a boundary width that approximates known leaf litterfall distances of common species."

5. Conclusion

This study serves to better understand mechanisms of mesophication in mixed pine and hardwood forests and is also a preliminary exploration of drivers of fire behavior in the important and understudied mountain longleaf pine ecoregion. The evidence reinforces that shifts in SCS occurring with mesophication reduce fire intensity. However, uncertainty remains concerning the relationships between SCS, the leaf litter characteristics, and fire behavior, highlighting the complex nature of these interactions. Although a clear mechanism of mesophication was not identified, this study supports the removal of mesophytic hardwoods from upland habitats as a priority in restoration of fire dependent ecosystems in the Southeastern U.S. Notably, mesophytes seem to inhibit fire even when they contribute relatively little to overall stand and fuel composition. Non-linear relationships should be investigated, as suggested by the potentially non-additive effects in the fuelbed. The timing of prescribed burns could also be adjusted to account for mesophytic litter. For example, if total leaf litter loads are largely stable over the dormant season then prescribed fires conducted relatively later in the season will minimize the fire inhibiting aspects of mesophyte litter by providing more time for it to decompose. Fires unencumbered by mesophyte litter likely have the potential for greater fire intensity allowing better control of mesophytic competition. Mesophytic leaf litter significantly reduced residence time, and longer residence time is associated with greater plant mortality (Gagnon et al., 2015; Varner et al., 2007). Additionally, this study showed that pyrophytic hardwoods in the mountain LLP ecoregion are not only fire tolerant, but fire promoting. This fire-promoting role contrasts the role of pyrophytic hardwoods in other LLP ecoregions. For instance, in the sandhill LLP communities, pyrophytic oaks are thought to create refugia of relatively lower fire intensity facilitating LLP recruitment (Johnson et al., 2021; Magee et al., 2022). However, pyrophytic hardwoods in the mountain LLP plots observed here significantly increased metrics of fire intensity indicating that functional groups have different effects in different communities based on different species, relative abundance, and dominance.

To improve management outcomes, land managers need the ability to predict fire behavior when conducting prescribed burns. In this analysis we did not find a significant relationship between SCS and leaf litter load and bulk density. Instead, we found that SCS alone significantly explains fire behavior. Therefore, simple measures of SCS may be enough to predict relative fire behavior in mixed pine and hardwood stands with primarily leaf litter fuel layers when considered in conjunction with weather and topography.

This work also provides insight into the contending hypotheses of how fuelbeds influence fire. Our findings indicate that both litter composition and structure influence fire behavior, and specifically that proxy effects of leaf litter composition appear to be stronger predictors of fire behavior than the mediated influence of litter composition on litter structure. For land managers, measuring leaf litter composition in the field is likely less practical than using SCS measurements as a proxy to predict fire behavior. However, identifying the most important drivers of fire behavior is important for future predictive models and improving management. Ecosystem responses and management outcomes depend on specific fire behaviors. To better control and predict these outcomes, understanding the links between vegetation, fuels, and fire is critical and future research should work to bridge the gap between drivers of fire behavior and the effects of fire behavior on the ecosystem.

CRediT authorship contribution statement

Nicholas Green: Writing – review & editing, Supervision, Methodology, Formal analysis. **Collin J. Anderson:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Heather D. Alexander:** Writing – review & editing, Methodology, Conceptualization. **Mario Bretfeld:** Writing – review & editing, Supervision, Resources, Methodology. **Matthew P. Weand:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors declare no use of generative AI during the preparation of this work.

Declaration of Competing Interest

The authors declare no knowledge of competing financial or personal interests that could influence the work reported here.

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Indigenous land acknowledgement

Long before Euro-American colonization and the forceful removal of Native Americans, our study area was the homeland of the Cherokee and Creek nations. Indigenous peoples used fire for land management but also considered it a sacred practice integral to their culture. While this research pertains only to the ecology of fire, we would like to acknowledge the cultural significance of prescribed fire and the cultural oppression that Indigenous peoples experienced when this practice was made illegal (Colenbaugh and Hagan, 2023).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122372.

Data availability

Data will be made available on request.

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