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Influence of Woody Vegetation Composition and Structure on Fuels and Prescribed Fire in Mountain Longleaf Restoration

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Abstract

Fire-dependent longleaf pine (LLP) ecosystems are valued for their open structure that supports hyperdiversity. In the last 200 years, these systems, which require a frequent (~ 2-3 year interval) fire regime, experienced a widespread ecological state shift largely due to decades of intentional fire exclusion. In many areas, fire exclusion allowed mesophytes, i.e., shade-tolerant, often fire-sensitive species to encroach, creating shady, moist understory conditions of lower flammability and reduced biodiversity through a process known as “mesophication.” Although prescribed fire is commonly used in an attempt to reverse mesophication and restore fire-dependent landscapes, fire behavior, and thus prescribed fire utility for this purpose, is poorly characterized in mixed pine-hardwood stands with mesophyte encroachment. This study aimed to identify mechanisms by which tree composition, structure, and fuels contribute to fire behavior, focusing on the understudied mountain longleaf pine (MLLP) ecoregion in northwest Georgia. I hypothesized that woody vegetation composition and structure indirectly influence fire behavior through fuel bed traits. Relative decreases in basal area and increases in the relative importance of pine and pyrophytic hardwoods (e.g., *Quercus* spp.) were expected to increase fuel load and reduce bulk density, thereby increasing fire rate of spread (RoS), fuel consumption, and residence time. To test this, I collected fuel and fire data across stands varying in woody vegetation composition and structure during dormant season prescribed burns and used Bayesian path analysis to estimate the effects of vegetation, fuel traits, and weather on fire behavior. Additionally, I tested the effects of prescribed fire variables that can influence fire behavior independently of vegetation and fuel bed traits, i.e., interactions between fire and topography, wind direction, and fuel moisture. Results showed that hardwood composition directly influenced fire behavior but lacked significant indirect effects through fuel bed traits. Pine importance and basal area did not significantly affect fuels or fire behavior. Despite lacking a significant relationship with the canopy, greater fuel bed bulk density significantly reduced RoS and duff consumption, but fuel load did not significantly influence fire behavior. The effects of mesophication, i.e., reduced fire intensity, were apparent, but woody vegetation composition and structure did not effectively predict fire behavior through fuel bed traits as expected. While precise mechanisms remain unresolved, mesophytic hardwoods reduce fire intensity, in part by reducing available fuel load, and should be targeted for removal in restoration efforts. In contrast, pyrophytic hardwoods significantly increased fire intensity in MLLP.

Keywords: Mountain longleaf pine, mesophication, fire behavior, restoration

Integrative aspects

Fire ecology inherently encompasses several scientific disciplines. Physics and chemistry are at the core of energy transformation and exchange that drive flammability and flame propagation. Plant physiology and ecology are used to understand interactions between communities and fire disturbance. Geography and meteorology also play a critical role in understanding how fire relates to the landscape. Importantly, the ecological issue at hand cannot be fully understood without the historical context of anthropogenic influence.

Contents

Introduction

History of the longleaf pine ecosystem

Prior to European settlement, longleaf pine (hereafter LLP, *Pinus palustris* Mill.) dominated the southeastern landscape of the United States covering an estimated 37 million hectares (Frost, 1993). Historical LLP ecosystems were open woodlands and savannas with understories comprised of grasses and forbs (Peet, 2007). These systems persisted because they were highly adapted to frequent, low- intensity fire. Fire is critical for facilitating LLP germination in bare soil and controlling competition (Boyer, 1990). LLP is considered a foundation species for its role in providing flammable fuels (e.g., pine needles) and an open canopy that allows light to support a species-rich and flammable herbaceous layer (Mitchell et al., 2009; Noss, 1989). Intact, fire-maintained LLP systems support a highly diverse range of organisms (Engstrom, 1993; Klaus et al., 2020; Platt et al., 2006; Sheehan & Klepzig, 2022). For instance, in the savanna community types, one square meter can contain up to 40 plant species in the herbaceous layer, among the highest richness at this scale for the temperate western hemisphere (Peet & Allard, 1993).

Today, the LLP ecosystem is a high conservation priority (*High Priority Species and Habitat Summary Data,* 2015) due to major reductions in range and the shift of its ecological state (Hanberry et al., 2018), both of which threaten the biodiversity and endemism it supports. As the southeast region was settled and developed by early Euro-Americans, the LLP ecosystem was reduced by timber cutting, naval stores production, and conversion to agriculture (Earley, 2004; Peet & Allard, 1993). Additionally, in the 1920s, fire suppression became a national policy in the United States that lasted for several decades (Stephens & Ruth, 2005) facilitating a state change from open forests with highly flammable herbaceous fuel beds to closed-canopy forests dominated by dense midstories of shade-tolerant, often fire-intolerant species and fire-inhibiting fuel beds (Babl et al., 2020; Nowacki & Abrams, 2008; Wade et al., 2000). A hypothesized feedback process termed mesophication describes how in the absence of fire, encroaching shade-tolerant, often fire-sensitive species (i.e., mesophytes) introduce self-reinforcing conditions of low light, high fuel moisture, and altered fuel beds which render fire less likely and less effectual (Alexander et al., 2021; Heyward, 1939; Nowacki & Abrams, 2008). Compared to fire-maintained, open forest stands, the resulting closed forest stands have greater canopy cover, fewer pyrophytic pines and hardwoods, and reduced understory biodiversity (Peet & Allard, 1993; Wade et al., 2000). By the end of the 20th century, direct removal, and fire exclusion reduced the historical LLP range by 97 percent (Frost, 1993). Most remaining longleaf pine stands are highly fragmented (Outcalt & Sheffield, 1996)

The mountain longleaf pine community

Biological conservation and ecological restoration efforts have prompted research to understand the relationship between LLP ecosystems and fire. Prescribed fire is currently used to maintain remnants and restore degraded LLP lands. However, the mechanisms by which mesophication influences fire in LLP ecosystems are not fully understood, and they may differ between the more frequently studied coastal plains LLP ecosystems and mountain (or montane) longleaf pine (MLLP) community types. Understanding the specific characteristics and historical nature of different longleaf pine communities is necessary to set realistic and appropriate restoration goals. This study focuses on the understudied MLLP community found in the upper piedmont, ridge and valley, and Blue Ridge ecoregions of northwest Georgia and northeast Alabama (Maceina et al., 2000). In contrast to the flat topography, sand or silt soils, and often monospecific overstories of the coastal plain LLP communities, the MLLP communities are characterized by dynamic topography with well-developed drainage systems, rockier clay soils (Peet, 2007), plant communities containing a unique mixture of Appalachian and coastal plain species, and overstories that are often mixed with hardwoods (Maceina et al., 2000). According to surveys of northwest Georgia, circa 1830, the MLLP overstory historically included LLP, shortleaf pine (*Pinus echinata* Mill.*)*, and Virginia pine (*Pinus virginiana* Mill.), as well as co-dominant hardwoods such as pyrophytic northern red oak *(Quercus rubra* L.*)* and post oak *(Quercus stellata* Wagenh.) Comparisons with modern surveys show that the relative abundance (RA) of pines and several pyrophytic hardwoods has since decreased in conjunction with increased RA of mesophytic species (e.g., *Acer rubrum*, *Nyssa sylvatica*) in the midstory following decades of fire exclusion (Knott et al., 2019; Waters, 2020).

In the past, LLP restoration often involved the indiscriminate removal of hardwoods (Brockway & Outcalt, 1998; Kush et al., 1999; Provencher et al., 2001). There is now a growing understanding that some pyrophytic hardwoods should be retained to some degree for their role in fire and several other ecological values such as mast production and wildlife habitat (Hiers et al., 2014). For example, pyrophytic turkey oak (*Quercus laevis* Walter) has been shown to facilitate LLP regeneration in the sandhill community (Johnson et al., 2021; Magee et al., 2022). In laboratory tests, some pyrophytic hardwoods display litter flammability traits rivaling longleaf pine needles (Kane et al., 2008; Varner et al., 2021), indicating a potentially important role in the MLLP community as well.

Influences on fire behavior

The use of prescribed burns for restoration has fostered research on factors influencing fire behavior (e.g., temperatures, residence times, rates of spread) including topography, weather, fuels, and interactions with vegetation. Topographic variables such as elevation, aspect, and slope influence vegetation composition (Crawley, 2013) and solar radiation exposure which dries the fuel bed (Byram & Jemison, 1943). Slope steepness can influence fuel bed accumulation via gravity and interacts directly with fire by changing the angle between the flame and the fuels. As the slope steepens, the rate of fire spread upslope increases as the fuels in front of the fire are pre-heated (Butler et al., 2007). This effect is magnified as wind pushes fire upslope (Weise & Biging, 1996). Regardless of slope, it is well understood that fires spreading with the wind (head fires) spread faster and with more intensity than fires spreading against the wind (back fires).

Weather also interacts with vegetation to affect fire. Mesophytic species often have crown and leaf types that keep the fuel bed cool by intercepting significantly more light than the sparse open crown of pines or pyrophytic hardwood species (Alexander et al., 2021; Babl et al., 2020; Kreye et al., 2018). Deeper, fuller crowns also block winds that would dry the fuel bed (Nowacki & Abrams, 2008). The loss of airflow could affect fire behavior during a burn by increasing humidity and reducing the rate of fire spread (Alexander et al., 2021; Rothermel, 1983; Weise & Biging, 1996). Windspeed, air temperature, humidity, and solar radiation influence fuels and fire behavior by heating and drying the fuel bed (Kreye et al., 2018a), and through influence on flame spread rate (Weise & Biging, 1996) during dormant season fires in the MLLP ecoregion.

Although topography and weather account for significant variation in fire behavior (Rothermel, 1983), fuel is the factor most strongly influenced by woody vegetation, and the factor most easily manipulated in restoration (Bale, 2009). The amount, type, and structure of fuels such as groundlayer vegetation, leaf litter, and downed woody debris are influenced by woody vegetation (both composition and structure) and can influence fire behavior in several ways. Leaf litter can be particularly important in LLP restoration as it is often the most continuous fuel, especially in more closed-canopy stands that are often targeted for restoration and can either promote or inhibit fire through traits such as litter chemistry and morphology (Varner et al., 2015). Needles from LLP and other pine species are highly flammable (Varner et al., 2022) and slowly decompose (Hendricks et al., 2002; Melillo & Aber, 1982). Needle structure (as opposed to broad-leaf structure) facilitates litter drying and supports fire (Kreye et al., 2013). Compared to mesophytic hardwood litter, pyrophytic hardwood litter decomposes more slowly (owing to greater lignin : nitrogen ratios) permitting fuel accumulation (Babl-Plauche et al., 2022; Alexander & Arthur, 2014; Melillo & Aber, 1982). Pyrophytic litter also curls when dried creating relatively deep and low-density litter beds with low surface area : volume ratios (Alexander et al., 2021; Babl-Plauche et al., 2022; McDaniel et al., 2021). Like pine needles, these traits permit faster drying, and compaction resistance (McDaniel et al., 2021; Kreye, 2013). In contrast, mesophytic leaf litter decomposes faster (Babl-Plauche et al., 2022; Hendricks et al., 2002; Melillo & Aber, 1982), traps moisture, and reduces airflow, suppressing fire (Babl et al., 2020; McDaniel et al., 2021). Faster decomposition reduces the amount of fuel in the litter layer but may decrease the amount of duff which retains moisture longer. Duff, the fuel layer comprised of partially decomposed leaf litter (Babl-Plauche et al., 2022) can also build up around tree boles and smolder for long durations, killing even mature fire-adapted trees (Varner et al., 2007)

Fire behavior and restoration success

Prescribed fire is commonly implemented with the goal of increasing or maintaining fire-adapted floral biodiversity (Brewer, 2016) and habitat for the many wildlife species that rely on the ecosystem (Engstrom, 1993). Vegetation interacts with topography, weather, and fuels to influence fire behavior and produce effects that determine restoration success.

For example, fire temperatures must be sufficient to consume the litter and duff layers for LLP germination and to control competition (Regelbrugge & Smith, 1994); however, excessive temperatures can damage the soil structure and alter the microbiome (Nelson et al., 2022). Residence time and rate of spread are also important. A fire that passes too quickly may not achieve the desired effects, e.g., mortality of undesired species. Conversely, if high temperatures remain for too long, excessive damage to the seed bank and even fire adapted vegetation could occur (Gagnon et al., 2015; Varner et al., 2007). Duration of fire is a good predictor of soil temperatures, both of which are negatively related to post-fire vegetation regeneration (Gagnon et al., 2015).

The aim of this study is to identify how vegetation influences fire behavior in forest stands targeted for MLLP restoration, i.e., containing LLP but also including mesophyte species, so that fire effects and ecosystem responses can be better understood and interpreted as responses of fire behavior, thereby improving ecosystem management. I hypothesize that fire behavior of dormant season prescribed fires in the MLLP community is largely explained by the indirect effect of woody vegetation composition and structure on fuel bed traits. Specifically, I predict relative decreases in basal area and increases in the relative importance of pine and pyrophytic hardwoods should promote fuel traits, i.e., greater fuel loads with lower bulk density, that increase fire rate of spread (RoS), residence time over 50°C, and fuel consumption.

Methods

Study site

This study examined mixed-species forests targeted for LLP restoration within the Sheffield Wildlife Management Area (WMA) in Paulding County, Georgia (34.020484, -84.904417). Sheffield WMA contains remnant patches of approximately 70-year-old LLP among a larger mosaic of mixed pine and hardwood forest. As a result of historical fire exclusion through the latter half of the twentieth century, regeneration of LLP was largely inhibited and mesophytic hardwood species like blackgum (*Nyssa Sylvatica* Marsh.) and red maple (*Acer rubrum* L.) now dominate in the mid-story and understory. Co-dominant species in the overstory include loblolly pine (*Pinus taeda* L.), shortleaf pine (*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 (*Cornis florida* L.), and American beech (*Fagus grandifolia* Ehrh.). Since 2008, prescribed fire has been re-introduced to much of the WMA at 2–5-year intervals (B. Womack, personal communication, March 7, 2023.)

Site Selection

Within WMA units scheduled for prescribed burns in 2022, I established 20-m diameter circular sample sites (Fig.1) to capture a gradient of woody vegetation structure and composition representing different restoration stages characterized by basal area (BA) and the ratio of pine to hardwood importance value (IV). Two sites were created in each of five planned burn units (10 sites total), all of which were unburned since at least 2019. The intent of this study was not to describe fire behavior at landscape scale, but rather to analyze fuels and fire across a restoration gradient. Therefore, sample sites do not represent the larger burn units they reside in. Site aspect ranged from 100 to 260 degrees, and all sites were located on upper slope positions ranging from 238 to 325 meters in elevation (Table 2). Sample sites were also selected based on the presence of mature LLP.

Woody vegetation survey

To examine the influence of woody vegetation on fuel traits and fire behavior within each site, I measured diameter at breast height (DBH) for all trees that were rooted inside the site and were at least 3-m tall. I calculated site BA and relative importance values (IV) for each functional group, i.e., pine, pyrophytic hardwood, and mesophytic hardwood. Importance was calculated as the sum of the relative density and relative dominance (BA) of each functional group. Species were classified as mesophytic or pyrophytic according to Nowacki & Abrams, 2015 and Thomas-Van Gundy & Nowacki, 2013. Understory stems less than 3-m tall were not measured due to low abundance and the relatively small amount of fine fuel they contribute. Site canopy openness was estimated by averaging the openness in each quadrant of the circular plot using a crown densiometer. I conducted k-means cluster analysis to determine how the sites differed along a gradient of BA and pine to hardwood IV ratio using the R packages “cluster” (v2.1.4; Maechler et al., 2022) and “factoextract” (v1.0.7; Kassambara & Mundt, 2020) (Fig. 3).

Characterizing fuel traits

Within six weeks prior to the burn date and after leaf fall, I measured fine fuel (leaf litter only) and duff depth using a ruler at four locations within eight 30-cm x 30-cm quadrats placed at 3, 6, 12, and 15-m along two intersecting transects (Fig.1) to examine the role of fuel bed traits on fire behavior within each site. I also collected the fine fuel from those quadrats to be sorted, dried, and weighed. Pre-burn fine fuels were sorted by functional group (pine, pyrophytic hardwood, mesophytic hardwood). Reproductive structures, twigs, and bark were removed due to low abundance and the decision to focus on leaf litter as the main influence on fire behavior. Fine fuel was oven dried at 60°C to a constant weight. The dry mass of pre-burn fine fuel was used to calculate mean fine fuel load and mean bulk density (dry mass/volume of sampling quadrat [900-cm^2 x litter depth]) for each site (Table 2). I observed *Andropogon* spp., *Smilax* spp., *Vaccinium* spp., *Vitis* spp., *Rubus* spp., and *Polystichum* spp., in the groundlayer vegetation, but only infrequently and in small amounts within sample sites therefore, I did not consider these as important fuels influencing fire behavior for this study.

Fire behavior measurements

Dormant season prescribed burns were conducted by the Georgia Department of Natural Resources (GA DNR) and The Nature Conservancy (TNC) between February 8 and March 4, 2022. To measure fire behavior within each site, I buried an enclosed CR1000 datalogger connected to two enclosed Am16/32 multiplexers (Campbell Scientific, Logan UT), in the center of each sample site within two hours prior to each burn. Multiplexers and central datalogger were each connected to two high temperature inconel overbraided silica fiber insulated k-type thermocouples (Omega Engineering Inc., Norwalk CT) 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 portions of the site (Fig. 1). Thermocouples measured temperature every two seconds, facilitating measurements of mean maximum temperature, mean rate of spread, and mean residence time over 50°C (Table 4). I 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.

Weather and topographic measurements

To account for the influence of weather on fire behavior, I made visual observations of each burn's progress whenever possible. Logistics and safety precautions prevented consistent on-site weather measurements, so I used data 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 sites). To correct for differences in the height of windspeed measurements collected by RAWS (6-m) as compared to site measurements taken at 2-m, I used the midflame windspeed conversion factor of 0.4 (Rothermel, 1983). I also used RAWS data for 10-hr fuel moisture estimations (Table 2). RAWS data is not linked to site characteristics but can account for how weather variables influence fire behavior temporally.

To measure how fire behavior changes due to the direction of fire spread in relation to wind direction and topography, I used on-site observation, thermocouple, and RAWS data to create indices representing fire heading and slope approach. For fire heading, one denotes back fire, two denotes flank fire (fire spreading perpendicular to wind direction), and three denotes head fire. For slope approach, "1" denotes approach from upslope, "2" denotes approach across slope, and "3" denotes approach from downslope. For sites that experienced a mixture of these conditions, the index values were averaged together. Within six weeks after each burn, I re-measured litter and duff depth within 0.5-m of the pre-burn quadrats to compare mean pre- and post-burn depths for fuel consumption estimation.

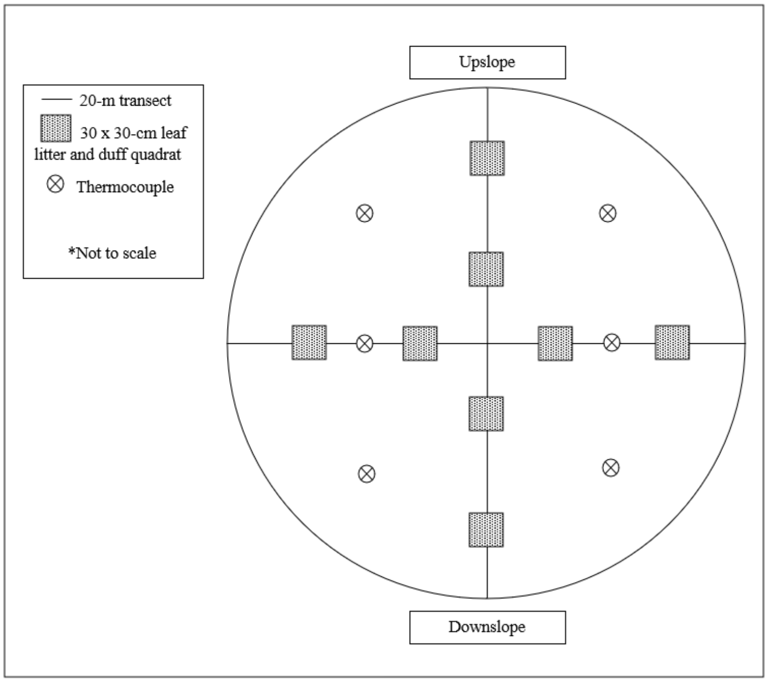


Figure 1: 20-m diameter sample site design for woody vegetation, fuels, and fire behavior measurements in mountain longleaf community of Sheffield WMA GA, USA. Thermocouples were placed away from any disturbed areas or anomalies. Post-fire leaf litter and duff quadrats are not shown but were located within 0.5-m of each pre-burn quadrat.

Analysis

I used path analysis to investigate hypothesized causal relationships between woody vegetation, fuel, weather, and fire behavior traits. Path analysis is a form of structural equation model (SEM) that includes only observed variables to fit systems of linear regressions and involves mediating variables that function as both predictor and response (Grace et al., 2015) (Fig. 2). Due to limited sample size (10 sites) I tested multiple smaller models rather than a single wholistic model where all direct and indirect effects could be quantified simultaneously. Models 1a-1d, describe pathways from woody vegetation structure traits to fuel traits to fire behavior, while models 2a-2d describe pathways from woody vegetation composition traits to fuel traits to fire behavior. Models 3a-3h have the same structure but describe pathways from fuel composition to fuel traits to fire behavior (Fig. 2). All sets of path models include a pathway between weather traits and fire behavior. I also fit variants of models 1a-2d with no direct path between woody vegetation and fire behavior, and variants with fuel moisture instead of weather variables for comparison (not shown). Models 4a and 4b are Bayesian multiple regression models that analyze the effects of prescribed fire variables that can influence fire behavior independently of vegetation and fuel traits, i.e., interactions between fire and topography, wind direction, and fuel moisture (Fig. 2).

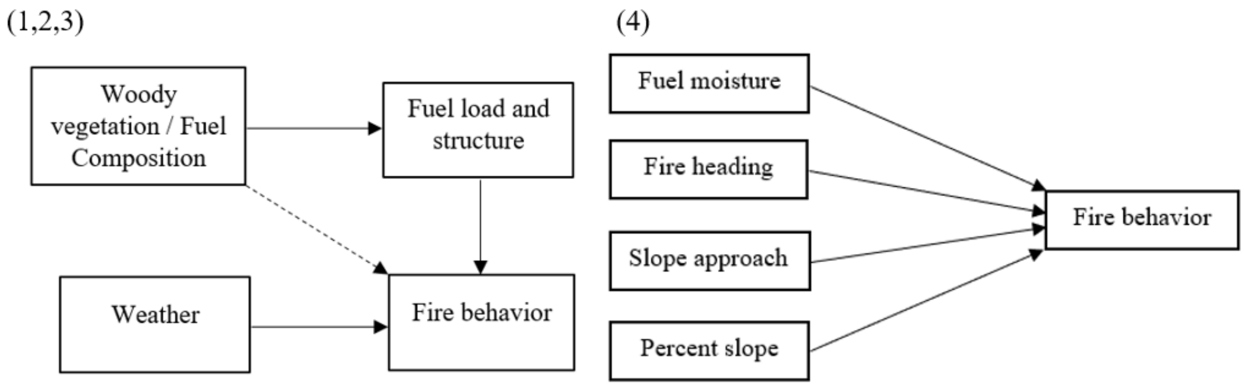


Figure 2: Generalized diagrams of hypothesized path models (1,2,3) and multiple linear regression model (4). Arrows represent causal pathways between variables (linear regression coefficients). (1,2,3) represents models 1a-1d that involve woody vegetation structure, 2a-2d that involve woody vegetation composition, 3a-3h that involve fuel composition, and 4a-4b that involve other prescribed fire variables that may influence fire behavior independently of vegetation and fuels. The dashed arrow represents a possible direct pathway to fire behavior.

Prior to modeling, all variables were tested for normality using the Shapiro-Wilk test (Shapiro & 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 fine fuel consumption and midflame windspeed varied minimally across sites (99.31 ± 1.50 percent and 1.95 ± 0.36 km h^{-1} respectively) and were also removed. To further reduce model complexity, I conducted a principal component analysis (PCA) on each of four datasets; woody vegetation composition and structure, fuel composition, weather, and fire behavior traits (Fig. 4 and Table 5), 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 models 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 & Legendre, 2012).

I 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 fit with three MCMC chains of 1000 burn-in and sampling iterations each. Relatively weak prior beliefs 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 1).

Table 1: Prior distributions for model parameters and a priori justifications. PC = principal component. WV1= first woody vegetation PC describing basal area and pine importance. WV2 = second woody vegetation PC describing mesophytic and pyrophytic hardwood importance. W = first weather PC describing air temperature and relative humidity (second PC not used). C1 = first fuel composition PC describing the amount of mesophytic hardwood and pine litter. C2 = second fuel composition PC describing the amount of pyrophytic hardwood litter. B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Distribution hyperparameters = (mean, standard deviation).

Model parameter	**Prior**	**Description**	**Justification**
$\beta_{\text{Fine fuel load}\sim\text{WV1}}$	norm(.5, .3)	Positive effect of PC_{WVI} on fine fuel load. Larger values on PC_{WV1} indicate greater pine importance while lower values indicate greater basal area.	Hendricks et al., 2002
$\beta_{\text{B1}\sim\text{Fine fuel load}}$	norm(.5, .3)	Positive effect of fine fuel load on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption. [1]	Graham & McCarthy, 2006 Kreye et al., 2013
$\beta_{\text{B1}\sim\text{W1}}$	norm(.5, .3)	Positive effect of PC_{W1} on PC_{B1}. Larger values on PC_{W1} indicate higher air temperatures while lower values indicate higher relative humidity. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Vaughan et al., 2021
$\beta_{\text{B1}\sim\text{WV1}}$	norm(.5, .3)	Positive direct effect of PC_{WV1} on PC_{B1}. Larger values on PC_{WV1} indicate greater pine importance while lower values indicate greater basal area. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	
$\beta_{\text{Bulk density}\sim\text{WV1}}$	norm(-.5, .3)	Negative effect of PC_{WV1} on fine fuel bulk density. Larger values on PC_{WV1} indicate greater pine importance while lower values indicate greater basal area.	Schwilk & Caprio, 2011

Table 1 continued:

Model parameter	Prior	Description	Justification
$\beta_{B1\sim\text{Bulk density}}$	norm(-.5, .3)	Negative effect of fine fuel bulk density on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Plucinski & Anderson, 2008 McDaniel et al., 2021 Kauf et al., 2019
$\beta_{B2\sim\text{Fine fuel load}}$	norm(-.5, .3)	Negative effect of fine fuel load on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.	Kreye et al., 2013 Gagnon et al., 2015
$\beta_{B2\sim W1}$	norm(-.5, .3)	Negative effect of PC_{W1} on PC_{B2}. Larger values on PC_{W1} indicate higher air temperatures while lower values indicate higher relative humidity. Larger values on PC_{B2} indicate shorter residence time.[2]	Rothermel, 1983 Menges et al., 2021
$\beta_{B2\sim WV1}$	norm(-.5, .3)	Negative direct effect of PC_{WV1} on PC_{B2}. Larger values on PC_{WV1} indicate greater pine importance while lower values indicate greater basal area. Larger values on PC_{B2} indicate shorter residence time.	
$\beta_{B2\sim\text{Bulk density}}$	norm(.5, .3)	Positive effect of fine fuel bulk density on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.[3]	Kreye et al., 2013a Kreye et al., 2018
$\beta_{\text{Fine fuel load}\sim WV2}$	norm(-.5, .3)	Negative effect of PC_{WV2} on fine fuel load. Larger values on PC_{WV2} indicate greater mesophytic hardwood importance while lower values indicate greater pyrophytic hardwood importance.	Bable-Plauche et al., 2022 Dickinson et al., 2016
$\beta_{B1\sim WV2}$	norm(-.5, .3)	Negative direct effect of PC_{WV2} on PC_{B1}. Larger values on PC_{WV2} indicate greater mesophytic hardwood importance while lower values indicate greater pyrophytic hardwood importance. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	

Table 1 continued:

Model parameter	Prior	Description	Justification
$\beta_{Bulk\ density\sim WV2}$	norm(.5, .3)	Positive effect of PC_{WV2} on fine fuel bulk density. Larger values on PC_{WV2} indicate greater mesophytic hardwood importance while lower values indicate greater pyrophytic hardwood importance.	Engber & Varner, 2012 Dickinson et al., 2016 McDaniel et al., 2021
$\beta_{B2\sim WV2}$	norm(.5, .3)	Positive direct effect of PC_{WV2} on PC_{B2}. Larger values on PC_{WV2} indicate greater mesophytic hardwood importance while lower values indicate greater pyrophytic hardwood importance. Larger values on PC_{B2} indicate shorter residence time.	
$\beta_{Fine\ fuel\ load\sim C1}$	norm(-.5, .3)	Negative effect of PC_{C1} on fine fuel load. Larger values on PC_{C1} indicate more mesophytic hardwood litter while lower values indicate more pine litter.	Bable-Plauche et al., 2022 Dickinson et al., 2016
$\beta_{B1\sim C1}$	norm(-.5, .3)	Negative direct effect of PC_{C1} on PC_{B1}. Larger values on PC_{C1} indicate more mesophytic hardwood litter while lower values indicate more pine litter. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Kreye et al., 2018
$\beta_{Bulk\ density\sim C1}$	norm(.5, .3)	Positive effect of PC_{C1} on fine fuel bulk density. Larger values on PC_{C1} indicate more mesophytic hardwood litter while lower values indicate more pine litter.	Babl-Plauche et al., 2022 Melillo & Aber, 1982
$\beta_{B2\sim C1}$	norm(.5, .3)	Positive direct effect of PC_{C1} on PC_{B2}. Larger values on PC_{C1} indicate more mesophytic hardwood litter while lower values indicate more pine litter. Larger values on PC_{B2} indicate shorter residence time.	Kreye et al., 2018
$\beta_{Fine\ fuel\ load\sim C2}$	norm(.5, .3)	Positive effect of PC_{C2} on fine fuel load. Larger values on PC_{C2} indicate more pyrophytic hardwood litter.	Babl-Plauche et al., 2022 Melillo & Aber, 1982

Table 1 continued:

Model parameter	Prior	Description	Justification
$\beta_{B1\sim C2}$	norm(.5, .3)	Positive direct effect of PC_{C2} on PC_{B1} . Larger values on PC_{C2} indicate more pyrophytic hardwood litter. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Kreye et al., 2018
$\beta_{Bulk\ density\sim C2}$	norm(-.5, .3)	Negative effect of PC_{C2} on fine fuel bulk density. Larger values on PC_{C2} indicate more pyrophytic hardwood litter.	Babl-Plauche et al., 2022 Melillo & Aber, 1982
$\beta_{B2\sim C2}$	norm(-.5, .3)	Negative direct effect of PC_{C2} on PC_{B2}. Larger values on PC_{C2} indicate more pyrophytic hardwood litter. Larger values on PC_{B2} indicate shorter residence time.	Kreye et al., 2018
$\beta_{B1\sim Fuel\ moisture}$	norm(-.5, .3)	Negative effect of fine fuel moisture on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Graham & McCarthy, 2006 Kreye et al., 2013a Varner et al., 2007
$\beta_{B1\sim Heading}$	norm(.5, .3)	Positive effect of fire heading on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption.[4]	
$\beta_{B1\sim Slope\ approach}$	norm(.5, .3)	Positive effect of slope approach on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption.[5]	Butler et al., 2007
$\beta_{B1\sim Percent\ slope}$	norm(.5, .3)	Positive effect of percent slope on PC_{B1}. Larger values on PC_{B1} indicate faster RoS and more duff consumption.	Butler et al., 2007 Schwilk & Caprio, 2011
$\beta_{B2\sim Fuel\ moisture}$	norm(.5, .3)	Positive effect of fine fuel moisture on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.	Menges et al., 2021
$\beta_{B2\sim Heading}$	norm(.5, .3)	Positive effect of fire heading on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.	Gagnon et al., 2015 Beaufait, 1965

Table 1 continued:

Model parameter	Prior	Description	Justification
$\beta_{B2\sim\text{Slope approach}}$	norm(-.5, .3)	Negative effect of slope approach on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.	Dupuy et al., 2011
$\beta_{B2\sim\text{Percent slope}}$	norm(-.5, .3)	Negative effect of percent slope on PC_{B2}. Larger values on PC_{B2} indicate shorter residence time.	Dupuy et al., 2011

1 No literature was found to directly support a significant effect of fine fuel load on RoS. However, fine fuel load has been shown to increase fire intensity which likely leads to faster RoS due to pre-heating of nearby fuels.

2 No literature was found to directly support an effect of air temperature and relative humidity on residence time. However, these weather variables are known to influence fuel moisture (Rothermel, 1983) and there is evidence of fuel moisture influencing residence time (Menges et al., 2021).

3 No literature was found to directly support an effect of fine fuel bulk density on residence time. However, higher bulk density fuels have been linked to slower drying rates (Kreye et al., 2013a) and more fuel moisture can truncate smoldering duration (Kreye et al., 2018).

4 By definition, headfires move with the wind and backfires move against it, therefore RoS will be greater with headfires. The effect of fire heading on duff consumption remains unclear. Slower moving backfires with lower intensity may consume more fuel over longer durations, or faster moving headfires with greater intensity may consume more fuel rapidly. Considering that PCB1 shows a positive correlation between duff consumption and RoS, duff consumption is expected to increase with RoS.

5 Fires approaching from upslope generally have slower RoS. It is unclear how duff consumption is affected. Considering that our PCB1 shows a positive correlation between duff consumption and RoS, duff consumption is also expected to decrease.

Model convergence was assessed using the Gelman-Rubin statistic ($\hat{R}$), effective sample size, and visual inspection of trace plots. Convergence was accepted if $\hat{R}$ was less than 1.01 for all parameters, and effective sample size was at least one hundred times greater than the number of chains used (Garnier-Villarreal, n.d.). Approximate fit was estimated with several indices that all assess different aspects of model fit; posterior predictive p-value (PPP), Bayesian root square mean error of approximation (BRMSEA), and Bayesian adjusted gammahat ($\hat{\Gamma}_{\mathrm{adj}}$) (Garnier-Villarreal & Jorgensen, 2020). Relative model fit was compared using the marginal log likelihood ratio and the rule of thumb for interpretation put forth by (Jeffreys, 1961). R^2 was calculated across the full posterior distribution for a model using the "ppmc" function in the "blavaan" R package (v0.4.3; Merkle et al., 2021). Due to the subjective nature of priors, a sensitivity analysis was conducted to examine the stability of posterior estimates (Table 7).

Results

Site characteristics and conditions

Site selections captured a gradient from open, pine dominated canopies (G, H, I) to closed, hardwood dominated canopies (A, B, D, J). As shown in Table 2, sample sites were located on 5 to 22 percent slopes with a mean of 14.2 ± 5.6 (Standard deviation) percent. Mean basal area was 27.14 ± 9.22 m^2 ha^{-1} and ranged from 11.89 m^2 ha^{-1} to 41.05 m^2 ha^{-1}. As noted earlier, basal area and canopy openness were highly correlated; for instance, the site with the lowest basal area I had the greatest canopy openness (75.92 percent), and the site with the greatest basal area (J) had a closed canopy (1.04 percent). The most pine dominated site (G) had a pine to hardwood importance ratio of 2.34 while the ratio of the most hardwood dominated site (B) was 0.13. The mean ratio among sites showed a balanced co-dominance (1.03 ± 0.78). When hardwoods were categorized as either pyrophytes or mesophytes, there was greater mean pyrophyte importance (61.43 ± 29.12) compared to mesophyte importance (42.52 ± 36.65) among sites. At most sites with low pine to hardwood importance ratios (B, D, F, J), the pyrophytic hardwoods tended to make up the majority of the hardwood component. Fine fuel load (leaf litter) ranged from 0.24 kg m^{-2} to 0.76 kg m^{-2} with a mean of 0.53 ± 0.15 kg m^{-2}. Fuel composition functional group means were 0.21 ± 0.14, 0.20 ± 0.06, and 0.03 ± 0.03 kg m^{-2} for pine, pyrophytic hardwood, and mesophytic hardwood leaf litter, respectively among sites. Pine leaf litter ranged from 0.06 ± 0.03 to 0.50 ± 0.13 kg m^{-2} and accounted for 13 to 72 percent of the fuel bed by mass. Pyrophytic hardwood litter ranged from 0.08 ± 0.03 to 0.34 ± 0.19 kg m^{-2} and accounted for 27-78 percent of the fuel bed by mass. Mesophytic hardwood litter ranged from 0.003 ± 0.005 kg m^{-2} to 0.10 ± 0.02 kg m^{-2} and accounted or 0.6-24 percent of the fuel bed by mass. Fine fuel bulk density varied from 4.31 kg/m^{-3} to 12.28 kg/m^{-3} with a mean of 7.7 ± 2.20 kg/m^{-3}. In comparison to fine fuel depth, duff depth was relatively shallow across all sites with a mean of 1.85 ± 0.61 cm and ranged from 1.08 cm to 3.13 cm. Mean fine fuel depth showed more variation ranging from 3.32 cm to 10.06 cm with a mean of 7.59 ± 2.13 cm.

Prescribed burns took place from February 8th to March 4th between 11am and 3pm with the exception of site C that did not burn until 5 pm. There was no relationship between burn times and air temperature or fuel moisture among sample sites. The lowest average air temperature at time of burn was 11.7 °C and the highest was 26.1 °C with a mean of 19.89 ± 5.50 °C. The lowest average relative humidity at time of burn was 13 percent and the highest was 34 percent with a mean of 24 ± 7 percent. Average midflame windspeeds were weak (National Weather Service, n.d.) and varied little between burns (1.95 ± 0.36 km h^{-1}). The lowest fuel moisture at time of burn was 7 percent and the highest was 10 percent with a mean of 8 ± 1 percent.

Table 2: Topography, woody vegetation, pre-burn fuel, and during-burn weather characteristics at sample sites (A-J) in Sheffield WMA GA, USA that experienced prescribed fire Feb-Mar, 2022. IV = importance value. Numbers in parenthesis are within site 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
Woody vegetation traits	Basal area ($m^2 ha^{-1}$)	34.75	29.21	32.74	36.78	11.89	23.44	19.18	22.66	19.66	41.05
	Canopy openness (%)	12.48	3.12	16.64	7.28	75.92	18.72	67.6	28.08	26	1.04
	Pine IV:Hardwood IV ratio	0.73	0.13	1.35	0.14	0.96	0.65	2.34	2.22	1.25	0.51
	Pine IV	84.43	22.34	71.76	18.15	98.08	78.43	140.19	137.89	111.01	67.43
	Pyrophytic hardwood IV	101.16	52.52	18.73	78.02	24.09	100.86	45.58	62.11	47.73	83.51
	Mesophytic hardwood IV	14.41	125.13	34.40	48.19	77.83	20.70	14.22	0.00	41.25	49.05
Fuel traits	Fine fuel load ($kg\ m^{-2}$)	0.60 (0.21)	0.60 (0.11)	0.58 (0.20)	0.54 (0.12)	0.24 (0.10)	0.43 (0.09)	0.61 (0.19)	0.76 (0.28)	0.58 (0.21)	0.38 (0.03)
	Pine ($kg\ m^{-2}$)	0.23 (0.07)	0.11 (0.08)	0.20 (0.12)	0.06 (0.08)	0.06 (0.03)	0.06 (0.04)	0.39 (0.26)	0.50 (0.13)	0.32 (0.15)	0.12 (0.04)
	Pyrophytic hardwood ($kg\ m^{-2}$)	0.18 (0.06)	0.20 (0.07)	0.25 (0.11)	0.34 (0.19)	0.08 (0.03)	0.28 (0.11)	0.15 (0.23)	0.19 (0.23)	0.14 (0.17)	0.17 (0.04)
	Mesophytic hardwood ($kg\ m^{-2}$)	0.01 (0.01)	0.10 (0.02)	0.02 (0.01)	0.06 (0.04)	0.01 (0.01)	0.02 (0.01)	0.003 (0.005)	0.01 (0.02)	0.03 (0.02)	0.05 (0.03)
	Bulk density ($kg\ m^{-3}$)	12.28 (5.69)	9.63 (1.80)	7.03 (2.20)	7.51 (1.80)	8.03 (2.41)	4.31 (0.92)	6.89 (4.08)	8.29 (3.99)	7.57 (2.93)	5.27 (0.94)
	Duff depth (cm)	2.13 (1.46)	1.57 (0.84)	1.58 (0.75)	2.06 (0.80)	1.09 (0.84)	2.13 (1.07)	1.08 (0.62)	3.13 (1.75)	2.2 (1.55)	1.51 (1.08)
	Fine fuel depth (cm)	5.83 (3.13)	6.30 (1.87)	8.21 (1.32)	7.19 (1.45)	3.32 (1.89)	10.06 (2.48)	10.03 (5.01)	9.88 (2.85)	7.74 (2.77)	7.29 (1.88)
Timing	Date of burn	8-Feb-22		9-Feb-22		2-Mar-22		3-Mar-22		4-Mar-22	
	Time of fire at site	3pm	2pm	5pm	1pm	1pm	2pm	2pm	1pm	11am	1pm
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 ($km\ h^{-1}$)	1.42	2.32	2.57	1.74	1.42	2	2	2	2	2
	Fuel moisture (%)	7.5	8	7.2	10	8.1	6.9	6.6	7.9	9.8	7.9

Table 3: Mean and median importance values (IV) of functional groups and the most important tree species that were present in at least half of all sample sites. Northern red, black, and scarlet oak were grouped together 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)

Importance values of functional groups and species were calculated to characterize woody vegetation (Table 3). Across sample sites, pines were the most important functional group, followed by pyrophytic hardwoods. Among pines, longleaf and shortleaf were most important. Among pyrophytic hardwoods, Northern red, black, scarlet, and Southern red oak were most important. The most important mesophytic hardwood was black gum, but collectively mesophytes were the least important functional group.

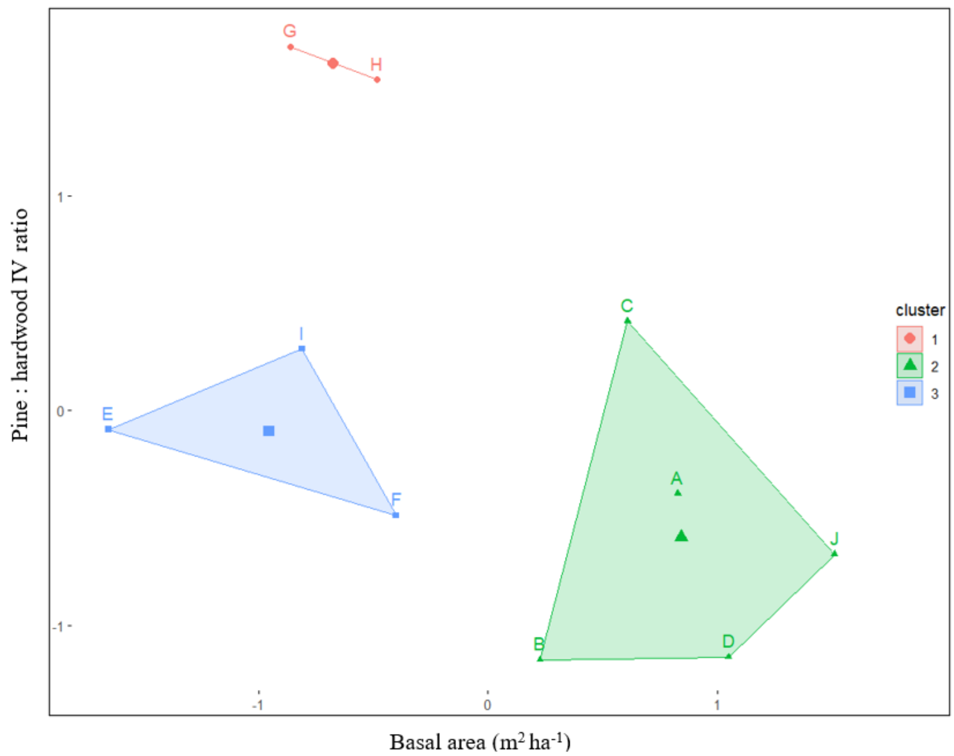


Figure 3: K-means cluster analysis of prescribed burn sites (A-J) in Sheffield WMA, Paulding County GA, based on standardized values of basal area and the ratio of pine to hardwood importance value (IV).

K-means cluster analysis was performed to visualize how sample sites partitioned along a gradient of woody vegetation composition and structure (Fig. 3). Three clusters maximized the within group similarity and between group dissimilarity of sample sites based on standardized basal area and pine to hardwood importance ratio values. Cluster one included sites with relatively low basal area and high pine importance with a standardized cluster mean of -0.67 for basal area and 1.62 for pine to hardwood importance ratio. Sites with relatively greater basal area and hardwood importance were grouped together in cluster two which had a standardized cluster mean of 0.84 for basal area and -0.59 for pine to hardwood ratio. Cluster three included sites with relatively low basal area, but a balance of pine and hardwoods and had a standardized cluster mean of -0.95 for basal area and -0.10 for pine to hardwood importance ratio.

Fire behavior

Table 4: Fire behavior and effects measurements from sample sites (A-J). Maximum fire temperature is the average of the maximum temperature from each thermocouple in a sample site. Mean residence time was calculated by averaging the amount of time each thermocouple in a sample site remained over 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 site. Numbers in parenthesis = within site standard deviation. Negative consumption values indicate an increase in fuel after fire.

	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**
Mean Max. temperature (°C)	77.98 (0.51)*	71.52 (5.02)*	77.00 (0.63)*	75.38 (0.38)*	162.40 (118.41)	474.17 (68.98)	457.82 (74.12)	465.43 (112.22)	373.73 (87.47)	403.30 (59.21)
Mean residence time (min)	4.06 (1.46)	3.06 (1.38)	4.76 (1.34)	3.82 (1.40)	3 (0.77)	5.74 (1.51)	11.67 (2.25)	7.81 (0.79)	9.69 (1.42)	8.21 (1.38)
Mean rate of spread (m/min)	0.91 (0.67)	0.62 (0.49)	2.91 (2.37)	0.70 (0.38)	0.10**	1.31 (0.45)	0.60 (0.26)	2.07 (2.14)	0.33 (0.07)	1.20 (0.36)
Fine fuel consumption (%)	100.00	100.00	100.00	100.00	95.39	99.53	98.13	100.00	100.00	100.00
Duff consumption (%)	28.46	-33.00	41.81	18.16	27.51	60.79	3.04	63.41	14.89	-5.58

* Thermocouples at sites A-D failed to measure temperatures over 80°C resulting in artificially low mean maximum temperatures.

** Thermocouples were not able to capture accurate RoS at sample site E due to the flame front failing to propagate across the site. 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.

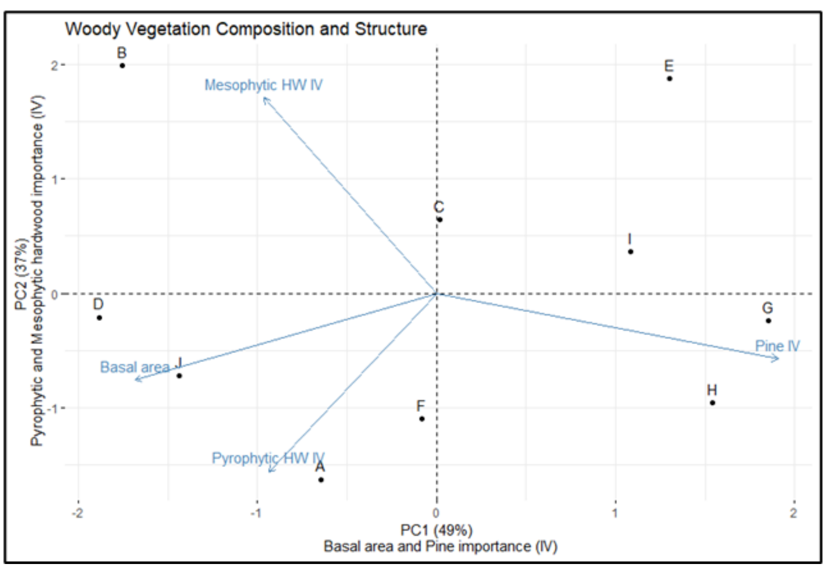
Although technical problems prevented measurement of fire temperatures above 80 °C in sites A-D, thermocouples successfully captured all flame temperatures at the other sites. As shown in Table 4, mean maximum fire temperature averaged among these sites was 389.48 ±118.00 °C. The coolest fire I was 162.40°C and the hottest fire (F) was 474.17°C. Mean residence time was 6.18 ± 1.05 minutes and ranged from 3 to 11.67 minutes (E and G respectively). Thermocouples were not able to capture accurate RoS at sample site E due to the flame front failing to propagate across the site, therefore 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. The other nine sites ranged from 0.33 to 2.91 m min^{-1} (I and C respectively) with a mean of 1.08 ± 0.97 m min^{-1}. All sites had complete or nearly complete fine fuel consumption (99 ± 2 percent), but more variable duff consumption. Maximum duff consumption was 63 percent (H), but sites B and J saw an increase of duff after fire (-33 and -6 percent respectively). Among sites where mean duff depth decreased, the average was 32 ± 22 percent.

Principal component analysis

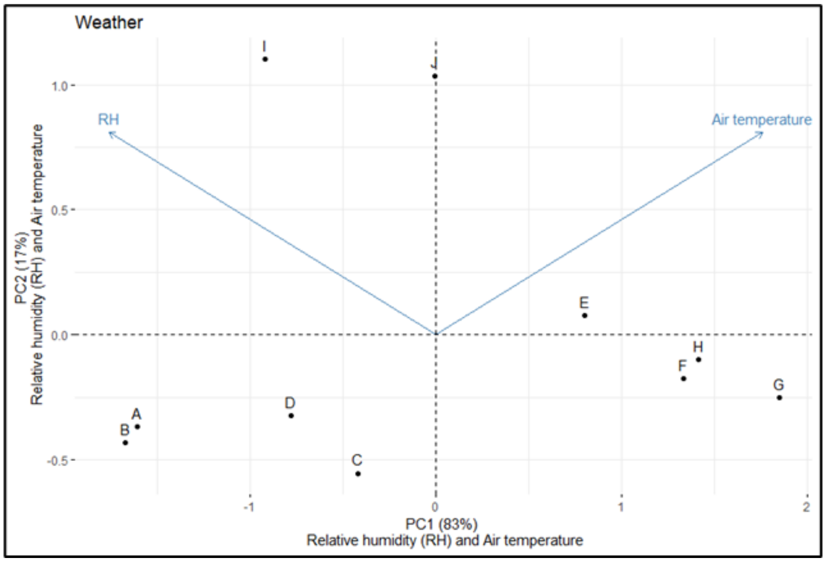
Table 5: Variable loadings for woody vegetation, weather, fuel composition, and fire behavior from principal component (PC) analyses of prescribed burn sample sites in Sheffield WMA. Percentages in parentheses indicate the proportion of variance explained by that PC. Loadings describe the Pearson correlation between variable and PC.

Woody Vegetation Composition and Structure		
	PC1 (49%)	PC2 (37%)
Basal area	-0.58	-0.3
Pine IV	0.66	-0.23
Pyrophytic hardwood IV	-0.33	-0.62
Mesophytic hardwood IV	-0.34	0.68
Weather		
	PC1 (83%)	PC2 (17%)
Relative humidity	-0.71	0.71
Air temperature	0.71	0.71
Fuel Composition		
	PC1 (58%)	PC2 (23%)
Mesophytic hardwood litter	0.6	-0.29
Pyrophytic hardwood litter	0.54	0.83
Pine litter	-0.59	0.48
Fire Behavior		
	PC1 (50%)	PC2 (33%)
Rate of spread	0.71	-0.03
Residence time	-0.04	-0.99
Duff consumption	0.71	-0.03

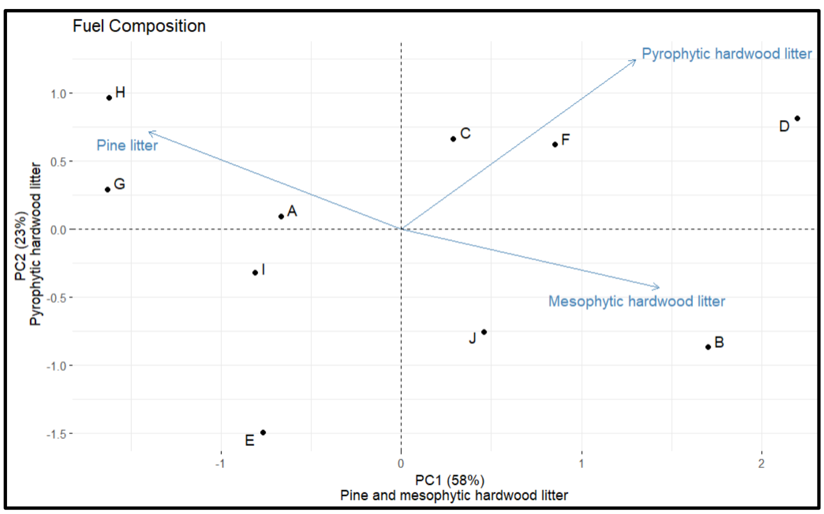
(A)



(B)


Weather
RH
Air temperature
PC2 (17%)
Relative humidity (RH) and Air temperature
PC1 (83%)
Relative humidity (RH) and Air temperature
A
B
C
D
E
F
G
H
I
J
1.0
0.5
0.0
-0.5
-1
0
1
2

(C)


Fuel Composition
Pyrophytic hardwood litter
Pine litter
Mesophytic hardwood litter
PC2 (23%)
Pyrophytic hardwood litter
PC1 (58%)
Pine and mesophytic hardwood litter
A
B
C
D
E
F
G
H
I
J
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1
0
1
2

(D)

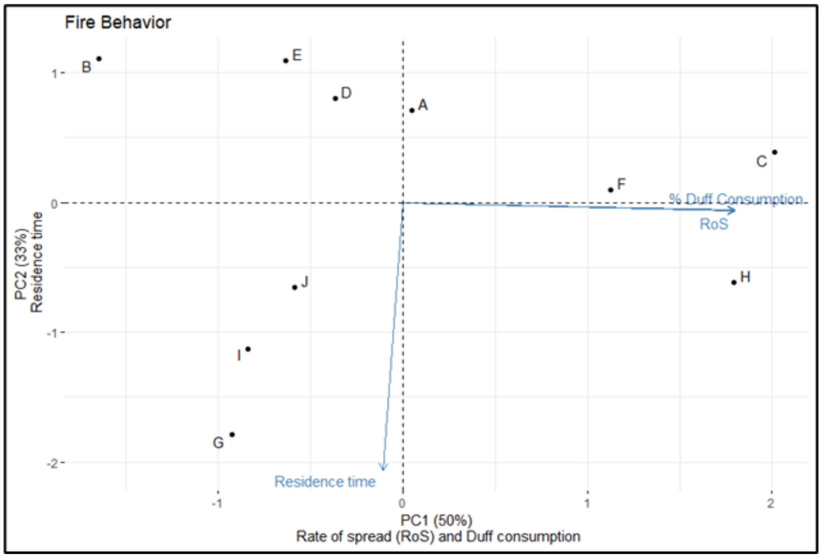


Figure 4: Principal component analysis biplots for woody vegetation composition and structure, weather variables, fuel composition, and fire behavior. Arrows show correlations between original variables and their associated principal components (PC). Numbers in parentheses = percent variation explained by that PC. Variables are standardized and centered.

The woody vegetation composition and structure PCA showed BA and Pine IV to be strongly and negatively correlated on PC1 while pyrophytic and mesophytic hardwood IV were strongly and negatively correlated on PC2 (Table 5 and Fig. 4A). In the weather PCA, air temperature and relative humidity loaded equally onto PC1 and PC2 (Table 5 and Fig. 4B). PC2 only explained 17 percent of the variance and was not used in further analysis. Air temperature and relative humidity had a strong negative correlation on PC1. In the fuel composition PCA, pine and mesophytic hardwood litter were strongly and negatively correlated to each other on PC1 and pyrophytic hardwood litter was positively correlated to PC2 (Table 5 and Fig. 4C). The fire behavior PCA showed RoS and duff consumption to be strongly and positively correlated on PC1 while residence time was strongly correlated to PC2 (Table 5 and Fig. 4C). Notably, sample sites did not show consistent similarities to each other across the PCAs.

Path analysis and multiple regression models

Table 6: Mean posterior parameter estimates, model fit (PPP), and R^2 for fitted Bayesian path analysis models relating fuel traits and principal components of woody vegetation, and weather variables to those of fire behavior (1,2). WV1= first woody vegetation principal component (PC) describing basal area and pine importance. WV2 = second woody vegetation PC describing mesophytic and pyrophytic hardwood importance. W = first weather PC describing air temperature and relative humidity (second PC not used). B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Lower and upper 95% PI = posterior credibility intervals. PPP = posterior predictive p-value. SD = standard deviation. R^2 is percent variation of fire behavior explained by model.

Model	Parameter (β)	Mean posterior estimate (SD)	Lower 95% PI	Upper 95% PI	PPP	R^2
Models of Forest Structure, Fuels, Weather, and Fire Behavior						
1a	Fine fuel load~WV1	0.277 (0.208)	-0.109	0.707	0.653	0.354
	B1~Fine fuel load	0.458 (0.252)	-0.047	0.956		
	B1~W1	0.37 (0.234)	-0.085	0.83		
	B1~WV1	0.24 (0.243)	-0.219	0.73		
1b	Bulk density~WV1	-0.232 (0.218)	-0.688	0.168	0.627	0.365
	B1~Bulk density	-0.396 (0.255)	-0.9	0.093		
	B1~W1	0.37 (0.239)	-0.099	0.852		
	B1~WV1	0.268 (0.245)	-0.198	0.761		
1c	Fine fuel load~WV1	0.282 (0.207)	-0.1	0.711	0.64	0.447
	B2~Fine fuel load*	-0.408 (0.222)	-0.856	0.017		
	B2~W1*	-0.345 (0.213)	-0.766	0.075		
	B2~WV1*	-0.274 (0.203)	-0.68	0.116		
1d	Bulk density~WV1	-0.244 (0.211)	-0.688	0.145	0.535	0.378
	B2~Bulk density*	0.235 (0.246)	-0.22	0.713		
	B2~W1*	-0.331 (0.223)	-0.783	0.084		
	B2~WV1*	-0.326 (0.21)	-0.737	0.086		
Models of Forest Composition, Fuels, Weather, and Fire Behavior						
2a	Fine fuel load~WV2	-0.377 (0.217)	-0.803	0.042	0.725	0.373
	B1~Fine fuel load	0.419 (0.248)	-0.075	0.903		
	B1~W1	0.396 (0.218)	-0.02	0.831		
	B1~WV2	-0.383 (0.231)	-0.845	0.056		
2b	Bulk density~WV2	0.065 (0.243)	-0.374	0.562	0.575	0.475
	B1~Bulk density	-0.491 (0.233)	-0.957	-0.037		
	B1~W1	0.393 (0.22)	-0.033	0.848		
	B1~WV2	-0.514 (0.231)	-0.961	-0.07		
2c	Fine fuel load~WV2	-0.365 (0.222)	-0.812	0.062	0.669	0.37
	B2~Fine fuel load*	-0.396 (0.229)	-0.849	0.026		
	B2~W1*	-0.426 (0.203)	-0.819	-0.025		
	B2~WV2*	0.287 (0.209)	-0.108	0.71		
2d	Bulk density~WV2	0.068 (0.248)	-0.391	0.583	0.507	0.38
	B2~Bulk density*	0.351 (0.241)	-0.106	0.818		
	B2~W1*	-0.422 (0.204)	-0.835	-0.023		
	B2~WV2*	0.428 (0.217)	0.007	0.871		

Table 7: Mean posterior parameter estimates, model fit (PPP), and R-squared for fitted Bayesian path analysis models relating fuel traits with principal components of fuel composition, and weather variables to those of fire behavior (3). C1 = first principal component (PC) describing the amount of mesophytic hardwood and pine litter. C2 = second PC describing the amount of pyrophytic hardwood litter W = first weather PC describing air temperature and relative humidity (second PC not used). B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Lower and upper 95% PI = posterior credibility intervals. PPP = posterior predictive p-value. SD = standard deviation. R^2 is percent variation of fire behavior explained by model.

Models of Fuel Composition, Fuel Structure, Weather, and Fire Behavior						
Model	Parameter (β)	Mean posterior estimate (SD)	Lower 95% PI	Upper 95% PI	PPP	R^2
3a	Fine fuel load~C1	-0.331 (0.211)	-0.754	0.067	0.687	0.341
	B1~Fine fuel load	0.436 (0.246)	-0.035	0.932		
	B1~W1	0.398 (0.247)	-0.093	0.889		
	B1~C1	-0.251 (0.234)	-0.742	0.201		
3b	Bulk density~C1	0.295 (0.221)	-0.179	0.692	0.48	0.358
	B1~Bulk density	-0.447 (0.253)	-0.95	0.025		
	B1~W1	0.45 (0.254)	-0.056	0.947		
	B1~C1	-0.286 (0.235)	-0.754	0.17		
3c	Fine fuel load~C1	-0.331 (0.223)	-0.791	0.09	0.58	0.443
	B2~Fine fuel load*	-0.375 (0.236)	-0.847	0.074		
	B2~W1*	-0.201 (0.24)	-0.704	0.243		
	B2~C1*	0.392 (0.202)	-0.002	0.791		
3d	Bulk density~C1	0.24 (0.222)	-0.168	0.701	0.213	0.39
	B2~Bulk density*	0.268 (0.247)	-0.206	0.773		
	B2~W1*	-0.257 (0.25)	-0.75	0.216		
	B2~C1*	0.426 (0.212)	0.006	0.831		
3e	Fine fuel load~C2	0.617 (0.237)	0.125	1.067	0.563	0.375
	B1~Fine fuel load	0.325 (0.247)	-0.141	0.826		
	B1~W1	0.391 (0.231)	-0.052	0.873		
	B1~C2	0.551 (0.255)	0.058	1.053		
3f	Bulk density~C2	-0.224 (0.262)	-0.753	0.27	0.402	0.569
	B1~Bulk density	-0.513 (0.232)	-0.96	-0.054		
	B1~W1	0.453 (0.21)	0.04	0.886		
	B1~C2	0.739 (0.251)	0.213	1.208		
3g	Fine fuel load~C2	0.627 (0.236)	0.159	1.087	0.657	0.29
	B2~Fine fuel load*	-0.371 (0.24)	-0.868	0.075		
	B2~W1*	-0.318 (0.231)	-0.775	0.121		
	B2~C2*	-0.326 (0.264)	-0.841	0.2		
3h	Bulk density~C2	-0.221 (0.262)	-0.749	0.278	0.427	0.318
	B2~Bulk density*	0.358 (0.247)	-0.12	0.861		
	B2~W1*	-0.37 (0.238)	-0.825	0.089		
	B2~C2*	-0.459 (0.255)	-0.973	0.017		

Table 8: Mean posterior parameter estimates, model fit (PPP), and R-squared for fitted Bayesian multiple regression models relating principal components of fire behavior to prescribed fire variables that may influence fire independently of fuel and vegetation traits (4). B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Lower and upper 95% PI = posterior credibility intervals. PPP = posterior predictive p-value. SD = standard deviation. R^2 is percent variation of fire behavior explained by model

Models of Topography, Wind Direction, Fuel Moisture, and Fire Behavior						
	Parameter	Mean posterior estimate (SD)	Lower 95% PI	Upper 95% PI	PPP	R^2
4a	B1~Fuel moisture	-0.322 (0.234)	-0.817	0.114	0.603	0.45
	B1~Heading	0.407 (0.269)	-0.103	0.944		
	B1~Slope approach	0.571 (0.273)	0.041	1.116		
	B1~Percent slope	0.083 (0.076)	-0.06	0.249		
4b	B2~Fuel moisture*	0.334 (0.214)	-0.08	0.767	0.542	0.31
	B2~Heading*	0.716 (0.264)	0.207	1.228		
	B2~Slope approach*	-0.289 (0.276)	-0.858	0.231		
	B2~Percent slope*	-0.081 (0.07)	-0.23	0.049		

* B2 represents the principal component (PC) on which residence time increases with lower PC values. Therefore, a negative posterior estimate for a path coefficient involving B2 is interpreted as a decrease in B2 which indicates longer residence time.

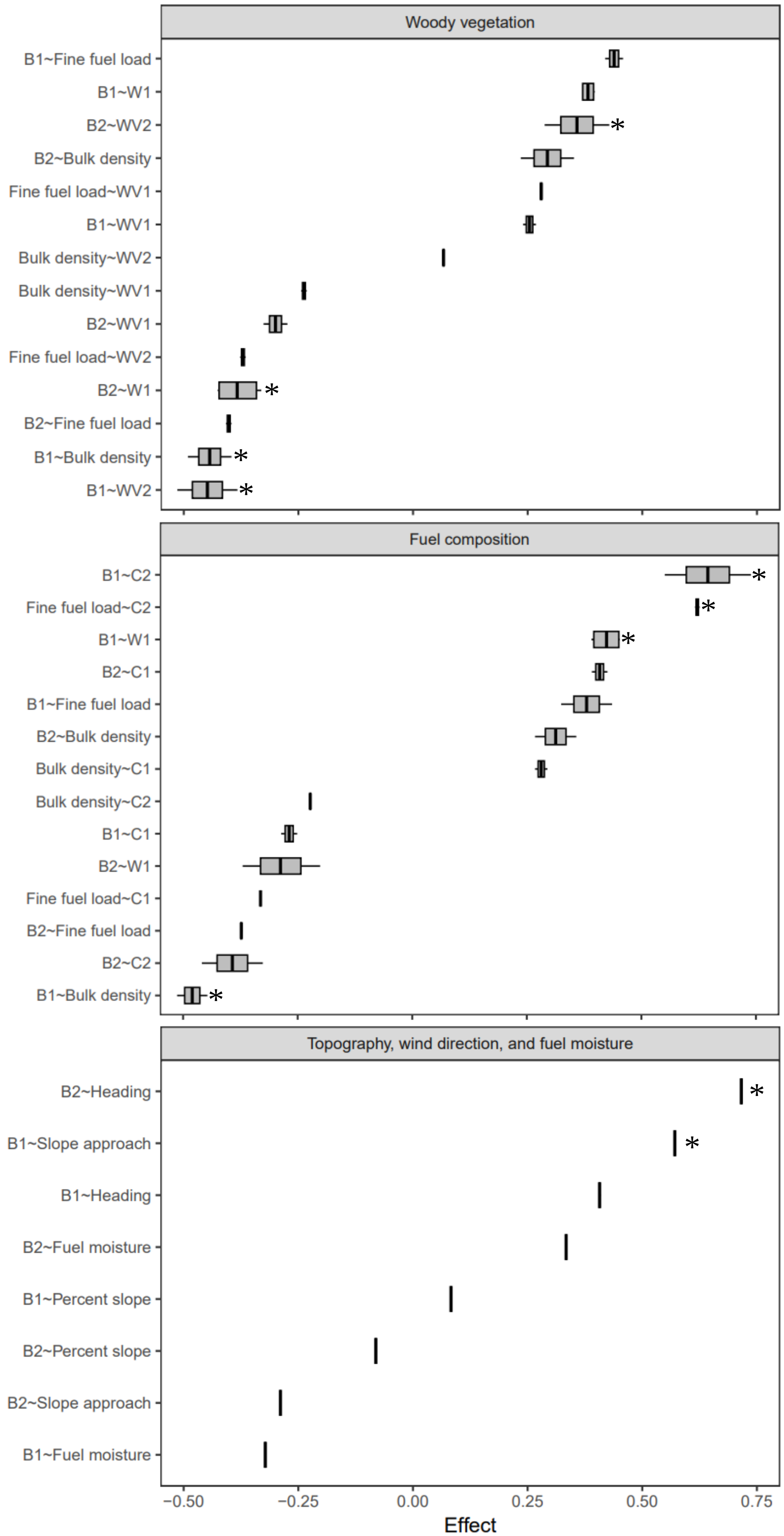

Woody vegetation
B1~Fine fuel load
B1~W1
B2~WV2
B2~Bulk density
Fine fuel load~WV1
B1~WV1
Bulk density~WV2
Bulk density~WV1
B2~WV1
Fine fuel load~WV2
B2~W1
B2~Fine fuel load
B1~Bulk density
B1~WV2
Fuel composition
B1~C2
Fine fuel load~C2
B1~W1
B2~C1
B1~Fine fuel load
B2~Bulk density
Bulk density~C1
Bulk density~C2
B1~C1
B2~W1
Fine fuel load~C1
B2~Fine fuel load
B2~C2
B1~Bulk density
Topography, wind direction, and fuel moisture
B2~Heading
B1~Slope approach
B1~Heading
B2~Fuel moisture
B1~Percent slope
B2~Percent slope
B2~Slope approach
B1~Fuel moisture
−0.50
−0.25
0.00
0.25
0.50
0.75
Effect

Figure 6: Boxplots of mean posterior estimates for parameters in models investigating woody vegetation, fuel composition, and the effects of topography, wind direction, and fuel moisture on fire behavior. WV1= first woody vegetation principal component (PC) describing basal area and pine importance. WV2 = second woody vegetation PC describing mesophytic and pyrophytic hardwood importance. C1 = first principal component (PC) describing the amount of mesophytic hardwood and pine litter. C2 = second PC describing the amount of pyrophytic hardwood litter W = first weather PC describing air temperature and relative humidity (second PC not used). B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Parameters that had statistically significant effects are marked with asterisks.

As shown in Table 6 and figure 6, models investigating the effects (mean posterior estimates of path coefficients β) of stand composition and structure on fuels and fire behavior (models 1a-2d) show that increased pine importance and decreased basal area (WV1) had a weak positive effect on fine fuel load (μ = 0.28 ± 0.003 for model 1a and 1c) and weak negative effect on fine fuel bulk density (μ = -0.24 ± 0.006 for model 1b and 1d). Fine fuel load also increased with greater pyrophytic hardwood importance relative to mesophytic hardwoods (WV2) (μ = -0.38 ± 0.006 for model 2a and 2c), but fine fuel bulk density was not affected (μ = 0.07 ± 0.002 for model 2b and 2d). As fuel load increased, RoS and duff consumption (B1) increased (μ = 0.43 ± 0.02 for model 1a and 2a). Greater fuel load also increased residence time (B2) (μ = -0.4 ± 0.006 for model 1c and 2c). Conversely, as bulk density increased, RoS and duff consumption (B1) decreased (μ = -0.44 ±0.05 for model 1b and 2b), as did residence time (B2) (μ = 0.29 ± 0.06 for model 1d and 2d). Higher air temperature and lower relative humidity (W1) increased RoS and duff consumption (B1) (μ = 0.38 ± 0.01 for model 1a, 1b, 2a, and 2b) and residence time (B2) (μ = -0.38 ± 0.04 for model 1c, 1d, 2c, and 2d) similarly to fuel traits.

Total effect sizes (sum of all direct and indirect pathways in a model) of woody vegetation traits on fire behavior were consistently similar to those of weather on fire behavior. For example, the mean total effect sizes of vegetation and weather had absolute values of |0.43| ± 0.07, and |0.38| ± 0.03. respectively. The direct effects of woody vegetation traits on fire behavior were consistently stronger than the indirect effects (product of path coefficients in a pathway) (|0.34| ± 0.09, and |0.09| ± 0.05 respectively).

Fuel composition (Table 7) and woody vegetation (Table 6) similarly influenced fuel traits and fire behavior, except fuel composition showed a stronger relationship with bulk density. Fuel load increased with more pine litter and decreased with mesophytic hardwood litter (μ = -0.33 ± 0.00 for model 3a and 3c). Bulk density decreased with more pine litter and increased with more mesophytic hardwood litter (β = 0.3 for model 3b). Greater fuel loads resulted in faster RoS, and more duff consumption (μ = 0.38 ± 0.06 for model 3a and 3e), as well as longer residence times (μ = -0.37 ± 0.002 for model 3c and 3g). More pyrophytic hardwood litter also increased fuel load (μ = 0.62 ± 0.005 for model 3e and 3g) and reduced bulk density (μ = -0.22 ± 0.002 for model 3f and 3h).

Total effect sizes of fuel composition on fire behavior were generally stronger than those of weather on fire behavior. The mean total effect sizes of fuel composition and weather had absolute values of |0.56| ± 0.15 and |0.35| ± 0.08. respectively. The direct effects of fuel composition on fire behavior were consistently stronger than the indirect effects (|0.43| ± 0.15, and |0.13| ± 0.05 respectively).

Models investigating the effects of prescribed fire variables that can influence fire behavior independently of vegetation and fuels, i.e., interactions between fire and topography, wind direction, and fuel moisture (Table 8 and figure 6) showed that RoS and duff consumption (B1) increased with head fires and when fires approached from downslope (β = 0.407 and 0.571 respectively) but decreased with fuel moisture (β = -0.322). Residence time (B2) decreased significantly with head fires and to a lesser degree with greater fuel moisture (β = 0.716 and 0.334 respectively). Fires approaching from downslope increased residence time slightly (β = -0.289) but slope percent had no effect on RoS, duff consumption, or residence time (β = 0.083 and -0.081 respectively).

All models converged with all parameter $\hat{R}$ values below 1.01 and, with the exception of model 3d, showed acceptable fit according to PPP and Bayesian $\hat{\Gamma}_{adj}$ values. Acceptable fit is indicated by a PPP close to 0.5 (Muthén & Asparouhov, 2012) and Bayesian $\hat{\Gamma}_{\mathrm{adj}}$ values close to one (Garnier-Villarreal & Jorgensen, 2020). However, all model posterior probability intervals (PPIs) were outside of the recommended limits for Bayesian root mean square error of approximation (BRMSEA) values, i.e., 90 percent PPI between 0.05 and 0.08 indicate good fit (Hoofs et al., 2018, Table S1 in supplementary materials). Model fit comparisons using the marginal log likelihood ratio showed that all models (with vs. without the direct path from woody vegetation traits to fire behavior, fuel moisture vs. W1, and woody vegetation vs. fuel composition) had similar model fit (Table S2 in supplementary materials). All sets of models also had relatively similar R^2 values (0.354-0.475, 0.29-0.569, and 0.31-0.45 for models 1a-2d, 3a-3h, and 4a-4b respectively).

Table 7: Sensitivity analysis of mean posterior parameter estimates averaged across models. Original subjective priors used in the reported fitted models are compared to three different alternative priors. WV1 = first woody vegetation principal component (PC) describing basal area and pine importance. WV2 = second woody vegetation PC describing mesophytic and pyrophytic hardwood importance. W = first weather PC describing air temperature and relative humidity (second PC not used). C1 = first fuel composition PC describing the amount of mesophytic hardwood and pine litter. C2 = second fuel composition PC describing the amount of pyrophytic hardwood litter. B1 = first fire behavior PC describing rate of spread and duff consumption. B2 = second fire behavior PC describing residence time. Prior distribution hyperparameters = (mean, standard deviation). Bold values indicate deviations of less than ten percent.

	Original Prior	Alternative Priors			Percent Deviation from Original		
		1	2	3	1	2	3
Mean	±0.5	±0.6	±0.5	0	-	-	-
Standard Deviation	0.3	0.3	0.5	1	-	-	-
Model Parameter	Mean Posterior Estimate						
$\beta_{\text{Fine fuel load\textasciitilde WV1}}$	0.28	0.33	0.19	0.09	17.90	-32.73	-68.90
$\beta_{\text{B1\textasciitilde Fine fuel load}}$	0.43	0.51	0.41	0.27	16.47	-6.68	-37.67
$\beta_{\text{B1\textasciitilde W1}}$	0.38	0.44	0.34	0.27	14.45	-10.33	-30.61
$\beta_{\text{B1\textasciitilde WV1}}$	0.25	0.21	0.09	0.01	-16.67	-65.45	-96.88
$\beta_{\text{Bulk density\textasciitilde WV1}}$	-0.24	-0.29	-0.13	-0.01	-23.32	44.96	94.33
$\beta_{\text{B1\textasciitilde Bulk density}}$	-0.44	-0.52	-0.39	-0.21	-18.86	10.51	52.00
$\beta_{\text{B2\textasciitilde Fine fuel load}}$	-0.40	-0.46	-0.37	-0.27	-13.57	**8.59**	31.63
$\beta_{\text{B2\textasciitilde W1}}$	-0.38	-0.43	-0.34	-0.27	-10.81	10.61	28.45
$\beta_{\text{B2\textasciitilde WV1}}$	-0.30	-0.33	-0.23	-0.23	-11.04	22.91	22.24
$\beta_{\text{B2\textasciitilde Bulk density}}$	0.29	0.37	0.15	-0.08	25.68	-49.32	-128.42
$\beta_{\text{Fine fuel load\textasciitilde WV2}}$	-0.38	-0.42	-0.32	-0.22	-12.10	15.69	41.89
$\beta_{\text{B1\textasciitilde WV2}}$	-0.45	-0.51	-0.44	-0.42	-12.72	**2.43**	**8.19**
$\beta_{\text{Bulk density\textasciitilde WV2}}$	0.07	0.14	-0.17	-0.36	95.14	-335.42	-598.61
$\beta_{\text{B2\textasciitilde WV2}}$	0.35	0.40	0.29	0.18	15.06	-17.50	-47.06
$\beta_{\text{Fine fuel load\textasciitilde C1}}$	-0.33	-0.38	-0.26	-0.16	-13.29	22.05	52.72
$\beta_{\text{B1\textasciitilde C1}}$	-0.27	-0.32	-0.15	0.00	-19.93	43.39	100.37
$\beta_{\text{Bulk density\textasciitilde C1}}$	0.24	0.29	0.12	-0.09	22.74	-51.37	-136.63
$\beta_{\text{B2\textasciitilde C1}}$	0.41	0.44	0.44	0.20	**7.58**	**7.09**	-50.61
$\beta_{\text{Fine fuel load\textasciitilde C2}}$	0.62	0.68	0.69	0.68	**8.60**	10.45	**9.65**
$\beta_{\text{B1\textasciitilde C2}}$	0.65	0.71	0.78	0.89	**9.84**	21.63	38.53
$\beta_{\text{Bulk density\textasciitilde C2}}$	-0.22	-0.31	0.02	0.36	-40.00	107.42	260.90
$\beta_{\text{B2\textasciitilde C2}}$	-0.39	-0.46	-0.42	-0.11	-18.22	**-7.52**	70.96
$\beta_{\text{B1\textasciitilde Fuel moisture}}$	-0.31	-0.37	-0.23	-0.13	-19.11	27.39	58.92
$\beta_{\text{B1\textasciitilde Heading}}$	0.39	0.45	0.32	0.13	15.05	-17.86	-67.09
$\beta_{\text{B1\textasciitilde Slope approach}}$	0.58	0.64	0.66	0.74	10.96	14.96	28.52
$\beta_{\text{B1\textasciitilde Percent slope}}$	0.08	0.08	0.08	0.09	**2.44**	**-4.88**	**3.66**
$\beta_{\text{B2\textasciitilde Fuel moisture}}$	0.33	0.40	0.30	0.24	19.46	-11.68	-29.04
$\beta_{\text{B2\textasciitilde Heading}}$	0.72	0.80	0.81	0.71	11.31	12.71	**-0.70**
$\beta_{\text{B2\textasciitilde Slope approach}}$	-0.29	-0.37	-0.15	0.17	-29.07	48.79	158.82
$\beta_{\text{B2\textasciitilde Percent slope}}$	-0.08	-0.09	-0.08	-0.06	**-7.41**	**6.17**	29.63

Almost all posterior estimates were highly influenced by the chosen priors. A deviation of more than ten percent indicates a large influence on estimates (Depaoli & van de Schoot, 2017). Deviations less than ten percent are in bold (Table 9). With the exception of B2~Bulk density, Bulk density~WV2, Bulk density~C1, Bulk density~C2, and B2~Slope approach, the directionality (positive or negative) of the parameter estimates remained consistent across alternative priors. The only parameter that maintained relatively stable effect size across all alternative priors was B1~Percent slope.

Discussion

The main goal of this study was to determine whether relative fire behavior could be predicted from the influence of woody vegetation on fuel bed trait. The relatively small indirect effects of woody vegetation on fire behavior and lack of statistical significance for relationships between woody vegetation and fuel bed traits indicate that the indirect path specified here is not a useful predictor of fire behavior. However, hardwood composition had significant direct effects on fire behavior. RoS, duff consumption, and residence time decreased significantly as mesophytic hardwood importance increased. Bulk density significantly reduced RoS and duff consumption. Fuel load did not influence fire behavior to a statistically significant degree, but all fire intensity metrics increased with greater fuel load. Fuel composition models showed similar relationships between functional groups, fuel traits, and fire behaviors, but they did not show a clear improvement in fit or explain more of the variation in fire behavior compared to woody vegetation models. The consistently stronger direct effects of woody vegetation and fuel composition on fire behavior suggest that flammability traits of leaf litter functional groups may be more important than fuel load and bulk density.

Effects of woody vegetation on fuels and fire

As sites shifted from forests with relatively closed structure and greater hardwood composition to open forest structure with greater pine importance, fuel load increased and bulk density decreased, but not to a statistically significant degree. Relative increases in pyrophytic hardwood importance also resulted in greater fuel loads, but the effect was not statistically significant and bulk density was not affected by hardwood composition.

RoS, duff consumption, and residence time all significantly increased as hardwood composition favored pyrophytic hardwoods (model 2b) despite the lack of significant relationship between hardwood composition and fuel traits. Several studies have shown mesophytic hardwood leaf litter to decompose faster than pyrophytic oaks and pines (Babl-Plauche et al., 2022; Alexander & Arthur, 2014; Melillo & Aber, 1982). Owing to this relatively faster decomposition along with often flatter, thinner, leaf morphology (Babl et al., 2020; McDaniel et al., 2021) I expected mesophytes to increase the bulk density of fuel beds as they provided leaf litter that lost rigidity and flattened into a compact fuel bed of smaller particles. There are several potential reasons why woody vegetation composition may be uncoupled from fuel bed traits. While mesophyte litter may contribute to an increase in bulk density, this effect may only be noticeable in fuel beds composed of a single species. Non-additive effects have been reported for mixed species fuel beds where the most flammable species determined the flammability of the fuel bed (de Magalhaes & Schwilk, 2012; Ellair & Platt, 2013). Kreye et al., 2018a also showed that mesophyte litter did not significantly impact flammability in fuel beds mixed with pyrophyte litter until mesophyte litter comprised two thirds of the fuel bed. This non-additive effect could also apply to bulk density where a threshold amount of pyrophytic litter could help maintain adequate aeration in the fuel bed, despite the mesophytic component.

Moreover, rapid decomposition may have dramatically reduced the abundance of mesophyte litter in the fuel bed at the time of collection, negating its effect on bulk density. Babl-Plauche et al., 2022 found that, in upland oak forests of North-central Kentucky, red maple litter lost ~40% of biomass three months after falling in early to mid-winter (November – December). Prescribed fires in the present study were conducted in February and March. To reduce complexity, woody vegetation models assumed that functional group proportions in the fuel bed would mirror woody vegetation importance, but mesophyte litter proportions were much lower than expected. The most mesophyte dominated site (B, Table 2) also had the greatest mesophyte litter proportion of all sites, but mesophyte litter only comprised 24 percent of the fuel bed, supporting the possibility of significant mass loss before collection. Although the effects were not statistically significant, fuel load trended downward as mesophytic hardwood importance and fuel composition increased, agreeing with Babl-Plauche et al., 2022 and Dickinson et al., 2016 that mesophytes reduce fire behavior through available fuel reduction.

Effects of fuel traits on fire

Despite lacking a significant link to woody vegetation, bulk density varied by site. Observed variation was possibly a function of fuel moisture at the time of measurement as damp leaves tend to lay flatter than dry ones. Bulk density significantly reduced RoS and duff consumption (models 2b and 3f), likely by restricting the amount of gas flow through the porous fuel bed (Kauf et al., 2019; Scarff & Westoby, 2006). Greater fuel loads had positive relationships with RoS, duff consumption, and residence time in agreeance with other experiments where fuel load and moisture were manipulated (Graham & McCarthy, 2006; Kreye et al., 2013); however, effects were not statistically significant. It is unclear why fuel load did not have a more pronounced effect on fire behavior considering that greater fuel loads can generate greater fire intensity relative to lesser fuel loads even as fuel moisture increases (Graham & McCarthy, 2006). It is possible that fuel load varied at finer scales than the within-plot sampling design accounted for. Spatial variability studies have shown that fuel bed traits can vary from fine scale (≈ 1-m) (Hiers et al., 2009) to medium scale (21 to 48-m) (Kennard & Outcalt, 2006). The present study aimed to summarize fuel heterogeneity in each sample site to detect variation in fuel bed traits along a gradient of woody vegetation composition and structure.

In addition to their effect on fuel load, and structure (this study), litter functional groups also influence fire behavior through distinct leaf litter flammability traits. For example, pine needles contain terpenes that increase flammability (Whelan et al., 2021; Ormeño et al., 2009), and pyrophytic hardwood litter tends to be faster drying than mesophytic litter (Kreye et al., 2013a; McDaniel et al., 2021) resulting in taller flames and more consumption (Kreye et al., 2018a). The relative importance of fuel load, structure, and flammability traits is contentious. Some work shows that leaf litter flammability controls fire behavior regardless of fuel structure (de Magalhaes & Schwilk, 2012) while others show that aerated fuel structure determines heat release regardless of litter flammability traits (Scarff & Westoby, 2006). Results presented here provide support for both mechanisms. RoS and duff consumption significantly increased with lower bulk density across fuel beds with varying litter composition, but fuel composition models showed that fire behavior was only partially mediated by fuel load and bulk density, suggesting that litter functional groups directly affect fire behavior through flammability traits as well. Specifically, an increase in pyrophytic hardwood litter significantly and positively increased RoS and duff consumption directly (models 3e and 3f). Considering the stronger direct effects of both woody vegetation and fuel composition on fire behavior compared to indirect effects through fuel load and bulk density and the lack of statistically significant effects of fuel load on fire behavior, specific litter flammability traits of different functional groups could explain the connection between the canopy and fire behavior better than fuel load and bulk density.

Another possible explanation for the weaker than expected indirect effect of woody vegetation on fire behavior is that other unexamined fuel bed components may be important. I focused on leaf litter as it is the most continuously distributed fuel in the study sites. However, other canopy derived fuels such as downed woody debris (DWD) and pinecones may play an important role. 1-hr fuels (DWD ≤ 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). Pine cones have been shown to smolder for long durations (Fonda & Varner, 2005). I did not observe pine cones in concentrated amounts, but they could represent a significant contribution to fire behavior after a masting event (Mitchell et al., 2009).

Fire Behavior and Restoration

Restoration success in the mountain longleaf and other fire dependent ecosystems depends on fire behavior. Reducing fuels and exposing mineral soil, increasing light to the understory to encourage fire adapted vegetation, and controlling competition all benefit longleaf pines and the associated fire dependent community and results vary with fire behavior (Mitchell et al., 2009). Inadequate fire intensity might fail to achieve these goals, and excessive fire intensity can bring undesired results such as soil damage (Nelson et al., 2022) and longleaf pine mortality (Varner et al., 2005). Understanding the drivers of fire behavior is necessary to maximize desired results and avoid unintentional damage.

Results of this study showed that fire behavior was also affected by fuel moisture and the direction of fire travel in relation to wind and topography. Intuitively, head fires increased RoS (not statistically significant) and decreased residence time (statistically significant), as head fires move quicker, reducing the amount of time the heat of the flame front remains in one location. This result supports the idea that faster spreading head fires may be useful when the intent is to consume dry fuels but reduce residence time and soil heating which can negatively impact vegetation regeneration (Gagnon et al., 2015). Interestingly, head fires reduced residence time even though duff consumption increased (consumption was positively correlated with RoS). Duff consumption has been implicated in longleaf pine mortality through long smoldering durations around mature tree boles with accumulated duff from periods of fire exclusion (Varner et al., 2005). Duff consumption and therefore mortality was reduced when duff had greater moisture content (Varner et al., 2007). Here, fuel moisture did not significantly reduce duff consumption, but did negatively relate to it, along with RoS and residence time. Thus, it is possible that, as with soil heating, residence time is part of the causal mechanism and smoldering duff may be avoidable with shorter residence times facilitated by either increased moisture or fast-moving head fires. However, increased moisture is likely safer considering the positive correlation between RoS and duff consumption. These contradictory results highlight the need for more research on the relationships between different fire behaviors.

Neither fire heading nor RoS are typically considered as predictors of fuel consumption. However, I used them as metrics of fire intensity with the hope that prescribed fire practitioners would find them relatively easy to visually estimate and helpful for better understanding their relationships with other fire behaviors. Similar fine fuel reduction has been reported for head and backing fires (Clark et al., 2020), but further research seems necessary given the findings presented here. The present study treated fuel consumption as a fire behavior though it is technically a fire effect, i.e., a result of fire behavior. Future work would benefit from direct investigation of the relationships between fire behavior and fuel consumption considering the apparent relationship with residence time and RoS.

Interestingly, RoS and residence time both increased with greater fuel load and lower bulk density reflecting greater fire intensity, but only RoS increased with head fires suggesting that fuel load and structure may exert more control over surface heating intensity. In other words, head fires could be fast moving due to wind, but variable in temperature, while greater fuel loads could cause faster RoS due to high temperatures generated from larger releases of combustion energy and result in longer heating durations.

Counter to expectations, percent slope had no effect on fire behavior. Slope steepness is considered an important variable for fire behavior and its impact is well supported by several studies showing RoS to increase with steeper upward slope (Butler et al., 2007; Morandini et al., 2018). It is less clear how sloped terrain influences fuel consumption and residence time, but I expected to see a positive effect due to changes in angle between flame and fuels as seen with slope approach where RoS, duff consumption (statistically significant), and residence time (not statistically significant) all increased when fire approached from downslope, likely from the pre-heating of upslope fuels (Butler et al., 2007). These models (4a and 4b) explained similar amounts of variation in fire behavior as woody vegetation and fuel composition models.

Effects of weather on fire behavior

Warmer, drier weather significantly increased RoS, duff consumption (model 3f), and residence time (models 2c and 2d). The effect of weather on fire behavior was similar to the total effect of woody vegetation and weaker than that of fuel composition. However, fire behavior may respond differently during growing season burns when canopy foliage is present and variation in microclimate between sites is likely much greater due to woody vegetation composition and structure.

Fire behavior in different ecoregions

Typical fire behavior varies across the southeastern U.S. with diverse topography and plant communities, even within the longleaf pine ecosystem. Much research has been conducted in the coastal plains, but this is the first study I am aware of to document fire behavior in the mountain longleaf ecoregion. Fire temperatures and residence times in the mountain longleaf sites examined here were intermediate compared to dormant season results from pine-oak-hickory forests of the southern Blue Ridge (Vaughan et al., 2021) and coastal plain longleaf communities of Florida (Menges et al., 2021). Relative to results reported here, fires in the southern Blue Ridge were much cooler, only averaging approximately 200 °C while the coastal plain fires were substantially hotter averaging 600 °C. Mean residence times were two minutes shorter in the southern Blue Ridge and two minutes longer in the coastal plains. Vaughan et al., 2021 also reported zero duff consumption in the Blue Ridge. To my knowledge, few studies have examined duff consumption as a response to fire behavior. As discussed earlier, duff consumption is a serious challenge when reintroducing fire after prolonged exclusion and should be further researched in relation to fire behavior and management objectives. Another coastal plain longleaf site in Alabama had cooler temperatures (177 °C), shorter residence times (4.3 minutes), and comparable spread rates (0.88 m min^{-1}) on average (Kennard & Outcalt, 2006), highlighting the diversity of possible fire behavior even within similar ecoregions.

Limitations

A sensitivity analysis of posterior estimates revealed that the model results were sensitive to priors which could be a consequence of small sample size (Depaoli & van de Schoot, 2017). Small sample size may also explain the wide credible intervals seen for all posterior estimates. Though Bayesian analysis does not rely on large sample sizes like the frequentist approach, expanding the size of this study could provide more robust results and clarify the validity of the theory-driven priors. Despite the limited sample size, R^2 values indicate that models explained non-trivial amounts of variation in observed fire behavior. A larger scale study could also allow for a more comprehensive model that could improve this further by including the various vegetation, fuels, weather, and topography variables for direct comparison of effects on fire behaviors and a clearer understanding of the mechanisms driving said fire behaviors. Due to the wide credible intervals that often included zero for many posterior estimates, I cannot be certain that those posterior estimates were reliable. Many parameters had credible intervals that included zero, suggesting that the coefficients were not statistically significant. However, in cases where zero was close to the edge of the interval, the credible interval still provides confidence that the directionality (positive or negative) of the parameter matched the prior expectation. The posterior estimates from this study can also be used as priors in future studies to further update understanding about the relationships in question. In this study, basal area was negatively correlated with pine importance because sample sites were chosen to represent a gradient of stand quality, i.e., open pine dominated or closed hardwood dominated. However, open stands dominated by pyrophytic oaks and closed stands dominated by pines (loblolly) can exist in MLLP systems as well. Therefore, in future analysis, basal area should be treated as a separate variable to distinguish its effect on fuels from that of composition. Additionally, this study compared the importance of pyrophytic hardwoods to mesophytic hardwoods (Table 6), but the relative importance of all three functional groups is interdependent. Thus, a direct comparison between pines and the hardwood functional groups would also be beneficial to quantify how they influence fire behavior differently and avoid a confounding effect. Ground layer vegetation was not observed in appreciable quantities, possibly because the restoration gradient did not include any fully restored sites where grasses and forbs can serve as important fuels. Relationships detected here may be stronger in future studies that sample a wider restoration gradient that includes sites with substantial ground layer vegetation. Lastly, non-linear relationships should be investigated, as suggested by the potentially non-additive effects of mesophytic litter.

Conclusion

This study is a preliminary exploration of in-situ fire behavior in the very important and understudied mountain longleaf pine ecoregion. The evidence reinforces that woody vegetation functional groups differentially contribute to the fuel bed, thereby influencing fire behavior. However, significant uncertainty remains concerning the indirect link between woody vegetation and fire behavior, highlighting the complex nature of these interactions. Although a clear mechanism of mesophication was not identified, this study corroborated that mesophyte encroachment on fire prone landscapes reduces the flammability of the environment. Notably, mesophytes seem to inhibit fire even when they contribute relatively little to overall stand and fuel composition, therefore removal and control of mesophytes should be a priority in restoring fire dependent ecosystems. The timing of prescribed burns could also be adjusted to account for mesophytes. For example, if total fuel 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.

Additionally, this study showed that pyrophytic hardwoods in the MLLP ecoregion are not only fire tolerant, but fire promoting. Some studies have shown that pyrophytic oaks facilitate longleaf recruitment by creating refugia of lower fire intensity in the sandhill LLP communities (Johnson et al., 2021; Magee et al., 2022). However, pyrophytic hardwoods in the MLLP sites observed here significantly increased metrics of fire intensity indicating their unique and important contribution to the MLLP ecoregion. Pine importance in the canopy and in the litter layer consistently related positively to fire promoting fuel traits and greater fire intensity, but effects were not statistically significant, and therefore played an unexpectedly limited role. This work also provided insight about the contending hypotheses of how fuels influence fire. This experiment suggests that both fuel bed composition and fuel bed structure (load and bulk density) influence fire behavior. However, while fuel composition drives fuel bed structure, thereby indirectly influencing fire, the direct effects of fuel composition appear to be more influential. 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 sites where fire is uniformly initiated under specific conditions (timing, direction, etc.), as opposed to sites being burned as part of a larger burn unit.

Greater RoS, residence time, and fuel consumption are not always the desired fire behaviors for restoration of longleaf pine ecosystems. In fact, these fire behaviors have potential detrimental effects as noted earlier regarding longleaf pine mortality. Faster, hotter fires that consume more fuel indicate a more flammable fuel bed which should benefit fire adapted vegetation in the LLP ecosystem that evolved with a frequent low intensity fire regime. The opposite fire behaviors generally indicate a less flammable environment related to mesophytic encroachment as demonstrated here. These fire variables were chosen for their potential relationships with important ecosystem responses such as vegetation mortality and regeneration (Gagnon et al., 2015; Magee et al., 2022; Varner et al., 2007) and their relative ease of estimation in the field to improve understanding of ecosystem responses in relation to fire behavior. However, this experiment suggests that a better determination of the relationships among drivers of fire behavior will be important for specific ecosystem outcomes and predictions to occur.

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Supplementary Information

Table S1: Model fit indices for models 1a to 4b. PPP = posterior predictive p-value, BRMSEA = Bayesian root mean square error of approximation, CI = credibility interval.

Model	PPP	Adj Bgammahat	BRMSEA	BRMSEA lower 90% CI	BRMSEA upper 90% CI
1a	0.653	0.974	0.023	0.000	0.109
1b	0.627	0.975	0.022	0.000	0.104
1c	0.64	0.968	0.026	0.000	0.122
1d	0.535	0.950	0.043	0.000	0.188
2a	0.725	0.989	0.010	0.000	0.000
2b	0.575	0.966	0.030	0.000	0.147
2c	0.669	0.978	0.019	0.000	0.082
2d	0.507	0.935	0.054	0.000	0.214
3a	0.729	0.985	0.014	0.000	0.000
3b	0.498	0.950	0.044	0.000	0.187
3c	0.58	0.966	0.030	0.000	0.145
3d	0.213	0.774	0.173	0.000	0.324
3e	0.563	0.973	0.026	0.000	0.120
3f	0.38	0.901	0.079	0.000	0.252
3g	0.66	0.985	0.015	0.000	0.000
3h	0.419	0.937	0.056	0.000	0.204
4a	0.603	0.999	0.001	0.000	0.000
4b	0.542	0.999	0.001	0.000	0.000

Table S2: Comparisons of marginal log likelihoods between 1.) woody vegetation models (1a-2d) with and without a direct pathway between woody vegetation traits (WV) and fire behaviors (B), 2.) with air temperature and relative humidity (W1) or fuel moisture, and 3.) between woody vegetation models and fuel composition models (3a-3h). The Marginal log likelihood ratio compares model fit and is assessed using the rule of thumb suggested by (Jeffreys, 1961).

Model	With direct path $_{(B\sim WV)}$	Without direct path $_{(B\sim WV)}$	Marginal log likelihood ratio
1a	-39.473	-38.325	1.030
1b	-40.351	-39.266	1.028
1c	-36.633	-35.846	1.022
1d	-37.975	-37.619	1.009
2a	-37.925	-37.52	1.011
2b	-38.82	-39.724	0.977
2c	-35.77	-35.069	1.020
2d	-37.692	-37.992	0.992
	W1	**Fuel moisture**	
1a	-39.473	-38.559	1.024
1b	-40.351	-39.765	1.015
1c	-36.633	-37.36	0.981
1d	-37.975	-39.155	0.970
2a	-37.925	-37.622	1.008
2b	-38.82	-39.852	0.974
2c	-35.77	-36.797	0.972
2d	-37.692	-39.579	0.952
	Woody vegetation	**Fuel composition**	
1a/3a	-39.473	-39.433	1.001
1b/3b	-40.351	-40.012	1.008
1c/3c	-36.633	-37.072	0.988
1d/3d	-37.975	-38.411	0.989
2a/3e	-37.925	-35.209	1.077
2b/3f	-38.82	-36.35	1.068
2c/3g	-35.77	-35.696	1.002
2d/3h	-37.692	-38.675	0.975