



Frequent fire slows microbial decomposition of newly deposited fine fuels in a pyrophilic ecosystem

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Abstract

Frequent fires maintain nearly 50% of terrestrial ecosystems, and drive ecosystem changes that govern future fires. Since fires are dependent on available plant or fine fuels, ecosystem processes that alter fine fuel loads like microbial decomposition are particularly important and could modify future fires. We hypothesized that variation in short-term fire history would influence fuel dynamics in such ecosystems. We predicted that frequent fires within a short-time period would slow microbial decomposition of new fine fuels. We expected that fire effects would differ based on dominant substrates and that fire history would also alter soil nutrient availability, indirectly slowing decomposition. We measured decomposition of newly deposited fine fuels in a Longleaf pine savanna, comparing plots that burned 0, 1, 2, or 3 times between 2014 and 2016, and which were located in either close proximity to or away from overstory pines (Longleaf pine, *Pinus palustris*). Microbial decomposition was slower in plots near longleaf pines and, as the numbers of fires increased, decomposition slowed. We then used structural equation modeling to assess pathways for these effects (number of fires, 2016 fuel/fire characteristics, and soil chemistry). Increased fire frequency was directly associated with decreased microbial decomposition. While increased fires decreased nutrient availability, changes in nutrients were not associated with decomposition. Our findings indicate that increasing numbers of fires over short-time intervals can slow microbial decomposition of newly deposited fine fuels. This could favor fine fuel accumulation and drive positive feedbacks on future fires.

Keywords Fire–microbe interactions · Decomposition · Microbial ecology · Pine savanna · Short-term fire history

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Introduction

Fire is a consistent disturbance in terrestrial ecosystems that profoundly changes biological and biogeochemical processes. Although often thought of as rare, catastrophic events (Bowman et al. 2009), frequent fires are necessary to maintain nearly 50% of terrestrial ecosystems including grasslands, savannas, and many Mediterranean-type ecosystems (Archibald et al. 2018). Since wildfire frequency is expected to increase due to human influence (Balch et al. 2017) and climate change (Liu and Wimberly 2016; Schoenagel et al. 2017), understanding how ecosystems respond to frequent fire is important for their preservation and maintenance. While directly manipulating aspects of fire regime is impossible in many systems, prescribed fire in naturally fire-frequented ecosystems may represent a conservative model to predict the pathways through which increased fire frequencies can impact systems that otherwise rarely experience fire.

Frequent fires in grasslands and savannas alter organisms and their environment in ways that can impact subsequent fires. The fine fuels produced by fire-adapted plants (i.e., their litter) are key examples, as frequent fires favor plant species that rapidly recover following fire and produce biomass that fuels future fires (Whitlock et al. 2003; Beckage et al. 2009; Cornelissen et al. 2017). By favoring fire-adapted plant species, characteristics of previous fires can create a feedback, through the rapid production of fine fuels that control the spread and intensity of new fires (i.e., short-term fire history; Neary et al. 1999, Ficken and Wright 2017). Fine fuel accumulation, however, is also governed by processes like microbial decomposition, which may also produce feedbacks based on fire history (Butler et al. 2019). Quantifying the pathways by which fire history impacts decomposition is critical for the maintenance of fire-frequented ecosystems and predicting potential mechanisms by which frequent fires impact other systems.

Repeated fires directly govern microbial decomposition by altering fine fuel loads and shaping the microbial communities that control fuel decay. The strength of fire's effect on decomposition is constrained by fire regime components like fire history, which can determine the quantity of available fine fuels and the intensity of future fires. For example, longer fire return intervals result in increased fuel loads (Archibald et al. 2013; Harris et al. 2016) and longer recovery times for microbes, while shorter fire return intervals, or frequent fires, can decrease plant fuel loads and microbial recovery times due to repeated combustion (Platt et al. 2016). When combined with natural variations in fuel load production (i.e., tree-grassland matrices of savannas; Platt et al. 2016), this can produce fires of varying frequencies and intensities that drive differential mortality of microbial decomposers and slow decomposition depending on location. Since fire can cause the mortality of microbial decomposers and filter communities for particular functional groups (Dooley and Treseder 2012; Ferrenberg et al. 2013; Brown et al. 2013), understanding how fire history and intensity alters microbial decomposition can clarify the dynamics of fire–microbe–plant interactions in pyrophilic ecosystems. If microbial decomposition is strongly altered by fire, this could directly shift new fine fuel accumulation rates and affect the intensity and likelihood of future fires.

Fire regimes also influence the substrates and nutrients available for microbial decomposition, which may create indirect pathways for fire feedbacks. Fine fuel traits (e.g., carbon-to-nitrogen ratio and lignin content) directly govern decomposition (Manzoni et al. 2010), and also determine the duration and intensity of fires (Demirbaş 2001). For example, the larger quantities of needles near longleaf pines can increase local fire intensities (Platt et al. 2016), and are also harder to decompose than grass and forb litter. As such, fire histories that change the composition of new fine fuels may

change both the substrates available to microbial decomposers, and fire's direct effects on them. Fire history can also govern stoichiometry through fire effects on limiting nutrients like nitrogen (N) and phosphorus (P) (Raison 1979; Butler et al. 2018). Rapid post-fire decomposition may be favored by N and P mineralization if enzyme production and microbial growth would be, otherwise, limited. Longer intervals between fires can allow fuels to build up, and increase fire intensity to the point where temperature-sensitive elements like N are volatilized (Raison 1979). N availability then may vary with fire due to interactions between fire history and intensity (i.e., maximum temperature and duration). Low N availability may a) slow decomposition if N-limited microbes cannot make enzymes or b) accelerate decomposition if microbes can make enzymes, and rapidly decompose new fuels to acquire N and other limiting nutrients lost with fire (Parnas 1975). Apart from individual fire intensity, repeated fires decrease nutrient availability (Bell and Binkley 1989) and drive leaching that could slow microbial decomposition.

These combined effects of short-term fire history on substrates and nutrients likely combine with direct fire effects to determine microbial decomposition of fuels. While single fires can slow decomposition and promote fuel accumulation (Semenova-Nelsen et al. 2019), increasing the number of fires within a short period could produce synergistic effects that further slow decomposition. These effects could result from both the direct and indirect effects of fire on microbial decomposition mentioned above. We hypothesized that increasingly frequent fires would slow decomposition, and that fire would impact decomposition through mechanisms related to fire characteristics and nutrient availability. We also hypothesized that natural variations in the type and quantity of fine fuels would slow decomposition independently of fire history due to substrate differences (Taylor et al. 1989).

We manipulated short-term fire history in an old-growth Longleaf pine savanna to evaluate the effect of fire history on the microbial decomposition of fine fuels. Pine savannas offer ideal systems for testing our hypotheses, because: organisms there have long co-evolutionary histories with fire (Noss et al. 2015), fire history can be experimentally manipulated, and the spatial heterogeneity of the savanna produces variation in dominant vegetation and the fuels that microbes decompose. We used mesh litter bags to measure microbial decomposition of new, post-fire fine fuels. Decomposition was assessed both near and away from pines, to reflect differences in fine fuel substrates (Ellair and Platt 2013; Platt et al. 2016) and microbial communities (Semenova-Nelsen et al. 2019). We first assessed the impact of fire history and pine proximity on microbial decomposition rate constants (k) during the year following 2016 fires. We then used structural equation

modeling (SEM) to assess the relative importance of direct and indirect mechanisms on decomposition following prescribed fires. Fire history, edaphic properties, fire characteristics, and fine fuel traits in 2016 were all analyzed as potential drivers of microbial decomposition. The resulting SEM model allowed us to identify the primary pathways through which fire history altered microbial decomposition of fine fuels.

Methods

Field site

We conducted our study on the Wade Tract (30° 45' N; 84° 00' W; Thomas County, Georgia, USA). Situated on moderately dissected terrain 25–50 m above sea level in the Red Hills region of northern Florida–southern Georgia, the 80 ha preserve is characterized by a warm-temperature climate, with a growing season of 10–11 months, a mean annual temperature of 19.6 °C, and average precipitation of ca. 1,350 mm that tends to bimodally distributed during the summer and winter months. Surficial soils are acidic, fine-textured sands with A horizons 50–100 cm deep over a clay hardpan (Typic and Arenic Kandiuults; Carr et al. 2009; Levi et al. 2010). Natural fires in this site tended to occur every 1–3 years, generally during a fire season that spanned dry springs-to-wet summers, when annual thunderstorms first occurred (Platt et al. 2015; Rother et al. 2018). Historical “open-woods burning” and more recently prescribed fires have maintained the open savanna/woodland physiognomy (Platt et al. 1988; Gilliam and Platt 1999; Mugnani et al. 2019). The ground layer vegetation and litter on the site has burned annually–biennially (return intervals averaging 1.5 years) during prescribed fires between March and June using drip torches, 1–2 weeks after rain at relative humidity of 50–60% and winds 10–20 km/h. Flame heights during burns can reach

1–2 m, and generally result in 60–90% removal of accumulated fine fuels.

Field plots

We established experimental plots in mid-June 2014, following 2014 prescribed fires. These fires produced large unburned patches in a matrix of burned vegetation. We randomly selected 24 unburned patches, 12 in each of two fire management units. Within each fire management unit, 6 patches were near (< 5 m) and 6 patches were away (> 10 m) from overstory pines. We then randomly selected 24 similar sized burned patches (12 near pines and 12 away from pines), such that each burned plot was near an unburned patch. Thus, 24 unburned and 24 burned patches were evenly distributed across two fire blocks and relative to overstory pines (Table 1). Each patch was at least 5 m in diameter to minimize fire-edge effects, and did not contain large amounts of woody debris such as fallen trees or large branches. Within each patch, we established randomly located, 1 × 1 m sampling plots for downstream measurements. Note that these plots were same as used in Semenova-Nelsen et al. 2019. This allowed us to test both the effects of increased fire frequency, as well as the presence/absence of fire on microbial decomposition.

Short-term fire regimes

We generated differences in short-term fire histories (2014–2016) by manipulating fire regimes. The different fire histories are depicted in Table 1. In 2014, unburned and burned plots were selected based on patchiness of prescribed fires conducted that year. In 2015, we manipulated prescribed fires by burning only one fire block, so that half of the experimental plots burned. Then, in 2016, all plots burned during prescribed fires. We thus generated replicated plots with patterns of 1, 2, and 3 fires; six plots with each fire history were located near and away from pines. Following the 2016 fires, we used fire maps to identify patches that did not burn in 2014, 2015, or 2016; we randomly selected

Table 1 Experimental field design for short-term fire history treatments (2014–2016) in plots located near and away from pines

	Near pines					Away from pines				
Short-term fire history										
2014	1	1	0	0	0	1	1	0	0	0
2015	1	0	1	0	0	1	0	1	0	0
2016	1	1	1	1	0*	1	1	1	1	0*
Number of plots	6	6	6	6	6	6	6	6	6	6
Number of fires	3	2	2	1	0	3	2	2	1	0

For each year, 1 indicates groups of plots that were burned and 0 indicates groups of plots that were not burned. The design produced five short-term fire history treatments that involved 0–3 fires, both near and away from pines. Of the total of 60 plots, 48 were established in 2014. Fire maps were used to establish an additional 12 plots (marked with *) in 2016 that did not burn in the 3 previous years

12 of these patches, 6 near pines, and 6 away from pines, and established an additional plot in each. This generated a total of five short-term fire histories that involved 0 (0–0–0), 1 (0–0–1), 2 (1–0–1, 0–1–1), and 3 (1–1–1) fires over the 3-year study period (Table 1).

We conducted prescribed fires similarly from 2014 to 2016. All were ignited and occurred under similar conditions. In all three years, head and flanking fires were ignited in the two fire management units between mid-March and early May under Keetch–Byram Drought Indices of 60–250 using drip torches. Fine fuel consumption in burned patches was estimated each year as 60–80%. Because fires were conducted under similar weather conditions and times of the year, short-term fire histories in Table 1 were considered to differ mainly in the numbers of fires.

In 2016, we explored fuel–fire relationships and measured characteristics of fires in the plots. First, we measured fine fuels, pre- and post-fire, in the 48 plots using procedures outlined in Platt et al. (2016). We established pairs of 30 × 30 cm subplots adjacent to each of the 1 m² plots. For each plot, we randomly selected one subplot and collected above ground fuels 1–2 days prior to fires, and then sorted those fuels into fine fuels using two categories: pine needles and non-pine fuels (graminoid, forb, shrub, and other non-woody fuels). Additionally, we recorded the total amount of fine fuels and proportion of fuel loads that were Longleaf pine needles. The fine fuels were air-dried and weighed. One day after 2016 fires, we collected the fine fuels from the other subplot. Remaining fine fuels were weighed to estimate fine fuel combustion. Average mass of woody fuels in plots was similar before and after fires, so we did not examine woody fuel effects on fire characteristics.

We assessed fire characteristics using temperatures recorded at the surface and in the soil during the prescribed fires. We placed two thermocouples in the center of each plot. One was placed 2–3 mm above the ground surface, not contacting litter or soil; the second was placed 1 cm in the soil, close to the surface thermocouple. Thermocouples recorded temperatures every second from the time of activation until 5–6 h after prescribed fires. The temperature data were used to estimate (1) *maximum surface & soil temperature increase*—the largest instantaneous rise in temperature recorded and (2) *duration of heating*—the time (in seconds) that the temperature at the soil surface remained > 60 °C (Platt et al. 2016).

Quantifying microbial decomposition

We measured microbial decomposition of recently deposited litter experimentally in 2016. In October 2015, we collected recently deposited, intact plant material (dead pine needles, grass culms, forbs, and oak leaves) from outside the 4 m² sample plots. Litter collected from patches of the same type

(i.e., near and away from pines) was pooled and then shipped to the University of Kansas where it was stored at – 20 °C until processing. Near and away litter was kept separate to account for inherent differences in litter chemistry (i.e., C:N ratios and lignin content) and composition (i.e., more pine needles near pines) between litter types. Plant litter was dried at 65 °C for 72 h, ground using a Model 4 Wiley Mill (Thomas Scientific, Swedesboro, USA) with a 6 mm opening, and sterilized via gamma irradiation to ~ 32 kGy at the Penn State Radiation Science & Engineering Center. Within a biological safety cabinet, we placed the sterilized plant litter in 15 × 15 cm, 30 μm nylon mesh bags, following (Robertson and Paul 2000). This mesh excludes non-microbes and isolates microbial decomposition of plant litter (Bradford et al. 2002). Each bag was filled with 5 g of plant litter collected either near or away from pines. Initial bag masses were recorded, and bags were stored sterilely until deployment.

Bags were deployed in June 2016, 2–3 months after experimental fires. Four decomposition bags with litter corresponding to pine proximity (i.e., near or away from pines) were selected and randomly placed on the soil surface in each plot. The small mesh size used in bag construction prevented photodegradation of bag contents. Bags were anchored along margins with sod staples, so that one surface of the bag contacted litter and soil. One bag from each plot was collected 2, 4, 6, and 8 months after deployment. Any soil or litter on the bag surface was cleared, and then, bags were placed in sterile plastic bags. Bags were shipped overnight to the University of Kansas. Litter contents were then removed, dried at 65 °C for 72 h, and weighed to determine mass loss. Decomposition rate constants (*k*) were determined by fitting decomposition from 2 to 8 months in each experimental plot to a negative exponential curve using the following equation:

$$\frac{M_t}{M_0} = e^{-k*t},$$

where the M_0 is the starting mass, M_t is the mass at time of collection, and t is the number of months which the bag was deployed in the field. A negative exponential curve was used to estimate k , as decomposition is well known to follow an exponential decay function when measured over time (Olson 1963; Karberg et al. 2008). This produced a decomposition rate constant (k) for each experimental plot during the year following 2016 prescribed fires.

Soil analysis

Soil samples were collected from all plots in June 2016 to measure post-fire nutrient pools. We collected soil at three randomly located points, avoiding ground layer plants. We

collected the upper 1.5 cm of soil within a 9×9 cm quadrat (i.e., the depth potentially affected by increasing fire temperatures; Mehlich 1984; Gagnon et al. 2015). Soil samples from each plot were combined, and kept cool until frozen at -20 °C within 6 h of sampling. Samples were overnighted to the University of Kansas, thawed, and homogenized by hand, before subsampling.

A 100 g subsample was sent to the Kansas State University Soil Testing Lab for analysis. Soil phosphorus was measured using the Mehlich-3 method (Mehlich 1984) on a Lachat Quickchem 8000 (Lachat Instruments, Loveland, USA). Total soil nitrogen and carbon were measured on an LECO TruSpec CN Carbon/Nitrogen combustion analyzer (LECO Corporation, St. Joseph, USA). Carbon-to-nitrogen ratio was also calculated. NH_4^+ and NO_3^- were extracted using 2 M KCl on 2 g of soil, and then, cadmium reduction for nitrate and colorimetric procedures were used, followed by flow analysis for ion quantification (Brown 1998).

Data Analysis

All analyses were conducted in R version 3.5.1 (R Core Team 2020). Analyses of variance (ANOVAs) assessed the effect of short-term fire history and proximity to pines on microbial decomposition rate constants (k). Differences in decomposition, fine fuels, nutrients, and fire characteristics between short-term fire history and pine proximity

treatments were first assessed using Type III analysis of variance (ANOVA) using the “Emmeans” package (Lenth 2018). Note that pine proximity treatments were considered in these analyses to account for inherent differences in litter chemistry, fuel traits, and flammability, between near pines fuels vs. away from pines fuels. Following ANOVAs, a priori contrasts regarding differences in decomposition based on the frequency of fires were assessed using the contrast function.

We then developed a structural equation model to assess the causal pathways by which fires impacted plot-level microbial decomposition rate constants (k). Based on existing literature, we hypothesized three specific pathways between fire history and microbial decomposition (Fig. 1). These pathways included both direct fire history effects and indirect effects through 2016 fire characteristics and initial changes to soil properties. Appendix Tables S1 and S1.5 describe variables and justifications for model pathways included in the SEM analysis. We also hypothesized that fuel characteristics play an independent role in determining both fire characteristics and decomposition. We hypothesized that frequent fires would (1) reduce microbial decomposition rates (Fig. 1; Path A; Ficken and Wright 2017), (2) reduce the severity of individual fires, thereby increasing decomposition rates (Fig. 1; Path B; Ficken and Wright 2017; Ellair and Platt 2013, and (3) modify the initial flux of nutrients mineralized by fire and slow decomposition (Fig. 1; Path C;

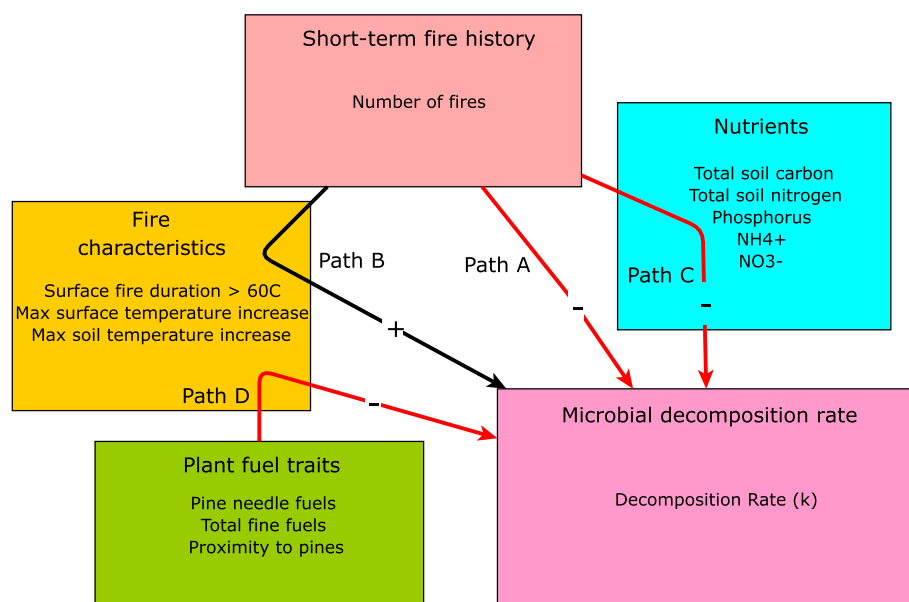


Fig. 1 Hypothesized pathways by which short-term fire history modifies microbial decomposition of fine fuels. Fire history shown in light red, nutrients in blue, fire characteristics in orange, fuel traits in green, and decomposition in pink. Path A: increasing recurrence of fire should slow decomposition through repeated negative effects on microbes. Path B: frequent fires should lessen fire severity char-

acteristics and the negative effect of fire on decomposition. Path C: frequent fires alter nutrient availability, which could lead to nutrient loss and slow decomposition. Path D: distinct from fires, increasing amounts of fine fuels should increase fire severity characteristics and slow decomposition. Citations for hypothesized pathways are detailed in Table S1.5

Bell and Binkley 1989; Czimczik et al. 2005; Butler et al. 2018). Distinct from short-term fire history effects, locational effects due to larger fine fuel loads and larger amounts of pine needles near pines should (4) increase fire intensity and slow decomposition (Fig. 1; Path D; Ellair and Platt 2013). Our SEM contained categorical, continuous, and ratio variables. All continuous variables were transformed and scaled prior to analysis (Appendix Table S1). After developing an initial model based on these hypotheses, the R Package: “lavaan” (Rosseel 2012) was used to evaluate the preliminary SEM for convergence. Upon convergence, fit measures and parsimony were used to assess the modification of model parameters. Further models were then evaluated per Hooper et al. (2008).

Results

Fine fuels

Pre-fire fine fuel loads varied based on proximity to over-story longleaf pines and short-term fire history treatment. The largest differences were between pine needle fuels, with near pines sites having larger amounts ($F_{1,59} = 33.4$, $p < 0.001$; Table S2, Fig. S1) and proportions ($F_{1,59} = 22.3$, $p < 0.001$; Table S2, Fig. S1) of Longleaf pine needles. Total fine fuels ($F_{4,59} = 7.34$, $p < 0.001$; Table S2, Fig. S1) and non-pine fuels ($F_{4,59} = 7.37$, $p < 0.001$; Table S2, Fig. S1) also differed between short-term fire history treatments, with sites experiencing two fires in the final 2 years having lower amounts of both. In summary, near pines sites had larger amounts of Longleaf pine needles, and more frequently burned sites had smaller fine fuel loads and amounts of non-pine fuels.

Soil nutrients

Post-fire nutrients levels varied based on the short-term fire history. As the number of fires increased, total soil nitrogen ($F_{4,59} = 5.17$, $p = 0.001$; Table S3, Fig. S2), inorganic phosphorus ($F_{4,60} = 4.49$, $p = 0.003$; Table S3, Fig. S2), ammonium ($F_{4,60} = 10.6$, $p < 0.001$; Table S3, Fig. S2), and nitrate ($F_{4,60} = 3.39$, $p = 0.02$; Table S3, Fig. S2) levels decreased. While nitrate levels decreased when there were two fires in the final two years, it is worth noting that sites burned in only the final year (0_0_1) or the first and final year (1_0_1) actually saw an increase in nitrate levels. Total soil carbon, however, did not vary between experimental treatments ($F_{4,60} = 1.02$, $p = 0.4$; Table S3, Fig. S2). While soil carbon did not vary between short-term fire history treatments in this analysis, C:N ratios increased as fires became more frequent ($F_{4,60} = 10.4$, $p < 0.001$; Table S3, Fig. S2). Frequent fires were associated with lower amounts of soil nutrients,

and changed nutrient levels in ways that shifted stoichiometric ratios of carbon and nitrogen.

Fire characteristics

2016 prescribed burn characteristics differed between short-term fire history treatments; however, these differences were primarily related to the presence or absence of fire. While there was some natural variation between maximum surface ($F_{4,51} = 105.1$, $p < 0.001$; Table S4, Fig. S3) and soil temperature ($F_{4,51} = 3.75$, $p = 0.009$; Table S4, Fig. S3) increases, surface fire duration > 60 °C ($F_{4,51} = 25.3$, $p < 0.001$; Table S4, Fig. S3), and percent fine fuel combustion ($F_{4,51} = 72.6$, $p < 0.001$; Table S4, Fig. S3), between burned sites, prescribed fires generally did not vary in intensity between our experimental treatments.

Microbial decomposition

Short-term fire history and pine proximity independently affected microbial decomposition rate. As fires increased in frequency, decomposition rates decreased ($F_{4,48} = 3.971$, $p = 0.007$; Table S5, Fig. 2a and S4) with contrasts, revealing that burning at least once during the 3-year period was associated with slower decomposition than not burning ($p = 0.01$; Table S5). Additionally, decomposition rates were lower in sites that burned at least two times as compared to sites that only burned once ($p = 0.009$; Table S5). There were no overall differences in decomposition rates between sites that burned two times and sites that burned three times ($p = 0.4$; Table S5).

Proximity to pines also altered microbial decomposition. During the year following 2016 prescribed fires, litter bags located near pines had slower decomposition rates than bags placed away from pines ($F_{1,48} = 3.921$, $p = 0.05$; Table S5, Fig. 2b). In summary, increasing the number of fires during the study period and close proximity to pines slowed microbial decomposition.

Structural equation modeling of causal pathways for fire history effects

We initially began with a highly saturated SEM based on our hypothesized pathways (Appendix; Table S1.5 and SEM model fitting section). The first model converged, but was poorly supported ($X^2 = 102.392$, $DF = 28$, $p < 0.00$). Through four iterations, poorly supported paths in the model were successively pruned to improve model fit using an increasingly conservative threshold for relationships (e.g., $p > 0.5$, $p > 0.2$). Model support was checked after each pruning step (support for each included in Appendix Table S6) with fit statistics assessed according to Hooper et al. (2008). The final model was well supported ($X^2 = 21.795$, $DF = 23$,

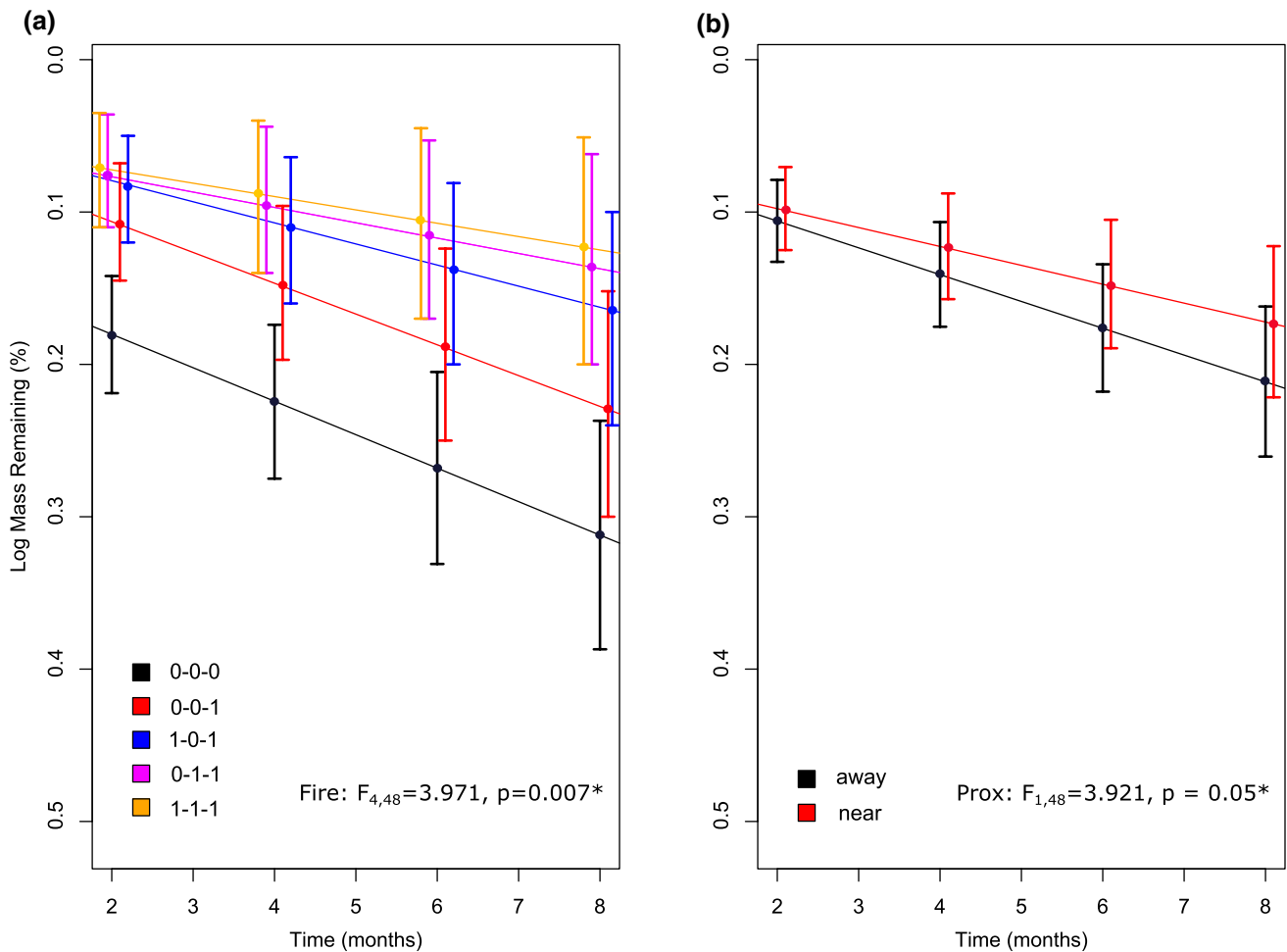


Fig. 2 Short-term fire history and pines proximity effects on microbial decomposition. Trend lines represent microbial decomposition rate constants (k) calculated by fitting decomposition measurements in each plot to a negative exponential decay function. Error bars and points represent 95% confidence intervals and means for microbial decomposition rate constants (k). ANOVA results are annotated in

the figures, fire=fire history and prox=pine proximity. (a) As fires became more frequent, decomposition rate constants (k) were lower, and larger amounts of plant fuels remained at the end of the experiment. (b) Experimental sites located near pines had lower decomposition rate constants (k) than sites located away from pines. Note that $*p \leq 0.05$

$p=0.533$; Table 2), and further removal of unsupported pathways did not improve overall fit. Final SEM pathways and coefficients along with literature support for these pathways are presented in Table 2.

SEM results

The final SEM model supported our hypotheses that short-term fire history altered the microbial decomposition of fine fuels. We used our initial hypotheses (Fig. 1) to construct pathways for relationships in our SEM model (Fig. 3). In this way, we could distinguish the underlying mechanisms through which fire history was postulated to modify microbial decomposition in the final model. Numbers in parentheses are the standardized regression coefficients (Table 2). These values indicate the direction (\pm) and strength of

relationships between variables, and allow for direct comparisons between model pathways.

SEM-direct Impact of short-term fire history

In line with our causal model (Fig. 1; path A), short-term fire history was linked to microbial decomposition rate (-0.517 ; Fig. 3). Specifically, as the number of fires a plot experienced increased, the decomposition rate constants (k) decreased, paralleling the ANOVA analyses above.

SEM-modification of edaphic factors

While short-term fire history directly modified edaphic pathways, changes to nutrient availability did not alter microbial decomposition rates (Fig. 3). Increased numbers of fires

Table 2 Final SEM pathway coefficients and justifications

Response variable	Explanatory variable	Stand. estim.	Stand. err.	<i>P</i> value	<i>R</i> ²	Justification
Microbial decomposition rate constant (<i>k</i>)	# of fires	− 0.517	0.123	< 0.001***	0.325	Ficken and Wright (2017)
	Pine proximity	− 0.268	0.236	0.021**		pine fuels are more recalcitrant than non-pine fuels
Maximum instant surface temp. increase (°C)	Surf. dur. > 60	0.169	0.129	0.181	0.441	Peay et al. (2009)
	# of fires	0.546	0.097	< 0.001***		Presence of fire = hotter temperatures
Maximum instant soil temp. increase (°C)	Pine needle fuels	0.335	0.11	0.002**	0.416	Ellair and Platt (2013)
	Max inst. surf. inc.	0.645	0.091	< 0.001***		Peay et al. (2009)
Surface fire duration > 60 °C (s)	# of fires	− 0.223	0.067	0.001***	0.843	Smaller fuel loads w/increased fire frequencies
	Max inst. surf. inc.	1.027	0.073	< 0.001***		Bárcenas-Moreno and Bååth (2009)
Total soil carbon (%)	# of fires	− 0.252	0.13	0.08*	0.06	Czimczik et al. (2005)
	Max inst. surf. inc.	0.241	0.146	0.102		Johnson and Curtis (2000)
	Surf. dur. > 60	− 0.279	0.121	0.032**		Johnson and Curtis (2000)
Total soil nitrogen (%)	# of Fires	− 0.551	0.111	< 0.001***	0.304	Christensen (1977)
Inorganic soil phosphorus (ppm)	# of fires	− 0.58	0.132	< 0.001***	0.519	Butler et al. (2018)
	Max inst. surf. inc.	− 0.494	0.304	0.071*		Butler et al. (2018)
	Surf. dur. > 60	0.861	0.252	< 0.001***		Butler et al. (2018)
NO ₃ [−] (ppm)	# of fires	− 0.368	0.15	0.008**	0.447	Christensen (1977)
	Max inst. surf. inc.	− 0.686	0.348	0.02**		Raison (1979)
	Surf. dur. > 60	1.094	0.289	< 0.001***		Longer, low-intensity fires release more N
NH ₄ ⁺ (ppm)	# of fires	− 0.774	0.1	< 0.001***	0.526	Christensen (1977)
	Surf. dur. > 60	0.195	0.096	0.041**		Longer, low-intensity fires release more N
Pine needle fuels (g)	Pine proximity	0.53	0.217	< 0.001***	0.281	More pine needles near pines

For each pathway in the model, the table identifies the response variable(s), explanatory variable(s), standardized estimate (effect size), standard errors, *P* values for significance, *R*² estimate for model pathway, and justification for inclusion in the final model

P* < 0.1, *P* < 0.05, ****P* < 0.001

during the study period were associated with decreases in ammonium (− 0.77), nitrate (− 0.37), phosphorus (− 0.58), and total nitrogen (− 0.55), and marginally significant decreases in soil carbon (*p* = 0.08, − 0.25). Overall, increasingly frequent fires were associated with decreased nutrient availability, but these changes were not associated with decomposition rates during the year following 2016 prescribed fires.

SEM-fire characteristics

As hypothesized in our causal model (Fig. 1; Path B), short-term fire history was associated with 2016 fire characteristics, but changes in fire characteristics were not associated with microbial decomposition. More fires during the study period corresponded with greater maximum surface temperature increases (0.55), although this was largely driven by the presence vs. absence (0–0–0) of fire in the final year. Additionally, increased numbers of fires during the study

were associated with shorter fire durations (− 0.22). Greater surface fire temperature increases were also correlated with increased surface fire durations (1.03) and larger soil temperature increases (0.65). Surface fire temperature increases and durations also altered edaphic properties as fires became hotter and longer. Hotter surface temperatures were associated with decreased nitrate (− 0.69) and phosphorus (− 0.49). Longer fire durations, however, were associated with increased phosphorus (0.86), ammonium (0.2), and nitrate (1.1), and decreased carbon (− 0.28). In summary, increasing the number of fires shifted 2016 fire characteristics, which were associated with altered edaphic properties, but not microbial decomposition.

SEM-fuel traits

Fuel traits were directly linked to microbial decomposition and 2016 fire characteristics (Fig. 1; path D). As shown in previous work (Ellair and Platt 2013), sites located near

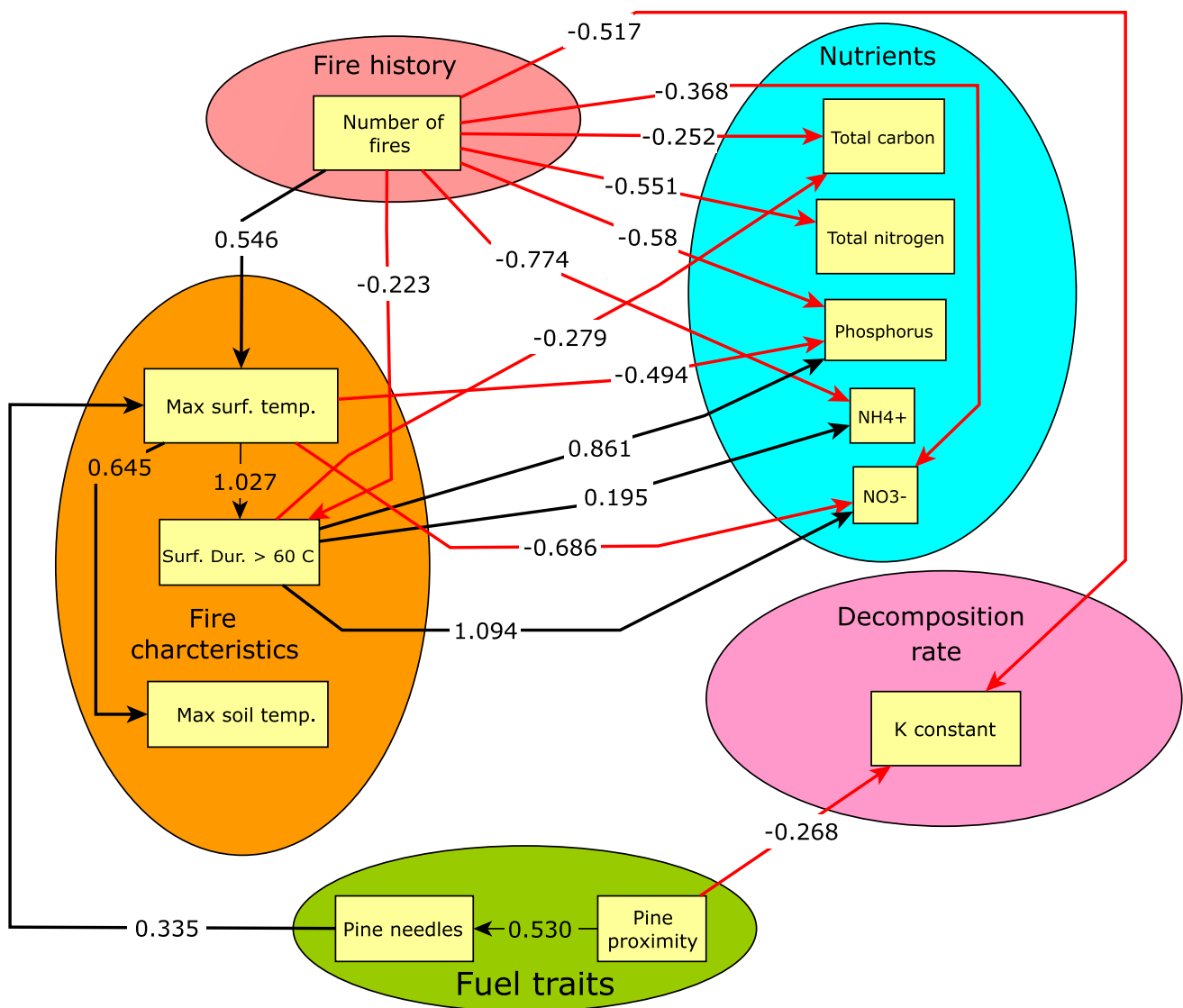


Fig. 3 SEM model for short-term fire history’s effect on microbial decomposition. Components are group by color as in Fig. 1. Coefficients are standardized regression coefficients. Red and black paths denote negative and positive associations between linked variables, respectively. Increasingly frequent fires were associated with lower

microbial decomposition rates; however, fire history-related effects on fire characteristics and nutrients did not affect decomposition. Additionally, sites located near pines had lower decomposition rates than sites located away from pines

pinus had more pine needles (0.53), which were directly linked with greater increases in maximum surface temperature (0.34) and indirectly linked to longer fire durations (0.34) and higher soil temperatures (0.22) through changes to surface temperatures. Fuel traits also had indirect effects on nutrient availability through their modification of fire characteristics (Fig. 3). Additionally, near pine sites had lower decomposition rate constants (*k*) than those located away from pines (− 0.27). Taken together, fuel traits modified the intensity of 2016 fire characteristics, and slowed decomposition in sites located near pines.

Discussion

Microbial decomposition of new fine fuels was slower in frequently burned sites during the year following 2016 prescribed fires. These fire-driven changes are consistent with studies that show repeated fires shift microbial community structure, cause the loss of key functional groups (Hart et al. 2005; Ferrenberg et al. 2013; Brown et al. 2013), and are associated with slower decomposition (Ficken and Wright 2017; Butler et al. 2019). While fire history in our

system did not suppress total fungal abundance (Hansen et al. 2019), it likely impacted microbial community structure (Semenova-Nelsen et al. 2019) in ways that slowed decomposition. This demonstrates that short-term variations in fire history are as important as single fires (Ficken and Wright 2017; Semenova-Nelsen et al. 2019) or long-term fire regime differences (Butler et al. 2019), in determining ecological functions like decomposition. Moreover, decomposition differences arose quickly (i.e., within 3 years) in this pyrophilic ecosystem, so rarely burned systems, which lack fire-adapted organisms, may respond more strongly to repeated fires. It is important to note, however, that the pathway linking fire history to microbial decomposition includes other unmeasured processes besides direct fire effects on microbial decomposers.

Although short-term fire history impacted nutrients, these effects were not linked to shifts in microbial decomposition. Our study confirms well-known impacts of fire on the availability of soil carbon and nutrients (Raison 1979; Neary et al. 1999; Certini 2005). While nutrient availability influences decomposition (Manzoni et al. 2010), significant fire-driven changes to carbon, nitrogen (NO_3 and NH_4), and phosphorus did not slow decomposition rates during the year following 2016 prescribed fires. Two key factors may explain the absence of this relationship. First, short-term nutrient effects directly after fire may have been obscured when evaluated on decomposition rate constants (k) that integrate seasonal variation. Stoichiometric controls on decomposition vary seasonally (Schmidt et al. 2007), and fire-induced differences in nutrient availability may have had decomposition effects that were balanced out at other time points. For example, frequent burning that reduced nutrients for decomposition directly after the 2016 spring fire, also likely reduced plant production throughout the year perhaps leaving greater soil nutrients for fall microbial decomposition. Second, the high frequency of fires at this site (return interval of ~1 year) may cause long-term nutrient limitations (Knicker 2007; Toberman et al. 2014; Butler et al. 2019), which could mask the effect of short-term changes in nutrient levels following single fires. Despite immediate C, N, and P losses in our study, the associations between microbial decomposition and fire history were stronger than associations between decomposition and altered nutrient availability. The long-term adaptation to frequent fires and low nutrient availability at this site likely had a stronger effect on decomposition rates (Butler et al. 2019) than short-term nutrient effects following the most recent fire. Other unmeasured factors, such as soil moisture, pH, and temperature, are also shifted by fire and can modify microbial decomposition, but past studies have not shown these factors were linked to microbial communities or decomposition at this site (Semenova-Nelsen

et al. 2019). In summary, short-term fire history altered nutrient availability, yet these changes were not linked to variation in microbial decomposition.

Short-term fire history also modified the intensity of 2016 fires, but this was not strongly linked to microbial decomposition rates. Larger temperature increases and longer burn durations are expected to kill more microbes (Bárcenas-Moreno and Bååth 2009, Dooley and Treseder 2012), and alter microbial decomposition rates due to microbial mortality. However, even in “long” unburned plots, prescribed 2016 fires at this site may not have reached sufficient intensity to cause significant microbial mortality (Hansen et al. 2019). As with nutrient effects, it is also possible that fire intensity related effects on microbial decomposition are strongest immediately after fires, and dissipate with time (or are even offset) as microbial communities recover (Bárcenas-Moreno et al. 2011). Consistent with this interpretation, while fire characteristics did not impact microbial decomposition, they did have strong effects on nutrient availability. High-intensity fires can increase nutrient volatilization (Neary et al. 1999), while longer, low-intensity fires (i.e., < 200 °C) may favor the release of nutrients from fine fuels (Certini 2005). These were born out by our data, as hotter fires (i.e., higher surface temperatures) were associated with decreased N and P, while longer fires (i.e., longer durations above 60 °C) were associated with increased N and P. Fire characteristics, including intensity and duration, may play a larger role in decomposition after wildfires, since wildfire intensity commonly surpasses that of prescribed fires (Certini 2005). Overall, short-term fire history modified fire characteristics and nutrient availability, but these changes were not associated with shifts in microbial decomposition rates.

The types of fuels present determined both fire characteristics and post-fire decomposition. While location and fuel composition covary, we show that microbial decomposition rates were slower in near pines sites. The direct link between pine proximity and decomposition suggests that the high lignin and C:N content of near pines fuels (Wardle et al. 2002) and location-based differences in microbial communities result in slower decomposition. While larger amounts of Longleaf pine needles increased the intensity of 2016 prescribed fires, this did not affect microbial decomposition rates following 2016 fires. Since microbial decomposition rates are slower near pines, the greater suppression of decomposition following fire may contribute to natural fuel accumulation that alters the likelihood or spread of future fires. At our study site, fires commonly consume more than 60% of fuels (see Appendix section “fuels”), and are primarily reliant on fuel accumulated in the last year. This may be a key difference, for example, from fire suppressed forests in the Western US, where the buildup of coarse woody debris (Brown 1983; Kalies and Yocom Kent 2016) can create fires so severe that upper soil horizons are completely lost

or sterilized. Fire-driven decomposition differences then may depend on the fuels accumulated since the last fire, and in fire-frequented systems, fuel loads may have a strong seasonal relationship.

Linking fire regime and microbial function elucidates the largely unconsidered, but important roles that microbes play in pyrophilic ecosystems. Historically, fire ecology has focused on the interaction of fire with above ground communities (i.e., plants) and biogeochemistry (Archibald et al. 2018), while rarely exploring microbial functions like decomposition. Our study identified pathways through which fire history governs microbial decomposition of fuels, fire characteristics, and soil nutrient availability. Short-term fire history's effects on microbial decomposition should modify fine fuel loads, which could ultimately impact future fires. Other microbial functions, however, may also contribute to (or mitigate) fire feedbacks. Fire regime impacts on microbial mutualists (i.e., mycorrhizae) could alter their benefits for post-fire plant survival and fuel production (Peay et al. 2009; Glassman et al. 2016; Carson et al. 2019). Microbial pathogen responses to fire history may also be important due to their role in plant productivity (Schnitzer et al. 2011), with pathogen suppression by fire potentially allowing for greater post-fire plant survival and faster fuel production. The indirect impact of microbe–plant symbioses on fuels may counterbalance, or even exacerbate the positive fire feedbacks from microbial decomposition. Future work can explore how fire–microbe interactions shape fire feedbacks through fuel load alterations (as seen here) and plant–microbe interactions.

In conclusion, we demonstrated that short-term fire history and microbial decomposition are closely connected through direct fire and fuel related pathways. Furthermore, we identified a feedback mechanism through which increased numbers of fires may increase fine fuel accumulation and the intensity of future fires. Understanding how different fire histories impact microbial decomposers and associated fine fuels is critical to our knowledge and maintenance of pyrophilic ecosystems, many of which are endangered (Bowman et al. 2009). Furthermore, our study system may provide a conservative model for predicting the effects of increasing fire frequencies in other ecosystems. Fire helps maintain more than 50% of terrestrial ecosystems, and its occurrence is becoming increasingly frequent due to anthropogenic change (Archibald et al. 2018). Including foundational microbial processes like decomposition in fire models can improve our understanding and management of fire-dependent and non-fire-dependent ecosystems alike.

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Data availability Data is available in Dryad: <https://doi.org/10.5061/dryad.3n5tb2rf2>.

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