Applied Soil Ecology 189 (2023) 104914

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Short-term prescribed fire-induced changes in soil microbial communities and nutrients in native rangelands of Florida

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ARTICLE INFO

Keywords:
Prescribed burning
Rangelands
Soil nutrients
Microbial diversity

ABSTRACT

Prescribed burning is widely used land management strategy to reduce the risks of wildfire and to achieve a wide range of ecological, economic, and societal benefits. However, it can also affect carbon (C), nitrogen (N), and phosphorus (P) cycling with potential subsequent effects on soil microbial communities. This study examined the short-term effects of prescribed burning on soil chemical properties, potential enzyme activities, and bacterial and fungal community composition in native rangelands of Florida. Fire-induced responses were assessed immediately (2 days) and 2 to 3 months after a prescribed fire event. Soil pH, total C, and extractable NH_4^+ and P concentration declined after fire. Total N concentration increased 2 days after fire but returned to initial level 2 to 3 months after fire. Prescribed fire elicited no observable effects on soil total P and extractable Ca, K, Mg, Mn, Fe, and Al concentration. Reductions in potential beta glucosidase and *N*-acetyl glucosaminidase activity were observed 2 days after fire but returned at pre-fire levels after 2–3 months. Bacterial and fungal diversity and community composition at the phylum level showed no short-term changes. At the Order level, bacterial Desulfurellales increased while fungal Eurotiales and Pleosporales decreased 2 days after fire. Prescribed burning had minimal effect on soil microbial community composition in the short-term, probably due to limited effects of fire on soil heating and rapid post-fire vegetative recovery. Although the impacts of prescribed fire on soil properties have been widely acknowledged, this study is the first to document short-term fire-induced soil microbial responses in subtropical native rangelands of Florida. This work contributes to a wealth of evidence indicating limited impacts of prescribed fire on soil microbial community composition.

1. Introduction

Prescribed burning is a land management tool in which fire is intentionally applied under specific weather, fuel, and topographic conditions to maintain ecosystem function and improve plant productivity (Carter and Darwin Foster, 2004; Fernandes et al., 2013; Limb et al., 2016). Among several ecological, economic and societal benefits, prescribed burning often reduces the likelihood of wildfires, controls growth of woody species, minimizes soil loss, increases plant biodiversity and wildlife habitat, and increases forage productivity for grazing animals (Carter and Darwin Foster, 2004; Harper et al., 2018; J. Vendramini, 2019; Ryan et al., 2013).

Fire has significant impacts on the biogeochemical cycle of nutrients, including carbon (C), nitrogen (N), and phosphorus (P) (González-Pérez et al., 2004). Some of the fire-induced responses include temporal changes in soil N availability through alterations in the rates of soil N mineralization and ammonia (NH_3) volatilization (Certini, 2005; Dannenmann et al., 2018; Hu et al., 2019), increases in soil pH (Alcañiz et al., 2018), and increases in soil erosion due to the formation of hydrophobic layers (Singh et al., 2017). Additionally, fire converts a fraction of plant biomass into charcoal, which contains highly recalcitrant black C (González-Pérez et al., 2004). Fire can impact P cycling and availability due to the combustion of organic P, soil organic matter (SOM) mineralization, and erosion (Durán et al., 2008; Lang et al., 2016). Previous studies in subtropical rangelands in Florida reported increases in soil extractable N and P levels within 3 h following a single

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https://doi.org/10.1016/j.apsoil.2023.104914
Received 1 December 2022; Received in revised form 14 February 2023; Accepted 5 April 2023
Available online 15 April 2023

fire event (Schafer and Mack, 2010).

Fire also alters the activity, abundance, and diversity of soil microbial communities (Alcañiz et al., 2018; Dove and Hart, 2017; Pressler et al., 2019) that play critical roles in nutrient cycling and ecosystem functioning (Nannipieri et al., 2017; Nannipieri and Badalucco, 2003). Fire may affect soil enzyme activity through alterations in substrate quantity and quality (Hart et al., 2005). Previous studies demonstrated that β-glucosidase (BGA) activity, commonly used as an indicator of C decomposition, decreases immediately after fire due to enzyme denaturation (López-Poma and Bautista, 2014). Similarly, *N*-acetyl glucosaminidase (NAG), an important enzyme that regulates soil N mineralization, may be affected by fire (Creamer et al., 2013; Knelman et al., 2017). Soil microbial communities may be affected by fire directly through mortality and indirectly through changes in soil physiochemical and biological properties (Barreiro and Díaz-Raviña, 2021; Certini, 2005). To date, contrasting results have been published on the effect of fire on soil microbial diversity and community composition, the extent of which was linked to changes in fire type and severity, fuel load, vegetation composition, climate, topography, soil properties, and area burned (Dove and Hart, 2017; Mikita-Barbato et al., 2015; Oliver et al., 2015; Pressler et al., 2019; Kranz and Whitman, 2019; Giuditta et al., 2019). For example, Rodríguez et al. (2017) found an increase in bacterial diversity and the relative abundance of Acidobacteria, Actinobacteria and Proteobacteria while Prendergast-Miller et al. (2017) found a decrease in fungal diversity following a wildfire in natural ecosystems. Recent meta-analyses reported significant negative effects of prescribed fire on fungal diversity due to alterations in soil pH and N pools (Dove and Hart, 2017; Pressler et al., 2019). Despite several reports on the impact of prescribed burning on soil microbial communities, it remains largely unknown how fast and how long these effects last and whether alterations in the diversity and community composition of bacteria and fungi can be restored after long-term recurring prescribed burning events.

Although the impacts of prescribed burning on soil responses are well documented in Mediterranean, boreal, and temperate climates (Barreiro and Díaz-Raviña, 2021), there is limited information for subtropical rangelands with repeated fire events. Rangelands cover about 48 % of the grazing lands in the United States and provide a wide range of ecosystem services including wildlife habitat, biodiversity management, environmental protection and C sequestration (Bracho et al., 2021; Duvall and Hilmon, 1965; Schuman et al., 2002). Subtropical rangelands in Florida are natural ecosystems that are dominated by grasses and grass-like plants, forbs and shrubs that are mainly used for cattle grazing during winter months (Kalmbacher et al., 1984). Fire-induced changes in nutrient dynamics are expected to have greater impacts in subtropical climates with high precipitation and temperature since warm and humid conditions favor SOM degradation (Lavelle et al., 1993; Zhong et al., 2018). Therefore, the objective of this study was to examine the short-term effects (2 days and 2 to 3 months after fire) of prescribed burning on soil properties, soil potential enzyme activities, and composition of bacterial and fungal communities in native rangelands of Florida where fire has been historically used to suppress shrub and woody vegetation. We hypothesized that: (i) prescribed burning would increase available soil nutrients, particularly N and P, within the first few days after prescribed burning but this effect may disappear 2 to 3 months after fire, (ii) soil enzyme activity would decrease after fire due to higher temperatures and decreased substrate availability, and (iii) prescribed burning would result in increases in the diversity of bacterial and fungal communities and variations in their composition due to increased soil nutrient availability.

2. Methods

2.1. Study site description

The study area was located at the Long-term Agroecosystem Research (LTAR)-Archbold/University of Florida, Range Cattle Research and Education Center site in Ona, Florida, USA (38°34′36″N and 92°10′25″W) (Supplementary Fig. S1). The site is characterized by a subtropical humid climate with a mean annual precipitation of 1283 mm and a mean annual air temperature of 23 °C from Florida Automated Weather Network (FAWN). The predominant soil series are Ona fine sand (sandy, siliceous, hyperthermic Typic Alaquods) and Smyrna sand (sandy, siliceous, hyperthermic Aeric Alaquods). Predominant vegetation consisted of shrubs, particularly saw-palmetto (*Sereona repens* (W. Bartram) Small), and perennial C_4 grasses including chalky bluestem (*Andropogon capillipes* Nash), broomsedge bluestem (*Andropogon virginicus* L.), and creeping bluestem (*Schizachyrium stoloniferum* Nash).

The experimental site consisted of 4 replicated units (W1U4, W2U2, W3U2, W4U1) of ~22 ha each. The experimental area has never been fertilized, periodically burned (every 3 to 8 years from mid-November to April), which is the recommended management practice for the region to prevent shrub encroachment, particularly saw-palmetto, and to promote the growth of desirable grasses for cattle grazing. All experimental units have been occasionally grazed during November to February at a stocking rate of 125 animal unit days ha^{-1} yr^{-1} (<60 days of grazing per year) for over 30 years (Adewopo et al., 2014). Detailed burn histories for each experimental unit are provided in Table 1. Fire is a critical tool in the southeast region to maintain vegetative species richness and prevent saw-palmetto encroachment, which has become a dominant shrub species in many degraded pine savannas (Willcox and Giuliano, 2010). Prescribed fire was implemented using the backing fire technique between March and May 2019, which corresponded to the dormant season in the region. Temperature (at soil surface) during prescribed burning was monitored using Type K thermocouples (TCW100-K, Onset Computer Corporation, Bourne, MA) equipped with dataloggers (U12-014 HOBO thermocouple data logger, Onset Computer Corporation). Sensors were deployed at six random locations within each experimental unit. Maximum recorded temperature during prescribed burning ranged from 168 to 316 °C (mean of 242 °C) with no detectable increase in temperature observed below 2.5 cm soil depth (Kohmann et al., 2022).

2.2. Soil sampling

Five 50 m transects were randomly established at each replicated units (W1U4, W2U2, W3U2, W4U1) (Supplementary Fig. S1). At each transect, five soil cores (2.2 cm in diameter x 10 cm depth) were collected at random locations and combined into composited samples. Soils were sampled before fire (BF, November 2018), within 2 days after fire (AF, between March and May 2019), and 2–3 months after fire (AF2, June 2019) (Table 1) and stored at 4 °C and −20 °C for soil biogeochemical and DNA analyses, respectively.

2.3. Soil characterization

Soil pH was measured using a 1:2 (solid/water) ratio with a glass electrode pH meter (Oakton instruments, Vernon Hills, IL). Soil total C and N concentration were determined by dry combustion using a Flash EA1112-NC elemental analyzer (CE Elantech, Lakewood, NJ). Total P concentration was measured using semi-automated colorimetry (EPA 200.7, Version 4.4). Extractable NH_4^+-N concentration was measured colorimetrically (EPA Method 350.1, modified). Mehlich-3 extractable P, potassium (K), calcium (Ca), manganese (Mn), magnesium (Mg),

Table 1
Experimental site fire history and prescribed burning date.

Experimental areas	Previous fire history (last 15 yr)	Prescribed burning date
W1U4	Burned in 2004, 2010, and 2018	May 2, 2019
W2U2	Burned in 2008, 2011, and 2018	May 1, 2019
W3U2	Burned in 2008, 2013, and 2018	March 13, 2019
W4U1	Burned in 2008, 2014, and 2018	April 04, 2019

aluminum (Al), and iron (Fe) were determined by Inductively Coupled Plasma (ICP) Spectrophotometer Spectro Arcos II (Spectro Analytical Instruments, Mahwah, NJ 07430). Soil moisture (SM) was determined gravimetrically by oven-drying the sub-samples at 105 °C for 24 h.

2.4. Potential enzyme activity

Two soil extracellular enzymes involved in C decomposition (β-glucosidase; BGA) and N mineralization (*N*-acetyl-glucosaminidase; NAG) were measured (within a week from collection) following procedures described by Sinsabaugh et al. (2005). Homogenate was prepared by dispensing 1 g of fresh soil sample with the corresponding substrate and buffer solutions into 96-well microplates. The amount of fluorescence was measured using a microplate fluorometer (Synergy HT, Biotek, Winooski, VT) with 365 nm excitation and 450 nm emission filters (German et al., 2012). Potential enzyme activity was calculated from the 4-methylumbelliferyl (MUB) standard curve following (German et al., 2011, 2012).

2.5. DNA extraction and sequencing

DNA extraction was performed in soil samples collected before fire (BF) and 2 days following fire (AF). DNA from 0.25 g of each frozen soil sample was extracted using the DNeasy Powerlyzer PowerSoil Kit (Qiagen, Germantown, MD, USA) following the manufacturer's instructions. The extracted DNA was quantified using a Qubit Fluorometer (Thermofisher Scientific) with the Quant-iT dsDNA HS Assay Kit and sent for sequencing at the DNA Services Facility at the University of Illinois Chicago (USA) on the Illumina Mi-Seq platform using a 2 * 250 paired end cycle sequencing mode. The V4 hypervariable region of bacterial 16S rRNA gene was amplified using universal primers forward 515Fa and 926R following the EMP protocol (Apprill et al., 2015). Similarly, the ITS1F and ITS2R primers were used to amplify ITS1 region of the fungal rRNA genes (Gardes and Bruns, 1993).

2.6. 16S and ITS rRNA gene analysis

Sequencing analysis was performed as described by Nuzzo et al. (2020) using Qiime2 (version 2018.8) (Bolyen et al., 2019). Briefly, the 16S reads were imported into Qiime2 and dereplicated using DADA2 with the paired-end setting (quality control, trimming, pair-joining). The ITS sequences were pair-joined using PEAR, and the 5.8S and ITS2 regions were trimmed using cutadapt before importing into Qiime2 (Martin, 2011; Zhang et al., 2014). ITS reads were dereplicated with the same algorithm as 16S but with single-end settings, resulting in amplicon sequence variant (ASV) tables containing read counts. The 16S and ITS representative ASVs were assigned to the SILVA 119 and UNITE 7.2 pre-trained gene databases (Quast et al., 2013; Tedersoo et al., 2018), respectively, producing taxonomy tables as described by Nuzzo et al. (2020). Amplicon sequencing of the 16S rRNA gene of the 18 (9 BF and 9 AF) samples resulted in 1,082,341 total sequences with an average of 60,130 demultiplexed sequences per sample, ranging from 22,893 to 102,882. A total of 637,754 demultiplexed ITS sequences were produced from 18 samples with an average of 35,431 per sample, ranging from 21,101 to 44,477. Raw reads used in this study can be found in the NCBI Sequence Read Archive (SRA) under accession number PRJNA808991.

2.7. Statistical analysis

All statistical analyses were performed using R v.3.6.1 software (R Core Team, 2020). Analysis of variance (ANOVA) was conducted to determine effects of fire (BF, AF, and AF2) on soil properties with a significance threshold $p < 0.05$ and post hoc comparisons were performed using Tukey test. Log transformations were used when the normality assumption was not met. Principal Component Analysis (PCA) was performed to explore the relationships between soil variables (pH, total C, total N, total P, C:N ratio, NH_4^+-N, P, K, Ca, Mg, Mn, Fe, Al, and SM) and potential enzyme activities (BGA, NAG and BGA:NAG ratio) with fire (BF, AF, and AF2) using“ggplot2” package (Wickham, 2011). Subsequently, Pearson's product moment correlation coefficients between the vectors representing soil properties and potential enzyme activities in the PCA plots were calculated using the “ggcorrplot” package.

Alpha (number of ASVs, Shannon and Simpson) and beta diversity analyses were performed using the R package “Phyloseq” (McMurdie and Holmes, 2013) on log-normalized data to avoid an increase in error rates due to rarefaction. Beta diversity analyses included nonmetric multidimensional scaling (NMDS) based on the Bray-Curtis distances. Permutational multivariate analysis of variance (PERMANOVA) was performed on Bray-Curtis dissimilarity metric with “vegan” package (Dixon, 2003). A paired *t*-test was used to compare changes in the relative abundance of the bacterial and fungal taxa from BF to AF at the phylum, order, and genus taxonomic levels with a significance threshold of $p < 0.05$. Redundancy analysis (RDA) was performed to investigate the relationship between soil variables (soil pH, total C, total N, C:N, total P, NH_4^+-N, BGA, NAG, BGA:NAG, extractable P, K, Ca, Mn, Mg, Al, and Fe) with bacterial and fungal genera. The Pearson's product moment correlation coefficients (r) among vectors representing soil variables and relative abundances of bacterial and fungal genera were determined.

Table 2
Selected soil chemical properties (0–10 cm) as affected by fire.

Soil property	Sampling event		
	Before fire (BF)	2 days after fire (AF)	2 to 3 months after fire (AF2)
Soil pH	4.7 ± 0.2b	4.3 ± 0.2a	4.3 ± 0.2a
Soil moisture (g kg^{-1})	240 ± 41a	248 ± 49a	220 ± 62a
Total C (g kg^{-1})	27 ± 7b	23 ± 6ab	19 ± 5a
Total N (g kg^{-1})	1 ± 0.3a	14 ± 0.2b	1 ± 0.3a
C:N ratio	28.0 ± 3.8b	16.1 ± 2.4a	26.2 ± 23.9ab
Total P (mg kg^{-1})	41.7 ± 14.2a	39.5 ± 8.7a	39.4 ± 9.7a
Extractable NH_4^+ (mg kg^{-1})	11.2 ± 2.8b	9.0 ± 2.5b	5.5 ± 1.3a
Extractable P (mg kg^{-1})	12.7 ± 3.6b	5.4 ± 3.4a	5.8 ± 3.2a
Extractable K (mg kg^{-1})	19.9 ± 4.8a	16.7 ± 4.6a	17.4 ± 3.2a
Extractable Mg (mg kg^{-1})	37.9 ± 18.5a	34.9 ± 14.3a	36.9 ± 14.3a
Extractable Ca (mg kg^{-1})	220.5 ± 79.2a	143.3 ± 53.5a	152.1 ± 56.7a
Extractable Mn (mg kg^{-1})	0.72 ± 0.4a	0.49 ± 0.2a	0.49 ± 0.3a
Extractable Fe (mg kg^{-1})	106.8 ± 45.0a	77.0 ± 46.6a	81.0 ± 42.8a
Extractable Al (mg kg^{-1})	178.1 ± 107.2a	169.2 ± 151.8a	170.6 ± 149.1a
BGA enzyme activity (nmol g^{-1}dry soil h^{-1})	24.0 ± 10.9a	5.8 ± 3.7b	24.1 ± 11.3a
NAG enzyme activity (nmol g^{-1}dry soil h^{-1})	51.0 ± 28.8ab	35.0 ± 17.7b	79.0 ± 39.6a
BGA:NAG ratio	0.51 ± 0.3a	0.24 ± 0.2b	0.33 ± 0.1ab

Soils were sampled before fire (BF), within 2 days after fire (AF) and 2 to 3 months after fire (AF2). Mean values (± standard deviation) followed by different letters within row indicate significant differences according to ANOVA and Tukey test ($p < 0.05$; $n = 9$). BGA - beta glucosidase activity; NAG - *N*-acetyl glucosaminidase activity.

3. Results

3.1. Effect of prescribed burning on selected soil properties and potential enzyme activity

Fire-induced changes in soil properties are shown in Table 2. Soil pH decreased significantly from BF to AF ($p < 0.001$), but remained unchanged afterwards. Soil total C concentration decreased at AF2 by 30 % compared to BF ($p = 0.03$), but AF values were intermediate between sampling events. There was a significant increase in soil total N concentration from BF (1 g kg^{-1}) to AF (1.4 g kg^{-1}), but it returned to pre-fire levels at AF2 (1 g kg^{-1}) ($p = 0.02$). The C:N ratio decreased by 43 % ($p < 0.001$) at AF, but returned to BF values at AF2. Soil extractable NH_4^+ concentration decreased from 11.2 mg kg^{-1} (BF) to 5.5 mg kg^{-1} (AF2) ($p < 0.001$). Soil extractable P concentration decreased by 57 % ($p < 0.001$) from BF to AF, but total soil P and extractable Ca, K, Mg, Mn, Fe, and Al concentration remained unchanged.

BGA activity at AF declined by 75 % ($p < 0.001$; Table 2) relative to BF levels, but it returned to pre-fire levels at AF2. There was no significant change in NAG activity from BF to AF, but it doubled from AF to AF2 ($p = 0.006$; Table 2). The BGA:NAG ratio decreased from BF to AF ($p = 0.03$), but no differences were observed between AF and AF2.

Principle component analysis showed that soil properties and potential enzyme activities differed significantly between sampling events ($R^2 = 0.24$, $p = 0.001$) (Fig. 1). Ordination of the sampling events was related to the first canonical axis (PC1 = 29 %) while the second axis explained 18 % of the variation. The first axis was correlated with total C concentration while the second axis was correlated with soil pH, extractable P concentration, and BGA activity. A significant positive correlation between BGA activity and soil pH ($r = 0.6$, $p = 0.004$), C:N ($r = 0.7$, $p = 0.002$), extractable P ($r = 0.6$, $p = 0.01$), and extractable Ca ($r = 0.6$, $p = 0.02$) were detected (Supplementary Fig. S2). NAG activity was positively correlated with NH_4^+ ($r = 0.7$, $p = 0.002$). BGA:NAG ratio showed positive correlation with soil pH ($r = 0.6$, $p = 0.02$) (Supplementary Fig. S2).

3.2. Effect of prescribed burning on soil bacterial community structure and diversity

Prescribed fire showed no significant differences in any of the alpha diversity indices of the bacterial communities (Fig. 2A). The average observed richness was 392 and 328 ASVs at BF and AF, respectively ($p = 0.16$). Values of the Shannon index varied from 5.58 (BF) to 5.46 (AF) ($p = 0.45$). The average Simpson diversity index remained unchanged from BF (0.99) to AF (0.99) ($p = 0.97$). A NMDS analysis on Bray-Curtis distances showed that bacterial beta diversity was not affected by the fire (PERMANOVA, $R^2 = 0.06$, $p = 0.21$) (Fig. 3A).

Across all samples, Acidobacteria, Actinobacteria, Planctomycetes, and Proteobacteria were the predominant phyla BF with mean relative abundances of 19 %, 18 %, 12 % and 30 %, respectively (Supplementary Fig. S3A). There were no significant changes in the relative abundance of any phyla from BF to AF ($p > 0.05$) (Supplementary Fig. S3A). Fire significantly increased the relative abundance of the bacterial order Desulfurellales by 26 % AF ($p = 0.009$), and impacted the relative abundance of *Variibacter* genera, which significantly increased from 2.1 % (BF) to 2.6 % (AF) ($p = 0.01$) (Supplementary Fig. S4A).

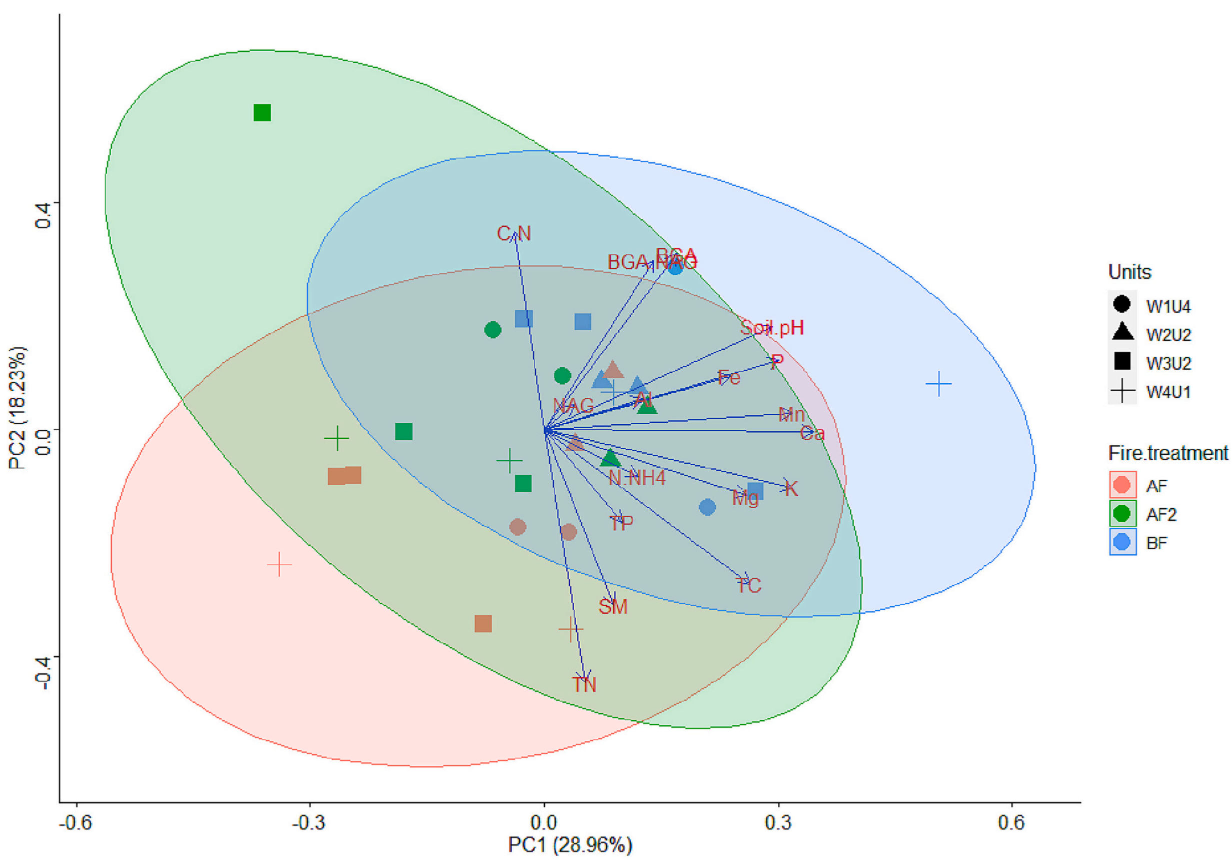


Fig. 1. Principal Component Analysis (PCA) relating selected soil chemical properties (pH, total C, N, P, C:N ratio, and extractable NH_4^+ P, K, Ca, Mg, Mn, Fe, Al concentrations) and microbial activity (BGA, NAG and BGA:NAG ratio) for 0–10 cm soil samples. Soils were sampled before fire (BF), within 2 days after fire (AF) and 2 to 3 months after fire (AF2). Each point represents an individual sample collected from the study site. Each PCA was grouped by fire event where BF is represented by a blue ellipse, AF by a green ellipse and AF2 by a red ellipse. BGA - beta glucosidase activity; NAG - *N*-acetyl glucosaminidase activity.

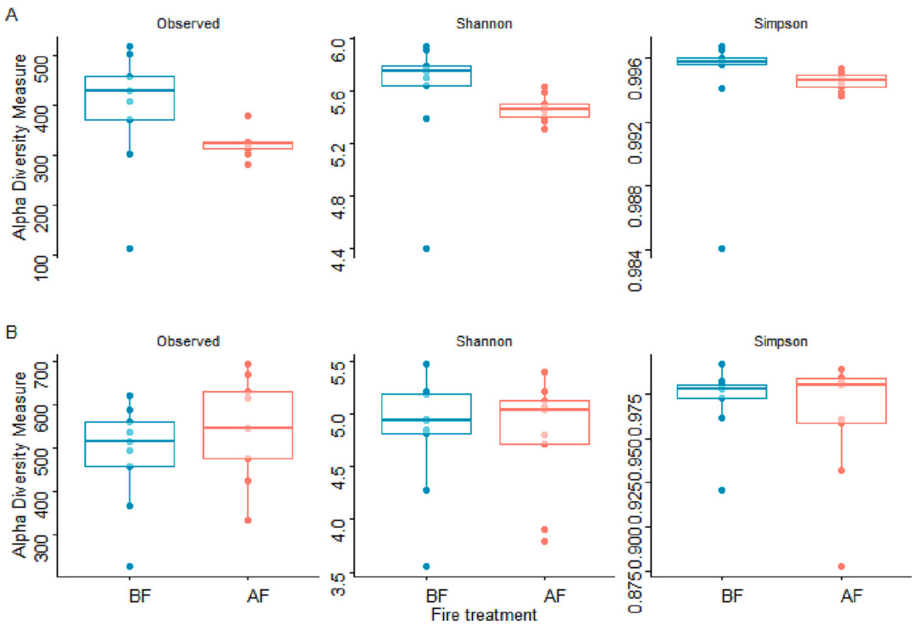


Fig. 2. Microbial diversity indices (richness, Shannon, and Simpson) for the bacterial (A) and fungal (B) community before fire (BF) - blue color and within 2 days after fire (AF) - red color (Tukey's HSD, $p \leq 0.05$). Values are expressed as mean with standard error.

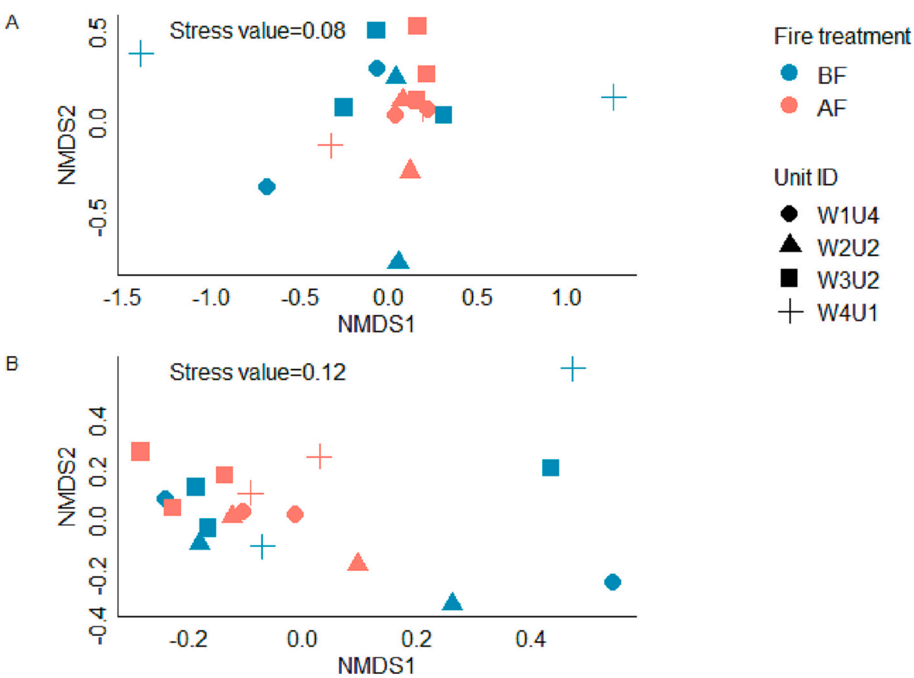


Fig. 3. Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity for the bacterial (A) and fungal (B) community. Each point represents an individual sample collected from the 4 experimental units either before fire (BF) - blue color and within 2 days after fire (AF) - red color.

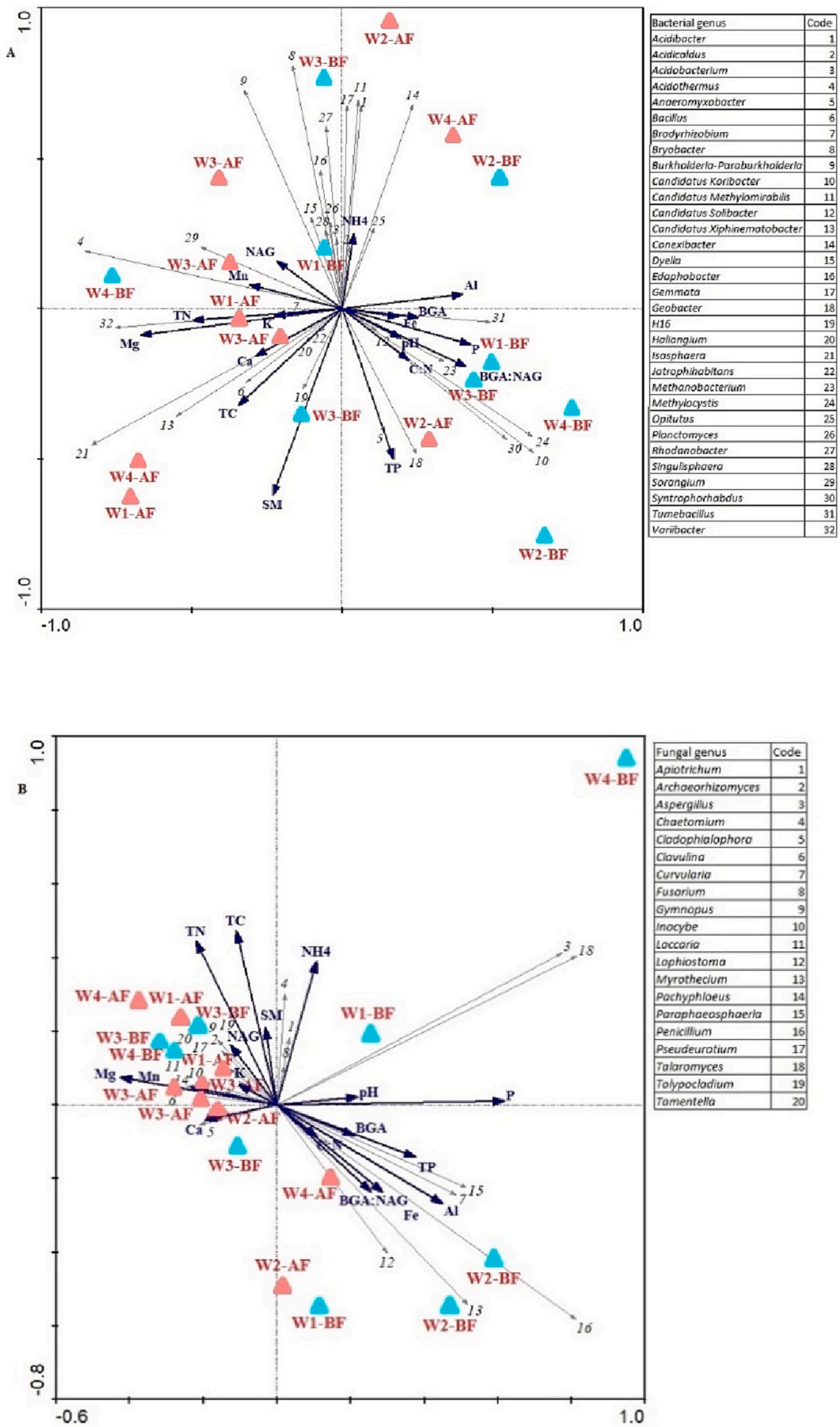
3.3. Effect of prescribed burning on soil fungal community structure and diversity

There were no significant differences in alpha diversity of the fungal communities from BF to AF (Fig. 2B). The average observed richness was 485 ASVs in BF vs 547 ASVs in AF ($p = 0.29$). The average Shannon diversity index was 4.81 and 4.78 at BF and AF, respectively ($p = 0.93$). Values of the Simpson index varied from 0.97 to 0.96 from BF to AF, respectively ($p = 0.53$). Soil fungal beta diversity did not change with fire as shown by a NMDS together with a PERMANOVA analysis ($R^2 = 0.07$, $p = 0.07$) (Fig. 3B).

Across all samples, Ascomycota, Basidiomycota, Mortierellomycota, and Rozellomycota were the dominant phyla BF with mean relative abundances of 81 %, 15 %, 2 %, and 1 % of the total relative abundance, respectively (Supplementary Fig. S3B). However, significant changes in the relative abundance of fungal phyla were not detected after the fire event. At the Order taxonomic level, fire significantly reduced the relative abundance of Pleosporales by 65 % ($p = 0.007$) and Eurotiales by 28 % ($p = 0.002$). The relative abundance of the *Talaromyces* genera decreased from 10.7 % to 6.1 % ($p = 0.005$; Fig. S4B).

3.4. Relation between soil microbial communities and soil properties

BF and AF samples clustered together in RDA suggesting that changes in soil properties due to fire had no effect on soil bacterial (Fig. 4A) and fungal (Fig. 4B) communities ($p > 0.05$). However, the RDA analyses showed that specific bacterial (Fig. 4A) and fungal (Fig. 4B) genera significantly ($p \leq 0.05$) correlated with soil properties (Supplementary Tables S1 and S2). Only significant correlation is described below. Soil pH was positively correlated with *Methanobacterium* and negatively correlated with *Acidothermus* and *Sorangium*. Total C concentration was positively correlated with various genera including *Bacillus*, *Candidatus Xiphinematobacter*, *Haliangium*, *Isosphaera*, *Jatrophihabitans*. A positive correlation was found between total N concentration and *Bradyrhizobium*, *Variibacter*, *Candidatus*



Bacterial genus	Code
Acidibacter	1
Acidicaldus	2
Acidobacterium	3
Acidothermus	4
Anaeromyxobacter	5
Bacillus	6
Bradyrhizobium	7
Bryobacter	8
Burkholderia-Paraburkholderia	9
Candidatus Koribacter	10
Candidatus Methylomirabilis	11
Candidatus Solibacter	12
Candidatus Xiphinematobacter	13
Conexibacter	14
Dyella	15
Edaphobacter	16
Gemmata	17
Geobacter	18
H16	19
Haliangium	20
Isosphaera	21
Jatrophihabitans	22
Methanobacterium	23
Methylocystis	24
Opitutus	25
Planctomyces	26
Rhodanobacter	27
Singulisphaera	28
Sorangium	29
Syntrophorhabdus	30
Tumebacillus	31
Variibacter	32

Fungal genus	Code
Apiotrichum	1
Archaeorhizomyces	2
Aspergillus	3
Chaetomium	4
Cladophialophora	5
Clavulina	6
Curvularia	7
Fusarium	8
Gymnopus	9
Inocybe	10
Laccaria	11
Lophiostoma	12
Myrothecium	13
Pachyphloeus	14
Paraphaeosphaeria	15
Penicillium	16
Pseudeurotium	17
Talaromyces	18
Tolypocladium	19
Tomentella	20

Fig. 4. RDA tri-plot showing the distribution of soil microbial community with soil properties (pH, total C, N, P, C:N ratio, and extractable NH_4^+ P, K, Ca, Mg, Mn, Fe, Al concentrations, BGA, NAG and BGA:NAG ratio) for the bacterial (A) and fungal (B) community. The vectors show the direction and strength of the relationships between the microbial community and soil variables before fire (BF) - blue color and within 2 days after fire (AF) - red color. Only bacterial and fungal general showing significant correlations with at least one of the soil variables are shown ($p \leq 0.05$). BGA - beta glucosidase activity; NAG - *N*-acetyl glucosaminidase activity.

Koribacter, *Candidatus Solibacter*, *Methanobacterium*, *Methylocystis* and *Syntrophorhabdus*. *Sorangium* was negatively correlated with total N concentration. Total P concentration was positively correlated with *Anaeromyxobacter*. *Acidibacter*, *Acidicaldus*, *Acidothermus*, *Bryobacter*, *Burkholderia-Paraburkholderia*, *Candidatus Methylomirabilis*, *Opitutus*, *Planctomyces*, *Rhodanobacter*, and *Singulisphaera* were positively linked to extractable NH_4^+ concentration.

Soil BGA activity was negatively correlated with *Acidothermus* and *Sorangium* and positively correlated with *Tumebacillus*. NAG activity was negatively linked to *Candidatus Koribacter*, *Candidatus Solibacter*, *Methanobacterium*, *Methylocystis*, *Syntrophorhabdus*, and positively linked with *Sorangium*. The BGA:NAG ratio was negatively linked to *Acidothermus* and *Sorangium* and positively linked with *Methanobacterium*.

For the fungal communities, a negative correlation was found between soil pH and *Cladophialophora*, while total C and total N concentration were negatively correlated with *Lophiostoma*, and *Myrothecium*. The C:N ratio was positively correlated with *Myrothecium* and negatively correlated with *Archaeorhizomyces*, *Gymnopus*, *Pseudeurotium,* and *Tolypocladium*. The fungal genera *Archaeorhizomyces*, *Clavulina*, *Gymnopus*, *Inocybe*, *Laccaria*, *Pachyphloeus*, *Pseudeurotium*, *Tolypocladium*, and *Tomentella* had a negative correlation with total P concentration and a positive correlation to *Curvularia* and *Paraphaeosphaeria*. Extractable NH_4^+ concentration was positively linked to *Apiotrichum*, *Chaetomium,* and *Fusarium* whereas *Fusarium* was negatively correlated with soil moisture. BGA activity was positively linked to *Curvularia* and *Paraphaeosphaeria* and negatively linked to *Archaeorhizomyces*, *Clavulina*, *Gymnopus*, *Inocybe*, *Laccaria*, *Pachyphloeus*, *Pseudeurotium*, *Tolypocladium*, and *Tomentella*. *Archaeorhizomyces*, *Gymnopus*, *Pseudeurotium*, and *Tolypocladium* was positively correlated with NAG activity and negatively with *Lophiostoma* and *Myrothecium*. BGA:NAG ratio was positively linked to *Myrothecium* and *Penicillium* and negatively linked to *Archaeorhizomyces*, *Gymnopus*, *Pseudeurotium*, and *Tolypocladium*.

4. Discussion

Prescribed burning plays a significant ecological role in maintaining vegetative species and soil nutrient cycling in rangelands (Bracho et al., 2021; González-Pérez et al., 2004b; Xu et al., 2022). We found that prescribed burning has transitory effects on soil properties and potential enzyme activities in native rangelands of Florida, as changes in these variables were observed only within 2 days after fire and tended to disappear after 2–3 months. Fire had no impacts on the diversity and composition soil microbial communities 2 days after fire compared to pre-fire levels. However, there were significant changes in the relative abundance of specific bacterial and fungal taxa. Significant correlations between microbial communities and soil properties revealed that prescribed burning impacts on the soil microbiome can be genus-specific and be controlled by different soil properties.

Prescribed burning decreased C availability 2 days after fire as shown by changes in soil properties (total C and C:N ratio) and potential enzyme activities involved in soil C decomposition (BGA) (Table 1). A previous study reported a decrease in soil C concentration and C–related enzyme activities after frequent fires across different ecosystems (Pellegrini et al., 2018). The authors attributed these responses mainly due to the loss of plant biomass after fire. In this study, decrease in total C concentration and potential BGA enzyme activity representative of the C cycle was observed within 2 days after fire. However, BGA significantly increased 2–3 months after fire to levels similar to pre-fire levels suggesting a recovery in microbial activity. Similarly, our previously published work showed fast (< 60 days) aboveground vegetation recovery following fire (Bracho et al., 2021). These observations are also in line with a previous study conducted in Florida native rangelands, which suggested that more favorable environmental conditions (greater soil temperature and soil moisture) for soil microbes in summer vs. winter can probably favor the recovery of BGA activity after fire (Xu et al., 2017). As documented in Kohmann et al. (2022), prescribed burning did not transfer large amounts of heat below 2.5 cm soil depth, therefore limiting impacts of fire on soil responses in the short-term. As the field sites in this study have been burned and grazed for about 15 years, we acknowledge that soil responses to prescribed burning should be also examined in comparison to areas that have never been grazed or burned in future studies.

In contrast to soil C, fire increased soil total N concentration 2 days after fire. Increases in soil total N concentration after fire have been previously reported and linked to surface charring and consumption of litter, SOM, and release of soil available nutrients in forest and flatwood ecosystems (Giardina and Rhoades, 2001; Schafer and Mack, 2010; Turner et al., 2007). Increased inorganic N levels immediately after fire can be due to the mineralization of organic N (Dannenmann et al., 2018; Prieto-Fernández et al., 2004; Schafer and Mack, 2010). However, in the current study, soil extractable NH_4^+ concentration decreased 2–3 months after fire, which is consistent with reports in other N-limited ecosystems (Turner et al., 2007; Vitousek and Matson, 1985). Decreases in NAG activity at 2 days after fire and its recovery after 2–3 months after fire suggests that prescribed fire has only short-term effects on soil potential enzymes activities, as previously observed (Menichetti et al., 2015). Other factors, such as vegetative regrowth, could also increase NAG activity to levels greater than pre-fire (Bracho et al., 2021; Ndiaye et al., 2000). However, it is expected that increases in NAG may eventually increase available soil N pools, as NAG was positively correlated with extractable NH_4^+ in our study and is often used as an index of N mineralization (Ekenler and Tabatabai, 2004).

Prescribed burning impacted soil pH and soil macro- and micronutrients. Slight decreases in soil pH 2–3 months after fire could be related to rapid uptake of nutrients by above-ground vegetation (Boerner et al., 1988). Conversely, other studies have shown an increase in soil pH after fire due to accumulated ashes and an influx of base cations from ashes (Bennett et al., 2003; Murphy et al., 2006). While no effect of fire was observed for Mehlich-extractable K, Mg, Ca, and Mg or total P concentration, we found a reduction in extractable P concentration 2 days after fire. Although the mechanism responsible for changes in soil P lability is unclear, one possible explanation is the formation of insoluble metal phosphates (Smith, 1970; Gray and Dighton, 2006).

In the current study, prescribed burning had no significant effects on the diversity of bacterial and fungal communities 2 days following fire. This is in line with previous studies which reported no changes in bacterial diversity 2 h (Li et al., 2019) and 2 weeks (Kranz and Whitman, 2019) post-fire in forests. This lack of response was mainly attributed to low fire intensity and short heating duration. It has been well established that the greater the consumption of duff and higher soil heating, the greater the immediate negative impact on soil microorganisms (Hungerford et al., 1995). It is also expected that fire severity will regulate the direction and magnitude of soil microbial responses (Lucas-Borja et al., 2019). In the current study, fire was characterized by low intensity with a short heating duration (Kohmann et al., 2022), which likely limited its impacts on soil microbial communities (González-Pérez et al., 2004; Jorgensen and Hodges, 1970). However, it is also expected that fire severity will regulate the direction and magnitude of soil microbial responses (Lucas-Borja et al., 2019). It is also worth noting that the main focus of this study was on short-term microbial responses. We did not examine changes in soil microbial communities 2–3 months post fire because we cannot elucidate whether variations in the diversity and compositions soil microbiota at that time, if any, would have been due to the prescribed burning event and/or the impact of many other abiotic and biotic variables (e.g., vegetation recovery, root exudates, and climatic factors, etc.). For example, vegetation recovery has been reported within 60 days following fire in the study sites (Bracho et al., 2021).

Although the diversity and composition of bacterial and fungal communities was not impacted by fire, there were significant changes in the relative abundance of specific bacterial and fungal taxa. In addition, we found that the impact of prescribed burning on specific soil properties 2 days after fire controlled variations in the relative abundance of specific bacterial and fungal taxa. That correlation between microbial communities and soil properties were genus- and soil property-specific suggests that prescribed burning impacts on the soil microbiome of the study Florida rangelands are not widespread. Acidobacteria, Actinobacteria, Firmicutes, and Proteobacteria were the dominant bacterial phyla in our study site. These results are consistent with previous studies in Entisols and marsh soils in Florida (Ho and Chambers, 2019; Khodadad et al., 2011). Among those phyla, taxa belonging to Firmicutes resist fire changes (Ferrenberg et al., 2013) and remain stable after fire due to their ability to cope abiotic stress (Lladó et al., 2017). Fire significantly increased the relative abundance of Desulfurellales order and *Variibacter* genera. Members of the Desulfurellales are obligate sulfur-metabolizing thermophiles (Flores et al., 2012) that have flourished after fire in our site, and they are involved in C, N, P and S cycles (Wang et al., 2016). *Variibacter* is often a dominant genus in karst soil, saline lakes, and forests controlling the ecosystem N cycle (Kim et al., 2014; Wan et al., 2021), and this genus was positively related with soil total N concentration in our study.

Fungi are generally dominant in less intensively managed ecosystems under a nutrient-limited environment, such as native rangelands, and can better utilize C substrates than bacteria (Bardgett et al., 1998; Strickland and Rousk, 2010). Ascomycota was the predominant phylum in our study, which is not surprising as it includes saprotrophs with enhanced capabilities to assimilate C and N after disturbances and the ability to tolerate environmental stresses like recurring fires (Egidi et al., 2019). Reduction in the relative abundance of Pleosporales and Eurotiales orders, and *Taloromyces* (mainly responsible for breakdown of SOM) was observed after fire (Pangging et al., 2019; Zhang et al., 2012).

It cannot be ruled out that relic DNA may have hindered the detection of spatial and temporal changes in microbial communities in the short-term as previously observed in other ecosystems (Carini et al., 2020). However, amplicon sequencing using total DNA is a commonly used method to characterize microbial community composition even in ecosystems subjected to prescribed burning (Hugerth and Andersson, 2017; Kranz and Whitman, 2019; Tremblay et al., 2015; Zhang et al., 2021).

Significant associations between soil properties and specific bacterial and fungal taxa revealed prescribed burning can influence variations in the soil microbiome to some extent. For example, soil pH often has a major influence on soil microbial communities (Rousk et al., 2010), and various acidophilic bacteria (*Acidibacter*, *Acidicaldus, Acidothermus*, and *Methanobacterium*) and fungi (*Cladophialophora*) genera showed a strong correlation with soil pH in our study. Thus, even slight changes in soil pH after fire might control the abundance of certain microbial communities as these taxa are often dominant in acidic soils (Kotsyurbenko et al., 2007; Grządziel and Gałązka, 2019). *Bacillus* are ubiquitous in nature being found in diverse environments, and in this study its abundance showed a strong positive correlation with total C concentration, as also found by Liu et al. (2019). Among different microbial groups associated with N cycling, *Bradyrhizobium, Candidatus Koribacter*, *Candidatus Solibacter*, *Methanobacterium*, and *Methylocystis* were correlated with total N concentration in our study (Acosta-Martínez et al., 2007; Lacerda-Júnior et al., 2019; Ormeño-Orrillo and Martínez-Romero, 2019; Szafranek-Nakonieczna et al., 2019). The positive correlation of NH_4^+ was observed with several bacterial genera that are known to contain nitrifiers (*Burkholderia-Paraburkholderia*, *Planctomyces*, and *Rhodanobacter*) and denitrifiers (*Candidatus Methylomirabilis*, and *Opititus*) in our study (Espenberg et al., 2018; Versantvoort et al., 2018).

BGA was negatively correlated with *Acidothermus*, *Sorangium* and positively correlated with *Tumebacillus*. Species of *Acidothermus* and *Sorangium* can harbor hydrolytic enzymes, which could explain their correlation with BGA in our study (Barabote et al., 2009; Krishna and Mohan, 2017). Saprotrophic basidiomycetes are responsible for fresh litter decomposition that produce hydrolytic enzymes. Some of the basidiomycetes species *Candidatus Koribacter*, *Candidatus Solibacter*, *Methanobacterium*, *Methylocystis*, and *Gymnopus* showed a positive correlation to BGA and NAG activity in our study (Valášková et al., 2007). NAG activity is correlated to the fungi *Pseudeurotium* and *Archaeorhizomyces*, which are responsible for decomposition found in rhizosphere soils (Rosling et al., 2013; Wang et al., 2021).

5. Conclusion

Our study evaluated short-term soil microbial and nutrient responses to prescribed burning in native rangelands of Florida. Results showed that prescribed burning causes only short-term changes (within 2 days) in selected soil properties, which generally returned to pre-fire levels after 2–3 months. Although the diversity and composition of bacterial and fungal communities was not significantly impacted by prescribed burning this study shows significant changes in the relative abundance of specific bacterial and fungal taxa occurred. In addition, prescribed burning impacts on the soil microbiome were genus-specific and appear to be controlled by different and specific soil properties. Although the impacts of prescribed fire on soil properties have been widely acknowledged, this study is the first to document short-term fire-induced soil microbial responses in Florida subtropical native rangelands. Our findings contribute to a wealth of evidence indicating limited effects of prescribed fire on soil microbial community diversity and composition, particularly in fire adapted habitats. Long-term studies are warranted to investigate the impacts of repeated prescribed burning events on the biogeochemical cycles of nutrients in rangeland ecosystems.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was a contribution from the Long-Term Agroecosystem Research (LTAR) network. The LTAR network is supported by the USDA.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2023.104914.

References

Acosta-Martínez, V., Cruz, L., Sotomayor-Ramírez, D., Pérez-Alegría, L., 2007. Enzyme activities as affected by soil properties and land use in a tropical watershed. Appl. Soil Ecol. 35 (1), 35–45. https://doi.org/10.1016/j.apsoil.2006.05.012.

Adewopo, J., Silveira, M., Xu, S., Gerber, S., Sollenberger, L., Martin, T.A., 2014. Management intensification impacts on soil and ecosystem carbon stocks in subtropical grasslands. Soil Sci. Soc. Am. J. 78 https://doi.org/10.2136/sssaj2013.12.0523.

Alcañiz, M., Outeiro, L., Francos, M., Úbeda, X., 2018. Effects of prescribed fires on soil properties: a review. Sci. Total Environ. 613–614, 944–957. https://doi.org/10.1016/j.scitotenv.2017.09.144.

Apprill, A., McNally, S., Parsons, R., Weber, L., 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. Aquat. Microb. Ecol. 75 (2), 129–137. https://doi.org/10.3354/ame01753.

Barabote, R.D., Xie, G., Leu, D.H., Normand, P., Necsulea, A., Daubin, V., Médigue, C., Adney, W.S., Xu, X.C., Lapidus, A., Parales, R.E., Detter, C., Pujic, P., Bruce, D., Lavire, C., Challacombe, J.F., Brettin, T.S., Berry, A.M., 2009. Complete genome of the cellulolytic thermophile Acidothermus cellulolyticus 11B provides insights into its ecophysiological and evolutionary adaptations. Genome Res. 19 (6), 1033–1043. https://doi.org/10.1101/gr.084848.108.

Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biol. Biochem. 30 (14), 1867–1878. https://doi.org/10.1016/S0038-0717(98)00069-8.

Barreiro, A., Díaz-Raviña, M., 2021. Fire impacts on soil microorganisms: mass, activity, and diversity. Curr.Opin.Environ.Sci.Health 22, 100264. https://doi.org/10.1016/j.coesh.2021.100264.

Bennett, L.T., Judd, T.S., Adams, M.A., 2003. Growth and nutrient content of perennial grasslands following burning in semi-arid, sub-tropical Australia. Plant Ecol. 164 (2), 185–199. https://doi.org/10.1023/A:1021253600712.

Boerner, R.E.J., Lord, T.R., Peterson, J.C., 1988. Prescribed burning in the oak-pine forest of the New Jersey pine barrens: effects on growth and nutrient dynamics of two quercus species. Am. Midl. Nat. 120 (1), 108–119. https://doi.org/10.2307/2425891. JSTOR.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J.E., Bittinger, K., Brejnrod, A., Brislawn, C.J., Brown, C.T., Callahan, B.J., Caraballo-Rodríguez, A.M., Chase, J., Caporaso, J.G., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat. Biotechnol. 37 (8), 8 https://doi.org/10.1038/s41587-019-0209-9.

Bracho, R., Silveira, M.L., Boughton, R., Sanchez, J.M.D., Kohmann, M.M., Brandani, C. B., Celis, G., 2021. Carbon dynamics and soil greenhouse fluxes in a Florida's native rangeland before and after fire. Agric. For. Meteorol. 311, 108682 https://doi.org/10.1016/j.agrformet.2021.108682.

Carini, P., Delgado-Baquerizo, M., Hinckley, E.-L.S., Holland-Moritz, H., Brewer, T.E., Rue, G., Vanderburgh, C., McKnight, D., Fierer, N., 2020. Effects of spatial variability and relic DNA removal on the detection of temporal dynamics in soil microbial communities. MBio 11 (1). https://doi.org/10.1128/mBio.02776-19.

Carter, M.C., Darwin Foster, C., 2004. Prescribed burning and productivity in southern pine forests: a review. For. Ecol. Manag. 191 (1), 93–109. https://doi.org/10.1016/j.foreco.2003.11.006.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143 (1), 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Creamer, C.A., Filley, T.R., Olk, D.C., Stott, D.E., Dooling, V., Boutton, T.W., 2013. Changes to soil organic N dynamics with leguminous woody plant encroachment into grasslands. Biogeochemistry 113 (1), 307–321. https://doi.org/10.1007/s10533-012-9757-5.

Dannenmann, M., Diaz-Pines, E., Kitzler, B., Karhu, K., Tejedor, J., Ambus, P., Parra, A., Sanchez-Martin, L., Resco, V., Ramirez, D.A., Povoas-Guimaraes, L., Willibald, G., Gasche, R., Zechmeister-Boltenstern, S., Kraus, D., Castaldi, S., Vallejo, A., Rubio, A., Moreno, J.M., Butterbach-Bahl, K., 2018. Postfire nitrogen balance of Mediterranean shrublands: direct combustion losses versus gaseous and leaching losses from the postfire soil mineral nitrogen flush. Glob. Chang. Biol. 24 (10), 4505–4520. https://doi.org/10.1111/gcb.14388.

Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14 (6), 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x.

Dove, N.C., Hart, S.C., 2017a. Fire reduces fungal species richness and in situ mycorrhizal colonization: a meta-analysis. Fire. Ecology 13 (2), 2. https://doi.org/10.4996/fireecology.130237746.

Durán, J., Rodríguez, A., Fernández-Palacios, J.M., Gallardo, A., 2008. Changes in soil N and P availability in a Pinus canariensis fire chronosequence. For. Ecol. Manag. 256 (3), 384–387. https://doi.org/10.1016/j.foreco.2008.04.033.

Duvall, V.L., Hilmon, J.B., 1965. New grazing research programs for southern forest ranges. J. Range Manag. 18 (3), 132. https://doi.org/10.2307/3895623.

Egidi, E., Delgado-Baquerizo, M., Plett, J.M., Wang, J., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., 2019. A few Ascomycota taxa dominate soil fungal communities worldwide. Nat. Commun. 10 (1), 1–9. https://doi.org/10.1038/s41467-019-10373-z.

Ekenler, M., Tabatabai, M.A., 2004. β-Glucosaminidase activity as an index of nitrogen mineralization in soils. Commun. Soil Sci. Plant Anal. 35 (7–8), 1081–1094. https://doi.org/10.1081/CSS-120030588.

Espenberg, M., Truu, M., Mander, Ü., Kasak, K., Nõlvak, H., Ligi, T., Oopkaup, K., Maddison, M., Truu, J., 2018. Differences in microbial community structure and nitrogen cycling in natural and drained tropical peatland soils. Sci. Rep. 8 (1), 4742. https://doi.org/10.1038/s41598-018-23032-y.

Fernandes, P.M., Davies, G.M., Ascoli, D., Fernández, C., Moreira, F., Rigolot, E., Stoof, C. R., Vega, J.A., Molina, D., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Front. Ecol. Environ. 11 (s1), e4–e14. https://doi.org/10.1890/120298.

Ferrenberg, S., O'Neill, S.P., Knelman, J.E., Todd, B., Duggan, S., Bradley, D., Robinson, T., Schmidt, S.K., Townsend, A.R., Williams, M.W., Cleveland, C.C., Melbourne, B.A., Jiang, L., Nemergut, D.R., 2013. Changes in assembly processes in soil bacterial communities following a wildfire disturbance. ISME J. 7 (6), 6 https://doi.org/10.1038/ismej.2013.11.

Flores, G.E., Hunter, R.C., Liu, Y., Mets, A., Schouten, S., Reysenbach, A.-L., 2012. Hippea jasoniae sp. nov. and Hippea alviniae sp. nov., thermoacidophilic members of the class Deltaproteobacteria isolated from deep-sea hydrothermal vent deposits. Int. J. Syst. Evol. Microbiol. 62 (Pt_6), 1252–1258. https://doi.org/10.1099/ijs.0.033001-0.

Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol. Ecol. 2 (2), 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x.

German, D.P., Marcelo, K.R.B., Stone, M.M., Allison, S.D., 2012. The Michaelis-Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study. Glob. Chang. Biol. 18 (4), 1468–1479. https://doi.org/10.1111/j.1365-2486.2011.02615.x.

German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L., Allison, S.D., 2011. Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. Soil Biol. Biochem. 43 (7), 1387–1397. https://doi.org/10.1016/j.soilbio.2011.03.017.

Giardina, C.P., Rhoades, C.C., 2001. Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. For. Ecol. Manag. 140 (1), 19–28. https://doi.org/10.1016/S0378-1127(00)00272-3.

Giuditta, E., Marzaioli, R., Esposito, A., Ascoli, D., Stinca, A., Mazzoleni, S., Rutigliano, F. A., 2019. Soil microbial diversity, biomass, and activity in two pine plantations of Southern Italy treated with prescribed burning. Forests 11 (1), 19.

González-Pérez, J.A., González-Vila, F.J., Almendros, G., Knicker, H., 2004a. The effect of fire on soil organic matter—a review. Environ. Int. 30 (6), 855–870. https://doi.org/10.1016/j.envint.2004.02.003.

Gray, D.M., Dighton, J., 2006. Mineralization of forest litter nutrients by heat and combustion. Soil Biology and Biochemistry 38 (6), 1469–1477.

Grządziel, J., Gałązka, A., 2019. Fungal biodiversity of the most common types of polish soil in a long-term microplot experiment. Front. Microbiol. 10 https://doi.org/10.3389/fmicb.2019.00006.

Harper, A.R., Doerr, S.H., Santin, C., Froyd, C.A., Sinnadurai, P., 2018. Prescribed fire and its impacts on ecosystem services in the UK. Sci. Total Environ. 624, 691–703. https://doi.org/10.1016/j.scitotenv.2017.12.161.

Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D., Boyle, S.I., 2005b. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. For. Ecol. Manag. 220 (1), 166–184. https://doi.org/10.1016/j.foreco.2005.08.012.

Ho, J., Chambers, L.G., 2019. Altered soil microbial community composition and function in two shrub-encroached marshes with different physicochemical gradients. Soil Biol. Biochem. 130, 122–131. https://doi.org/10.1016/j.soilbio.2018.12.004.

Hu, T., Hu, H., Li, F., Zhao, B., Wu, S., Zhu, G., Sun, L., 2019. Long-term effects of post-fire restoration types on nitrogen mineralisation in a Dahurian larch (Larix gmelinii) forest in boreal China. Sci. Total Environ. 679, 237–247. https://doi.org/10.1016/j.scitotenv.2019.05.008.

Hugerth, L.W., Andersson, A.F., 2017. Analysing microbial community composition through amplicon sequencing: from sampling to hypothesis testing. Front. Microbiol. 8 https://www.frontiersin.org/article/10.3389/fmicb.2017.01561. https://www.frontiersin.org/article/10.3389/fmicb.2017.01561.

Hungerford, R.D., Frandsen, W.H., Ryan, K.C., 1995. Ignition and burning characteristics of organic soils. In: Tall Timbers Fire Ecology Conference, 19, pp. 78–91.

J. Vendramini, R.S.K., 2019. Managing South Florida Range for Cattle. July 3. https://edis.ifas.ufl.edu/ag173.

Jorgensen, J.R., Hodges, C.S., 1970. Microbial characteristics of a forest soil after twenty years of prescribed burning. Mycologia 62 (4), 4. https://doi.org/10.2307/3757661. JSTOR.

Kalmbacher, R.S., Long, K.R., Johnson, M.K., Martin, F.G., 1984. Botanical composition of diets of cattle grazing south Florida rangeland. J. Range Manag. 37 (4), Article 4. https://doi.org/10.2307/3898706.

Khodadad, C.L.M., Zimmerman, A.R., Green, S.J., Uthandi, S., Foster, J.S., 2011. Taxa-specific changes in soil microbial community composition induced by pyrogenic carbon amendments. Soil Biol. Biochem. 43 (2), 385–392. https://doi.org/10.1016/j.soilbio.2010.11.005.

Kim, K.K., Lee, K.C., Eom, M.K., Kim, J.-S., Kim, D.-S., Ko, S.-H., Kim, B.-H., Lee, J.-S., 2014. Variibacter gotjawalensis gen. nov., sp. nov., isolated from soil of a lava forest. Antonie Van Leeuwenhoek 105 (5), 915–924. https://doi.org/10.1007/s10482-014-0146-z.

Knelman, J.E., Graham, E.B., Ferrenberg, S., Lecoeuvre, A., Labrado, A., Darcy, J.L., Nemergut, D.R., Schmidt, S.K., 2017. Rapid shifts in soil nutrients and decomposition enzyme activity in early succession following forest fire. Forests 8 (9), 9. https://doi.org/10.3390/f8090347.

Kohmann, M.M., Silveira, M.L., Brandani, C.B., Sanchez, J.M.D., da Silva, H.M.S., Vendramini, J.M.B., 2022. Plant litter chemical characteristics drive decomposition in subtropical rangelands under prescribed fire management. Rangel. Ecol. Manag. 84, 22–30. https://doi.org/10.1016/j.rama.2022.05.002.

Kotsyurbenko, O.R., Friedrich, M.W., Simankova, M.V., Nozhevnikova, A.N., Golyshin, P. N., Timmis, K.N., Conrad, R., 2007. Shift from acetoclastic to H2-dependent methanogenesis in a West Siberian peat bog at low pH values and isolation of an acidophilic Methanobacterium strain. Appl. Environ. Microbiol. 73 (7), 2344–2348.

Kranz, C., Whitman, T., 2019b. Short communication: surface charring from prescribed burning has minimal effects on soil bacterial community composition two weeks post-fire in jack pine barrens. Appl. Soil Ecol. 144, 134–138. https://doi.org/10.1016/j.apsoil.2019.07.004.

Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. EnergyEcol.Environ. 2 (4), 236–249. https://doi.org/10.1007/s40974-017-0064-9.

Lacerda-Júnior, G.V., Noronha, M.F., Cabral, L., Delforno, T.P., de Sousa, S.T.P., Fernandes-Júnior, P.I., Melo, I.S., Oliveira, V.M., 2019. Land use and seasonal effects on the soil microbiome of a Brazilian dry forest. Front. Microbiol. 10, 648. https://doi.org/10.3389/fmicb.2019.00648.

Lang, F., Bauhus, J., Frossard, E., George, E., Kaiser, K., Kaupenjohann, M., Krüger, J., Matzner, E., Polle, A., Prietzel, J., Rennenberg, H., Wellbrock, N., 2016. Phosphorus in forest ecosystems: new insights from an ecosystem nutrition perspective. J. Plant Nutr. Soil Sci. 179 (2), 129–135. https://doi.org/10.1002/jpln.201500541.

Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. Biotropica 25 (2), 130–150. https://doi.org/10.2307/2389178.

Li, W., Niu, S., Liu, X., Wang, J., 2019. Short-term response of the soil bacterial community to differing wildfire severity in Pinus tabulaeformis stands. Sci. Rep. 9, 1148. https://doi.org/10.1038/s41598-019-38541-7.

Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Miller, R.F., 2016. Synthesis paper: assessment of research on rangeland fire as a management practice. Rangel. Ecol. Manag. 69 (6), 415–422. https://doi.org/10.1016/j.rama.2016.07.013.

Liu, J., Cui, X., Liu, Z., Guo, Z., Yu, Z., Yao, Q., Sui, Y., Jin, J., Liu, X., Wang, G., 2019. The diversity and geographic distribution of cultivable bacillus-like bacteria across black soils of northeast China. Front. Microbiol. 10 https://doi.org/10.3389/fmicb.2019.01424.

Lladó, S., López-Mondéjar, R., Baldrian, P., 2017. Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. Microbiol. Mol. Biol. Rev. 81 (2), 2 https://doi.org/10.1128/MMBR.00063-16.

López-Poma, R., Bautista, S., 2014. Plant regeneration functional groups modulate the response to fire of soil enzyme activities in a Mediterranean shrubland. Soil Biol. Biochem. 79, 5–13. https://doi.org/10.1016/j.soilbio.2014.08.016.

Lucas-Borja, M.E., Miralles, I., Ortega, R., Plaza-Alvarez, P.A., Gonzalez-Romero, J., Sagra, J., Soriano-Rodriguez, M., Certini, G., Moya, D., Heras, J., 2019. Immediate fire-induced changes in soil microbial community composition in an outdoor experimental controlled system. Sci. Total Environ. 696 https://doi.org/10.1016/j.scitotenv.2019.134033. UNSP 134033.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.Journal 17 (1), 1. https://doi.org/10.14806/ej.17.1.200.

McMurdie, P.J., Holmes, S., 2013. Phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PLOS ONE 8 (4), e61217. https://doi.org/10.1371/journal.pone.0061217.

Menichetti, L., Reyes Ortigoza, A.L., García, N., Giagnoni, L., Nannipieri, P., Renella, G., 2015. Thermal sensitivity of enzyme activity in tropical soils assessed by the Q10 and equilibrium model. Biol. Fertil. Soils 51, 299–310.

Mikita-Barbato, R.A., Kelly, J.J., Tate, R.L., 2015. Wildfire effects on the properties and microbial community structure of organic horizon soils in the New Jersey Pinelands. Soil Biol. Biochem. 86, 67–76. https://doi.org/10.1016/j.soilbio.2015.03.021.

Murphy, J.D., Johnson, D.W., Miller, W.W., Walker, R.F., Carroll, E.F., Blank, R.R., 2006. Wildfire effects on soil nutrients and leaching in a Tahoe Basin watershed. J. Environ. Qual. 35 (2), 479–489. https://doi.org/10.2134/jeq2005.0144.

Nannipieri, P., Ascher, J., Ceccherini, M.T., Landi, L., Pietramellara, G., Renella, G., 2017. Microbial diversity and soil functions. Eur. J. Soil Sci. 68 (1), 12–26. https://doi.org/10.1111/ejss.4_12398.

Nannipieri, P., Badalucco, L., 2003. Biological processes. In: Handbook of Processes And Modelling in the Soil-Plant System, pp. 57–82.

Ndiaye, E.L., Sandeno, J.M., McGrath, D., Dick, R.P., 2000. Integrative biological indicators for detecting change in soil quality. Am. J. Altern. Agric. 15 (1), 26–36.

Nuzzo, A., Satpute, A., Albrecht, U., Strauss, S.L., 2020. Impact of soil microbial amendments on tomato rhizosphere microbiome and plant growth in field soil. Microb. Ecol. 80 (2), 2 https://doi.org/10.1007/s00248-020-01497-7.

Oliver, A.K., Callaham, Jumpponen, A., 2015. Soil fungal communities respond compositionally to recurring frequent prescribed burning in a managed southeastern US forest ecosystem. For. Ecol. Manag. 345, 1–9.

Ormeño-Orrillo, E., Martínez-Romero, E., 2019. A genomotaxonomy view of the Bradyrhizobium genus. Front. Microbiol. 10 https://doi.org/10.3389/fmicb.2019.01334.

Pangging, M., Nguyen, T.T.T., Lee, H.B., 2019. New records of four species belonging to eurotiales from soil and freshwater in Korea. Mycobiology 47 (2), 154–164. https://doi.org/10.1080/12298093.2018.1554777.

Pellegrini, A.F.A., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzik, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R.L., Randerson, J.T., Jackson, R. B., 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. Nature 553 (7687), 194–198. https://doi.org/10.1038/nature24668.

Prendergast-Miller, M.T., de Menezes, A.B., Macdonald, L.M., Toscas, P., Bissett, A., Baker, G., Farrell, M., Richardson, A.E., Wark, T., Thrall, P.H., 2017. Wildfire impact: natural experiment reveals differential short-term changes in soil microbial communities. Soil Biol. Biochem. 109, 1–13. https://doi.org/10.1016/j.soilbio.2017.01.027.

Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128 (3), 309–327. https://doi.org/10.1111/oik.05738.

Prieto-Fernández, Á., Carballas, M., Carballas, T., 2004. Inorganic and organic N pools in soils burned or heated: immediate alterations and evolution after forest wildfires. Geoderma 121 (3), 291–306. https://doi.org/10.1016/j.geoderma.2003.11.016.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41 (D1), D590–D596. https://doi.org/10.1093/nar/gks1219.

R Core Team, 2020. R Core Team R: a language and environment for statistical computing. Foundation for Statistical Computing.

Rodríguez, J., González-Pérez, J.A., Turmero, A., Hernández, M., Ball, A.S., González-Vila, F.J., Enriqueta Arias, M., 2017. Wildfire effects on the microbial activity and diversity in a Mediterranean forest soil. Catena 158, 82–88. https://doi.org/10.1016/j.catena.2017.06.018.

Rosling, A., Timling, I., Taylor, D.L., 2013. Archaeorhizomycetes: patterns of distribution and abundance in soil. In: Horwitz, B.A., Mukherjee, P.K., Mukherjee, M., Kubicek, C.P. (Eds.), Genomics of Soil- and Plant-associated Fungi. Springer, pp. 333–349. https://doi.org/10.1007/978-3-642-39339-6_14.

Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J. 4 (10), 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11 (s1), e15–e24. https://doi.org/10.1890/120329.

Schafer, J.L., Mack, M.C., 2010. Short-term effects of fire on soil and plant nutrients in palmetto flatwoods. Plant Soil 334 (1), 433–447. https://doi.org/10.1007/s11104-010-0394-2.

Schuman, G.E., Janzen, H.H., Herrick, J.E., 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environ. Pollut. 116 (3), 3 https://doi.org/10.1016/S0269-7491(01)00215-9.

Singh, G., Schoonover, J.E., Monroe, K.S., Williard, K.W.J., Ruffner, C.M., 2017. Prescribed burning and erosion potential in mixed hardwood forests of southern Illinois. Forests 8 (4), 4. https://doi.org/10.3390/f8040112.

Sinsabaugh, R.L., Gallo, M.E., Lauber, C., Waldrop, M.P., Zak, D.R., 2005. Extracellular enzyme activities and soil organic matter dynamics for northern hardwood forests receiving simulated nitrogen deposition. Biogeochemistry 75 (2), 2. https://doi.org/10.1007/s10533-004-7112-1.

Smith, D.W., 1970. Concentrations of soil nutrients before and after fire. Can. J. Soil Sci. 50 (1), 17–29. https://doi.org/10.4141/cjss70-003.

Strickland, M.S., Rousk, J., 2010. Considering fungal:bacterial dominance in soils – methods, controls, and ecosystem implications. Soil Biol. Biochem. 42 (9), 1385–1395. https://doi.org/10.1016/j.soilbio.2010.05.007.

Szafranek-Nakonieczna, A., Wolińska, A., Zielenkiewicz, U., Kowalczyk, A., Stępniewska, Z., Błaszczyk, M., 2019. Activity and identification of methanotrophic bacteria in arable and no-tillage soils from Lublin region (Poland). Microb. Ecol. 77 (3), 701–712. https://doi.org/10.1007/s00248-018-1248-3.

Tedersoo, L., Sánchez-Ramírez, S., Kõljalg, U., Bahram, M., Döring, M., Schigel, D., May, T., Ryberg, M., Abarenkov, K., 2018. High-level classification of the fungi and a tool for evolutionary ecological analyses. Fungal Divers. 90 (1), 135–159. https://doi.org/10.1007/s13225-018-0401-0.

Tremblay, J., Singh, K., Fern, A., Kirton, E., He, S., Woyke, T., Lee, J., Chen, F., Dangl, J., Tringe, S., 2015. Primer and platform effects on 16S rRNA tag sequencing. Front. Microbiol. 6 https://www.frontiersin.org/article/10.3389/fmicb.2015.00771. https://www.frontiersin.org/article/10.3389/fmicb.2015.00771.

Turner, M.G., Smithwick, E.A.H., Metzger, K.L., Tinker, D.B., Romme, W.H., 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. Proc. Natl. Acad. Sci. 104 (12), 4782–4789. https://doi.org/10.1073/pnas.0700180104.

Valášková, V., Šnajdr, J., Bittner, B., Cajthaml, T., Merhautová, V., Hofrichter, M., Baldrian, P., 2007. Production of lignocellulose-degrading enzymes and degradation of leaf litter by saprotrophic basidiomycetes isolated from a Quercus petraea forest. Soil Biol. Biochem. 39 (10), 2651–2660. https://doi.org/10.1016/j.soilbio.2007.05.023.

Versantvoort, W., Guerrero-Cruz, S., Speth, D.R., Frank, J., Gambelli, L., Cremers, G., van Alen, T., Jetten, M.S.M., Kartal, B., Op den Camp, H.J.M., Reimann, J., 2018. Comparative genomics of candidatus methylomirabilis species and description of Ca. Methylomirabilis lanthanidiphila. Front. Microbiol. 9 https://doi.org/10.3389/fmicb.2018.01672.

Vitousek, P.M., Matson, P.A., 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66 (4), 1360–1376. https://doi.org/10.2307/1939189.

Wan, Y., Li, W., Wang, J., Shi, X., 2021. Bacterial diversity and community in response to long-term nitrogen fertilization gradient in citrus orchard soils. Diversity 13, 282. https://doi.org/10.3390/d13070282.

Wang, C., Chen, D., Shen, J., Yuan, Q., Fan, F., Wei, W., Li, Y., Wu, J., 2021. Biochar alters soil microbial communities and potential functions 3–4 years after amendment in a double rice cropping system. Agric. Ecosyst. Environ. 311, 107291 https://doi.org/10.1016/j.agee.2020.107291.

Wang, W., Wang, H., Feng, Y., Wang, L., Xiao, X., Xi, Y., Luo, X., Sun, R., Ye, X., Huang, Y., Zhang, Z., Cui, Z., 2016. Consistent responses of the microbial community structure to organic farming along the middle and lower reaches of the Yangtze River. Sci. Rep. 6 (1), 1 https://doi.org/10.1038/srep35046.

Wickham, H., 2011. Ggplot2. WIREs Comput.Stat. 3 (2), 180–185. https://doi.org/10.1002/wics.147.

Willcox, E.V., Giuliano, W.M., 2010. Seasonal effects of prescribed burning and roller chopping on saw palmetto in flatwoods. For. Ecol. Manag. 259 (8), 8 https://doi.org/10.1016/j.foreco.2010.01.034.

Xu, S., Eisenhauer, N., Pellegrini, A.F.A., Wang, J., Certini, G., Guerra, C.A., Lai, D.Y.F., 2022. Fire frequency and type regulate the response of soil carbon cycling and storage to fire across soil depths and ecosystems: a meta-analysis. Sci. Total Environ. 825, 153921 https://doi.org/10.1016/j.scitotenv.2022.153921.

Xu, S., Silveira, M.L., Inglett, K.S., Sollenberger, L.E., Gerber, S., 2017. Soil microbial community responses to long-term land use intensification in subtropical grazing lands. Geoderma 293, 73–81. https://doi.org/10.1016/j.geoderma.2017.01.019.

Zhang, J., Kobert, K., Flouri, T., Stamatakis, A., 2014. PEAR: a fast and accurate Illumina Paired-End reAd mergeR. Bioinformatics 30 (5), 614–620. https://doi.org/10.1093/bioinformatics/btt593.

Zhang, M., Wang, W., Tang, L., Heenan, M., Wang, D., Xu, Z., 2021. Impacts of prescribed burning on urban forest soil: minor changes in net greenhouse gas emissions despite

evident alterations of microbial community structures. Appl. Soil Ecol. 158, 103780 https://doi.org/10.1016/j.apsoil.2020.103780.
Zhang, Y., Crous, P.W., Schoch, C.L., Hyde, K.D., 2012. Pleosporales. Fungal Divers. 53 (1), 1–221. https://doi.org/10.1007/s13225-011-0117-x.
Zhong, Z., Chen, Z., Xu, Y., Ren, C., Yang, G., Han, X., Ren, G., Feng, Y., 2018. Relationship between soil organic carbon stocks and clay content under different climatic conditions in central China. Forests 9 (10), 10. https://doi.org/10.3390/f9100598.