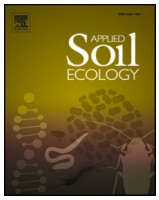
Applied Soil Ecology 185 (2023) 104795

Contents lists available at ScienceDirect

Applied Soil Ecology

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



Prescribed versus wildfire impacts on exotic plants and soil microbes in California grasslands

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ARTICLE INFO

Keywords:
California grasslands
prescribed burns
Tenaja fire
bacteria
fungi
invasive plants
microbial succession

ABSTRACT

Prescribed burns are often used as a management tool to decrease exotic plant cover and increase native plant cover in grasslands. These changes may also be mediated by fire impacts on soil microbial communities, which drive plant productivity and function. Yet, the ecological effects of prescribed burns compared to wildfires on either plant or soil microbial composition remain unclear. Grassland fires account for roughly 80 % of global annual fires, but only roughly 12 % of research on belowground impacts of fires occurs in grasslands, limiting our understanding of aboveground belowground connections in these important habitats. Here, we took advantage of the serendipitous opportunity of a wildfire burning through the same reserve where we had previously sampled a prescribed burn. This enabled us to investigate the impacts of a spring prescribed burn versus a fall wildfire on plant cover and community composition and bacterial and fungal richness, abundance, and composition. Our California grassland sites were thus within the same reserve, limiting environmental, vegetation, or climate variation between the sites. We used qPCR of 16S and 18S to assess impacts on bacterial and fungal abundance and Illumina MiSeq of 16S and ITS2 to assess impacts on bacterial and fungal richness and composition. Wildfire had stronger impacts than prescribed burns on microbial communities and both fires had similar impacts on plants with both prescribed and wildfire reducing exotic plant cover but neither reducing exotic plant richness. Fungal richness declined after the wildfire but not prescribed burn, but bacterial richness was unaffected by either. Yet, fire exposure in both fire types resulted in reduced bacterial and fungal abundance and altered bacterial and fungal composition. Plant diversity differentially impacted soil microbial diversity, with exotic plant diversity positively impacting bacterial richness and having no effect on arbuscular mycorrhizal richness. However, the remainder of the soil microbial communities were more related to aspects of soil chemistry including cation exchange capacity, organic matter, pH and phosphorous. Our coupled plant and soil community sampling allowed us to capture the sensitivity to fire of the fungal community and highlights the importance of potentially incorporating management actions such as soil or fungal amendments to promote this critical community that mediates native plant performance.

1. Introduction

Land managers increasingly need to grapple with the effects of fire on their management objectives, particularly in the Western United States, where prescribed burns and wildfires are becoming more frequent (Running, 2006; Ryan et al., 2013; Westerling et al., 2006). Comparisons between the effects of prescribed burns and wildfires have centered on forests where long-term fire suppression has altered the baseline conditions and can create undesirable negative effects (Ryan et al., 2013). However, similarities between prescribed burns and wildfires in other systems, such as grasslands, have yet to be fully explored. It is especially critical to research grassland fires since approximately 80 % of annual global fires occur in grasslands (Leys et al., 2018).

Within grasslands, leveraging insights from cultural burning practices, land managers are using prescribed burns as a management tool to

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https://doi.org/10.1016/j.apsoil.2022.104795
Received 12 May 2022; Received in revised form 27 November 2022; Accepted 27 December 2022

reduce the negative impacts of exotic plant species and increase native plant establishment and performance (Blackburn and Anderson, 1993; McKemey et al., 2020). Prescribed burns typically occur in spring, under higher moisture conditions that minimize fire spread and intensity (Ryan et al., 2013). In contrast, wildfires in the Western United States historically occur during the summer and fall, under drier fuel conditions (Stephens and Collins, 2004), thus leading to more intense burns. This difference in burn intensity may be a key factor in the beneficial management outcomes of prescribed burns (Knapp et al., 2009). A meta-analysis found that native plant species performance was enhanced after 81 % of prescribed burns and negatively affected after 28 % of wildfires (Alba et al., 2015), suggesting differential responses to fire types. Therefore, more studies are needed that compare the ecological effects of prescribed burns and wildfires in grasslands to improve the use of fire as a management tool.

The impacts of fire for land management have classically focused on native plant recovery but have overlooked the impacts that the soil microbial communities may have on vegetation recovery. Soil microbes are critical drivers of all major biogeochemical cycles (Crowther et al., 2019) and plant diversity and productivity (van der Heijden et al., 1998). Fungi play particularly critical roles in plant regeneration since up to 90 % of vascular plant species are associated with mycorrhizal fungal symbionts that increase access to nutrients in exchange for carbon (Brundrett and Tedersoo, 2018). Arbuscular mycorrhizal fungi (AMF) are especially important in driving grassland plant community dynamics (van der Heijden et al., 2006). AMF also co-occur with soil bacteria and fungi that are critical to plant growth, productivity, nutrition, and tolerance to drought and other abiotic stresses (Auge, 2001; Garbaye, 1994; Marro et al., 2022; Vacheron et al., 2013; Yuan et al., 2021). While it is clear that high severity fires negatively impact the richness and colonization of mycorrhizal fungi (Dove and Hart, 2017), microbial biomass (Dooley and Treseder, 2012), and bacterial and fungal richness and composition (Pressler et al., 2019), how prescribed burns versus wildfires affect microbiomes and subsequent plant successional dynamics is largely unknown. Since even a one-time soil inoculation can have long lasting impacts (up to 20 years) on grassland plant successional trajectories (Wubs et al., 2019), how prescribed burns versus wildfires influence soil microbiomes in grasslands is an important knowledge gap.

Exotic plant species, which are often the impetus for prescribed burns (Knapp et al., 2009), may create soil legacies that limit the recovery of native species (Kulmatiski et al., 2008). These soil legacies may interact with disturbances such as fire to synergistically reduce native plant performance (Suding et al., 2013). For example, many exotic plant species succeed and become invasive through reduced reliance on mycorrhizal symbionts (Pringle et al., 2009) or by suppressing native symbiotic communities in an invaded area (Mummey and Rillig, 2006; Vogelsang and Bever, 2009; Zubek et al., 2016), thus promoting the growth of invasive over native plant species. Alternatively, exotic plant species may alter the soil microbial community by enhancing pathogens (Eppinga et al., 2006) or promoting soil communities that enhance resource acquisition (Hawkes et al., 2006). These dynamics can result in a positive feedback loop (Callaway et al., 2004; Kulmatiski et al., 2008) and may interact with disturbances to further promote the performance of exotic species (Suding et al., 2013). They can also limit the outcomes of restoration efforts for native plant species (Lankau et al., 2014). Therefore, understanding the resilience of soil microbial community richness and composition in an invaded grassland is key to identifying and refining further management efforts. For example, it may be necessary to intervene and amend with bioinoculants from belowground soil communities beneath healthy native plant communities to achieve desired management outcomes (Aprahamian et al., 2016).

California grasslands are an ideal system to explore these dynamics. Prescribed burns are an important management tool for reducing the dominance of exotic species in once biodiverse native perennial grasslands (DiTomaso et al., 2006; Dyer, 2002; Menke, 1992). But prescribed burns have had mixed effects in helping to eliminate noxious weeds, especially in systems where invasive annual grasses within the genera *Avena* and *Bromus* outcompete native perennial bunchgrasses, thus failing to promote native plant species establishment (Corbin and D'Antonio, 2010; D'Antonio et al., 2002; Holmes and Rice, 1996; Meyer and Schiffman, 1999). These annual grasses can differentially impact biogeochemical cycling and soil communities for their benefit (Eviner and Hawkes, 2008; Hawkes et al., 2005; Vogelsang and Bever, 2009). Plant invasions can also lead to losses in soil mycorrhizal fungal biomass, colonization, and richness because many invasive plants either do not associate with mycorrhizal fungi or are less reliant on mycorrhizal fungal partners than native plants (Pringle et al., 2009). However, soil amendments to offset the impacts of these invaders can result in positive native plant responses (Emam, 2016; Sandel et al., 2011). Together, these dynamics suggest that a closer investigation of how soil microbial communities are changing with fire may provide some insight into improving the efficacy of grassland management.

Here, we explore the impacts of a prescribed burn versus a wildfire in a remnant perennial grassland on a Southern California reserve. While this study focuses on only a single prescribed burn and wildfire, the strength of this study is that both fires occurred in the same exact reserve, thereby limiting variation in environment, climate, and vegetation that would ordinarily obscure direct comparisons of prescribed and wildfires effects. We coupled time-series sampling of the soil microbial community with plant recovery data to ask how a prescribed burn versus wildfire impacts: Q1) native versus exotic plant cover and richness Q2) soil bacterial and fungal abundance and richness Q3) soil bacterial and fungal composition over time, and finally, Q4) how does AMF and soil microbial regeneration relate to native plant regeneration?

2. Materials and methods

2.1. Description of field site

Field work was conducted at the Santa Rosa Plateau Ecological Reserve, Riverside County, CA, USA in the location of the Burro prescribed burn unit and the Tenaja wildfire (Fig. 1; Table A.1). In Southern California grasslands, managers use spring prescribed burns in an effort to reduce exotic species cover and to retain cover of the native perennial bunchgrass *Stipa pulchra* (Valliere et al., 2019), but summer and fall wildfires also typically occur in California grasslands every 2–6 years (Fryer and Luensmann, 2012). The Burro prescribed burn took place on May 23, 2018 and burned 0.6 km^2. The Tenaja wildfire occurred serendipitously in a nearby location within the same reserve, lasted from Sept 4, 2019 through Sept 14, 2019, and burned 7.8 km^2. While the reserve consists of expanses of grassland intermixed with chaparral, coastal sage scrub, and oak woodlands (Valliere et al., 2019), both sites were in grasslands dominated by invasive annual grasses from the genus *Bromus*. The reserve has a Mediterranean climate where most precipitation falls from October through May, and rainfall was greater in 2018–19 compared to 2019–20 (Fig. A.1). Specifically, precipitation was approximately 648 mm for the 2018–19 growing season and 506 mm for the 2019–20 growing season, which was greater than the historical average of 446 mm (1970–2020) (PRISM Climate Group 2021). Both soils are Alfisols with the soil at the Tenaja site belonging to the Vallecitos series and the soil at the Burro site in the Murrieta series (https://casoilresource.lawr.ucdavis.edu/gmap/). The Burro Burn Unit is one of ten active prescribed burn management units in the reserve and has experienced four prescribed burns between 2004 and 2018. In contrast, the Tenaja site was retired from the prescribed management plan and experienced its last prescribed burn in 2006 (Dickens and Allen, 2009).

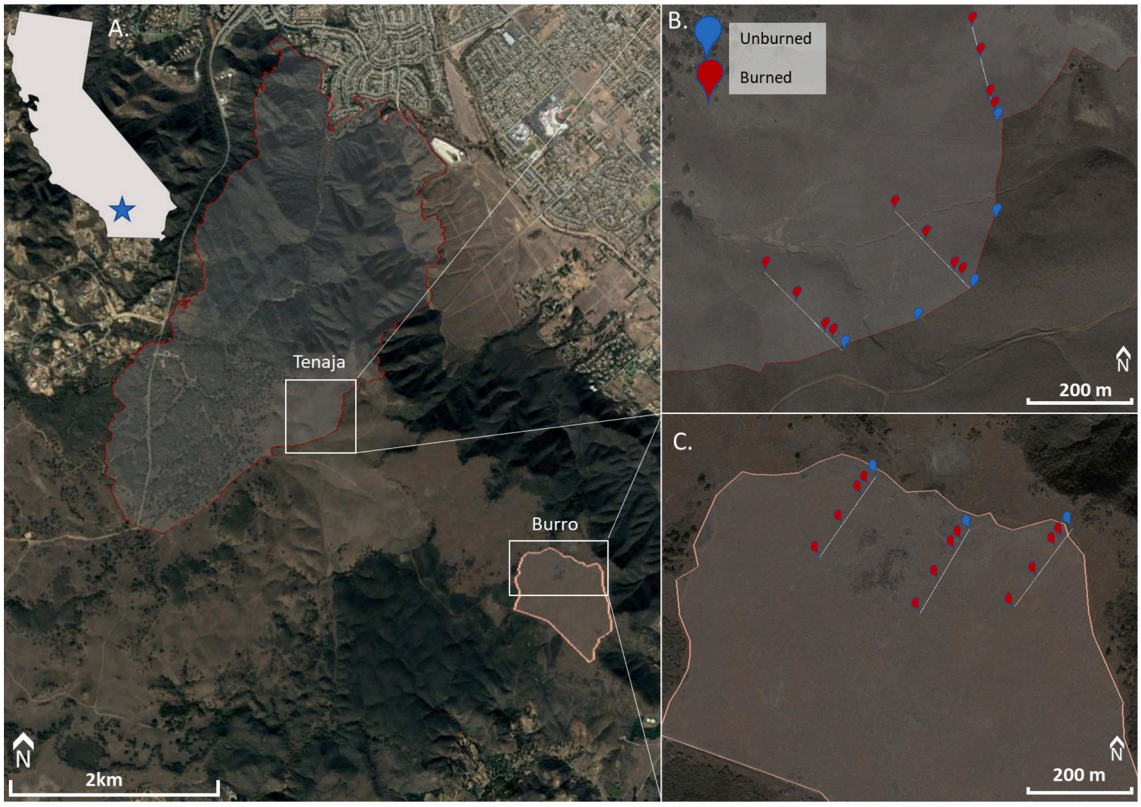

Fig. 1. Map of study site with both fire perimeters displayed (A) and insets show the sampling transects within the Tenaja wildfire (B) and Burro prescribed burn (C). Samples were collected 5 m outside the burn (blue), and 5 m, 20 m, 100 m, and 200 m (red) within the burn. Two additional unburned samples were sampled between transects within the Tenaja wildfire.

2.2. Sampling methods

We established three replicated transects with $1m^2$ plots at 5 m outside the burn line (A), and inside the burn line at 5 m (B), 20 m (C), 100 m (D) and 200 m (E) (Fig. 1). Transects were established based on proximity to contiguous habitat opposite from the burn section outlined by a firebreak. All transects were set up to be as far as possible from the access road, to cover as much area of the burn unit as possible, and to represent varying distances from the burn edge that might be of relevance to plants and microbes dispersing in from unburned edges. While the design was initially established to test the effects of time since fire and distance from burned edge on recovery of bacterial, fungal and plant communities, we observed no effect of distance from burned edge in our preliminary statistical analysis and dropped that variable from the analyses presented here. For the Tenaja wildfire, we added an additional 2 unburned plots in between the three transects for a total of 5 unburned plots and 12 burned plots. Therefore, we had 15 plots within the Burro prescribed burn unit and 17 within the Tenaja wildfire burn scar.

These plots were sampled at three time points post-fire. Within the Burro prescribed burn, soils were collected on June 2, 2018 at 2 weeks post-fire (1st post-fire), on November 28, 2018 at 6 months post-fire, and on May 6, 2019 at 12 months post-fire. The Tenaja wildfire soils were sampled on November 5, 2019 at 2 months post-fire (1st post fire), on November 19, 2019 at 2.5 months post-fire, and on May 13, 2020 at 7 months post-fire. The first time point captured the immediate effects of fire on the soil microbial community. Unfortunately, due to access constraints for the wildfire, this time frame differs between both burn units. The remaining two sampling points paralleled growing season phenology to account for the effects of intra-seasonal variation in precipitation on soil communities.

At every time point, for each plot, three ~5 cm deep subsamples (8 cm diameter and 10 cm deep releasable bulb planter filled half depth) were collected haphazardly from the $1m^2$ plot and combined for a single homogenized sample per plot. Between plots, gloves and soil corers were sterilized with 70 % ethanol. All soils were placed on ice in the field and stored in −80 °C freezer that night. A total of 45 soil samples were collected for the prescribed burn (3 transects × 5 plots × 3 time points) and 51 soil samples were collected for the wildfire (3 transects × 5 plots +2 additional unburned plots x 3 time points). At the first post-fire sampling, the amount of bare ground, rock, litter, char material and live plant cover was estimated for each $1m^2$ plot. Litter was identified as any plant growth from previous growing seasons that had not decomposed, and char material was identified as any ash or blackened charred residue present on the ground surface post fire. We used initial char as a proxy for fire severity as these post-fire residues may mediate nutrient pulses associated with fire and can be linked to fire severity (Neary et al., 1999). We visually estimated the plant community composition in each plot in the spring, which is peak growing season in this habitat. The cover of each species was estimated such that percent cover could be over 100 to capture species cover in the overlapping layers. Observers used reference squares of known percentages (i.e., 1 %, 5 %, and 10 %) to help estimate cover and increase consistency across different observers and any species with a single individual was given a value of 0.5 %. Additionally, for cover estimates above 15 and below 95, cover was rounded to nearest value divisible by 5 (i.e., 30 not 32), since more precise estimates are not possible with this method. Species names and classification of origin followed the Jepson Flora (Jepson Flora Project, 2022).

2.3. Soil chemistry

Soil from 32 soil samples from the first post-fire sampling were selected for nutrient analysis, which consisted of 15 samples from 2 weeks post-fire for prescribed burn and 17 samples at 2 months post-fire

for the wildfire as this provided the best temporal comparison between the two sites (i.e. the closest sampling after the fire). Soils were air-dried in a fume hood, and sent to A&L Western Laboratories, Inc. (Modesto, CA, USA) for analysis (http://www.al-labs-west.com/fee-schedule.php?section=Soil%20Analysis; soil test suite S1B) including ppm of sulfur (S), potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na), soil pH, cation exchange capacity (CEC), hydrogen concentration, organic matter (OM) in lbs./acre, and phosphorous (weak Bray and Sodium Bicarbonate-P; ppm). To minimize redundancy in some of the soil variables, we dropped variables that were estimates of similar pools (e.g. weak Bray and sodium bicarbonate —P) and variables with strong correlations that indicated similar dynamics (e.g. both Mg and Ca were strongly correlated with CEC at $r > 0.8$, therefore just CEC was kept). This reduced our soil variables to OM, phosphorous (Sodium Bicarbonate-P; ppm), soil pH, K, Na, CEC, and S.

2.4. DNA extractions, PCRs, and Illumina MiSeq sequencing

To identify microbial abundance, richness, and composition, DNA was extracted from 0.25 g soil using Qiagen DNeasy PowerSoil Kits (Qiagen, Maryland, USA) following the manufacturer's protocol and stored at −20 °C for subsequent analysis. Extracted DNA was amplified using the primer pair ITS4-fun and 5.8 s (Taylor et al., 2016) to amplify the fungal Internal Transcribed Spacer 2 (ITS2), and the primer pair 515F-806R to amplify the V4 region of the 16S rRNA gene for archaea and bacteria (Caporaso et al., 2012) using the Dual-Index Sequencing Strategy (DIP) (Kozich et al., 2013). Although the 515F-806R amplifies both archaea and bacteria, from here on we say only bacteria for simplicity since bacterial reads were so dominant (Fig. A.2). We conducted polymerase chain reaction (PCR) in two steps, each with 25 μl aliquots. The first PCR amplified gene-specific primers, and the second PCR ligated the DIP barcodes for Illumina sequencing. For fungi, we combined the gene-specific primers at 0.5 μl each at 10 μM, 5 μl of undiluted fungal DNA, 6.5 μl of Ultra-Pure Sterile Molecular Biology Grade water (Genesee Scientific, San Diego, CA, USA) and 12.5 μl of AccuStart II PCR ToughMix (Quantabio, Beverly, MA, USA). Thermocycler conditions were: 94 °C for 2 min, followed by 31 cycles of 94 °C for 30 s, 55 °C for 30 s, 68 °C for 2 min followed by a 10 min extension at 68 °C. For bacteria, we combined 1 μl of 1:10 diluted DNA, 10.5 μl of water, 12.5 μl of AccuStart II PCR ToughMix and 0.5 μl each of the 10 μM 515F-806R primers. Thermocycler conditions were: 94 °C for 2 min, followed by 30 cycles of 94 °C for 30 s, 55 °C for 30 s, 68 °C for 1 min followed by a 2 min extension step at 68 °C and ending with a 4 °C hold. PCR products were then cleaned with AMPure XP magnetic Bead protocol (Beckman Coulter Inc., Brea, CA, USA). The DIP PCR2 primers containing the barcodes and adaptors for Illumina sequencing were ligated to the amplicons during the second PCR step in a 25 μl reaction containing 2.5 μl of the 10 M DIP PCR2 primers, 6.5 μl of water, 12.5 μl of Accustart II PCR ToughMix and 1 μl of PCR1 product. Thermocycler conditions for PCR2 were: 94 °C for 2 min followed by 10 cycles of 94 °C for 30 s, 60 °C for 30 s, 72 °C for 1 min, and ending at a 4 °C hold. Bacterial and fungal PCR products were then separately pooled based on gel electrophoresis band strength and cleaned with AMPure following established methods (Glassman et al., 2018). The 16S and ITS pools were each checked for quality and quantity with an Agilent 2100 Bioanalyzer, then pooled at 0.4 bacteria to 0.6 fungi ratio prior to sequencing with Illumina MiSeq 2x300bp at the University of California-Riverside Institute for Integrative Genome Biology. Sequences were submitted to the National Center for Biotechnology Information Sequence Read Archive under BioProject PRJNA761493.

2.5. Bacterial and fungal abundance

For all soil samples, bacterial and fungal abundance as a proxy of biomass were estimated by qPCR copy number. Bacterial biomass was estimated based on bacterial 16S rRNA genes with Eub338/Eub518 primers (Fierer et al., 2005) and fungal biomass was estimated based on fungal 18S rRNA genes using FungiQuant-F/FungiQuant-R primers (Liu et al., 2012). QPCR reactions were performed in triplicate with 1 μl of undiluted DNA added to 9 μl of qPCR master mixer containing 1 μl of 0.05 M Tris-HCl ph 8.3, 1 μl of 2.5 mM $MgCl_2$ (New England BioLabs; NEB; Ipswich, MA, USA), 0.5 μl of 0.5 mg/ml BSA, 0.5 μl of 0.25 mM dNTPs (NEB), 0.4 μl of both forward and reverse primer at 0.4 μM, 0.5 μl of 20× Evagreen Dye (VWR), 0.1 μl of Taq DNA polymerase (NEB) and the remaining volume of 4.6 μl with the molecular grade water. Each reaction was run in triplicate in 384 well plates on CFX384 Touch Real-Time PCR Detection System starting at 94 °C 5 min, followed by 40 cycles of a denaturing step at 94 °C for 20 s, primer annealing at 52 °C for bacteria or 50 °C for fungi at 30 s, and an extension step at 72 °C for 30 s. Standards were generated by cloning the 18S region of *Saccharomyces cerevisiae* or the 16S region of *Escherichia coli* into puc57 plasmid vectors, which were constructed by GENEWIZ, Inc. (NJ, USA) as previously established (Averill and Hawkes, 2016; Pulido-Chavez et al., 2022). Melt curves were generated and copy number extracted using the following equation: $10^{(Cq-b)/m}$ where Cq is the average of 3 technical replicates of the quantification cycle value and b is the y intercept and m is the slope generated with CFX Maestro software.

2.6. Bioinformatics

All Illumina MiSeq data were processed using QIIME2 Version 2019.10 (Bolyen et al., 2019). Forward and reverse adaptors were removed with the cutadapt trim-pair function, and reads were denoised, trimmed to remove low quality regions, and forward and reverse reads were merged using the dada2 denoise-paired functions. Bacterial reads were then aligned against the Silva 132 16S classifier (Quast et al., 2013) and fungal reads against the UNITE classifier (Köljalg et al., 2005). For fungi, all reads not identified to Kingdom Fungi were removed, and for bacteria, all mitochondrial and chloroplast reads were removed.

2.7. Statistical analysis

All statistical analyses were conducted in R version 4.0.2 (R Core Team, 2017). To evaluate the plant community response to the prescribed burn (Burro) and wildfire (Tenaja), we ran mixed effects model for species richness, Shannon-Weiner diversity, and cover of the exotic and native plant community as a function of fire exposure (burned, unburned) and fire type (prescribed burn, wildfire). Sampling plot was nested within transect as a random effect. To evaluate microbial community responses to the two different fires, we ran mixed effect models on bacterial and fungal richness and abundance (as estimated by copy number) separately for each fire as a function of initial char, or the char measured at the first time-point following fire, time, and their interaction. Since initial char measurements are most representative of fire severity for the plants and microbes, we analyzed all effects as a function of initial char cover. Bacterial and fungal richness were estimated as observed species number after rarefying all samples to same number of sequences (9,009 for bacteria, 12,532 for fungi). We included sampling plot as a random effect and specified an autoregressive correlation structure to account for the lack of independence of samples over time. We compared differences among factors by least square means using the "emmeans" package in R (Lenth et al., 2020). Bacterial and fungal abundance were natural log transformed to meet assumptions of normality for the above data analysis.

To assess recovery of the microbial communities to the fires, we first calculated a Bray-Curtis dissimilarity matrix for the bacterial and fungal communities after rarefaction. For each fire, we used this distance matrix as the response variable in a PERMANOVA (permutational multivariate analysis of variance) with fire exposure (burned/unburned), time, and their interaction as predictor variables. We visualized these differences using a nonmetric multidimensional scaling (NMDS) plot. We also compared the dispersion of the microbial communities between

burned and unburned sites for each fire type. These analyses were done using the "vegan" package in R (Oksanen et al., 2012).

We took a model fitting approach to relate soil properties and plant community attributes to bacterial and fungal communities. These seven soil variables were analyzed in a principal components analysis to get two axes that described the soil attributes of the sites. The first axis, which captured 30.74 % of the variation, described plots with high soil pH, P, and K availability at negative values of PC1 but high Na values at positive values of PCA1. The second axis, which captured 26.96 % of variation, described plots across a CEC, S, and OM gradient where negative values indicated plots with high CEC and positive values plots with low CEC (Fig. A.3).

We began with a global model that included initial char estimates, soil PCA1 and PCA2, and exotic plant diversity and cover as fixed effects, and transect as a random effect. Fire exposure was measured based on initial char estimates. For the plant community attributes, we selected exotic plant Shannon-Weiner diversity and cover after adjusting for correlations among various community attributes such as richness, cover, and diversity of the total community, native, and exotic species. Since we measured plant community attributes in spring at peak biomass of their growing season, these models were run with only the May timepoint data for bacterial, fungal, and plant communities. We conducted stepwise model selection and selected the model with the lowest Akaike information criterion (AIC). We also repeated this analysis with AMF richness as the response variable. The model fitting was done using the "MuMIn" package (Barton, 2020). Given that the AMF community may be more sensitive to native plants, we conducted an additional analysis where we ran a mixed effects model for AMF richness as a native plant diversity and fire type. Sampling plot was nested within transect as a random effect.

3. Results

3.1. Summary description of fire severity

The burned plots within the prescribed burn site were covered by 44 ± 9.5 % (average ± standard error) char and still had on average 35 ± 8.9 % cover of intact litter. The burned plots within the wildfire site had on average 74 ± 60 % char cover and no litter was present. In contrast, litter in unburned control plots made up about 78 ± 2 % of the plot cover in the first post fire sampling in the prescribed burn site and about 77 ± 17.9 % cover in the wildfire site. By the spring peak growing season sampling, char was no longer observed after the prescribed burn but was on average 10 ± 2.3 % in the plots exposed to wildfire.

3.2. Summary description of site plants

We observed 65 unique plant species within the prescribed burn site with an average per plot species richness of 13 ± 0.65 species/m^2. In contrast, we observed 41 unique plant species within the wildfire site with an average per plot richness of 8 ± 0.98 species/m^2. In the prescribed burn site, the plots exposed to fire were dominated by the following four plant species (average cover ± standard error): the exotic grass *Festuca myuros* (17.91 ± 20.44), exotic forb *Erodium botrys* (8.75 ± 10.64), and native forbs *Calandrinia menziesii* (8.83 ± 6.98) and *Deinandra fasciculata* (8.71 ± 7.03) whereas the plots not exposed to fire were dominated by exotic annual grasses (*F. myuros* 23.33 ± 22.55; *Bromus hordeacous* 16.83 ± 28.72) and the native forb, *C. menziesii* (13.33 ± 11.54) (Fig. A.4). The most dominant species in the wildfire site regardless of fire exposure were exotic annual grasses, mainly *Bromus diandrus* and *Avena fatua*, with *B. diandrus* covering 45.1 ± 43.31 % in control plots versus 11.79 ± 21.36 % in burned plots, and *A. fatua* covering 19 ± 19.8 % in control plots versus 37 ± 30 % in burned plots (Fig. A.4). *Stipa pulchra*, the native perennial bunchgrass that is a focal species for management at the reserve, averaged ~1 % cover at both fire types but was absent in the prescribed burn control plots.

3.3. Summary description of site soil bacteria and fungi

Overall, after rarefaction, we identified 5,216 fungal and 17,722 bacterial Amplicon Sequence Variants (ASVs), which are similar to operational taxonomic units (OTUs), and approximate microbial species (Glassman and Martiny, 2018). At the first time point post-fire, there were a total of 6,602 bacterial and 1,991 fungal ASVs in the prescribed burn site and 3,884 bacterial and 1,995 fungal ASVs in the wildfire site. In the May following fire, we observed a total of 6,705 bacterial and 1,948 fungal ASVs in the prescribed burn site and 3,699 bacterial and 1,439 fungal ASVs in the wildfire site. Mean bacterial and fungal richness and abundance were both higher in prescribed burn than wildfire (Table A.2). The prescribed burn and wildfire plots were both dominated by the bacterial phyla Proteobacteria and Actinobacteria, followed by Acidobacteria, Bacteroidetes, Verrucomicrobia, Chloroflexi, Planctomycetes, Gemmatimonadetes, and Cyanobacteria (Fig. A.5). Fungi were always dominated by the phylum Ascomycota regardless of site, followed by Basidiomycota, then Glomeromycota (Fig. A.6), with larger turnover from unburned to burned at the family level (Fig. A.7).

3.4. Effect of prescribed versus wildfire on exotic and native plant species richness, diversity, and cover

Exotic plant species richness and Shannon-Weiner diversity were greater in the prescribed burn than wildfire site (richness: $F_{1,27.3} = 7.79$, $p < 0.01$, Fig. 2A; diversity: $F_{1,16.6} = 17.05$, $p < 0.001$) and did not differ by fire exposure (richness $F_{1,27.3} = 0.12$, $p = 0.73$; diversity: $F_{1,15} = 1.04$, $p = 0.32$). Both the prescribed burn and wildfires reduced exotic species cover, which was greater in the unburned plots ($F_{1,28} = 4.15$, $p = 0.05$), but did not vary by fire type ($F_{1,28} = 0.60$, $p = 0.44$, Fig. 2B). Native species richness, diversity, and cover were all greater in the prescribed burn site compared to wildfire site and were not affected by fire exposure (Fig. 2; Table A.3).

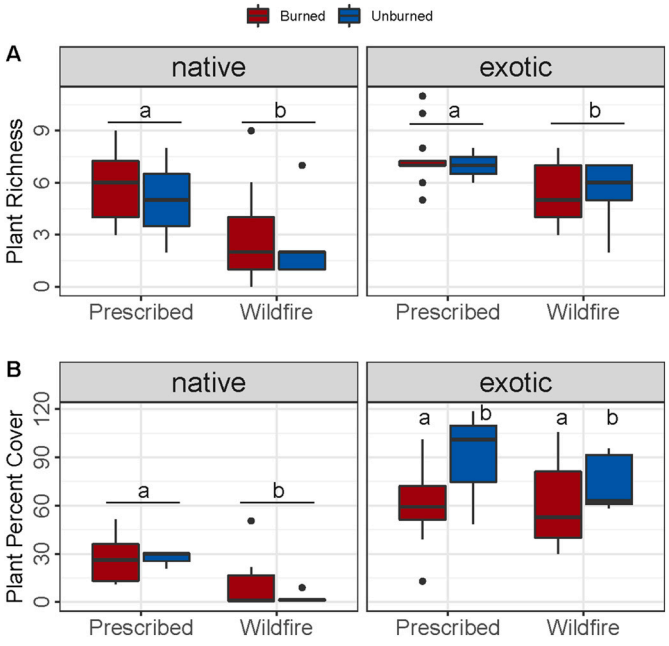

Fig. 2. Plant community metrics of species richness (A) and percent cover (B) for native and exotic species in burned and unburned plots within the Burro prescribed burn and Tenaja wildfire sites. Plant communities were sampled the first spring post fire, thus April 2019 and April 2020 respectively for the Prescribed and Wildfire. Segments and letters indicate significant differences between main effects of Prescribed and Wildfire at $p < 0.05$. Letters in the exotic cover panel indicate pairwise differences at $p < 0.05$ for a significant fire exposure and fire type interaction.

3.5. Effect of prescribed versus wildfire on soil bacterial and fungal richness

Within the prescribed burn site, bacterial richness was not influenced by fire exposure but did vary over time across the three sampling points (Char $F_{1,13} = 0.39$, $p = 0.55$; Time $F_{2,26} = 3.5$, $p < 0.05$; Fig. 3A, Fig. A.8, Table A.4), where bacterial richness decreased significantly between November and May but did not vary among the other time points (post hoc Nov-May $p < 0.05$). Within the wildfire site, bacterial richness was similarly not affected by fire exposure but did vary over time, with richness being the greatest in November and not differing between the 1st post-fire sampling and May (Char $F_{1,29} = 0.17$, $p = 0.69$; Time $F_{2,29} = 7.3$, $p < 0.01$; post hoc 1st-Nov $p < 0.05$; Nov-May $p < 0.01$; Fig. 3B, Fig. A.8). Fungal richness was not impacted by the prescribed burn such that it did not vary with initial char or over time (Char $F_{1,13} = 0.15$, $p = 0.7$; Time $F_{2,26} = 0.11$, $p = 0.89$; Fig. 3C, Fig. A.8). Within the wildfire, fungal richness decreased with increasing initial char (Char $F_{1,29} = 22.4$, $p < 0.001$) and gradually decreased over time ($F_{2,29} = 16.4$, $p < 0.001$, Fig. 3D, Fig. A.8).

3.6. Effect of prescribed versus wildfire on soil bacterial and fungal abundance

Bacterial and fungal abundance were more responsive than richness to initial char across both fires (Table A.4). In the prescribed burn site, the relationship between bacterial abundance and initial char tended to shift depending on the sampling point (Char x Time $F_{2,26} = 2.86$, $p = 0.08$; Fig. 4A). For instance, there was no relationship between abundance and char at the first post-fire sampling, but it shifted to positive in November (i.e. abundance increased with char) and then negative in spring. Conversely in the wildfire site, bacterial abundance slightly decreased with increasing char (Char $F_{2,29} = 7.8$, $p < 0.01$, Fig. 4B). Bacterial abundance did increase in the wildfire over the sampling periods (Time $F_{2,29} = 29.1$, $p < 0.0001$; post hoc at $p < 0.05$ 1st Post fire = Nov < May). Fungal abundance also varied with initial char depending on the sampling point within the prescribed burn site (Char x Time $F_{2,26} = 5.88$, $p < 0.01$; Fig. 4C). For the first sampling post-fire, fungal abundance increased with increasing char but for the subsequent two sampling periods the relationship was negative. Within the wildfire site, fungal abundance showed a similar trend to bacterial abundance with a small decrease with increasing char (Char $F_{2,29} = 6.3$, $p < 0.02$, Fig. 4D). While the relationship between char and fungal abundance did not change with time, average fungal abundance tended to decrease from

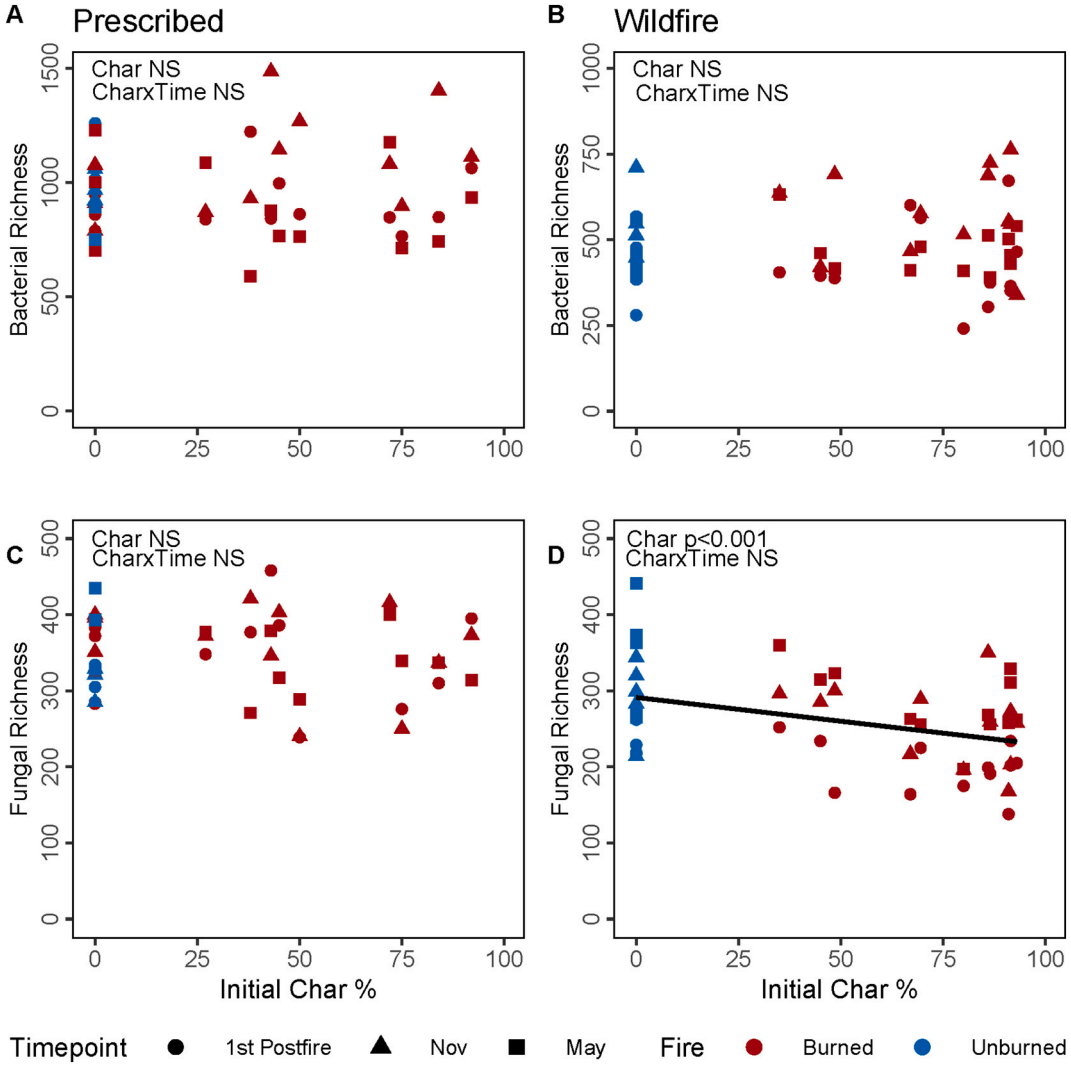

Fig. 3. Relationship between Bacterial (A,B) and Fungal (C,D) richness and percent initial char for burned and unburned plots sampled over three time points, within the Burro Prescribed Burn (A,C) and the Tenaja Wildfire (B,D). The percent char present at initial sampling was only significantly related to fungal richness within the wildfire site.

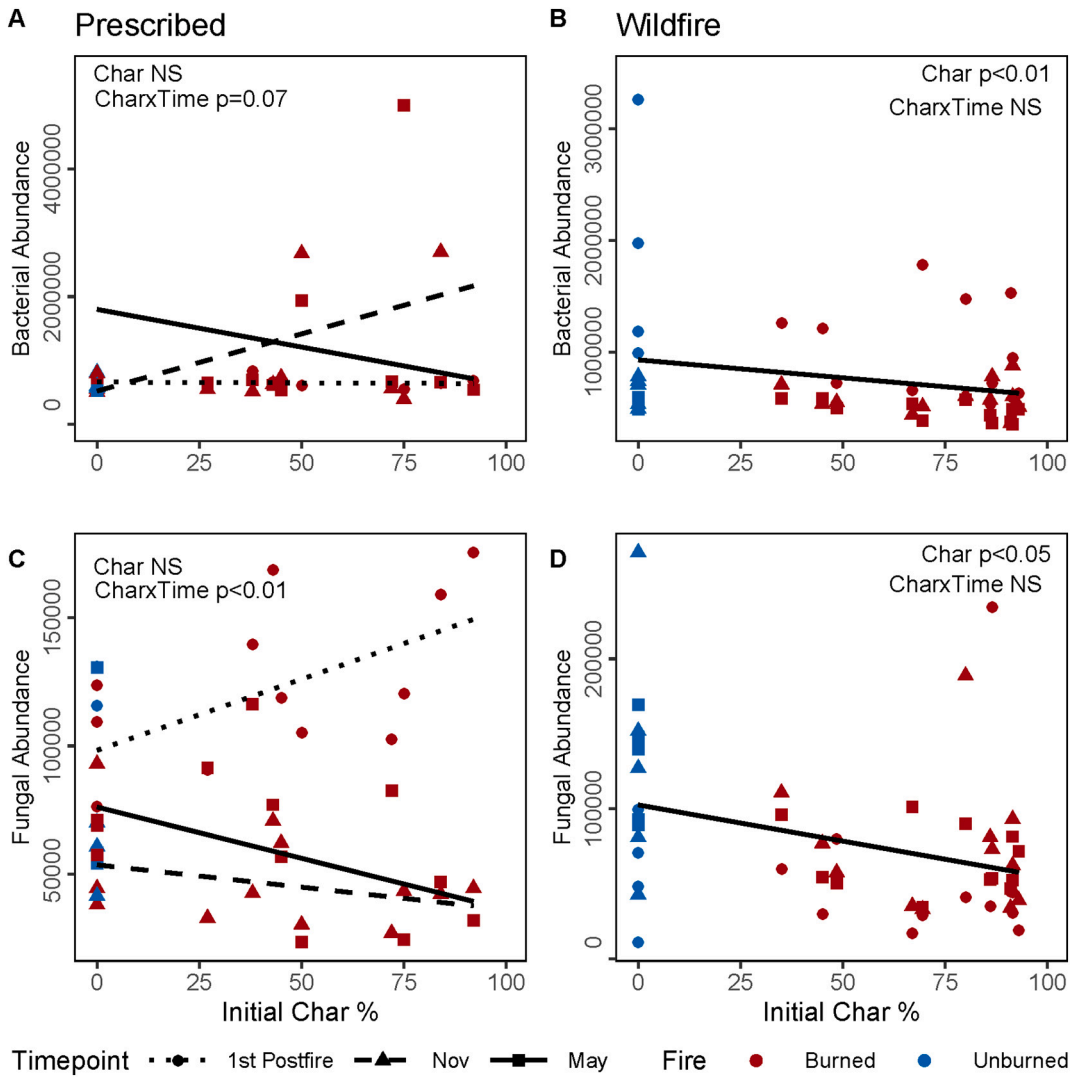

Fig. 4. Bacterial abundance, estimated as 16S copy number, at the A) Burro prescribed burn and the B) Tenaja wildfire. Fungal abundance, estimated as 18S copy number, at the C) Burro prescribed burn and the D) Tenaja wildfire. Lines represent significant relationships for either main effect of char on abundance or two-way interactions of Char and Time ··· 1st Postfire, - - Nov, — May.

the initial post-fire sampling point to May (Time $F_{2,29} = 6.04$, $p < 0.01$; post hoc at $p < 0.05$ 1st Post fire = Nov < May).

3.7. Effect of prescribed versus wildfire on soil bacterial and fungal composition

Bacterial composition was similarly affected by fire exposure in both the prescribed burn (PERMANOVA: $F_{1,39} = 1.45$, $p < 0.05$, $R^2 = 0.03$; Fig. 5A) and wildfire ($F_{1,45} = 1.46$, $p < 0.05$, $R^2 = 0.03$; Fig. 5B) but did not vary over time (PERMANOVA: prescribed-Time $F_{2,39} = 1.23$,$p = 0.07$, $R^2 = 0.06$; wildfire-Time $F_{2,45} = 1.07$, $p = 0.28$, $R^2 = 0.04$). Fungal composition was also affected by fire exposure in both the prescribed burn (PERMANOVA: $F_{1,39} = 1.82$, $p < 0.01$, $R^2 = 0.04$; Fig. 5B) and wildfire ($F_{1,45} = 2.39$, $p < 0.01$, $R^2 = 0.05$; Fig. 5C), with slightly more compositional change in the wildfire than prescribed burn. Like bacteria, fungal composition did not vary over the three sampling periods in either fire type (PERMANOVA: prescribed: $F_{2,39} = 1.06$, $p = 0.32$, $R^2 = 0.05$; wildfire: $F_{2,45} = 1.05$, $p = 0.33$, $R^2 = 0.04$). The variation in community composition differed by fire exposure for fungal communities in both fires (prescribed, $p < 0.05$, wildfire, $p < 0.001$) but not for bacterial communities (prescribed, $p = 0.27$, wildfire, $p = 0.70$).

3.8. Predictors of bacterial and fungal richness in spring

Bacterial and fungal richness were predicted by different soil properties at each site when pooled across burned and unburned plots in spring (Fig. 6). Within the prescribed burn site, bacterial and fungal richness increased with decreasing cation exchange capacity (CEC) and organic matter (OM) (Fig. 6A, B, blue dots). Bacterial richness was also influenced by the plant community such that it increased with increasing exotic plant richness. For the wildfire site, bacterial and fungal richness both responded to PCA1 but in different directions. Bacterial richness decreased as soil pH and phosphorus concentrations decreased (Fig. 6A, red dots); however, fungal richness increased as soil pH and phosphorus concentrations decreased (Fig. 6B, red dots). AMF richness on its own was not related to soil properties or to the exotic plant community in either fire type (Fig. 6C). AMF richness followed similar patterns to native plant richness in that the prescribed burn site had higher AMF average richness (31 ± 5) than the wildfire site (17.3 ± 4.3; Fire type: $F_{1,26} = 9.76$, $p < 0.01$). AMF richness was not related to exotic plant diversity at either of our fire sites; however, it was marginally related to native plant diversity within the wildfire, such that AMF richness increased with native plant diversity (Fire x Native $F_{1,27} = 3.14$, $p = 0.09$; Fig. A.9).

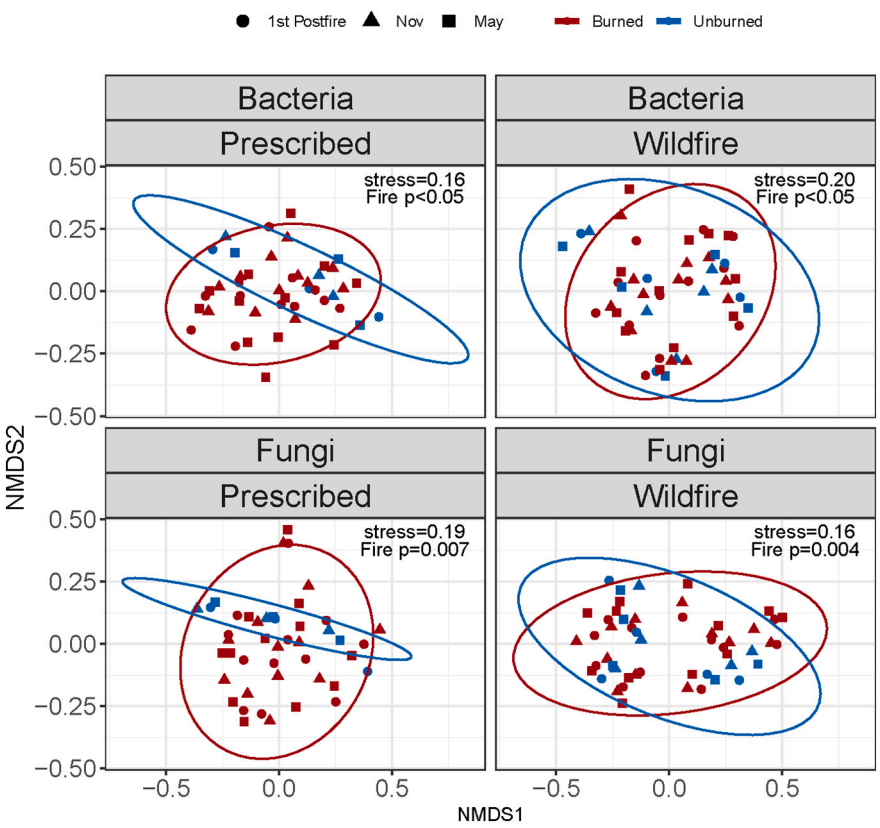

Fig. 5. Nonmetric Multidimensional Scaling ordination of burned versus unburned soil microbial composition for bacteria and fungi in the Burro prescribed burn versus Tenaja wildfire at the three time points. Ellipses represent 95 % confidence interval and visualize statistical diffences between fire exposure (burned, unburned plots).

4. Discussion

Wildfire had stronger impacts on soil microbial communities and both fire types had similar impacts on plants. Both fire types significantly reduced the amount of exotic plant cover but neither reduced exotic plant richness (Q1). Regardless of fire exposure, the prescribed burn site had higher cover and diversity of native plants than the wildfire site. Soil microbial richness was differentially impacted by fire type. Specifically, fungal richness decreased with increasing char levels only within the wildfire, but bacterial richness was not impacted by either fire. Bacterial and fungal abundance were impacted by char levels within both the wildfire and prescribed burn (Q2). Both prescribed burn and wildfire significantly altered bacterial and fungal composition, but fungal composition was more altered by wildfire than prescribed burn (Q3). The factors that predicted spring peak growing season bacterial, fungal, and AMF richness differed by fire type (Q4). In the prescribed burn, bacterial and fungal richness was predicted by soil cation exchange capacity and organic matter (PCA2), and bacterial richness was additionally predicted by exotic plant diversity. In the wildfire, bacterial and fungal richness were not related to the plant community but were predicted by soil pH and phosphorus concentrations (PCA1). AMF richness was not related to soil attributes or the exotic plant community but was related to native plant diversity.

While prescribed burns are often used as a tool to reduce exotic plant abundance and recover native plant species in grasslands (DiTomaso et al., 2006; Dyer, 2002; Menke, 1992), here we found that both fire types reduced exotic plant cover but neither recovered native plant cover or richness. Our results thus recapitulate the findings of a meta-analysis that neither prescribed burns nor wildfires resulted in increased native plant performance (Alba et al., 2015). This may be because there was not enough propagule pressure of native seeds even after exotic plant cover was reduced post-fire. Appropriately timed fires may reduce viable seeds of exotic plants and allow establishment of native species from the seedbank if a seedbank exists (Meyer and Schiffman, 1999), but without a native seedbank, exotic species can readily re-establish within a few years either after prescribed burns (Dickens and Allen, 2009) or after wildfire (Larios et al., 2013). Indeed, lack of plant dispersal post-fire is increasingly preventing native plant regeneration post-fire in Western North America (Gill et al., 2022). Overall, the prescribed burn site, which has a long history of management, did possess a higher richness and diversity of native species suggesting that periodic prescribed burns maintain the integrity of the native seedbank. For example, native forbs like *Deinandra fasciculata* slightly increased in cover after the prescribed burn. Yet, despite the long history of management, exotic plant species were more abundant than native in both fire types, suggesting that regular burning does not necessarily alter the abundance of exotics but may ameliorate the long-term impacts of invasion.

Bacterial and fungal communities often respond differently to disturbances (Griffiths and Philippot, 2013) and to prescribed versus wildfires (Dooley and Treseder, 2012; Pressler et al., 2019) and indeed showed different responses to fire types in our study. Bacteria have high regeneration times that allow them to readily resist and recover post disturbance (Shade et al., 2012). The lack of any shifts in bacterial richness between fire exposure in either fire type, suggest that bacterial richness is highly resistant to fire in grasslands, which is in line with a study of a prescribed burn in a Northern California grassland (Yang et al., 2020) and a wildfire in a different Southern California grassland (Barbour et al., 2022). Due to these similarities with other California grassland fires, we think it is unlikely that our results were seriously hindered by the fact that our prescribed burn and wildfire occurred in different seasons and the timing of the initial post-fire sampling differed

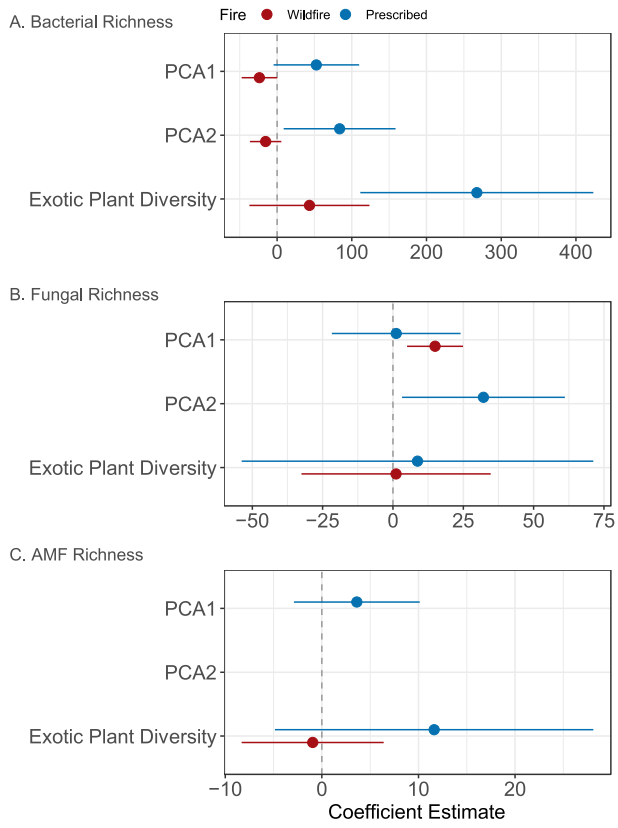

Fig. 6. Best fit model parameter coefficients for relating soil variables (PCA1, PCA2) and plant community diversity (exotic Shannon-Weiner diversity) to richness of A) bacteria B) fungi and C) arbuscular mycorrhizal fungi (AMF) for the Tenaja wildfire versus the Burro prescribed burn. Error bars not overlapping 0 indicate significant parameters in model. Note: the best fit models often contained parameters that were not significant.

slightly by fire type. In those instances when bacterial richness was affected by grassland fires, recovery occured at a scale of specific functional groups (e.g. ammonia-oxidizing bacteria) versus at a community level (Docherty et al., 2012). This contrasts with fungi, where richness decreased by 13–17 % in the wildfire site. While heat penetration may not be as deep in fast moving grassland fires (Bruns et al., 2020), it is possible that fungal richness is more affected than bacterial richness because it is more directly tied to plant mortality (Hart et al., 2005), especially in grasslands where fungi are closely coupled to plant successional dynamics (Cheeke et al., 2019; Koziol and Bever, 2016). Moreover, a recent study of microbial succession after a Southern California chaparral shrubland fire also found that fungal richness was more negatively affected by fire than bacterial richness (Pulido-Chavez et al., 2022). However, in the shrubland fire, which burned hotter than the grassland due to higher fuel loads and much higher char levels, both bacterial and fungal richness declined post-fire. Yet, like the shrubland study, bacterial richness varied more over time than fungal richness, likely because bacteria are more likely than fungi to rapidly respond to changes in soil moisture (Blazewicz et al., 2014; Schimel, 2018).

Our findings that wildfire had stronger impacts on soil microbial abundance than prescribed burns and that fire had stronger impacts on fungi than bacteria are largely in line with the literature (Dooley and Treseder, 2012; Pressler et al., 2019). However, there are some key differences in that we were able to detect significant reductions of bacterial and fungal biomass following grassland wildfires whereas most previous studies did not. Grassland fires typically are lower severity due to low fuels and quick-moving fires and are thus thought to have small impacts on the soil microbial community, as indicated by a meta-analysis finding that microbial biomass declined after fires in boreal and temperate forests but not after grassland fires (Dooley and Treseder, 2012). Indeed, a study examining effects of prescribed burns of varying fire intensity on Northern Great Plain grasslands found no effect of fire on microbial biomass, as measured by Phospholipid-derived fatty acids (PLFAs) (Reinhart et al., 2016). In our study, fungal and bacterial abundance were sensitive to the amount of char present immediately after both fire types. Since we did find a significant interaction between char and time in the prescribed burn, our ability to detect reductions in microbial abundance could be due to our rapid post-fire sampling, which is not always commonly done (Pressler et al., 2019). Furthermore, our usage of char percentage as an index of soil burn severity, which is not typically measured, likely helped us detect impacts of fire severity on microbial abundance which might be missed using coarse soil burn severity maps. Finally, we speculate that the usage of qPCR helped us to detect impacts on microbial abundance that previous studies using PLFA or chloroform fumigation might have missed due to the coarse nature of those methods.

Disturbances such as fire can also impact the mean community state and the variation within communities (Houseman et al., 2008). Severe wildfires can often be homogenizing for both plants (Turner et al., 1994) and soil microbes (Enright et al., 2022; Pulido-Chavez et al., 2022), yet low severity fires common in grasslands might have the opposite effect and in fact increase community dispersion, perhaps by increasing variation in soil chemistry by adding in bits of char or removing leaf litter, but not being hot enough to cause severe mortality (Allen et al., 2011), such as we found here. We found that wildfire resulted in a more noticeable shift in fungal community composition compared to prescribed burn. Yet, the prescribed burn resulted in greater heterogeneity in soil microbial community with increased dispersion in fungal composition following the prescribed burn in comparison to the wildfire. This greater dispersion in fungal communities within the prescribed burn is likely due to the greater variation in remaining litter and char levels in the prescribed burn than the wildfire. In contrast to fungi, the prescribed burn and wildfire similarly affected bacterial composition. Bacteria often have high resilience to fire (Ferrenberg et al., 2013; Maquia et al., 2021; Xiang et al., 2014), likely due to their high rates of dispersal and fast generation times (Hanson et al., 2012). A prescribed fire in a Northern California grassland also resulted in small but significant shifts in bacterial composition but not richness, which had important functional consequences for carbon and nitrogen cycling genes (Yang et al., 2020). While we acknowledge that the small number of control samples in our study might limit our inference, we were still able to detect differences in composition, suggesting that a larger sample size might have found larger effect sizes.

The presence of exotic plants can interact with soil microbiomes to mediate the impacts of prescribed versus wildfire. Indeed, which plants colonize first post-fire can exert strong influences on the initial microbial community that will subsequently mediate plant recovery in old fields (Cheeke et al., 2019; Kardol et al., 2006) and in other *Bromus* and *Avena* dominated California grasslands (Hausmann and Hawkes, 2009; Hausmann and Hawkes, 2010). In the wildfire site with lower overall plant diversity, microbial communities were not sensitive to the aboveground exotic plant community compared to in the prescribed burn, suggesting that intensity of disturbance may have damped some of the exotic plant impacts. Indeed, bacterial richness in the prescribed burn site increased with exotic plant diversity while remaining unaffected by fire. Meta-analyses have demonstrated that bacterial diversity increases with the presence of invasive plants either by allelopathy (Torres et al., 2021) or production of higher quality leaf litter (Liao et al., 2008). *Bromus* (Holzapfel et al., 2010) and *Avena* (Perez and Ormenonunez, 1991) have each been found to exude allelochemicals, which are speculated to provide resources for bacteria to increase their diversity (Torres et al., 2021). The fact that AMF richness on its own was not related to the exotic plant community in either fire type is also supported by meta-analysis (Torres et al., 2021). Within the prescribed burn that has a

history of regularly timed burns, we found that bacterial and fungal richness was sensitive to increasing organic matter, in addition to CEC, and also to soil pH, which is supported by the literature (Fierer and Jackson, 2006; Glassman et al., 2017). Thus, it is possible that in our system the high abundance of exotic species offset some of the impacts of fire.

While native plant communities did not completely recover in this study, we did observe an emerging trend at the peak of the first post-fire spring growing season, between native plant diversity and AMF richness in the wildfire site. This relationship may be expected due to the lower overall AMF richness within the wildfire site (wildfire: average 15 AMF taxa per sample, with a range from 5 to 30 AMF per sample; prescribed burn: average 30 AMF taxa per sample, with a range from 14 to nearly 60 AMF per sample). The benefit of AMF richness on plant richness tends to saturate after 12–14 AMF species (van der Heijden et al., 1998). Therefore, we would expect this trend to only emerge within the wildfire site since it is likely that the positive impact of AMF on native plant diversity has already met the saturation point at the more biodiverse prescribed burn site. Further, the prescribed burn site that has a history of regularly timed burns had greater native plant richness and diversity, potentially increasing the resistance of the AMF community to fire by buffering some of the degradation of mutualistic fungi that can occur with plant invasion (Callaway et al., 2008). These findings highlight the additional components of an ecosystem that benefit from maintaining and/or increasing the abundance of native plant taxa in California grasslands land management.

Unexpected wildfires may provide opportunistic management windows to re-establish native species in degraded grasslands; however, the success of these efforts are contingent on mediating some of the recovery constraints associated with long-term invasion (Larios and Suding, 2013). While our findings support the idea that consistent management actions such as periodic prescribed burns may promote native plant diversity (Steenwerth et al., 2002), they do not indicate that periodic burns or wildfires will increase native plant performance or cover without intervention. Soil inoculations are likely required to recover native soil microbial and plant diversity in these situations (Aprahamian et al., 2016; Balshor et al., 2017; Emam, 2016), and these strategies are more likely to be successful if local soil inocula are used (Maltz and Treseder, 2015), since mycorrhizal partnerships tend to be context dependent (Klironomos, 2003). Broadcast inoculation can be done with either local soil which would likely contain spores and hyphal and root fragments or commercial inoculants, which tend to contain a few common AMF species (Aprahamian et al., 2016; Balshor et al., 2017; Emam, 2016). Moreover, research shows that a single time-point inoculation can be highly effective in modifying plant successional trajectories (Wubs et al., 2019). Thus, the success of an opportunistic management action capitalizing on a wildfire would be contingent on addressing invader legacies (e.g., adding seeds, soil amendments) and implementing periodic management actions (e.g., prescribed burns) to regularly clear out persistent plant invaders.

In summary, here we demonstrate the multi-faceted response of grassland soil microbial communities to wildfire and prescribed burns. While this study focused on a single prescribed burn and wildfire, the strength of the study lies in that both fires occurred in the same exact reserve, thereby limiting variation in environment, climate, and vegetation which would ordinarily obscure direct comparisons. Our findings point to the strong role that long-term management may have in mediating invader legacies and promoting native plant diversity and ultimately soil microbial communities.

Authors' contributions

SIG conceived of the field experiment with joint project development and experimental design by SIG and LL. JC, JWJR, LL, SIG, SSS conducted field work. JWJR performed molecular work. JC, JWJR, MFPC, and SIG conducted bioinformatics. SIG and JWJR created rarefied ASV tables and calculated richness and beta-diversity metrics. JWJR created the microbial taxonomy figures. LL conducted statistical analyses and made the figures. SIG and LL wrote the manuscript. All authors contributed edits to the manuscript and approved the final submission.

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 are available via Dryad Digital Repository https://doi.org/10.6086/D1VQ36 (Larios & Glassman, 2022) and sequences were submitted to the National Center for Biotechnology Information Sequence Read Archive under BioProject PRJNA761493.

Acknowledgements

We thank Hailey Laskey, Carole Bell, and Zachary Principe for allowing us access to the Santa Rosa Ecological Plateau Reserve, and Judy Chung, Lachlan Charles, Stuart Schwab, Miguel Solis, and Soren Weber for aid in field work and plant data collection. This project was supported by UC Riverside funds to SIG and LL and Bureau of Land Management California Forest and Woodlands Resource Management Award L19AC00280 to SIG.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2022.104795.

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