



Vegetation type and fire severity mediate short-term post fire soil microbial responses

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Abstract

Background Wildfire severity mediates key dynamics, such as nutrient pulses, that regulate the recovery of ecosystem functioning. Large shifts in vegetation communities associated with plant invasions are often coupled with changes in soil communities; thus, it's critical to understand how fire severity may interact with vegetation type and soil communities to mediate ecosystem recovery.

Methods Following a 2017 wildfire in southern California, soils from areas dominated by native coastal sage scrub or exotic annual grasses that experienced a low or high severity fire event were analyzed for nutrient concentrations and two proxies for ecosystem

function—microbial respiration and enzymatic activity potentials over the first-year post-fire.

Aims We predicted that increasing fire severity would positively correlate with soil nutrient concentrations. Thus, higher severity burned soil would experience a greater downregulation of enzyme activity as potential microbial nutrient limitation was alleviated, a relationship that would be stronger in shrub dominated soil.

Results We observed a strong soil nitrogen (N) pulse post-fire, which was greatest in shrub dominated soil; however, dominant vegetation had a variable effect on microbial responses. Enzyme activities were downregulated in CSS soil, but the grass dominated soil response was inconsistent. After 1 year, soil N remained elevated in burned soil, suggesting that basal soil N concentrations were altered.

Conclusions Persistent, residual soil N concentrations are of particular concern in high fire risk ecosystems, which will likely experience increasing fire frequency associated with environmental change; thus, encouraging the regrowth of opportunistic vegetation in subsequent growing seasons will be key to minimize long-term changes to these ecosystems.

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Exotic grasses · Soil respiration potentials

Introduction

Wildfires can have strong impacts on soil communities and ecosystem functioning that can potentially feedback to the recovery of ecosystem properties such as plant community composition (Allen et al. 2011; Dickens et al. 2013; Neary et al. 1999). The severity of a fire can mediate these impacts on ecosystem functioning in two key ways: 1) changing the concentration and availability of soil carbon (C) and nitrogen (N) due to volatilization, leaching or conversion from organic to inorganic forms and/or 2) changing water infiltration dynamics due to ash deposition, which can create a hydrophobic layer on the soil surface (Neary et al. 1999). These impacts are mediated by the relative proportion of charred (incomplete combustion) and ashed (complete combustion) residues present post-fire, which is dependent on fire temperature and duration. Nutrient pulses post-fire are dependent on the progression of charred material becoming increasingly ashed. In low severity burns, charred material is often comprised of more labile C relative to the more ashed residues that are produced at higher burn intensities (Baldock and Smernik 2002; Certini et al. 2011, and references within). In addition to burn severity affecting C quality, a corresponding shift from charred (incomplete combustion) to ashed (complete combustion) residues often corresponds to an increased conversion of organic- to inorganic N forms. As temperatures continue to increase (upward of 500 °C) up to half of the organic N can be volatilized (Úbeda et al. 2009) and lost from the system.

Pulses of available soil nutrients post-fire can alter nutrient limitation and the need to upregulate the production of inducible enzymes for nutrient acquisition, affecting microbial function. Thus, microbial enzyme activity is often used as a proxy to evaluate early responses to disturbance events (Winding et al. 2005), such as fires. As discussed above, lower severity burns can result in a pulse of available N, leading to the downregulation of N-acquiring enzymes in ecosystems limited by N. In high severity burns, P liberation can result in the downregulation of P-acquiring enzymes in ecosystems limited by P (Wang et al. 2020). Decreased nutrient limitation can stimulate microbial processing, which can be quantified by respiration potentials. Nutrient pulses can result in either the downregulation or upregulation of ecosystem processes, but the strength of change is mediated

by factors that influence the quality and quantity of charred and ash material such as the aboveground vegetation prior to the fire. Thus, evaluating the impacts of fire severity on soil ecosystem function will also require investigating dynamics across different plant communities.

Ecosystem functioning is tightly coupled to aboveground plant communities (Hobbie 1992) and may create legacies post-fire that influence the recovery of ecosystem functioning (Hart et al., 2005). For example, grassland fire surface temperatures can be lower than shrubland fire temperatures impacting the depth and extent to which soils are affected (Christensen 1985; Neary et al. 1999). Vegetation type can interact with moisture content in an ecosystem to have a large effect on the resultant vegetation-derived fire residues (char or ash) deposited on the soil surface post fire (Hogue and Inglett 2012). The additions of nutrient rich vegetation-derived fire residues can indirectly affect the soil microbial communities by alleviating nutrient limitation (Medvedeff et al. 2013) and can facilitate shifts in dominant microbial communities (Pietikäinen et al. 2000). While these effects may be transient (Allen et al. 2011), they often occur at a critical stage of regeneration for plant communities.

Due to widespread environmental change, many landscapes are now characterized by a mosaic of native and exotic vegetation. Exotic species are often characterized by faster growing, nitrophilic species that alter soil functioning (Vilà et al. 2011). These changes to the communities can result in feedbacks that promote the exotic species (Ehrenfeld 2003). In uninvaded communities, plant-soil feedbacks can mediate ecological succession such that early to late successional species responses vary from negative to positive feedbacks (Kardol et al. 2013, 2006) with nutrient cycling and ecosystem functioning changing over time (Hobbie 1992; Odum 1969; Wardle et al. 2004). In invaded communities, plant invaders can alter these successional dynamics in a system by altering soil communities (Vitousek and Walker 1989; Yelenik and D'Antonio 2013), and a quick recovery of these altered soil microbial communities post disturbance may help in the stability of the invaded systems. More research is needed to understand how the recovery of ecosystem functioning may differ between invaded and uninvaded sites.

Coastal sage scrub (CSS) communities are a dominant vegetation type in coastal California (Barbour

2007). This threatened habitat has already been reduced from 60–90% of its range from the late 19th Century (Westman 1981) and is increasingly vulnerable to exotic plant invasions due to multiple interacting environmental change factors such as fire, atmospheric pollution and drought (Cox et al. 2014; Talluto and Suding 2008; Valliere et al. 2017). Many of southern California's landscapes are now a mosaic of uninvaded CSS and invaded CSS. Invaded CSS can exist along a gradient of invasion where CSS is still dominant but with an understory of exotic species including annual grasses to completely invaded and type converted to exotic annual grasslands (Cox et al. 2014). These different community types vary in their total aboveground primary production and in their plant leaf nutrient traits (Wolkovich et al. 2010). The differences in fire residue inputs post-fire may mediate the recovery of CSS and exotic grasslands. For example, Dickens and Allen (2014a) found that in a southern California shrub dominated ecosystem of chaparral, exotic grass species altered soil inputs and slowed the rate of plant recovery post fire. Moreover, long-term dominance of exotic annual grasses can result in altered microbial communities (Dickens et al. 2015; Sigüenza et al. 2006), that vary in their responsiveness to environmental change factors from those naturally associated with CSS shrubs (Finks et al. 2021). Understanding how fire severity may differentially mediate the recovery of ecosystem functioning in distinct microbial communities can provide some insights into future shifts in nutrient cycling with changing fire regimes.

In the current study, we evaluated ecosystem functioning within paired exotic grassland and CSS patches after a wildfire in southern California, where we ask 1.) How do ecosystem processes recover after a fire? and 2.) to what extent does dominant vegetation type and fire severity impact ecosystem recovery? We measured soil respiration and microbial enzymatic activity as proxies for ecosystem functioning and additionally, monitored soil nutrient availability and physico-chemical properties to provide insights to how changes in nutrient availability may mediate shifts in ecosystem functioning that we observe. Lastly, we measured plant community composition and biomass in the first-year post fire.

If charred material (as opposed to ash) dominated as the resultant fire residue in all sites, we predicted that available soil N concentrations would increase

with increasing burn severity. An increase in soil nutrient availability (largely N) would result in the downregulation of microbial enzyme activity and would be coupled with elevated microbial respiration. This would only occur if the microbes were nitrogen limited. Given that exotic grassland fires tend to burn at lower temperatures and are more modest than fires in shrub dominated areas (Christensen 1985; Neary et al. 1999), we predict that the effect of fire severity on nutrient availability and enzyme activity would be weaker in exotic grass relative to CSS dominated areas.

Materials and methods

Study site

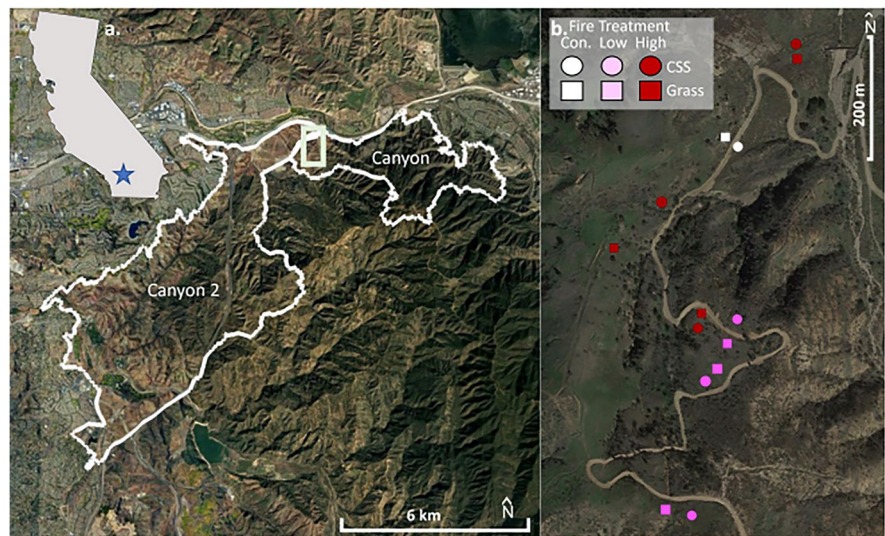
The objective of this study was to investigate the effects of fire on ecosystem properties within exotic grasslands and CSS vegetation within Coal Canyon in Chino Hills State Park (Anaheim, CA; 33°52'13.96"N, -117°41'15.42"W). This area experienced two distinct wildfires (Canyon Fire and Canyon 2 Fire) that collectively burned about 4800 hectares of grassland, shrubland and riparian vegetation. The Canyon Fire lasted from September 25, 2017 to October 4, 2017 and the Canyon 2 Fire burned from October 9–17, 2017. The pre-fire grassland communities were defined by exotic annual grasses such as *Avena fatua*, *Bromus diandrus*, *Schismus barbatus*, and forbs such as *Brassica nigra* and *Hirschfeldia incana*, while the coastal sage shrublands were dominated by *Artemisia californica*, *Eriogonum fasciculatum* and *Salvia mellifera*. The study site is characterized by Mediterranean cool-wet winters and hot-dry summers with a mean annual growing season (Nov–June) rainfall of 291 mm (based on 1989–2019 Irvine station precipitation data, <https://cimis.water.ca.gov/Default.aspx>). Rainfall during the 2018 sampling was 75% below average at 72 mm.

We identified six sites that were stratified by fire severity (low and high) as estimated by char cover (low severity: $\leq 40\%$ char cover; high severity: char cover $\geq 60\%$; Table 1; Fig. 1). We recognize that the residual char cover post-fire does not fully capture the factors that determine fire severity, but we used char cover as a proxy for burn severity in the current study. Within each site, three 1 m²

Table 1 Initial characterization of the burn severity (low: $\leq 40\%$ char cover; high: char cover $\geq 60\%$) and percent vegetation cover of 7 sites dominated by CSS and 7 sites dominated by exotic grass following the 2017 Canyon Fires. Vegetation cover was sampled in May 2018. Data are reported as average ± 1 SE

Site	Dominant site vegetation	Burn severity classification	Char cover (%)	Vegetation cover (%)
1	CSS	High	86.67 (1.67)	15 (15)
2	CSS	High	95 (0)	10.67 (3.84)
3	CSS	High	80.00 (2.89)	5.67 (3.28)
4	CSS	Low	6.67 (1.67)	24.33 (7.88)
5	CSS	Low	15 (7.64)	36.67 (4.41)
6	CSS	Low	16.67 (3.33)	21.33 (9.13)
7	CSS	Control	0 (0)	95 (0)
8	Grass	High	83.33 (1.67)	78.33 (8.33)
9	Grass	High	73.33 (3.33)	63.33 (3.33)
10	Grass	High	65 (2.89)	63.33 (3.33)
11	Grass	Low	16.67 (6.01)	50 (2.89)
12	Grass	Low	25 (8.66)	61.67 (11.67)
13	Grass	Low	18.33 (7.26)	41.67 (13.02)
14	Grass	Control	0 (0)	62.33 (22.56)

Fig. 1 Map of Canyon Fire perimeters (a.) and experimental sites (b.) within the fire scars. Inset describes general location of the study site within California. Experimental plots were placed in coastal sage scrub (CSS) shrublands and exotic dominated grasslands at three different fire treatments: no (control plots, white), low (pink) or high (red) severity during this fire event



plots within an exotic grassland area and another three within a CSS dominated area were identified for a total of 36 plots (2 fire severities \times 3 sites \times 2 vegetation types \times 3 plots). We identified one unburned vegetation site, containing six 1 m² plots split evenly between a grassland and CSS patch. Control plots served as a baseline for comparison of potential changes in soil and vegetation post-fire and are referred to as the control plots. Samples (as described below) were collected on April 30th, 2018 (6 mo. post-fire), July 10th, 2018 (9

mo. post-fire) and October 22nd, 2018 (1-year post-fire). It is important to note that the distinction of a “low severity” and “high severity” burned plot is a relative term. Moreover, based on differences in vegetation type and the % char cover (Table 1), it is plausible that the soil dominated by CSS experienced an overall higher severity burn relative to the soil dominated by grasses thus, the “low severity” and “high severity” terms are used as comparisons within a vegetation type.

Soil & Vegetation sampling

Prior to sampling, each plot was further divided into four quadrants to ensure sampling was representative of the variation within a plot. Soil cores (0–5 cm) were composited from each quadrant within each plot until ~200 g of soil was collected. In the CSS control plots, soil collection via a soil corer was not feasible so a gardening spade was used for soil collection to a depth of 5 cm. Soils were immediately placed on ice and transported to Chapman University (Orange, CA) for processing. Once in the lab, soils were sieved through a 2 mm sieve, pH was measured (1 soil: 1 nanopure), and subsamples were dried at 105° C to a constant mass for moisture content determinations.

Soil nutrients

To estimate available soil N, 10 g of field-moist soil and 40 mL 2 M KCl were added to 50 mL falcon tubes, placed on a shaker at 150 RPM for 1 h, centrifuged at 4000 RMP for 10 min and filtered through a Whatman 42 filter for NO_3^- and NH_4^+ analyses. Soils were extracted within 48 h of sample collection and were frozen prior to analysis. Briefly, for NO_3^- analysis, we used a 96 well plate method with a vanadium chloride, sulfanilamine solution, NED solution, and nanopure reagent. 10 μL of sample and 160 μL of reagent were incubated, in the dark, for 6 h prior to measurement at 540 nm on a spectrophotometer. For NH_4^+ analysis, we used a 96 well plate method with sodium salicylate and bleach reagents (Weatherburn 1967). 15 μL of sample were added to 92.5 μL of salicylate solution and bleach reagents, incubated for 50 min and analyzed at 650 nm on a spectrophotometer. Available N was measured at all time points.

Six months after the fire, total organic carbon (TOC) and microbial biomass carbon (MBC) were measured to determine if the fire affected the quantity of microbes and/or the soil dissolved organic carbon. Microbial biomass carbon was measured following the chloroform fumigation method (Brookes et al. 1985). 0.5 g of soil was added to 2 sets of conical tubes. Chloroform was added to one of the two sets for a 24-h period in a desiccator. After 24 h, chloroform fumigated and non-fumigated soils were extracted with 40 mL of 0.5 M K_2SO_4 , centrifuged for 10 min at 4000 RMP, and

filtered through a Whatman 42. Extracts were frozen and sent to the Center for Applied Isotope Studies at the University of Georgia for TOC and MBC analysis.

Microbial activity

To quantify microbial respiration potentials, 10 g of soil (adjusted to a 20% moisture content) was added to a 470 mL mason jar fitted with a sampling port. 60 mL of room air was injected into each mason jar to maintain positive pressure. Mason jars were incubated at 25 °C and 10 mL of headspace gas was injected into a EGM-4 environmental gas analyzer (PP systems) every hour over a four hour period to determine CO_2 concentrations.

Enzyme assays for liberation of nitrogen (leucine aminopeptidase (LAP) and N-acetyl-glucosidase (NAG)), phosphorus (Phosphatase (PHOS)), and carbon (β -glucosidase (BGA) and cellobiohydrolase (CBH)) were quantified using substrates tagged with a methylumbelliferone fluorophore or methylcoumarin fluorophore (LAP). Enzymes quantified in this study are inducible, meaning that the microbes can choose to up or downregulate production based on changing metabolic needs (Allison et al. 2010). Soils were diluted with nanopure water (1 g soil: 19 mL nanopure) in 20 mL scintillation vials and placed on a shaker at 150 RMP for 30 min to ensure adequate mixing. 150 μL slurry aliquots were added to 96 well plates with 100 μL of the appropriate fluorescently tagged substrate at T_0 (start of incubation) and at T_2 (after 2 h). After incubation, enzyme activity was measured at an excitation of 350 nm and emission of 450 nm. Fluorescence measured at T_2 was subtracted from fluorescence measured at T_0 and enzyme activity rates were calculated using a standard curve.

Vegetation sampling

At peak biomass (May 2018), plant composition was sampled in all plots. Cover for each species was visually estimated, and this cover was allowed to sum to more than 100 due to overlapping canopy layers. Any species that occurred as a single individual were recorded as 0.5%. Species cover data were used to estimate species richness and Shannon Diversity. Total vegetation cover out of 100% was also visually

estimated. In the 6 burned sites, aboveground plant biomass was additionally sampled in a 25 cm × 25 cm on the outer edge of the 1 m² plot. Biomass was sorted into live biomass and litter, dried at 60 °C for 48 h and weighed.

Statistical analysis

To assess how soil N and the microbial activity differed between vegetation types and fire severity, a repeated measures ANOVA model with vegetation type, fire severity, and time and all their interactions as fixed factors was run for each response variable (Soil, pH, moisture, NO₃⁻, NH₄⁺, extracellular enzyme assays, and microbial respiration). Microbial biomass carbon, TOC, and plant diversity and biomass were sampled only once and were analyzed with two-way ANOVA with vegetation type and fire severity as fixed factors and sampling block as a random factor. All repeated measures statistical tests were performed using JMP v. 13.0 (SAS Institute, Cary, N.C.). Two-way ANOVAs were performed in R v4.1 (R Core Team 2020). All variables were natural log X + 1 transformed to meet assumptions of normality for analyses except for Shannon diversity and Tukey HSD was used for any post-hoc comparisons.

Results

Soil resources and attributes

Soil pH was lower in the low severity plots relative to control and high burn plots (Fire; $p < 0.0001$; Table 2A) regardless of vegetation type (Vegetation; $p = 0.62$). Soil pH was affected by the time post fire and fire treatment interaction such that control plots at 6, 9, and 12 months and high severity plots at 6 and 9 months had the highest soil pH (Fire*time; $p = 0.034$; Fig. 2a. and b.). Soil moisture was not affected by vegetation type but was lowest in burned plots (Control > Low severity = High severity; Fire; $p = 0.0006$, Table 2A). Additionally, soil moisture varied with time post fire with the highest soil moisture at 12 months after the fire (12 months > 6 = 9; Time; $p < 0.0001$; Fig. 2c. and d.)

Soil nitrogen (NO₃⁻ and NH₄⁺) availability varied among the experimental treatments (Fig. 3, Table 2B). Soil NH₄⁺ concentrations were greatest in high severity plots, followed by the low severity plots and with control plots maintaining the lowest concentrations at all time points, but the differences between high severity plots and control plots tended to decrease over time (Fire*time; $p = 0.0028$; Fig. 3a. and b.). Coastal sage scrub dominated plots were elevated in soil NH₄⁺

Table 2 Summary model statistics for main and interactive effects of char level, vegetation type, and time post fire on soil attributes (A.), soil nutrients (B.), and soil processes (C.). F statistics and degrees of freedom are reported based on Ken-

ward-Roger approximations. All response variables were natural log transformed (i.e. Ln(x + 1)) to meet assumptions of normality prior to analysis.

Response variable	Char	Vegetation	Time	Char*Veg	Char*Time	Veg*Time	Char*Veg*Time
A. Soil Attributes							
Soil pH	45.76 _{2,16.6} ***	0.26 _{1,47.26}	7.25 _{2,97.9} **	0.99 _{2,16.6}	2.92 _{4,38.29} *	0.13 _{2,97.9}	0.61 _{4,38.3}
Soil Moisture Content	14.3 _{2,12.3} ***	0.14 _{2,16.15}	181.2 _{2,51.9} ***	3.49 _{2,12.3} †	0.70 _{4,34.9}	0.71 _{2,51.9}	2.01 _{4,34.9}
B. Soil Nutrients							
Soil NH ₄ ⁺	96.8 _{2,13.5} ***	16.4 _{1,22} ***	4.23 _{2,83.9} *	18.2 _{2,13.5} ***	5.0 _{4,34.2} **	4.09 _{2,83.9} *	0.79 _{4,34.2}
Soil NO ₃ ⁻	23.44 _{2,6.8} ***	2.30 _{1,8.4}	2.32 _{2,85.6}	4.97 _{2,6.8} *	1.95 _{4,36.6}	5.14 _{2,85.6} **	3.43 _{4,36.6} *
C. Soil Processes							
Soil CO ₂ Respiration	63.0 _{2,18.0} ***	4.93 _{1,48.4} *	42.4 _{2,90.1} ***	1.02 _{2,18.0}	0.22 _{4,35.4}	0.03 _{2,90.1}	0.20 _{4,35.4}
BGA	20.64 _{2,11.7} ***	5.98 _{1,21.5} *	109.34 _{2,75.1} ***	3.22 _{2,11.7} †	4.57 _{4,32.8} **	1.55 _{2,75.1}	3.89 _{4,32.8} *
CBH	4.59 _{2,10.4} *	4.76 _{1,13} *	106.62 _{2,79.9} ***	6.09 _{2,10.4} *	19.37 _{4,35.3} ***	2.27 _{2,79.9}	1.74 _{4,35.3}
PHOS	15.59 _{2,16.3} ***	2.00 _{1,25.1}	199.58 _{2,54.1} ***	14.33 _{2,16.3} ***	4.26 _{4,32.5} **	6.14 _{2,54.1} **	4.38 _{4,32.5} **
NAG	40.31 _{2,15.4} ***	7.05 _{1,34.4} *	120.89 _{2,51.6} ***	5.78 _{2,15.4} *	3.79 _{4,28.0} *	0.47 _{2,51.6}	1.25 _{4,28.0}
LAP	10.00 _{2,16.4} **	12.65 _{1,31.8} **	96.48 _{2,76.8} ***	11.96 _{2,16.4} ***	1.75 _{4,37.1}	3.74 _{2,76.8} *	1.17 _{4,37.1}

Note: † $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

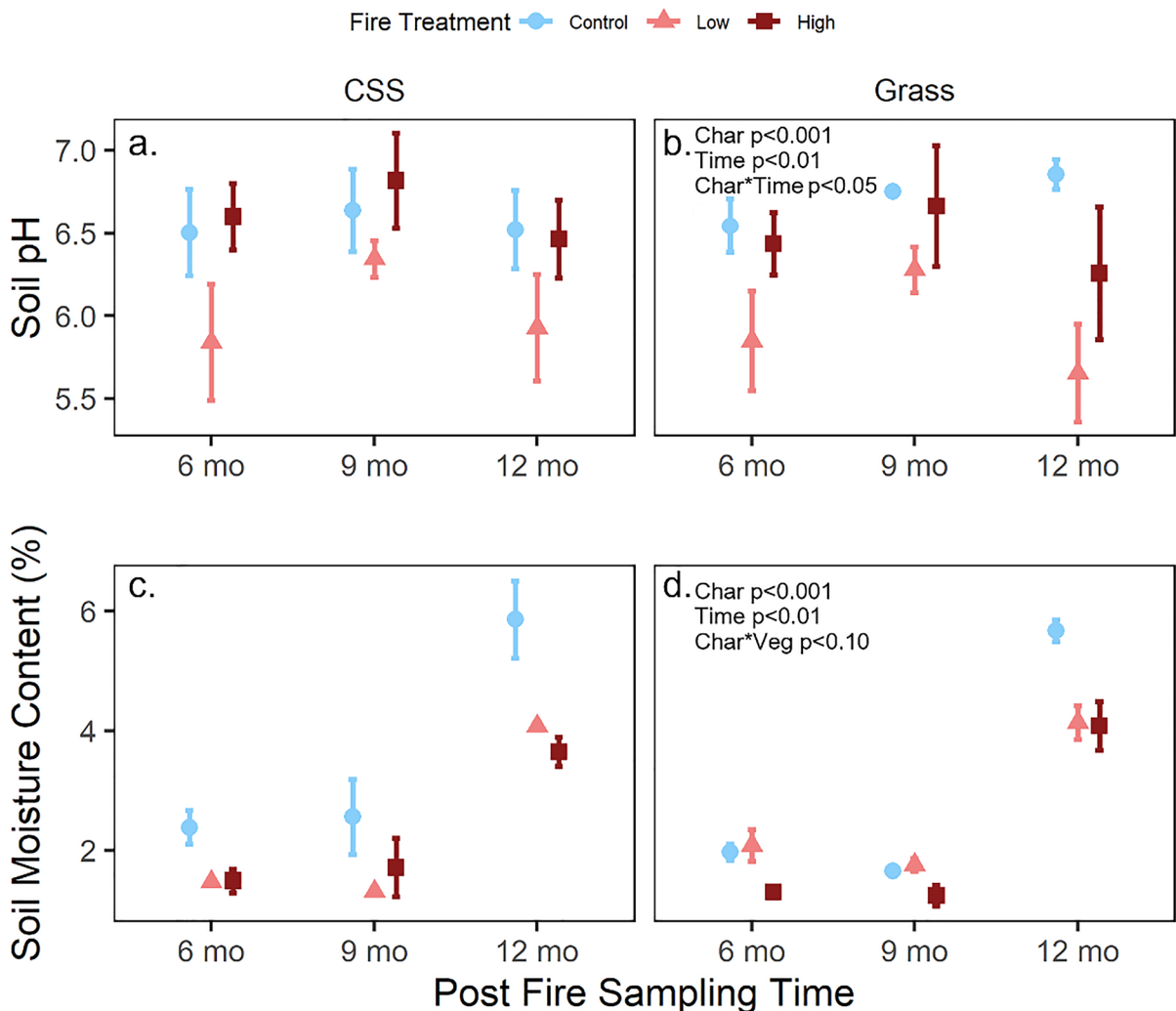


Fig. 2 Soil pH (a) and percent soil moisture content (b) from plots dominated by differing vegetation (Exotic grass or Coastal sage scrub) following the Canyon Fires in October

2017. Note: plots were exposed to either no (control plots, ●), low (▲) or high (■) severity during this fire event. Data reported are average ± 1 SE

relative to exotic grass dominated plots (Vegetation; $p = 0.0005$; Fig. 3c. and d.). Control plots had the lowest soil NO_3^- concentrations, and concentrations did not vary over time or by vegetation type (Fire; $p = 0.0009$; Fig. 3c. and d.). Vegetation type and time post fire did not significantly affect soil NO_3^- availability independently but did interact with fire severity to affect concentrations. While there were some nuanced differences among the multiple levels of the three-way interactions, generally, regardless of vegetation, low severity plots

had the greatest soil NO_3^- concentrations, followed by concentrations in high severity plots; with control plots containing the lowest soil NO_3^- levels (Fire*veg*time; $p = 0.0177$; Fig. 3c. and d.).

Total organic carbon (TOC) differed across fire severity regardless of vegetation type (Fire; $p = 0.039$, Fire*veg; $p = 0.014$; Table S1; Fig. 4a.), with the low severity plots tending to have the lowest TOC (Low severity < Control, post hoc $p = 0.056$). TOC did not differ between the vegetation types (Vegetation; $p = 0.10$).

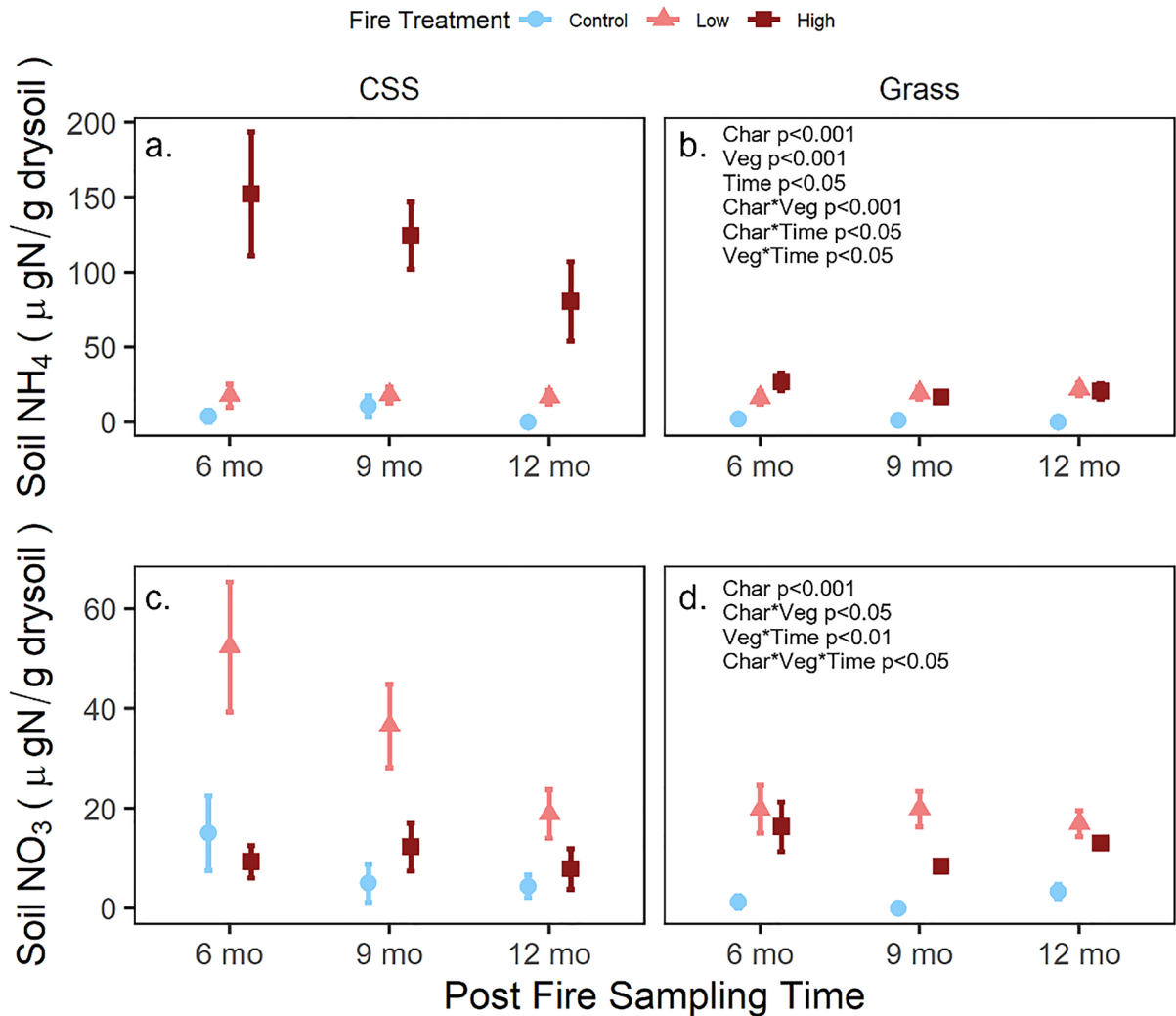


Fig. 3 Soil NH_4^+ (a.) and NO_3^- (b.) concentrations from plots dominated by differing vegetation (Exotic grass, orange or Coastal sage scrub, blue) following the Canyon Fires in Octo-

ber 2017. Note: plots were exposed to either no (control plots, ●), low (▲) or high (■) severity during this fire event. Data reported are average ± 1 SE

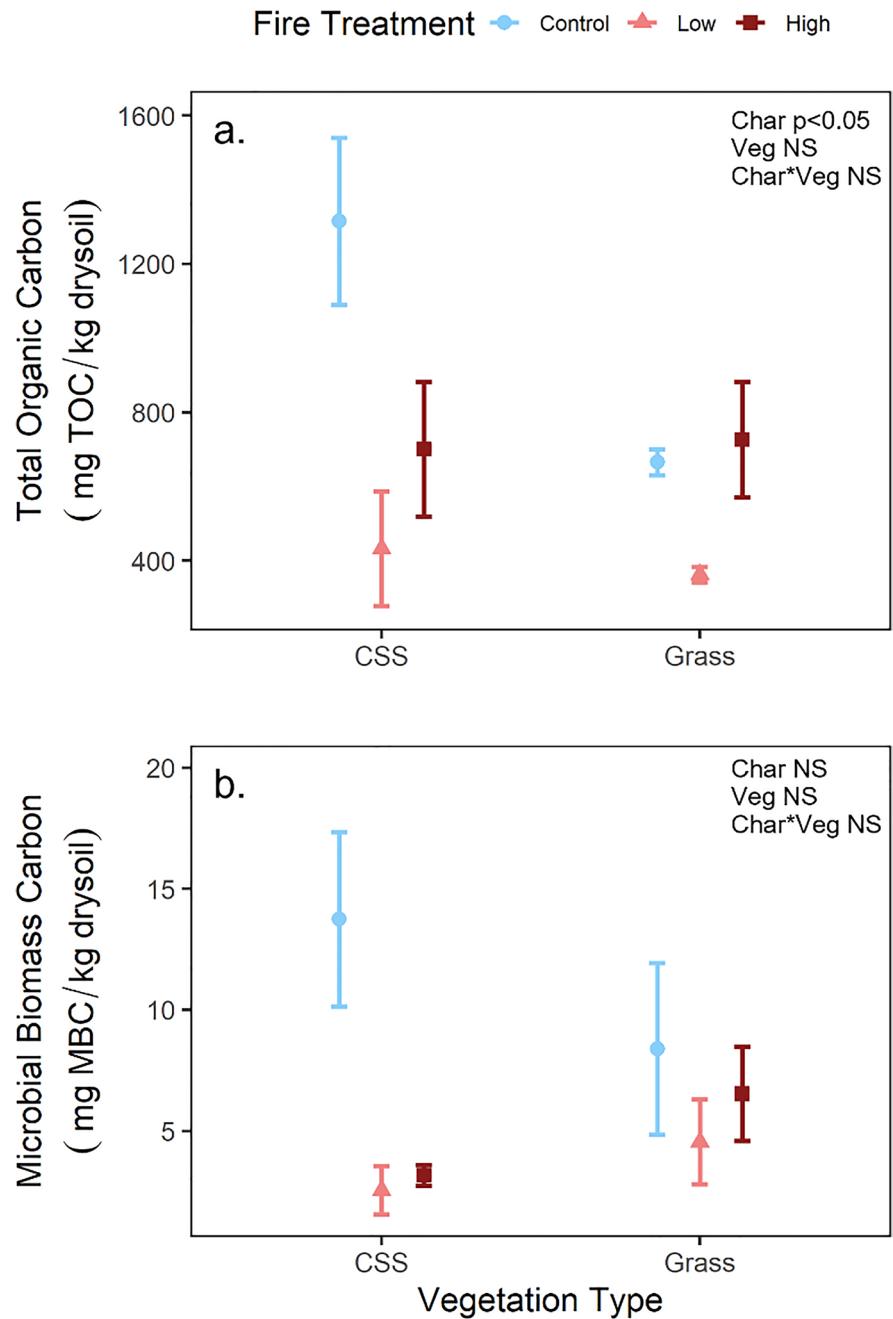
Soil microbial activity

Soil microbial respiration was influenced by fire severity, vegetation type and time post fire but no interactive effects influenced respiration (Table 2C). Soil microbial respiration was suppressed in low severity plots relative to control and high severity plots, regardless of vegetation type (Fire; $p < 0.0001$; Fig. 5). Exotic grass plots had higher respiration rates relative to CSS plots (Vegetation; $p = 0.031$; Fig. 5), and respiration was affected by time post fire with elevated CO_2 production at 6- and 9-months post fire

relative to 12 months post fire (Time; $p < 0.0001$; Fig. 5). Although trends suggest lower MBC in burned plots relative to control plots, these differences were not statistically significant, regardless of vegetation (Fig. 4b; Table S1).

Generally, enzyme activity had more variable responses relative to the soil resources and attributes described above; however, the interactions of 1.) fire severity * time and 2.) fire severity * vegetation type most consistently impacted enzyme activity (Table 2C). β -glucosidase activity was suppressed in low severity plots relative to high severity and

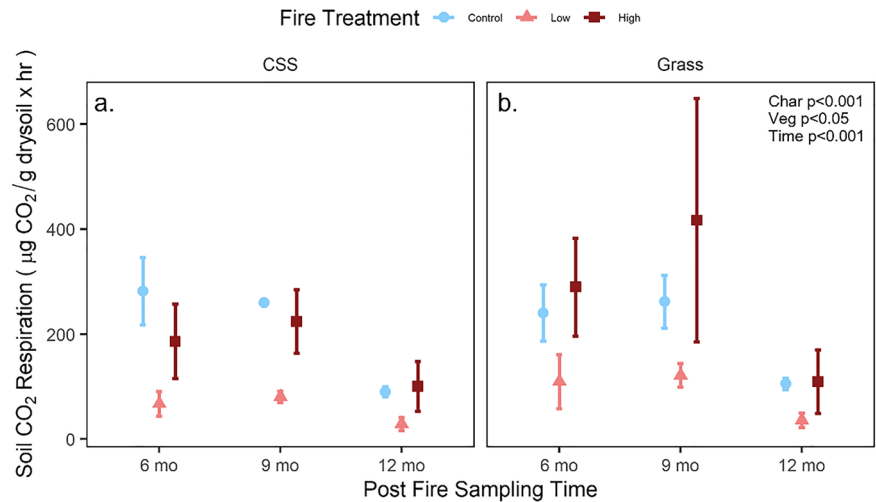
Fig. 4 Soil total organic carbon (a.) and microbial biomass carbon (b.) concentrations from plots dominated by differing vegetation (Exotic grass or Coastal sage scrub) following the Canyon Fires in October 2017. Note: data are from soils collected 6 months post-fire, and plots were exposed to either no (control plots), low or high severity during this fire event. Data reported are average \pm 1 SE



control plots (Fire; $p = 0.0001$ (BGA); Fig. 6a. and f.); while, CBH tended to be upregulated in high severity plots compared to others (Fire; $p = 0.037$ (CBH); Fig. 6b. and g.). Activity of BGA and CBH was elevated in exotic grass relative to CSS dominated soils (Vegetation; $p = 0.023$ (BGA), $p = 0.048$ (CBH); Fig. 6b. and g.). β -glucosidase activity was lowest 9 months post fire in control and low severity exotic

grass plots and CSS plots, with the lowest activity 12-month post fire (October) across a mix of vegetation and burn treatments (Fire*veg*time; $p = 0.023$; Fig. 6a. and f.). In contrast to BGA, CBH activity was lowest 9-months post fire (July) and was greatest in high severity plots at 12 months post fire (October) (Fire*time; $p < 0.0001$; Fig. 6b. and g.). The greatest CBH activity was in the high severity grass

Fig. 5 Soil respiration potentials from plots dominated by differing vegetation (Exotic grass or Coastal sage scrub) following the Canyon Fires in October 2017. Note: plots were exposed to either no (control plots, ●), low (▲) or high (■) severity during this fire event. Data reported are average \pm 1 SE



dominated plots with similar activity across all other (low severity and control) plots (Fire*veg; $p=0.018$; Fig. 6b. and g.).

Fire severity, vegetation, and time post fire all significantly impacted phosphatase activity among soils (Table 2C). The time post fire had a large effect on phosphatase activity (12 mo > 6 mo > 9 mo; time; $p<0.0001$; Fig. 6c. and h.). Phosphatase activity was the lowest in low severity plots regardless of vegetation type (Fire; $p=0.002$). The interactive effects of fire, vegetation and time post fire were strongly structured by time, where phosphatase activity was greatest at 12 months (October) across burn and vegetation types and lowest in 9 months (July) post fire in control and low severity exotic grass plots and CSS plots (Fire*veg*time; $p=0.006$; Fig. 6c. and h.).

N enzyme activity was also significantly impacted by fire severity, vegetation, and time post fire (Table 2C). N-acetyl-beta-D-glucosamine (NAG) activity was greatest in the high severity plots regardless of vegetation type (Fire*veg; $p=0.014$; Fig. 6d. and i.) and in all plots 12-months (October) post fire (Fire*time; $p=0.014$; Fig. 6). NAG activity was also elevated in exotic grass relative to CSS dominated soil (Vegetation; $p=0.012$; Fig. 6d. and i.). Leucine aminopeptidase (LAP) activity was greatest in the control and high severity exotic grass plots and was lowest in the low severity (CSS- and grass dominated plots) and high severity CSS dominated plots (Fire*veg; $p=0.0006$; Fig. 6e. and j.). LAP was suppressed in burned relative to control soil (Fire; $p=0.0014$; Fig. 6e. and j.) and was elevated in CSS

relative to exotic grass dominated soil (Vegetation; $p=0.0012$; Fig. 6e. and j.). LAP activity was affected by season with the greatest activity at 12 months (regardless of vegetation) and the lowest activity in CSS dominated plots at 6 months (April) (Vegetation*time; $p=0.028$; Fig. 6e. and j.).

Vegetation

Aboveground plant cover differed by vegetation community and fire severity (Table S2). Burned CSS plots had lower plant cover compared to control plots (High severity: 11 ± 5.94 , Low severity: 27.4 ± 5.94 , Control: 95 ± 10.3) or burned grass plots (Fire*veg; $p<0.001$). Exotic grass burned and control plots had similar cover (High severity: 68.3 ± 5.94 , Low severity: 51.1 ± 5.94 , Control: 62.3 ± 10.3). Plant community diversity also strongly differed by vegetation type and fire severity (Fire*veg; $p<0.001$). Plant diversity was similar for the exotic grass plots regardless of fire severity (High severity: 1.14 ± 0.13 , Low severity: 1.128 ± 0.13 , Control: 0.57 ± 0.23); however, diversity differed for CSS, with diversity being the highest in the low severity plot (Control = High severity < Low severity; Control: 0.11 ± 0.23 , High severity 0.38 ± 0.13 , Low severity: 1.60 ± 0.13). Aboveground plant biomass was the greatest in exotic grass plots regardless of burn severity (High severity: 11.8 ± 0.27 , Low severity: 9.8 ± 0.27) and lowest in the high severity CSS plots (High severity: 0.38 ± 0.27 , Low severity: 3.96 ± 0.27 ; Vegetation*fire; $p<0.001$).

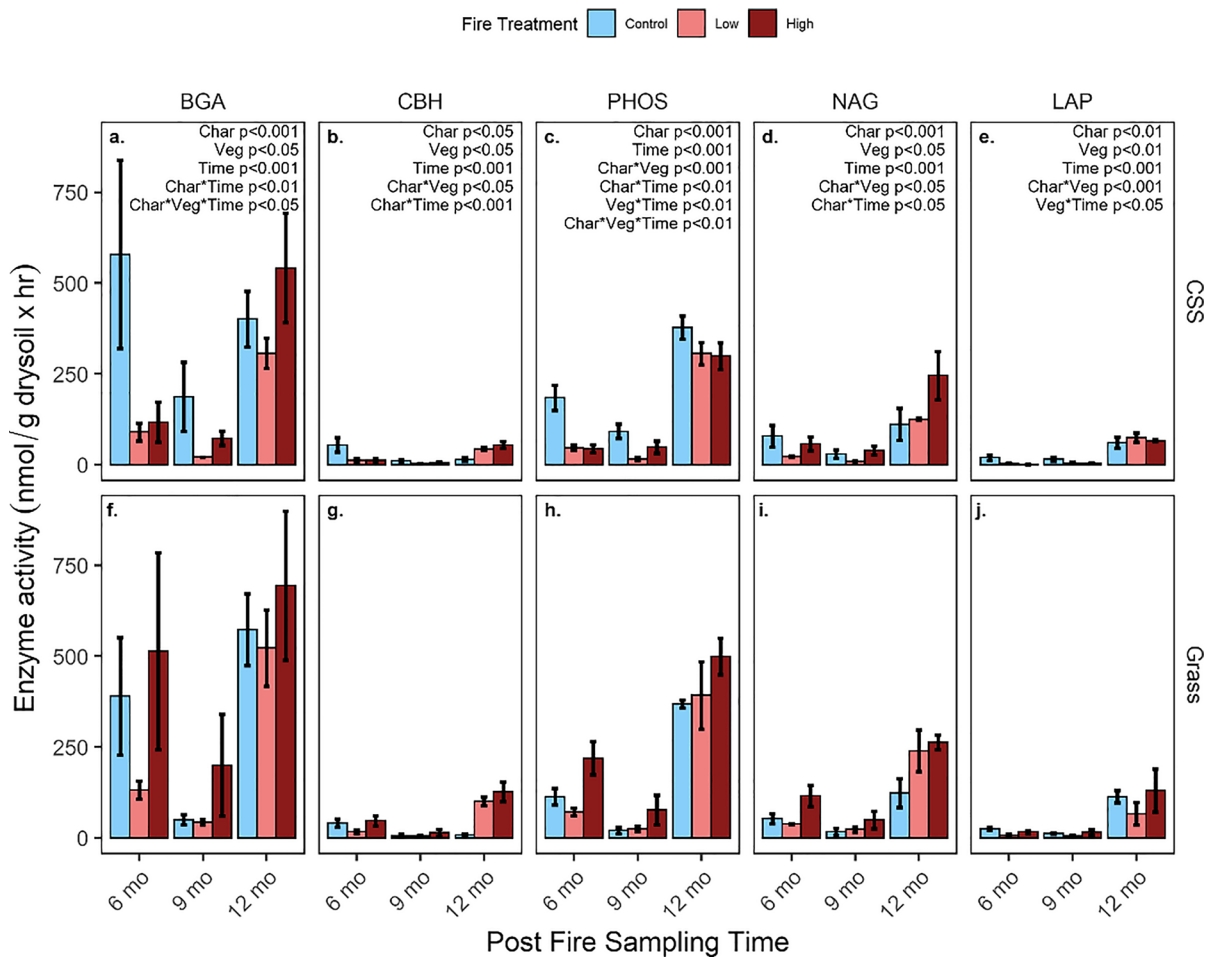


Fig. 6 Microbial enzyme activity of β -glucosidase (BGA), Cellobiohydrolase (CBH), Phosphatase (PHOS), N-acetylglucosidase (NAG), and Leucine aminopeptidase (LAP) from soils dominated by Coastal sage scrub (panels a–e., respectively) or exotic grasses (panels f.–j., respectively) following the Canyon Fires in October 2017. Note: plots were exposed

to either no (control plots), low or high severity during this fire event. Data reported are average \pm 1 SE. Note: Methylcoumarin (MCA) fluorophore was only used to determine LAP activity; all other enzyme assays used the methylumbelliferone (MUF) fluorophore

Discussion

Our results highlight that ecosystem processes in this Mediterranean system are sensitive to fire severity and are strongly impacted by growing season dynamics. We did observe an increase in available nitrogen (N) following fire; however, only soil NH_4^+ (and not soil NO_3^-) concentrations increased with burn severity. Thus, our initial hypothesis that soil N would increase with burn severity was partially supported. Additionally, we predicted that elevated N availability associated with increasing fire severity would stimulate soil microbial respiration

following the downregulation of microbial enzyme production. The fire effects would be more pronounced in CSS relative to exotic grassland dominated soil. We did find a differential effect of fire on microbial respiration and enzyme activity, but we did not see a consistent trend of downregulation. We did not observe that any fire effects on soil respiration were weaker in exotic grassland soils compared to CSS soils as we predicted. Shifts in enzyme activity varied across vegetation type, fire severity and enzyme type. Overall, our predictions were partially supported as we found key differences in soil nutrient and enzyme dynamics driven

by burn severity and recovery time, which we expand on below.

Microbial community responses and their subsequent recovery to fire are dependent on the initial dominant vegetation (Hart et al. 2005) and the extent of vegetation combustion. Fire duration and severity can dictate the combustion completeness of the vegetation; ultimately affecting the proportion of fire residues (ash and/or char) produced and the magnitude of nutrient pulses post-fire (Hogue and Inglett 2012). The combustion of organic matter can result in the direct production of NH_4^+ thus, we would expect a high severity burn to deposit more NH_4^+ on the soil than a low severity burn. In the current study, N was elevated in all burned soils, with soil NH_4^+ concentrations greatest in high severity soil. The pulse of NH_4^+ was more pronounced in the CSS community consistent with other studies (Esque et al. 2010; Fenn et al. 1993) and in agreement with our prediction that the effects of fire would be more evident in CSS (relative to exotic grass) dominated soil. In contrast, NO_3^- is often indirectly produced post fire through the process of nitrification (Certini 2005). Soil NO_3^- concentrations were greatest in soils exposed to low severity conditions, although concentrations remained elevated in high severity relative to control soils. With concentrations of NO_3^- regulated by microbial processes, this result was not surprising. While Total N and Total Carbon (C) were not measured in the initial vegetation, the combustion of the CSS community (which had a greater standing biomass) likely contributed to the heightened pulse of soil N observed in CSS (relative to grass) dominated soil. Dickens and Allen (2014b) reported CSS (*Artemisia californica*) to contain more than twice the tissue N concentrations relative to exotic grasses (*Avena fatua*) and forbs (*Brassica nigra*) found in our study site, suggesting that when completely combusted, there is a potential for more N deposition on CSS dominated soil. Consistent with our findings, Romanyà et al. (2001) reported that higher severity burns correlated with elevated soil NH_4^+ concentrations in shrub dominated communities. Additionally, they reported that in shrub dominated soil, increased fire severity resulted in only a small increase in soil NO_3^- concentrations (relative to the increase in soil NH_4^+ concentrations). These data suggest that the observed response in soil N availability post-fire in our study was similar to the response observed in

other Mediterranean ecosystems. An increase in soil N availability would suggest that microbial activity, such as enzyme production and respiration potentials, would be indirectly affected by fire.

Microbial enzyme activity shifted in this study across vegetation type post fire in line with changes to nutrient availabilities. The combustion of standing biomass results in the deposition of C (among other nutrients) rich charred or ashed residues on the soil surface. Microbes release enzymes to break down the C within residues targeting β -1,4 linked to glucan chains to release C from cellobiose dimers (CBH enzyme) or cellobiose (BGA enzyme) resulting in a C form that may be more accessible to microbes (Sinsabaugh et al. 2008). Exotic grass dominated soil exhibited higher C enzyme activities relative to CSS dominated soil suggesting a greater need for additional available C in grass dominated soil. These findings are consistent with soil TOC concentrations in CSS dominated soil being almost double that of concentrations in grass dominated soil. Microbes exposed to low severity conditions suppressed β -glucosidase activity relative to high severity and control soil suggesting that the low severity fire alleviated any potential C limitation. Time was an important factor regulating C enzyme activity but was driven by seasonality as opposed to time post fire. Seasonality affected C enzyme activity with the greatest down-regulation in July during the summer drought and the greatest upregulation in October at the start of the growing season.

Soil N cycling post shrubland fires can be very dynamic with multiple components such as soil inorganic N pools and N liberating enzyme production impacting overall cycling (Hanan et al. 2016; Vourlitis et al. 2021). The control plots had the lowest soil inorganic N estimates supporting previous hypotheses that mature vegetation may rapidly uptake soil N preventing its accumulation in the soil and resulting in high plant/microbe competition (Fenn et al. 1993; Hanan et al. 2016). The pulse of soil N that commonly occurs post-fire (Esque et al. 2010) could therefore temporarily alleviate microbial N limitation in ecosystems with high plant/microbe competition (Sinsabaugh and Foreman 2001). Leucine aminopeptidase (LAP) was downregulated in low and high severity soils and down regulated more strongly in CSS plots suggesting that microbial N limitation may be greater in this soil. This is consistent with the

slower nutrient cycling associated with CSS ecosystems relative to grass invaded CSS (Allen et al. 2011; Dickens et al. 2013; Neary et al. 1999). While LAP activity was heightened in grass dominated soil, NAG activity was greatest in CSS dominated soil. This differential response in NAG may be a result of some native shrubs relying heavily on mycorrhizal fungal associations. Some dominant species are arbuscular mycorrhizal (e.g. *Artemisia californica*) while others are both arbuscular and ectomycorrhizal (*Adenostoma fasciculatum*) (Wang and Qiu 2006). Fungal partners can be key players in extracellular chitinase production (Treseder and Lennon 2015). CSS communities that have been invaded by annual grasses often tend to see a shift in mycorrhizal communities both in diversity and abundance (Egerton-Warburton and Allen 2000). This suggests that microbes residing in CSS and grass dominated soil may upregulate different N acquiring enzymes when N availability is limited (Sinsabaugh et al. 2005).

As vegetation is increasingly combusted, N can be volatilized and lost from a system; however, high combustion temperatures are needed for P release in the form of ashed residue which can deposit on the soil surface (Pérez-Cabello et al. 2009). Thus, PO_4 deposition would be more likely in high severity, relative to low severity and control plots where the temperatures would not be high enough for P liberation. Surprisingly, PHOS activity was downregulated in low severity (and not high severity) soil suggesting that adequate concentrations of soil P were available for microbial processing. However, downregulation may be in response to increased nutrient pulses aside from P. Allison and Vitousek (2005) investigated PHOS activity following the combined addition of C (sodium acetate) and N (NH_4Cl) to rainforest soil. Data suggest that increased availability of these two nutrients can result in stimulated PHOS activity whereas the addition of PO_4 resulted in the downregulation of PHOS. In the current study, the activity of PHOS in high severity soil was not statistically different from PHOS activity in the control soil; however, increased soil NH_4^+ in high severity soil may explain the lack of downregulation of PHOS following the fire. Similar to other enzymes assayed, activity was greatest in October regardless of burn severity or vegetation type.

Overall changes in soil attributes, nutrient concentrations, as well as microbial activity (changes in

enzyme production) were more pronounced in low severity soil. The downregulation of several key C, N, and P acquiring enzymes coupled with a more pronounced pulse of soil N (as NO_3^-) suggests that the activity of the remaining microorganisms should be heightened relative to activity rates in control soil, particularly in soil exposed to low severity conditions. Although trends suggest potential microbial respiration was lower in low severity soil, this was not statistically significant. Decreased microbial biomass carbon (MBC) is common post fire (Heydari et al. 2016), suggesting that the quantity of microbes (in addition to type of microbes present) can vary across sites. A disproportional decrease of the microbial abundance within the low severity sites is a plausible explanation for the decreased microbial respiration observed. A reduction in microbial abundance is often in response to direct fire effects, unfortunately MBC was only measured at one time point during the current study. In our study, vegetative cover was significantly reduced in all burned plots, which can increase microbial exposure to elevated temperatures while simultaneously reducing the soil moisture content (Neary et al. 1999). Consistent with this theory, soil moisture content was significantly reduced in burned soil, regardless of dominant vegetation type or burn severity.

Microbial activities were greatly affected by seasonality and trends were relatively consistent across sites, regardless of burn severity or dominant vegetation type. Data collected 6-months post fire (April 22nd) coincided with the peak of herbaceous growth, data collected 9-months post fire (July 10th) coincided with mid-summer drought conditions, and data collected 12-months post fire (October 22nd) coincided with the beginning of the growing season (October–May in Mediterranean climates). These events would affect soil moisture concentrations and potential microbial and plant competition for nutrient availability across all plots (Jackson et al. 1988). The largest effect on microbial activity occurred at the start of the growing season (October) when the demand for vegetation resources would be elevated. During this time, microbes upregulated the production of key N acquiring enzymes while simultaneously decreasing overall respiration potentials. These findings suggest that the microbial communities may have become nutrient limited and were allocating resources to maintain necessary nutrient ratios. Consistent with Machmuller

et al. (2016), we observed increasing enzyme activities with soil moisture content; however, this relationship only occurred in CSS dominated soil. With the highest soil moisture contents during October in all sites, it is likely that a combination of factors are controlling the rate of microbial activity in our sites and that the main controls may vary by dominant vegetation type.

Conclusions

The overarching objective of the current study was to determine how burn severity would affect microbial activities and soil nutrient availabilities in soil dominated by CSS or exotic grasses in a Mediterranean climate. While decreased soil moisture and vegetative cover coupled with elevated soil N concentrations were evident regardless of burn severity, the N form (NH_4^+ or NO_3^-) deposited to the soil varied by burn severity with the greatest pulse of NO_3^- and NH_4^+ in low and high severity soils, respectively. The microbial response in low severity soils was more pronounced with downregulation of key nutrient acquiring enzymes and lower microbial respiration potentials relative to activities in control and high severity soil. While we expected a stronger effect of burn intensity, this was still an important finding. Surprisingly, dominant vegetation type was not a strong control on the microbial responses post fire although soil dominated by CSS did contain greater concentrations of key nutrients relative to grass dominated soil post fire. After 1 year, soil N concentrations remained elevated in burned soils suggesting that the regrowth of opportunistic vegetation in subsequent growing seasons is probable. The conversion of CSS to exotic grassland has been linked to soils with elevated N deposition in this region (Cox et al. 2014) suggesting that CSS vegetation may be particularly vulnerable in our sites post-fire. Furthermore, increased fire frequency associated with climate change, has the potential to have a much larger effect on ecosystems that are at a high risk for fire, such as this study site. Based on our data, an increase in fire frequency could result in a vegetation type conversion, which would continue to affect microbial activity and dictate long term changes to this ecosystem and its ecosystem functioning. These findings suggest that the management and continuous monitoring of soil attributes and

microbial activity following fire events can provide insight into potential long term ecological changes that could affect conditions for plant regrowth.

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Author contributions CZ and LL designed the study and experimental design; CZ, EH, JR, KB, LL collected the samples, CZ, EH, JR, KB ran analyses, CZ and LL analyzed data and prepared figures, CZ and LL wrote the manuscript. EH, JR, and KB provided edits to the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest Authors declare no conflicts of interest.

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