2013-12-01

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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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December 2013

ABSTRACT

Exploring Post-Fire Recovery of Biocrusts and Desert Ecosystem Services

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Biocrusts and the ecosystem services they provide are becoming more susceptible to fire as exotic annual grass invasions facilitate the spread of desert wildfires. Further, precipitation patterns across the western United States are predicted to change over the next century, and have the potential to dramatically influence fire regimes and the recovery of burned biocrusts. Despite these changes to desert fire and precipitation cycles, our understanding of post-fire biocrust recovery is limited, especially regarding the first two years after fire. To investigate biocrust recovery, we created burn manipulations (i.e., unburned and burned) and tracked crust form and function over two years in one cold and one hot desert ecosystem (UT, USA). We evaluated the entire bacterial community, but focused on Cyanobacteria species that confer soil stability and N fixation capabilities to biocrusts. Specifically, we quantified shifts in biocrust bacterial community composition using target metagenomics of 16S rDNA; monitored biocrust moss and lichen cover; measured N fixation potential; and assessed soil infiltration rates and soil stability. We found little evidence that biocrust form or function recovered from fire within two years. Based on pyrosequencing results, fire altered biocrust community composition in interspace and shrub biocrusts. Cyanobacteria species were almost completely eliminated by fire, constituting 9-21% of unburned plots and less than 0.01% of burned interspace and shrub biocrust communities. Based on cover estimates, no lichen or moss species survived the fire or recovered within two years. N fixation potentials decreased by at least six-fold in burned interspace biocrusts, representing a reduction in soil N inputs into already N-limited desert soils. Soil infiltration rates also drastically declined in burned biocrusts and remained depressed, but only remained depressed for one year. To investigate the interactions between biocrust recovery, fire, and precipitation, we nested precipitation treatments manipulating the amount of monthly rainfall (i.e., ambient, plus 30% and minus 30%) within burn treatments during the second year. Soil NH_4^+ was the only parameter to be affected by precipitation, and exhibited a positive relationship with precipitation magnitude at the end of one year. Our results demonstrate that fire is a strong destabilizer of the bacterial components of biocrust communities and that the ecosystem services provided by crusts recover at different rates, with N dynamics recovering more slowly than soil ecohydrology.

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CHAPTER 1: ABSTRACT

Wildfires Open Niches for Rare Bacteria to Exploit, Leading to a Reduction in Ecosystem
Services from Recovering Biocrusts

Biocrusts and the ecosystem services they provide are becoming more susceptible to fire as
exotic annual grass invasions facilitate the spread of desert wildfires. Despite this, our
understanding of biocrust recovery is limited, especially regarding the first year after fire. To
investigate biocrust recovery, we created burn manipulations and tracked crust form and function
over one year in a cold desert ecosystem (UT, USA). We evaluated the entire bacterial
community, but focused on Cyanobacteria species that confer soil stability and N fixation to
biocrusts. Specifically, we quantified shifts in biocrust bacterial community composition using
target metagenomics of 16S rDNA; monitored biocrust moss and lichen cover; measured N
fixation potential; and assessed soil infiltration rates. Biocrust dynamics were evaluated one
week, two months, and one year post-fire. We found little evidence that biocrust form or function
recovered within one year. Based on pyrosequencing results and principle coordinate analysis,
fire altered crust community composition in barren plant interspaces and beneath shrubs.
Cyanobacteria species were almost completely eliminated by fire, constituting 9-21% of
unburned plots and less than 0.01% of burned interspace and shrub biocrust communities.
Bacteria from the Firmicutes phylum filled the resulting gap in community composition,
increasing from 0% in unburned to 12-35% relative abundance in burned biocrust, signifying that
Firmicutes thrive in post-fire conditions. Fire did not alter bacterial species diversity, but did
lower the total amount of 16S rDNA gene copies in shrub biocrusts. Thus, fire may reduce
biomass, but community complexity was unchanged. Based on cover estimates, no lichen or
moss species survived the fire, but the structural remnants of burned lichens and mosses
remained attached to soil surfaces, and total crust cover, albeit severely damaged, did not
decline. N fixation potentials decreased by at least six-fold in burned interspace biocrusts,
representing a reduction in soil N inputs for establishing plant species. Additionally, soil
infiltration rates drastically declined in burned biocrusts and remained depressed after one year.
Our results demonstrate that fire is a strong destabilizer of biocrust communities and biocrust-
mediated processes, and opens new niches for other bacteria to exploit. Due to the absence of
Cyanobacteria recovery, we predict that burned shrub and interspace biocrusts remain
susceptible to potential wind and water erosion. Additionally, inorganic N may be available in
the short-term as burned residues are mineralized, but eventually the lack of incoming N may
cause soils to become N limited.

1. CHAPTER 1: INTRODUCTION

1.1 Biocrusts and their ecological importance

Biological soil crusts (i.e., biocrusts) are complex mosaics of cyanobacteria, green algae, lichens, mosses, microfungi, and other bacteria, and may constitute more than 70% of the living biomass in desert ecosystems (Belnap, 2003). Cyanobacteria and other bacteria are essential to form and function of biocrusts in arid and semi-arid systems as they colonize the top millimeters of soils, physically weaving soil particles together with filaments of bacterial strands, and producing exopolymeric substances that glue soil particles together. Thus, cyanobacteria, along with mosses, lichens, and microfungi help armor desert soils against wind- and water-erosive forces. Biocrusts also influence soil-water relations by altering the topography of soil surfaces. For example, infiltration rates, which are controlled by water residence time and surface permeability, may increase where crusts create rough surfaces, and decrease where crusts are flat (Brotherson & Rushforth, 1983; Belnap & Lange, 2003; Madsen et al, 2008). Lastly, Cyanobacteria species perform N fixation, providing the dominant input of N for higher plants to utilize in these chronically poor N systems (Belnap, 2002). The ecological importance of crusts in arid and semi-arid environments is immense and undeniable; unfortunately, biocrusts and the ecosystem services they provide may be extremely fragile, taking decades for a fully developed crust to regenerate following disturbance (Belnap & Eldridge, 2001).

1.2 Wildfire damages biocrusts and inhibits their ecosystem services

Catastrophic wildfires are threatening to eliminate biocrust form and functions. Although some deserts are fire-adapted systems, invasions annual grasses, including *Bromus tectorum*, create fire cycles of high frequency, size, and intensity, causing many systems to shift from

mosaics of barren plant interspaces and shrub-islands of fertility to exotic annual grasslands in the western United States (Knapp, 1996). Exotic grasses reduce light levels reaching the soil surface, effectively threatening phototrophic mosses, lichens, and cyanobacteria (Keeley et al, 2009; Brooks & Matchett, 2006). Eventually, as the system burns, the lack of recovery of burned lichens, mosses, and Cyanobacteria may lead to declines in soil stability, water infiltration, and N fixation rates, and if biocrusts do not recover fast enough annual grass may force them from soils altogether. For example, depending on biocrust composition, fire drastically reduced the ability of biocrusts to defend soil surfaces from water-erosive forces, and N fixation rates in burned crusts were reduced 2-fold following fire, further limiting N in desert shrub communities (Bowker, 2004; Hobbs & Schimel, 1984; Belnap, 2003). Additionally, the combustion of plant materials releases hydrophobic volatile organic compounds that may clog soil pore spaces upon cooling, effectively inhibiting soil ecohydrology (Finley and Glenn, 2009). Based on linear extrapolations of visual estimates of mosses and lichens, biocrust recovery may occur within six to one-hundred years depending on disturbance intensity and precipitation variability (Belnap & Eldridge, 2001; Johansen et al, 1984). Unfortunately, during the time required for mosses and lichens to recover, annual grasses may displace biocrusts. However, Cyanobacteria and other crust bacteria have the potential to recover more quickly after fire, restore biocrust functions, and influence higher plant establishment across burned landscapes.

1.3 Fire effects on bacteria

Fire violently alters bacterial communities, however, bacteria utilize a vast array of strategies to withstand and recover from fire (Bárcenas-Moreno & Bååth, 2009). Fire creates surface soil temperatures reaching nearly 100°C, causing bacteria to experience extreme desiccation stress and the denaturing of biomolecules essential for metabolism and growth

(Daniel and Cowan, 2000). Some strategies include formation of endospores or sporulation (Nicholson et al, 2000), the creation of persister cells that are relatively dormant until environmental conditions improve (Keren et al, 2004), and metabolic plasticity (Justice et al, 2008). Bacterial communities may recover from fire in a matter of months (Goberna et al, 2012). Bacterial biomass can even be stimulated 29-42% by fire (D'Ascoli et al, 2005). Cyanobacteria may be more affected by fire than other bacteria. For example, cyanobacterial pigments decreased more than other bacterial pigments in burned crusts one year following an Oregon wildfire (Bowker et al, 2004). Alternatively, diversity of 16S rRNA *nifH* gene copies (responsible for N fixation) from N-fixing Cyanobacteria increased in biocrusts one month after fire (Yeager et al, 2005). Further, following disturbance, cyanobacteria species often follow secondary successional patterns where fast-growing generalists like *Microcoleus* species are the first to recover followed by other cyanobacteria (i.e., *Nostoc* and *Scytonema*). Unfortunately, *Microcoleus* species are not heterocystous and do not fix N unless the crusts are well developed and composed of many layers of cyanobacterial filaments to create anaerobic conditions (Belnap 1996; Ehlering et al, 1998; Yeager et al, 2007). Therefore, the recovery of crust bacterial communities remains in question, and the restoration of some crust services is likely dependent on the bacterial species that recover.

1.4 Study description and hypotheses

In this study, we evaluated the post-fire recovery of all biocrust components (i.e., bacteria, lichens, and mosses) and the desert ecosystem services they provide. We created burn manipulations and tracked crust form and function in barren plant interspaces and beneath *Artemisia* shrubs through time in a cold desert ecosystem (UT, USA). Specifically, in burned and unburned interspaces and shrub biocrusts, we: quantified shifts in biocrust bacterial community

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composition using target metagenomics of 16S rRNA; quantified bacterial 16S rRNA sequences using quantitative PCR; monitored the cover of biocrust moss and lichen species; measured N fixation potential with acetylene reduction assays; quantified soil inorganic nitrogen; and assessed soil infiltration rates. Biocrust dynamics were evaluated after the fire over a year (i.e., one week, two months, and one year). We evaluated recovery in interspace and shrub biocrusts because these microsites are prominent features across deserts, and biocrust species composition is strikingly different in these microhabitats due to soil moisture and light variability (Housman et al, 2007). We hypothesized that the bacterial component of biocrusts recovers more quickly than mosses and lichens following fire, and that ecosystem services recover more slowly than the recovery of bacterial biocrust communities.

2. CHAPTER 1: MATERIALS AND METHODS

2.1 Site description

We conducted our study at a location in a cold desert ecosystem of the Great Basin Desert in Rush Valley, UT (40°05'27.43"N - 112°18'18.24"W). Biocrusts at the site were dominated by *Collema* and *Toninia* lichens in barren plant interspaces, and *Syntrichia* mosses beneath shrubs. The annual exotic grass, *Bromus tectorum*, has altered fire regimes of the surrounding area, but our site had minimal *Bromus* present. The shrub community was dominated by *Artemisia tridentata, ssp. Wyomingensis*, and other dominant plant species at the site included perennial grass *Elymus elymoides* (Raf.) Swezey and several annual forbs: *Halogeton glomeratus* (Bieb.) C.A. Mey., and *Ceratocephala testiculata* (Crantz.) Bess. Mean annual precipitation at the site is 27.57 cm year^{-1} (± 1.39, n=30) and mean annual temperature is 8.87°C (± 0.056, n=30). Soils were derived from Lake Bonneville sediments with a Taylorsflat series silt loam texture. The series consists of well drained, fine-loamy, mixed, mesic Xerollic Calciorthids with 3 to 15% calcium carbonate. Surface soils are strongly alkaline and have a pH of 8.6.

2.2 Fire manipulation, experimental design, and biocrust sampling

We created fire manipulations with controlled burns on 20 September 2011. The burns were conducted in five randomly selected plots (30 m width x 30 m length) balanced with five unburned plots of the same dimensions. To ensure that the fire carried through the plots we spread 20 bales of straw onto the soil surface (Esque et al, 2010). This straw has similar above and below ground heating patterns to invasive grasses (Biederbeck et al, 1980). Also, the ash from burned straw blew away from soil surfaces within two weeks, reducing the likelihood of

long term increases in C and N from straw. We also created five unburned plots of the same dimensions. Within each plot, we sampled from two biocrust microsites, interspace and shrub biocrusts. The interspace biocrusts were at least 30 cm away from the nearest shrub, and shrub biocrusts were located at the edge of shrub canopies. Sampling in all replicates (i.e., 2 burned manipulations x 2 biocrust microsites x 5 replicates = 20 samples) occurred after the fire at four time points: one week (27 September 2011), two months (4 November 2011), eight months (1 June 2012), and one year (1 October 2012) post-fire. We removed two samples at each sampling time. The first sample consisted of three cores (diameter = 2 cm, depth = 2 mm) extracted with a soil probe and then homogenized. The composite sample was then split into two and was either transferred to a cyrovial and immediately frozen in liquid N for bacterial molecular analyses or stored at 5º C for inorganic N determination. The second sample consisted of one intact soil core (diameter = 2 cm, depth = 1 cm) that was used in N fixation analysis.

2.3 Biocrust bacterial community composition

We performed pyrosequencing of bacterial DNA to characterize the bacterial community in burned and unburned soils. We extracted genomic DNA from 0.5 g of soil using the PowerSoil DNA Isolation Kit (MoBio, Carlsbad, CA) from three of the five biocrust replicates in three treatment by time combinations (2 burned manipulations x 2 crust microsites x 3 replicates x 3 times = 36 samples). Samples from June were not included in the molecular analyses. The genomic DNA was used in target-metagenomics where we pyrosequenced (Hamady et al, 2008; Fierer et al, 2009) 16S rDNA. We used the bacterial specific primer set 515F and 806R with a 12-nt error correcting Golay barcodes to amplify the V4-V5 region of the 16S rRNA gene. We performed 25μl PCR reactions containing 5μl of 5X KAPA2G Buffer A, 0.5μl of dNTPs, 1.25μl of modified 515F and 806R, and 0.1μl of KAPA2G Robust HotStart DNA Polymerase

(5units/µl, Kapa Biosystems, Inc., Woburn, MA) to amplify extracted DNA. We used the following thermal cycle for PCR reactions: an initial denaturation step at 94ºC for 3 minutes followed by 35 cycles of denaturation at 94ºC for 45 seconds, annealing at 55ºC for 30 seconds, and an extension at 72ºC for 90 seconds. The amplified DNA was purified using Agencourt AMPure XP PCR Purification (Beckman Coulter Inc., Brea, California, USA) and quantified using a Quant-iT^{TM} PicoGreen dsDNA Kit (Invitrogen Corporation, Carlsbad, California, USA) to create approximately equimolar concentrations prior to pyrosequencing. Samples were sequenced at the Brigham Young University DNA Sequencing Center (http://dnasc.byu.edu/) in a 454 Life Sciences Genome Sequence FLX instrument (Roche, Branford, Connecticut, USA).

We used *mothur* open-source, expandable software to analyze the 16S rDNA sequences (Schloss & P.D., et al, 2009). Sequences less than 260 bp in length were excluded from the analysis to ensure accuracy of post-sequencing analysis. We identified bacterial operational taxonomic units (OTUs) using Megablast with a minimum coverage of 99%, and minimum pairwise identity of 97%. We used the SILVA database (http://www.arb-silva.de/) to align the phylogenetic identity of each sequence. Sequences aligned via Kmer searching, pairwise alignment with the de-gapped template, and Needleman-Wunsch Gotoh and Blastn algorithms with the NAST algorithm to reinsert gaps.

To analyze shifts in bacterial communities following the burn manipulations, we conducted principle coordinate analysis (PCoA) based on pyrosequenced bacterial DNA sequences. PCoAs were constructed using Vegan package in the R Statistics Environment (R Development Core Team, 2008). We used permutational multivariate analysis of variance (PERM-ANOVA; Anderson, 2001), with the *adonis* function in the Vegan package of the R Statistics Environment (R Development Core Team, 2008), to assess the effects of the fire

treatment on bacterial communities. We also calculated the relative abundance, or percent, of bacterial sequences by major phylum or subclass. Shifts in phyla and subclasses were evaluated using repeated measures analysis of variance (RM-ANOVA) in the stats package of the R Statistics Environment (R Development Core Team, 2008). The effects of fire on bacterial species richness (Chao-1 diversity estimation) and species diversity (Inverse Simpson diversity index) was evaluated using RM-ANOVA (Chao, 1984; Aanderud and Lennon, 2011b).

2.4 Microbial biomass

We assessed the reduction and recovery of microbial biomass in the burn manipulations with quantitative PCR. We performed qPCR on the same DNA samples and primer set, 515F and 806R, used for pyrosequencing, and analyzed the quantity of 16S rDNA with SYBRGreen for fluorescent detection of PCR products on a Mastercycler ep realplex (Eppendorf International, Hamburg, Germany). Each qPCR reaction was performed in duplicate and each 12 µl reaction consisted of 5.4 µl KAPA SYBR Fast qPCR Master Mix (KAPA Biosystems), 0.2 µl of each primer (10 µM Invitrogen), 5.2 µl molecular grade water, and 2 µl of DNA template DNA. PCR conditions were as follows: 5 minutes at 95ºC followed by 40 cycles of 95ºC for 1 minute, a 72ºC annealing temperature for 1 minute, and the final extension at 72ºC for 7 minutes. We confirmed amplification for each product by observing melting curves. We generated qPCR standards from a soil bacterium using the TOPO TA Cloning® Kit (Invitrogen). We extracted plasmids from transformed cells (Qiagen Sciences, Germantown, MD, USA) that we used for our standard curve, which captured a range of $10^1 - 10^8$ copies μL^{-1}. The coefficient of determination (r^2) for our assay was 0.98, while amplification efficiency was 1.5. Our melting curves confirmed the lack of primer-dimers. We analyzed biocrust biomass in the treatments

through time with RM-ANOVA in the Stats package from the R Statistics Environment

(R Development Core Team, 2008).

2.5 Visual crust species identification

We conducted visual estimates of lichens, mosses, and cyanobacteria percent ground cover to identify the recovery of all biocrust components following fire. We used a sixteen-point grid and a modified, step point-intercept transect technique (Bowker and Belnap, 2008) to estimate the average percent ground cover of cyanobacteria, lichen, mosses, bare ground, and rock in burned and unburned plots. The grids were placed in fixed locations at each sampling time point to more accurately reevaluate crust components through time.

2.6 Ecosystem services

We measured a suite of biocrust ecosystem services in shrub and interspace biocrusts. We evaluated N fixation, inorganic N concentrations, infiltration and soil stability. All measurements were evaluated (2 burned manipulations x 2 crust microsites x 5 replicates x 4 times = 80 samples) using RM-ANOVA in the stats package of the R Statistics Environment (R Development Core Team, 2008).

2.6.1 N fixation and inorganic N concentrations

To determine the effects of fire on the input of N into the ecosystem following fire, we measured N fixation (μmol h^{-1} m^{-2}) using the acetylene reduction assay, ARA, and inorganic N concentrations (ppm). We followed ARA protocols outlined by Belnap (2002). Briefly, the enzyme responsible for N fixation, nitrogenase, reduces acetylene to ethylene at approximately the same rate as it reduces N to NH_4^+, allowing for a simulated measurement of N fixation. We

brought all soil cores, described in section *2.2 Fire manipulation, research design, and biocrust sampling*, and incubated cores for two days on a 12 hour light, 12 hour dark schedule with daily nanopure water additions of 1 mL. The cores were then sealed and a 10% acetylene atmosphere was created in the headspace by injecting 5 mL of pure acetylene through a septum with a gas-tight syringe. Four hours later, we removed a 4 mL headspace gas sample. Concentrations (ppm) of ethylene in the headspace were measured with an Agilent Technologies 6890A gas chromatograph with a PoraPak R column (Agilent Technologies, Santa Clara, CA) with an attached flame ionization detector. The injection chamber of the gas chromato ra h a s e t at 50 C, the col m n a s 250 C We sed the ideal as la   to convert m e thylene to μmol ethylene h^{-1} m^{-2}.

We measured inorganic soil N to identify the impact of fire on nitrogen availability. We measured soil ammonium (μ $N-NH_4^+$ g $soil^{-1}$) and soil nitrate (μ $N-NO_3^-$ g $soil^{-1}$) in soil N extracts consisting of 2 grams of soil with 4 mL 0.5 M K2SO4 (1:2 w/v). Following 30 minutes of shaking, the extracts were centrifuged for 30 minutes at 4,000 rpm. We colorimetrically quantified the $N-NH_4^+$ and $N-NO_3^-$ species in the supernatant using a SpectraMax Plus 384 (Molecular Devices Corporation, Sunnyside, CA) (Forster 1995; Miranda et al, 2001).

2.6.2 Infiltration and stability

To investigate the effect of fire on soil infiltration rates, we measured changes in infiltration rates   ith a Deca on Device's Mini Dis Te nsion Infiltrometer (Deca on Devices, Pullman, WA). Due to the rugose nature of the biocrusts at this site, the infiltrometer was only able to form a seal with the soil when approximately 16 grams of sterilized sand was deposited in a thin layer on the soil s rf ace. The sand did not affect infiltration rates d e to the infiltrometer's pressure chamber which allows one to target the specific texture of the soil, and effectively

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ignore the sand. This sand covered a 5 cm diameter circle under a shrub canopy and in a nearby interspace in every plot. We then measured infiltration accordin to Deca on De vice's rotocol (Decagon Devices, Pullman, WA), and calculated infiltration rates (cm s^{-1}) following Zhang et al (1997).

To understand how fire impacts soil stability, we measured soil stability according to the Jornada Experimental Range Test (Herrick et al, 2001). This test involves timed water immersion and wet sieving of soil aggregates between 6 and 8 mm diameter. We then visually estimated the material remaining on the sieve and assigned stability values based on predetermined parameters. We used kits designed by Synergy Resource Solutions, Inc. (Montana, USA).

3. CHAPTER 1: RESULTS

3.1 Biocrust community recovery following fire and fire effects on bacterial diversity

Both interspace and shrub biocrust bacterial communities were altered by fire, but only shrub biocrusts demonstrated evidence of recovery. Based on principle coordinates analysis (PCoA) and PERM-ANOVA results, fire created distinct interspace (PERM-ANOVA: fire*time, F=5.27, *P*<0.001, *df*=17, Fig. 1A) and shrub biocrust communities (PERM-ANOVA: fire*time, F=2.85, *P*<0.025, *df*=17, Fig. 1B). The effects of fire explained 22.7% variation and 13.8% variation in principle component 1 and 2 respectively for interspace biocrusts, and 17.2% variation and 10.1% variation in principle component 1 and 2 respectively in shrub biocrusts. Bacterial communities in burned and unburned shrub biocrusts started to resemble each other after one year (PERM-ANOVA: fire, F=1.29, *P*<0.28, *df*=5, Fig. 1B), while the interspace burned and unburned communities were still marginally different from one another (PERM-ANOVA: fire, F=4.45, *P*<0.09, *df*=5, Fig. 1A). Although fire caused shifts in community makeup, community complexity was unaltered. Bacterial OTU diversity (Inverse Simpson index, Fig. 2) was not statistically different in burned and unburned treatments with diversity ranging from 16±3 to 25±5 in interspace and 10±4 to 26±3 in shrub biocrusts. Although there were no statistical differences, there was a trend of lower diversity in burned than unburned shrub and interspace biocrusts. Diversity was three- and two-fold lower in burned than unburned shrub biocrust communities at two months and one year respectively. Interspace biocrust communities in burned plots had lower mean diversity than unburned plots at both two months and one year, but standard errors of burned and unburned diversity overlapped.

3.2 Fire effects on the relative abundance of bacterial phyla

Fire caused shifts in three dominant phyla in interspace and shrub biocrusts. Based on relative abundance (%) from 16S rDNA pyrosequencing results, interspace Cyanobacteria and Acidobacteria and shrub Cyanobacteria and Bacteroidetes experienced a decline one week after fire, and these taxa recovered little one year following the fire. One week after fire, Cyanobacteria basically disappeared from burned crusts with relative abundance decreasing at least four-fold in burned interspace (RM-ANOVA: fire, F=21.73, *P*<0.01, *df*=5, Fig. 3A) and one-hundred-and-fifty-fold burned shrub biocrusts (RM-ANOVA: fire*time F=13.96, *P*<0.02, *df*=5, Fig. 3B) compared to unburned plots. Two months later, Cyanobacteria in interspace crusts were thirteen-times lower in burned (1.1%±0.3) than unburned crusts (14.2%±5.2), and after one year, were only slightly detectable in burned crusts (0.1%±0.1). Two months later, Cyanobacteria in shrub biocrusts were seventy-times lower in burned (0.1%±0.1) than unburned crusts (8.6%±2.6), and at one year, Cyanobacteria were not detectable. In interspace crusts, the relative abundance of Acidobacteria was reduced by seven-times, from 9.7%±0.8 to 1.4%±0.9, just one week after the fire and remained four-times lower, from 9.1%±1.8 to 2.6%±0.3, two months after the fire (RM-ANOVA: fire*time, F=6.98, *P*<0.05, *df*=5). One year after the fire; however, relative abundance of Acidobacteria was similar in unburned (2.1%±0.6) and burned (3.0%±1.3, Fig. 3A) interspaces. The relative abundance of Bacteroidetes in shrub biocrusts decreased by at least two-and-a-half-times following the burn and remained depressed one year later (RM-ANOVA: fire, F=25.46, *P*<0.008, *df*=5, Fig. 3B).

Fire stimulated bacteria in the phylum Firmicutes in both interspace and shrub biocrusts. Firmicutes were not even detectable in unburned interspace and shrub communities; however, two months following the fire this phylum constituted 11.9%±5.3 of burned interspace

communities (RM-ANOVA: fire, F=33.72, *P*<0.005, *df*=5, Fig. 3A) and 34.9%±16.3 of burned

shrub biocrust communities (RM-ANOVA: fire, F=4.99, *P*<0.09, *df*=5, Fig. 3B). One year after

the fire, Firmicutes remained a dominant phylum in burned interspace (13.2%±5.8) and

(9.2%±6.0) shrub communities.

Unclassified bacteria abundance also shifted following fire, while other phyla remained

relatively unaltered by fire. For example, the relative abundance of unclassified bacteria spiked

in both shrub and interspace burned biocrusts. Unclassified bacteria ranged from 27.9%±4.6 to

44.4%±4.5 in unburned interspaces, and from 35.0%±13.0 to 44.6%±2.8 in the burned treatments

throughout the duration of the experiment (Fig. 4A). In unburned shrub biocrusts, unclassified

bacteria ranged from 19.9%±2.2 to 40.7% ±8.2, and in the burned treatments ranged from

15.5%±7.8 to 43.8%±21.7 (Fig. 4B). The relative abundance of Actinobacteria, Proteobacteria,

Deinococcus-Thermus, Chloroflexi, Gemmatimonadetes, Planctomycetes, and Verrucomicrobia

were unaffected by fire in either shrub or interspace biocrusts: (Fig. 4). The three most dominant,

but unaffected, interspace phyla were Actinobacteria (ranging from 17.5%±3.1 to 29.5%±3.5),

Proteobacteria (ranging from 4.3%±0.7 to 11.5%±2.6), and Bacteroidetes (ranging from

5.1%±0.7 to 11.2%±4.2), and their shrub counterparts were Actinobacteria (ranging from

26.1%±13.3 to 40.5%±5.8), Proteobacteria (ranging from 4.3%±2.5 to 12.7%±1.3), and

Deinococcus-Thermus (ranging from 1.0%±0.6 to 9.3%±2.2).

3.3 Biocrust biomass and fire

Fire reduced bacterial biomass in shrub but not interspace biocrusts. In shrub biocrusts,

bacterial biomass (16S rDNA copy number) declined an order of magnitude at one week, and

two orders of magnitude at two months, following fire respectively (RM-ANOVA: fire*time,

F=296.3, *P*<0.004, *df*=9, Fig. 7). Interspace biocrust bacterial gene copy numbers were lower in burned soils, but this difference was not statistically significant (Fig. 7).

3.4 Biocrust cover estimates

None of the lichens or mosses that compose the visible portion of biocrusts recovered one year after the fire. In the unburned treatments, four lichen species, two moss species, and Cyanobacteria comprised interspace biocrusts, and leaf litter, Cyanobacteria, and two moss species dominated shrub biocrusts. Interspace biocrust cover was as follows: Cyanobacteria = 50.6% ±2.8, lichens = 24.2%±6.9, mosses = 15.6%±2.5, and plant litter = 3.6%±1.0. Interspace lichen cover was dominated by *Collema tenax*, 10.4% ±2.0, and *Toninia sedifolia*, 8.5% ±1.7. The two dominant interspace mosses were *Syntrichia caninervis*, 11.5% ±1.6, and *S. ruralis*, 4.02% ±0.9. Shrub biocrusts were mostly covered with shrub leaf litter, 65.1% ±4.7. Cyanobacteria crusts 18.6%±3.4 and the mosses *S. ruralis* and *S. caninervis* also made up a significant portion of shrub biocrusts, 5.9%±1.5 and 4.7%±0.9, respectively. *Toninia sedifolia* was the dominant lichen in shrub biocrusts, 2.3%±0.8.

3.5 Biocrust nitrogen

Fire impacted the ability of biocrusts to add new N to soils through fixation and had varying effects on inorganic N in shrub and interspace soils. N fixation rates were six-times lower in burned than unburned interspaces one week after the fire, and thirty-one-times lower at two months (RM-ANOVA: fire*time, F=12.53, *P*<0.0001, *df*=3, Fig. 5A). Although fixation in unburned interspaces was much lower after a year, it was still three-and-a-half-times higher than burned soils. N Fixation in shrub biocrusts was less affected by fire, but after two months, burned soils exhibited a four-fold decrease (RM-ANOVA: fire*time, F=3.87, *P*<0.022, *df*=3,

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Fig. 5A). Fire increased $N-NH_4^+$ concentrations in burned interspace (RM-ANOVA: fire*time, F=43.27, $P<0.0001$, df=3, Fig. 5B) and shrub biocrusts (RM-ANOVA: fire*time, F=7.99, P<0.0008, df=3, Fig. 5B) over the one-year experiment. The largest $N-NH_4^+$ increase in interspace crusts, 0.38±0.07 to 3.13±0.19 ppm, and in shrub biocrusts, 0.55±0.05 to 2.65±0.19 occurred two months after the fire. $N-NO_3^-$ concentrations demonstrated more variability through time, but fire caused an increase in interspace soils two months after fire, from 0.64±0.35 to 1.19±0.17 ppm (RM-ANOVA: fire*time, F=3.02, $P<0.05$, df=3, Fig. 5C). Shrub biocrust $N-NO_3^-$ was variable through time (RM-ANOVA: time, F=6.78, $P<0.002$, df=3, Fig. 5C) but was not different in burned and unburned plots.

3.6 Infiltration rates and soil stability

Fire depressed soil infiltration rates and stability initially but fire effects on these two variables decreased through time. One week after the fire, infiltration rates (cm s^{-1}) were at least five-and-a-half-times lower in burned than unburned soils (RM-ANOVA: fire*time, interspace F=7.21 $P<0.0002$; shrub F=31.13, $P<0.0001$, Fig. 6). Two months following the fire, neither interspace nor shrub biocrust infiltration rates differed by treatment, however at one year they were depressed at least one-and-a-half-fold in both interspace and shrub soils. Soil stability decreased in shrub biocrusts at least one-and-a-half-fold in burned compared to the unburned treatments one week after the fire (RM-ANOVA: fire*time, F=3.01, $P<0.05$, data not shown). There were no measured differences in stability between treatments at any other time points.

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4. CHAPTER 1: DISCUSSION

4.1 Crust community recovery

In support of our first hypothesis, the bacterial component of biocrusts is recovering more quickly following fire than mosses and lichens. Fire-altered bacterial biocrust communities eliminated mosses and lichens and reduced bacterial biomass, but did not change bacterial diversity. Only shrub biocrust bacterial communities demonstrated some evidence of recovery in their composition and bacterial biomass within one year after fire. The recovery of communities in shrub biocrusts was unexpected because leaf litter and woody shrub material most likely increased fire intensity and duration of soil heating underneath shrubs (Blank et al, 1995). The observed recovery may be due to thick mats of mosses underneath shrubs shielding or buffering bacterial communities from the full effects of a hotter and longer burn. Following fire, components of the microbial communities were potentially replaced by more resilient species that were better adapted to survive burned biocrust conditions. Based on cover estimates, none of the 15 species of lichens or mosses survived the fire, but burned biocrusts remained attached to soil surfaces and total crust cover, however burned biocrust structure did not decline. This severe burning of biocrusts is common. For example, in an Idaho shrubland, lichen and moss diversity and richness decreased following fire (Hilty et al, 2004).

4.2 Fire effects on bacterial phyla

Cyanobacteria species, and to a lesser extent Acidobacteria and Bacteroidetes species, disappeared following fire. Cyanobacteria constituted 9-21% of unburned and less than 0.01% of burned interspace and shrub biocrust communities. Cyanobacteria species were dominated primarily by *Microcoleus*, in both interspace and shrub biocrusts. *Microcoleus* species establish a

foundation for desert biocrust communities. They are pioneer colonizers of bare soil surfaces and provide stability, improve ecohydrology, fix N, and protect future colonizing species from UV damage (Garcia-Pichel & Wojciechowski, 2009; Belnap & Gardner, 1993; Belnap, 1996; Chen et al, 2009). Acidobacteria and Bacteroidetes, were also reduced by fire in interspace and shrub biocrusts respectively. One year later, Bacteroidetes remained suppressed but Acidobacteria concentrations recovered. The dominant Acidobacteria species in unburned and burned crusts were in the genus *Candidatus Chloracidobacterium*, which has prominent members in Yellowstone hot spring phototrophic mats. These Acidobacteria are anoxygenic photoheterotrophs that can withstand alkaline conditions, making them adapted to extreme conditions and able to forage residual carbon after fire (Bryant et al, 2007). Similar to Cyanobacteria, members of the *Candidatus Chloracidobacterium* genus were not able to recolonize surface soils. Bacteroidetes species were most commonly found in the family Chitinophagaceae, whose species are thermophilic and have glycoside hydrolase activity associated with breakdown of plant compounds including cellulose and hemicellulose (Eichorst et al, 2013). The lack of plant materials in burned plots or the lack of a specific C substrate may have slowed the recovery of these bacteria.

Firmicutes filled the resulting gap in community composition. These bacteria increased in relative abundance from 0% in unburned to 12-35% in burned biocrusts, suggesting that the phylum tolerates desiccation and is well adapted to survive and thrive in the extreme conditions of surface desert soils. Firmicutes may be filling a niche vacated by Cyanobacteria or other gram-negative phyla following fire. As gram-positive bacteria, Firmicutes have a thick, external peptidoglycan layer and produce endospores that may make them more resilient to fire and post-fire soil conditions (Onyenwoke et al, 2004; Ferrenberg et al, 2013). Firmicutes and

Cyanobacteria may occupy the same location in the environment in the uppermost millimeters of the soil surface, but gain C from different sources. Cyanobacteria are photoautotrophs, while Firmicutes are chemoheterotrophs that consume organic C sources.

4.3 What makes Firmicutes able to survive fire and post-fire conditions

Burned communities were dominated by two Firmicutes species from the genera *Planococcus* and *Sporosarcina*. These two Firmicutes genera may have the capacity to provide essential ecosystem services, including N fixation following fire. Both genera are resilient to extreme conditions and have been isolated from sulfurous springs, the Arctic, Antarctica, and a cold desert in the Himalayas (Mykytczuk et al, 2012; Romano et al, 2003; Mayilraj et al, 2005). They have also been described as psychrophilic, alkaliphilic, and halophilic (Reddy et al, 2002; Yu et al, 2008; Claus et al, 1983). Additionally, *Sporosarcina* species form spores to withstand hostile conditions, providing a potential escape from fire (Kämpfer et al, 2010). *Planococcus antarcticus* may have nitrogen fixation potential (Margolles et al, 2012). One *Sporosarcina* species is also a urea decomposer and is active in environments with up to 13% ammonium carbonate (Benini et al, 2013). However, fire caused a decrease in N fixation potential that did not recover within one year, even though Firmicutes were abundant in burned biocrusts and had the potential to fix N. Therefore, Firmicutes did not posses the potential to fulfill some of the N fixation services once provided by Cyanobacteria.

4.4 Recovery of ecosystem services after fire

In support of our second hypothesis, ecosystem services are recovering more slowly than bacterial biocrust communities. For example, shrub biocrust bacterial communities showed signs of recovery within one year, but N fixation rates did not recover in the same time frame. Fire

negatively affected biocrust ecosystem services including: N fixation, soil stability, and ecohydrology, and it altered soil inorganic N concentrations. However, soil $N-NH_4^+$ concentrations reflected a net increase over the year following fire. This increase could be due to bacteria mineralizing residual unburned material in and on top of surface soil layers (Prietofernandez et al, 1993), or the release of NH_4^+ from heat-induced oxidation of organic matter (Raison et al, 1990). Shrub communities were also decimated by fire treatments, eliminating the uptake of NH_4^+ by higher plants in the system. Additionally, two months after fire, burned interspace $N-NO_3^-$ was higher than unburned areas, again possibly due to a lack of plants immobilizing N from soils. $N-NO_3^-$ levels were unusually low, less than 1 ppm, in almost all treatments and time periods. This was to be expected since we sampled the topmost layers, 2 mm, of the soil surface and $N-NO_3^-$ may be readily leached to deeper soils with precipitation.

Soil ecohydrology and stability were also impacted by fire and exhibited varying recovery. Fire causes hydrophobicity in soils through volatilization of plant compounds that settle and cool into a hydrophobic layer on soil surfaces (Huffman et al, 2001). Burned biocrusts in shrub and interspace soils immediately experienced reduced infiltration rates, indicating the possible creation of a hydrophobic layer. However, at one year, interspace infiltration rates remained severely depressed in burned crusts, indicating a lack of recovery. Again, this difference in recovery between shrub and interspace biocrusts could be due to the moss acting as buffers in burned shrub biocrusts. Another vital ecosystem service provided by biocrust bacterial communities is the stabilization of soil particles. Fire reduced soil stability in burned biocrusts, but only in the short term. Burned shrub biocrust stability recovered within two months and interspace stability recovered in one year, indicating that other bacteria produce exopolymeric substances that glue soil particles together just as well as Cyanobacteria. It remains unclear if

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burned biocrusts still armor soil surfaces against water and wind erosive forces, but our

measurements of stability indicate the potential for continued protection.

5. CHAPTER 1: CONCLUSIONS

Our results support our hypotheses that the bacterial components of biocrusts recover more quickly following fire than mosses and lichens, and that ecosystem services recover more slowly than bacterial biocrust communities. Fire is a strong destabilizer of biocrust bacterial species and biocrust-mediated processes, and opens new niches for other bacteria to exploit. In shrub biocrusts, bacterial communities, infiltration rates, and soil stability showed some signs of recovery within one year of fire, but interspace biocrusts were more severely altered by fire and exhibited a lack of recovery in biocrust form and function. Last, inorganic N may be available to plants colonizing soils, including *Bromus tectorum,* but this may only be a short-term pulse as soils may eventually become more N limited due to less N entering the system through N fixation.

6. CHAPTER 1: REFERENCES

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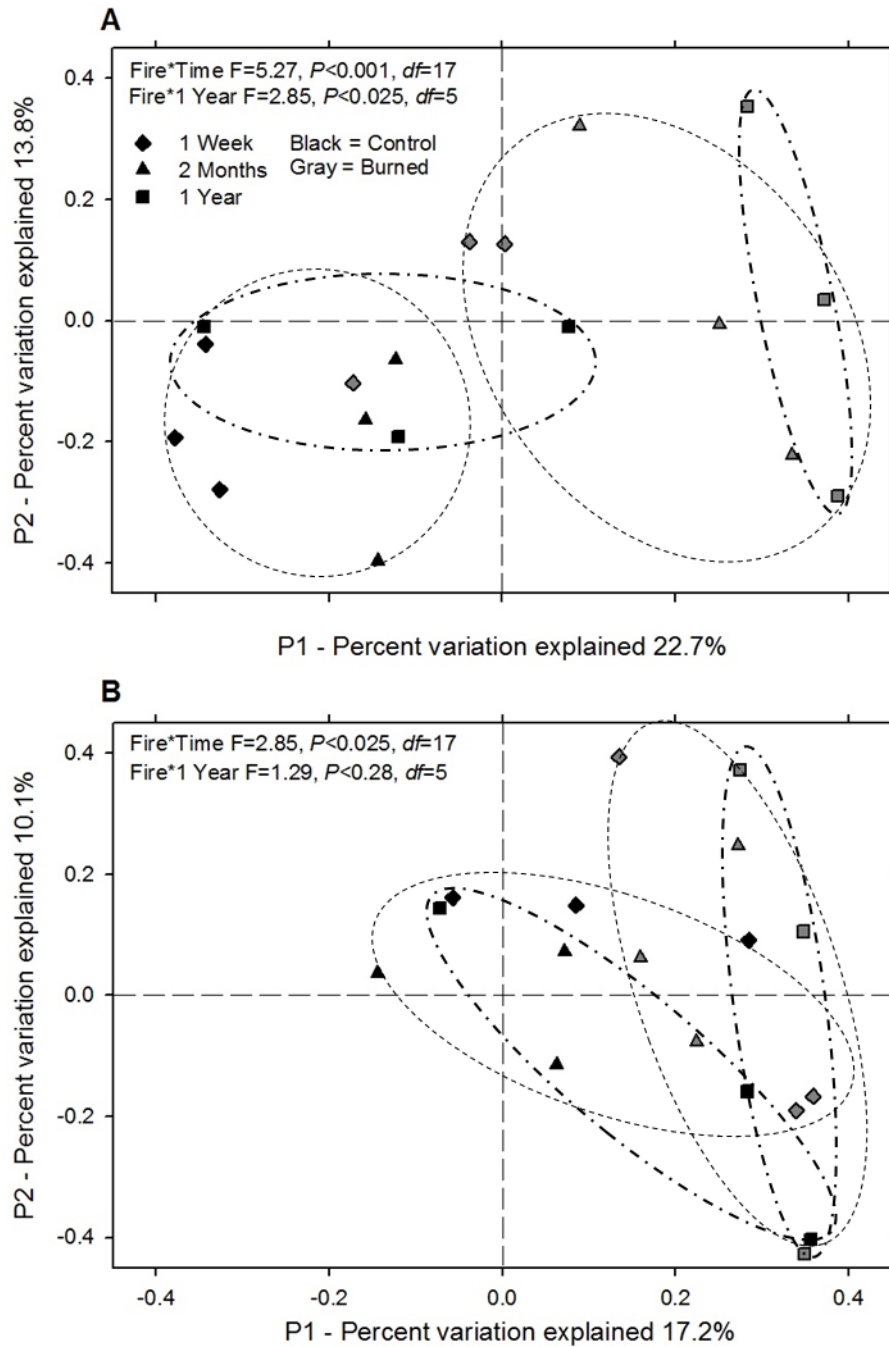
Figure 1. Principle component analysis (PCoA) of bacterial communities from biocrusts in unburned and burned soils in interspaces (A) and underneath shrubs (B) from three time points, one week, two months, and one year following fire. Communities (*n*=3) are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S rDNA pyrosequence libraries. Significant differences between burned and unburned communities through time are based on permutational multivariate analysis of variance (PERM-ANOVA) comparisons with attending F statistics and P values. PERM-ANOVA results are in the upper left of the figures.

Figure 2. Bacterial species diversity in unburned and burned interspace and shrub biocrusts. Values are means (*n*=3) ± SEM. Species richness and diversity are reported as Chao1 and inverse Simpson values, respectively.
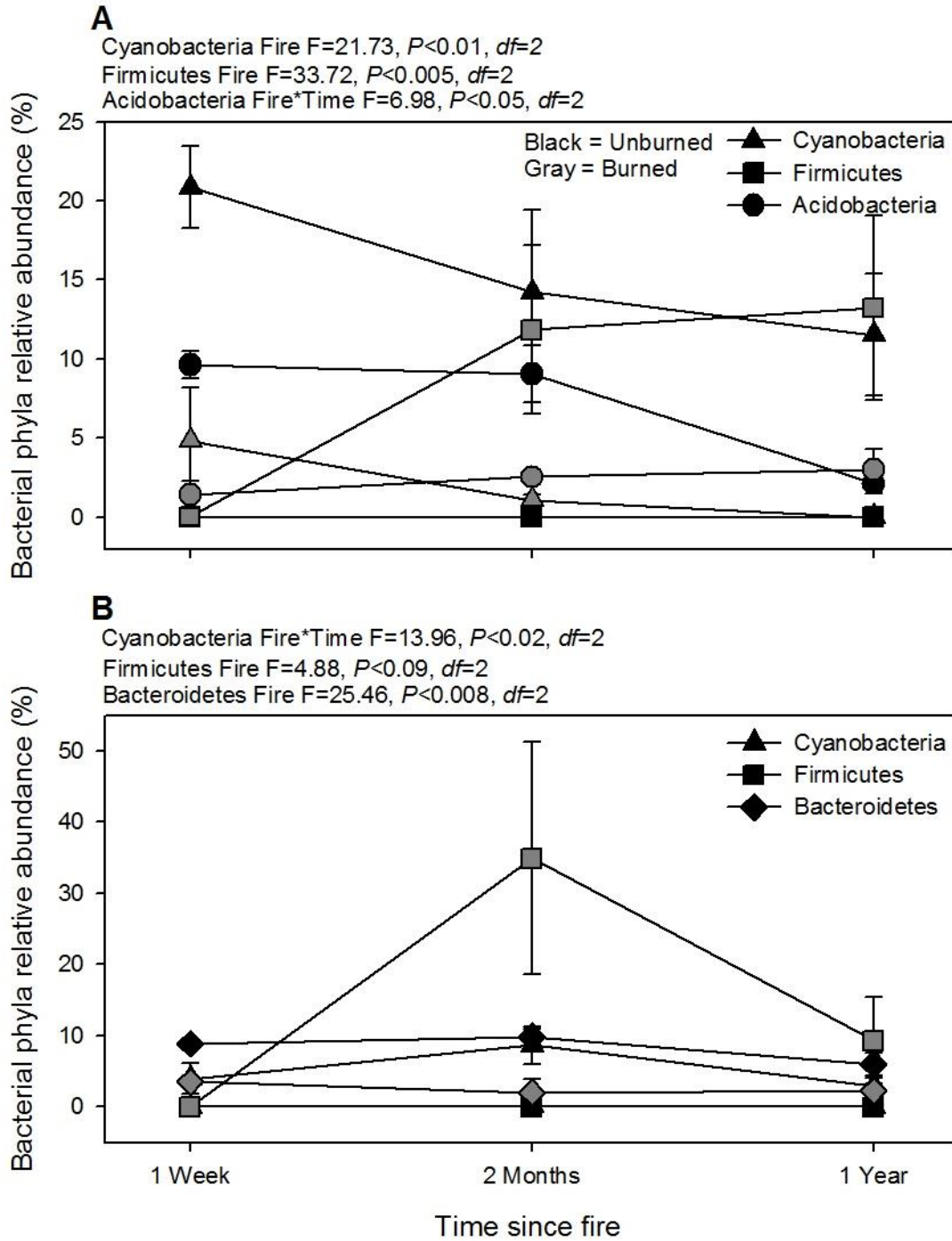
Figure 3. Relative abundance (%) of bacterial phyla in biocrusts from unburned and burned soils in interspaces and underneath shrubs (B) that responded to fire over one year. Bacterial phyla relative abundance values are means (*n*=3) ± SEM calculated from the same OTU data from PCoAs. Significant differences between burned and unburned phyla through time are based on RM-ANOVA. The RM-ANOVA F statistics and *P* values for each phylum are in the upper left.
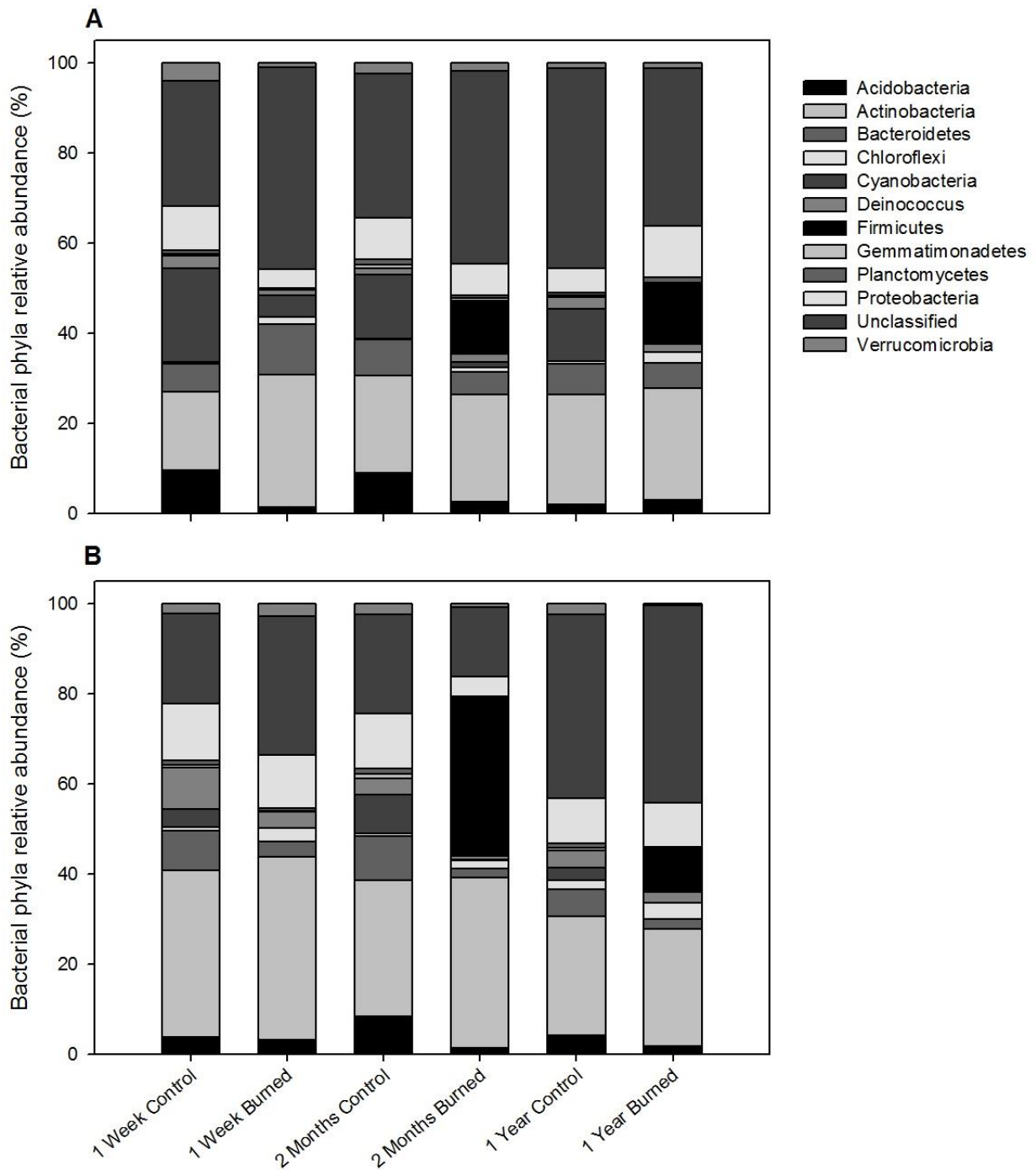
Figure 4. Relative abundance (%) of bacterial phyla in unburned and burned interspace (A) and shrub (B) biocrusts at three time points following fire over one year. Values are means (*n*=3) ± SEM based on pyrosequencing of 16S rDNA.
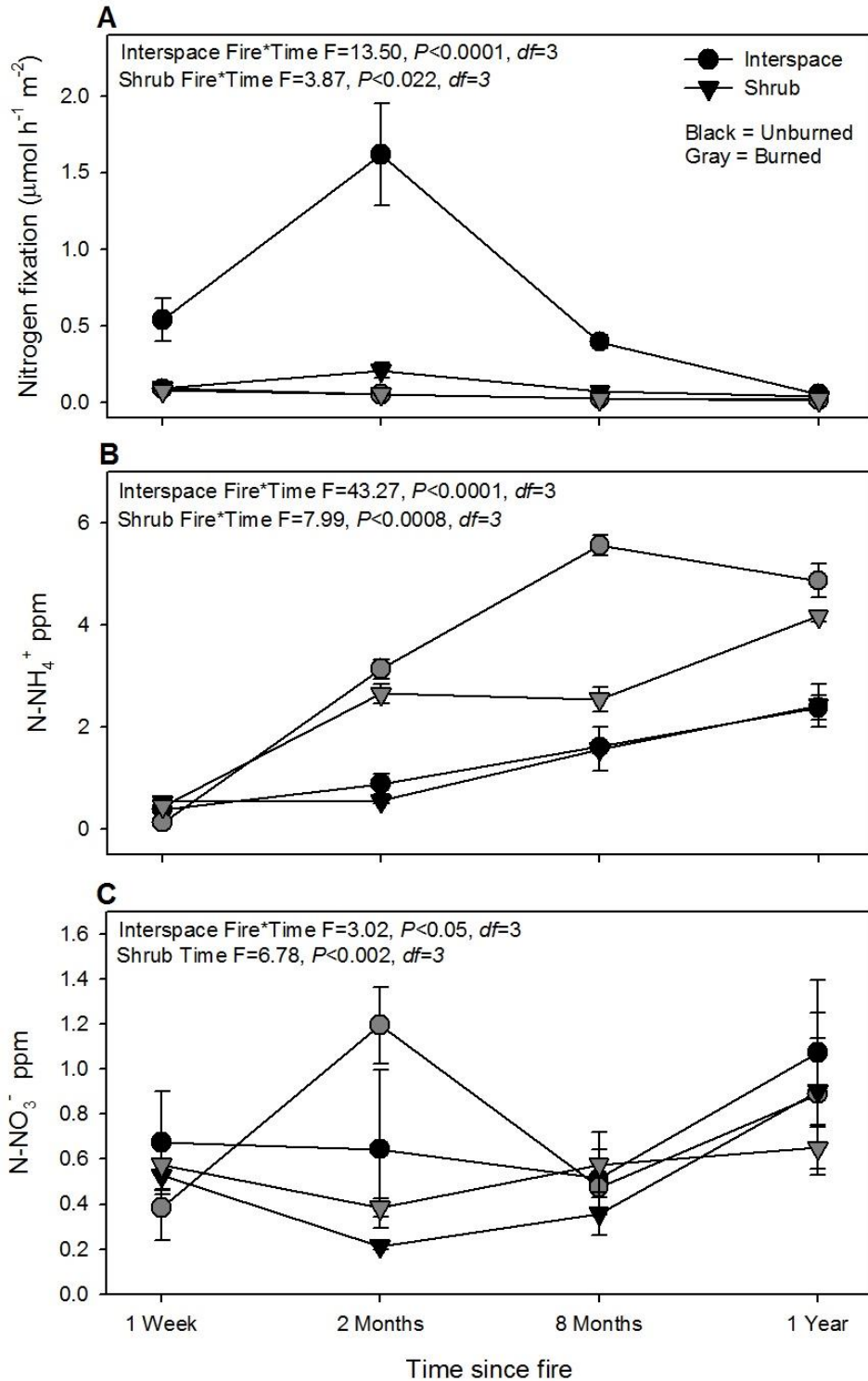
Figure 5. N fixation rates (A), and inorganic N concentrations (N-NH$_4^+$ (B) and N-NO$_3$ (C)) in unburned and burned biocr sts over one year follo in fire. N fixation (μmol h^{-2} m^{-2}) and inorganic N (ppm) values are means (*n*=5) ± SEM. Differences in N characteristics between burned and unburned biocrusts through time are based on RM-ANOVA with attending F statistics and *P* values for significant interactions.
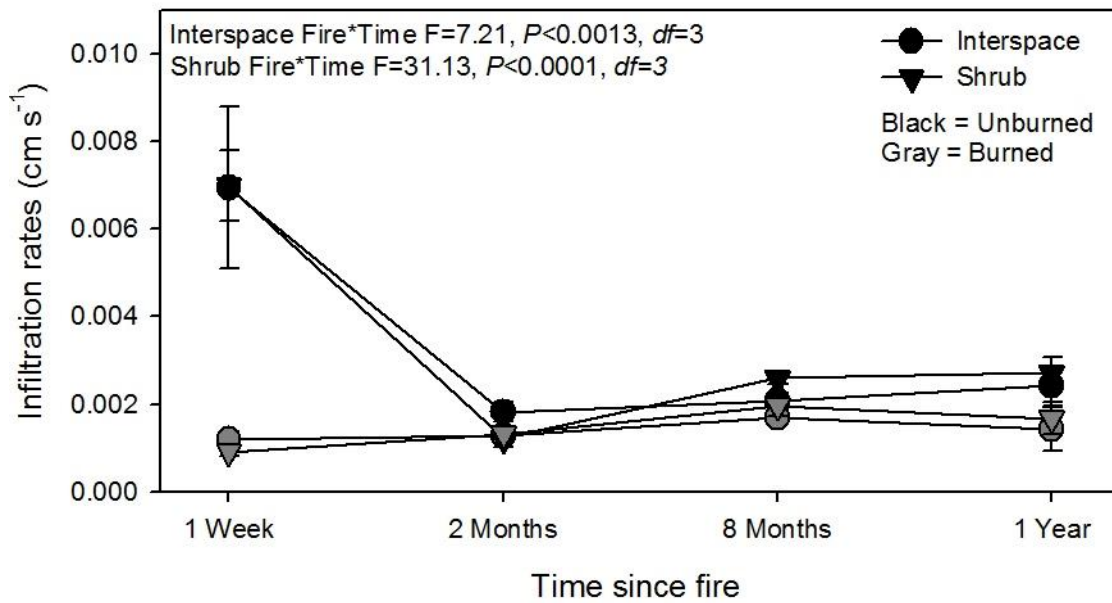
Figure 6. Soil infiltration rates following fire in burned and unburned biocrusts. Values are means (*n*=5), ± SEM, reported in cm s^{-1}. Differences are based on RM-ANOVA with attending F statistics and *P* values for significant interactions.
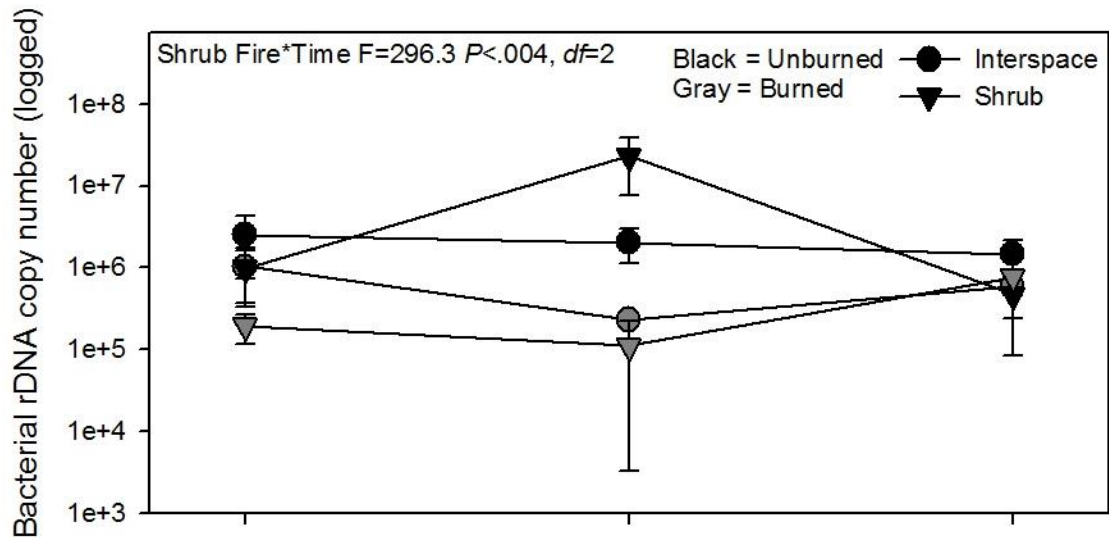
Figure 7. Bacterial biomass in interspace and shrub biocrusts. Values are means (*n*=3) ± SEM, measured with quantitative polymerase chain reaction (qPCR) and reported as rDNA gene copy number. Differences between burned and unburned soils through time are based on RM-ANOVA with F statistic and *P* value for significant interactions.

CHAPTER 2: ABSTRACT

Exploring post-fire recovery of biocrust ecosystem services under different precipitation regimes

Biocrusts and the ecosystem services they provide are increasingly threatened by fire and precipitation regime shifts in the western United States. Despite this, our understanding of the interactions between wildfire, precipitation, and biocrust recovery is limited. To investigate these interactions, we created burn manipulations (i.e., unburned and burned) and precipitation treatments (i.e., ambient, plus and minus 30%) and monitored biocrust cover and ecosystem services over two years in the Great Basin and Mojave deserts (UT, USA). Specifically, we: monitored biocrust moss and lichen cover; measured N fixation potential and soil inorganic N; and assessed soil infiltration rates and soil stability. We burned biocrusts in summer 2011 and measured biocrust recovery one week following fire and every subsequent fall and spring season over the duration of the study. In the Great Basin, no lichen or moss species survived burn treatments, but visual burned biocrust structure persisted through time. Many biocrust ecosystem services did not recover within two years following the fire, but infiltration rates may be the one service that did recover. Fire reduced N fixation potential at least four-fold in burned interspace and shrub biocrusts. Also, soil stability decreased two- to three-fold in interspace and shrub biocrusts and did not recover within two years. Infiltration rates initially decreased at least six-fold in interspace and shrub biocrusts, but began to recover within two months. The burn manipulations increased the availability of soil $N-NH_4^+$ concentrations but this pulse may be short because N fixation remains limited in burned soils. In the Mojave, the burn manipulations were less severe and biocrust function was more influenced by seasonality than fire. Infiltration rates in shrub biocrusts decreased almost two-fold, one week following fire, but recovered within two months. Precipitation manipulations began one year into the experiment so the impact of increased or decreased precipitation is yet to be determined. However, inorganic N levels in shrub biocrusts in the Great Basin did respond to precipitation variability. Soil $N-NH_4^+$ concentrations were positively related to precipitation, but $N-NO_3^-$ concentrations were lower in both precipitation treatments than biocrusts exposed to ambient precipitation.

1. CHAPTER 2: INTRODUCTION

1.1 The ecological role of biocrusts

The top 0-2 mm of arid land soil surfaces are inhabited by a biofilm consortium of cyanobacteria, green algae, lichens, mosses, and microfungi known as biocrusts (Belnap, 2003). Biocrusts are well adapted to harsh desert conditions including large variations in temperature, moisture, and UV radiation (Grote et al, 2010). Moreover, biocrusts are essential to the health of arid lands due to their ability to provide ecosystem services including: defending desert soils from erosion, improving ecohydrology, and fixing C and N into these nutrient limited systems (Muscha & Hild, 2006; Beaty & Smith, 2012). Biocrusts stabilize soil particles by producing exopolysaccharide and microfungal filaments under moist conditions. These filaments weave through the soil matrix, binding soil particles together (Mazor et al, 1996). Upon desiccation, the exopolysaccharide filaments harden, forming sheaths that help soil particles and organisms withstand the erosive forces of wind and water (Belnap & Lange, 2003). Biocrusts also increase soil infiltration rates by increasin ater residence time thro h "hill-valley," or r ose, topography. The infrequent nature of large precipitation events in deserts makes this biocrust function even more important for capturing variable precipitation and moving moisture belowground. Last, biocrust lichen and cyanobacteria species fix N contributing the dominant source of nitrogen in deserts, making biocrusts an invaluable resource to desert systems (Holst et al, 2009). Unfortunately, biocrusts and the ecosystem services they provide are increasingly exposed to fire as exotic annual grass invasions facilitate the spread of catastrophic wildfires (Haubensak et al, 2009).

1.2 Fire and biocrusts

Wildfire has historically been an infrequent stressor in deserts of the American West. Over the past century, invasive grasses, including *Bromus tectorum* and *Bromus rubens* have increased wildfire frequency, size, and intensity in the Great Basin and Mojave deserts (Keeley et al, 2009; Brooks & Matchett, 2006). These new fire regimes are causing both systems to shift from stable mosaics of shrub-islands of fertility and barren plant interspace to annual grasslands. For example, Mojave wildfires in 2005 and 2006 lightly or completely burned approximately 80% of shrubs and biocrusts and the frequency of *B. rubens* increased across much of the landscape in the northeastern Mojave (Personal Communication, Kevin Horn). In the Great Basin, *B. tectorum* has effectively replaced shrubs and biocrusts across large areas. Even when biocrusts remain, fire threatens biocrust health and their ability to perform ecosystem services. Fire destabilizes biocrusts, thus increasing erosion potential (Bowker et al, 2004; Johansen et al, 1984) and decreasing N fixation potential. Last, fire drastically alters soil ecohydrology, especially through increasing soil water repellency or hydrophobicity (Beatty & Smith, 2012).

1.3 Precipitation and biocrusts

Biocrusts are well adapted to the precipitation variability present in arid and semi-arid systems (Lange et al, 1994). Exopolymeric substances, exuded by bacteria and other biocrust organisms, have high absorptivity and increase infiltration rates, maximizing the amount of water that can enter the soil in a short amount of time. The Mojave and Great Basin deserts experience high-levels of precipitation intra- and inter-annual variability with most precipitation occurring d rin the inter and early s rin months. Each desert's precipitation regime is generally characterized by 3- to 5-year wet and dry periods that are largely dictated by Pacific sea surface temperatures (Anderson et al, 2010). The El Niño Southern Oscillation (ENSO) is linked to

maximum levels of winter precipitation in the Mojave (McCabe & Dettinger, 1999). The northern Great Basin experiences wet and dry periods based on a 12-year cycle influenced by the Pacific Quasi-Decadal Oscillation (PDO). The ENSO and PDO also interact with other sea surface temperature patterns along longer time scales to form the multi-decadal precipitation regimes experienced by the Mojave and Great Basin (Hua & Ma, 2009). Additionally, future climate models predict either an increase or decrease of approximately 30% in precipitation levels throughout the American southwest (Seager et al, 2007; Cubasch et al, 2001). It has been predicted that climate change will alter precipitation intensity and frequency even further throughout the 21st century (Sun et al, 2007; Easterling et al, 2000). Due to the intense precipitation variability in these systems and the dominant role of biocrusts, it is essential to better understand interactions between precipitation, fire and biocrust recovery.

1.4 The Great Basin and Mojave deserts

Biocrusts inhabit most of the soil surface in interspaces and beneath plants in deserts worldwide, including the Great Basin and Mojave. The Great Basin and Mojave deserts cover large geographical areas in the American west, and encompass valuable natural resources. They provide habitat for many native species and are important lands for cattle grazing and agriculture. Large portions of The Great Basin make up most of Nevada and Utah, but it also extends into California, Oregon, Idaho, and Wyoming covering nearly 185,000 m^2. The Mojave expands over 25,000 m^2 throughout southeastern California, southern Nevada, northwestern Arizona, and the southwest corner of Utah. Land managers over these areas are faced with the task of managing these violently changing systems. Further understanding the complex interactions between fire, precipitation, and biocrusts, will help land managers better manage biocrust and soil resources following fire.

1.5 Study objectives and hypotheses

We lack knowledge regarding how wildfire and altered precipitation regimes affect the ecosystem services provided by biocrusts. In this study, we investigated the impacts of invasive grass fires and altered precipitation regimes on biocrust ecosystem services. We conducted burn manipulations and measured ecosystem services from burned and unburned plots, with nested precipitation treatments, at different time points over a period of nearly two years, including summer (after the burn) and the next two fall and spring seasons. Specifically, in burned and unburned interspace and shrub biocrusts we: measured N fixation, soil infiltration rates, soil stability, and inorganic N concentrations, and monitored biocrust cover. We hypothesize that fire will drastically reduce ecosystem services in both deserts and the addition of precipitation will shorten the time needed for ecosystems to recover.

2. CHAPTER 2: MATERIALS AND METHODS

2.1 Site descriptions

We conducted our study at one location in both the Great Basin and Mojave Deserts. The Great Basin site was in Rush Valley, UT, (40°05'27.43"N - 112°18'18.24"W). Biocrusts were dominated by *Collema* and *Toninia* in plant interspaces and *Syntrichia* beneath shrub-islands. The annual exotic grass, *Bromus tectorum*, has altered fire regimes of the surrounding area, but our site was minimally invaded and was more indicative of a pristine shrubland. Shrub-islands were composed of *Artemisia tridentata, ssp. wyomingensis* with other dominant plant species including the perennial grass *Elymus elymoides* (Raf.) Swezey and several annual forbs: *Halogeton glomeratus* (Bieb.) C.A. Mey., *Ceratocephala testiculata* (Crantz.) Roth. Mean annual precipitation at the site is 27.57 cm year^{-1} ($\pm$ 1.39, n=30) and mean annual temperature is 8.87°C ($\pm$ 0.056, n=30). Soils are derived from Lake Bonneville sediments in the Taylorsflat series. This series consists of well drained, fine-loamy, mixed, mesic Xerollic Calciorthids with 3 to 15 percent calcium carbonate. Surface soils are strongly alkaline and have a pH of 8.6.

The Mojave study site was located in the Beaver Dam Wash in southwest Utah (37°08'55.14"N - 114°00'50.49"W). Interspace and shrub biocrusts were dominated by cyanobacteria. When present, *Collema*, *Placidium*, and *Peltula* lichens and *Syntrichia* mosses inhabited both interspace and shrub biocrust surfaces. The annual exotic grass, *Bromus rubens*, was common throughout the site. Dominant native plants included *Coleogyne ramosissima (Torr.), Larrea tridentata (DC.) Coville, Ambrosia dumosa (A. Gray) Payne, and Yucca brevifolia (Engelm)*. Mean annual precipitation is 17.32 cm year^{-1} ($\pm$ 0.0017, n=30) and mean annual temperature is 18.87°C ($\pm$ 0.064, n=30). Soils are in the Quazo series. This series consists of shallow well drained, sandy loams. Surface soils are alkaline and have a pH around 8.

2.2 Visual crust estimates

We conducted visual estimates of biocrust cover to track the impacts of fire and precipitation on the recovery of lichens, mosses, cyanobacteria, and leaf litter. We used a sixteen-point grid and a modified, step point-intercept transect technique (Bowker and Belnap, 2008) to estimate the percent ground cover of the above groups in fire treated and unburned plots. Each replicated treatment microsite had one permanent grid location that was used for all evaluations through time and cover estimates were based on the sixteen points in each grid. The grid dimensions were 16 squares, spaced ~2 inches apart, in a 4x4 pattern.

2.3 Fire manipulations, precipitation treatments, and research design

We created fire manipulations with controlled burns in early July 2011, Mojave, and late September 2011, Great Basin. In each desert, the burns were conducted in ten randomly selected plots (30 m width x 30 m length). To ensure that the fire carried through the plots, at the Great Basin site we spread 20 bales of straw onto the soil surface (Esque et al, 2010). This straw has similar above and below ground heating patterns to invasive grasses (Biederbeck et al, 1980). Also, the ash from burned straw blew away from soil surfaces within two weeks, reducing the likelihood of long term increases in C and N from straw. We also created ten unburned plots of the same dimensions. Within each plot, we constructed 2 or 3 precipitation shelters (2 m x 3 m x 1 m tall). Precipitation treatments consisted of plus and minus 30% monthly averages. If present, the third shelter was an ambient precipitation control. All precipitation shelters were permanent structures built from painted, metal bars with clear polycarbonate v-shaped gutters spaced evenly on top to manipulate the amount of precipitation reaching the soil surface (Yahdjian and Sala 2002). Gutters in minus treatments were spaced over 30% of the shelter area and oriented inhibit

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natural precipitation, guiding water outside of the shelters. Gutters in plus and unburned

treatments were also spaced over 30% of the shelter area, but were oriented to allow precipitation

to drip into plots. Precipitation additions in plus shelters were based on 20 year averages for each

month, and applied every three weeks. Shelter boundaries were lined with 8 inch metal flashing,

buried to hydrologically isolate the area beneath each shelter. The gutters transmitted >90% of

photosynthetically active radiation and were UV transmissive, effectively providing near natural

levels of light to plants and biocrusts.

2.4 Biocrust sampling

Under each shelter, we selected two biocrust microsites, an interspace and a shrub-island

biocrust. The interspace biocrusts were at least 30 cm away from the nearest shrub and shrub

biocrusts were located at the edge of shrub canopies. Sampling in all replicates (i.e., 2 fire

manipulations x 2 crust microsites x 2 precipitation treatments x 5 replicates = 30 replicates)

occurred after the fire at five time points. Time points in the Mojave were one week (17 July

2011), 3 months (13 October 2011), 10 months (24 April 2012), 15 months (15 October 2012),

and 21 months (4 April 2013) post-fire. Time points in the Great Basin were one week (27

September 2011), two months (4 November 2011), 8 months (1 June 2012), 1two months (1

October 2012), and 20 months (3 May 2013) post-fire. We removed two samples from both

microsites at each sampling time. The first sample consisted of three homogenized cores

(diameter = 2 cm, depth = 1 cm) extracted with a soil probe. The sample was stored at 5º C for

inorganic N determination. The second sample consisted of 1 intact soil core (diameter = 2 cm,

depth = 1 cm) that was used in N fixation analysis.

2.5 Estimation of Ecosystem services

We monitored the impacts of fire and precipitation treatments on the following biocrust ecosystem services and characteristics: N fixation, inorganic N concentrations, infiltration rates, and soil stability. All measurements (2 fire manipulations x 2 precipitation treatments x 2 crust microsites x 5 replicates x 5 time points = 200 replicates) were compared within each desert via RM-ANOVA in the Stats package of the R Statistics Environment (R Development Core Team, 2008).

2.5.1 Biocrust N fixation and inorganic N concentrations

We measured the effects of fire and varying precipitation on N fixation, and inorganic N availability. N fixation (μmol h^{-1} m^{-2}) was estimated using acetylene reduction assay, ARA, protocols outlined by Belnap (2002). Briefly, the enzyme responsible for N fixation, nitrogenase, reduces acetylene to ethylene at approximately the same rate as it reduces dinitrogen gas to NH_4^+, allowing for a simulated measurement of N fixation. We brought all soil cores, described in section *2.2*, to uniform conditions by incubating for two days on a 12 hour light, 12 hour dark schedule and watering with 1 mL of nanopure water. A 10% acetylene atmosphere was then created by sealing cores and injecting 5 mL of pure acetylene through an airtight septum. Incubations continued for another 4 hours and then a 4 mL headspace gas sample was removed. Ethylene in the gas sample (ppm) was measured with an Agilent Technologies 6890A gas chromatograph with a PoraPak R column (Agilent Technologies, Santa Clara, CA) with an attached flame ionization detector. The in ection chamber of the a s chromato ra h a   s   e t at 50 C,the col m n a s 250 C We sed the ideal as la   to convert m e thylene to μmol ethylene h^{-1} m^{-2}.

Inorganic nitrogen concentrations were measured via spectrophotometry. Soil ammonium (μ N-NH$_4^+$ g soil^{-1}) and soil nitrate (μ N-NO$_3^-$ g soil^{-1}) extracts consisted of 2 grams of soil with 4 mL 0.5 M K2SO4 (1:2 w/v). Extracts were shaken for 30 minutes and then centrifuged for another 30 minutes at 4,000 rpm. We then quantified each N species in the supernatant colorimetrically using a SpectraMax Plus 384 (Molecular Devices Corporation, Sunnyside, CA) (Forster, 1995; Miranda et al, 2001).

2.5.2 Soil ecohydrology and stability

To investigate the effect of fire and precipitation on soil ecohydrology, we measured chan es in infiltration rates ith a Deca on Device's Mini Dis Te nsion Infiltrometer (Deca on Devices, Pullman, WA). Due to the rugose nature of the biocrusts at the Great Basin site, and presence of rocks in the Mojave, the infiltrometer was only able to form a seal with the soil when approximately 16 grams of sterilized sand was deposited in a thin layer on the soil surface. The sand did not affect infiltration rates d e to the infiltrometer's r ess re chamber hic h allo s one to target the specific texture of the soil, and effectively ignore the sand. Infiltration measurements were conducted accordin to Deca on De vice's rotocol (Deca on Devices, Pullman, WA), and rates (cm s^{-1}) were calculated following Zhang et al (1997).

We measured soil stability according to the Jornada Experimental Range Test (Herrick et al, 2001) in order to understand how fire and precipitation impact soil stability. This test involves timed water immersion and wet sieving of soil aggregates between 6 and 8 mm diameter. We then visually estimated the material remaining on the sieve and assigned stability values based on predetermined parameters. Test kits were designed by Synergy Resource Solutions, Inc. (Montana, USA).

3. CHAPTER 2: RESULTS

3.1 Biocrust cover in the Great Basin and Mojave Deserts

Visual estimates of biocrust species reflected losses from fire in the Great Basin, and no fire effects in the Mojave. Great Basin interspaces were dominated by Cyanobacteria crusts (50.6% ±2.8), but lichen (24.2% ±6.9) and moss (15.6% ±2.5) cover was also common. Lichen cover in interspaces was predominantly *Collema tenax*, 10.4% ±2.0, and *Toninia sedifolia*, 8.5% ±1.7. There were also two dominant mosses, *Syntrichia caninervis*, 11.5% ±1.6, and *S. ruralis*, 4.02% ±0.9. Shrub biocrusts were mostly covered with shrub leaf litter, 65.1% ±4.7. Cyanobacteria crusts comprised 18.6% ±3.4 and *T. sedifolia* was the dominant lichen, 2.4% ±0.8. *S. ruralis* and *S. caninervis* also made up a significant portion of shrub biocrust cover, 5.9% ±1.5 and 4.7% ±0.9, respectively. Mojave crusts exhibited little visual evidence of fire, and only one shelter covered any mosses or lichens. Visual estimates were reduced primarily to surface cover of bare cyanobacteria crusts, presence of *B. rubens*, and presence of rock. Mojave interspaces were dominated by cyanobacteria crusts (38.4% ±3.2), but were also covered by *B. rubens* (16.2% ±2.8) and a substantial amount of rock (38.9% ±3.3). Mojave shrub biocrusts were covered by 46.0% ±3.9 Cyanobacteria, 26.2% ±3.9 *B. rubens*, and 19.5% ±2.4 rock.

3.2 N fixation recovery following fire

Fire had varying effects on N fixation rates and inorganic N concentrations in Great Basin and Mojave shrub and interspace biocrusts. Fire initially decreased Great Basin N fixation rates in interspaces six-fold, and rates declined to as low as forty-three-times lower in burned than unburned biocrusts two months following the fire (RM-ANOVA: fire*time, F=114.7, *P*<0.0001, *df*=4, Fig. 8A). Shrub biocrust N fixation rates were less affected by fire, but at two

months, burned soils exhibited a three-fold decrease compared to unburned soils (RM-ANOVA: fire*time, F=67.56, $P<0.0001$, df=4, Fig. 8A). N fixation rates remained higher in unburned than burned biocrusts through the final time point in interspace and shrub soils. Conversely, in the Mojave, fire had no measurable effect on N fixation rates in either interspace or shrub biocrusts. N fixation rates were the same for both shrub (RM-ANOVA: time, F=2149, $P<0.0001$, df=4, Fig. 8B) and interspace (RM-ANOVA: time, F=1826.9, $P<0.0001$, df=4, Fig. 8B) biocrusts and reflected strong seasonality with rates highest in spring and lowest in the fall.

Fire effected an overall increase in $N\text{-}NH_4^+$ in both interspace and shrub biocrusts in the Great Basin. $N\text{-}NH_4^+$ was initially two-and-a-half-fold less in burned interspaces, but at two, eight, and twelve months, burned biocrusts had up to three-fold more $N\text{-}NH_4^+$ than unburned soils (RM-ANOVA: fire*time, F=47.66, $P<0.0001$, df=3, Fig. 9A). Shrub biocrust $N\text{-}NH_4^+$ did not initially differ between unburned and burned biocrusts. At two months following the burn, burned soils had five-fold more $N\text{-}NH_4^+$ than unburned soils, and still had almost two-fold more at one year (RM-ANOVA: fire*time, F=42.57, P<0.0001, df=3, Fig. 9A). Additionally, interspace and shrub biocrust $N\text{-}NH_4^+$ concentrations in the Great Basin were the only parameters affected by precipitation treatments. This effect was only detectable at twelve months when $N\text{-}NH_4^+$ concentrations in interspace biocrusts were lower in plus and minus treatments than ambient controls (RM-ANOVA: precip*time, F=25.05, $P<0.0001$, df=6, Fig. 10B) and shrub biocrust $N\text{-}NH_4^+$ concentrations were greatest in plus and least in minus treatments (RM-ANOVA: precip*time, F=3.35, $P<0.01$, df=6, Fig. 10B). In the Mojave, $N\text{-}NH_4^+$ concentrations in interspaces were altered by fire. At one week, burned plots had one-and-a-half-fold less $N\text{-}NH_4^+$ than unburned soils, but at two months $N\text{-}NH_4^+$ was two-fold greater in unburned than burned biocrusts (RM-ANOVA: fire*time, F=10.85, $P<0.0002$, df=3, Fig. 9B). After two

months, fire had no effect on interspace $N-NH_4^+$. Fire did not alter soil $N-NH_4^+$ in Mojave shrub biocrusts, but there was a seasonality effect in which summer had the highest levels of $N-NH_4^+$ and spring had the lowest (RM-ANOVA: time, F=107.86, $P<0.0001$, df=3, Fig. 9B).

Fire had varying effects on biocrust $N-NO_3^-$ concentrations in the Great Basin. $N-NO_3^-$ in burned interspaces was almost three-fold lower than unburned soils one week after the fire, but this effect was reversed after two months with concentrations six-fold greater in burned than unburned soils (RM-ANOVA: fire*time, F=18.99, $P<0.0001$, df=3, Fig. 9C). Shrub biocrust $N-NO_3^-$ was up to one-and-a-half-times higher in burned than unburned biocrusts at two and eight months following fire (RM-ANOVA: fire*time, F=2.59, $P<0.08$, df=3, Fig. 9C). Mojave interspace $N-NO_3^-$ was also affected by fire. Fire initially decreased $N-NO_3^-$ four-fold, but from two months to one year following fire $N-NO_3^-$ was higher in burned soils (RM-ANOVA: fire*time, F=20.92, $P<0.0001$, df=3, Fig. 9D). Shrub biocrust $N-NO_3^-$ concentrations exhibited similar trends to interspaces, with initial decreases followed by increases in burned soils through time (RM-ANOVA: fire*time, F=8.19, $P<0.0007$, df=3, Fig. 9D).

3.3 Infiltration rates and soil stability following fire

Fire reduced Great Basin soil infiltration rates and stability in interspace and shrub biocrusts. Infiltration rates in burned interspace and shrub biocrusts were initially depressed five and seven-fold respectively, interspace (RM-ANOVA: fire*time, F=19.21 $P<0.0001$, df=4, Fig. 11A), shrub (RM-ANOVA: fire*time, F=116.49, $P<0.0001$, df=4, Fig. 11A). Infiltration rates remained roughly one-and-a-half-fold lower in burned than unburned crusts through the rest of the time points. Mojave infiltration rates were initially one-and-a-half-fold lower in burned than unburned interspace (RM-ANOVA: fire*time, F=3.99, $P<0.01$, df=4, Fig. 11B) and shrub (RM-

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ANOVA: fire*time, F=10.89, $P<0.0001$, $df=4$, Fig. 11B) biocrusts. By three months infiltration rates returned to similar levels as unburned soils.

Fire decreased soil stability in Great Basin interspace and shrub biocrusts. Burned biocrusts remained three-fold less stable in interspace soils (RM-ANOVA: fire*time, F=2.78, $P<0.045$, $df=4$, Fig. 12A) and two-fold less stable in shrub soils (RM-ANOVA: time, F=5.24, $P<0.003$, $df=4$, Fig. 12A) at the final time point. Soil stability in Mojave biocrusts was unaffected by fire, but was seasonally variable. The initial and final measurements were both two- to three-fold higher than the first spring and both fall measurements, interspace (RM-ANOVA: time, F=15.02, $P<0.0001$, $df=4$, Fig. 12B), shrub (RM-ANOVA: F=11.67, $P<0.0001$, $df=4$, Fig. 12B).

4. CHAPTER 2: DISCUSSION

4.1 Differences in burn manipulations between deserts

Contrary to our first hypothesis, fire drastically reduced ecosystem services in the Great Basin but not in the Mojave. The intensity of burn treatments differed between deserts. In the Great Basin, burn treatments had a continuous fuel load that connected shrubs and interspaces, creating a relatively even burn which removed nearly all plants, lichens, and mosses, and visually darkened biocrusts. This continuous fuel load was more representative of a landscape that is beginning to be invaded by the exotic annual grass, *B. tectorum*. The Mojave burn treatments were less even due to the lack of a continuous fuel load. The Mojave fire burned shrubs and occasionally darkened shrub biocrusts, but fewer biocrusts in interspaces were directly exposed to fire. This disparity in burn intensity resulted in biocrust ecosystem services being more severely impacted by fire in the Great Basin than the Mojave, and our Mojave results predominantly highlighting seasonal effects on biocrust ecosystem services.

4.2 Great Basin recovery of biocrust ecosystem services following fire

Fire impacted the efficiency of biocrusts to stabilize soils, enhance infiltration rates, fix N, and it altered inorganic N concentrations in the Great Basin. N fixation initially decreased when biocrusts were burned, but did not differ between burned and unburned crusts during spring 2013. N fixation rates may have started to recover by spring 2013; however, this potential recovery was confounded by a drought that persisted from winter 2011 to spring 2013. *Collema* lichens and cyanobacteria including *Microcoleus* species conduct N fixation, but only under ideal moisture and anoxic (for *Microcoleus*) conditions that occur infrequently in desert systems (Zaady, 2005). The drought likely lowered N fixation rates in unburned crusts during fall 2012,

with rates nearly sixty-times lower under drought than the pre-drought conditions of fall 2011. A previous study in the Great Basin found that recovery of N fixation occurred within five years of fire disturbance and that this recovery was linked to greater than average precipitation three and four years after fire (Terry and Burns, 1986). Thus, although the current dataset still holds some uncertainty regarding N fixation recovery, further monitoring of biocrusts in burned plots under different precipitation treatments will clarify the importance of time and precipitation for post-fire recovery of N fixation.

Fire had varying effects on inorganic N concentrations. The overall fire effects on inorganic N availability were increased $N-NH_4^+$ concentrations and initially varying soil $N-NO_3^-$ concentrations that leveled out after one year. The increase of $N-NH_4^+$ is likely due to bacteria mineralizing partially burned substrates and the absence of plants immobilizing inorganic N in the burned areas. $N-NO_3^-$ levels were unusually low, less than 1 ppm, in almost all treatments and time periods. This might be because we only sampled he top 1 cm of soil where $N-NO_3^-$ leaching is common.

Many biocrust ecosystem services did not recover within two years following the fire, but infiltration rates may be the one service that did recover. Fire can create hydrophobic layers in soils by volatilizing plant compounds that settle and cool on soil surfaces (Huffman et al, 2001). Fire generally reduced infiltration rates in both shrub and interspace biocrusts, indicating the possible creation of a hydrophobic layer, but the effects of fire on infiltration seem to be declining through time. Infiltration rates are influenced by air temperatures and humidity (Houser, 2005), and evidence for recovery could again be confounded by the observed drought from winter 2011 to spring 2013. The potential recovery of soil infiltration is not likely due to the recovery of soil stability since Great Basin soil stability decreased with fire and the

differences between the treatments increased through time.

4.3 Mojave

Most ecosystem services in the Mojave were not impacted by the more natural fire treatments; however, they exhibited strong seasonality with peak activity occurring in spring. Steady patterns of winter precipitation in the Mojave drove N fixation rates. N fixation was highest in the spring, when crusts were moist and temperatures were not high enough to cause desiccation stress. N fixation was lowest during both fall measurements before the onset of winter precipitation. Inorganic N concentrations were altered by fire in shrub and interspace biocrusts. Burned Interspace $N-NH_4^+$ was only affected in the short-term, experiencing an initial decrease in concentrations, but at two months concentrations increased. This increase could be due to residual unburned material in and on top of surface soil layers that bacteria are breaking down. Burn treatments effectively thinned shrub communities, reducing a dominant $N-NH_4^+$ sink. This resulted in a net increase in $N-NH_4^+$ concentrations. Interspace biocrust $N-NO_3^-$ was not immediately affected by fire, but in spring and fall 2012 burned interspaces had higher levels than unburned biocrusts. One reason for this could be the lack of shrubs to draw $N-NO_3^-$ from interspaces. Shrub biocrust $N-NO_3^-$ also was also higher in burned than unburned soils. Microbes could be breaking down burned plant material and causing a release of N in burned shrub and interspace biocrusts.

Infiltration rates in burned interspace and shrub biocrusts were depressed immediately following the burn, but recovered rapidly by fall 2011. This indicates that wildfires in the Mojave may not have long-term effects on water infiltration, an important characteristic of ecohydrology. Soil stability was unaffected by fire and was highest at the initial measurement and spring 2013.

4.4 Precipitation effects

We hypothesized that the addition of precipitation will shorten the time needed for ecosystems to recover. Contrary to our hypothesis, $N-NH_4^+$ in shrub biocrusts was the only parameter in either desert that was positively related to precipitation magnitude. We initiated precipitation treatments approximately six months and one year after burn manipulations in the Mojave and Great Basin respectively. Accordingly, our results reflect less than two years of precipitation treatments. We are only beginning to see the impact of precipitation variability in the Great Basin and Mojave. Precipitation treatments in the Great Basin altered soil $N-NH_4^+$ concentrations in shrub and interspace biocrusts one year after fire. During fall 2012, $N-NH_4^+$ concentrations in shrub biocrusts were positively related to precipitation. However, both plus and minus 30% precipitation treatments reflected a loss of soil $N-NO_3^-$ in shrub biocrusts. Moisture is essential for the formation of biological soil crusts, but too much moisture at the wrong time is detrimental to overall crust health. For example, increased precipitation frequency reduced biocrust chlorophyll *a* content, nitrogenase activity, and protective pigments, during summer months (Belnap et al, 2004). Another study in the Mojave revealed that increased levels of precipitation stressed *Syntrichia* mosses, causing C deficits (Stark et al, 2011). Contrarily, biocrusts are only metabolically active when moist, and multiple studies have found that greater levels of precipitation can stimulate biocrust recovery from disturbance (Harper & Marble, 1988; Johansen et al, 1993). We will continue monitoring biocrust ecosystem services over the next five years to better understand the interactions of fire, precipitation, and biocrust recovery.

5. CHAPTER 2: CONCLUSIONS

We hypothesized that fire will drastically reduce ecosystem services in both deserts. Contrary to this hypothesis, fire greatly impacted Great Basin biocrust cover and ecosystem services, but the less even burn conditions in the Mojave only subtly impacted a few biocrust characteristics. Fire reduced the capacity of biocrusts to stabilize soils, enhanced ecohydrology, and provided N to Great Basin soils. Fire also increased levels of soil $N-NH_4^+$. Our results indicated potential recovery of N fixation, but recovery was confounded by a drought that reduced N fixation in all biocrusts. Soil stability remained depressed at the end of two years, but infiltration rates showed signs of recovery. In the Mojave, N fixation rates were strongly influenced by seasonality with the highest activity occurring in spring, following winter precipitation. Fire did not initially affect soil $N-NO_3^-$ in interspace or shrub biocrusts, but later time points exhibited increased soil $N-NO_3^-$. These increases could be due to the absence of adjacent shrub species drawing N into shrub-islands or the enhanced breakdown of unburned material. Fire also inhibited soil infiltration rates in shrub and interspace biocrusts. Infiltration recovered within two months of fire, indicating that fire may not significantly decrease ecohydrology in the short-term. Contrary to our second hypothesis, $N-NH_4^+$ concentration in Great Basin shrub and interspace biocrusts was the only parameter to respond to precipitation treatments. Shrub biocrusts reflected a positive relationship between precipitation and $N-NH_4^+$ concentrations. However, interspace biocrusts exposed to plus and minus precipitation treatments had lower N-NH4+ concentrations than those exposed to ambient precipitation. Our interpretations regarding precipitation are currently premature due to precipitation treatments being in effect for only one year. However, monitoring efforts will continue for the next five

years, a more realistic time frame to capture potential interactions between fire, precipitation, and

biocrust recovery.

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7. CHAPTER 2: FIGURES
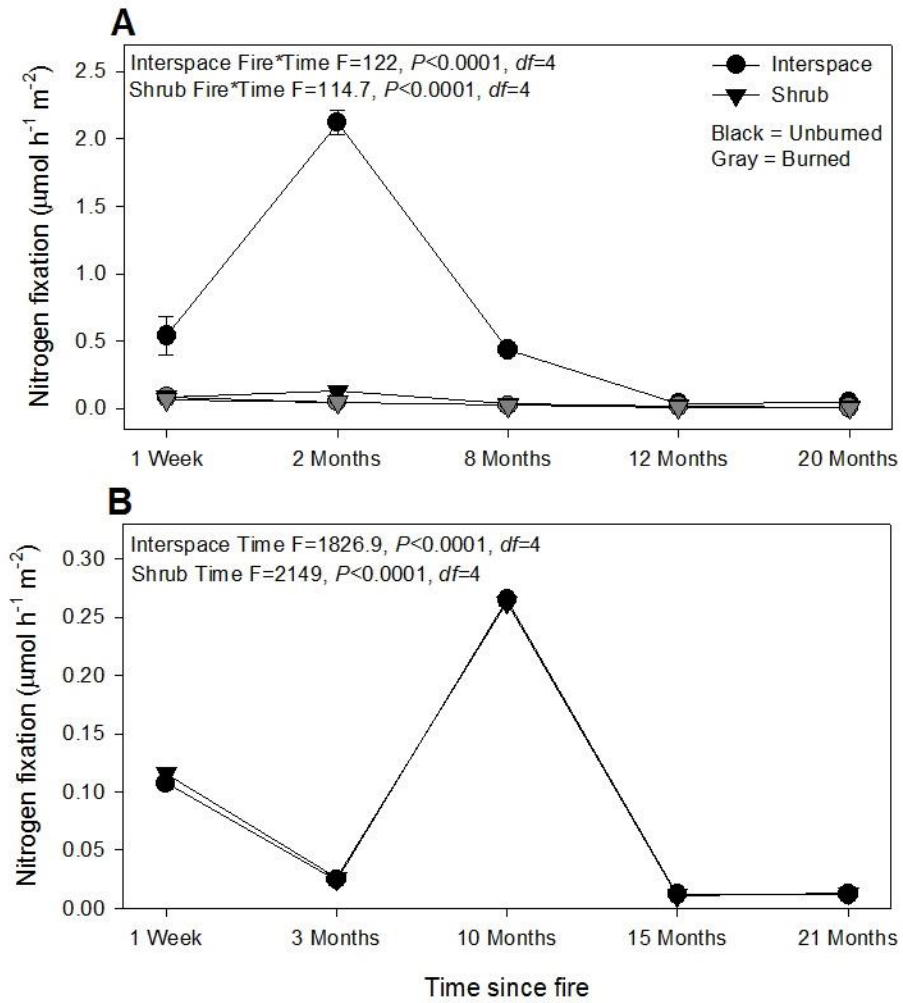
Figure 8. Great Basin (A) and Mojave (B) N fixation rates in unburned and burned biocrusts over ~20 months follo in fire. N fixation ($\mu mol\ h^{-1}\ m^{-2}$) values are means ± SEM (*n*=5). Differences through time and by fire treatment are based on RM-ANOVA with attending F statistics and *P* values for significant interactions.
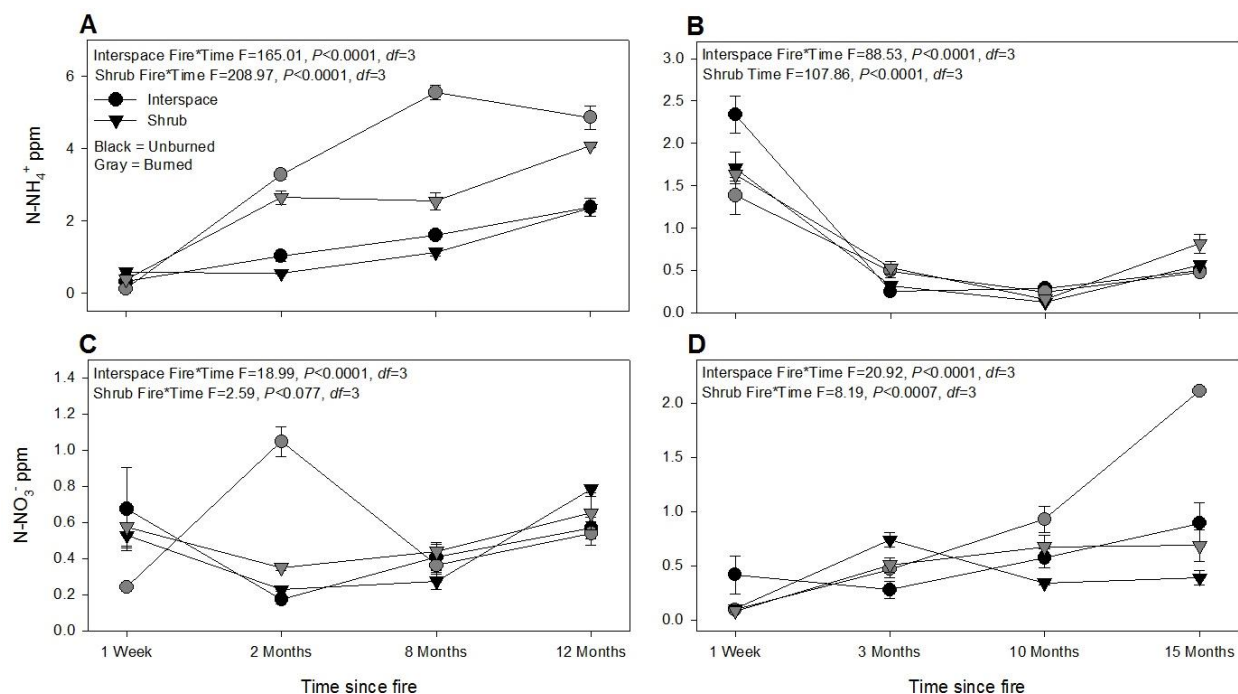
Figure 9. Soil $N-NH_4^+$ and $N-NO_3^-$ concentrations in Great Basin (A and C) and Mojave (B and D) biocrusts following fire over ~15 months. $N-NH_4^+$ and $N-NO_3^-$ concentrations are given in ppm and are means ± SEM (*n*=5). Significant differences between burned and unburned soils through time are based on RM-ANOVA comparisons with attending F statistics and P values.
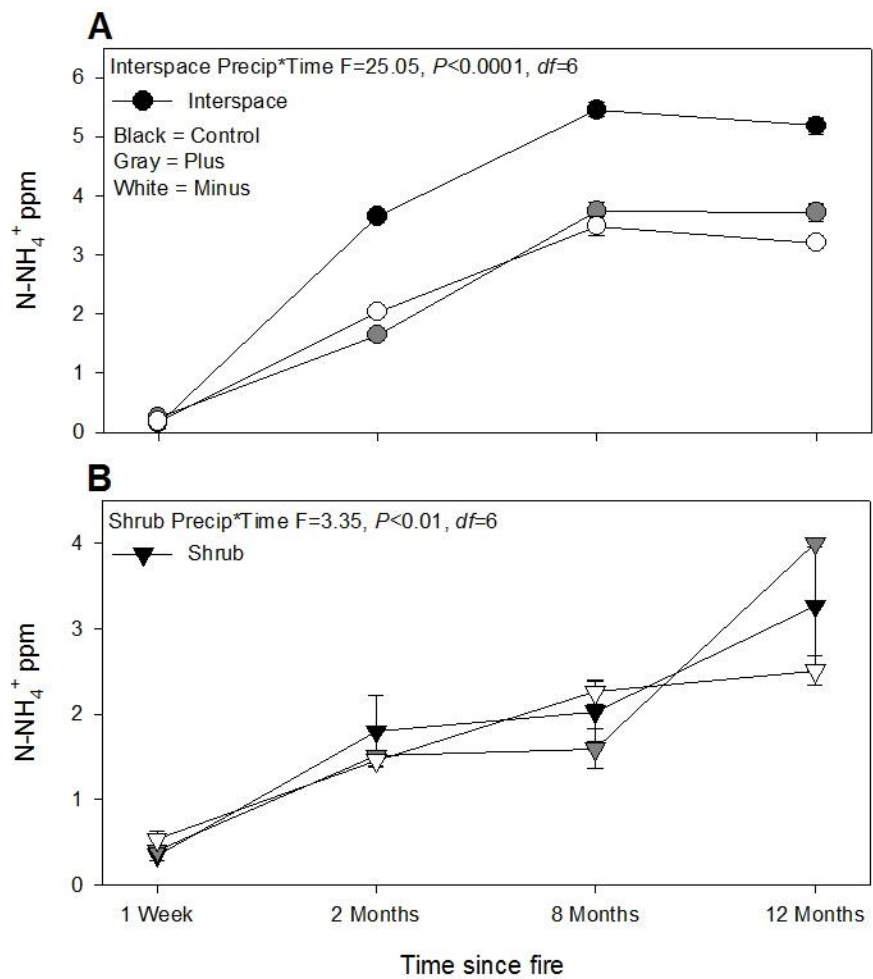
Figure 10. Great Basin interspace (A) and shrub (B) $N-NH_4^+$ concentrations over 12 months following fire. Biocrusts were subjected to three precipitation treatments: ambient precipitation, plus 30% mean annual precipitation, and minus 30% mean annual precipitation. $N-NH_4^+$ concentrations are given in ppm and are means $\pm$ SEM (n=5). Significant differences between treatments through time are based on RM-ANOVA comparisons with attending F statistics and P values.
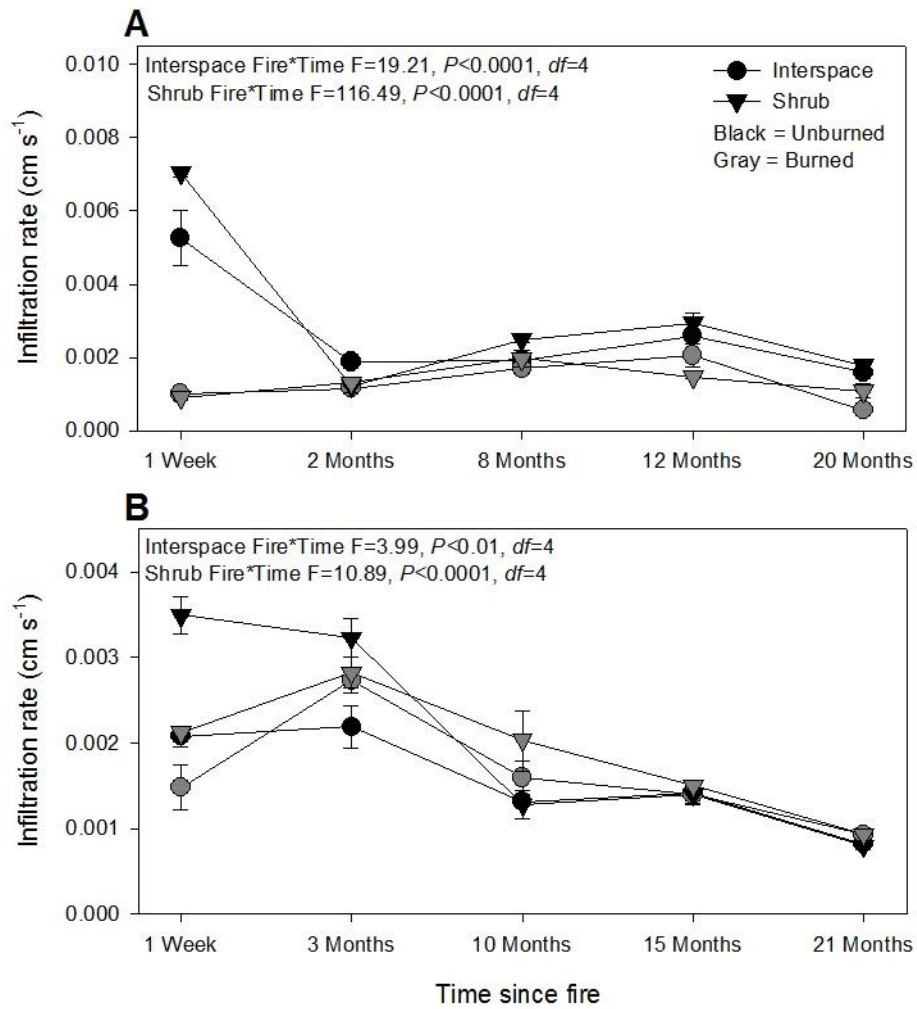
Figure 11. Great Basin (A) and Mojave (B) soil infiltration rates in biocrusts following fire over ~20 months. Infiltration rates (cm s^{-1}) are means ± SEM (*n*=5). Significant differences between burned and unburned soils through time are based on RM-ANOVA comparisons with attending F statistics and P values.
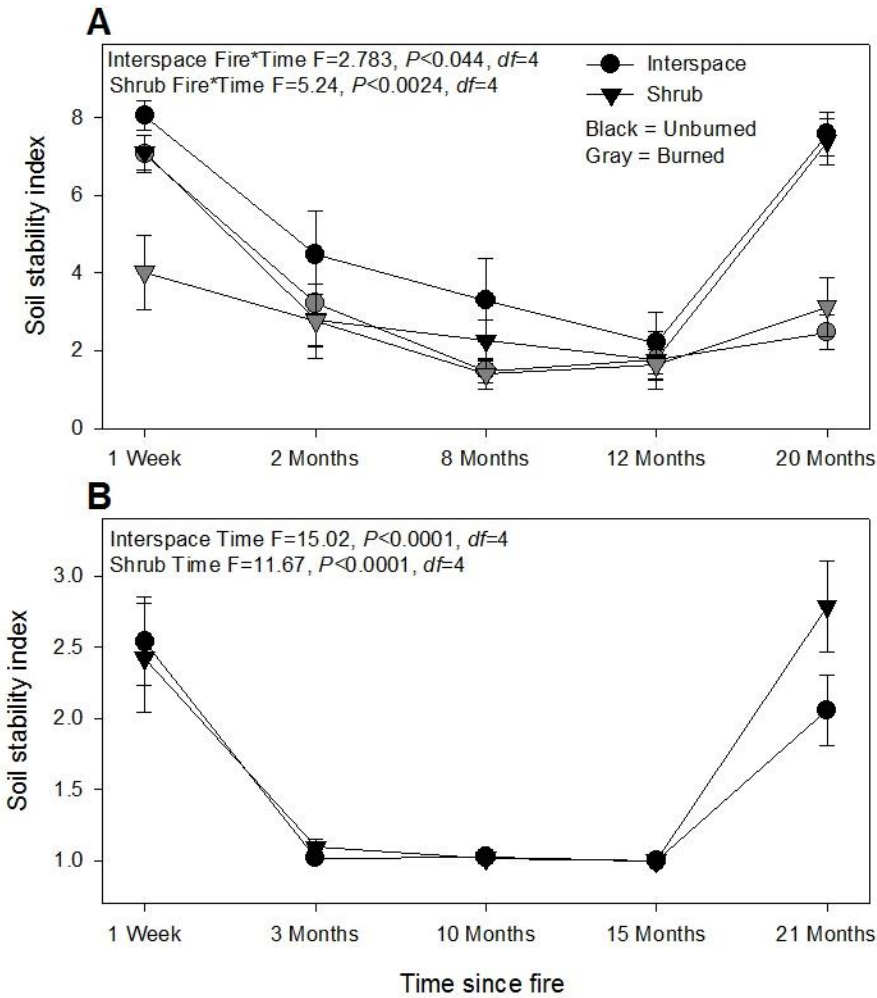
Figure 12. Great Basin (A) and Mojave (B) soil stability over ~20 months following fire. Soil stability is reported as the soil stability index and values are means ± SEM (*n*=5). Significant differences between burned and unburned soils through time are based on RM-ANOVA comparisons with attending F statistics and P values.