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The Microscopic and Macroscopic Response of Biological Soil Crust to Fire

By

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DISSERTATION

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DAVIS

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2022

Dedication

To my parents – without our camping trips and your willingness to let me explore this dissertation would not have been possible.

Acknowledgments

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I would like to dedicate this dissertation to my parents who took me on countless camping trips as a child and let me explore. I would not be the person I am today without you, and without our trip to Arches National Park, I wouldn't even know biocrusts existed. I would also like to thank all the people who supported me on this journey and helped me push off the imposter syndrome. Thanks to my wonderful husband, Jason Spar, who was there from the time I applied to graduate school, moved to California for me, and supported me the whole time. Thanks to the 2017 San Diego State ecology cohort: Azeem Rahman, Kylie Curtis, Craig Fisher, Greta Schmidt, Emma Tomaszewski, and Madison Davis – from our study groups to breweries, I always knew I could lean on you. Thanks to the 2018 UC Davis Ecology cohort, you made my experience in Davis unforgettable and enjoyable.

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Looking back on my academic career, several people shaped my path and led me here today. First, Mrs. Zolle (HHS) who helped me get my first research job in high school. Dr. Karen Mock (USU) guided me through research as an undergraduate. And Dr. Fee Busby (USU) was a great advisor and friend and taught me to follow my passions.

There are so many more people who influenced my path to get here but, in an effort, to keep this brief, I will end it here. I appreciate all of you who took the time to read this dedication.

Abstract

Fires are becoming increasingly frequent and more severe across the Western United States and there is a need to understand how all ecological systems respond to this disturbance, including the soil microbial community. Biological soil crusts (biocrusts) house a diverse soil microbial community and are common in drylands and are composed of visible macroscopic constituents (lichens, bryophytes, cyanobacteria biofilms) and a diverse microscopic community. These communities have been historically understudied in California grasslands, which frequently experience both prescribed and wildfires. The purpose of this research is to understand how biocrusts recover after grassland fires by measuring changes in the macroscopic community cover, microscopic community composition, key biocrust ecosystem functions, and understand mechanisms of biocrust recovery.

The first chapter is a meta-analysis of the current understanding of biocrust response to fire. It revealed that overall, fire reduced biocrust cover, particularly cyanobacteria coverr, and demonstrated that over time, lichen, and bryophyte cover gradually recover 200-300 months after the initial burn. The meta-analysis confirmed the gap in our knowledge about the response of biocrusts in California grasslands which is addressed in the subsequent chapter.

The second chapter uses a recently burned grassland on San Clemente Island (SCI) to understand how fire changes biocrust cover in a California coastal grassland. This is the first biocrust study on San Clemente Island and we found that the biocrusts are primarily dominated by cyanobacteria with some lichens and bryophytes. One year after a prescribed fire, biocrust cover surpasses the cover of biocrusts in unburned control plots. Two years after the fire, the total biocrust cover declined but still had greater cover than the controls. I collected biocrust samples from the same SCI sites for my third chapter.

Chapter three uses laboratory measurement and shotgun metagenomics to understand how the microscopic community and the ecosystem function changes after a fire by comparing communities in

paired burned and unburned plots on SCI. My analyses showed that one year after a prescribed fire and six years after a wildfire, the biocrust microbial community is similar between both fire types and the controls. Additionally, photosynthetic biomass, nitrogen fixation, and exopolysaccharide content did not vary between treatments, indicating similar ecosystem function. Although, there were differences in the functional genes present between the wildfire and control samples and difference configurations of the microbial network. There are several reasons for this result. The biocrust microbial community may be similar because in the year(s) between the fire and the time of sampling, the microbes recolonized the area, perhaps from a nearby source population or some of the key biocrust formation microbes could have survived the low-severity grassland fire.

My final chapter addresses the hypothesis that some biocrust microbes can survive a fire and determined how deep soil microbes must live to avoid the heat from the fire. Using a simulated burn in the lab, we cultured microbes from each soil depth up to 10cm and used RNA and DNA sequencing to understand what microbes are present at each soil layer. The results indicate that biocrust microbes are able to grow in culture from 2cm. The microbes that survived in culture and were sequenced span four Cyanobacteria orders, one Alphaproteobacteria order, and two algal orders. Some microbes were only cultured from deeper soil depths suggesting a low level of thermotolerance or the ability to be motile and survive in deeper soil depths, while others were able to grow and survive in the top few centimeters where the heat from the fire was concentrated.

The coalition of these four chapters adds more insight into the complex community interactions of biocrusts in California grasslands, improves our understanding of how they recover after fire, and reveals further gaps in our understanding of these important and often overlooked microbial communities.

CHAPTER 1

The fate of biological soil crusts after fire: a meta-analysis

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This chapter is already published.

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Abstract

Fire is a global disturbance that is predicted to increase in frequency and severity in many parts of the world due to climate change. Biological soil crust (biocrust) communities are often overlooked in fire studies despite having a substantial effect on ecological function and the adjacent communities. The goal of this study is to synthesize and analyze existing data elucidating the recovery of biocrust cover following fire at the global-scale and suggest avenues for future research. We performed a meta-analysis of studies from 1984 to 2019 to address the response of biocrust after fire and determine the moderating factors governing their response. Overall, fire reduced biocrust cover by 50% and had a significantly negative effect on biocrusts classified as cyanobacteria or algal dominated. Additionally, as time since fire increased, total biocrust cover increased but this response was modulated by biocrust type indicating compliance with traditional biocrust successional models. However, there was significant unexplained heterogeneity within the meta- analysis. This reflects a critical need for more studies specifically addressing the effect of fire on biocrust communities as they are an ecosystem engineer in drylands around the world. We suggest more thorough characterization of biocrust organisms through field and laboratory studies to understand the mechanisms of biocrust response to fire. Additionally,

research is needed across a broader geographic range to represent the known distribution of biocrust communities, particularly as fires increase in severity and scope.

Introduction

Disturbances, such as fire, change the community structure and diversity of an ecosystem at all scales (Sousa 1984). Fires are highly heterogeneous across both spatial and temporal scales which makes their effect on ecosystems difficult to generalize (Turner et al. 1989). As fires are becoming increasingly destructive and ubiquitous globally, their occurrence has been met with an increase in scientific and public concern over the complex, potentially deleterious interactions between fire and ecological communities, particularly since fires are shifting from their historic averages, increasing in frequency andseverity, and fire effects are often unpredictable (Stephens 2005, Westerling et al. 2006, Marlon et al. 2008, Pausas and Keeley 2009). Fires affect all components of the ecological community from the macro-fauna, flora, and soil dwelling organisms.

Several studies have assessed how fires impact micro-fauna and soil microbes in fire-prone ecosystems (Pressler et al. 2019). Soil microorganisms are relatively fire resistant (Pressler et al. 2019) but may enter a dormant state to avoid thephysiological toll of the fire, which can inhibit critical biogeochemical activities that may otherwise occur (Lennon and Jones 2011, Wang et al. 2015). The amount of heat transferred into the soil and the duration of heating have varying impacts on the community depending on the soil depth, meaning the most at-risk soil microbial communities reside at the soil surface. The extreme heat from the fire may result in instantaneous and widespread mortality on the soil surface while organisms deeper in the soil may experience alterations in various properties in their microhabitat but survive in the near term (DeBano 2000, Hart et al. 2005, Cairney and Bastias 2007).

In dryland ecosystems, biological soil crusts (biocrusts) serve as the biogeochemical interface between the soil surface and the belowground soil community and are directly exposed to the heat of the fire. Biocrusts are a unique assemblage of micro and macro organisms located directly on the soil surface often adjacent or under fuels (Belnap and Eldridge 2001, Belnap et al. 2001, Hilty et al. 2004). Despite the growing body of knowledge demonstrating their role as ecosystem engineers, biocrusts are often neglected in studies assessing the effect of fire on dryland ecosystems, an issue not only systematicof biocrusts but belowground communities in general (Zaitsev et al. 2016). Disturbed biocrusts lose their ability to inhibit wind and water erosion (Eldridge and Leys 2003, Rodríguez-Caballero et al. 2015), modulate water infiltration and soil water content (Belnap 2006, Chamizo et al. 2012b), and fix atmospheric nitrogen and carbon (Belnap 2002, Morillas and Gallardo 2015). Changes to or loss of biocrust cover, can thus result in a loss of ecosystem function at larger scales (Belnap 2002, 2006, Barger et al. 2006, Chamizo et al. 2012a).

Given the diversity of organisms that reside in biocrusts (generally referred to as “biocrust types”), different biocrust assemblages may have different responses to fire. Biocrust communities are composed of two broad groups of organisms: the macroscopic components and the microscopic components. Macroscopic components of biocrusts are primarily lichens andbryophytes, including mosses and liverworts, and are characteristic of well-developed, late successional biocrusts. These complex communities often necessitate decades to recover from disturbance, including heat damage from fire (Johansen et al. 1984, Belnap et al. 2003, Root et al. 2017). The microscopic components are the microorganisms living in the bio-crusts on the uppermost millimeters of the soil surface (Belnap et al. 2003), such as cyanobacteria and algae. Cyanobacteria and algae are the early colonizers of biocrusts and may have swifter recovery times after fire (Büdel et al. 2016). Some cyanobacteria are also motile and can move up and down the soil profile to avoid UV stress (Belnap et al. 2008).Recolonization of fire-impacted communities can occur with the transfer of inoculum suspended

in air from unburned, intact soils supporting biocrust communities nearby or the colonization and growth of surviving organisms (e.g., those existingdeeper in the soil); however, undisturbed soils capable of serving as sources may not exist while biocrust organisms occupying surficial niches may be completely extirpated (Choudoir et al. 2018, Dastrup et al. 2018).

There are several variables that may influence how biocrusts respond to fire. Since fire disrupts the successional process, biocrust type may be a significant moderator of biocrust response. Early successional species such as cyanobacteria, algae, or ruderal mosses may be more resilient to fire than later successional constituents (Calabria et al. 2016, Weber et al. 2016, Grover et al. 2019). In line with the successional processes, time since fire (TSF) may also modulate biocrust response. Biocrustcover and TSF may have a positive relationship since biocrusts generally increase in cover as the time since disturbance increases, although this relationship is often nonlinear and depends on other biotic and abiotic factors (Belnap et al. 2001, Weber et al. 2016). Abiotic factors such as climate and substrate type can determine what types of organisms live within the biocrust and the overall biocrust abundance on the landscape (Bowker and Belnap 2008, Veste et al. 2011, Concostrina-Zubiri et al. 2014). Fire type (e.g., wildfire versus prescribed fire) and the fire regime may also affect the response of biocrusts to fire. Fires vary in their severity which produces heterogeneity and may allow some biocrust organisms to recover swiftly after a fire, while those that experience greater fire severity may have a slower recovery time. Similar patterns are observed for above-ground and belowground communities (Neary et al. 1999, González-De Vega et al. 2016).

Previous work summarizes the current knowledge on how biocrusts respond to local disturbance including fire (Zaady et al. 2016). However, there is no quantitative consensus on how biocrusts respond to fire, given the variety of biocrust types, the heterogeneity of the ecosystems the biocrusts reside in, and differences in fire severity, frequency, and disturbance history. In order to fill this knowledge gap and elucidate areas of further research, we performed a meta-analysis on the

available literature measuring changes in biocrust communities after fire to determine if there is a global response and understand what factors modulate biocrust response to disturbance. Specifically, we addressed the following objectives: 1)determine the net effect of fire on biocrusts globally, 2) assess the differences in fire response between biocrust types, 3) understand how fire type (e.g. prescribed fire vs wildfire) impacts biocrust cover, and 4) determine how the time since the fire changes the total biocrust cover. Finally, inferring from these results, we provide recommendations for future ecological,experimental, and geographic research on the fire ecology of biocrusts as well as potential implications for dryland management.

Methods

Experimental design

To assess the effect of fire on biocrust communities, we performed a meta-analysis using the literature compiled in theWeb of Science Core Collection database (Fig. 1). In December of 2019, we performed a search for title, abstract and keyword for terms in the Web of Science Core Collection across all years (1900 - 2019). Specifically, we search for keywords and theirplurals such as "biological soil crust", "biocrust", "cryptobiotic crust", "cryptogramic crust", "cyanobacterial crust", "lichencrust", "bryophyte crust", and "moss crust". These search terms were combined with the "AND" operator followed by either "fire", "wildfire", "controlled fire", "prescribed fire", "burn", "prescribed burn", or "controlled burn." This analysis only includes papers accessible from the authors' institutions in English. Web of Science returned 81 results, of which 20 matched our criteria for biocrust cover. We specifically chose studies that measured percent cover or proportion cover of biocrusts orany biocrust components living on the soil (i.e., studies documenting % soil moss or lichen cover) with a control. The control may be an adjacent unburned area, pre-fire measurements, or in the case of Eldridge and Bradstock (1994) and Nicholas et al. (2009), the control was set as plots with a long amount of time since the fire, greater than 100 and 24 years respectfully, with burn plots representing

more recently burned fire periods. Studies that did not report the percent cover of biocrusts were not used, nor were studies that did not report standard deviations or standard error. For those studies that included multiple sites,time since fire (TSF), or other treatments, we classified each treatment combination as a distinct "experiment" with its own effect size. Throughout this analysis, peer-reviewed papers are referred to as "studies" while the individual observationswithin those papers are called "experiments." For each experiment we determined the time since fire (in months). For studies that did not report the actual time be-tween the fire and the sampling date, we assumed TSF would be in increments of years (12 months) since fire. For example, ifa study reported a fire in 2015 and sampling in 2017, we assumed the TSF to be 24 months. For studies that reported theseason of the fire and subsequent sampling, we determined TSF using three-month intervals (each season lasts 3 months). Forexample, if a fire that occurred in the fall of 2015 and sampling occurred in the spring of 2017, the TSF would be 15 months.Biocrust type was defined as the functional group of the biocrusts categorized into cyanobacteria/algae, lichen, bryophyte, or unknown, as described in the original papers. Data were extracted directly from tables, published supplementary mate- rials, and from digitized figures using 'Web Plot Digitizer (Rohatgi 2020). Fire type was assigned as either 'wildfire' or 'prescribed' based on the descriptions within the studies. One unpublished study (Palmer et al. *in prep*) was also included in this meta-analysis as it explicitly measured biocrust cover for both fire types. Climate variables including average temperature, average precipitation, average radiation, average wind speed, and aridity from the WorldClim database were matched with corresponding coordinates from the studies (Fick and Hijmans 2017). Three studies, Evangelista et al. (2004), Haubensak et al. (2009), and Johansen et al. (1984), did not include coordinates of thestudy location. Coordinate systems used in each study were not published, therefore all coordinates were plotted using the WGS1984 coordinate projection. We also used the LandFire map layer to determine the fire regimes for experiments that occurred in the United States and had specific coordinates listed in the study (*LANDFIRE: Fire Regime*

Groups 2013). The fireregimes are categorical variables that range from Fire Regime Group I to Fire Regime Group V. Group I experiences less thanthirty-five years between fires and fires are typically low to mixed severity. Group II also has a fire return interval of less than35 years but is characterized as having stand replacing fires. Group III have a thirty-five to two hundred years fire return interval with low and mixed severity fires. Group IV is characterized by having thirty-five to two-hundred-year fire returnintervals with a stand replacing fire. And finally, Group V fires have a fire return interval greater than two hundred years withfires of any severity.

Statistical analysis

To understand the relative importance of the moderators and their effect on burned biocrust cover, we performed a boosted regression tree (BRT) analysis on all the variables except 'Study ID' using the 'gbm.step' function in the gbm and dismo packages as described in Elith and Leathwick (2017). This and all subsequent analyses were performed using R studio version 1.2.1335. Potential interactions between moderators were also explored using the 'gbm.interaction' function (Elith and Leathwick 2017). We used the root mean standard error (RMSE), mean actual error (MAE) and the coefficient of determination (R-sq) to assess the accuracy of the BRT.

For each comparison between burned and unburned plots, we calculated the effect size of the response variable (percent cover) using mean values. The effect size is the log response ratio: ln ($X_{burn}/X_{control}$). A negative effect size indicates the percent cover of biocrusts was greater in the control (unburned) plots compared to the burned plots suggesting that fire reduced the cover of biocrusts. The magnitude of the effect size indicates the degree to which the response variable was affected by the fire. We log transformed the response ratio to create a more normally distributed variable that is equallyaffected by both the control and burned group means (Hedges et al., 1999). Based on the calculation of the effect size, experiments that had zero biocrust cover

in the burned plots and positive percent cover of biocrust cover in the control plotsresulted in a null effect size. This occurred for 48 experiments from Aanderud et al. (2019), 28 from Calabria et al. (2016), eight from Dettweiler-Robinson et al. (2013), five from Hilty et al. (2004), four from Bowker et al. (2004), and one from Johansen et al. (1984). Because we were unable to calculate an effect size from these experiments, they were omitted from the analysis.

To determine the overall effect of fire on biocrust cover, we performed a random effect meta-regression model using the'metafor' package (Viechtbauer 2010) with restricted maximum likelihood. We performed the Egger's Regression Test toassess publication bias.

Using all the moderators and interactions determined from the BRT model, we created a full model with study ID as a random effect using the 'rma.mv' function that was used for model selection. Model selection was used by comparing the corrected Akaike information criterion (AICc) scores using the package 'MuMIn' (Barton´ 2020). Biocrust type, fire type, and TSF were required to be in the model to test our hypotheses. The best model had the lowest AICc score. As a post-hoc test, for each moderator included in the best model, we used a Wald-Type test, using the "anova.rma" function in 'metafor,' to determine the extent to which that individual variable influences biocrust cover. We then performed separate meta- regressions for each significant moderator and performed the same post-hoc tests. We used results from our meta- analysis to identify gaps in our knowledge and propose future avenues of research to further our understanding of these interactions.

Results

Summary of experiments

We obtained 237 useable experiments from 20 unique studies found in the database search and one unpublished study (Table 1). Nineteen studies used the Burn-Control method where some plots were burned, others were not burned, and thetwo treatments were compared. Johansson and Reich

(2005) used a pre and post fire method, where the same plots were measured before and after the fire. Huffman et al. (2013) included both types of methods. Thirty-one percent (n = 74) of the experiments used either the line intercept or point intercept methods to record percent cover of biocrusts while the remaining 69%(n=163) used plots ranging from 0.25 to 2 m^2 to measure percent cover. The studies span 1984-2019 with 86% (n=203) of the experiments occurring in the continental United States, 13% were performed in Australia (n=30) and 1% (n=4) from theSouth Island of New Zealand. Of the individual experiments performed in the United States, Washington accounted for 30% ofthe studies (n=70), followed by Utah (n=58), Oregon (n=23), Idaho (n=20), California (n=15), New Mexico (n=7), Arizona (n=4), Minnesota (n=3), and Nevada (n=2). It is worth noting the lack of papers from all other countries other thanthe United States, Australia, and New Zealand (Fig. 2). Of the experiments included, 77 experiments were performed in grasslands, 150 in shrublands, eight were in deserts, and one was characterized as mixed. Most of the experiments (n=143) tested the effects of wildfire, 93 tested prescribed fire, and one study did not characterize fire type. The minimum time since fire (TSF) was 0, indicating measurements were taken immediately after the burn while the maximum TSF was 420 months. This analysis included four groups of biocrust types: bryophytes (n=66), cyanobacteria/algae (n=25), lichen (n =118), and unknown (n =28). All five fire regime groups were represented in this dataset. Thirteen experiments were categorized as having frequent and low severity fire, fire regime group I. Seven and eight were categorized as fire regime II and III, respectively. Most of the studies (n=143) were categorized as having infrequent and stand replacing fire, fire regime group IV. Thirty-one experiments were categorized as fire regime group V. To account for the low sample size for fire regime groups II and III, we grouped the fire regimes by the fire return interval. Regimes I and II were classified as “short”, Regime III and IV were classified as “medium.” and Regime V was classified as “long.” This “fire return interval” variable was included in thesubsequent analyses.

Effect of Moderating Variables on biocrust cover

The BRT model determined location, biocrust type, TSF, and average temperature to be important moderators for burned biocrust cover (Fig. 3A). It also indicated interactions between biocrust type, TSF, location, temperature, radiation, aridity, andwater vapor. Experiment type and ecosystem type were dropped in the simplified BRT model. Overall, the BRT accurately represented the data based on the RMSE, MAE, and R^2 (Table 2).

The random effects model indicates fire reduces overall biocrust cover by 50% (Figs. 3B and 4). The Egger's Regression testfor biocrust cover showed no publication bias (Table 2). However, there was significant unexplained heterogeneity(Q 76,736, $p < 0.0001$). Based on the AICc scores, the best meta-regression model included average temperature, biocrust type, TSF, fire type, location, the interaction between biocrust type and location, and the interaction between biocrust type and TSF as fixed effects and study ID as a random effect (Table 3). We then performed separate meta-regressions on these moderators to determine the extent to which they impact biocrust cover.

In the meta-regression performed to identify the effect of biocrust type, only cyanobacteria/algae biocrusts were negatively affected by fire. Bryophyte, lichen, and unknown biocrusts had a neutral response to fire (Fig. 4A). However, there is significant heterogeneity that may be influencing the results (Table 3). Bryophytes from Washington, USA and cyanobacteria/ algae from the Northern Territories, Australia had a significantly negative response to fire, though individual locations did notinfluence biocrust response (Table 3).

TSF prompted a positive response of biocrust cover to fire (Fig. 5). As TSF increased, algae and cyanobacteria cover decreased while lichen, bryophyte, and unknown biocrust cover increased (Fig. 5). In both the TSF and the TSF- biocrust typeinteraction models, there was significant unexplained heterogeneity (Table 3).

Fire type was considered a significant moderator (Table 3), although there was no difference in the

response of biocruststhat experienced prescribed fires or wildfires. Additionally, there was no significant influence location nor average temperature on biocrust cover, although like the other moderating variables, there was a significant amount of residual heterogeneity (Table 3). Much of the residual heterogeneity within these meta-regression models may be driven by the between study heterogeneity which was included as random effect in this analysis (Fig. 4B), though there was no study that had greaterinfluence on the results than the others as indicated by the Egger's publication bias test (Table 2).

Discussion

Our meta-analysis revealed that fire reduced the cover of biocrusts by 50%. However, only cyanobacteria/algae biocrusts had a significantly negative response to fire. There is a large amount of residual heterogeneity within the models and indicatesthese studies and the response to fire is highly variable and noisy. A portion of the residual heterogeneity may be due to the between study variation which was included as a random effect (Fig. 4B). This could be due to differences in the way the researchers measured the biocrust cover, the knowledge of biocrust identification of the researchers, or other variables that are not accounted for in this analysis. Variation between studies is common in meta-analyses and we attempted to minimize that variation by adding moderating variables. Despite this, a significant amount of heterogeneity remains.

A negative response of cyanobacteria and algae to fire is somewhat unexpected. Cyanobacteria are generally considered early biocrust colonizers and recover quickly after a fire (Wang et al. 2009, Büdel et al. 2016, Weber et al. 2016). However, inthis study their cover significantly declined after a fire. This is likely due to the timing of the studies. Since cyanobacteria and algal biocrusts are early successional species, their recovery after fire may be missed if the sampling occurs after other late-successional species colonize the area (Weber et al. 2016, Zaady et al. 2016). Bryophytes also

responded negatively to fire (P=0.06), though not significantly. Although bryophytes are often characterized as being part of late-successional, well- developed biocrusts, some bryophytes are also highly ruderal and recover quickly after a fire. In forest ecosystems, ruderalmoss biocrusts are often the first colonizers (Bowker et al. 2004, Zaady et al. 2016, Grover et al. 2019).

The neutral response of lichen cover to fire was unexpected. Lichens are slow-growing organisms and are often thought to be late-colonizers and highly sensitive to disturbance (Weber et al. 2016), though in the scope of this analysis they did notsignificantly decline in cover. There may be other factors such as biotic and abiotic interactions that promote lichen cover thatwere not accounted for in this analysis. Furthermore, these groupings of biocrust types are broad and may be too general to gauge the true effect of fire on these communities especially given genera within these groupings vary widely in their response to disturbance. Some cyanobacteria, for example, may be disturbance intolerant and would likely not increase incover after a fire (Belnap and Eldridge 2001) and the resilience of lichens and bryophytes may vary depending on the species composition (Belnap and Eldridge 2001, Belnap et al. 2003 p. 2003, Lan et al. 2015, Weber et al. 2016). Although it is valuable to know that, in general, these groups of biocrust organisms respond neutrally to fire, it is equally important to understand how individual species and communities respond. Some of the studies included focused on a particular biocrust type and identified the organisms to the genus or species level. However, this targeted sampling may lead to bias in a meta-analysis since they were classified within the broader group to be compared to other less descriptive studies. For example, if the goal of the study was to quantify the changes in biocrust lichen cover after a fire, a biased sampling of lichens over other biocrust constituents may result. Additionally, if the focus of the study was on plants or another organism or process, and biocrustswere included as a minor experimental component, the biocrust data may lack breadth, which can increase the between study heterogeneity (Fig. 4B). Additionally, biocrust communities are often spatially patchy. Therefore,

measuring percentcover is tricky and prone to human error. Moreover, biocrust communities are often cryptic. Many species are only active aftera rainfall and may be difficult to see during the dormant season (Bowker et al. 2004). Some biocrusts are located under thecanopies of shrubs and trees and thus may be missed in the percent cover estimates that only assess cover in interspaces. Interestingly, there was no effect of fire type on biocrust cover. The neutral response to fire type may be due to the timing of the fires in relation to the period when the biocrusts are active. Perhaps if both wildfires and prescribed fires burned thebiocrusts when they were dormant, they responded similarly. Fires that occur during the growing season have different effects on biocrust function compared to dormant season fires. In New Mexico grasslands, Ford and Johnson (2006) compared nitrogen fixation and chlorophyll-a content, a measure of photosynthetic biomass, in biocrusts between growing season and dormant season wildfires. Dormant season fires led to reduced nitrogen fixation rates and reduced chlorophyll-a content.Growing season fires have less negative impact on biocrusts. Ford and Johnson specifically addressed the effect of wildfires during two seasons while this study emphasized the difference between wildfire and prescribed fires which may differ inseverity. Timing of the fire (i.e., growing season versus non-growing season) was not included in this study but may be animportant moderating variable and requires further research.

Adding more specificity and variables to the “fire type” may reduce the overall residual heterogeneity of the model. Fires produce heterogeneous environments, especially at small scale (Thaxton and Platt 2006, Sankey et al. 2012) and may therefore allow for small refugia from the heat of the fire. Furthermore, biocrust types vary in their surface roughness (Rodríguez-Caballero et al. 2012) creating microsites that may be shaded from the heat of the fire and patches that are more exposed. For now, this is just conjecture as fire severity (i.e., maximum temperature and duration) and surface roughness werenot reported in any of these studies so we cannot quantitatively assess how changes in fire intensity affect biocrust cover and the relationship between fire type.

In this analysis, time since fire (TSF) can be used to look at changes in biocrust cover as succession progresses. As TSF in-creases, we expect the biocrust cover to follow a successional pathway, generally moving from early successional cyanobacteriaand algae to late successional bryophytes and lichens (Weber et al. 2016). We saw this trend reflected in the cover of individual biocrust types (Fig. 5). Early successional biocrust types, algae and cyanobacteria, decreased as TSF increased while the latersuccessional species, lichens and mosses, increased indicating that globally, biocrusts follow the general successional pathway.Despite this pattern with time since fire, the inclusion of the fire return interval did not improve the model. One possible explanation is understanding the difference in scale between the LandFire dataset and the microscopic scale that biocrustsexperience. Many of the experiment coordinates on the LandFire map were near different fire regime groups; a change in the mapping coordinate system may have moved the points into a different fire regime group and different fire return interval.Additionally, we only included the fire regimes from the United State experiments (86%) and did not have any measure of fire regime for the Australia and New Zealand experiments. The LandFire database consists of 30-meter pixels which providesvaluable information about the fire regime on the landscape scale. However, biocrusts in this study were studied on scalesranging from 0.25 m^2 to 2 m^2 and soil biogeochemical properties can exhibit high variability on the millimeter scale depending on the soil moisture and temperature (Wanzek et al. 2018).

Interestingly, although temperature was ranked fourth in relative importance based on the BRT model and its inclusion inthe model reduced the AICc, it was not a significant moderator nor were any other climate variables. However, previous work indicates the type of organisms living in the biocrust and overall biocrust abundance is dependent on climatic variables (Veste et al. 2011, Concostrina-Zubiri et al. 2014). This is another area to explore to understand the heterogeneity of biocrust responses to fire. Perhaps the climate data included in this study was not measuring the appropriate variables to

understand biocrust response. Additionally, like the LandFIRE data, the WorldClim data represents landscape level climate on the scale of1 km^2 and is not indicative of the environment the biocrusts live in.

Another potential variable that may help explain the complexity of these results is the history of the site and under- standing how often fire occurs and what other disturbances came prior. The legacy of disturbances can be seen in the soilmicrobial community and soil properties which may affect how these communities respond to future disturbances (Vacchiano et al. 2014, Fernández-García et al. 2019). This was not included in this meta-analysis however because the site history was not reported in the studies. This should be explored further in the future.

A consequence of fires, smoke, may also be an important variable governing biocrust response. Although as noted in (Bell and Adams (2008), the effect of smoke on soil properties is rarely considered in fire studies. However, wildfire smoke may be important in transporting microorganisms, such as biocrust forming cyanobacteria, to new areas and promoting colonization (Kobziar et al. 2018). This could be an important microbial source for the passive restoration of biocrust communities in the future.

The presence of refugia, such as shrubs, may also help explain the heterogeneous response. Biocrusts are sometimes located under or near shrub cover (Ochoa-Hueso et al. 2011). Shrubs may provide shade and moisture but when burned, may increase biocrust mortality compared to more open habitats. None of the experiments included in this analysis specificallymeasured the effect of shrub or overall plant cover on biocrust response to fire. In the future, connecting these two com- munities may provide insight on how biocrust communities respond and recover to fire and other disturbances.

Furthermore, the nature of this study alone could have led to large amounts of heterogeneity. Although there was nopublication bias based on the Egger's regression test, random

effects meta-analysis inherently gives more weight to smaller studies, thus making it more vulnerable to small-study effects (Moreno et al. 2012).

Based on these results, we know that fire reduces biocrust cover in grasslands and shrublands in the United States, Australia, and New Zealand but given the extent of biocrust cover on every continent and in a variety of ecosystems this analysis reveals little about the global pattern of biocrust response to fire and but rather reveals the large gaps in our knowledge and highlights the need for further research to extend to more countries, continents, and ecosystems, particularly as the threat of more frequent and severe fires increases worldwide. Additionally, it highlights the need for high quality species or genus data for biocrust constituents as well as more data regarding the interactions between fire, biocrust biomass, diversity, and ecosystem processes. We need more information about the organisms within in these biocrust types and their specific resistance and resilience strategies. Currently, biocrust research is integrating soil ecology, plant ecology, and microbial ecology to understand the complex dynamics within these systems. These methods and interdisciplinary approaches can be applied to understand the biocrust disturbance ecology.

Given the gaps that this analysis has identified, we composed a table of recommendations for future research (Table 4). Wegrouped these recommendations into ecological, experimental, and geographic. The ecological recommendations suggestareas to expand our knowledge about interactions between biocrusts and biotic and abiotic environments. The experimental recommendations focus on areas where we need to understand the mechanisms of how biocrusts function in the environment. The geographical recommendations suggest geographical areas where biocrust research needs to be expanded to encompass the range of ecosystems where they are found. All these recommendations are in the context of fire ecology although they can be expanded to include all disturbances impacting biocrusts.

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Tables and Figures

Table 1 - Experiment Descriptions. Peer-reviewed journal articles included in the meta-analysis and the moderating variables included in the study.

Study	Location	Fire Type	TSF (months)	Fire Regime	Plot Size (m^2)	Biocrust Type	Successional State
Aanderud et al. 2019	Utah	Prescribed	0, 12	IV	Line Intercept	cyanobacteria, lichen, moss	early, late
Bowker et al. 2004	Oregon	Wildfire	11	IV	Point Intercept	lichen, moss	late
Calabria et al. 2016	Washington	Wildfire	7,17,19	V	0.1	lichen, moss, liverwort	late
(Davies and Dean 2019)	Oregon	Prescribed	24,48,72	I	0.3721	NA	unknown
Dettweiler-Robinson et al. 2013	Washington	Wildfire	132	IV	2	lichen, moss, liverwort, mixed	late

Eldridge and Bradstock 1994	New South Wales	Prescribed	12,36,48,84,156,192,216,420	NA	0.25	algae, lichen, moss	early, late
Evangelista et al. 2004	Utah	Wildfire	24,36,48	NA	1	NA	unknown
Ford and Johnson 2006	New Mexico	Prescribed	3,6,15,18,30	II	Line Intercept	cyanobacteria	early
Haubensak et al. 2009	Nevada	Wildfire	60	NA	1	NA	unknown
Hilty et al. 2004	Idaho	Wildfire	120	IV	Line Intercept	lichen, moss, mixed	late
Huffman et al. 2013	Arizona	Prescribed	60	III	0.625	NA	unknown
Johansson and Reich 2005	Minnesota	Prescribed	0.5	I	0.25	lichen	late
Johansen et al. 1984	Utah	Wildfire	60	NA	0.25	lichen, moss	late
Michel et al. 2013	South Island, NZ	Prescribed	108	NA	0.25	moss	late
Nicholas et al. 2009	Northern Territory	Wildfire	48,264	NA	Line Intercept	NA	unknown

Palmer et al. *in prep*	California	Prescribed	11,24	IV	1	cyanobacteria, lichen, moss	early, late
Palmer et al. *in prep*	California	Wildfire	72	IV	1	cyanobacteria, lichen, moss	early, late
Root et al. 2017	Idaho	Wildfire	144,180,192	III	1	lichen	late
Root et al. 2017	Idaho	Prescribed	192	III	1	lichen	late
Schulten 1985	Iowa	NA	17	I	0.25	moss	late
Strong et al. 2010	Northern Territory	Wildfire	72	NA	0.625	cyanobacteria	early
Warren et al. 2015	Utah	Prescribed	0.5,13,22	IV	0.25	lichen, moss	late

Table 2 - Summary Statistics. Summary of the statistics for the boosted regression tree model (BRT), random effects model (RE), and the Egger's regression test.

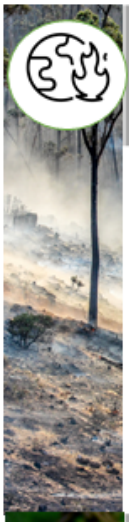
BRT Model			**RE Model**					**Egger's Test**	
RMSE	**Rsq**	**MAE**	**Estimate**	**s.e.**	**CI lower**	**CI upper**	**p-val**	**z-val**	**p-val**

6.09	0.84	3.27	-0.70	0.27	-1.22	1.17	0.01	-0.65	0.52

Table 3 - Significant Moderating Variables. The QE statistics is the test for residual heterogeneity. A p-value less than 0.05 indicates significant residual heterogeneity within the mode. The QM (chi-square statistic) and p-value indicates whether the moderating variables included in the model were significant predictors of the effect size.

Model	**QE**	**df**	**p-value**	**QM**	**df**	**p-value**
Average Temperature	45113.30	150	<0.0001	2.0017,	1	0.16
Biocrust Type	55830.75	166	<0.0001	12117.38	3	<0.0001
Fire Type	76605.40	167	<0.0001	1751.42	2	<0.0001
Location	36650.67	157	<0.0001	10.4639	0.58	0.58
Location:Biocrust Type	50142.51	165	<0.0001	16198.05	4	<0.0001
TSF	74162.30	168	<0.0001	2557.99	1	<0.0001
TSF:Biocrust Type	45360.30	162	<0.0001	16401.60	7	<0.0001

Table 4 - Future research needs**.** Critical research gaps for describing, mapping, and predicting biocrust-fire interactions.



Ecological Research Gaps in Biocrust-Fire Interactions

Determine

- How smoke associated with fire may impact biocrusts
- If fire related disturbance impact biocrusts in the interspaces versus under plant communities differently
- If there are fire adaptations within biocrust communities

Experimental Research Gaps in Biocrust-Fire Interactions

Quantify

- Morphological measurements (e.g. cover) and physiological differences (e.g. photosynthesis) for each macro constituent within the experimental design
- Impacts on individual biocrust species in controlled, laboratory setting
- Appropriates scales to assess biocrust-fire relationships
- The fire severity, history, and frequency when possible
- Biocrust fire response in predictive ecosystem models

Geographical Research Gaps in Biocrust-Fire Interactions

Increase

- Fire studies in ecosystems where biocrusts are present such as desert, alpine, arctic, and temperate ecosystems
- Number of studies in countries that are underrepresented in the dataset, and are, or, likely to be impacted by a changing fire regime such as those in Europe, Asia, Africa, and South America

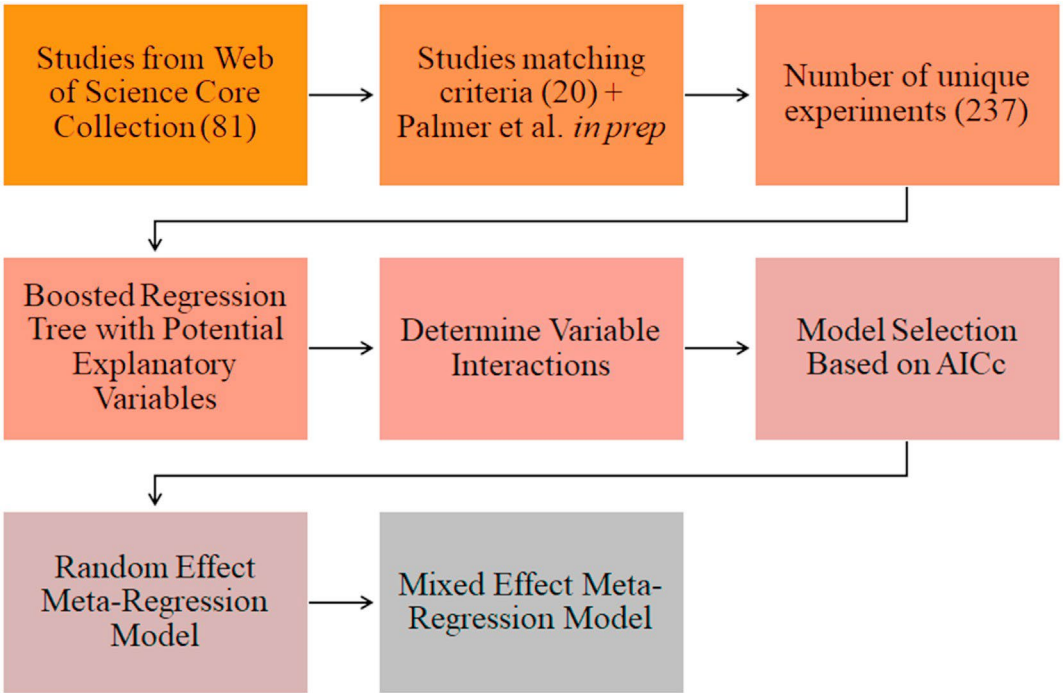


Figure 1 - Flow chart depicting the data collection. A schematic of the data preparation and analysis process from the initial Web of Science database search to the total number of unique experiments analyzed. Numbers in the parentheses indicate the total number of studies or unique experiments included in each step. Unique experiments are defined as those including an empirical comparison of observations between a burn and control plot for a subset of the data (e.g., comparison between burned and control plots of cyanobacteria biocrust). This can result in multiple 'unique experiments' for an individual study.

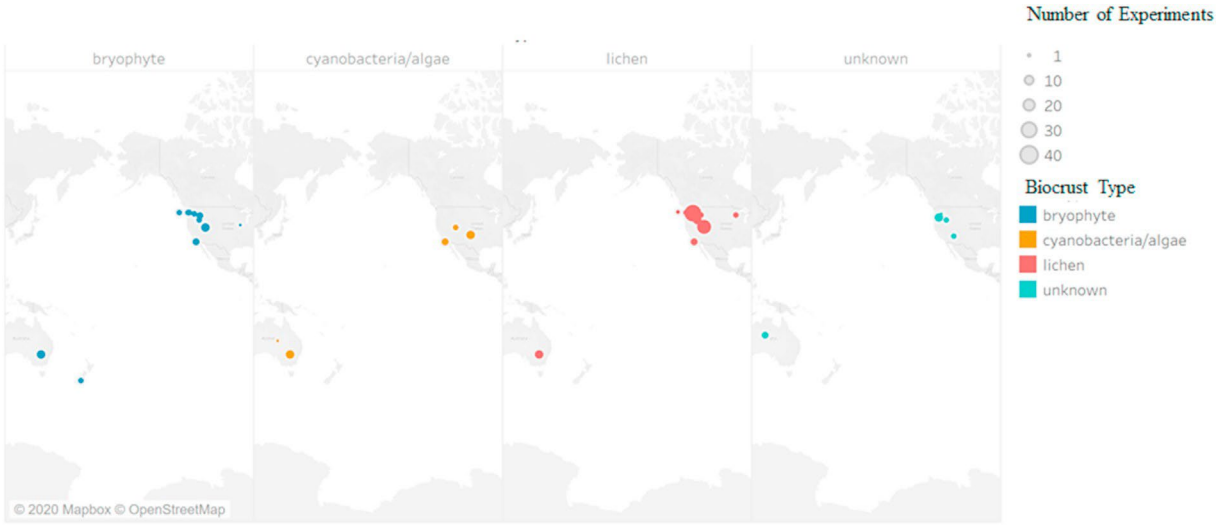


Figure 2 - Experiment Map. Locations of all experiments included in this study categorized by biocrust type (color). Global regions not shown lack sufficient or appropriate data. The larger the circle, the more experiments performed in that location. Figure was made using Tableau ("Tableau (version. 9.1)" 2016). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

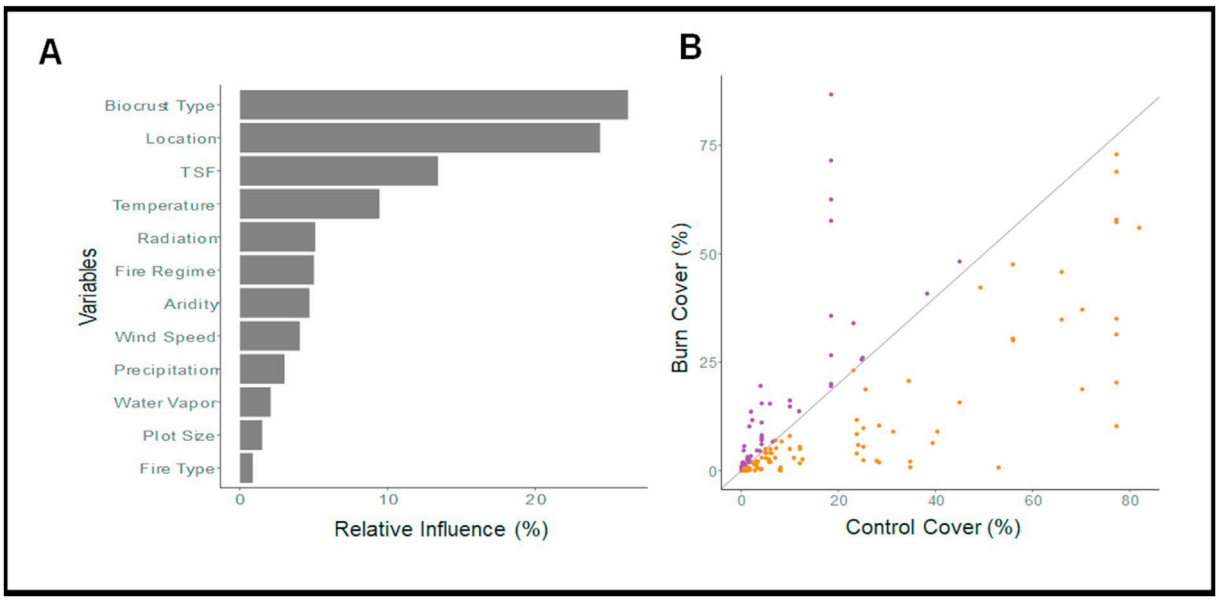


Figure 3- Relationship between treatments and fire. A) The relative influence of the moderating variables from the simplified gradient boosted regression tree model. B) L'Abbé plot showing biocrust cover data, both burn and control for all experiments. Any points above the line indicate experiments where the burnt plots had greater cover than the control plots (purple). Any points below the line indicate experiments where the control outperformed the treatment plots (orange).

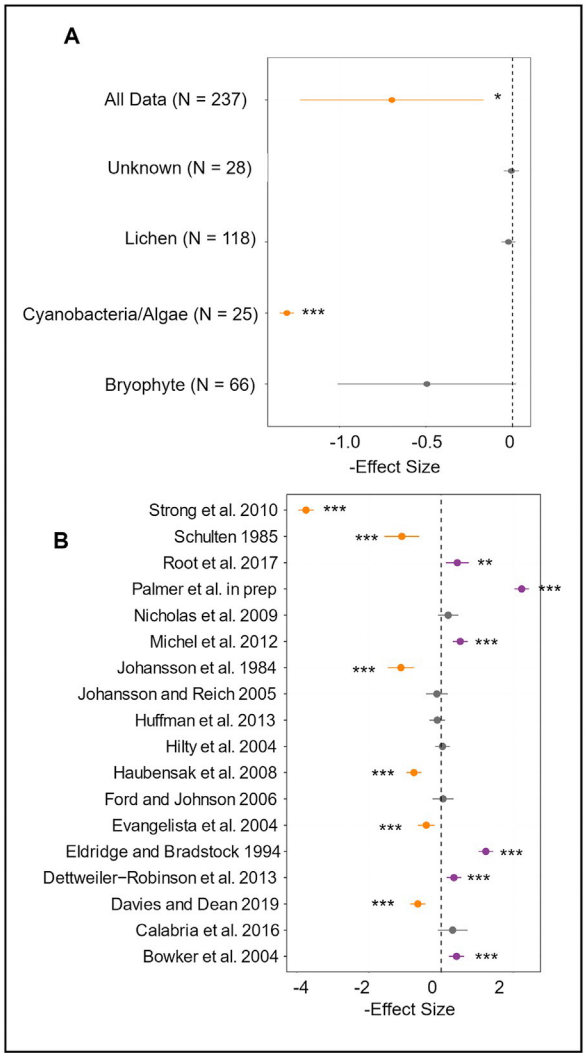


Figure 4- Effect of Moderating Variables. Data in purple indicate the biocrust cover had a significant positive response to fire ($P < 0.05$). Data in orange indicate a significantly negative response to fire. Data in gray indicate no response to fire ($P < 0.05$). A) The effect size and 95% confidence intervals of all the data and each ofthe biocrust types. 'All' is the total response based on all the data. The dashed line represents an effect size of zero, indicating no difference between the cover ofburn and control plots. B) The effect sizes for all the studies which were included as a random effect in all the analyses. Asterisks represent significant re- lationships based on meta-regression modeling (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). (For interpretation of the references to color in this figure legend, the readeris referred to the Web version of this article.)

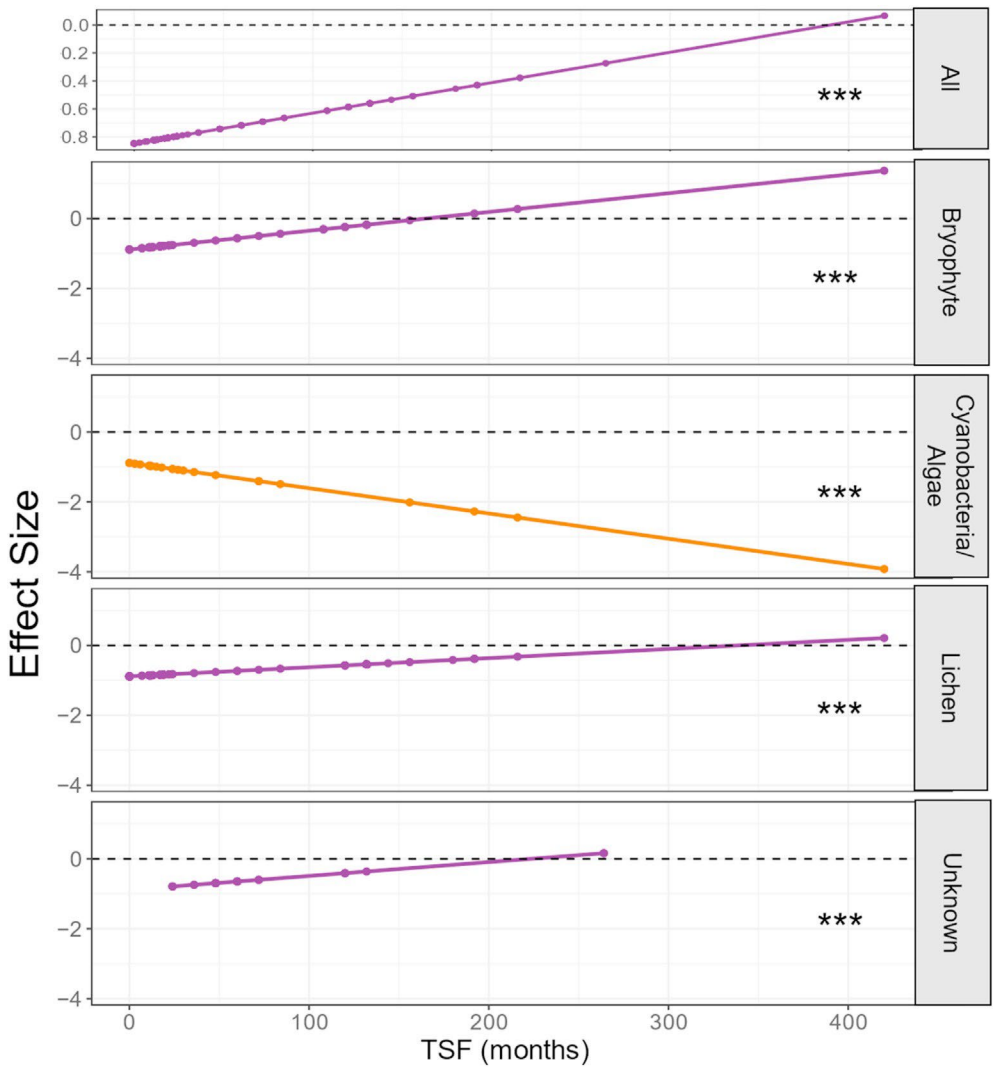


Figure 5- Relationship between biocrust cover and time since fire. Positive (purple) and negative (orange) relationships between time since fire (TSF) in months and the effect size by biocrust type. Asterisks represent significant relationships based on meta-regression modeling (***P < 0.001). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

CHAPTER 2

Biocrust cover is greater than unburned controls one year after a prescribed fire

Brianne Palmer, Dawn Lawson, David Lipson

Abstract

Prescribed fires are often used as a management tool in grasslands to promote the growth of desired plant species. These fires also impact other ecological communities where they occur. One ecological community that is often overlooked regarding fire is biological soil crusts (biocrusts). Biocrusts contain an assemblage of cyanobacteria, lichens, and bryophytes living on the soil surface and are important for nutrient cycling and soil stability. Here, we used prescribed burns in a California coastal grassland on San Clemente Island (SCI) to understand how fire impacts biocrust cover. Two sites were burned in a prescribed fire in 2012 and then again in 2017 and one site was burned in a wildfire in 2012 and prescribed fire in 2017. We measured the percent cover of biocrusts in 2018 and 2019. Additionally, we assessed the role of precipitation in moderating biocrust cover. On SCI, the biocrusts are cyanobacteria dominated in both the burned and unburned areas. In 2018, one year after the last prescribed fire, the burned plots had more biocrust cover than the controls. Although in 2019, the percent cover declined, it was still greater than the controls. The abundance of biocrusts in the burned plots suggests a level of recovery after the fire or the ability of biocrusts to withstand a grassland fire. It indicates that biocrusts may play a role in the ecosystem trajectory after a fire.

Introduction

Fire is a common ecological disturbance that affects all communities within an ecosystem (Pausas and Keeley 2009). Due to changes in land use (Andersson et al. 2004) and climate change (Marlon et al. 2008), fires are increasing in frequency and severity globally (Westerling et al. 2006). In California, fires will likely burn more frequently and with greater intensity (Fried et al. 2004). This is of

particular importance since California's coastal grasslands are home to a variety of rare and ecologically important species (U.S. Navy 2013). These grasslands experience both wildfire and prescribed fires and a variety of studies have assessed the effect of fires on the community composition (Parsons and Stohlgren 1989, DiTomaso et al. 2001, 2006, D'antonio and Meyerson 2002). The response of ecological communities to fire is dependent on the climate (Batllori et al. 2013). On the California Channel Islands, plant populations are impacted by the timing of and quantity of precipitation from winter storms, temperature, and coastal fog (Levine et al. 2011, Clemesha et al. 2021).

There is, however, a key ecological community missing from much of the literature regarding community response to fire in grasslands – biological soil crusts (biocrusts). Biocrusts are communities of microorganisms, lichens, and bryophytes living on the soil surface (Belnap et al. 2003). The recovery of biocrust communities after an ecological disturbance range from less than a year to many centuries to reach the pre-disturbance cover and community composition (Weber et al. 2016). Cyanobacteria are generally the first organisms to recolonize after a disturbance, followed by larger organisms such as lichens and bryophytes (Belnap et al. 2003, Büdel et al. 2016). These communities are important for soil stability (Eldridge and Leys 2003, Rodríguez-Caballero et al. 2015), fixing atmospheric nitrogen and carbon (Belnap 2002, Morillas and Gallardo 2015), and influence the germination and establishment of plants (Havrilla et al. 2019).

Previous studies have shown that fire can reduce overall biocrust cover (Schulten 1985, Evangelista et al. 2004, Haubensak et al. 2009, Strong et al. 2010, Davies and Dean 2019) while others show a positive (Eldridge and Bradstock 1994, Bowker et al. 2004, Michel et al. 2013, Dettweiler-Robinson et al. 2013a) or neutral (Hilty et al. 2004, Johansson and Reich 2005, Nicholas et al. 2009, Huffman et al. 2013, Calabria et al. 2016) effect of fire on biocrust cover. The influence of fire on biocrust cover depends on the biocrust type, time since fire, and site location (Palmer et al. 2020). The relationship between biocrust cover and fire has not been assessed in California coastal grasslands.

To expand on the previous research, we studied the effect of fire on biocrust cover within a California coastal grassland by comparing biocrust cover between burned and unburned plots. We hypothesized that fire would reduce the cover of biocrusts, particularly biocrusts dominated by lichens and bryophytes since they often colonize later than cyanobacteria (Weber et al. 2016) and have more distinct biomass above the surface. We predict that cyanobacteria-dominated biocrusts will be more abundant in the burned plots as they are often early successional colonizers. This study improves our understanding of how biocrust communities within California coastal grasslands respond to fire and provides insights on management strategies to improve fire recovery.

Methods

This study occurred on San Clemente Island (SCI) (32°53'58.76"N, 118°29'24.46"W), part of the Channel Island chain in Southern California (Figure 1). Biocrusts have been documented on the California Channel Islands previously (Rosentreter and Belnap 2001). The climate is Mediterranean, with most of the annual precipitation falling between November and April (Figure 1). Natural fires do not occur often and there is no evidence of historical Indigenous burning (US Department of the Navy 2001). However, a wildfire did occur on SCI in May 2012 and prescribed burns have been used to facilitate the growth of native plants (Keeley and Brennan 2015). Further information on the recent prescribed fire and wildfire history can be found in Keeley and Brennan (2015) and Keeley et al. (in prep).

Plot Design and Fire History

This study focuses on three sites on SCI that experienced recent prescribed fires. Perennial grasslands east (PGE) and perennial grasslands west (PGW) were established by the United States Geological Survey (USGS) to study the impact of prescribed fire on native vegetation on SCI (Keeley and Brennan 2015). They were burned in a prescribed fire in 2012 and 2017. Ranch Canyon (RC) was burned

in a wildfire in 2012. The wildfire occurred in the spring of 2012 and 100% of the vegetation in each plot was burned. Ten unburned plots were established outside of the wildfire perimeter in 2012. The RC plots were established in an area with similar soil and vegetation to PGE and PGW and were also included in the Keeley and Brennan (2015) study. In 2017, the ten $10m^2$ plots within the wildfire perimeter established in 2012 were burned in separate prescribed fires at the same time as the plots in PGE and PGW. All sites are located at a similar elevation and slope on soils derived from volcanic substrates, primarily alfisols and vertisols (United States. Navy 2008, Keeley and Brennan 2015). The prescribed burns in 2012 and 2017 consumed most of the vegetation in the plots with an average burn area of 95%. A description of the fires is documented in Keeley and Brennan (2015) and Keeley et al. *in prep.* For the prescribed burns, within each site, ten plots were burned in the spring of 2012 and 2017. Each plot was $10m^2$ and the boundaries were treated with the fire retardant Phos Check (NWCG Fire Equipment Working Team 1991). Ten unburned plots were established near the burned plots. The result is twenty plots across two sites burned in prescribed fires in 2012 and 2017, referred to as 'prescribed fire plots', and ten plots in one site which were burned in a wildfire in 2012 then prescribed fire in 2017, referred to as 'wildfire/prescribed plots.'

Biocrust Cover Sampling

Each $10m^2$ plot was divided into quadrats and within each quadrat, we used a Daubenmire frame to estimate the percent cover of three biocrust types: cyanobacteria dominated, lichen dominated, or bryophyte dominated (Figure 1) for a total of four cover measurements within each plot. The biocrust cover was measured in the springs of 2018 and 2019.

Statistical Analyses

All analyses were performed in R version 4.02. The biocrust cover was analyzed using a generalized mixed linear model with the lme4 package (Bates et al. 2015). We examined the effect of treatment (control, prescribed fire, prescribed/wildfire) on biocrust cover for each year (2018, 2019). We also included the annual precipitation for 2017, 2018, and 2019. We log-transformed biocrust cover to meet the assumptions of the generalized linear model. The plot was included as a random effect and significance was assessed using Tukey post-hoc tests using the emmeans package (Lenth et al. 2018). We ran separate models, replacing "Cover" with total biocrust, cyanobacteria, lichen, and bryophyte.

Results

Biocrust Cover was Greater in Burned Plots Compared to Controls

Overall, there was greater biocrust cover in both the prescribed burn and wildfire/prescribed burn plots compared to the unburned plots ($P<0.0001$, Table 1, Figure 3). Across all sites – both burned and unburned-- the majority of the biocrust cover was dominated by cyanobacteria. There was more cyanobacterial cover in the prescribed and wildfire/prescribed plots compared to the unburned plots. Overall lichen cover was greater in the prescribed burn plots compared to the control plots. For bryophytes, the cover was greater in the prescribed, and wildfire/prescribed compared to the control. Furthermore, PGE had more lichens than PGW. There was more precipitation in 2019 compared to 2018 and the annual precipitation during the year that we sampled was a significant predictor of biocrust cover for all the biocrust types (Figure 1, Table 2).

Discussion

Here we show the ability of the biocrust cover in burned plots to recover to and even surpass, levels of biocrust cover in unburned plots. In both the burned and unburned plots, the dominant biocrust type was cyanobacteria. We expected to see an increase in lichen and bryophyte cover as

cyanobacteria decreased, which was true in both the unburned and burned plots. However, surprisingly, there was greater lichen and bryophyte cover in the burned plots which is contrary to our hypotheses.

Evidence of biocrust recovery or resilience to fire

The biocrusts in these sites either recovered quickly after the fire or were unaffected by the fire. Fire-resistant or resilient biocrusts are not unheard of. In Australian eucalypt shrublands, frequent fire intervals, such as those simulated in this study (5 years between fires), can maintain low biocrust cover and create an environment for the early successional biocrust organisms (Eldridge and Bradstock 1994). The frequency of the fires in this study – two fires within five years – may have selected for a biocrust community in the plots that are accustomed to a frequent fire interval and may recover faster after a fire or are able with withstand the fire. Similarly, in the Columbia Basin, recent fires did not change the overall cover of biocrust cover but there was higher species loss and species turnover (Dettweiler-Robinson et al. 2013b). In the Palouse prairies, there were more species in unburned areas but a negligible difference in biocrust cover between the unburned areas and those burned in a wildfire (Bowker et al. 2004). These sites have some similarities to San Clemente Island. Like the eucalypt shrublands, SCI experiences a Mediterranean climate and like the grasslands and prairies in Eastern Oregon, the SCI sites were dominated by grass species and likely experience lower severity fire than those in woodier systems.

Additionally, the biocrust cover may be higher in the burned plots because the biocrusts that were present before the fire survived then quickly expanded to monopolize on the newly available bare soil. Both the wildfire and the prescribed fires were characteristic of grassland fires with low fuel loads and were both considered low-severity fires (Johansen 2001). Previous work has documented biocrusts surviving these types of fires (Johansen 2001, Bowker et al. 2004). Biocrust cyanobacteria, for instance, have exopolysaccharides (EPS) that can bind the soil particles together but also allow the cyanobacteria

to survive under extreme conditions including high temperatures up to 100°C (Mager 2010, Kimura et al. 2017b). Fire temperatures 2cm below the surface of a low severity fire may reach 88ºC despite the upwards of 250ºC temperatures on the surface (DeBano et al. 1979). Therefore, biocrust microbes living the in deeper soil layers (~ 2cm deep) may be able to survive the fire and establish a biocrust, as the EPS also allows them to move through the soil (Mager and Thomas 2011). Additionally, though mosses were not dominant in this environment, moss crusts – often called fire moss—is a common early colonizer after fire (Grover et al. 2019, Silva et al. 2019). Similar to cyanobacteria, this is due to the wide diversity of spores and the ability to establish on unstable soils (Esposito et al. 1999). Due to this ability to recolonize soil after a fire, biocrust cyanobacteria and mosses are used to restore post-fire ecosystems (Muñoz-Rojas et al. 2021).

Plant competition as a driver of biocrust cover

Eventually, the bare space colonized by biocrusts may become less available as plants re-establish after the fire. We found that biocrust cover decreased as the time since fire increased. This has been documented previously with cyanobacterial dominated biocrusts (Palmer et al. 2020). This could be due to reduced competition with plants after the fire, then increased competition as the plants reestablish leading to lower biocrust cover in subsequent years. Cyanobacteria are able to quickly recolonize if there is a nearby undisturbed source location, like in this experiment, because they can readily aerosolize and establish on a patch of bare ground (Warren et al. 2019). After a fire, there is ample bare ground and no vegetation. In this experiment, the fire consumed 95-100% of the existing vegetation (Keeley and Brennan 2015, Keeley et al in prep). Therefore, without the shade from plants, the biocrusts can maximize the amount of light they receive for photosynthesis. In a mesocosm experiment, Dettweiler-Robinson et al. found that biocrust chlorophyll content increased with the removal of plants and found that plants and biocrusts can directly compete with each other for

resources (Dettweiler-Robinson et al. 2018). As plants become dominant in the ecosystem, as they are in the unburned plots, biocrust cover declines.

Precipitation as a Driver for Biocrust Cover

Another driver of biocrust cover is annual precipitation. On SCI in 2018, the average precipitation was 71.51 and 66.71mm at the two SCI weather stations. This is in stark contrast with 2019, when the SCI weather stations recorded 354.7 and 435.75mm of precipitation (Figure 2). Like plants, biocrusts benefit from additional moisture which can improve their overall growth (Fick et al. 2020). This may be why we saw an increase in lichens and bryophytes in 2019. In this sense, the cover of more complex biocrust types like lichens and bryophytes may act as an indicator of the year-to-year variability within the sites. In this ecosystem, the cover of cyanobacteria-dominated biocrusts may be related to the post-fire dynamics like competition with plants while the cover of lichens and bryophytes is positively correlated with the annual precipitation.

Disturbance history may influence both burned and unburned biocrust

Another variable that may influence both the types of biocrust present and their percent cover is the disturbance history. The control plots in this study were also dominated by cyanobacteria with scattered lichens and bryophytes indicating that that the biocrusts that reestablished after the burn are similar to the existing community composition, perhaps because even the unburned plots has a history of disturbance which can influence the type of biocrusts that establish (Weber et al. 2016). This is supported by the complex ecological history of the island. SCI is an active military base with frequent man-made disturbances and the island was historically grazed by feral goats until the 1990s. This study occurred nearly thirty years after the goats left the island (Keegan et al. 1994), but legacy effects of that

disturbance may linger in the biocrust community in both the burned and unburned plots (Concostrina-Zubiri et al. 2014, Condon et al. 2020).

Conclusion

Under the right conditions and with the right biocrust species, biocrusts can recover from or tolerate low severity fires. In this experiment, the low-severity fire, absence of plants, presence of a nearby source population with organisms that can survive on disturbed soils, and the increase in precipitation the following year may have helped the biocrusts recover. However, these hypotheses need to be explicitly tested. Overall, in this coastal grassland on San Clemente Island, fire initially increases the amount of biocrust and is primarily dominated by cyanobacteria. This is an important aspect of ecosystem recovery after the fire to understand since biocrusts are directly and indirectly involved in several ecosystem processes such as nutrient cycling and soil stability. Furthermore, this study – the first of its kind on San Clemente Island – shows that the effect of fire on biocrusts is related to the ecosystem and thus more work in a variety of habitats where fire and biocrusts cooccur is needed to understand the relationships between them.

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Tables and Figures

Table 1: Results of the Tukey post-hoc test for each type of biocrust cover. Data were log-transformed to meet the model assumptions. Rx means the plot was burned in a prescribed fire in PGE and PGW. Wild/rx means that it was burned in a prescribed fire and a wildfire in RC. Annual precipitation is the precipitation of the year that the plots were sampled. Bold values indicate where the p-value is less than 0.05.

		Log(total biocrust +1)			Log(cyanobacteria + 1)			Log(Lichen + 1)			Log(bryophyte + 1)		
		Estimate	s.e	p-value	Estimate	s.e	p-value	Estimate	s.e	p-value	Estimate	s.e	p-value
Fire Type	Rx – none	0.61	0.048	**<0.001**	1.26	0.11	**<0.001**	0.23	0.68	**0.0016**	0.53	0.076	**<0.001**
	Rx/wild – none	0.72	0.085	**<0.001**	1.11	0.18	**<0.001**	0.24	0.11	0.074	0.76	0.12	**<0.001**
	Rx/wild-rx	0.11	0.85	0.38	-0.14	0.21	0.76	0.0018	0.13	0.99	0.23	0.14	0.22
Site	PGW-PGE	-0.093	0.075	0.43	-0.047	0.19	0.96	-0.013	0.11	0.99	-0.28	0.094	**0.0076**
	RC-PGE	-0.15	0.087	0.199	0.047	0.22	0.97	-0.12	0.14	0.65	-0.088	0.12	0.75
	RC-PGW	-0.056	0.087	0.79	0.095	0.22	0.90	-0.11	0.14	0.70	0.19	0.12	0.26
Annual Precipitation		-0.099	0.040	**0.013**	-0.72	0.091	**<0.001**	0.24	0.057	**<0.001**	0.46	0.64	**<0.001**

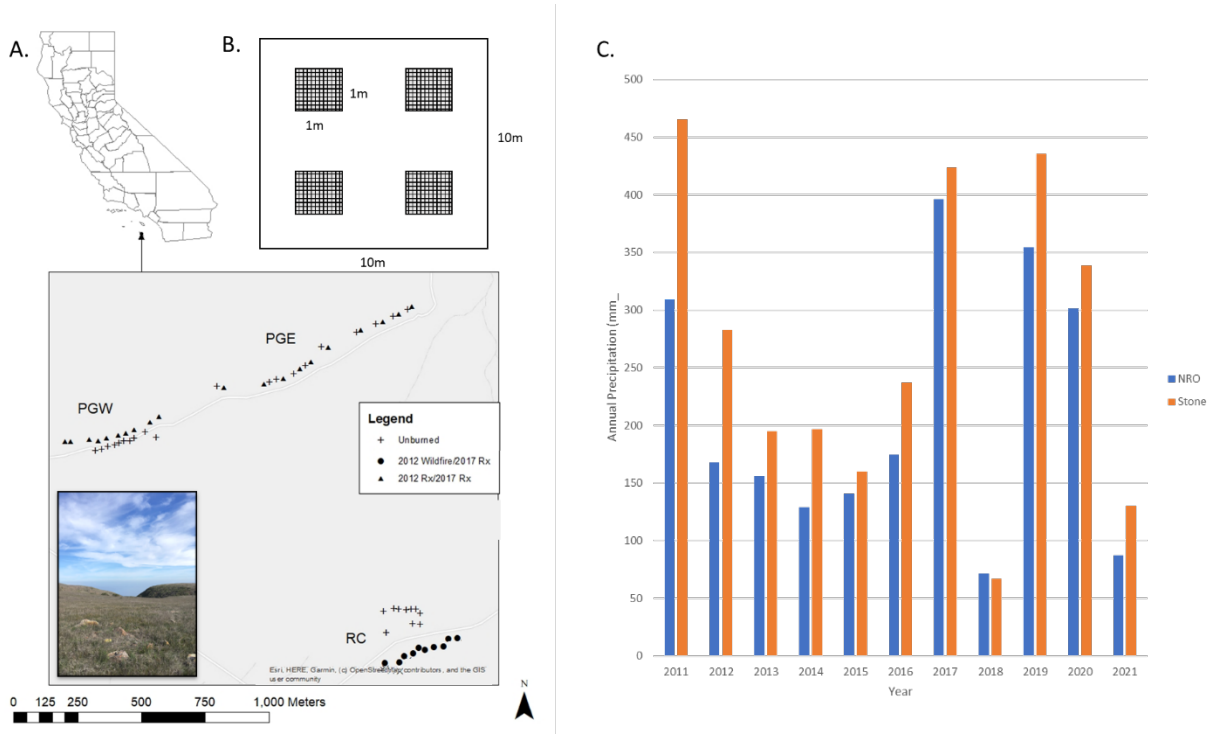

Figure 1: A) The location of the biocrust sampling sites on San Clemente Island. PGE and PGW were burned in two prescribed fires in 2012 and 2017. RC was burned in a wildfire in 2012 and a prescribed fire in 2017. The + denotes controls, ● are burned plots in RC, and ▲ are burned plots in PGE and PGW. The burns only occurred within a 10m² plot B) A layout of the plot design, Biocrust, and plant cover was measured in four quadrats within a 10m² plot. C) Annual precipitation (mm) from two locations on SCI from 2011 to 2021

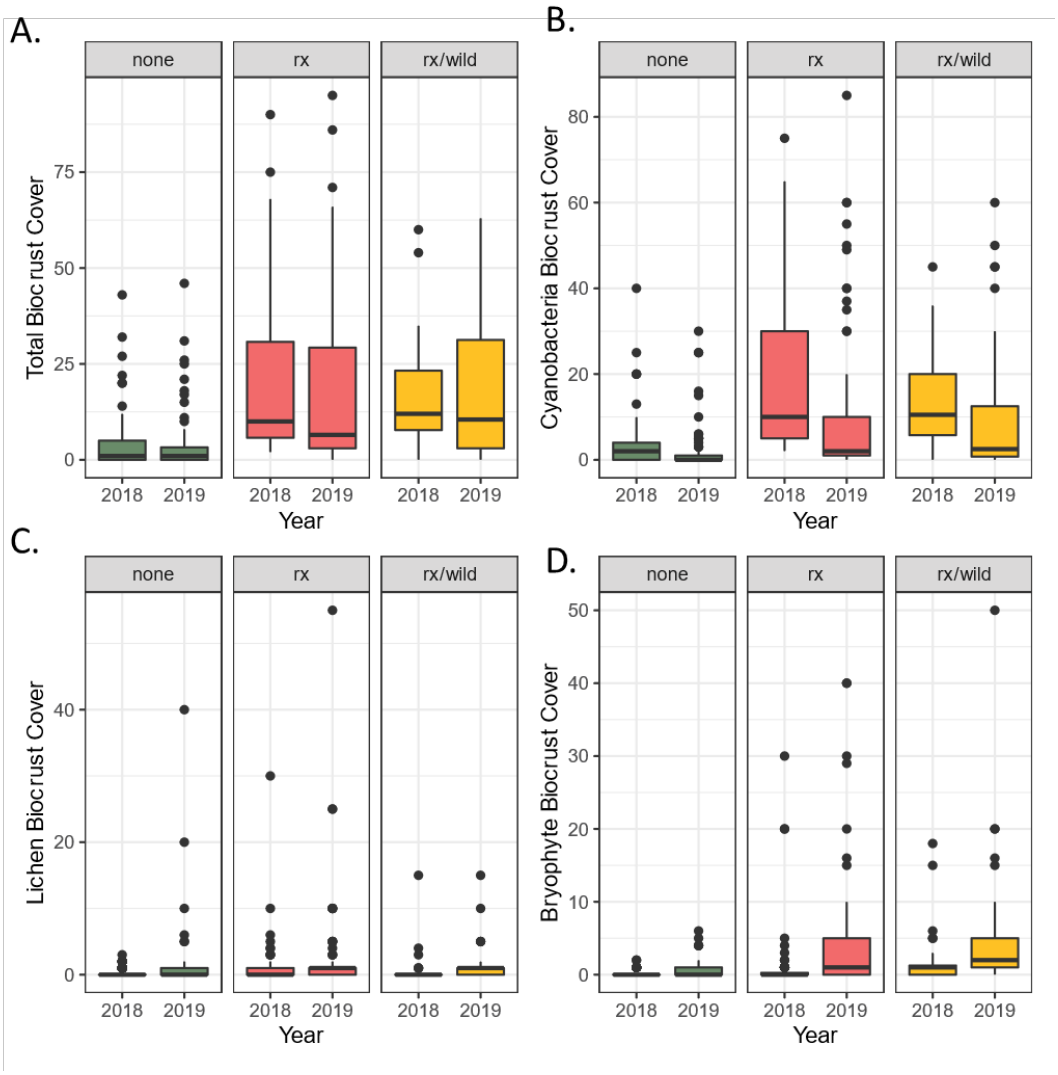

Figure 2: The percent cover of total biocrust (A), cyanobacterial dominated (B), lichen dominated (C), and bryophyte dominated (D) for each site and year. "none" includes all plots that were not burned in either fire. "rx" includes all the plots burned in the prescribed fires in 2012 and 2017. "rx/wild" includes all plots that were burned in the 2012 wildfire and subsequent 2017 prescribed fire.

CHAPTER 3

Years after a fire, biocrust microbial communities remain similar to unburned communities in a coastal grassland

This chapter is under review in *Microbial Ecology*.

Palmer, B., D.A. Lipson, D. Lawson. *In review.* Years after a fire, biocrust microbial communities remain similar to unburned communities in a coastal grassland. Microbial Ecology.

Abstract

Microbial communities are integral for ecosystem processes and the taxonomic composition and functions may be altered by a disturbance such as fire. Biocrusts are communities composed of macroscopic and microscopic organisms and are important for a variety of ecosystem functions where they occur, such as nutrient cycling and erosion control. We sought to understand if the biocrust community composition and function were altered one year after a prescribed fire and six years after a wildfire in a coastal California grassland. We used shotgun metagenomic sequencing, and laboratory-based measurements of photosynthetic biomass, exopolysaccharide production related to soil stability, and nitrogen fixation. Based on the shotgun metagenomic sequencing, there were no differences in the community composition between unburned samples and the samples burned in the prescribed fire and wildfire. Additionally, there were no measured differences in total photosynthetic biomass, exopolysaccharide production, and nitrogen fixation. However, the wildfire and their respective unburned samples had different functions based on the gene annotations. We compiled one Actinobacteria metagenome-assembled genome from the shotgun sequences which had genes for oxidative and heat stress tolerance. These results suggest that the biocrust community on San Clemente Island can reach a community composition and function similar to the unburned biocrusts within a year after a prescribed burn and six years after a wildfire. However, legacy effects of the wildfire may present

themselves in the differences between functional gene sequences. Due to their ability to match the undisturbed community composition and function within years and without intervention, future restoration work should consider the biocrusts in their restoration plans as they may provide valuable ecosystem functions after a disturbance.

Introduction

Microbial communities are an integral part of ecosystems worldwide with important influences on ecosystem and community structure and function. Because they are cryptic and difficult to study our understanding of their contributions is limited. Though growing advances in methodology have reduced costs and made next-generation sequencing methods more accessible allowing us to apply sequencing methods to understand the complex interactions between microbial communities and their environment.

Wildland fire regimes are an important driver of ecosystem processes and are changing due to climate change (Westerling et al. 2006, Pausas and Keeley 2009). These changes have important implications for ecosystem dynamics and community structure and function (Westerling et al. 2006). Improving our understanding of microbial community response to fire will contribute to the projection of ecosystem effects of climate change and developing ecosystem management strategies. Fire can have indirect influences on the soil microbial community and through this, indirect effects on vascular plants. California coastal grasslands are home to a variety of rare and ecologically important species and experience both wildfire and prescribed fires.

Fire can change nutrient inputs, soil temperature, and soil moisture (Hart et al. 2005). Fire can also directly kill soil microbes by heating the soil surface (Hart et al. 2005). Microbial groups differ in their fire tolerance, with fungi being the most sensitive to heat from a fire followed by nitrite oxidizers, and other heterotrophic bacteria (Dunn et al. 1985).

Fire can alter the microbial community by changing both the taxa and the functional genes (D'Ascoli et al. 2005, Prendergast-Miller et al. 2017, Rodríguez et al. 2017, Lucas-Borja et al. 2019). Often the magnitude of the effect depends on the severity of the fire (Pourreza et al. 2014). The effects of fire can be seen immediately after a burn and may result in an increase in *Acidiobacteria*, *Proteobacteria, Actinobacteria,* and *Firmicutes* (Prendergast-Miller et al. 2017, Rodríguez et al. 2017, Lucas-Borja et al. 2019). In a Mediterranean ecosystem in Spain, soils burned in a wildfire had a higher diversity of Bacteria and Archaea but there was no difference in the microbial communities at the genus level (Rodríguez et al. 2017). Fire can also alter the soil properties and change microhabitats, thus changing the microbial community composition(Hamman et al. 2007, Pereira et al. 2019). A metagenomic analysis of burned rhizosphere soil showed an increase in the number of nitrogen fixation genes and a reduction in the number of sequences for denitrification genes after a fire (Cobo-Díaz et al. 2015), however relating total number of sequences to ecological function requires direct measurement (Bier et al. 2015, Hall et al. 2018). The time since fire is an important factor in considering the changes in the microbial community. The community composition changes immediately after the fire (Lucas-Borja et al. 2019) and it may take several years for the community structure to become similar to undisturbed sites (Dangi et al. 2010). In a sagebrush-grassland ecosystem, microbial communities were determined to be similar to the mature soil within seven years after a fire (Dangi et al. 2010). Often, the most severe impacts of fire occurs within the top few cm of the soil surface (DeBano et al. 1979). Therefore, fire studies should emphasize the effect of fire on the soil microorganisms on the soil surface, including biological soil crusts (biocrusts).

Biocrusts are communities of microorganisms, lichens, and bryophytes bound to the soil surface and are directly exposed to fires (Belnap et al. 2003). These communities are important for soil stability, nitrogen fixation, and photosynthesis (Elbert et al. 2012, Rodríguez-Caballero et al. 2015). Previous research has emphasized the recovery of biocrusts after fire and the successional trajectory of the

microbial community and functions. The recovery of biocrust communities after an ecological disturbance ranges from less than a year to many centuries (Weber et al. 2016), depending on the type of disturbance. Fire, has a varying effect on biocrusts but it is estimated range of biocrust recovery after fire is less than five years to fifteen years, often depending on the biocrust type (Hawkes and Flechtner 2002, Hilty et al. 2004, Palmer et al. 2020). Cyanobacteria are generally the first organisms to recolonize after a disturbance, followed by larger organisms such as lichens and bryophytes (Büdel et al. 2016). Ecological functions, like photosynthesis, interactions with vascular plants, soil stability, and nitrogen fixation by biocrusts also change with biocrust age due to changing community composition (Langhans et al. 2009, Dojani et al. 2011, Havrilla et al. 2019, Chock et al. 2019). For example, the abundance of photoautotrophic organisms may decline (Zhang et al. 2018). Additionally, biocrust communities differ in their taxa and function depending on the biocrust type or successional stage (Li et al. 2020). A comparative metagenomic study in from the Tengger Desert, China found that *Actinobacteria* was the most abundant phyla in both early and late successional biocrusts but the biocrust types differed in the abundance of other common phyla – *Proteobacteria, Acidobacteria, Cyanobacteria, Planctomycetes,* and *Bacteroidetes* (Li et al. 2020). The genera *Rubrobacter, Microcoleus*, and *Geodermatophilus,* were among the seven genera more abundant in early successional biocrusts. These biocrust communities also differed in their functional composition (Li et al. 2020).

Burned biocrust may experience similar changes in the microbial community composition and be more similar to early successional communities, even if the undisturbed biocrust is at a similar successional state. Recent research in a cold desert of the southwestern United States found that one year after fire biocrusts had fewer Cyanobacteria and were dominated by chemoheterotrophic bacteria and fixed less nitrogen (Aanderud et al. 2019). However, there is little understanding of how biocrust microbial communities respond to fire in grasslands, despite fire being an important ecological disturbance in this ecosystem (Keeley 2000). Previous work has shown that some biocrusts and their

functions can survive low-severity fires (Johansen et al. 1998, Johansen 2001, Bowker et al. 2004). Despite this, fire may ultimately reduce the total biocrust cover depending on the biocrust type and the time since fire (Palmer et al. 2020). However, there is little research on the impact of fire on the biocrust microbial community which may differ from previous work emphasizing biocrust cover and macroscopic community composition.

To expand on the previous research, we studied the effect of prescribed fire and wildfire on biocrust community composition and ecological function within a California coastal grassland. We had two objectives:

1. To determine the effect of fire on biocrust microbial community composition
2. To determine the effect of fire on the biocrust functional gene profile and measured ecological function.

We analyzed the microbial community composition and functions between prescribed fire plots measured 1 year after a fire, wildfire plots measured 6 years after a fire and compared them to unburned control plots. We predicted that there would be a difference in the biocrust microbial community composition between wildfire, prescribed fire, and unburned biocrusts. Since the prescribed fire and wildfire occurred in different years, we predict that the community composition and function in the wildfire plots will be more similar to the controls because it has had a longer time to recover. Six years is an adequate timeframe to observe microbial recovery after a wildfire (Dangi et al. 2010), however biocrust communities have been shown to take five to fifteen years to recover from fire (Hawkes 2004, Hilty et al. 2004). Biocrusts in the wildfire and prescribed fire plots are expected to have fewer genes relating to ecosystem functions such as chlorophyll biosynthesis, nitrogen fixation, and exopolysaccharide biosynthesis. Although these specific gene sequences have not previously been assessed in regard to fire, biocrust functions may be more preserved in undisturbed biocrust. This study

improves our understanding of how biocrust communities within California coastal grasslands respond to fire and provides insights on management strategies to improve fire recovery of grassland ecosystems.

Methods

The study area (32°53'58.76"N, 118°29'24.46"W) was located on San Clemente Island (SCI), the southern-most island of the Channel Island chain of the coast of southern California (Figure 1). Biocrusts are an important component of the Channel Island ecosystem (Flechtner et al. 2008). The vegetation community is a mix of perennial and annual grasslands (Keeley and Brennan 2015). The climate is Mediterranean Dry Summer Subtropical with an average of 20.5 cm of annual rainfall from 2005-2016 with much of the rainfall occurring between November and April (US Department of the Navy 2001) and persistent coastal low clouds and fog in the warm season (Clemesha et al. 2021). Natural fires are rare on the island with only 3 lightning-caused fires in 140 years and there is no evidence of historical Indigenous burning (US Department of the Navy 2001). However, a wildfire did occur on SCI in May 2012 and prescribed burns have been used to facilitate the growth of native plants (Keeley and Brennan 2015). Further information on the recent prescribed fire and wildfire history can be found in Keeley and Brennan (2015) and Keeley et al. (in prep).

Plot Design and Fire History

The grassland soils are clay derived from volcanic substrates, primarily alfisols and vertisols (United States. Navy 2008, Keeley and Brennan 2015). Perennial Grasslands East (PGE) and Perennial Grasslands West (PGW) were burned in prescribed fires in 2012 and 2017 (Keeley and Brennan 2015). The burns consumed most vegetation in the plots, in both years the average area burned exceeded 95% (Keeley et al in prep). Within each site, ten plots were burned, and ten unburned plots were established. The boundaries of the $10m^2$ plots were treated with the fire-retardant Phos Chek. Phos Chek is

composed of monoammonium phosphate and ammonium sulfate and is frequently used as a fire retardant (NWCG Fire Equipment Working Team 1991). Ten plots were burned in the Ranch Canyon (RC) wildfire in May 2012 and 100% of the plots were burned. Ten unburned plots were established outside of the wildfire perimeter (Figure 1)(Keeley and Brennan 2015). Characteristics of grassland fires with low fuel loads, both the prescribed fire and wildfire were determined to be low severity (Johansen 2001). PGE and PGW plots were established by the United States Geological Survey (USGS) to determine the impact of prescribed fire on native vegetation in 2012 and represent the typical soil type and vegetation of SCI grasslands (Keeley and Brennan 2015). Wildfire plots were established in an area (RC) with similar soil and vegetation to PGE and PGW that burned around the same time as the prescribed burns. The wildfire control plots were established on the other side of a road that did not burn in the wildfire. Importantly, there are differences between these treatments beyond the fire type. PGE and PGW each experienced two prescribed fires (2012 and 2017) and RC only had one fire in 2012. Therefore, we will only be comparing each fire type (prescribed and wildfire) against their respective controls to account for differences in the fire history and differences between sites.

Biocrust Sampling

In April 2018 and May 2019, we collected approximately 20 grams of biocrust from each plot by scraping the biocrust off with a sterile pie server and placing each sample into a sterile plastic bag. To avoid sampling the bulk soil, we only collected the first centimeter. We avoided collecting samples growing directly adjacent to large rocks, or under shrubs and cacti. All biocrusts were classified as cyanobacteria-dominated based on visual assessments, though lichen and bryophytes were present in low abundance (Palmer et al. *in prep*). At the time of sampling, cyanobacteria-dominated biocrusts were the most common biocrust type within the plots (Palmer et al. *in prep*). These biocrusts were used for the laboratory analyses.

DNA Extraction and Shotgun Metagenomics

In April 2018, we collected four biocrust samples for DNA extraction from each site and treatment resulting in 24 total samples (Table 1). The biocrust samples were stored in 15 ml polypropylene tubes on ice then moved to the -80° freezer. We extracted DNA using a Qiagen DNeasy PowerSoil Pro DNA extraction kit with an added proteinase K incubation to improve DNA yield (Rubin et al. 2014). Libraries were created by the Genome Center at UC Davis. Initial taxonomic and functional classifications for the shotgun metagenomic data were determined using the MG-RAST pipeline (Meyer et al. 2008). We uploaded the sequences in FASTQ format to MG-RAST and used the default settings which removes sequences with less than 75 bp, artificial replicates, human sequences, and sequences with a Phred score below 15. The average number of base pairs was 83Mbp (standard deviation 37, 170,485) with a total of 5,773,395 sequences and an average of 240,550 sequences per sample. The MG-RAST project can be found here: https://www.mg-rast.org/linkin.cgi?project=mgp89409. Significant matches had a sequence identity of over 15 amino acids and an e-value $<10^{-5}$. Taxonomy was determined using the 'Representative Hit' classification with the RefSeq database as a reference. For functional classification, MG-RAST classifies sequences into subsystems which are grouped into hierarchal categories. 'Functions' is the most detailed category (e.g., Assimilatory nitrate reductase large subunit (EC:1.7.99.4)) to 'Level 1' which is the least detailed category (e.g., Nitrogen Metabolism). 'Level 2' and 'Level 3' are intermediate categories.

We used applications developed for KBase (Arkin et al. 2018) to assemble and annotate metagenome-assembled genomes (MAG). Reads from both the burned and control samples which were quality checked using Fast-QC (Andrews 2017), combined into one read library and trimmed using Trimmomatic (Bolger et al. 2014)to remove the TruSeq3-PE-2 adapters with the default Trimmomatic settings. Trimmed reads were assembled using metaspades with a minimum contig length of 1000 bp. Assemblies were binned using MetaBAT2 (Kang et al. 2019) and the resulting genome quality was

checked with CheckM (Parks et al. 2015). Assemblies were classified using GTDB-tk (Chaumeil et al. 2019)classify and annotated with Rasttk (Brettin et al. 2015). The quality of the MAG was assessed by comparing the completeness and contamination scores. Using HHMER3 within KBase, we extracted the 16S rRNA genes and used them to create a bootstrapped maximum likelihood tree. We used reference sequences from NCBI and MEGA 11 to create the tree (Kumar et al. 2018). The tree was annotated using FigTree (Rambaut 2020).

Laboratory Analyses

For nitrogen fixation, chlorophyl content, and EPS content we used biocrusts collected from each site in 2018 and 2019. For chlorophyll and EPS, we used one sample from each plot (N = 60 per year) and performed the analyses in triplicate. For nitrogen fixation, we used six samples for each site, treatment, and year (N = 36 per year) (Table 1).

Total chlorophyll concentration was determined using the DMSO method (Caesar et al. 2018). All the samples were dried in a drying oven at 60°C for 24 hours and the dry weight was measured, the average dry weight was 3.35g. Then, each sample was sprinkled with distilled water to activate the biocrust organisms. Each biocrust sample was added to a 15ml tube with a spatula tip of $CaCO_3$. We added 6ml of DMSO to each tube and placed it in a Hybridization Incubator with Isotemp Rotisseries (Fisher Scientific) where the tubes were incubated at 65°C for 90 minutes and continuously rotated. Following this, the supernatant was transferred to a separate vial, and 6ml of DMSO was added to the original sample tubes for the second extraction cycle. Both supernatants were pooled and centrifuged for 10 minutes at 3000 x g at 15°C. Then, 100ul of the extractant was loaded into a 96-well plate in triplicate and the absorption was measured on a SpectraMax 190 microplate reader (Molecular Devices,

San Jose, CA) at 648, 665, and 700. Chlorophyll a+b concentrations were calculated using the following equations.

Equation 1 Total Chl a+b amount in the sample

$$Chl\ a+b\ [ug] = [(A_{665} - A_{700}) * 8.02 + (A_{648} - A_{700}) * 20.2] * DF * S$$

Equation 2: Chl a+b based on a dry weight

$$Chl\ a+b[ug *\ g^{-1}] = Chl\ a+b[ug]/DW$$

Where:

A_x = absorbance at wavelength 'x'

DF = dilution factor

S = amount of solvent (ml)

DW = dry weight

Exopolysaccharide (EPS) concentration was measured using the weak acid extraction method (Redmile-Gordon et al. 2014). Five grams of biocrust for each sample were air-dried and added to 100 ml Nalgene bottles containing 50 ml 0.5M H_2SO_4 and autoclaved for 60 minutes at 121°C and 103 KPa. Following this, each sample was centrifuged at 5200 x g for 20 minutes at 4°C. The supernatant was transferred to 50ml tubes which were immediately stored at -80°C. Total EPS content was determined by combining 400 µl of the supernatant, 10 µl of 80% phenol, and 1ml 0.5M sulfuric acid (DuBois et al. 1956). After ten minutes, the plates were read on the microplate reader at 490 nm using 10mg/100 ml and 1mg/100ml glucose as standards.

To determine nitrogen fixation, we placed 0.5 grams of biocrust samples inside desiccators, each sample was approximately 1cm thick. All samples were hydrated with 3ml distilled water 24 hours before incubation. This was enough water to fully saturate the biocrust, without the water pooling. The desiccators were vacuum sealed and ^{15}N was injected using a gas bag attached to a syringe. We added

enough labeled ^{15}N to create an 8.3% ^{15}N atmosphere. The desiccators were placed in a growth chamber at 25°C with a radiance of 20.3µmol m^{-2} s^{-1}, and with 12 hours of light or two weeks (Holst et al. 2009). Samples were then removed from the desiccator and ground up for analysis on the mass spectrometer. For each sample, we also analyzed the baseline ^{15}N from samples that were not exposed to the enriched atmosphere from the same biocrust sample (N=72). Nitrogen fixation was calculated using the following equation:

Equation 3:

$$Y = ((atom\%\ ^{15}N\ exess))/100 * \ (Total\ N * 10^9)/(t\ * 28) * \ 100/(\%^{15}N\ air)$$

Where Y (nmol N*mgDW^{-1}day^{-1}) is the rate of N_2 uptake, atom% ^{15}N excess is the difference between the atom% ^{15}N of the incubated samples and the control samples, total N is the total nitrogen in the incubated samples (g*100 gDw^{-1}), t is the incubation time, and 28 is the relative molecular mass of N_2(g mol^{-1}), and %^{15}N air is the percentage of ^{15}N out of the total amount of N gas in the desiccator (8.3%). Atom% for both incubated and control were calculated using equation 4. δ15N is the stable isotope ratio of ^{15}N: ^{14}N and 0.3363 is the standard for the percent of ^{15}N of all the nitrogen gas in the atmosphere.

Equation 4:

$$atom\%^{15}N = \left(\frac{\delta^{15}N}{1000} + 1\right) * 0.3663$$

Statistical Analyses

All analyses were performed in R version 4.02. Separate generalized mixed linear models were used to look at the results of the lab analyses using the lme4 package (Bates et al. 2015). For all the models we examined the fire type (control in 2017, control in 2012, prescribed, wildfire) and sample year (2018, 2019). The plot was included as a random effect and significance was assessed using Tukey post-hoc tests using the 'emmeans' package (Lenth et al. 2018). We calculated the Shannon-diversity

index and richness of the genus level for all the biocrust metagenomes using the package 'vegan' (Dixon 2003). We compared the differences in these measurements between treatment and site using the 'Anova' function in the 'car' package then used a Tukey post-hoc test (Fox and Weisberg 2018). Additionally, we calculated the Bray-Curtis Dissimilarity distances based on the genus for each community and performed a PERMANOVA using 'vegan' to determine the similarities between community make-up (Dixon 2003). These data were visualized using non-metric multidimensional scaling (NMDS) plots. Differences between gene abundance of specific taxa and functional genes were determined using the 'Anova' function and Tukey post-hoc tests (Parks et al. 2014). We used 'phyloseq' and 'igraph' to create a network of the microbial community (Csardi and Nepusz 2006, McMurdie and Holmes 2013). We performed this analysis for the burned and unburned communities separately. All code can be accessed via GitHub at https://github.com/briannepalmer/San-Clemente-Biocrust-.

Results

The average chlorophyll content, EPS content, and nitrogen fixation rates for the biocrusts were 6.89 (±5.93) $mg \cdot g^{-1}$, 3.79 (±2.24) $mg \cdot g^{-1}$, and 0.15 (±1.85) $nmolN \cdot mg^{-1} \cdot g \cdot h^{-1}$. Overall, chlorophyll content (mg/g) did not differ between the prescribed fire and the adjacent controls nor between the wildfire and the adjacent controls (Table 2, Figure 2). Similarly, there was no difference in the total EPS concentration (mg/g) between the fire types and their corresponding controls (Table 2, Figure 2). Nitrogen fixation also did not vary between the fires and their controls (Table 2, Figure 2).

Microbial Community Composition

The total metagenomic dataset consists of 0.5% Archaea, 2.1% Viruses, 6.3% Eukarya and 91.1% Bacteria. There was no difference in the relative abundance between the controls, prescribed fire, and wildfire treatments for Archaea, Bacteria, or Eukarya and the control plots had a greater mean

proportion of viruses than the wildfire plots (P<0.0001). The most abundant phyla across all samples were Actinobacteria (32.3 %), Proteobacteria (30.1 %), and Cyanobacteria (8.7 %) (Figure 3). *Nostoc* was the most abundant cyanobacteria genus, and the abundance of all cyanobacterial genera did not vary between treatment or site. Nor were there significant differences in the microbial community composition between sites.

Based on the PERMANOVA and subsequent post-hoc analyses, there was no difference in the microbial community composition between the wildfire, prescribed fire, and the control plots (Table 3, Figure 4). Diversity and richness were also similar across treatments (Figure 4). However, seven genera varied in their relative abundance between the prescribed fire and the control, and nine genera varied between the wildfire and the control (Figure 5). The wildfire and control samples also had a different composition of functions based on the Subsystem annotations ($P = 0.025$, $R^2 = 0.223$, Figure 4, Table 3). There was no difference in the number of genes for nitrogen fixation, exopolysaccharide biosynthesis, or chlorophyll biosynthesis between treatments as indicated by the level 2 and level 3 functional gene characterizations from the Subsystems database in MG-RAST. However, twelve function sequences were more abundant in the prescribed fire samples compared to the control and seven were more abundance in the wildfire compared to the control (Figure 5).

Network Analysis

Each treatment (prescribed, wildfire, and the two controls) have different network shapes (Figure 6). The prescribed fire control had the most network connections (154) and the wildfire control had the least (92) (Table 4). Across all networks, Proteobacteria and Actinobacteria had the most connections (Table 4).

Both the prescribed burn, and the associated controls, have three genera of cyanobacteria that are separate from the network—*Anabaena, Cyanthece*, and *Microcoleus*. The eukaryotic Ascomycota

formed a separate network in the control plot (Figure 6A). In the prescribed burn community, the same three cyanobacteria genera formed a separate network. However, Ascomycota, though still primarily connected to each other, have a connection with the larger network (Figure 6B). The wildfire controls also had the same three cyanobacteria genera forming their own network with an addition of *Physcomurella*, in the phylum Steptophyta. This network lacks the large cyanobacterial network shown in the prescribed fire and other control networks (Figure 6C). The wildfire network does not have the network of three isolated cyanobacteria, rather, it is all connected. It still has a group of Ascomycota which are connected to each other, but this is also connected to the larger network (Figure 6D). The cyanobacteria genera *Anabaena* and *Nostoc* are connected to the Ascomycota (Table 4). The prescribed fire network had more connections to Actinobacteria; however, the associated controls had more connections to Ascomycota, Bacteroidetes, Cyanobacteria, and Proteobacteria. The wildfire network also had more connections to Actinobacteria compared to the associated controls and more connections between Ascomycota. The controls associated with the wildfire did not have any connections between Ascomycota but did have more connections to Bacteroidetes, Cyanobacteria, Proteobacteria, and Verucomicrobia (Table 4).

Metagenome Assembled Genome

We found one medium quality MAG that is 77.78% complete with 3.14% contamination within the family Pseudonocardiaceae. The GC content is 66.34%. The Rasttk annotations revealed that genes related to clustering-based subsystems and carbohydrates with other gene groups are necessary for cell function. Interestingly, there were 7 genes for oxidative stress, 10 genes for heat shock, 28 for capsular and extracellular polysaccharides, 10 genes for ammonia assimilation, and 7 for nitrate and nitrite ammonification. Using the 16S genes and reference sequences from NCBI, we placed the MAG in a clade with *Microbispora bispora* (Figure 7).

Discussion

This is the first study to analyze biocrust metagenomes from a coastal grassland and provides insight into how biocrusts recovery from fire which can inform restoration and land management in the future – particularly due to the outsize role biocrusts play in ecosystem function (Belnap 2002, Belnap et al. 2003, Elbert et al. 2012, Rodríguez-Caballero et al. 2015).

Our results provide insight into the microbial community composition and function of biocrusts 1 year after a prescribed fire, 6 years after a wildfire, and from plots that did not experience fire. Interestingly, the community composition and measured functions were similar between both fire types and their respective controls. However, there were some differences in the relative abundance of function sequences between the fires and their controls. Additionally, there were differences in the microbial networks. This has implications for understanding how grassland biocrust communities respond to fire.

After one year, the prescribed fire microbial community is similar to the unburned controls, suggesting a level of recovery one year after the fire or indicating that the fire did not impact the microbial community. Furthermore, seven years after the wildfire the microbial community is similar to the control community, as expected, but there are differences in the relative abundance of functional genes that suggests there may be legacy effects of the fire impacting microbial function. This should be explored further.

Measured Functions were Similar Between Treatments

The chlorophyll content is a measure of how much of the biocrust is photosynthetic. Both burned and unburned samples had similar amounts of photosynthetic biomass – for both the prescribed fire and the wildfire. This differs from other studies. After a grassland fire in New Mexico and the Palouse prairies, burning reduced chlorophyll-a content in biocrusts up to one year after the fire

(Bowker et al. 2004, Ford and Johnson 2006), although in the case of the wildfire, seven years may be sufficient time for the chlorophyll to reach the same level as the unburned biocrust. Interestingly, previous literature suggests that cyanobacteria are less resistant to fire based on pigment analyses like chlorophyll-a (Johansen 2001, Bowker et al. 2004). In this study we found similar amounts of chlorophyll-a between treatments, all the biocrusts were classified as cyanobacteria-dominant, and there was no difference in the relative abundance of Cyanobacteria between the treatments (Figure 2). However, chlorophyll measurements provide an estimate of how much of the sample is photosynthetic, it is not a direct measure of photosynthetic activity. Future work should directly measure the effect of fire on the photosynthetic capacity of biocrusts.

EPS is often used as a measure of soil stability (Rossi et al. 2018). Since EPS concentrations were similar between the treatments in this study, this suggests that the ability of the biocrusts to hold the soil aggregates together is the same in all the treatments. This is important in terms of fire ecology and management because increased erosion is a significant effect of wildland fires (Shakesby 2011). All plots – prescribed, wildfire, and both controls—were dominated by cyanobacteria biocrust (Palmer et al. in prep) and similar biocrust types have similar EPS content (Pietrasiak et al. 2013). Therefore, it is not surprising that EPS was similar between two similar biocrust types, but what is important in terms of restoration, is that the EPS content within the biocrusts in the prescribed fire plots recovered to unburned levels within a year or were not impacted by the fire originally.

Like EPS, nitrogen fixation often increases with biocrust age (Pietrasiak et al. 2013). Since the crusts in both fire treatments and the controls were all classified as cyanobacteria-dominated, it is unsurprising that there is no difference in the nitrogen fixation rates between treatments. A previous study in the New Mexico shortgrass-steppe found that nitrogen fixation was initially reduced one year after a fire, but was similar to the unburned sample after 2.5 years (Ford and Johnson 2006). This is similar to our results, although we found similar nitrogen fixation rates within one year after the

prescribed burn. Our calculated nitrogen fixation rates are similar to those documented previously in biocrust (Belnap 2002).

Microbial community composition was similar between both fires and their controls

The abundance of each phylum on SCI is similar to estimates from previous biocrust sequencing studies and contains several of the bacterial species previously detected within biocrusts including *Acaryochloris, Anabaena, Arthospira, Conexibater, Cyanothece, Geodermatophilus, Leptolyngbya, Lyngbya, Microcoleus, Micromonospora, Mycobacterium, Nitrospira, Nocardioides, Nostoc, Pyyamimonas, Rubrobacter, Sphingomonas, Streptomycetes, and Synechococcus* (Steven et al. 2012, Schulz et al. 2016, Mogul et al. 2017, Maier et al. 2018, Li et al. 2020).

Contrary to our hypothesis, there was no difference in the microbial community composition between burned and control plots at any of the phylogenetic levels. We were surprised by the composition of the cyanobacterial communities, as these communities are studied in a variety of dryland ecosystems. We expected *Microcoleus*, traditionally an early successional filamentous bacterium (Garcia-Pichel 2003), to be the dominant genera in the burned plots, but found the community dominated by nitrogen-fixers like *Nostoc, Anabaena,* and Cyanothece. The abiotic environment like soil temperature and pH can determine what cyanobacteria genera are dominant (Machado de Lima et al. 2021). In biocrusts in Brazil, nitrogen-fixing cyanobacteria were more abundant in arid environments (characterized as 200-800mm of rainfall) while filamentous cyanobacteria were more abundant areas with greater rainfall (Machado de Lima et al. 2021). SCI receives between 200 and 500 mm of rainfall annually (US Department of the Navy 2001) and has persistent coastal fog in the warm season (Clemesha et al. 2021). The combination of low rainfall and using fog as a water source when it is available (Lehnert et al. 2018, Jung et al. 2020) may have impacted the composition of cyanobacteria in the SCI biocrusts.

We compared our cyanobacterial sequences to previous cyanobacteria inventory on the nearby San Nicolas Island (SNI). Unlike our study, the SNI inventory used culture-dependent methods to identify community members (Flechtner et al. 2008). The only genera that are common between this study and the inventory of SNI were *Microcoleus, Nostoc,* and *Synechocystis.* This may be due to the difference between culture-independent and dependent techniques. Additionally, several of the genera identified in the metagenomes are known from aquatic rather than terrestrial environments. Other reasons for this finding may be the maritime climate and proximity to the ocean or due to an underrepresentation of terrestrial cyanobacterial genomes in the SEED database (Steven et al. 2012).

One explanation for the similarities between the burned and control communities is that the bare soil after the fire could be quickly recolonized by a nearby source population. Due to the setup of our plots, with burned plots adjacent to unburned areas, there was a nearby source population that could have recolonized after the fire. Cyanobacteria, the initial colonizers, readily aerosolize and can travel long distances and land on the soil to form a biocrust (Warren et al. 2019).

Another explanation may be that the biocrust microbes were able to withstand the fire. Deeper soil layers (~ 2cm deep) are protected from the heat of fire (DeBano 2000) and biocrust microbes have a demonstrated ability to rehydrate quickly after severe drought stress which may be valuable after fire (Xu et al. 2021). Additionally, the EPS produced by cyanobacteria and other biocrust microbes can allow the microbes to survive extreme temperatures (Mager 2010) and terrestrial cyanobacteria can survive temperatures of 100°C (Kimura et al. 2015)which is within the range of soil temperatures during a low severity wildfire 1 cm below the soil surfaces (DeBano et al. 1979).

Previous work on biocrust recovery described the years to decades to centuries it takes for biocrusts to recover from fire (Weber et al. 2016). However, more recently other papers have described a new understanding of resistance and resilience in biocrust communities in the recovery of biocrust

microbial communities after physical and climate disturbances (Steven et al. 2021). Biocrust microbial recovery or the ability to withstand the fire could be a phenomenon unique to the Mediterranean climate. Fog and low-cloud formation on the SCI are important in structuring plant communities (Clemesha et al. 2021) and may be important in the recovery of biocrust communities as well, due to the moisture in the clouds that could aid in the recovery of desiccation-tolerant biocrust organisms.

Difference in Functional Gene Sequences

There was, however, a difference in functional gene composition between the wildfire and the control samples. Changes in the functional gene profile without changes to the taxonomical composition suggest that there may be unaccounted for diversity below the taxonomic levels addressed in this study – at the species or strain level. Shotgun metagenomics often does not provide accurate information at lower taxonomic ranks (Steven et al. 2012) .

Although it was not a significant difference based on the PERMANOVA, 16 functional gene sequences varied between the prescribed fire and the controls and 12 of the sequences were more abundant in the prescribed burn samples including cannabinoid biosynthesis and pyrroloquinoline quinone biosynthesis which were also more abundant in the wildfire samples (Figure 6). Pyrroloquinoline quinone is a bacterial cofactor involved in redox reactions (Rucker et al. 2008). Exosome sequences were only found in the wildfire samples (Figure 6). Exosomes are important for intracellular transport and communication (Nazimek et al. 2016). The wildfire samples also had more sequences for cell division and bacterial chemotaxis suggesting that the microbes in that environment may be dividing more and have more genes to sense chemicals in the environment. Metabolic pathways that have been found in previous biocrust shotgun metagenomic studies were found in these samples as well (Li et al. 2020) and did not differ between the treatments.

Although there were some differences in the functional gene sequences between the fire types and the controls, the key metabolic pathways biogeochemical pathways important for the biocrust ecosystem functions were similar between the treatments.

Insights from the Network Analysis

The network analysis revealed difference between the treatments. Although each phylum was connected to a similar number of genera (Table 4), there are differences in the shape of the networks. For one, the Ascomycota are connected to the larger network in the prescribed fire but not the control, suggesting that although the microbial community is similar between the treatments, the microbes differ in the communities that they cooccur with. These two networks, also have a group of cyanobacteria that are disconnected – *Anabaena, Cyanothece*, *and Microcoleus—these are common cyanobacteria in biocrusts and often early successional* (Garcia-Pichel 2003) and previous network analyses in the Namib Desert showed that Cyanobacteria are often network hubs, not separated from the network (Valverde et al. 2015).

Metagenome Assembled Genome Provides Insight into Potential Ecological Function

The MAG was placed within Actinobacteria, the most abundant phylum in the samples. Since it was created with all 24 metagenomes, we cannot draw conclusions about whether or not this MAG can survive fire or may be an early colonizer after a fire – rather we can extrapolate that it is a common microbe in SCI biocrusts. It has gene sequences that hint at its functional role in the biocrust including genes for nitrogen cycling, although it is not a nitrogen fixer. Importantly, it has genes for EPS formation which suggest that it may play a role in soil stability and the EPS can act as a protective layer for the cell (Mager and Thomas 2011). The MAG also included gene sequences for oxidative and heat stress, which would be beneficial for a microbe living on an island in a Mediterranean climate. Based on the extracted 16S sequences, the MAG is phylogenetically related to *Micobispora.* Several species within the genera

Micobispora are thermotolerant (Lechevalier 1965, Boondaeng et al. n.d.). Of course, the recovery of one MAG is interesting as this is the first metagenomic study in this ecosystem, but future studies should increase the sequencing depth to potentially find more MAGs and to be able to identify the MAG beyond the phylum level.

Relevance to Restoration

Here we show that within one year of a prescribed fire and six years after a wildfire, the biocrust microbial community has a similar composition to unburned biocrust in a coastal grassland with cyanobacterial dominated biocrust. However, there are some differences in the gene sequences coding for microbial functions between the wildfire and control samples, even six years after the fire. Furthermore, each of the treatments (prescribed, wildfire, and the two controls) had different microbial networks.

If the biocrusts indeed recovered from the fire, this may be considered a form of passive restoration – the recovery of a community without intervention (Shimamoto et al. 2018). Restoring biocrusts leads to the recovery of other ecosystem functions (Bowker 2007). understanding how biocrust recovery occurs without intervention is important to understand so that time and resources may be delegated to communities with the most need for intervention. Passive restoration of biocrusts damaged by grazing occurred in the Great Basin (Condon et al. n.d.), though the success of passive restoration is dependent on climate and the disturbance type (Weber et al. 2016). On SCI, perhaps the right biotic and abiotic conditions were available to facilitate passive restoration of the biocrust community.

Another possibility is that the biocrust microbes were able to withstand the fire in which case, active restoration of biocrusts in a coastal grassland may not be necessary after a fire. Rather, the surviving biocrusts may be used to facilitate post-fire restoration. Previous researchers have used

biocrust microbial inoculum as a tool to aid in post-fire restoration (Chamizo et al. 2020, Muñoz-Rojas et al. 2021). Using existing biocrusts, particularly the cyanobacteria, as inoculum can quickly improve ecosystem functioning after a fire (Chamizo et al. 2020, Muñoz-Rojas et al. 2021).

Biocrusts in coastal grasslands are understudied and there is still much to learn about their macroscopic and microscopic components. Although in the face of global change and increasing fire frequency and severity globally, it is valuable to know how these diverse and ecologically important communities survive. As evidenced by this study at least some biocrust microbial communities may reach similar microbial community composition and function to the pre-fire communities. Understanding how microbial communities recover from disturbance will improve restoration of other ecosystem components. Future work should continue to address how biocrust microbial communities recover from a variety of ecological threats and seek to understand biocrust resilience in a variety of biocrust habitats.

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Tables and Figures

Table 2 The number of samples in each analysis. Within each plot (N=20 at each site), we collected biocrust. Then, a subset of those biocrust were used for each analysis. For metagenomics, 4 plots were chosen randomly within each site. For nitrogen fixation, six plots were chosen randomly, the same plots were used in 2018 and 2019. We could comfortably fit 72 samples in the desiccator. Chlorophyll and EPS content were measured at all plots.

		RC Samples		**PGE and PGW**		
Method	**Sample Year**	**Wildfire (2012)**	**Control**	**Prescribed (2012 and 2017)**	**Control**	**Total**
Metagenomics	**April 2018**	**4**	**4**	**8**	**8**	**24**
Nitrogen Fixation	**April 2018**	**6**	**6**	**12**	**12**	**36**
Nitrogen Fixation	**May 2019**	**6**	**6**	**12**	**12**	**36**

Chlorophyll Content	**April 2018**	**10**	**10**	**20**	**20**	**60**
Chlorophyll Content	**May 2019**	**10**	**10**	**20**	**20**	**60**
EPS Content	**April 2018**	**10**	**10**	**20**	**20**	**60**
EPS Content	**May 2019**	**10**	**10**	**20**	**20**	**60**

Table 3 Results of the Tukey post-hoc tests for all the functions measured in the lab. Chlorophyll measurements include both chlorophyll a and b. Bold values indicate a p-value <0.05.

Variable	Regression Coefficient	Std. Error	P-Value
Chlorophyll			
Wildifre-Control2012	1.82	1.72	0.713
Prescribed-Control2017	-2.46	1.33	0.244
Exopolysaccharides			
Wildifre-Control2012	-0.383	0.684	0.943
Prescribed-Control2017	0.341	0.484	0.894
Nitrogen Fixation			
Wildifre-Control2012	-0.497	0.665	0.876
Prescribed-Control2017	-0.0421	0.436	1

Table 4 Results of the PERMANOVA for the taxonomic community on the genus and function levels. Bold values represent p-values <0.05.

Pairs	Df	SS	F Model	R2	P value
Genus Level					
Prescribed vs. Control2017	1	0.0280	0.935	0.0626	0.415
Wildfire vs. Control2012	1	0.0296	1.19	0.165	0.313
Function Level					
Prescribed vs. Control2017	1	0.00597	0.930	0.623	0.441
Wildfire vs. Control2012	1	0.0061	1.72	0.223	**0.025**

Table 5 The total number of connections to individual genera that each phylum has based on the treatment.

	# Genera Connected to			
Phlym	Prescribed Fire Control	Prescribed Fire	Wildfire Control	Wildfire

Acidobacteria	4	4	4	4
Actinobacteria	36	37	25	27
Ascomycota	17	13	0	10
Bacteroidetes	9	8	5	3
Chlorobi	1	1	0	0
Chloroflexi	5	5	3	3
Cyanobacteria	12	11	5	4
Deinococcus-Thermus	1	1	1	1
Firmicutes	4	4	2	2
Gemmatimonadetes	1	1	1	1
Planctomycetes	5	5	5	5
Proteobacteria	56	58	36	33
Streptophyta	1	0	1	0
unclassified (derived from Bacteria)	1	1	0	1
unclassified (derived from Viruses)	1	1	1	1
Verrucomicrobia	4	4	3	2
Grand Total	158	154	92	97

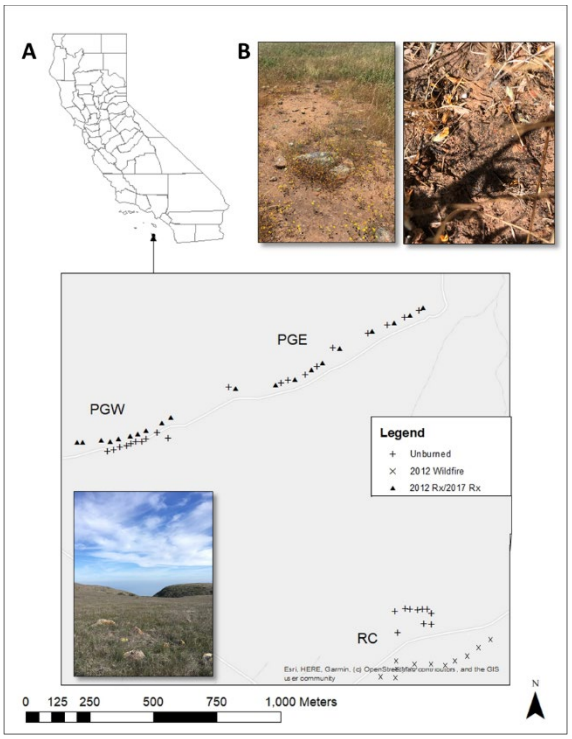


Figure 2 A) Map of the Plots on San Clemente Island with a photo of PGE. Ten plots each 10m^2 were burned in a prescribed fire in PGW and PGE in 2012 and 2017. Adjacent unburned plots were established as controls. In RC, we collected biocrust from ten locations within the 2012 wildfire perimeter and included ten unburned plots outside of the wildfire perimeter. B) Typical habitat for SCI biocrusts. Biocrusts on SCI are often found growing in large patches in open spaces or nestled between dense plant clumps.

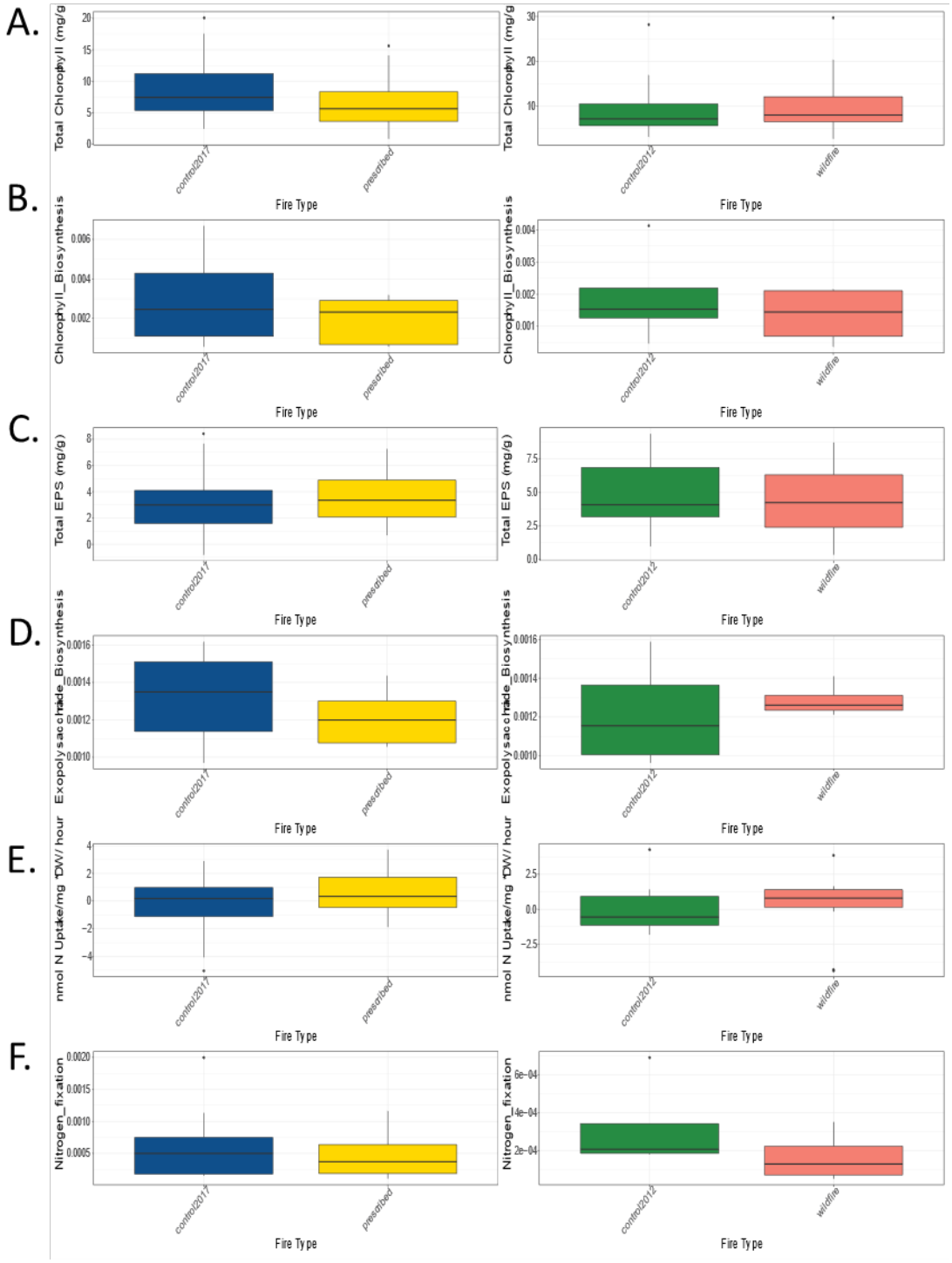


Figure 3 A) The total measured chlorophyll for each fire type and their respective controls; B) The relative abundance of nitrogen fixing genes; C) The measured EPS content ; D) The relative abundance of the exopolysaccharide biosynthesis genes; E) The measured nitrogen fixation; F) The relative abundance of nitrogen fixing genes.

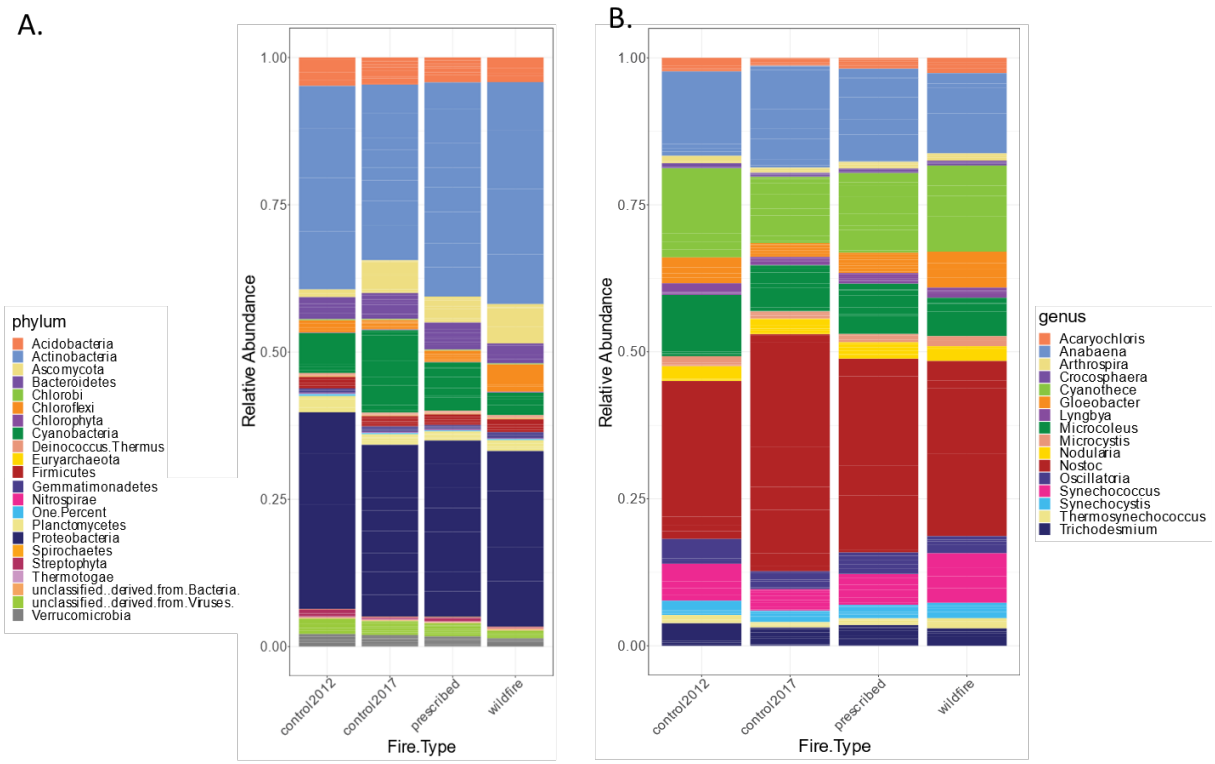
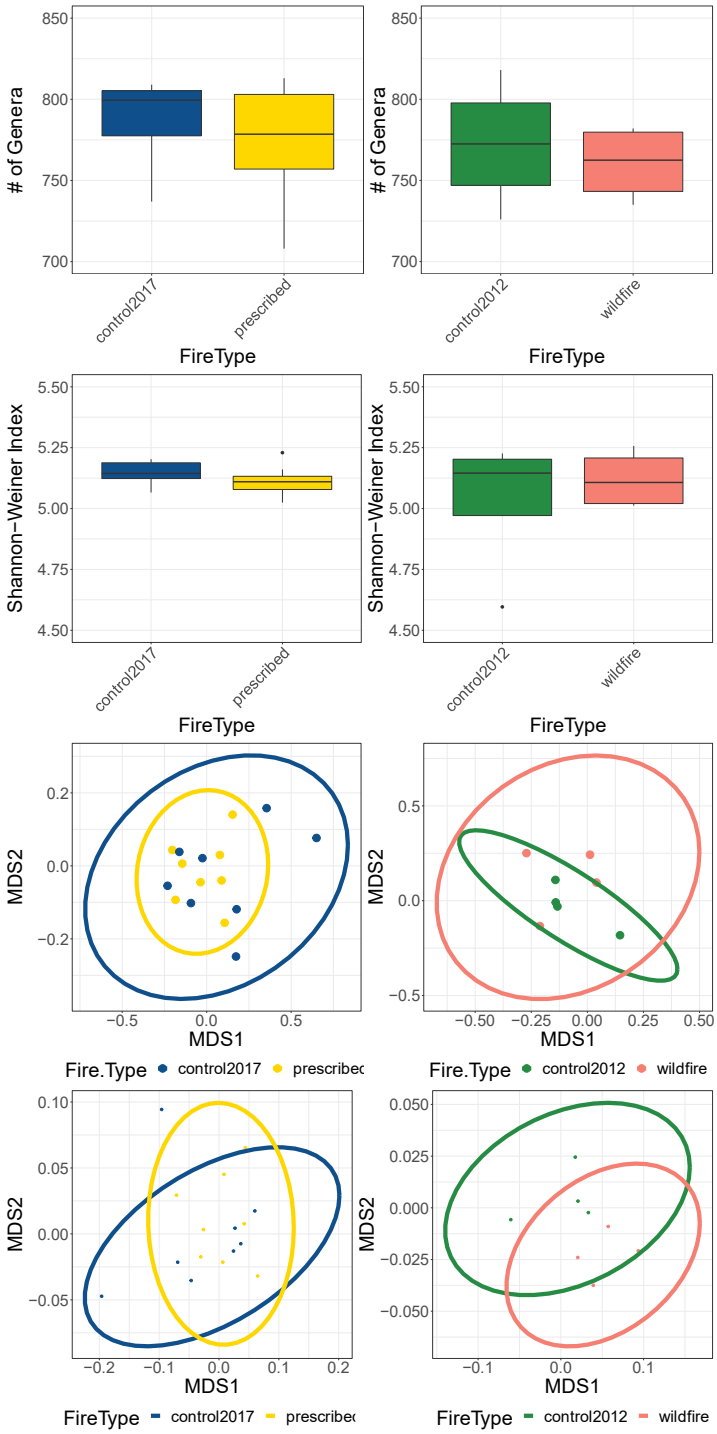


Figure 4 A) Relative abundance of each phylum. Phyla that had less than 1% relative abundance are grouped. B) Relative abundance of cyanobacteria genera.


# of Genera
850
800
750
700
control2017
prescribed
FireType
control2012
wildfire
Shannon−Weiner Index
5.50
5.25
5.00
4.75
4.50
MDS2
MDS1
0.2
0.0
−0.2
−0.5
0.5
−0.50
−0.25
0.25
0.50
Fire.Type
control2017
prescribed
control2012
wildfire
0.10
0.05
−0.05
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−0.025
−0.050

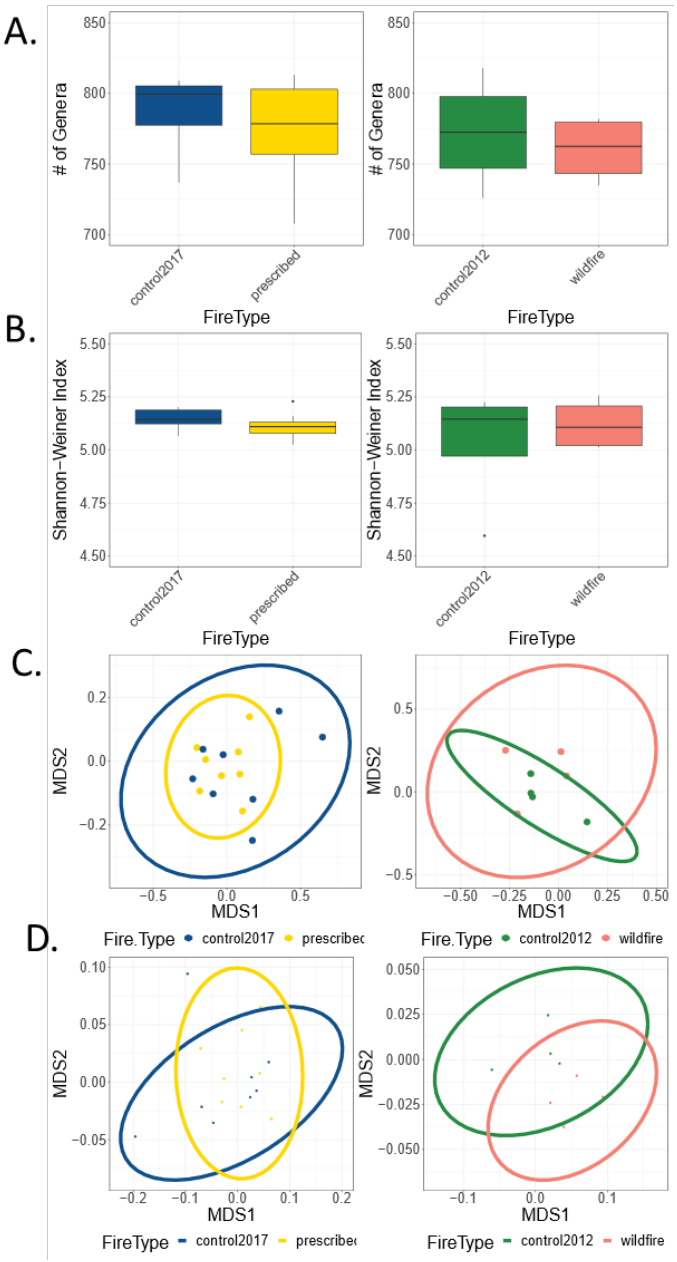

Figure 5 A) Richness values for each treatment There was no difference in the total number of genera within each treatment. B) Shannon Diversity Index for each treatment. There was no difference in the Shannon diversity between treatments. C) NMDS plot based on genera in each treatment. The community composition between the treatments was similar. D) NMDS plot based on the functions level of the SEED database. The functional genes present are similar between the wildfire and prescribed fire and the prescribed fire and controls. There is a difference in the functional genes present between the wildfire and control samples (P= 0.043).

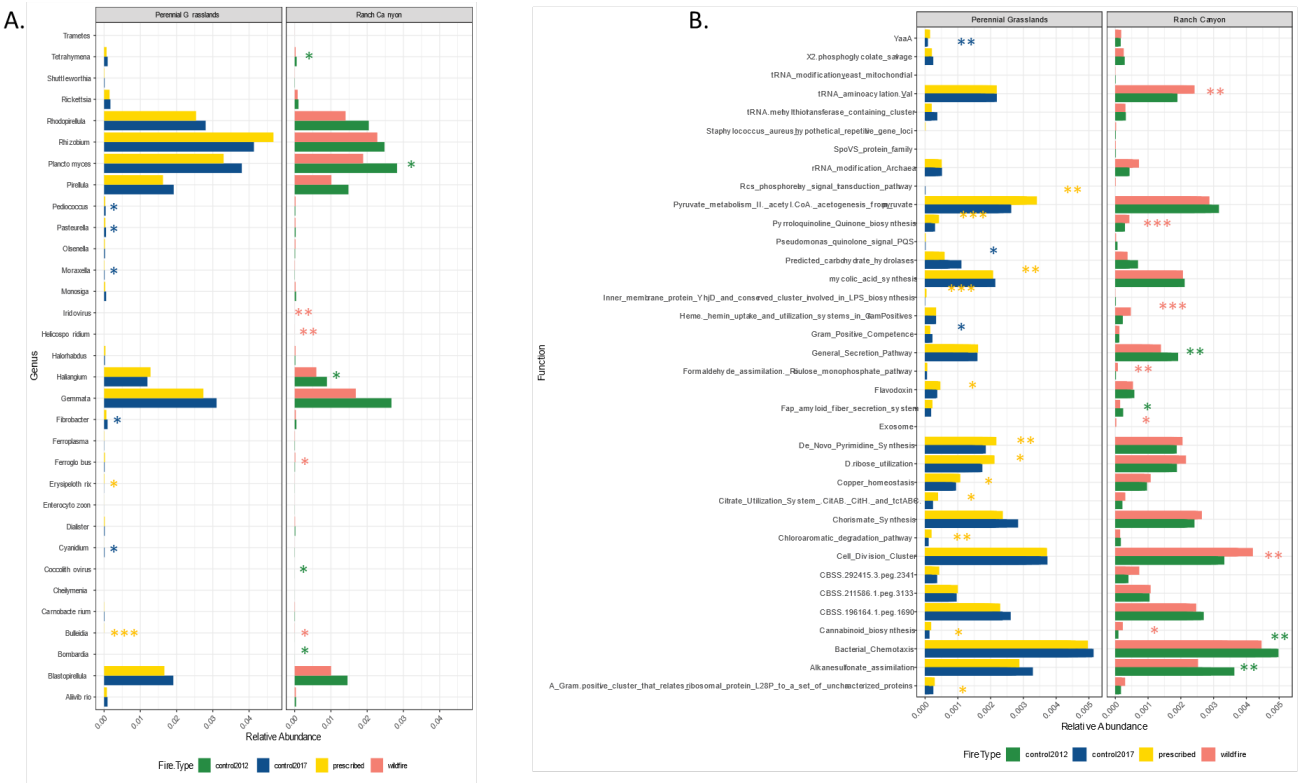

*Figure 6 The genera (A) and the functional gene sequences (B) that varied between the treatments. The color of the * indicates which treatment had a greater relative abundance. Perennial grasslands include the prescribed fires in PGE and PGW and Ranch Canyon (RC) includes the wildfire. The * represents a p-value <0.05, ** represents a p-value <0.01, and *** represents a p-value <0.001.*

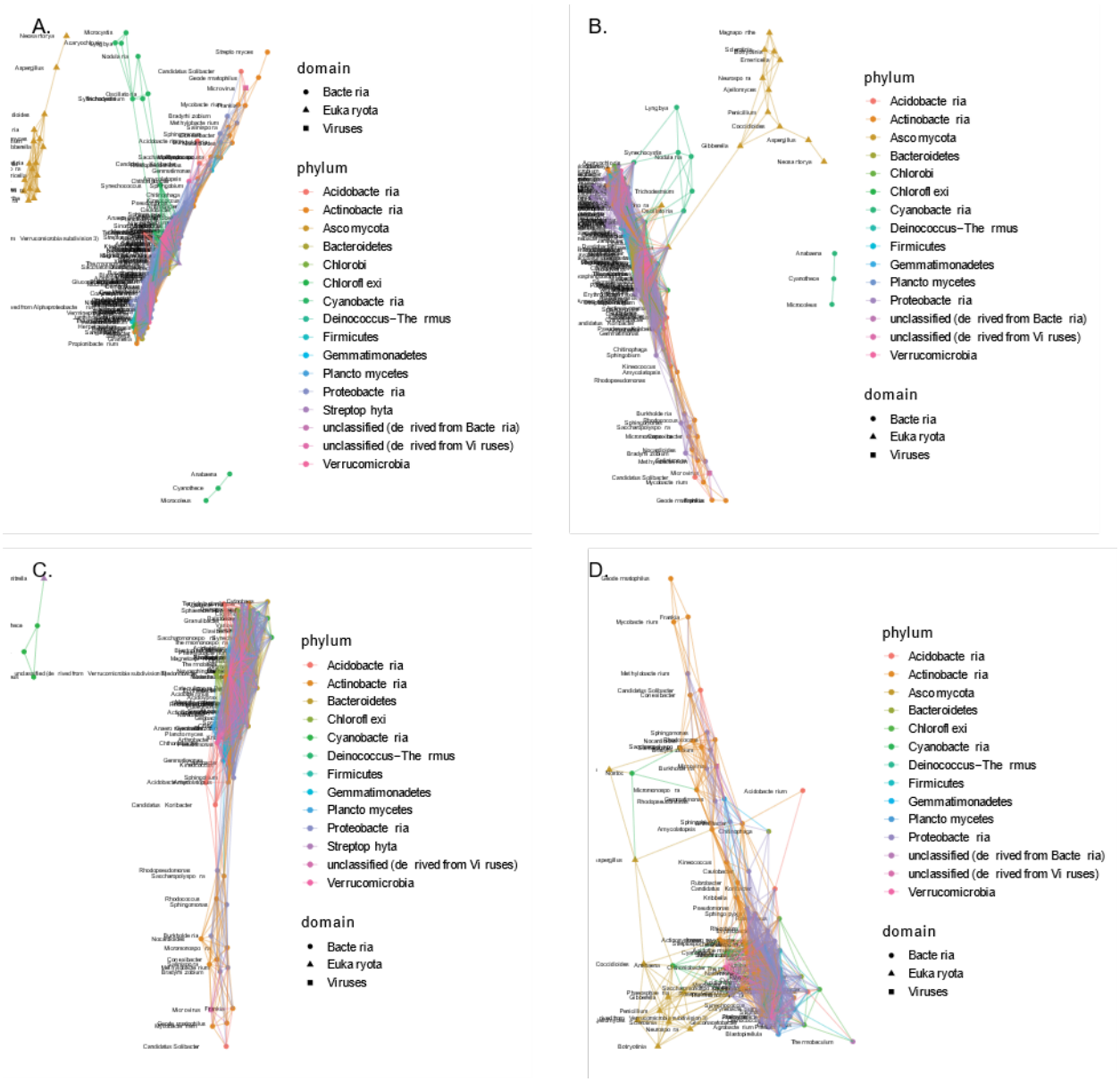

Figure 7 A-B) Networks for control samples associated with the 2017 prescribed burn (n=8) (A), prescribed burn samples (n=8)(B), control samples associated with the wildfire in 2012 (n=4)(C), and samples that were burned in the 2012 wildfire (D). Each point represents a genus, the shapes depict different domains, and the colors represent different phyla.

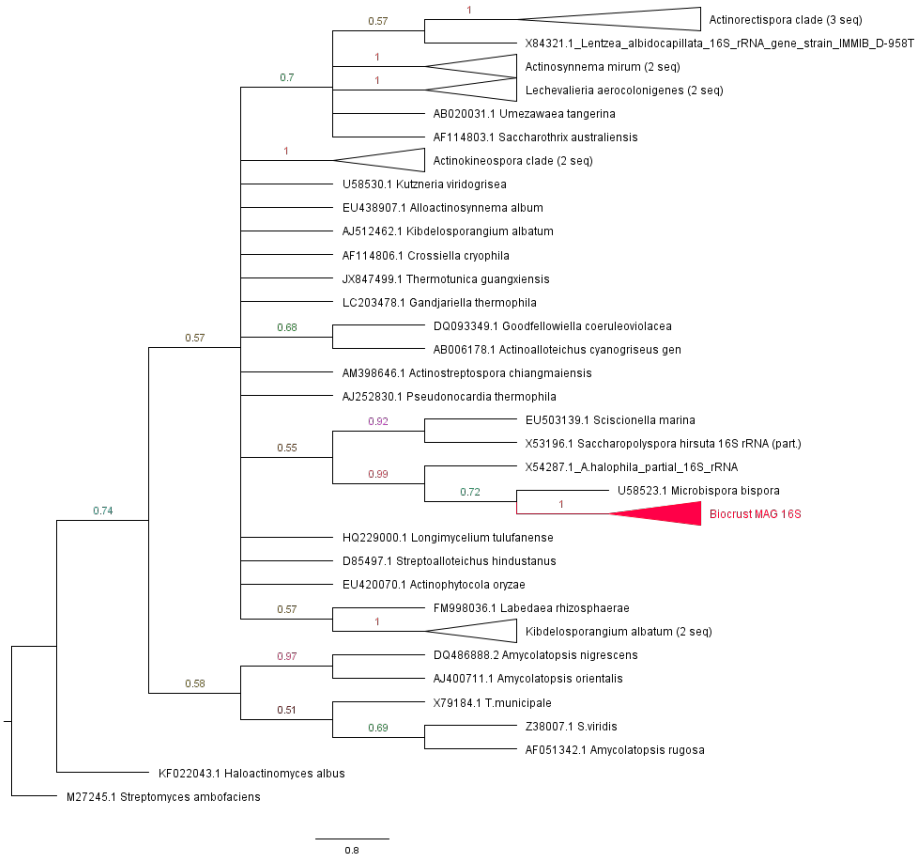

Figure 8 Bootstrapped Maximum likelihood tree with the extracted 16S rRNA genes from the MAG and reference sequences from NCBI. The numbers are the bootstrap value. The higher the number the more confidence there is in the branch placement. Bootstrap values >0.70 are considered well supported.

Chapter 4

Using simulated wildland fire to assess microbial survival at multiple depths from biocrust and bare soils

Brianne Palmer, Nicole Pietrasiak, David Lipson

Abstract

Surface soil microbial communities are directly exposed to the heat from wildland fires. Due to this, the microbial community composition may be stratified within the soil profile with more heat tolerant microbes near the surface and less heat tolerant microbes, or mobile species found deeper in the soil. Biological soil crusts, biocrusts, are found on the soil surface and contain a diverse microbial community that is directly exposed to the heat from wildland fires. Here, we used a simulated fire mesocosm along with a culture-based approach and molecular characterization of isolates to understand the stratification of biocrust and bare soil microbes after low severity (450°C) and high severity (600°C) fires. We cultured and sequences microbial isolates from 2cm – 6cm depth from both fire types. The OTUs were stratified along the soil depth. Green algal OTUs were less thermotolerant and found in the deeper depths (4-6cm) and the control soils. While several cyanobacteria in Oscillatoriales, Synechoccales, and Nostocales were found at 2-3cm depth for both fire temperatures. An Alphaproteobacteria OTU was common across several depths, both fire types, and both fire temperatures. Here we show evidence of stratification of soil and biocrust microbes after a fire and provide evidence that these microbes are able to survive the heat from the fire by living just below the soil surface. This is a steppingstone for future work on the mechanisms of microbial survival after fire and the role of soil insulation in creating resilient communities.

Introduction

The recovery of microorganisms after a disturbance is a key component of ecosystem restoration. There are several theories and experiments that attempt to explain microbial recovery

through resistance or resilience. A resistant microbial community is insensitive to disturbance while a resilient community may be altered but eventually return to the original state (Shade et al. 2012). How microbes respond depends on if the disturbance is a press disturbance that occurs over long time scales (i.e. climate change) or a pulse disturbance which is s short-term disruption (i.e. fire) (Shade et al. 2012).

We know that fire, as pulse disturbance, can alter the microbial community in a variety of ways. Fire can reduce microbial biomass (Dooley and Treseder 2012, Fontúrbel et al. 2012) and is mediated by the severity of the fire (Dooley and Treseder 2012). Low severity fires do not alter microbial diversity but high severity fires do (Pourreza et al. 2014). Sometimes, fire may have a small effect on soil functioning due to the relatively low soil temperatures during a fire (Fontúrbel et al. 2012).

Fire severity describes the interactions between the fire temperatures, duration, and other biotic and abiotic factors (Neary et al. 1999). In a simplified model, a high severity fire would have a high temperature and a long duration, and a low severity fire would have a relatively low temperature and short duration. For microbes, the temperature of the soil and the amount of time that the soil is exposed to heat may determine the survival of microorganisms (Hart et al. 2005). The duration is determined by the type and the amount of fuel (Neary et al. 1999). For example, a fire may have a high release of heat but burn so quickly that much of the initial heat fails to penetrate deep into the soil depths (Neary et al. 1999). In grasslands and shrublands, heat is transferred into the soil primarily through radiation and convection and is dependent on the water content, structure, and organic matter in the soil (Neary et al. 1999).

During a fire, there is a heat-stratified profile where temperatures drop precipitously as depth increases (Campbell et al. 1994, Massman 2012), suggesting there is also stratified mortality with a mortality rate at the soil surface and increased survival at greater depths, although survival is highly dependent on the type of organism (Pingree and Kobziar 2019). Soil microbial communities can be

relatively resistant to fire (Pressler et al. 2019). In some cases, microbes can enter a dormant state during the fire and be reactivated after the heat from the fire dissipates (Lennon and Jones 2011, Wang et al. 2015). In chaparral ecosystems where shrubs and grasses are dominant, peak fire temperatures on the soil surface range from approximately 250 to 700°C (DeBano et al. 1979). At 2.5 cm depth, temperatures ranged from approximately 70 to 280°C (DeBano et al. 1979), well within the temperature range of thermophilic microorganisms (Brock 2012).

Studying the effect of these fire processes on soil microbial communities is challenging and has been addressed in several studies (reviewed in Dove and Hart 2017, Pressler et al. 2019) but these types of studies often use space-for-time replacements, comparing burned and unburned plots which allows for little room for manipulation to explore fire parameters. As a result of this gap in experimental fire and microbial community studies, Bruns et al. (2020) developed a "pyrocosm" system to experimentally test the effects of fire on a microbial community in a controlled setting.

Here, we use our own form of pryrocosum and microbial genomic techniques to evaluate the effect of fire on a particular soil microbial community – biological soil crusts (biocrusts). Biocrusts contain communities of microscopic and macroscopic organisms living on the soil surface and cover about 12% of the soil surface globally (Rodriguez-Caballero et al. 2018). They are important for a variety of ecosystem functions including nutrient cycling (Belnap 2002, Elbert et al. 2012), water retention (Eldridge et al. 2020), and soil stability (Rodríguez-Caballero et al. 2012). Fire can have varying impacts on biocrusts from altering their cover (reviewed in Palmer et al. 2020), changing the photosynthetic biomass (Johansen 2001), and changing the microbial community (Aanderud et al. 2019). As biocrusts, by definition, reside at the soil surface, they are at immediate risk of mortality by high-temperature fires on the soil surface while microbes in the deeper layers may survive (DeBano 2000, Hart et al. 2005, Cairney and Bastias 2007).

However, in a California coastal grassland, we previously found that the biocrust microbial community is unaltered one year after a fire (Palmer et al. *in review*). This suggests that biocrusts may have the potential to swiftly recover from a fire. Therefore, using our pyrocosm system, we sought to understand the depth of mortality of biocrust microorganisms after low and high temperature fires using a culture-based approach with subsequent molecular characterization of microbial isolates.

Methods

Biocrust Collection

In June 2020, we collected twenty 10cm cores of biocrusts and twenty cores of bare soil from the coastal sage scrub habitat at the Santa Margarita Ecological Reserve (33.44128 N, 117.1644 W) in Riverside Country, California, USA. The biocrusts are classified as lichen and cyanobacteria dominant and comprise much of the open space at the reserve. Cores were stored in 15cm silicon cups at room temperature before burning.

Fire Simulation

We developed a model using the Campbell et al. 1994, 1995 soil heat transfer model which includes a variable for soil moisture to understand what to expect from the simulated fire. Additionally, we used the equations described by Mercer and Weber 2001 to create a right-skewed curve as is typical during a fire. We calculated the bulk density and the volumetric water content from the SMER soils and used the soil organic matter, mineral soil by volume, and organic matter by volume measurements from previous work at SMER (Pérez Castro et al. 2019). The thermal conductivity (gamma) was set to 0.03bW/cm*K based on estimates from Ochsner et al. 2001. The initial temperature was set to 20°C for both models. The low-intensity fire had a maximum temperature of 450°C, and the high-intensity fire had a maximum temperature of 600°C. These values were based on soil temperature estimates in chaparral (DeBano et al. 1979). For each fire type, it took 900 seconds to reach the maximum

temperature then stayed at the maximum temperature for 60 seconds. There was an 1800 second decay period as it returned to the basal temperature. The result was a model of the temperature fluctuations every second for every 0.1cm depth.

The fire simulation within the pyrocosum was performed using a blow torch in a controlled laboratory setting. This ensures control over the soil temperature. Previous studies have used this method to test the effects of fire on small scales (Hean and Ward 2012, Bruns et al. 2020). A blowtorch may more closely model a wildland fire than a similar temperature in the muffler furnace due to the difference in heat conduction. Before the burn, the samples were moved to ceramic mugs. Each mug had a small hole in the bottom where we inserted thermocouples at 8cm, 5cm, and 2cm depth before transferring the soil from the silicon cups used in the field. The thermocouples were used to track the temperature of the soil at three different depths and the values were compared to the model we developed. We compared the temperatures between each treatment using a t-test. The surface of the soil was monitored using a laser thermometer pointed at the hottest area of the soil, directly under the blowtorch flame. The blowtorch was attached to a stand, and we calibrated the height of the stand for each treatment to ensure consistency between samples (Figure 1). The mug was placed in a tray full of sand to reduce heat transfer from the bottom of the mug. For each sample, we recorded the ramp-up time and ensured it stayed at the maximum temperature (450°C or 600°C) for 60 seconds before turning off the blowtorch and letting the mugs cool for ten minutes. This cooling period allows the heat from the surface to dissipate into the deeper soil layers, similar to wildland fire, and was accounted for in our model. After the cool-down period, we separated the soil into each cm depth by using a sterile spoon and ruler to scoop out each cm and placed it in a sterile plastic bag. The spoon and ruler were sterilized with 95% ethanol between every centimeter. In total, we had six treatments: low-temperature biocrust, high-temperature biocrust, low-temperature bare soil, high-temperature bare soil, biocrust control, and

bare soil control. Each treatment was replicated 6 times. After sampling, each plastic bag containing 1cm of soil was stored at 4°C. In total, we had 10 1cm samples per cup for a total of 360 individual samples.

Culturing, DNA Extraction, and PCR

After the burn, we cultured each sample (n= 360) on individual Petri-dishes with BG-11 medium. For each sample, we created a soil slurry with five grams of the soil sample and diluted it to 10^{-2}. This dilution was streaked onto BG-11 plates and placed in an incubator at 25°C with a radiance of 20.3µmol m^{-2} s^{-1}, and with 12 hours of light. Every week, we recorded the presence or absence of colony-forming units on the plates. After three months, there were mixed cultures growing on the plates. We moved individual isolates to fresh BG-11 plates made with low-temperature melting agar. This is because of the often-filamentous nature of biocrust organisms. The cyanobacteria often grow into the agar, and it can be difficult to remove the culture for DNA extraction. After growing on the low-melt agar for one month, we began DNA extraction. We chose isolates that were cultured from the top 6cm of the soil. For each sample, we scraped the biomass and agar off the plate with a sterile loop and placed it into a 1.5 ml collection tube. We then added 1 ml of sterile water that was warmed to 60°C to help melt the agar. The collection tubes were centrifuged for 5 minutes at 13,000 rpm, incubated for 30 minutes at 65°C, then centrifuged again for 5 minutes. Incubation and centrifuging were repeated until the agar was completely melted. After the agar was melted, we removed the supernatant, leaving the pellet of biomass, and continued with DNA extraction. We then used the phenol-chloroform DNA extraction method. We placed each sample in a 1.5 ml collection tube and filled it with 100 mg of UV sterilized beads. Then, we added 500 µl of lysis buffer (TE with SDS) to each sample and vortexed for ten minutes. We then added 5 µl proteinase-k and incubated the samples at 37°C for 30 minutes. Next, we added 25µl 0.5M NaCl, 20µl ctab NaCl, and 500µl chloroform. The samples were vortexed and centrifuged at

13,000 rpm for five minutes. Then, we added 500µl of phenol-chloroform, vortexed, and centrifuged for 5 minutes. We moved the aqueous solution into sterile collection tubes and precipitated it with 0.7 volumes of isopropanol. After 30 minutes, we rinsed with 500µl cold ethanol and centrifuged at 13,000 rpm for ten minutes. We removed the supernatant and let the pellet air dry in the fume hood for 24 hours. We resuspended the DNA pellet in 100 µl Tris buffer.

The DNA was amplified using PCR. The PCR settings include an initial denaturation at 94°C for 3 minutes and the following cycle repeated thirty times: denaturation at 94°C for 30 seconds, annealing at 55°C for 30 seconds, elongation at 72°C for 60 seconds, then a final elongation at 75°C for 6 minutes and cooled to 4°C. The quality of the PCR product was assessed using gel electrophoresis, only samples with a clear band were sequenced. Because there are a variety of different types of photosynthetic organisms found in biocrust, we used both prokaryotic and eukaryotic primers. Six bacteria cultures were sequenced using f8-27 (5'-AGAGTTTGATCCTGGCTCAG-3') and r1510(5'-GGTTACCTTGTTACGACTT-3'. Seventeen bacteria cultures were sequenced using more specific cyanobacteria primers cyanoF (5' – GGGGAATTTTCCGCAATGGG -3') and r1510cy (5' – ACGGCTACCTTGTTACGACTT -3'). One algae sample was sequenced using algSSU1 (5' -TGGTGGACTCTGCCAGTAG -3') and algSSU2 (5' -TGATCCTCCCGCAGGTCCAC -3'). A further nine algae samples were sequenced using ITS1F (5' – TCCGTAGGTGAACCTGCGG -3') and ITS4 (5´-TCCTCCGCTTATTGATATGC-3´). All 16s rRNA samples were sequences at Eton Biotech (San Diego, CA). We focused the DNA extractions and sequencing to samples from 1-6cm depths in all treatments.

Phylogenetic Trees

Sequenced data were first compared with published sequences in GenBank using n-BLAST to screen which phylum and order the taxonomic units were the closest match. We selected matching

reference sequences with high sequence similarities (>90%) as well as sequences from organisms known to be abundant in soils and biocrusts. The sequences were aligned in Mega 11 using ClustalW. We used the maximum-likelihood tree tool in Mega 11 to create bootstrapped maximum likelihood trees with 100 bootstraps. We separated the cyanobacteria into three different trees, one for each represented order – Synechoccales, Oscillatoriales, and Nostocales. For the Cyanobacteria, the trees were rooted with *Gloeobacter violaceus* (NR074282). We included one tree for Alphaproteobacteria with *Caulobacter vibrioides* (AJ227754) as the root. We also created trees for the algal orders Chlamydomonadales and Chlorellales.

Results

Three months after the simulated burns, CFUs were growing on 72% of the plates (n = 259), based on presence-absence (Figure 2). For the bare samples, after the 450 °C and 600 °C burns, there was growth from 2-10cm and there was growth on every cm for the control. For the biocrust samples, the 450 °C had growth from 3-10cm and the 600 °C burn and controls had growth from 1-10cm. One month later, there was one CFU on one plate burned at the top cm at 450 °C.

Thermocouple Measurements and Model

The thermocouples were placed at 2, 5, and 8cm depths which we compared with the values from the model. Overall, our model captured the overall shape of the temperature curve, but for biocrust, was 1cm off. The maximum temperature during the experiment occurred in the bare 600°C treatment at 502. 1°C (Table 1, Figure 3). We compared the average temperatures at each depth during the first 30 minutes of the experiment which included the ramp up time, ten minutes of maximum heat burn time, and a cool down period and found that the biocrust treatments had consistently lower temperatures at each soil depth (Table 1).

Culture Sequence Results

Nineteen sequences are from bare soil and twelve were from biocrust. Eleven were from the controls, fifteen were from the high temperature fire, and five were from the low temperature fire. Seven sequences were low quality and had ambiguous hits within the NCBI database, these were not included in the trees. The Blast sequences with the highest percent identity are Table 2.

For bacteria, the sequences spanned four orders: Oscillatoriales, Nostocales, Synechoccales, and Caulobacterales. The green algae sequences were in Chlamydomonadales and Chlorellales.

Oscillarotiales

One sequence fell within Oscillatoriales. It was from 2cm deep from a bare soil sample burned at 450°C. It is within a clade containing *Phormidium* and *Wilmottia* (Figure 4, bootstrap value = 0.82).

Synechoccales

Six sequences fell within the order Synechoccales. A CFU obtained and sequenced from bare soil at 4cm depth burned at 600°C is likely *Trichocoleus desertorum* (bootstrap value = 0.98). Three other sequences fell within a clade with *Phormidesmis* including Bare soil burned at 450°C at 6cm, a biocrust sample from 5cm burned at 600°C, and an unburned biocrust sample from 4cm (bootstrap value = 0.63). A bare sample from 2cm burned at 600°C has ambiguous relatives but was placed within a clade with *Droutiella, Leptognbya,* and *Trichoaquatus* (bootstrap value = 0.8). A biocrust sample from 6cm deep burned at 600°C is in a clade with *Stenomitos* (Figure 5, bootstrap value = 0.75).

Nostocales

One sample – biocrust at 3cm depth burned at 600°C—was placed in Nostocales within a clade that contains *Tolypothrix* and *Nostoc* (Figure 5, bootstrap value = 0.79).

Alphaproteobacteria

Eight sequences were placed within Caulobacterales and are all closely related to each other. Although, the sequences initially blasted to Brevundimonas, the maximum likelihood tree shows that they are related to *Phenylobacterium* isolated from farmland soil which are heavy metal resistant (Li et al. 2019). Although this placement has weak support with a bootstrap value of 0.68. Generally, bootstrap values 0.7 and above are considered supported.

Chlamydomonadales

Five of the algal sequences are within Chlamydomonadales and all the isolated from the burned samples are from the deeper soil layers (5-6cm). There is one control sample at 2cm that is in a clade with *Spongiochloris spongiosa*. Although this branch is weakly supported with a bootstrap value of 0.5. The other sample from a biocrust sample burned at 450ºC from 5cm deep is more supported (bootstrap value = 0.87) and it is in a clade with *Chlamydomonas rubra* and *Chlamydomonas pygmaea.* It was placed with the same node as *C. pygmaea* in every bootstrap iteration.

Chlorellales

One algal sample was placed within Chlorellales and is in a clade with *Chlorella sorokiniana* (bootstrap value 0.92, Figure 5). This sample is the only burned algal sample from the top few cm. It was isolated from a biocrust burned at 600ºC 2cm deep.

Discussion

Here we show evidence that microbes can survive a fire and grow, given the right conditions from 1-10cm depth in the soil after an experimental fire. Based on the presence-absence of CFUs on the agar plates, we can conclude that both cyanobacteria, algae, biofilm forming alphaproteobacterial colonies, and even moss as depicted in Figure 2 can survive fire. The sequences from these isolates reveal a phylogenetically diverse community of cyanobacteria, alphaproteobacteria and green algae.

Importantly, we showed different organisms can be found and survived at each soil depth, suggesting differences in the thermotolerance of biocrust and soil microbes.

Insights from 1-3cm

Microbes collected from the hottest parts of the soil, were able to survive and grow after the fire. These organisms may have adaptations that allowed them to persist in the inhospitable environment. For example, *Phenylobacterium,* a genus closely related to the alphaproteobacterial OUT found after the low-temperature fire, is related to an isolate from soils with heavy metals (Li et al. 2019). Furthermore, *Phenylobacterium* is known to be abundant after a fire. In an outdoor controlled fire, Lucas-Borja et al. 2019 found that *Phenylobacterium* was relatively more abundant in soils that were burned in a high severity fire (595ºC) compared to the low severity fire (547ºC) (Lucas-Borja et al. 2019). Additionally, Woolet and Whitman (2020) found that genera within *Phenylobacterium* increased in soil after fire. *Phenylobacterium* may be common in burned soils due to their ability to degrade aromatic compounds (Lingens et al. 1985). In a savanna ecosystem, *Phenylobacterium* OTUs were present in soils after the first rain following the fire season (de Souza and Procópio 2022). Although, the identity of the sequence found in this study is unknown with 68% of the bootstrapped trees supporting its placement, we know that is can survive a fire at 2cm depth.

The green algae found in the top cm is related to *Chlorella sorokiniana.* Although, *C. sorokiniana* has not been associated with burned soils previously, there is evidence that it is adapted to survive extreme environments. *C. sorokiniana* can biomineralize lead in the soil (Tan et al. 2022). Adding *C. sorokiniana* to degraded desert soils alters the soil bacterial community and may be used for bioremediation (Lopez et al. 2013). Additionally, *C. sorokiniana* is capable of taking up heavy metals (Yoshida et al. 2006, León-Vaz et al. 2021). In a Florida pine forest, algae quickly recolonized soil after a fire including *Chlorella* (Myers et al. 2003). *Chlorella sp.* were also present after a fire in a juniper

woodland (Warren et al. 2015). A *Chlorella* isolate from biocrusts in Negev, Israel is closely related to *C. sorokiniana* and was resistant to photoinhibition (Treves et al. 2013).

One of the cyanobacterial isolates that survived the fire in the top centimeters is similar to the filamentous *Wilmottia murrayi.* Previously, researchers have described *Wilmottia murrayi* as being found exclusively in cold and temperate regions of the world, although more recent evidence suggest is has a wider distribution (Machado-De-Lima et al. 2017), and perhaps a wider range of thermotolerance. Cyanobacteria within Oscillatoriales form sheaths and are able to move within the soil (Garcia-Pichel and Pringault 2001) which may allow them to move away from the heat. Another cyanobacteria isolate was placed within Synechoccales is in a clade with *Trichotorquatus. Trichotorquatus maritimus* was isolated from this site and recently described in Pietrasiak et al. (2021), though little is known about the thermal tolerance of this genus.

Additionally, we isolated two species from the 3cm deep biocrusts burned at 600°C closely related to *Tolypothrix sp./Nostoc sp.* and *Phenylobacterium sp.* The estimate from our model predicts that these species experienced temperatures >100°C. *Tolypothrix* is a genus often found in biocrusts (Giraldo-Silva et al. 2020). However, in one study testing the thermotolerance of biocrust cyanobacterial species *Tolypothrix* only grew up to 4°C, though the thermotolerance changed in the presence of nitrogen suggesting it may be the inability to form heterocyte at high temperatures that impeded their growth (Giraldo-Silva et al. 2020). All the cultures in the present study were grown on media with nitrogen so we did not test the thermotolerance of nitrogen-fixing cyanobacteria specifically, but it would be an interesting avenue to explore in future research. A similar study, testing the thermal limits of EPS production, *Tolypothrix bouteillei*, also found that *T. bouteillei* had a lower temperature limit to produce the maximal amount of EPS (27-34°C) (Kvíderová et al. 2019). Here, we found an organism similar to *Tolypothrix* that survived temperature conditions greater than the congeners in the literature. Although our isolate was also in a clade with *Nostoc. Nostoc* can be dry heat tolerant (Kimura et al.

2015, 2017b, 2017a), meaning it can survive temperatures up to 100°C and revive after being rehydrated. The dormant form of some cyanobacteria, including *Nostoc*, called the akinete, are dry-heat tolerant (Kimura et al. 2015). We also found *Phenylobacterium* growing in this treatment and this genus is ubiquitous among treatments as it is found in the bare control at 2, 3, and 4 cm, biocrust 600°C burn at 3 and 5cm, and in the biocrust control at 4cm. It was not found on the soil surface or in any of the burned bare treatments.

Insights from 4-6cm

The soil from 4-cm deep experienced a broad temperature range from approximately 50-100°C and in these depths, we found two common cyanobacteria and two green alga in biocrusts in the deeper layers of the bare soil – *Phormidesmis sp.,Trichocoleus deserotum, Spongiochloris spongiosa,* and *Clainomonas sp.* Interestingly, *Phormidesmis sp.*and *Spongiochloris spongiosa* were only isolated from the deeper soil depths. *Phormidesmis* is common in soils and is not heat tolerant (Chrismas et al. 2015, Raabova et al. 2019). *Spongiochloris spongiosa* was found in soils from Joshua Tree National Park, though the sequence data available for the *Spongiochloris* genus is limited (Flechtner et al. 2013). *Trichocoleus desertorum* is common in dryland soils and biocrusts. It is mobile and produces EPS (Muhlsteinova et al. 2014). *Trichocoleus* isolates were only found in unburned soils during an assessment of biocrust recolonization after a fire in a juniper woodland (Warren et al. 2015), suggesting that this genera is not fire resistant.

Bare versus Biocrust Soil

The burned and bare samples were also collected within 1m of each other in an area with a patchy distribution of biocrusts and bare ground. Therefore, regardless of the formation of a biocrust, the microbial communities, especially below the first cm are likely to be similar. Here we found cyanobacteria genera common to both biocrust and soils in the bare treatment. We also had more

success extracting the DNA and performing PCR with the samples collected from the bare soils, biasing our results towards a more complete picture of the bare soils. Future research should use more robust DNA extraction and sequencing methods to understand what microbes are found after fire at each depth.

There were also mixed cultures initially growing on the plates, so there was likely a mix of cyanobacteria and alphaproteobacteria in both cover types. Additionally, the PCR and sequencing was unsuccessful for several of our isolates due to the contamination or the presence of a mixed culture. Attempting to classify cyanobacteria through mixed cultures leads to a risk of misidentification (Anagnostidis and Komarek 1999). We took care to isolate individual cultures by transferring them to their own BG-11 plate where they were allowed to grow alone, however contamination may have occurred.

Based on the thermocouple data, the biocrust treatments had lower temperatures at each depth, which may have altered the types of microbes we were able to culture. This may be because biocrusts are known to increase soil moisture in the deeper soil layers (Chamizo et al. 2012a), and this property may improve overall fire resistance.

However, this result should not be taken at face value. The placement of the thermocouples was haphazard. We used a ruler to place the thermocouples at the exact locations prior to each burn, but they could have shifted as we moved the mug into the pyrocosm. This may also explain why the thermocouples are about a cm off from the values predicted by our model. The purpose of this experiment was not to test if biocrusts cooled deeper soil layers during a fire, but based on these results, future research should examine this hypothesis with most predictable and accurate measurements at each depth.

Conclusion

This is a step towards understanding how biocrust and soil microbes respond to fire. We showed that culturable microbes can grow from 2-10 cm deep after a fire. However, culture independent methods like metagenomics or RNA sequencing would provide more information about the microbial community at different depth and may provide sequences from the top cm of the soil that we were unable to successfully culture and sequence since the majority of soil microorganism have not been identified in culture (Pham and Kim 2012).

Furthermore, we showed that a simulated fire with a blowtorch can be used to answer small scale questions related to how organisms respond to fire. The method can be modified for future studies to fit their research needs.

The survival of biocrust and soil microorganisms a few cm below the soil surface has implications for overall ecosystem recovery and improves our understanding of resiliency in soil microbes. To understand how this might impact the microbial community recovery from fire there are several further research questions that need to be addressed. First, we need to determine if the microbes that survived can ultimately form a new biocrust. Here, we showed that biocrust forming microorganisms could survive but future research needs to test how or if they can form new biocrusts and at what rate. Second, further research should address how these microbes survive fire. Some bacteria are motile (Schuergers et al. 2017) and may be able to move deeper in the soil to escape the initial heat from the fire. Others might enter a fire resistant dormant state and form an akinete (Kimura et al. 2017a). Currently, we know that biocrusts can be recolonized through aerial transport (Warren et al. 2019) and now, we should pursue further research to understand if the microbes in the soil after a fire can also act as a source for recolonization.

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Tables and Figures

Table 1: Results from the t-test comparing the temperatures at each depth recorded by the thermocouples for the first 30 minutes of the experiment which included the ramp-up, ten-minute burn at the treatment temperature, and a cooldown period.

Fire Temp. (°C)	Depth (cm)	t-value	p-value	Bare Mean (°C)	BSC Mean (°C)	Bare Max (°C)	BSC Max (°C)
450	2	6.44	<0.001	123.14	94.80	304. 4	301.7
450	5	12.69	<0.001	53.91	36.88	106.2	68.93
450	8	11.89	<0.001	30.28	23.30	48.52	32.37
600	2	12.85	<0.001	190.95	94.07	502.1	479.3
600	5	13.17	<0.001	46.76	31.36	85.1	51.95
600	8	14.12	<0.001	38.37	23.55	75.86	29.89

Table 2: The first hit from the NCBI database for each culture.

NCBI Hit	Query Cover	Per. Ident	Accession	Type	Temp	Depth
Wilmottia murrayi 23PC	92%	97.25%	KY288988.1	Bare	450	2
uncultured fungus genomic DNA sequence	95%	90.05%	OU940418.1	Bare	450	6
uncultured fungus genomic DNA sequence	95%	88.90%	OU940418.1	Bare	450	6
Pseudophormidium americanum KT18	66%	97.75%	MK861905.1	Bare	600	2

Leptolyngbya cf. frigida ACT684	96%	98.32	MK248006.1	Bare	600	4
Trichocoleus desertorum	93%	96.88%	MK478718.1	Bare	600	4
Uncultured Vahlkampfiidae	96%	90.42%	EU812478.1	Bare	600	4
Spongiochloris spongiosa	82%	94.71%	KM020025.1	Bare	600	5
Uncultured Chlamydomonadales isolate soil	24%	94.74%	MF482975.1	Bare	600	6
Spongiochloris spongiosa	60%	93.55%	KM020025.1	Bare	600	6
Leptolyngbya cf. frigida ACT684	93%	95.94%	MK248006.1	Bare	Control	1
Brevundimonas sp. LY-2	94%	97.32%	GU003879.1	Bare	Control	2
Chlorococcum isabeliense	70%	92.08%	LT594563.1	Bare	Control	2
Brevundimonas sp. MF30-B	92%	98.52%	CP038440.1	Bare	Control	3
Brevundimonas sp. MF30-B	93%	99.12%	CP038440.1	Bare	Control	4
Leptolyngbya cf. frigida	93%	97.69%	MK248006.1	Bare	Control	5
Brevundimonas sp. GENT16	74%	79.51%	LC094574.1	BSC	450	2
Heterochlamydomonas sp.	94%	99.53%	MT735195.1	BSC	450	5
Uncultured bacterium gene for 16S rRNA, partial sequence, clone: L1CLN37	95%	97.45%	AB696310.1	BSC	600	2
Edaphochlorella mirabilis	30%	94.90%	OM472009.1	BSC	600	2
Tolypothrix sp. Es_Yyy1600	90%	94.30%	KC463187.1	BSC	600	3
Brevundimonas sp. MF30-B	77%	78.68%	CP038440.1	BSC	600	3
Brevundimonas sp. FrW-Ado30	95%	98.16%	LC324780.1	BSC	600	5
Phormidesmis sp. WJT36-NPBG20	88%	96.55%	KJ939034.1	BSC	Control	4
Brevundimonas sp. SCU-B193	91%	84.98%	KJ000827.1	BSC	Control	4
Brevundimonas sp. FrW-Ado30	94%	98.83%	LC324780.1	BSC	Control	4

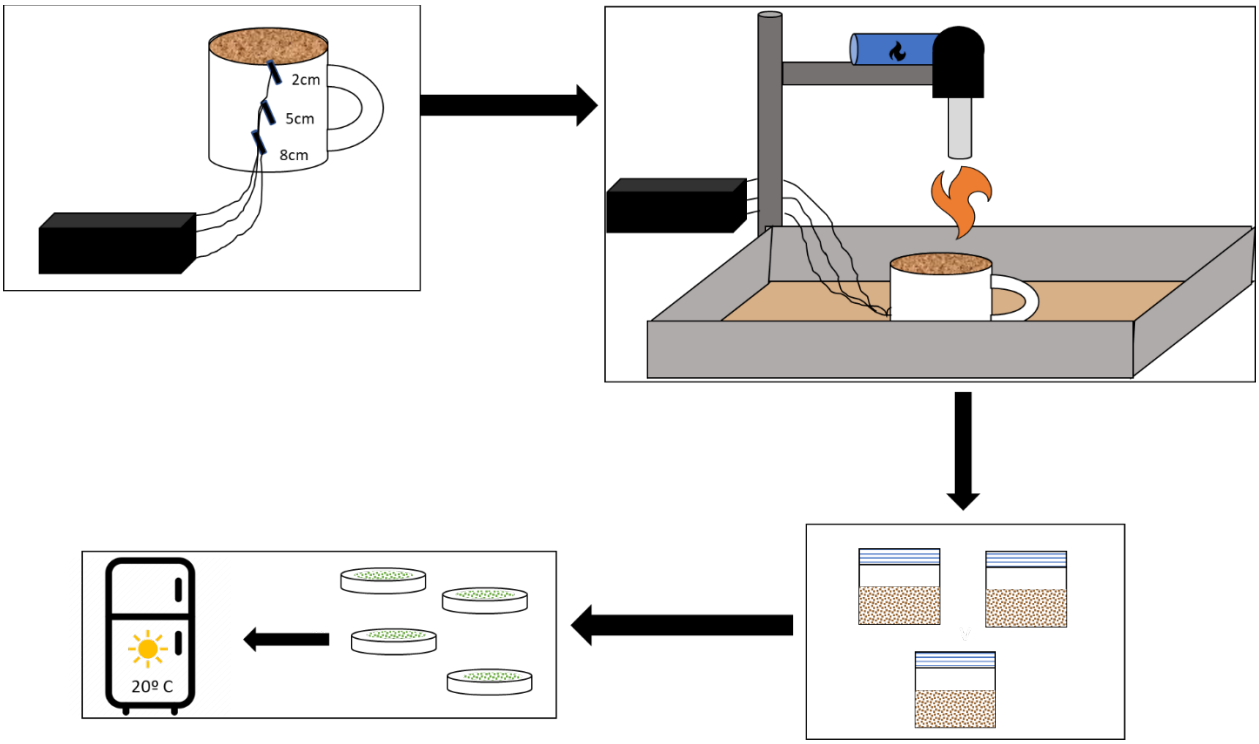

Figure 9: Schematic of the burn methods and downstream analyses. Thermocouples were placed at 2cm, 5cm, and 8cm depth in a ceramic mug which was then placed in a tray of sand below a calibrated blow torch. After burning the soil and biocrusts in the mug, each cm was separated into separate sterile bags. We used soil from each depth to inoculate BG-11 agar plates and allowed the microbes to grow in a growth chamber.

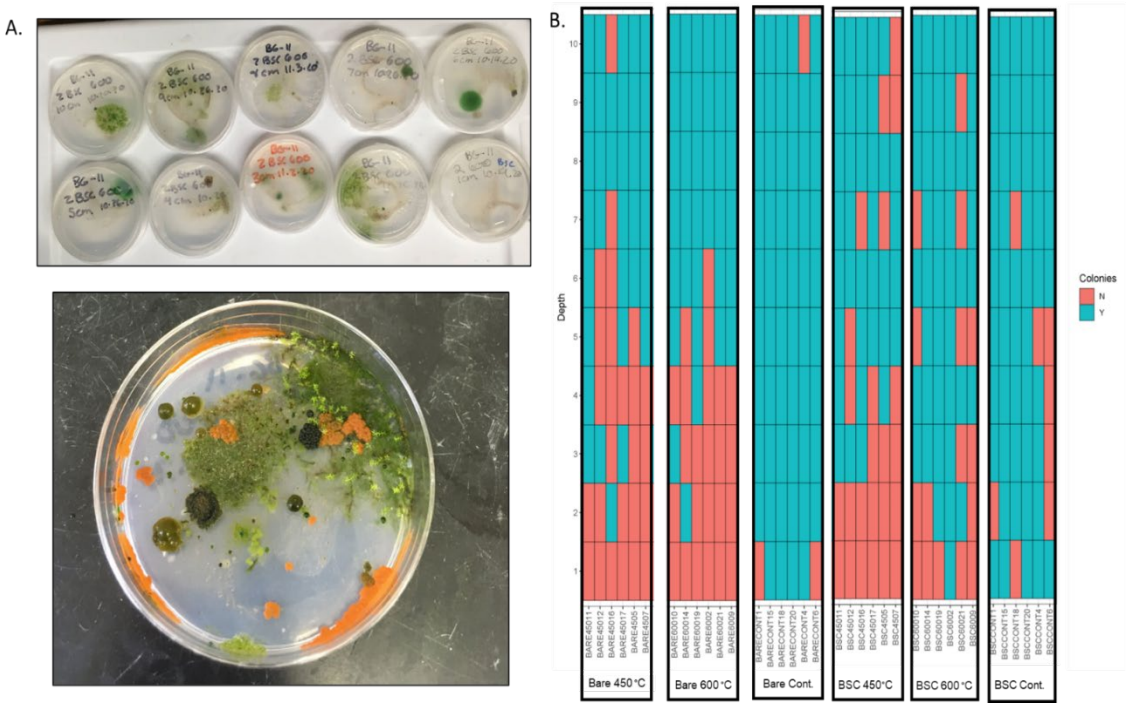

Figure 10: A) Photo of ten culture plates from 1-10cm depth for biocrust burned at 600°C and a photo of an open culture plate revealing the diversity of microorganisms found in the samples. B) The presence/absence of cultures on BG-11 agar plates for each sample at each depth (1-10cm). Red rectangles indicate there was no growth after 3 months and blue rectangles indicate there was >1 CFU on the plate after 3 months.

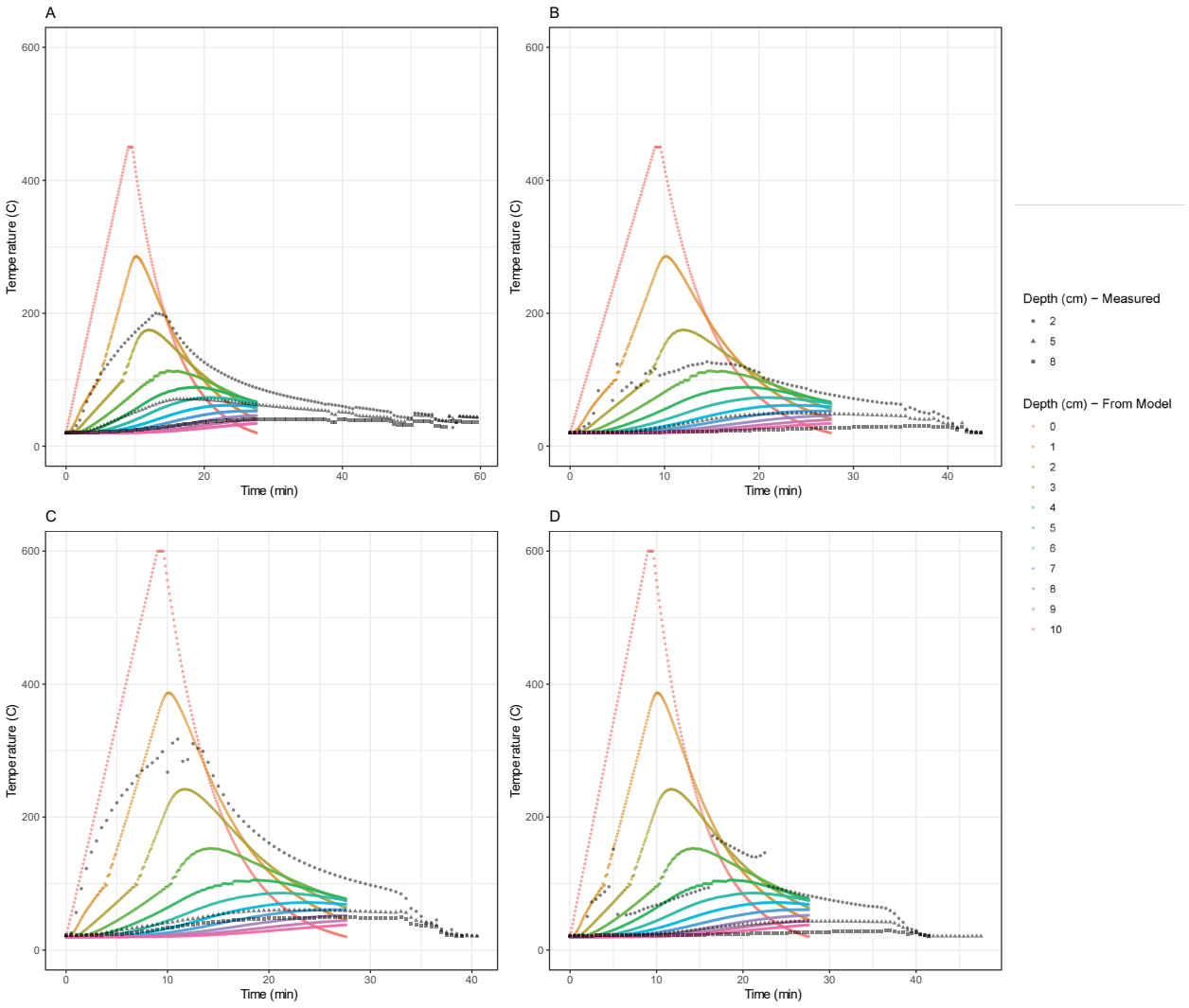

Figure 11: The model predictions of soil temperature for A) Bare soil burned at 450°C; B) Biocrust burned at 450°C C) Bare soil burned at 600°C, and D) Biocrust burned at 600°C. Gaps in the thermocouple data occurred when the thermocouples overheated, particularly at the lower depths. The actual depth of the thermocouples is assumed to be 2cm, 5cm, and 8cm but they may have shifted during the experiment. Surface temps remained consistent throughout with both fire treatments reaching 450°C and 600°C respectively.

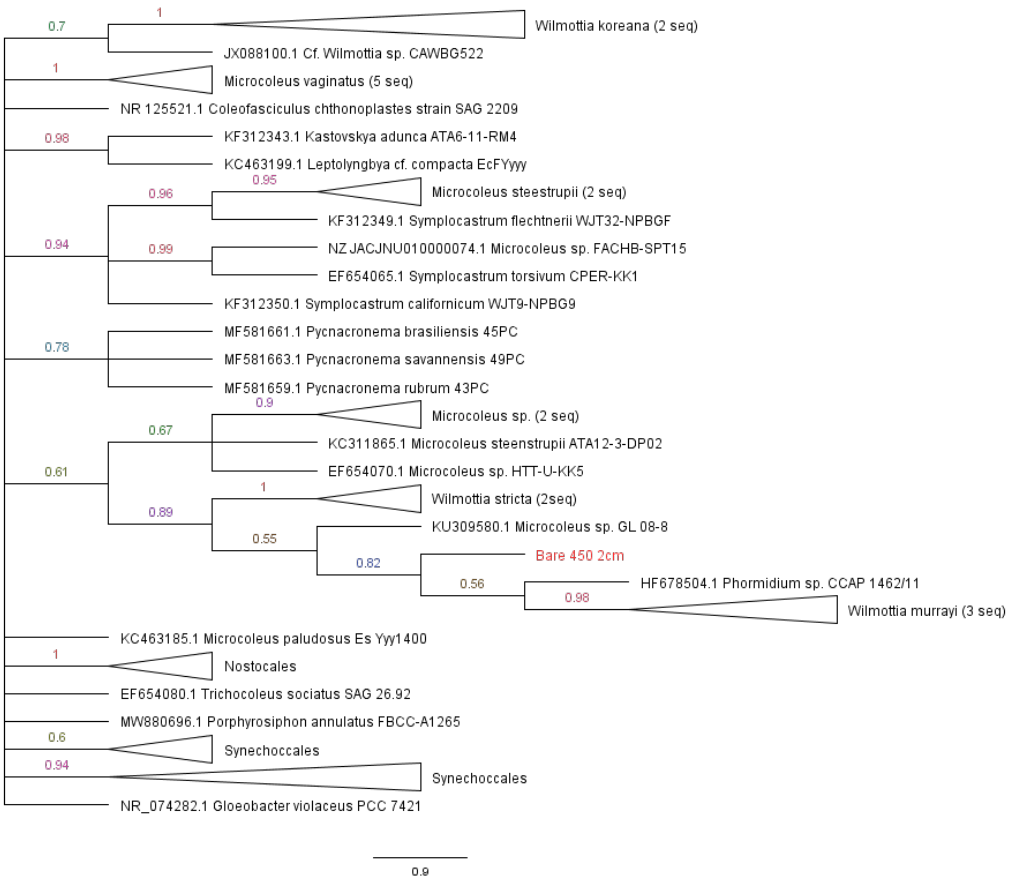

Figure 12 Maximum likelihood tree for Oscillatoriales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.

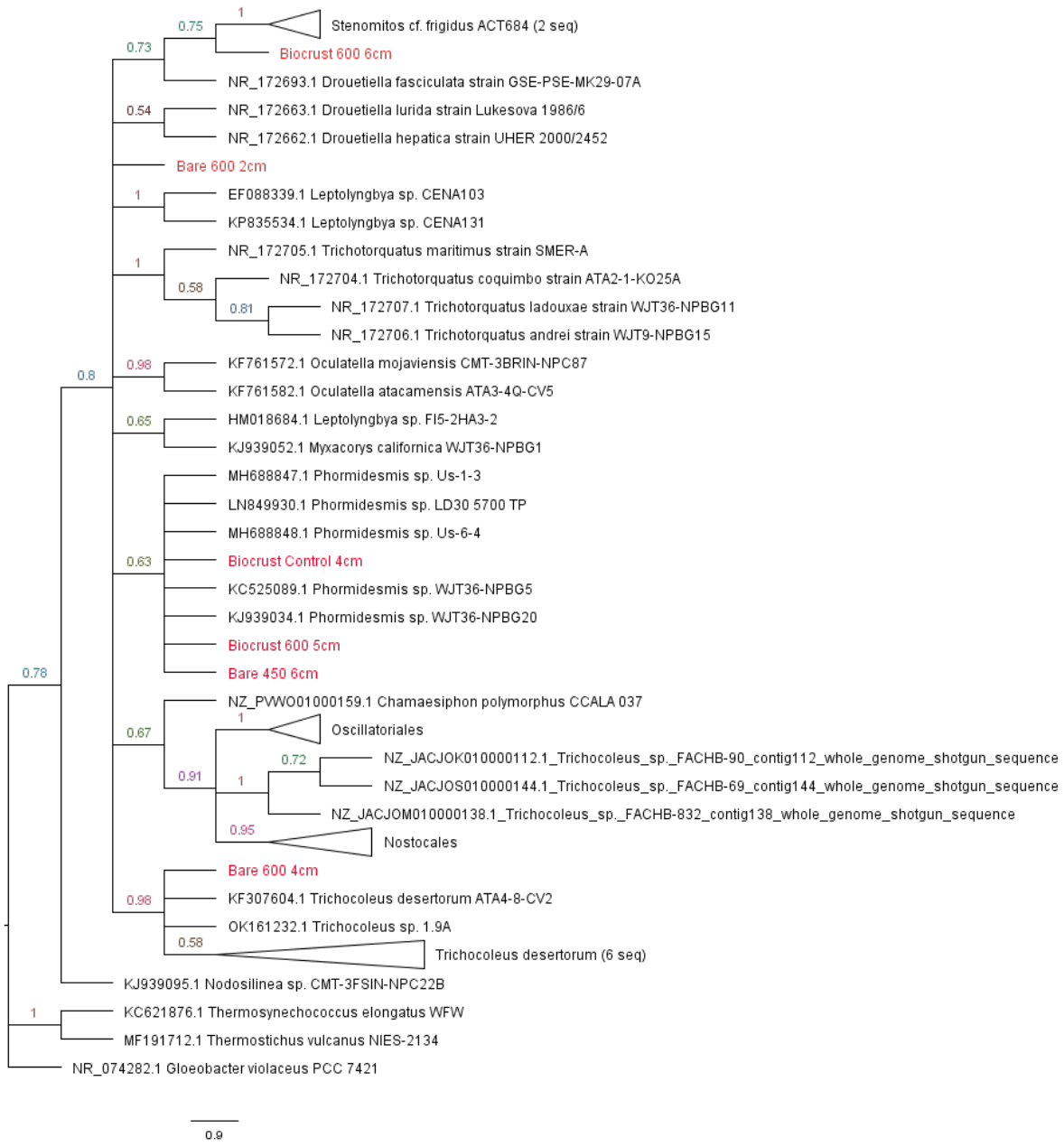

Figure 13 Maximum likelihood tree for Synechoccales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.

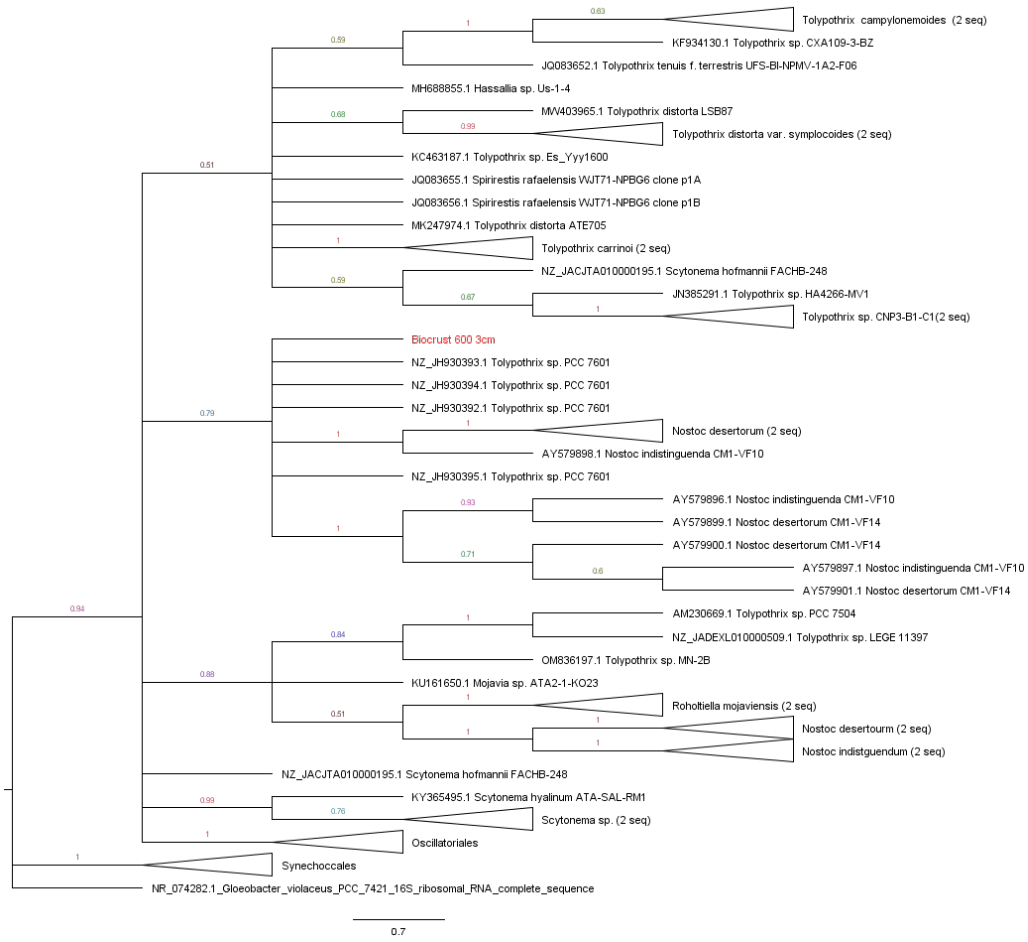

Figure 14 Maximum likelihood tree for Nostocales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.

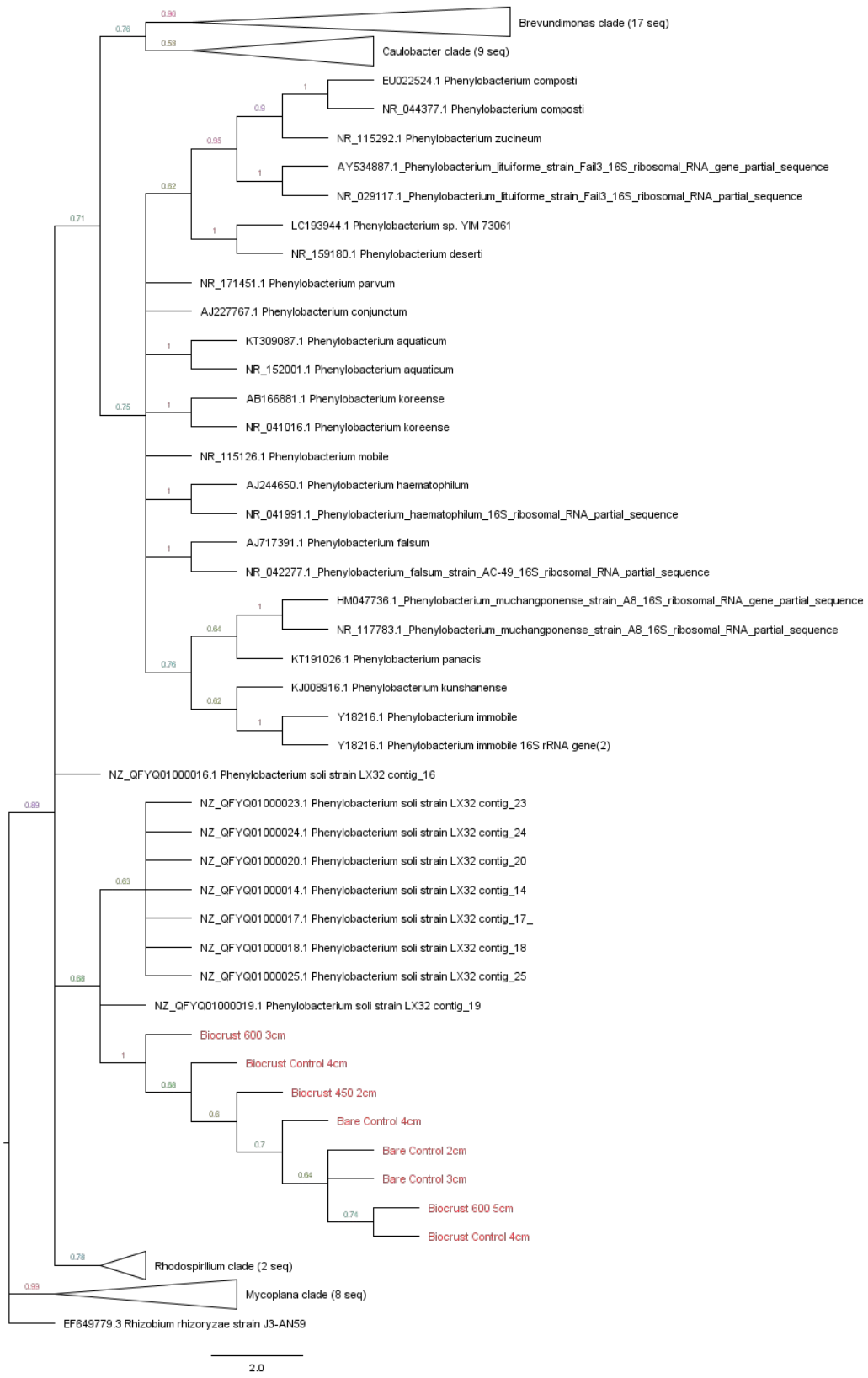
Brevundimonas clade (17 seq)
Caulobacter clade (9 seq)
EU022524.1 Phenylobacterium composti
NR_044377.1 Phenylobacterium composti
NR_115292.1 Phenylobacterium zucineum
AY534887.1_Phenylobacterium_lituiforme_strain_Fail3_16S_ribosomal_RNA_gene_partial_sequence
NR_029117.1_Phenylobacterium_lituiforme_strain_Fail3_16S_ribosomal_RNA_partial_sequence
LC193944.1 Phenylobacterium sp. YIM 73061
NR_159180.1 Phenylobacterium deserti
NR_171451.1 Phenylobacterium parvum
AJ227767.1 Phenylobacterium conjunctum
KT309087.1 Phenylobacterium aquaticum
NR_152001.1 Phenylobacterium aquaticum
AB166881.1 Phenylobacterium koreense
NR_041016.1 Phenylobacterium koreense
NR_115126.1 Phenylobacterium mobile
AJ244650.1 Phenylobacterium haematophilum
NR_041991.1_Phenylobacterium_haematophilum_16S_ribosomal_RNA_partial_sequence
AJ717391.1 Phenylobacterium falsum
NR_042277.1_Phenylobacterium_falsum_strain_AC-49_16S_ribosomal_RNA_partial_sequence
HM047736.1_Phenylobacterium_muchangponense_strain_A8_16S_ribosomal_RNA_gene_partial_sequence
NR_117783.1_Phenylobacterium_muchangponense_strain_A8_16S_ribosomal_RNA_partial_sequence
KT191026.1 Phenylobacterium panacis
KJ008916.1 Phenylobacterium kunshanense
Y18216.1 Phenylobacterium immobile
Y18216.1 Phenylobacterium immobile 16S rRNA gene(2)
NZ_QFYQ01000016.1 Phenylobacterium soli strain LX32 contig_16
NZ_QFYQ01000023.1 Phenylobacterium soli strain LX32 contig_23
NZ_QFYQ01000024.1 Phenylobacterium soli strain LX32 contig_24
NZ_QFYQ01000020.1 Phenylobacterium soli strain LX32 contig_20
NZ_QFYQ01000014.1 Phenylobacterium soli strain LX32 contig_14
NZ_QFYQ01000017.1 Phenylobacterium soli strain LX32 contig_17_
NZ_QFYQ01000018.1 Phenylobacterium soli strain LX32 contig_18
NZ_QFYQ01000025.1 Phenylobacterium soli strain LX32 contig_25
NZ_QFYQ01000019.1 Phenylobacterium soli strain LX32 contig_19
Biocrust 600 3cm
Biocrust Control 4cm
Biocrust 450 2cm
Bare Control 4cm
Bare Control 2cm
Bare Control 3cm
Biocrust 600 5cm
Biocrust Control 4cm
Rhodospirillium clade (2 seq)
Mycoplana clade (8 seq)
EF649779.3 Rhizobium rhizoryzae strain J3-AN59
2.0

Figure 15 Maximum likelihood tree for Caulobacterales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.

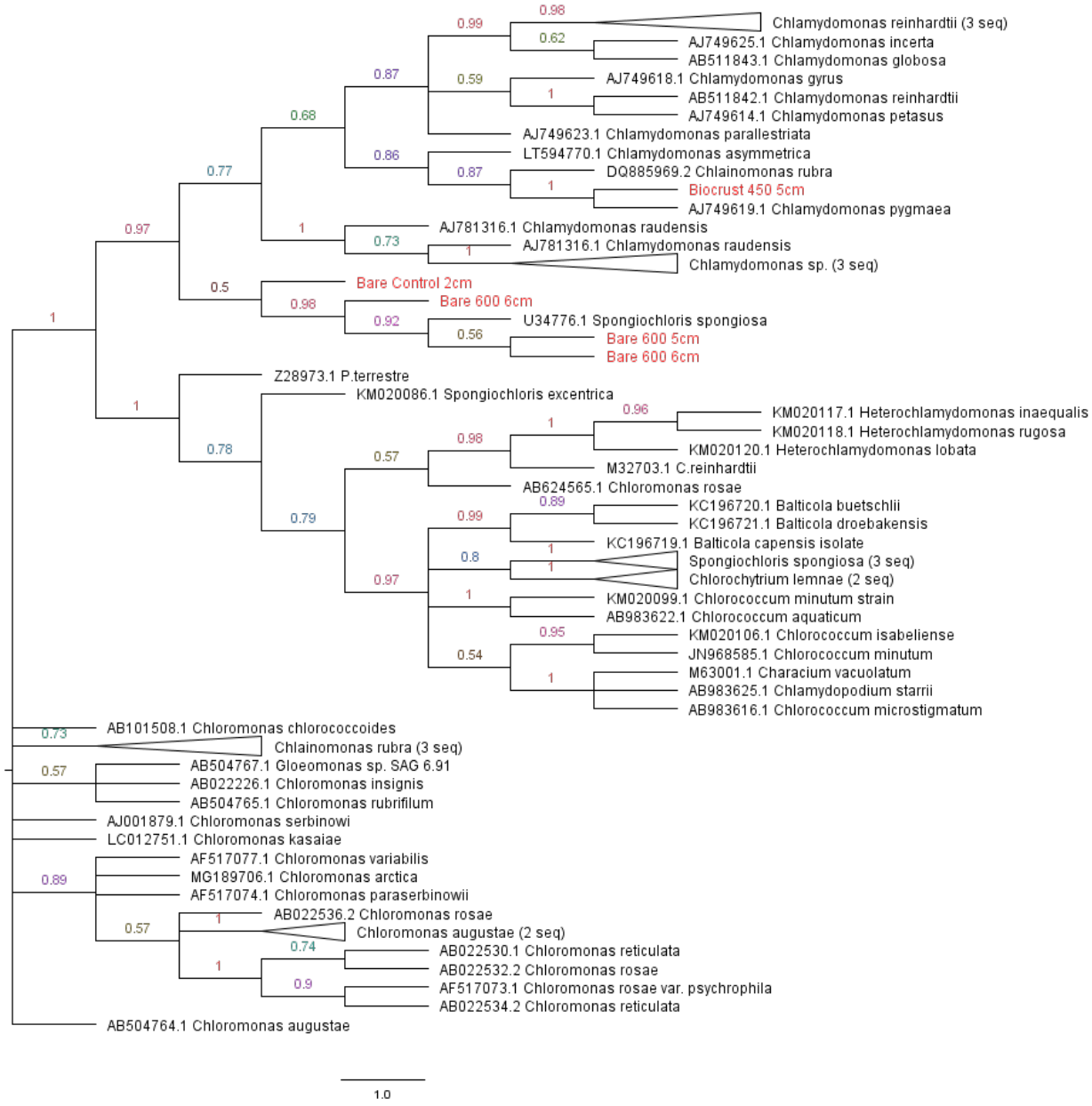

Figure 16 Maximum likelihood tree for Chlamydomonadales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.

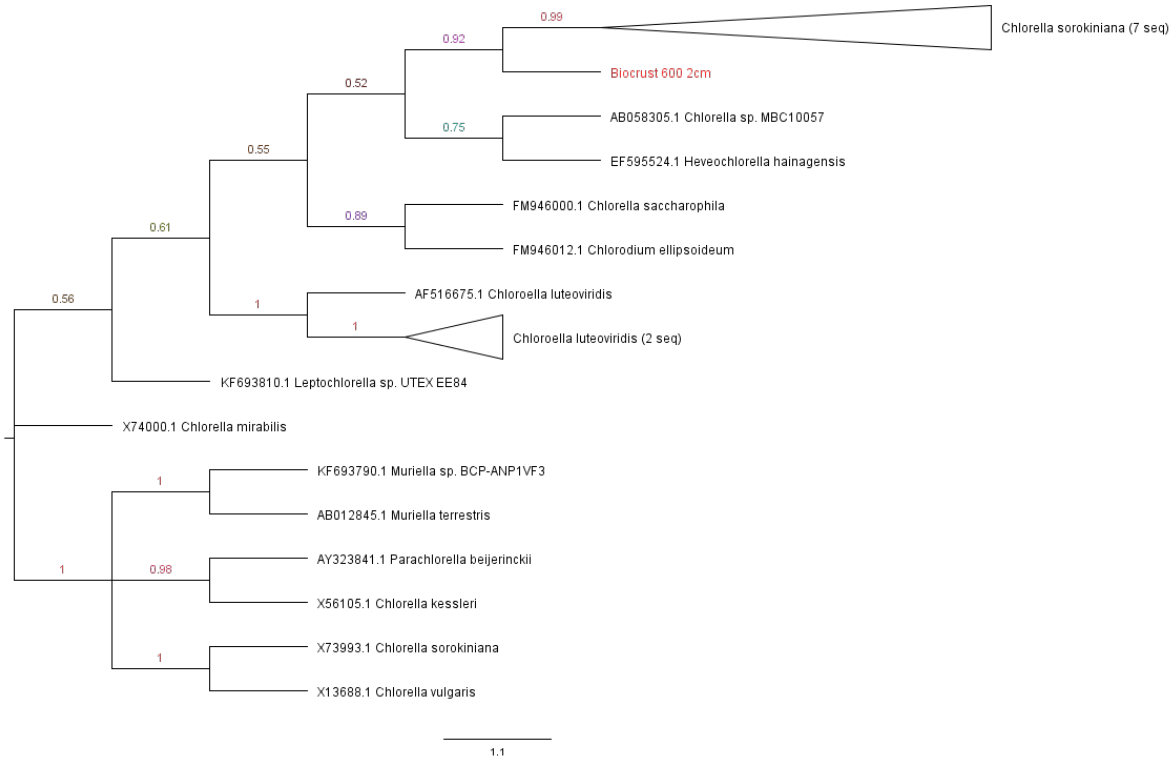

Figure 17 Maximum likelihood tree for Chlorellales. Bootstrap values are denoted on the branches. Bootstrap values indicate the percent of the trees with that particular branch placement. Bootstrap values >0.70 are considered well supported.