

THESIS

UNDERSTANDING SOIL TREATMENT EFFECTIVENESS IN DRYLAND
RESTORATION: ECOLOGICAL BARRIERS, CONTEXTS, AND BASELINE CONDITIONS

Submitted by

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ABSTRACT

UNDERSTANDING SOIL TREATMENT EFFECTIVENESS IN DRYLAND RESTORATION: ECOLOGICAL BARRIERS, CONTEXTS, AND BASELINE CONDITIONS

Land degradation is one of the greatest environmental issues our planet faces today, with over 33% of Earth's soils currently degraded. Drylands are especially vulnerable to soil degradation given their history of intensive land use and desertification. However, dryland restoration can be very difficult, and often fails when seeding is used as a sole treatment. Soil-based restoration, which includes abiotic treatments like organic amendments and water collection pits, and biotic treatments like microbial inoculation, may be needed for ecosystem recovery in drylands. Compared to plant-based restoration, however, less is known about how and when to use active soil restoration for optimal results. To improve our understanding of how to best use active soil restoration to restore degraded drylands, we conducted two research studies: (1) a global meta-analysis of dryland soil restoration treatment effectiveness across environmental gradients (Chapter 1), and (2) a regional field study comparing microbial communities across degraded, intact, and revegetated dryland sites to understand baseline conditions and when active soil restoration (e.g., inoculation) may be needed to improve soil conditions (Chapter 2).

For project 1, we generated a global database from 155 publications and 1,403 unique studies of responses of soil health variables [i.e., aggregate stability, bulk density, soil moisture, soil organic carbon, soil nitrogen, mycorrhizal colonization, and basal respiration] to soil restoration relative to untreated controls. We then used quantitative meta-analysis techniques to analyze soil restoration effect sizes. In Chapter 2, we collected soil samples from paired reference, degraded, and revegetated plots across seven different dryland sites across the southwestern United

States, sequenced the 16S and ITS rRNA gene regions from extracted DNA for bacteria/archaeal and fungal communities (respectively), and analyzed differences in microbial community composition among samples. Results from the meta-analysis suggested that active soil restoration generally improves soil health and is most effective in arid, fine-textured soils. Organic amendments were most effective at increasing soil organic carbon, while fungi inoculation treatments were most effective at increasing mycorrhizal colonization. From the regional microbiome study, we found that soil microbial communities differ between paired degraded and intact sites, and that degraded sites have lower abundances of biocrust-forming bacteria and dark septate endophytic fungi, which are both indicative of reference/intact conditions, making these taxa potential targets for inoculation treatments. However, we found that microbial communities do not differ between degraded and revegetated sites, suggesting that degraded sites may require active interventions beyond revegetation, such as direct microbial inoculation, to replenish microbial communities. These findings advance understanding of the effects of dryland degradation and restoration on soil health and have actionable implications for improving restoration decision-making, and thus improve outcomes in dryland restoration.

ACKNOWLEDGEMENTS

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summer with me reading, analyzing, and collecting data from papers for the meta-analysis. I could not have completed this without her!

I have also been lucky to have many mentors and role models in science throughout my life. As an undergraduate student at Tufts University, I was unsure of what I wanted to do with my life, what I was really passionate about, and how I wanted to make a difference in this world. I began as an Anthropology major, but struggled to feel passionate about the work I was doing. It wasn't until I took Biological Anthropology with Dr. Zarin Machanda, a primatologist, that things really clicked, and I realized how much I loved learning about the natural world, and discovering things through the scientific process. It was then that I learned about all the intricacies of evolution and how uniquely ecosystems are adapted to their environment, that I decided that I really wanted to study ecology. From there, I had several other incredible professors and mentors that have further inspired me. Dr. Kate Tully, at the University of Maryland, was the first person who really believed in me as someone with a limited scientific background, and gave me an opportunity to gain research experience by working in her amazing agroecology lab for a summer. Dr. Andrew Kemp, professor of paleoclimate at Tufts University, was also a great inspiration and incredible educator, and has always supported me in my research pursuits.

I have also had an incredible support system outside of CSU, which I am very grateful for. Firstly, I would like to thank my parents, who have always supported me in pursuing my passions and who have never doubted my ability to succeed, even when things have been hard. I am really lucky to come from a large family, where truly everyone has supported me in my path as a scientist and environmentalist. I especially appreciate so many of my family members' (successful!) attempts to better understand soil science, including my grandfather who frequently sends me books and articles about advances in environmental soil science! Additionally, I have so many

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INTRODUCTION

Land degradation, the deterioration or loss of the productive capacity of the soils, is one of the greatest environmental issues our planet faces today, with over 33% of Earth's soils currently degraded and the potential for over 90% to become degraded by 2050 (FAO & ITPS, 2015). Globally, at least 3.2 billion people are directly impacted by land degradation, especially those whose livelihoods depend on agriculture, natural resource use, and ecosystem services (IPBES 2018). This issue is particularly pervasive in Earth's semi-arid and arid (dryland) ecosystems (Chambers & Wisdom, 2009) which cover 46% of Earth's land surface and contain half of the world's agricultural systems (Maestre et al., 2021). Drylands are especially vulnerable to land degradation given their water limitation, and long history of intensive agriculture, urbanization, resource extraction, and escalating aridification in the face of climate change (IPBES, 2018). Once degraded, dryland ecosystem functionality often cannot be recovered within the timescale of human lives in the absence of active ecological restoration, the process of applying active management techniques to overcome physical and biotic barriers that limit ecosystem recovery (Gann et al., 2019).

Land degradation has disproportional consequences in drylands (Chambers & Wisdom, 2009), and ecological restoration is particularly difficult in these systems. Novel methods may be needed to achieve multidimensional management goals such as increasing soil health, ecosystem functioning, native plant establishment, and forage quality (Hardegree et al., 2016). Dryland restoration has historically focused mainly on revegetation through native plant seeding (Palma & Laurance, 2015), yet seeding alone is often ineffective in recovering ecosystem functioning in degraded drylands (Shackelford et al., 2021). This may be due to the fact that seeding only addresses the barrier of a lack of plant propagules in the soil of a particular site and does not

address other barriers such as low moisture and nutrient availability or a lack of beneficial microbial taxa, which commonly limit ecosystem recovery in degraded dryland systems (Anaya-Romero et al., 2015; Muñoz-Rojas et al., 2016). As such, although often ignored in the restoration process, active soil restoration, meaning non-vegetation restoration treatments that specifically target soil health, may be needed to overcome physical and biotic barriers limiting restoration success to achieve soil health and plant establishment goals (Rorive & Bainbridge, 1993; Stroosnijder et al., 2012; Stanturf et al., 2021). Despite this growing need, we have a limited understanding of how active soil restoration techniques can be used to overcome physical and biotic barriers to ecosystem recovery and improve soil health across environmental gradients in degraded drylands.

Restoration of degraded soils is also important given that healthy soils support critical ecological functions including biodiversity, plant productivity, erosion control, and carbon sequestration (Doran and Safley, 1997, Van Der Heijen et al., 2008, Paustian et al., 2016, Magdoff and Van Es, 2021). Depending on the degree of degradation and what barriers limit ecosystem recovery, either physical (abiotic) or biotic soil restoration treatments may be needed to recover ecosystem functioning in degraded drylands (Suding et al., 2004). Degraded drylands face a number of abiotic barriers to ecosystem recovery including low moisture and nutrient availability and highly erodible soils (Noy-Meir, 1973). Treatments such as water catchments, organic amendments, and soil stabilizers could be used to address such physical barriers (Chaudhary et al. 2020; Faist et al. 2020).

Restoration of diminished soil biotic communities may also be critical for ecosystem recovery. Soil microbial communities including bacteria, archaea, and fungi can support soil health by increasing structural stability, water-holding capacity, and nutrient cycling (Bowker 2007). In

drylands, soil microbes can also facilitate plant recruitment, survival, and productivity by increasing consistency of plant access to water and nutrients in space and time (Pointing & Belnap, 2012; Naylor & Coleman-Derr, 2018). As such, restoration of degraded soil biotic communities could have promising implications for use in ecological restoration (Zhang et al. 2021, Harris 2009).

In recent decades, physical and biotic soil-based restoration techniques including soil amendments, soil stabilizers, water collection devices, and microbial inoculations have been increasingly used with the goal of re-establishing soil health and alleviating barriers to plant recruitment in degraded drylands. However, these treatments have shown varying success in promoting ecosystem recovery (Chaudhary et al., 2020; Faist et al., 2020; Román et al., 2021). One potential reason underlying this variation in success may be that restoration practitioners often lack a predictive understanding of the ecological contexts in which soil-based treatments may be most beneficial, including the types of treatments shown to be most effective across environmental gradients, and site-specific conditions under which restoration is most effective. Additionally, for biotic treatments specifically, we often lack information on baseline microbial conditions in degraded dryland sites, making it difficult to choose proper inoculation treatments. A greater understanding of how, when, and where to use soil-based restoration could help improve decision making in dryland restoration by allowing practitioners to select treatments that will be most effective and identify sites where restoration will be most useful. This information will help improve restoration outcomes and is thus a critical knowledge gap in dryland restoration ecology and management.

This thesis includes two research studies that aim to address this knowledge gap:

1. A global meta-analysis of how soil-based restoration treatment success varies across environmental gradients in drylands
2. A regional field study comparing soil microbial communities across paired degraded, intact, and revegetated sites in dryland ecosystems of the western United States

CHAPTER 1 - SOIL RESTORATION INCREASES SOIL HEALTH ACROSS GLOBAL DRYLANDS: A META-ANALYSIS

Introduction

Restoration of degraded landscapes is of urgent need in order to help sustain livelihoods (George et al., 2018), enhance natural carbon sequestration (Di Sacco et al., 2021), and mitigate other impending environmental crises such as poor water quality and loss of biodiversity (Rey Benayas et al., 2009), yet, drylands are particularly difficult to restore. Dryland restoration has historically focused on revegetation through native plant seeding (Palma & Laurance, 2015), though seeding alone is often ineffective in recovering ecosystem functioning in degraded drylands (Shackelford et al., 2021). Even when native plant seeding is successful in increasing plant establishment, it may not improve soil health conditions without additional intervention (Yang et al., 2022). Other methods, such as active soil-based restoration, meaning non-vegetation restoration treatments that specifically target soil health, may be needed (Farrell et al., 2020). Active soil restoration treatments include anything that can be applied to the soil that is not just a plant or seed, such as organic amendments, erosion control structures, water retention agents, microbial inoculations, and more (Fig. A1.2 in Appendix 1). Soil restoration addresses various abiotic and biotic barriers to ecosystem recovery in drylands, while seeding alone only addresses the barrier of a lack of plant propagules. Abiotic barriers include low moisture and nutrient availability, as well as soil erodibility, while biotic barriers include diminished beneficial soil microbial communities, which commonly limit ecosystem recovery in degraded dryland systems (Anaya-Romero et al., 2015). Despite this growing need for active soil restoration, we have a

limited understanding of how these techniques can be best used to improve soil health across environmental gradients in degraded drylands.

In recent decades, soil-based restoration techniques have been increasingly used with the goal of re-establishing soil health in degraded drylands (Chaudhary et al. 2020; Faist et al. 2020; Roman et al., 2021). However, these soil treatments have shown varying degrees of success in promoting recovery of soil function. Some studies suggest that certain treatments may work better than others at improving soil health, such as Antoninka et al. (2019), which found that biocrust inoculation increased aggregate stability, but straw barriers and soil tackifiers did not. Additionally, Luna et al. (2016) found that organic amendments were more effective than mulch at improving multiple aspects of soil health. Other studies suggest that environmental conditions largely control whether or not restoration efforts are successful. For example, a study by Bateman et al. (2019) suggests that the effectiveness of restoration treatments depends on how water-limited the system is. Similarly, Chua et al. (2019) found that soil type was a more important determinant of soil health than whether a plot was treated or not. Such variability in restoration outcomes highlights a current lack of a predictive understanding of the ecological contexts in which soil-based restoration treatments may be most beneficial for improving soil health.

To address this knowledge gap of how to best use soil-based restoration to improve soil health in drylands, we compiled available literature on soil-based restoration in drylands and conducted meta-analyses to determine how the effects of soil-based restoration vary across ecological and restoration context factors. We used our results from this analysis to answer the following questions:

1. How does soil restoration affect various measures of soil health?

2. Do these effects of soil restoration vary across environmental stress gradients of aridity and soil texture?
3. Could other restoration intervention factors, such as the type of treatment used, additional revegetation, and time since restoration, impact the effect of soil restoration?
4. What information on soil restoration in drylands are we still lacking and where should future research focus?

We predicted that overall, soil restoration would benefit soil health, and that the effectiveness of soil restoration would increase with aridity and percent soil sand. We made this prediction under the assumption that soil health could improve by larger margins in areas facing more limited moisture and nutrient availability (typical of arid and sandy soils) than it would in areas that already had high levels of moisture and nutrients (Augustin & Cihacek, 2016; Klemmedson, 2009). Additionally, we predicted that treatment type, revegetation, and time since restoration would all impact soil restoration effectiveness.

Methods

Literature search and database creation

To identify relevant literature we searched the Web of Science Core Collection database (<http://www.webofknowledge.com/>) using the following search terms:

dryland OR desert* OR arid* OR shrubland* OR rangeland* AND
restor* OR rehabilitat* OR reclamation* OR revegetat* AND soil**

From the records that came up from our search, we only selected articles that

1. examined some type of active, soil-based restoration treatment, as opposed to passive restoration (i.e. letting land regenerate naturally by providing protection only), or restoration through seeding or revegetation only,
2. took place in a dryland, defined by having an aridity index of less than 0.65 (Cherlet et al. 2018), on land that was not being currently cultivated (previous meta-analyses have covered agroecosystems),
3. quantified at least one of the chosen soil health metrics (aggregate stability, bulk density, volumetric water content (%VWC) (as a measure of soil moisture), soil organic carbon (SOC), soil nitrogen (N), mycorrhizal colonization, or basal respiration, and
4. contained an untreated control, meaning an adjacent plot or area where soil restoration treatments were not applied.

After this screening process we selected 155 articles, which included 1,403 unique studies, each quantifying the effect of a soil-based restoration treatment versus an untreated control for the seven chosen soil health metrics (Fig A1.1 in Appendix 1). These metrics were chosen based on their representation of physical, chemical, and biological properties of soils, as well as their common presence in the literature. Specifically, aggregate stability and bulk density are useful in determining nutrient holding capacity, aeration and infiltration, and susceptibility to erosion or compaction (Raghavendra et al., 2020). Volumetric water content, which was the most commonly reported measure of soil moisture, indicates water availability to plants and microbes and also influences aeration (Voroney 2019). Organic carbon and nitrogen are essential nutrients for plants and microbes, and are therefore major aspects of soil health (Raghavendra et al., 2020). Lastly, mycorrhizal colonization and basal respiration are both ways to quantify the presence of microbes in the soil that can be integral in aiding plant nutrient uptake (Raghavendra et al., 2020). Other

biotic soil health metrics, such as microbial diversity, were considered but were not reported enough in the literature to yield sufficient data for meta-analysis.

From each study, we extracted the mean, standard deviation or standard error, and the number of replicates for the treatment and control groups. When data were represented in figures rather than numerical values, we used the online tool *graphreader* to extract values from figure images (Graphreader, 2022). We also recorded information on candidate moderator variables. These included what type of restoration treatment was used in the study (i.e., Treatment_Type; Table 1.1), as well as the aridity index (Aridity_Index) and soil texture (Percent_Sand) of the study site. We chose aridity and soil texture as representative environmental stress variables because these are two of the most influential variables in controlling ecosystem functioning in drylands, given that both are related to water availability (Maestre et al., 2021). These two variables were found to be only weakly correlated to each other (24%) from a correlation analysis using the `corrplot()` function in R. To calculate Aridity_Index for each study, we extrapolated precipitation and potential evaporation data from the geographic coordinates of each study using the TerraClimate dataset (Abatzoglou et al., 2018). When soil texture data were not reported for a given study, we extrapolated sand percentages using SoilGrid spatial data from the World Soil Information Service database (Hengl et al., 2014).

Lastly, we extracted data on whether treated plots were seeded or revegetated in addition to a soil treatment (Revegetation), and how long it had been since the treatment(s) were implemented when data were collected (Time). We also collected data on the soil depth at which measurements had been taken. Soil depth is important when considering variables such as SOC, which has been shown to generally decline with soil depth (Liu et al., 2021). However, this information was only reported in about 60% of studies for SOC, and when analyzed using

generalized boosted regression models from the *gbm* package (Greenwell et al., 2022), had a relative influence of less than 3% on the effect size for SOC. In order to avoid a large reduction in sample size, we did not include soil depth in our models. See Appendix 1 for supplementary methods.

Table 1.1. Descriptions of each moderator variable.

Variable name	Variable type	Variable description
Treatment_Type	Categorical	Type of treatment used; Seven levels: Organic amendment, Inorganic NPK fertilizer, Water retention treatment, Erosion control structure, Soil tackifier, Bacteria inoculation, Fungi inoculation (Fig. A2 in Appendix)
Aridity_Index	Continuous	The calculated aridity index of the site from 0 – 0.65; (low values meaning more arid, high values meaning more mesic)
Percent_Sand	Continuous	Percent of sand particles (0.5-2 mm diameter) of the study site's soil (Soil Survey Staff, 1999)
Revegetation	Categorical	Whether or not treatment plots were seeded or revegetated in addition to soil treatment(s); Two levels: Yes, No
Time	Continuous	Time since restoration treatment application in years

Calculation of meta-analysis metrics

To obtain the metrics needed for meta-analysis, we calculated the log response ratio (LnRR) as a measure of the effect size of soil restoration on each soil health metric, using equation 1 (Hedges et al. 1999):

$$\text{LnRR} = \ln(X_{\text{treatment}}/X_{\text{control}}); \text{eqn 1}$$

In this equation $X_{\text{treatment}}$ signifies the mean of the treatment group, and X_{control} signifies the mean of the control group. For bulk density, we took the inverse of the LnRR, as lower values for bulk density indicate better soil health, given that high bulk density usually means lower soil porosity,

which limits nutrient and water holding capacity and can lead to soil compaction (Raghavendra et al., 2020). We calculated within-study variance using equation 2 (Hedges et al., 1999):

$$\sigma^2 = [SD^2_{treatment}/(n_{treatment} * X^2_{treatment})] + [SD^2_{control}/(n_{control} * X^2_{control})]; \text{ eqn 2 (Appendix 1)}$$

When standard deviation (or standard error) were not reported (45% of studies), we used Taylor's Law, which describes the linear relationship between the natural log of the mean and standard deviation within a given dataset (Nakagawa, 2015). Equation 3 describes this relationship for our dataset:

$$\log(SD_{pooled}) = (\log(X_{pooled}) * 0.8878) - 1.951; R^2 = 0.6143; \text{ eqn 3}$$

Publication bias

To determine whether publication bias was detected in our data, we performed a p-curve analysis using the pcurve() function from the metasens package in R (Schwarzer et al., 2015). This p-curve is an alternative to the trim-fill method, as the p-curve tests for bias towards studies with low p-values, rather than just for effect sizes (Harrer et al., 2021). During this analysis, a curve of p-values is created for all studies and then right and left skewness are measured to test for bias towards studies with low p-values (Harrer et al., 2021). The results from this test indicated that evidential value was present in our study, meaning that publication bias was unlikely a main driver of the observed effect sizes produced from our models (Harrer et al. 2021).

Meta-analysis

We performed a separate meta-analysis for each soil health metric, totaling seven separate meta-analyses. All analyses were conducted in R version 1.4.1103 (R Core Team, 2022) using the metafor package (Viechtbauer, 2010). First, we used pure random effects models to determine the

overall effect size of soil restoration on each soil health metric without the influence of moderator variables using the `rma()` function. (2) Next, we used the `rma.mv()` function to run multivariate mixed-effects models for each response variable using the five moderator variables listed in Table 1. In these models we included interaction terms that were found to be significant from a boosted regression tree analysis using the `gbm.interactions()` function from the `gbm` package (Greenwell et al., 2020). For the `Treatment_Type` variable, we only included treatment types with sample sizes of at least 20.

From the multivariate models, we determined which moderator variables had a significant effect on LnRR in the presence of other moderator variables ($p < 0.05$), which then allowed us to select moderator variables to run in univariate mixed-effects models (Hoeksema et al. 2010, Havrilla et al. 2019). We chose to analyze univariate models because this allowed us to maximize the number of studies that could be analyzed as not all moderator variables were reported in every study, and calculate the intercept and slope or mean effect size values that described the relationship between each moderator variable and its effect on the LnRR of soil restoration. This approach allowed us to calculate these values while still taking into account the effects of all moderator variables to ensure that each moderator variable analyzed still had a significant effect on LnRR in the presence of other moderators. In all models, studies were nested within publications as well as within independent observations, where repeated observations of the same treatment made over multiple time points were analyzed as one group of observations (Harrer et al. 2021; Fernández-Castilla et al. 2020).

Results

Database summary

Studies included in our database spanned all continents excluding Antarctica (Fig. 1.1). The majority of studies took place in Europe ($n = 486$), Asia ($n = 463$), and North America ($n = 290$), while fewer took place in South America ($n = 86$), Australia ($n = 52$), and Africa ($n = 26$). Most of our studies assessed the effects of soil-based restoration on soil nutrients (SOC: $n = 518$; soil N: $n = 464$) and soil moisture ($n = 427$), while fewer analyzed effects on soil structure (aggregate stability: $n = 167$; bulk density: $n = 129$) and microbial communities (mycorrhizal colonization: $n = 164$; basal respiration: $n = 62$). See Appendix 1 for detailed database summary.

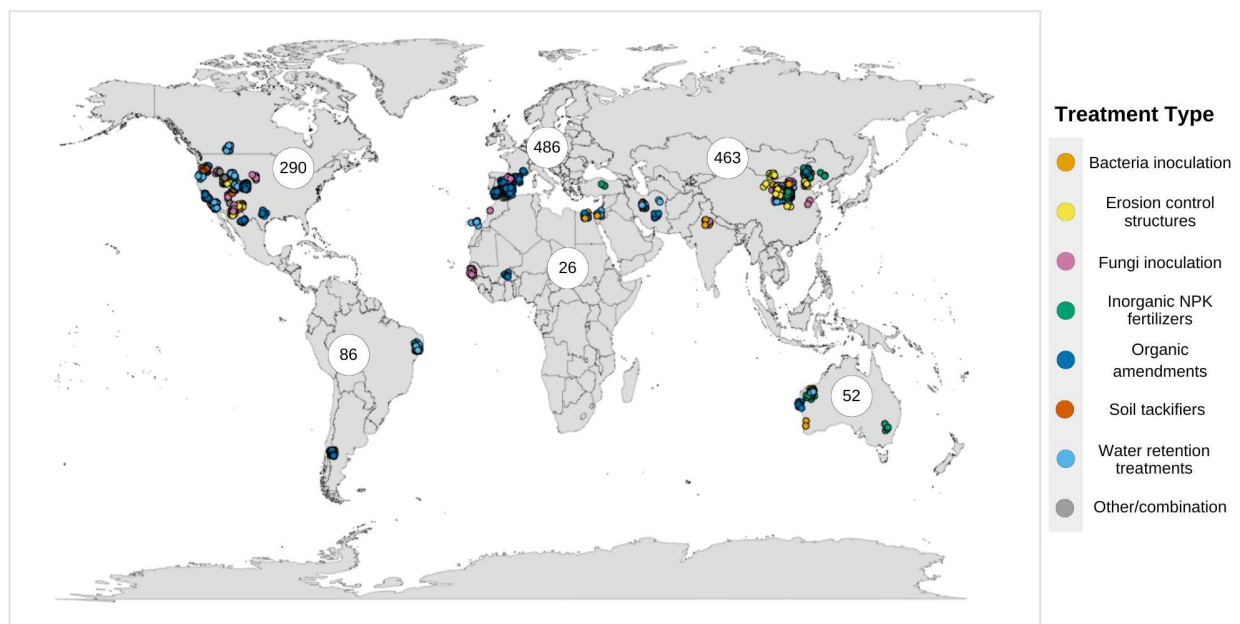


Fig. 1.1. Geographic locations of the 1,403 unique studies analyzed, with points colored by treatment type. See Fig. A1.3 in Appendix 1 for a map of study locations for each individual soil health metric.

Soil restoration increases soil health

Soil restoration had an overall positive effect on all soil health metrics included in our study (Fig. 1.2). Positive effects of soil restoration were particularly large for microbial metrics, amounting to a +6,967% increase in mycorrhizal colonization and a +277% increase in basal respiration following soil restoration, on average (Fig. 1.2). These high averages may be partially due to the fact that most studies that examined microbial metrics used inoculation treatments, which in some cases could increase a condition of near 0% colonization to near 100% (e.g., Solís-Dominguez et al., 2011). Effects were also relatively large for nutrient availability (SOC: +72%; soil N: +76%), but lower for physical soil components (aggregate stability: +18%; bulk density (inverse): +11%; soil moisture: +19%).

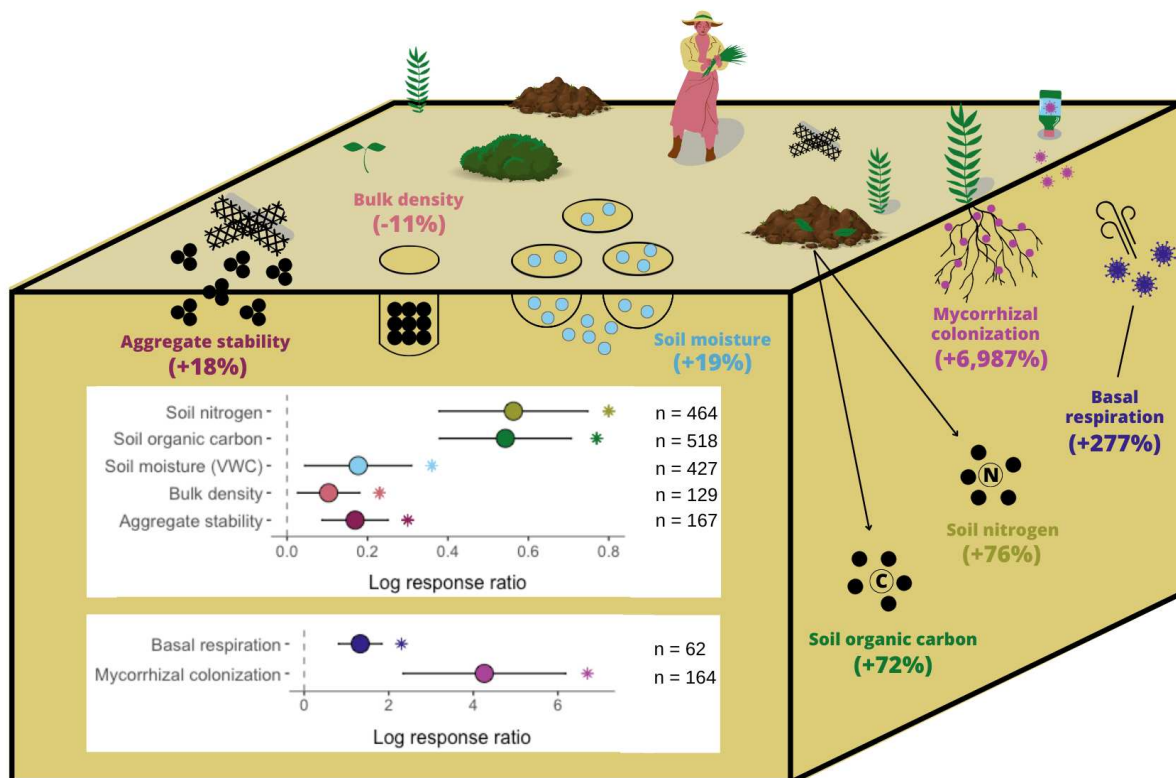


Fig. 1.2. Pure random effects of soil restoration on soil health metrics (aggregate stability, bulk density, SOC, soil N, soil moisture, mycorrhizal colonization, and basal respiration). Error bars

represent 95% confidence intervals. Percentages represent the average percent change of each soil health metric following soil restoration.

Effects across environmental gradients vary by soil health metric

Effects of restoration on soil health decreased with increasing aridity index (more mesic climates) for SOC and N, (Fig. 1.3, Table 1.2), meaning that restoration was found to be less effective in relatively mesic dryland systems. For aggregate stability, soil texture was a significant moderator of the effect size of soil restoration, where effect size increased with percent sand (Fig 1.4., Table 1.2).

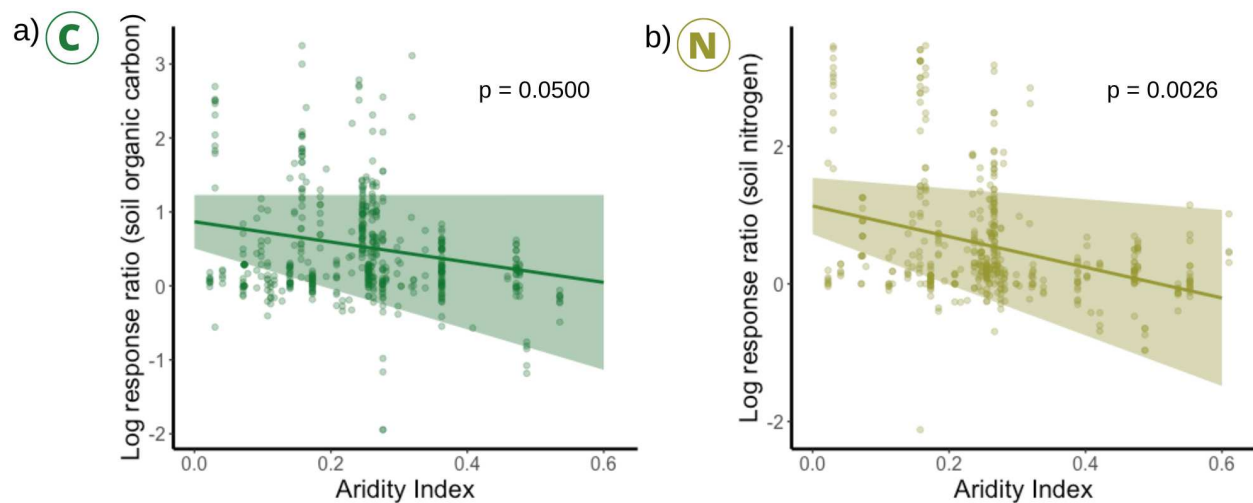


Fig. 1.3. Variation in the effect of restoration across an aridity gradient for soil health metrics: (a) SOC, and (b) soil N, measured as a log response ratio. Solid lines are meta-regression lines, and shaded areas represent the 95 percent confidence intervals.

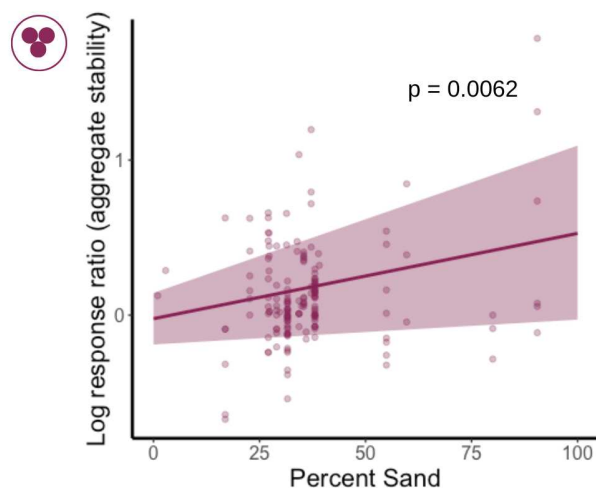


Fig. 1.4. Variation in the effect of restoration across a soil texture gradient for aggregate stability, measured as a log response ratio. The solid line is a meta-regression line, and shaded area represents the 95 percent confidence interval.

Table 1.2. Results from univariate mixed-effects models for Aridity_Index, Percent_Sand, Time, and their interactions, when applicable. Estimates are regression line slope values. 95% confidence intervals (CI), reported as a +/- value from the estimate, and p-values are also included. * indicates values that are statistically significant using an alpha of < 0.05.

		Aridity Index	Percent Sand	Time	Aridity Index * Percent Sand	Percent Sand * Time
Aggregate Stability	estimate	-	0.0055	-	-	-
	CI	-	0.0040	-	-	-
	<i>p</i> - val	-	0.0062*	-	-	-
Soil Organic Carbon	estimate	-1.3669	0.0005	-	0.0697	0.0007
	CI	1.3672	0.0047	-	0.0497	0.0006
	<i>p</i> - val	0.0500*	0.8318	-	0.0060*	0.0073*

Soil Nitrogen	estimate	-2.2266	-0.0046	-	0.0850	-
	CI	1.4500	0.0059	-	0.0670	-
	<i>p</i> - val	0.0026*	0.1171	-	0.0134*	-
Basal Respiration	estimate	-1.6883	-	-0.0771	-	-
	CI	4.3725	-	0.0852	-	-
	<i>p</i> - val	0.4492	-	0.0766	-	-

Additionally, we found a significant interaction between Aridity_Index and Percent_Sand as moderator variables for SOC and N (Table 1.2). This suggests the effect of aridity on restoration effectiveness for these two metrics is moderated by percent sand, and vice versa. Using our modeled results, we calculated that when the aridity index was below 0.19 and 0.26 for SOC and N, respectively, effect size decreased with percent sand, but when aridity index was above these values, effect size increased with percent sand. These threshold values were calculated using the modeled interaction coefficients, which were 0.0697 and 0.0850 for SOC and soil N, respectively. This means, using SOC as an example, for a one unit increase in aridity index, the slope of the relationship between LnRR and percent sand increases by 0.0697, and vice versa (Table 1.2). We used these coefficients to calculate the aridity index value at which the slope of the relationship between LnRR and percent sand changed from negative to positive. Using the same method, we found that when percent sand was below 68% and 78% for SOC and N, respectively, effect size decreased with aridity index, but increased with aridity index when percent sand was above these values. Combining these two results, we find that overall soil restoration has the greatest effect on

SOC and N in fine-textured soils in more arid environments, as well as sandy soils in more mesic environments (Fig. 1.5; Fig. A1.4 in Appendix 1).

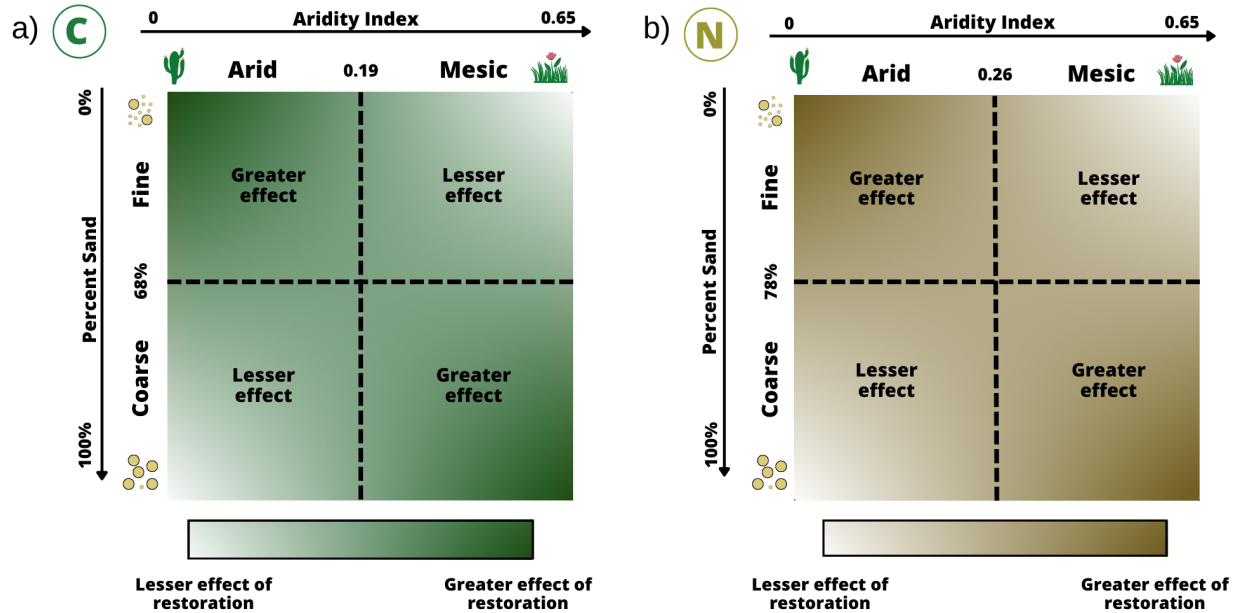


Fig. 1.5. The combined influence of aridity and percent soil sand on the effect of soil restoration on SOC (a) and soil N (b). Darker colors represent conditions where soil restoration has a greater effect size, and lighter colors represent conditions where soil restoration has a lesser effect size. The values next to the dotted lines represent threshold values for aridity index and percent sand above and below which soil restoration has a greater or lesser effect.

For just SOC, we found that the effect of Percent_Sand was also moderated by time since restoration, as there was a significant interaction between these two variables (Table 1.2). The coefficient for this interaction was 0.0007, meaning that as time increases, the slope describing the relationship between the LnRR and percent sand increases. Using the same method described above, we calculated that when percent sand was less than 36%, the effect size of restoration on SOC decreases with time, but when it is greater than 36%, the effect size increases with time (Fig. A1.4 in Appendix 1).

Treatment type influences effectiveness

Treatment type had a significant effect on restoration effectiveness for certain soil health metrics. For aggregate stability, erosion control structures had a significantly lesser effect size than all other treatments analyzed. For SOC and mycorrhizal colonization, however, certain treatments had significantly higher effect sizes than others. Organic amendments significantly had the greatest effect size on SOC, while fungi inoculation had the greatest for mycorrhizal colonization. (Fig 1.6; Table 1.3). For soil N, organic amendments had a significantly higher effect size than fungi inoculation. Revegetation did not have a significant effect on the effect size of restoration for any soil health metric.

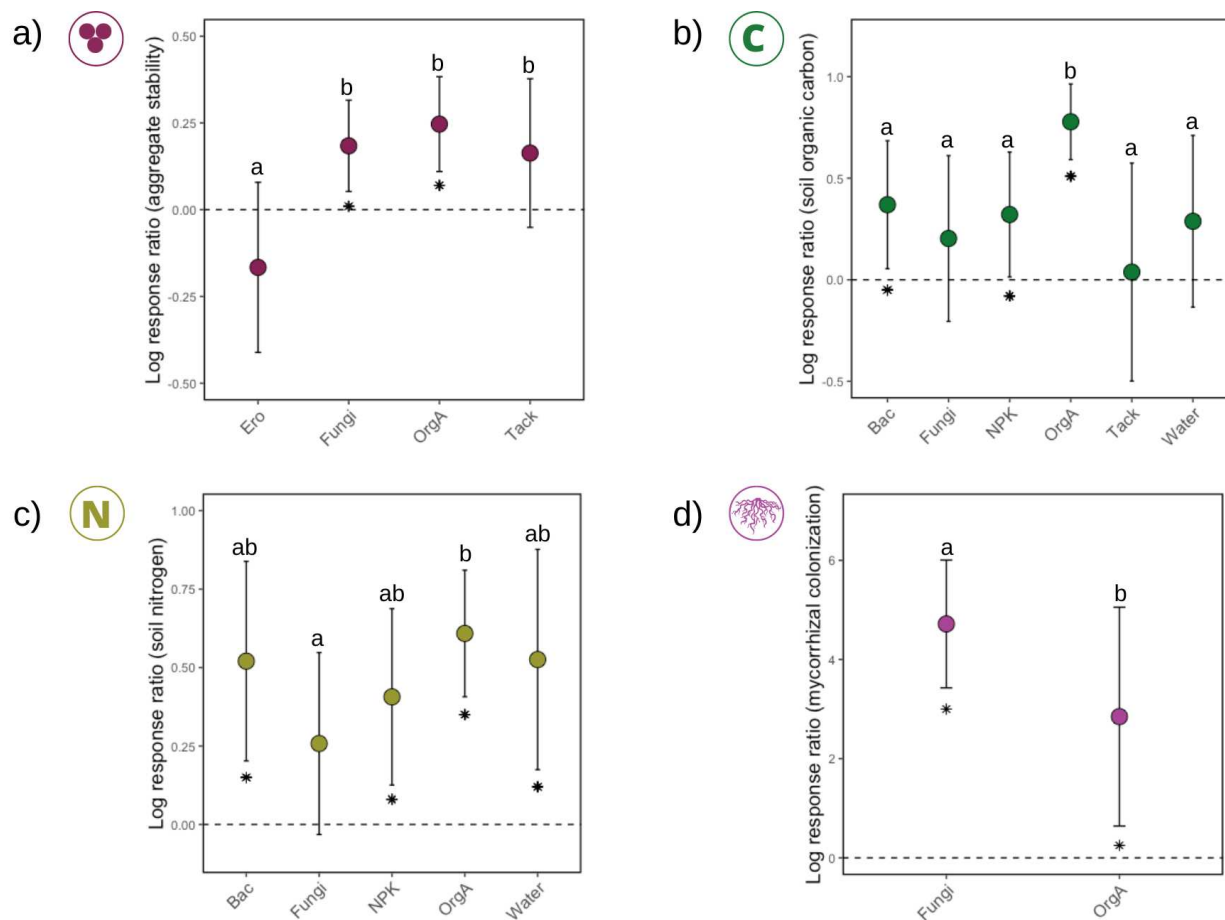


Fig 1.6. Effect sizes and differences between different soil restoration treatment types for six soil health metrics (aggregate stability, SOC, soil N, and mycorrhizal colonization). Error bars

represent 95% confidence intervals. * indicates values that are statistically significant from zero using an alpha of < 0.05. Letters represent treatment types that are significantly different from each other. “Bac” = bacteria inoculation, “Fungi” = fungi inoculation, “NPK” = inorganic NPK fertilizer, “OrgA” = organic amendment, “Ero” = erosion control structure, “Tack” = soil tackifier, and “Water” = water retention treatment.

Table 1.3. Results from multivariate mixed-effects models for Treatment_Type and Revegetation. Estimates (est.) are mean effect sizes for each factor level. 95% confidence intervals (CI), reported as a +/- value from the estimate, and p-values (*p*) are also included. * indicates values that are statistically significant using an alpha of < 0.05. See Fig. 7 for treatment type codes.

		Treatment Type						
		Bac	Fungi	NPK	OrgA	Ero	Tack	Water
Aggregate Stability	est.	-	0.1840	-	0.2466	-0.1662	0.1632	-
	CI	-	0.1315	-	0.1366	0.2450	0.2141	-
	<i>p</i>	-	0.0061*	-	0.0004*	0.1836	0.1352	-
Soil Organic Carbon	est.	0.3695	0.2033	0.3214	0.7780	-	0.0378	0.2880
	CI	0.3152	0.408	0.3075	0.1861	-	0.5366	0.4228
	<i>p</i>	0.0216*	0.3288	0.0405*	<0.0001*	-	0.8902	0.1818
Soil Nitrogen	est.	0.5204	0.2579	0.4066	0.6087	-	-	0.5256
	CI	0.3179	0.2899	0.2811	0.2017	-	-	0.351
	<i>p</i>	0.0013*	0.0814	0.0046*	<.0001*	-	-	0.0033*
Mycorrhizal Colonization	est.	-	4.7167	-	2.8474	-	-	-
	CI	-	1.8839	-	2.2064	-	-	-
	<i>p</i>	-	<0.0001*	-	0.0114*	-	-	-

Discussion

Soil restoration increases soil health across global drylands

Results from our meta-analysis show soil restoration had a beneficial effect on aggregate stability, bulk density, soil moisture, SOC, soil N, mycorrhizal colonization, and basal respiration across global drylands. Soil restoration had very large effects on the measured microbial soil health metrics, suggesting that soil restoration is particularly effective at improving certain biotic conditions such as mycorrhizal colonization and microbial respiration (Fig. 1.2). Collectively, results suggest that active soil restoration has the potential to improve many aspects of soil health and could be an important tool in combating dryland soil degradation.

Restoration effectiveness on abiotic metrics of soil health varies across environmental gradients

We found that the effectiveness of soil restoration increased with aridity for SOC and N, meaning that restoration is most effective at increasing soil nutrients in drier climates (Fig. 1.3). This may be because in more mesic climates, soils can recover more easily on their own post-disturbance (Crouzeilles et al., 2017) as there tends to be a greater availability of moisture and nutrients, meaning that active restoration efforts may not provide many additional ecosystem benefits. In drier climates, there are likely more barriers to natural recovery, such as a lack of soil moisture and nutrients (Klemmedson, 2009), meaning that replenishing soil nutrients through active restoration could have a greater impact. Soil texture also influenced restoration effectiveness on aggregate stability. For aggregate stability, restoration effectiveness increased with percent sand, meaning restoration was most effective at improving aggregate stability in sandier soils (Fig. 1.4). This may be because aggregate stability is usually low in sandier soils, so it is possible for

aggregate stability to increase by larger margins following restoration than it would be for soils that already have high aggregate stability (Almajmaie et al., 2016).

However, we did not find any significant influence of environmental variables on the effect size of restoration for biotic soil health metrics. Given the relatively smaller number of studies that examine biotic soil health metrics, more studies that test restoration effectiveness on biotic soil health across environmental gradients will need to be conducted in order to better determine these relationships.

Effects of aridity and soil texture are moderated by other variables

Soil nutrient responses to restoration were mediated by interactions between aridity and soil texture. While we found that overall restoration effectiveness increases with aridity, this relationship was contextualized by soil texture. Overall, restoration is most effective at increasing SOC and N in finer-textured soils in drier environments, and coarser-textured soils in more mesic environments. (Fig. 1.5).

One explanation for this could be that soil restoration may be most effective at increasing soil nutrients when a site is facing just one major barrier to nutrient accumulation, rather than multiple at once. As discussed previously, high levels of aridity may be a barrier to nutrient accumulation due to a lack of organic matter in these environments (Klemmedson, 2009). Additionally, high sand content can prevent soils from holding nutrients effectively due to poor aggregation (Augustin and Cihacek, 2016). Therefore, it may be so difficult to increase nutrients in sandy soils in arid environments that restoration is not very effective. Additionally, soil restoration may also be less effective in soils that do not face any barrier associated with aridity or soil texture (i.e. mesic, fine-textured soils) because they may be able to recover nutrient levels on

their own (Crouzeilles et al., 2017, Augustin and Cihacek, 2016), meaning a smaller net effect of restoration. These findings are interesting in the context of restoration decision making, as they suggest choosing a site that will likely not recover without active intervention, but also has the capacity to recover if proper treatments are applied. This also suggests that arid sites with very sandy soils may have a greater need for protection and conservation, as they are very difficult to restore post-degradation.

For SOC, the influence of soil texture was also moderated by time since restoration (Fig. A1.4 in Appendix 1). The interaction between these two variables suggests that in less sandy soils, the effect of restoration decreases over time, but that in more sandy soils it increases over time. Because less sandy soils can generally accumulate nutrients more easily (Augustin and Cihacek, 2016), it makes sense that the effect of restoration treatments would dampen over time in these types of soils. In sandy soils, restoration treatments that promote SOC persistence such as increasing inputs and aggregation can create a positive feedback of SOC, which may amplify this time response in sandy soils (Liu et al., 2019). So that while on short time scales restoration may be less effective at increasing SOC in sandy soils, perhaps on longer time scales restoration can be effective across soil textures (De Rouw and Rajot, 2004).

Restoration effectiveness varies by treatment type for different soil health metrics

For some soil health metrics, certain treatments showed greater effectiveness than others, meaning that treatment type is an important factor for restoration success. For SOC and mycorrhizal colonization, organic amendments and fungi inoculation had the greatest effectiveness, respectively (Fig 1.6). This is likely because many commonly used organic amendments, such as compost, are a direct source of carbon for the soil (Zmora-Nahum et al., 2005), and fungi inoculation directly adds colonizing fungi to the soil (Smith and Read, 2008). It

is important to note that the majority of studies examining SOC had a duration of one year or less (55%), meaning SOC was measured within one year after treatments were implemented. The remaining studies had durations of 1-5 years (31%), 6-10 years (10%) and greater than 10 years (4%). Therefore, this finding is most relevant for relatively short-term studies.

For aggregate stability and soil N, most treatments had roughly the same effectiveness, except for erosion control structures and fungi inoculation, which had the smallest effect sizes for their respective soil health metrics (Fig 1.6). The fact that erosion control structures were least effective for increasing aggregate stability is interesting given that aggregate stability is often associated with erodibility, which is usually what erosion control structures aim to decrease (Stanchi et al., 2015). It is possible that because these structures are placed above-ground, they are ineffective at improving the stability of subsurface aggregates. Additionally, our finding that fungi inoculation was the least effective treatment for soil N is noteworthy since this was found to be the most effective treatment for mycorrhizal colonization. This highlights how different aspects of soil health may respond differently to certain treatments, and that specific goals for soil health improvement are important when choosing restoration treatments. It is likely that fungi inoculation is less effective at improving soil N because, although mycorrhizal fungi, particularly arbuscular mycorrhizal fungi that are commonly found in drylands (Begum et al., 2019), can help plants acquire N from the soil, they generally do not fix atmospheric N like certain types of bacteria and are not direct sources of N like many soil amendments (Hestrin et al., 2019).

Study limitations and future research directions

Our study has several limitations that highlight opportunities for future research:

1. *Global data availability.* This meta-analysis did not have global representation for all variables included. While our database included studies of SOC and N responses to

restoration in drylands across six continents, the remaining five metrics only had data points from two to five continents.

2. *Soil health responses.* This study only includes seven commonly measured metrics of soil health, and is therefore not comprehensive of all aspects of soil health. Other important aspects of soil health, including pH, electrical conductivity, and exoenzyme activity (Raghavendra et al., 2020), had low representation in the literature and were not included in this meta-analysis.
3. *Land use and disturbance legacies.* Other potential moderator variables, such as land usage and land disturbance, were not reported in most studies, so we did not have sufficient data to include these variables in our analyses. Future work should investigate how land use or disturbance legacies could influence soil restoration effectiveness (Meli et al., 2017).
4. *Combined abiotic and biotic restoration treatments.* Future work should also examine abiotic and biotic soil treatments used simultaneously. We found several publications that examined these types of treatments (e.g., Antoninka et al., 2019, Faist et al., 2020), but there were not enough unique studies to be used for meta-analysis.
5. *Microbial responses to restoration.* Soil-based restoration field studies should explore the effects of restoration on microbial community metrics, as these soil health metrics were much less commonly reported than abiotic soil characteristics, and are very important indicators of soil health (Raghavendra et al., 2020).
6. *Effects of soil restoration on plants.* Although outside the scope of our study, future studies should examine the effects of soil restoration on plant responses like recruitment and growth.

Key takeaways and implications

From this meta-analysis we found that soil restoration can be an effective tool for improving physical and biological soil health in drylands. However, for certain abiotic soil health metrics, this effectiveness is dependent on environmental stress (aridity and soil texture). Soil restoration was most effective at improving nutrient levels in fine-textured soils in arid environments as well as coarse-textured soils in mesic environments. This suggests that sites with these conditions may be optimal targets for restoration, whereas sites that are very arid with very sandy soils could be prioritized for conservation, as restoration has shown to be less effective under these conditions. Additionally, we found that organic amendments are most effective at increasing SOC, while fungi inoculation is effective at increasing mycorrhizal colonization, highlighting that treatment selection should be based on specific restoration goals. Reversing land degradation through ecological restoration can produce myriad environmental and social benefits, including carbon sequestration (Di Sacco et al., 2021), improved water quality (Rey Benayas et al., 2009), and long-term sustainability of natural resources (George et al., 2018). Results from our study can be used by land managers and restoration practitioners to prioritize areas for soil restoration and choose restoration treatments based on soil health targets. More informed decision-making could improve restoration effectiveness and efficiency, and will help combat escalating land degradation in global drylands (IPBES, 2018).

CHAPTER 2 - DIFFERENCES IN SOIL MICROBIOMES BETWEEN REFERENCE AND DEGRADED SITES SUGGEST OPPORTUNITIES FOR SOIL RESTORATION IN SOUTHWESTERN U.S. DRYLANDS

Introduction

Land degradation, or the loss of land productivity and ecosystem functioning, has become an increasing issue across the globe, occurring in over 30% of Earth's terrestrial lands (Olsson et al., 2019). This has the potential to impact at least 1.3 billion people, whose livelihoods depend on natural resources, rendering many populations highly vulnerable as the effects of land degradation worsen under a changing climate (Olsson et al., 2019). Land degradation is particularly pervasive in Earth's semi-arid and arid (dryland) ecosystems (Chambers & Wisdom, 2009) which cover 46% of Earth's land surface (Maestre et al., 2021), and are highly subject to intensive land use practices, resource extraction, and water limitations (IPBES, 2018). One way to potentially reverse the effects of land degradation is ecological restoration, which aims to improve ecological functioning through active intervention (Vaughn et al., 2010). This may be especially useful in drylands, which are often unable or very slow to recover on their own post-disturbance due to extreme climates and severe resource limitation (Estruch et al., 2018, Monroe et al., 2020).

Soil microorganisms, or microbes, are critical to dryland ecosystem health given their ability to form symbiotic relationships with plants and improve soil conditions, which could have promising implications for their use in ecological restoration (Zhang et al., 2021, Harris, 2009). Specifically, soil microbes in drylands can increase consistency of plant access to water and nutrients in space and time (Pointing & Belnap, 2012; Naylor & Coleman-Derr, 2018), while also supporting soil health by increasing soil stability, water-holding capacity, and nutrient cycling

(Bowker, 2007). Ecologists have experimented with various microbial restoration techniques in dryland environments, including microbial inoculation (manually adding microbes into soils) (Alori and Babalola 2018), as well as biopriming or seed-coating with microbes (coating seeds in solutions containing microbes) (Muñoz-Rojas et al., 2018, Chua et al., 2019). However, these techniques have shown varying success across drylands (Antoninka et al., 2019, Chaudhary et al., 2019, Faist et al., 2020). One reason for this may be that use of biotic soil restoration treatments is often not guided by a preliminary understanding of soil community structure and what organisms and/or functions are lacking in degraded communities. Therefore, it would be useful to have more information on the microbial community composition and diversity differences between degraded ecosystems and relatively healthy reference sites, in order to identify microbial taxa that could be used in restoration efforts.

Revegetation by planting native plant species has also been used to restore dryland functionality, yet these efforts have similarly not always been successful in promoting microbial community health (Yang et al., 2021). However, with a lack of baseline information of microbial community composition under reference conditions, it is difficult to assess the effects of plant-based restoration on the health of microbial communities. So, it is also important to understand the differences between reference, degraded, and revegetated sites to assess whether plant-based restoration can help restore microbial communities, or if other interventions are needed.

In order to address this gap in our knowledge, we conducted a soil microbiome study to assess how soil microbial community composition and diversity differ across reference (which we refer to as “intact”), degraded, and revegetated site conditions using plots from the RestoreNet project (Havrilla et al., 2020, Yang et al., 2021). This study explored three major research questions:

1. How do microbial community composition (including bacteria, fungi, and archaea) and species diversity differ across paired intact, degraded, and revegetated dryland sites?
2. Are there certain taxa that serve as indicators of each of these site conditions?
3. Do disturbance and revegetation influence physical indicators of soil health (e.g., bulk density, pH, nutrient concentrations), and which of these soil characteristics are related to microbial community composition?

We predicted that microbial community composition and diversity would differ between degraded, intact, and revegetated sites due to associated differences in plant cover and soil conditions. At intact dryland sites, there is usually higher plant cover and diversity because the plants have not been majorly disturbed (Manhaes et al., 2022). This is sometimes true of revegetated sites, but only when revegetation efforts have been successful, which is often not the case in drylands (Shakelford et al., 2021). Due to the symbiotic relationships between certain microbes and plants, we would therefore expect that areas with different plant community composition and diversity would have different microbial community composition and diversity, and that microbial diversity would be higher in intact systems (Zhang et al., 2021). We also predicted that degraded sites would have the highest abundance of stress-tolerant microbial taxa, as certain types of microbes have adapted to survive in extreme, resource-limited conditions (Torsvik and Ovreas, 2008). Lastly, we predicted that changes in bulk density, water content, pH, organic matter, and nitrate associated with degradation would also correlate with changes in microbial community composition, as microbe community structure is often highly dependent on soil conditions (Harris, 2009).

Methods

To address our research objectives, we compared soil microbial community composition across paired intact, degraded, and revegetated plots that had undergone revegetation with native plants. Our study leveraged eight existing field sites within the RestoreNet project located in the southwestern U.S. within Arizona, New Mexico, and Utah (Table 2.1, Fig. 2.1). RestoreNet is a co-produced, networked restoration study established in 2018 to systematically test the suitability of a broad range of restoration techniques across environmental gradients in dryland ecosystems in the western United States (Havrilla et al., 2020; Laushman et al. 2021). Each RestoreNet site consists of a fenced, 50 x 50-m plot, with certain sites containing a series of replicated revegetation treatments in 2x2-m plots, and a nearby paired intact reference plot (Figs 2.2 & 2.3).

Study sites and experimental design

The eight sites sampled for our study are all located in the southwestern United States in semi-arid and arid regions. Mean annual precipitation (MAP) across sites ranged from 225 to 535 mm, and mean annual temperatures (MAT) ranged from 11 to 21 °C. Soil texture also somewhat varied across sites, ranging from silt loams to loamy sands, with most sites as sandy loams. Most sites were disturbed by grazing or farming/irrigation, with a few cases of disturbance from prairie dogs, foot/vehicle traffic, and invasive plants (Table 2.1).

Each site includes degraded and intact reference plots, and five sites (BART, CRC, FLYM, PEFO, SPID) also contain revegetated plots (Table 2.1, Fig. 2.2). Degraded plots are within RestoreNet site fencing (Laushman et al., 2021) in areas that have undergone past disturbances but have not received restoration treatments. Revegetated plots are also within RestoreNet site fencing, but have undergone a treatment of transplanted native plant seedlings that were transplanted three years prior to sampling (Balazs et al., 2021). Intact reference sites have minimal historical

disturbance, no or low current livestock grazing, and high cover of desirable native plants. Paired intact reference and degraded/revegetated plots are all within the same soil series and have similar potential plant communities.

Table 2.1. RestoreNet site characteristics. MAP = mean annual precipitation (30 year average). MAT = mean annual temperature (30 year average).

Site Name	MAP (mm)	MAT (°C)	Aridity	Soil Type	Disturbance	Includes revegetation?
Bar T Bar Ranch (BART)	311	11	Semi-arid	Loam	Grazing, prairie dogs	Yes
Canyonlands Research Center (CRC)	225	12	Arid	Sandy loam	Farming, irrigation	Yes
Flying M Ranch (FLYM)	359	11	Semi-arid	Silt loam	Grazing	Yes
McDowell-Sonoran Preserve (MDSP)	371	21	Semi-arid	Sandy loam	Foot/vehicle traffic	No
Mesquite College Ranch (MESQ)	275	16	Semi-arid	Sandy loam	Grazing	No
Petrified Forest (PEFO)	245	13	Arid	Loam	Farming, irrigation	Yes
Spiderweb Ranch (SPID)	171	13	Arid	Sandy loam	Grazing	Yes
Santa Rita Experimental Range (SRER)	535	18	Semi-arid	Loamy sand	Invasives, Grazing	No

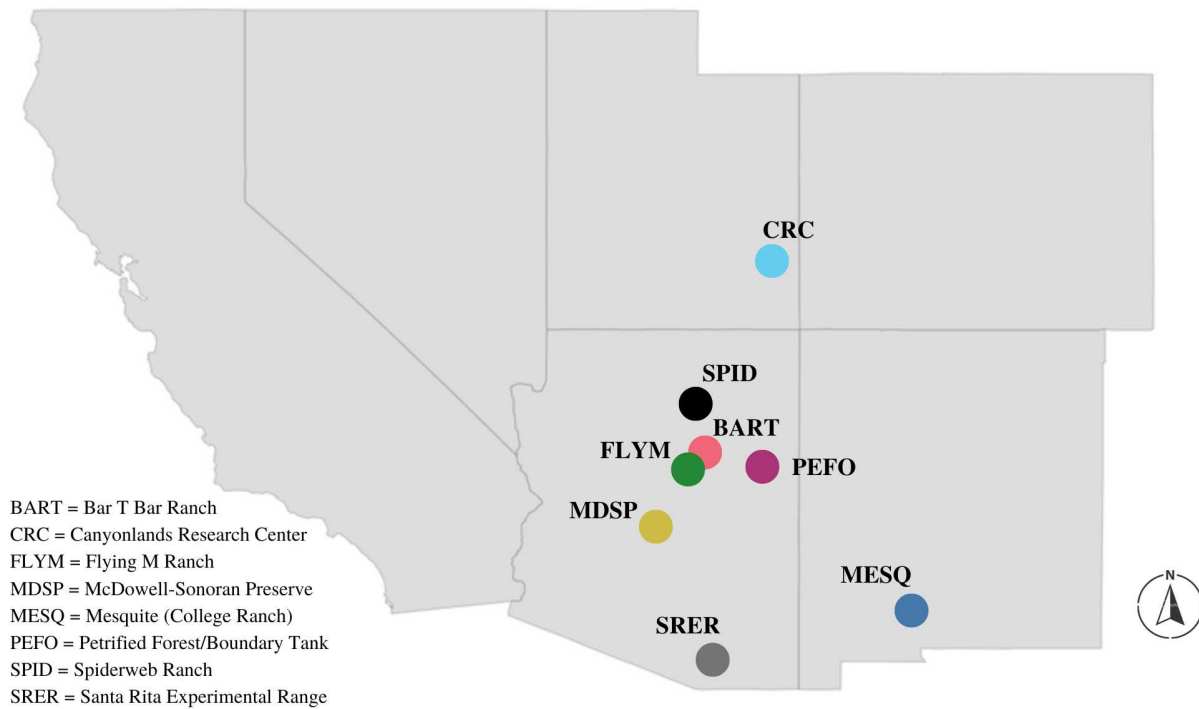


Fig. 2.1. Map of RestoreNet sites and nearby reference sites that were sampled for this study.

Physical soil sampling and analysis

At the five sites containing revegetated plots (BART, CRC, FLYM, PEFO, SPID), soil samples were collected from intact, degraded, and revegetated plots. At the three remaining sites (MDSP, MESQ, SRER), no revegetation treatments had been implemented so soil samples were only collected from degraded plots. For physical analysis, three soil samples were collected to a depth of 10 cm from three, 2x2-m subplots within each intact/degraded/revegetated plot in a diagonal (Fig. 2.3). Replicated soil samples collected from each subplot ($n = 3$ each) were then pooled and homogenized for 63 samples total. All samples were stored in plastic bags at room temperature prior to analysis. Before conducting physical analysis, rocks were sieved out of all samples. Samples were then sent to the Colorado State University Soil and Plant Testing Lab (<https://agsci.colostate.edu/soiltestinglab/>) where the following characteristics were measured:

bulk density, organic matter content, electrical conductivity, pH, nitrate content, phosphorus content, and potassium content. Organic matter was measured using the loss on ignition method. Bulk density was measured with a mass per volume calculation using oven-dried 200 mL subsamples. Electrical conductivity and pH were measured using a 1:1 soil to water suspension test. Nitrate was measured using a KCl extraction. Lastly, phosphorus was measured using a Mehlich III test, while potassium was measured using an ammonium acetate replacement.



Figure 2.2. Intact (left), degraded (center), and revegetated (right) plots at Petrified Forest. Photos by Katie Laushman.

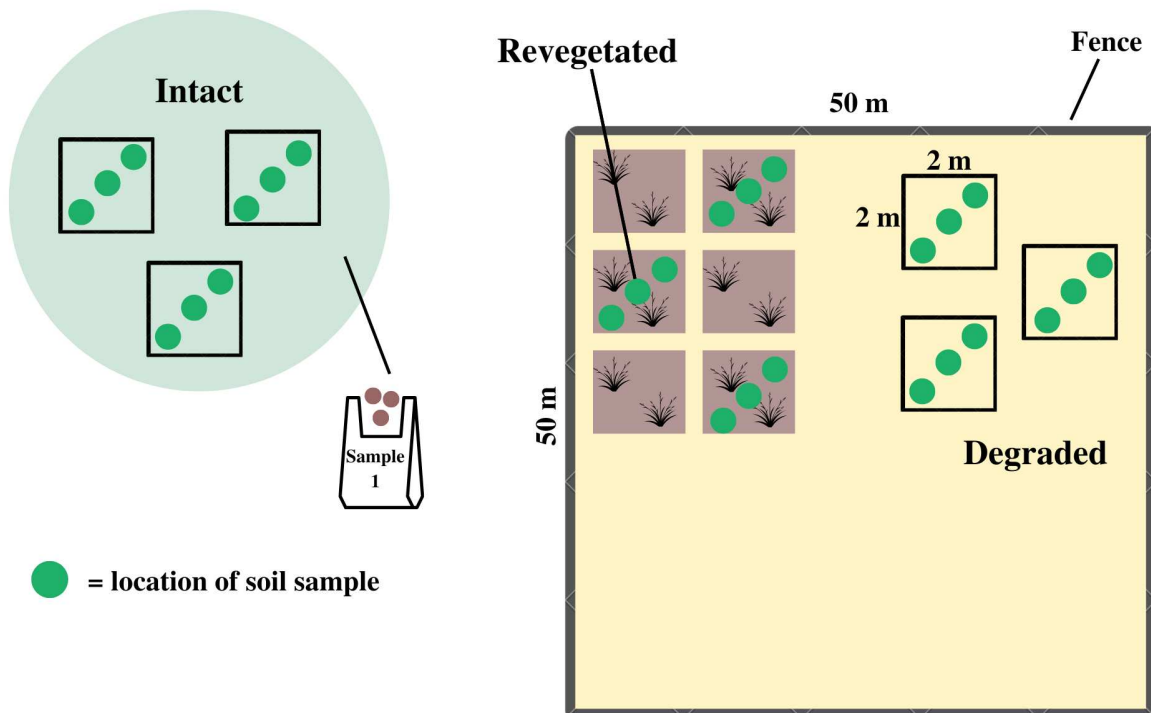


Figure 2.3. Diagram of sampling design at each RestoreNet site containing revegetated plots.

Microbial soil sampling

Soil samples for microbial analysis were collected from the same subplots using the same sampling design as was used for the soil samples for physical analysis (Fig. 2.3). Sampling of all plots was done within the same week in July of 2021. For these samples, however, a smaller amount of soil (10 gram samples; Penton et al., 2016) were collected from three, 2x2 m subplots within each intact/degraded/revegetated plot to a depth of 10 cm. Replicated soil samples collected from each subplot (n = 3 each), collected in a diagonal line across the subplot, were also pooled and homogenized prior to DNA extraction in an effort to minimize the signal of within-plot microheterogeneity in the soil communities (Bailey et al., 2013) for a total of 63 pooled soil samples. All samples were collected in sterile Whirl Paks, stored in a cooler on dry ice during transport to Colorado State University, and then stored in a -40 °C freezer until further analysis.

Soil DNA extraction, PCR, and gene amplicon sequencing

First, DNA was extracted from 0.25 grams of the 63 soil samples using the Qiagen DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany). Next, we used 515F/806R primers to amplify the V4 region of the 16S rRNA gene for bacteria and archaea (Apprill et al., 2015; Caporaso et al., 2011; Parada et al., 2016), and ITS1-F/ITS2 primers for the ITS gene region for fungi (Bellemain et al., 2010; Smith and Peay, 2014). Each sample was assigned a 12-bp barcode, homogenized, and then randomly assigned a location on a 96-well plate. Four blank samples were included as negative controls. Duplicated PCR reactions were run for all samples using Invitrogen's Platinum II Hot-Start PCR Master Mix (Invitrogen, Waltham, MA). After confirming amplification and length via gel electrophoresis, amplicons were then normalized using the ThermoFisher Scientific SequalPrep Normalization plates (Thermo Fisher Scientific Inc. USA). Both libraries were then

sequenced with the Illumina MiSeq platform. The 16S library was sequenced using a 300-cycle v2 paired end kit and the ITS was sequenced using a 500-cycle v2 paired end kit. Both runs included a 15% phiX spike. DNA extraction was done in the Dryland Ecology and Management Lab at Colorado State University, while PCR and sequencing was done at the University of Colorado Boulder Fierer Laboratory. After sequencing, reads were demultiplexed with idemp (idemp <https://github.com/yhwu/idemp>) and adaptors were trimmed using cutadapt (Martin, 2011).

We then used the *dada2* package in R (Callahan et al., 2016) to characterize the microbial communities in each sample. First, we used the `filterAndTrim()` function (settings: 16S `truncLen = c(150,140)`, ITS `truncLen = c(200,220)`, `maxEE = 2`, `truncQ = 2`, `rm.phix = T`) to trim all sequences to the same length by filtering based on the number of ambiguous bases, a minimum quality score, and the expected number of errors in the read. Next we learned error rates from 1×10^8 bp chosen from a random subset of the samples. Then we used the `derepFastq()` function to depuplicate the sequences, which output a list of unique sequences and their abundances, where identical sequences were grouped together. We next applied a denoising algorithm using the `dada()` function. This involved partitioning the sequences where the most abundant sequence was made the center of the partition, and then all sequences were compared to the center. Sequences were first compared based on kmer distance and banded alignment. Then an error rate was calculated based on differences in bases between sequences, cross-referenced with quality scores. These error rates then allowed for the calculation of abundance p-values, where low values indicate that a certain sequence is too abundant to be considered an error in sequencing, and will then get partitioned out of the algorithm as a new taxonomic unit (here we used amplicon sequence variants, or ASVs). After the partitioning algorithm was run, we used the `isBimeraDenovo()` function to

identify and remove bimeras (two-parent chimeric sequences), and the mergePairs() function to merge paired forward and reverse reads. Finally, we used a Bayesian taxonomic identifier (want2009) as implemented in the dada2 package to assign taxonomy based on UNITE (Oct. 2021 release for ITS) and Silva (v 138.1 for 16S).

Statistical analyses

Before performing statistical tests, we first filtered the 16S and ITS community composition data for quality control. This involved removing from the datasheet all ASVs where taxonomy was unknown at the phylum level, since only the kingdom was known for these organisms, which was not useful to answer our questions. We also removed all ASVs that were chloroplasts or mitochondria, as this DNA likely came from plant and animal matter. Lastly, we removed the extraction and no-template control samples from the datasheet after verifying that none of our samples significantly overlapped with the control samples when visualized in a non-metric multidimensional scaling (NMDS) plot (created using the metaMDS() function in the vegan package; Okansen et al., 2022).

We then rarefied the data to the lowest number of reads, which was 7,641 for the 16S data, and 19,141 for the ITS data. For the 16S data, one of our samples from the revegetated plots at Bar T Bar Ranch (BART) (Fig. 2.1) had only 2,412 reads, so we removed the three samples from the revegetated plots at this site, as this was assumed to be a failed sample. Additionally, when visualized in an NMDS plot, we noticed that samples from Spiderweb Ranch (SPID) (Fig. 2.1) appeared to be outliers, as these points were very spatially separated from all other points on the plot (Fig. A2.1 in Appendix 2). So, we removed the samples from Spiderweb Ranch from the 16S dataset to avoid misinterpreting variation that was only explained by community composition differences from this one site. For the ITS data, several of the samples from the degraded and

revegetated plots at Spiderweb Ranch had reads of less than 1,000, so we also removed the samples from Spiderweb Ranch from the ITS dataset as these values were not large enough for statistical testing. After this filtering process, we analyzed seven degraded and intact plots from the 16S and ITS datasets, three revegetated plots from the 16S dataset, and four revegetated plots from the ITS dataset.

To analyze differences in community composition between degraded, intact, and revegetated plots within each site, we used nested PERMANOVA (permutational analysis of variance) and PERMDISP (permutations of dispersion) tests using the `adonis2()`, `pairwise.adonis2()`, `betadisper()`, and `permutest()` functions of the *vegan*, *pairwiseAdonis*, and *smartsnp* packages in R Studio (Herrando-Perez et al., 2021; Martinez, 2020; Okansen et al., 2022). In these models, disturbance condition (i.e. degraded vs intact vs revegetated) was the predictor variable, stratified by site, and Bray-Curtis dissimilarity matrices were the response variables for both bacteria/archaea and fungi communities. To compare differences in diversity between degraded, intact, and revegetated plots within each site, we first calculated the Shannon index and species richness for each sample using the `diversity()` and `specnumber()` functions of the *vegan* package (Okansen et al., 2022). We then used ANOVA (analysis of variance) tests to compare the Shannon indices and species richness', first making sure the data met assumptions of normality and equality of variances using the `shapiro.test()` and `leveneTest()` functions of the *car* package (Fox et al., 2022). We also performed an indicator species analysis to determine taxa indicative of degraded, intact, and revegetated conditions. For this analysis we used the `multipatt()` function of the *indicspecies* package (De Cáceres et al., 2022).

Lastly, we used multiple regression on distance matrices (MDRM) (Goslee and Urban 2012) to test for soil characteristics known to be responsive to degradation that may be related to

differences in microbial community composition. To do this we first used the `cor()` function of the *corrplot* package (Wei and Simko, 2021) to assess correlations among the soil physical characteristics tested (only including variables with a priori hypotheses about how they could be impacted by degradation or revegetation). We then used ANOVA and Tukey HSD tests to determine differences in soil characteristics between degraded, intact, and revegetated sites, in order to determine if there was a significant relationship between site condition and physical soil characteristics. Log transformed data were used when assumptions of normality and equality of variances were not met. When log transformed data did not meet assumptions, we used Kruskal-Wallis tests instead of ANOVA tests. To run the MDRM, we used the `MRM()` function of the *ecodist* package (Goslee and Urban 2022), and included only soil characteristics with correlation coefficients of less than 0.7 (Nettleton, 2014), along with disturbance condition (degraded, intact, or revegetated), and site (representing each of the seven different sites) to account for site level differences in the model.

Results

Database summary and exploratory community analysis

For the 16S (bacteria and archaea) dataset, we found 14,232 ASVs total across all samples. There were 6,577 ASVs across all seven degraded sites and 7,316 across all intact sites. Across the three revegetated sites, there were 2,435 ASVs, compared to the 2,658 degraded and 3,232 intact at those same three sites. The most abundant ASV was an archaea in the Nitrososphaeraceae family of Crenarchaeota phylum. The most abundant bacteria (and third most abundant ASV) was the genus *RB41* of the Pyrinomonadaceae family, a type of Acidobacteriota. For the ITS (fungi) dataset, we found 5,115 ASVs across all samples. Across all seven degraded sites, there were 2,093 ASVs, and 2,685 ASVs across the seven intact sites. 1,281 ASVs were found across the four

revegetated sites, compared to 1,169 and 1,551 ASVs at the same four degraded and intact sites, respectively. The most abundant fungal ASV was *Naganishia albida*, a type of Basidiomycota.

Soil community composition differs between degraded and intact dryland sites

PERMANOVA tests (nested by site) showed that across all seven sites, composition of bacterial/archaeal communities differed between degraded and intact plots within each site ($p < 0.001$, $R^2 = 0.030$) (Fig. 2.4, Table 2.2). Specifically, this indicates that the midpoints of the polygons (depicted in Fig. 2.4) representing soil communities of degraded and intact plots are significantly different from one another. However, the R^2 of 0.03 indicates that disturbance condition (degraded versus intact) only accounts for about 3% of the variation in community composition. Across the three sites containing revegetated plots, PERMANOVA tests also indicated compositional differences in bacterial/archaeal communities within each site ($p < 0.001$, $R^2 = 0.136$) (Fig. 2.4, Table 2.2). Results from pairwise comparisons, however, did not indicate compositional differences between pairs of degraded, intact, and revegetated plots (likely due to low sample sizes). Although, there is a trend towards marginal differences between degraded and intact and revegetated and intact plots, but no significant differences between degraded and revegetated plots (Fig. 2.4., Table A2.1 in Appendix 2). PERMDISP tests (grouped by site), on the other hand, indicated no difference in the dispersion of bacterial/archaeal communities between degraded and intact plots within each site ($p = 0.541$) (Table A2.2 in Appendix 2), or between degraded, intact, and revegetated plots across the subset of three sites ($p = 0.983$) (Table A2.2 in Appendix 2). This suggests that the dispersion, or distance from midpoint to endpoint of the polygons representing each plot were not significantly different from one another (Fig. 2.4).

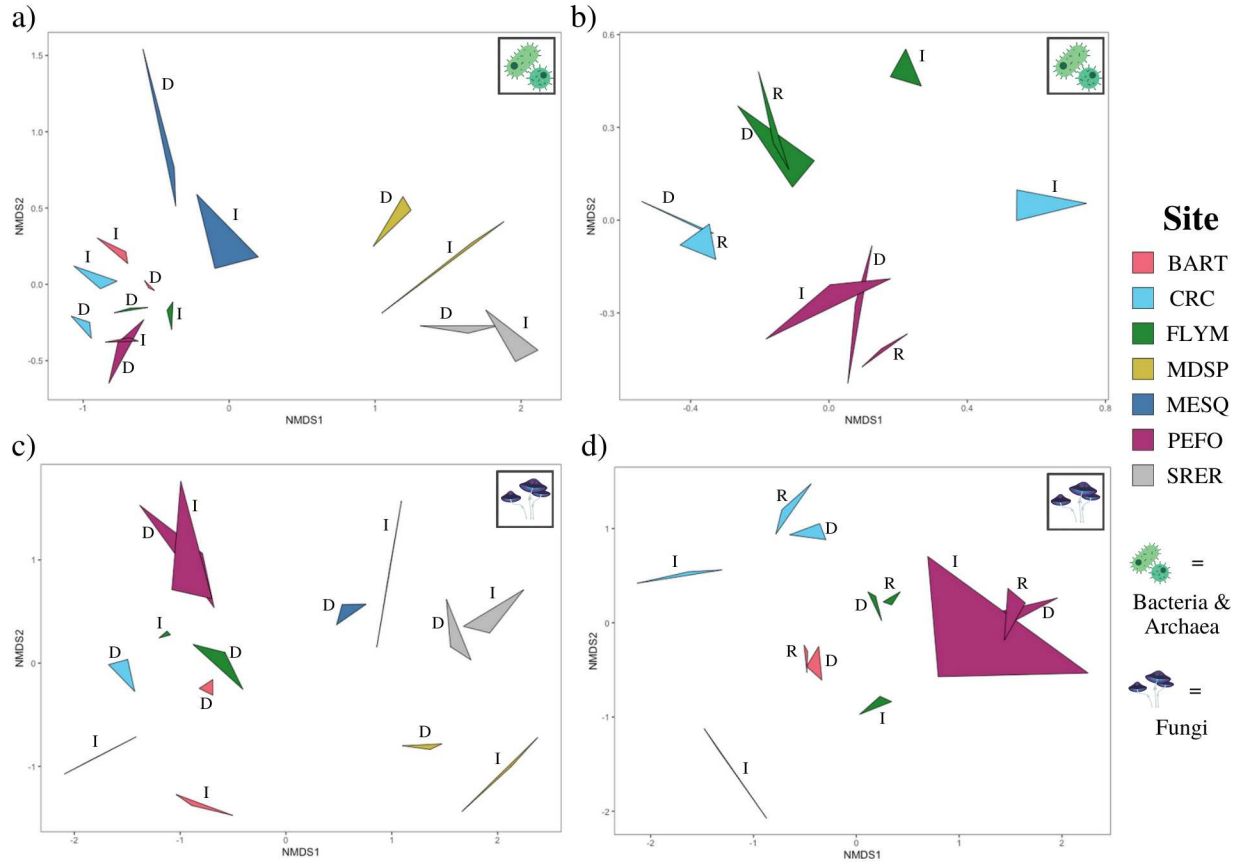


Fig. 2.4. Non-metric multidimensional scaling (NMDS) plots displaying dissimilarity in community composition between (a) degraded and intact plots for bacteria/archaea, (b) degraded, intact, and revegetated plots for bacteria/archaea, (c) degraded and intact plots for fungi, and (d) degraded, intact, and revegetated plots for fungi. Polygons represent soil microbial communities for each plot. Polygons that are more spatially dissimilar represent greater dissimilarity in microbial communities. I = intact, D = degraded, R = revegetated.

Table 2.2. Results from PERMANOVA tests for differences in microbial community composition between degraded and intact, and degraded, intact, and revegetated plots. Samples sizes (n), correlation coefficients (R^2), and p -values (p) are included.

	Degraded vs Intact			Degraded vs Intact vs Revegetated		
	n	R^2	p	n	R^2	p
Bacteria/ Archaea	21	0.03	<0.001*	9	0.136	<0.001*

Fungi	21	0.037	<0.001*	12	0.082	<0.001*
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Similarly, for soil fungal communities, PERMANOVA tests indicate that among all seven sites degraded and intact plots were compositionally different ($p < 0.001$, $R^2 = 0.037$). Though again, the R^2 value of 0.037 suggests that only about 4% of this variation in community composition is accounted for by disturbance condition (degraded versus intact). For the three sites with revegetated plots, results from nested PERMANOVA tests also indicate that fungal community composition differed between degraded, intact, and revegetated plots ($p < 0.001$, $R^2 = 0.082$) (Fig. 2.4, Table 2.2). But similarly to bacteria/archaea, results from pairwise comparisons did not show significant differences between pairs of degraded, intact, and revegetated plots. However, results indicated a trend towards marginal differences between degraded and intact and revegetated and intact plots, but no differences between degraded and revegetated plots (Fig. 2.4, Table A2.1 in Appendix 2). PERMDISP tests for fungal communities also indicate no significant differences in community composition among degraded and intact plots for all seven sites ($p = 0.062$), or degraded, intact, and revegetated plots for the subset of four sites ($p = 0.128$) (Table A2.2 in Appendix 2).

Microbial diversity does not differ among disturbance conditions at most dryland sites

For bacterial/archaeal communities, results from ANOVA tests (nested by site), did not indicate significant differences in Shannon index or species richness between degraded, intact, and revegetated plots (Table 2.3). Additionally, results from a linear regression model did not suggest significant correlation between plant survival in revegetated plots and Shannon index ($p = 0.273$, $R^2 = 0.049$, $F = 1.414$) or species richness ($p = 0.308$, $R^2 = 0.025$, $F = 1.208$) (Figure A2.2 in

Appendix 2). For fungal communities, nested ANOVA results indicate only a significant difference in Shannon index between degraded and intact plots at Flying M Ranch ($p = 0.005$). For the subset of four sites with revegetated plots, nested ANOVA results also indicate significance differences in both Shannon index and species richness between degraded and intact, and revegetated and intact plots at only site FLYM (Table 2.3). At all other sites, there were no significant differences in Shannon index or species richness between degraded, intact, and revegetated plots (Table 2.3). For fungal communities, results from linear regression models actually indicated a negative correlation between survival rate and Shannon index ($p = 0.03$, $R^2 = 0.328$, $F = 6.365$) and species richness ($p = 0.021$, $R^2 = 0.371$, $F = 7.499$) (Figure A2.2 in Appendix 2).

Table 2.3. Differences in Shannon index (exponent) and species richness between degraded, intact, and revegetated plots ($n = 3$).

		Degraded		Intact		Revegetated	
		Shannon Index (exp)	Species Richness	Shannon Index (exp)	Species Richness	Shannon Index (exp)	Species Richness
Bacteria/Archaea	BART	367	753	322	831	N/A	N/A
	CRC	321	643	383	770	276	555
	FLYM	340	736	312	736	292	534
	MDSP	555	906	423	724	N/A	N/A
	MESQ	341	672	431	843	N/A	N/A
	PEFO	390	781	466	861	350	718
	SRER	432	757	548	927	N/A	N/A

Fungi	BART	41	206	39	213	48	246
	CRC	29	151	30	178	19	150
	FLYM	35 a	170 a	82 b	293 b	33 a	177 a
	MDSP	38	144	50	212	N/A	N/A
	MESQ	24	157	35	206	N/A	N/A
	PEFO	38	177	48	184	45	217
	SRER	62	236	53	229	N/A	N/A

Certain microbial taxa are indicative of disturbance conditions

Indicator species analyses determined taxa that were both commonly and close to exclusively found at certain disturbance conditions (degraded, intact, or revegetated plots). Results from the indicator species analysis suggest that there are four bacterial/archaeal ASVs that are indicative of degraded conditions, 38 indicative of intact, and 233 indicative of revegetated conditions. Additionally, results suggest that there are five fungal ASVs indicative of degraded conditions, 12 indicative of intact, and 89 indicative of revegetated.

Bulk density and organic matter content vary by disturbance condition

Correlation analysis helped us identify four relatively orthogonal soil characteristics (i.e., $R^2 < 0.70$): bulk density, pH, organic matter content, and nitrate concentration (Fig. A2.3 in Appendix 2). Nested ANOVAs and Kruskal-Wallis tests for each variable showed significant differences in bulk density ($p < 0.001$) and organic matter content ($p < 0.001$) by disturbance condition (degraded vs intact vs revegetated), but no significant differences in pH ($p = 0.425$) or nitrate concentration ($p = 0.091$) between these three conditions, within each site (Fig. 2.5).

Pairwise comparisons from Tukey HSD and Dunn tests suggest, however, that there were only significant differences in bulk density and organic matter content between degraded and intact, and revegetated and intact plots, and not between degraded and revegetated plots (Fig. 2.5). These differences between degraded and intact were also only present at certain sites (Fig. 2.5).

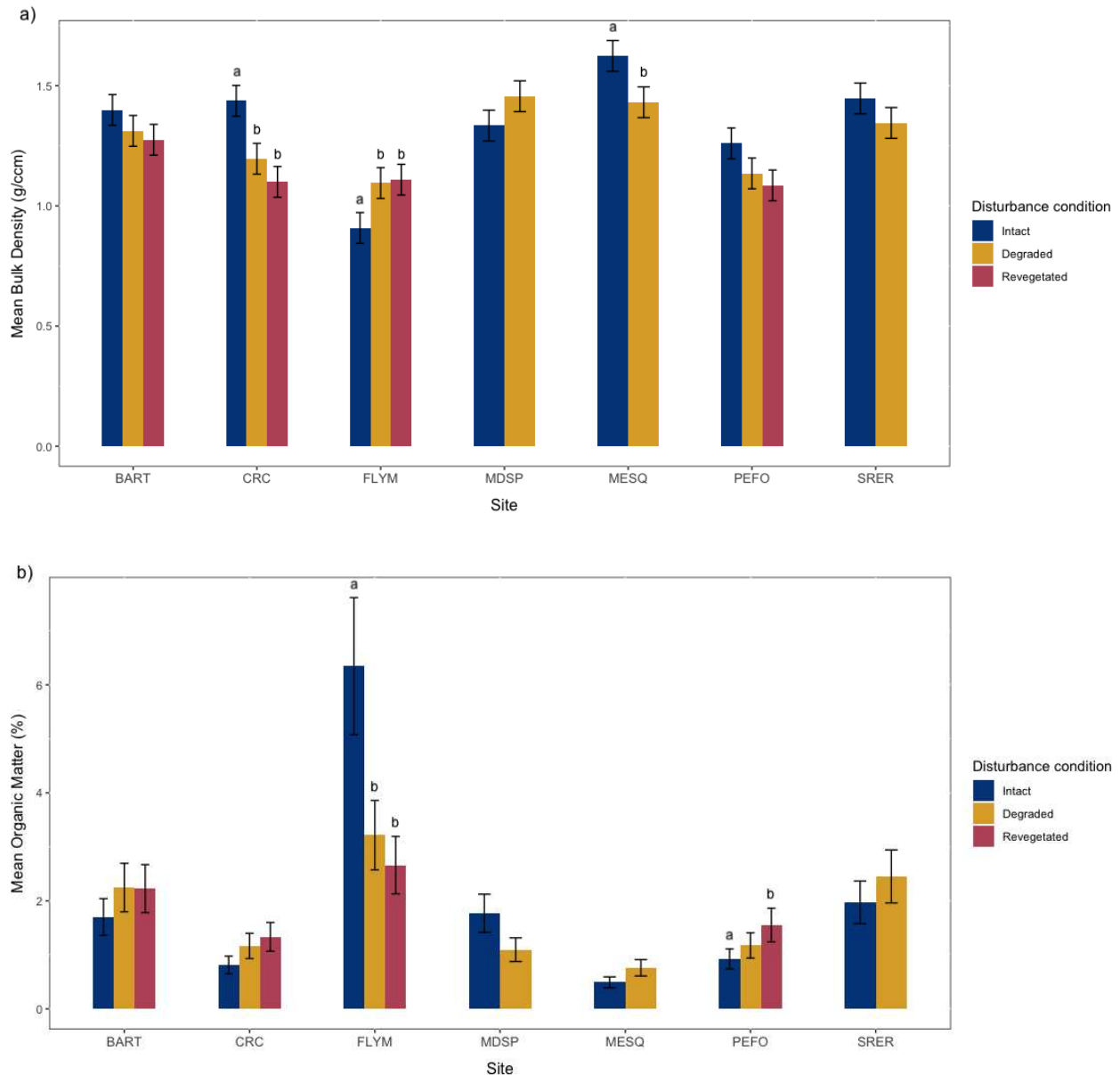


Fig. 2.5. Differences in mean bulk density (a) organic matter content (b) across intact, degraded, and revegetated plots at each site. Letters represent values that are significantly different using an alpha of 0.05. Error bars represent 95% confidence intervals.

Bulk density and pH are related to differences in microbial community composition

After running MRDM models, we found that bulk density ($p = 0.001$), pH ($p = 0.001$), and site ($p = 0.001$) are all significantly related to differences in bacterial/archaeal community composition. However, organic matter content, nitrate concentration, and site condition were not significantly related to differences in bacterial/archaeal community composition. Similarly, bulk density ($p = 0.001$), pH ($p = 0.001$), site ($p = 0.001$), and site condition ($p = 0.01$) were significantly related to differences in fungal community composition, but organic matter content ($p = 0.328$) and nitrate concentration were not ($p = 0.341$).

Discussion

In support of our hypothesis, soil microbial communities differed between paired intact reference and degraded plots. This suggests that soil disturbances, such as those from grazing and tilling for example, may alter belowground microbial communities in drylands. This finding establishes an opportunity for the potential restoration of microbial communities following soil disturbance and degradation, including treatments such as microbial inoculations that aim to directly add beneficial microbes back into degraded soils (Alori and Babola, 2018). However, disturbance likely only plays a small role in determining microbial community composition, given disturbance condition only accounted for about 3-4% of variation in community composition, and community response to disturbance varied by site. This, along with our findings from the MDRM analysis, suggest that there are likely other factors, such as soil pH and bulk density, that play a larger role in structuring microbial communities, which is important to consider when choosing inoculation treatments.

Soil microbial community composition, but not diversity, differs between reference and degraded dryland sites

Microbial community composition differed between degraded and intact plots within sites. While PERMDISP tests did not indicate differences in the dispersion of microbial communities among disturbance conditions, PERMANOVA tests did indicate differences in the midpoints of polygons representing intact and degraded plots. Therefore, we can infer that there are some differences in microbial communities between degraded and intact plots. This supports our prediction, given that microbes are often dependent on the types of plants present, which differ between degraded and intact plots (Zhang et al., 2021). Our finding matches findings from other literature on microbial communities in degraded grassland and agricultural soils, which similarly found differences in microbial compositions along degradation gradients that may have been associated with changes in soil properties and the presence of pathogens (Chao et al., 2022, Zhang et al., 2017). It is important to note, however, that the R^2 values from PERMANOVA tests of 0.030 for bacteria/archaea and 0.037 for fungi indicate that, while significant, disturbance condition only explains a relatively small amount of the total variation in microbial community composition. Additionally, the direction of compositional shifts was not uniform across all sites, suggesting that degradation does not affect microbial communities in the same way at every site (Fig. 2.4). This suggests that additional factors, such as pH, which has been found to be one of the main drivers of microbial community composition (Jin and Kirk, 2018, Rousk et al. 2010), are important to consider for decision-making in the restoration of dryland soil microbial communities.

Surprisingly, we did not find significant differences in diversity between degraded and intact plots for bacteria/archaea or fungi, as there was only a significant difference in diversity for fungi at one site in northern Arizona (FLYM) (Table 2.3). This does not support our prediction

that intact sites would have greater microbial diversity given that they often have greater plant diversity (Chen et al., 2019, Manhães et al., 2022). However, several studies have found that factors such as aridity are major drivers of microbial diversity in drylands, specifically (Maestre et al., 2015, Pan et al., 2022). So, it is possible that other environmental factors such as aridity may play a larger role in determining microbial diversity in drylands. Looking at community composition and diversity together, since degraded and intact plots have roughly the same levels of diversity, then there are likely just different species present with different relative abundances, as we have evidence that microbial communities at degraded versus intact plots are compositionally different. This finding indicates that direct actions besides revegetation may need to be taken to address shifts in microbial community composition where soil degradation has occurred.

Microbial community composition and diversity do not differ between degraded and revegetated sites

Neither bacterial/archeal nor fungal community composition varied between degraded and revegetated plots. In fact, for the subset of sites containing revegetated plots, we did not find significant differences between any pairs of degraded, intact, or revegetated plots, though we did observe a trend towards marginally significant differences between degraded and intact, and intact and revegetated plots. This result may have been partially due to the low sample size ($n = 3$) when only a subset of all sites was analyzed. Still, there was no trend towards significance between degraded and revegetated plots. There were also no significant differences in diversity between degraded and revegetated plots. One reason for this could have been the relatively low survival rates of transplanted seedlings (Fig. A2.2 in Appendix 2), causing revegetated plots to have similar plant cover and soil physical conditions as degraded plots, in some cases. However, we found no correlation between seedling survival at revegetated plots and diversity, meaning that diversity

was not significantly higher in plots with higher seedling survival rates. This suggests that low survival of revegetated seedlings is likely not the only reason for similar levels of diversity in degraded and revegetated plots.

The lack of difference in microbial communities of degraded versus intact plots that we observed agrees with the findings of a similar study by Yang et al. (2021), which used some of the same study sites, and also found no significant differences in microbial community composition or diversity between degraded and intact plots. This study presents a relatively short-term observation of microbial communities post revegetation, as samples were only collected one year post revegetation. While our study was slightly longer term (three years post-revegetation), three years may not be enough time for microbial communities to recover to pre-degradation conditions, as some studies suggest recovery of microbial communities often takes between six and ten years (Steven et al., 2021, Zhang et al., 2021 b). Conversely, other studies have found relatively short-term responses (one to two years) of microbial communities to restoration or the cessation of disturbance (Selari et al., 2021, Xu et al. 2022), yet these studies took place in humid tropical environments, and varied for fungi and bacteria communities. So, it may be that microbial community recovery is slower in dryland systems given water and nutrient limitations that may limit microbial activity (Harris, 2009, Klemmedson, 2009). Overall, the similarity in microbial communities between degraded and revegetated plots suggests that revegetation may not be sufficient for restoring microbial communities, or at least not within a time frame of three years.

Biocrust-forming bacteria and endophytic fungi are indicative of intact dryland conditions

Indicator species analyses suggest many different taxa that are indicative of intact, degraded, and revegetated site conditions. Interestingly, we found that several bacterial and fungal ASVs associated with biological soil crusts (biocrusts) were indicative of intact conditions, which

makes sense given that many “intact” reference sites in this study were selected in part due to the presence of biocrusts. Biocrusts are soil surface dwelling communities composed of organisms including cyanobacteria, lichens, and bryophytes that increase soil stability and resource availability in drylands (Weber et al., 2022). As such, biocrusts are commonly used as indicators of healthy dryland soils, especially given their observed potential to initiate succession and recovery of degraded systems through functions such as increasing aggregate stability, moisture storage, and nutrient accumulation through carbon and nitrogen fixation (Bowker, 2007, Eldridge and Leys, 2003, Eldridge et al., 2020, Elbert et al. 2012). Bacterial indicator species for intact sites included ASVs in the AKIW781 family of the Chloroflexi phylum. Several species in this family have been found in biological soil crust (biocrust) samples (Mogul et al., 2017). Another bacteria that was identified as indicative of intact conditions was an ASV in the genus *Rubellimicrobium*. Some species that make up this genus have been found in lichen samples (Jiang et al., 2019), which are often part of the biocrust community (Belnap and Lange, 2017).

Several fungal ASVs were found to be indicative of intact conditions as well, including multiple in the Lentitheciaceae family of Ascomycota phylum. This family includes many types of saprobic, or decomposing, fungi (Liu et al., 2022 b), which are important for soil health given their large role in the decomposition of organic matter and nutrient cycling (Baldrian and Valášková 2008). Additionally, this family also includes certain types of dark septate endophytic fungi (Liu et al., 2022 b, Romero-Jimenez et al., 2022), which are also thought to be important constituents of biocrusts (Maier et al., 2016) and are especially important in drylands due to their potential abilities to enhance seedling growth and increase drought resistance (Liu et al. 2022, a). Additionally, some research has also suggested that these types of fungi may be able to help link plants with carbon and nitrogen-fixing biocrusts, known as the fungal-loop hypothesis (Collins et

al., 2008). Given these beneficial qualities, it makes sense that many of these taxa are found to be indicative of intact conditions where greater cover of biocrust and plant communities exist.

Unlike intact conditions, we did not find biocrust-associated indicator species within degraded plots. In contrast, indicator species in degraded plots included several potentially stress-tolerant and pathogenic taxa. For example, one bacterial taxa found to be indicative of degraded conditions was the genus *Kineococcus*, which includes several species of bacteria that have been found to be radiotolerant (Phillips et al., 2022). In some cases, this means tolerant to high levels of solar radiation (Molina-Menor et al., 2020). Radiotolerant bacteria may be indicative of degraded conditions given that degraded plots likely have lower plant cover, and therefore less shade and higher exposure to solar radiation. Several fungi of the genus *Alternaria* were also found to be indicative of degraded conditions. This genus includes a common plant pathogen that produces phytotoxins and can cause tissue damage and growth inhibition in plants (Patriarcha et al., 2014, Xu et al., 2021). This could explain a potential cause of degradation at sites that are experiencing plant death due to pathogens. Or, it may be that plants experiencing difficult growing conditions in degraded sites (such as water deficiency) are more susceptible to pathogens like *Alternaria*, so it can spread more easily in these communities (Chojak-Koźniewska et al., 2018).

Overall, these results suggest that certain beneficial microbes like biocrust-forming bacteria and dark septate endophytes, may be much less abundant at degraded sites than at their intact counterparts, making them potentially good targets for inoculation treatments (Chaudhary et al., 2020). These differences in functionality between indicator species of intact versus degraded conditions indicate that there may be significant functional differences between degraded and intact microbial communities. So, while we found that only a relatively small (3-4%) of variation in microbial community composition was explained by disturbance condition, this small percent

of variation could be significant to ecosystem functioning if large differences in microbial functions exist. This presents opportunities for future research specifically examining differences in functional diversity between degraded and intact conditions.

Changes in bulk density are related to both disturbance condition and concomitant differences in microbial community composition

Activities causing soil degradation, such as intensive grazing and tilling/plowing, often impact soil physical characteristics, usually leading to higher compaction, lower moisture retention, and less nutrient accumulation (Lema et al., 2019, Gregory et al., 2015). When comparing changes in soil physical characteristics across degraded, intact, and revegetated plots, we found that bulk density and organic matter content differed across disturbance conditions, but varied greatly by site. For example, bulk density was lower in the degraded plot than the intact at Canyonlands Research Center, but higher at Flying M Ranch. Similarly, organic matter was lower in the degraded plot at Flying M Ranch, but higher at Petrified Forest.

While we expected to see higher bulk density and lower organic matter content in degraded plots in general, some of the site-specific variation we observed may have to do with different types of disturbances. Intensive grazing, for example, has been shown to increase bulk density by causing soil compaction (Chanasyk and Naeth, 1995), so this may explain the higher bulk density values at degraded plots at Flying M Ranch. Agricultural tilling, on the other hand, often decreases bulk density by breaking up compacted soil (Osunbitan et al., 2005), so this could explain lower bulk density in degraded plots at Canyonlands Research Center, where cropping was the main historical disturbance (Table 2.1). For organic matter content, grazing can have varied effects on soil organic matter, often depending on climate, where grazing tends to decrease organic matter levels in more arid regions (Abdallah et al. 2018), as observed at Flying M Ranch. While

agricultural activity is often associated with lower soil organic matter (Yavitt et al., 2021), it is possible that farming practices in this study region included applications of organic amendments, which are commonly applied in dryland farming systems, and may increase soil organic matter levels (Parr et al., 2009). So, this could explain the higher levels of organic matter at Petrified Forest, which historically had been cultivated land (Table 2.1).

After analyzing differences in soil physical characteristics across disturbance conditions, we used MRDM models, which identify correlation in dissimilarity matrices to look for relationships between physical soil characteristics and dissimilarity in microbial communities. Understanding soil characteristics that are associated with changes in microbial communities could help us infer some of the possible mechanisms for how degradation might impact microbial communities. Through MRDM models, we found that only bulk density and pH are correlated with differences in microbial communities. These analyses suggest that soil degradation affects bulk density, which has been also found in other research (Chanasyk and Naeth, 1995), and that bulk density is associated with differences in microbial communities. So, perhaps changes in bulk density following activities such as intensive grazing are part of what is driving the differences in microbial communities between degraded and intact plots (Li et al., 2002). For example, we see the greatest differences in bulk density between degraded and intact plots at Canyonlands Research Center (CRC) and Flying M Ranch (FLYM), but no significant differences in bulk density at Petrified Forest (PEFO). According to our NMDS plots, we also see that degraded and intact communities are more spatially separated at CRC and FLYM than they are at PEFO (Fig 2.4 panel b), so this may be related to the greater disparity in bulk density between plots at CRC and FLYM.

However, as discussed above, at certain sites we actually found that bulk density was higher at intact plots and lower at degraded plots, which is not what we would expect given that

soils with relatively lower bulk density benefit plant growth due to increased soil pore space for moisture and nutrient retention (Stirzaker et al., 1996). This could be partially due to past management practices (e.g., tilling, invasive plant removal) at certain sites that could have caused soil decompaction and lowered bulk density within degraded plots. Either way, changes in bulk density associated with degradation could be part of what is driving changes in microbial communities associated with degradation.

Soil pH was also significantly correlated with dissimilarity in microbial communities, but was not affected by disturbance condition (soil degradation) overall. So, while previous research has also found pH to be the main driver of microbial community composition in general, (Fierer et al., 2017, Jin and Kirk, 2018, Rousk et al. 2010), it is likely not a direct mechanism underlying changes in microbial communities following degradation specifically, at least across the sites in this study. Overall, the relationship between soil degradation, bulk density, and microbial community composition suggests that changes in microbial composition following degradation may be associated with changes in soil bulk density following degradation. So, if degradation occurs and causes changes in bulk density, it is likely that microbial communities will shift, and action may be needed to aid in their recovery.

Limitations and opportunities for future research

This study had several limitations that could be addressed with future research. One of the major limitations is that our final analyses only included three revegetated plots for bacterial/archaeal communities, and four for fungal communities. Because there were only three replicate samples per plot, this yielded relatively low sample sizes that might have impacted our ability to detect ecological signals. Future studies should sample from a greater number of sites with more replicate samples to allow for greater potential sensitivity in analyses to detect soil

microbial community responses to degradation and revegetation. Additionally, for this study we only took samples three years post-revegetation, making this study relatively short term. While soil communities have been shown to be early indicators of changes in soil health following restoration interventions in some cases (Selari et al., 2021, Xu et al. 2022), longer term studies may be needed in order to assess the full recovery of soil microbial communities, as this may take more in the range of six to ten years (Steven et al., 2021, Zhang et al., 2021 b). We also utilized revegetated plots that in many cases had low seedling survival. It is possible that we might see greater differences in microbial communities in degraded versus revegetated plots where revegetation had been more successful in terms of higher seedling survival, so this would be interesting to examine in the future as well. Overall, studies on dryland soil microbial communities with greater sample sizes, longer time intervals, and more successful revegetation would be useful in assessing soil microbiomes across gradients of disturbance in drylands.

Shifts in soil microbiomes following dryland degradation indicate the importance of active soil restoration

Degradation of dryland soils is a major global issue, and, given their importance in ecosystem health and functioning, microbes may play a significant role in soil recovery. In this study, we aimed to help improve our general understanding of soil microbial sensitivity to degradation and revegetation efforts in order to better assess the need for direct intervention in replenishing microbial communities in degraded drylands. We found that soil microbial community composition varied between degraded and intact dryland plots, but not between degraded and recently revegetated plots. This small, but significant difference first suggests that if a site has been degraded, then the soil microbial community has likely shifted from the intact reference condition, meaning that direct action may need to be taken to help microbial

communities recover, such as active microbial inoculation (Alori and Babola 2018). This also tells us that revegetation with plants may not be sufficient to restore microbial communities, at least in the relative short term, especially since revegetated seedling survival is often low in drylands without additional treatments that directly target increasing physical and/or biotic soil health (Shackelford et al., 2021). Other findings from this study also suggest that some of the changes in microbial communities associated with degradation may be partially due to changes in bulk density associated with degradation (Li et al., 2002). So, if soil degradation causes changes in bulk density, then restoration of microbial communities may be especially important. Lastly, degraded sites in U.S. drylands seem to often have lower abundances of beneficial taxa such as biocrust-forming bacteria and dark septate endophytic fungi, so these taxa may be particularly useful in restoration inoculation treatments, and that differences in microbial functionality between degraded and intact conditions may be significant. The results from this study can help lead us towards more informed restoration of microbial communities in degraded drylands, which will help improve restoration outcomes and combat degradation in global drylands.

CONCLUSIONS

Given the serious threat to billions of livelihoods, land degradation is an issue that must be addressed. In global drylands, which make up over 40% of the world's terrestrial land surface, reversing degradation through ecological restoration has shown to be very difficult (Shackelford et al. 2021, Antoninka et al., 2019). Seeding or revegetating alone often fails, potentially due to the many abiotic and biotic barriers drylands face such as water and nutrient limitation, as well as diminished microbial communities (Shackelford et al. 2021, Antoninka et al., 2019). Soil-based restoration treatments may be key in overcoming some of these barriers to ecosystem recovery, yet to date we have not had sufficient information on which treatments are most effective, and conditions under which their benefits may be maximized. Too often, treatments are administered without a preliminary understanding of site-specific conditions and barriers or optimal treatments. This research aims to provide more information on how, when, and where to use soil based restoration treatments in order to inform land managers and restoration practitioners about how to restore soils efficiently and effectively in degraded drylands.

Chapter 1 of this thesis suggests that across global drylands, soil restoration is most effective at increasing nutrients in arid environments with fine-textured soils, making sites with these conditions good targets for restoration. We also found that for increasing soil organic carbon, organic amendments work particularly well, while for increasing mycorrhizal fungi colonization of plant roots, direct inoculation with fungi is likely the best option. Additionally, findings from Chapter 2 suggest that soil microbial communities in degraded sites differ from intact reference site counterparts, but not from paired revegetated sites, indicating that active soil-based restoration treatments are likely needed to help degraded microbial communities recover. Certain taxa including biocrust-forming bacteria and dark septate endophytic fungi, which were found to be

indicative of intact sites but less abundant or missing from degraded sites, may be good options for inoculation treatments. All of this information can be used by land managers and restoration practitioners to inform site selection and optimal treatments for dryland restoration. More informed decision-making in restoration planning will hopefully improve restoration success and make better use out of the limited resources available for restoration. Improved restoration success could mean the potential reversal of degradation in certain areas, a shift towards healthier ecosystems, and more sustainable livelihoods for decades to come.

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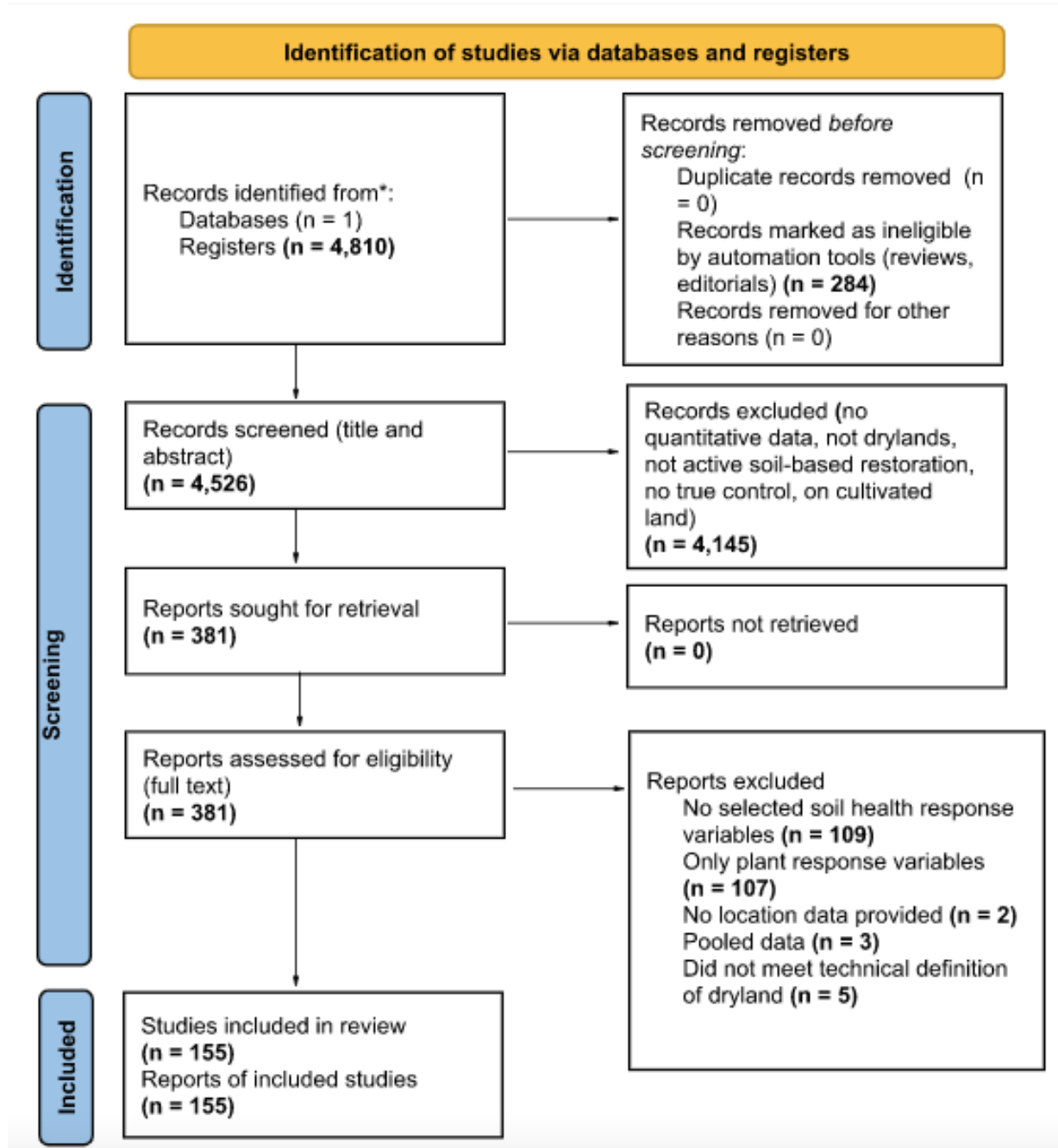
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APPENDIX 1



From: Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 2021;372:n71. doi: 10.1136/bmj.n71

For more information, visit: <http://www.prisma-statement.org/>

Fig. A1.1. Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) diagram.

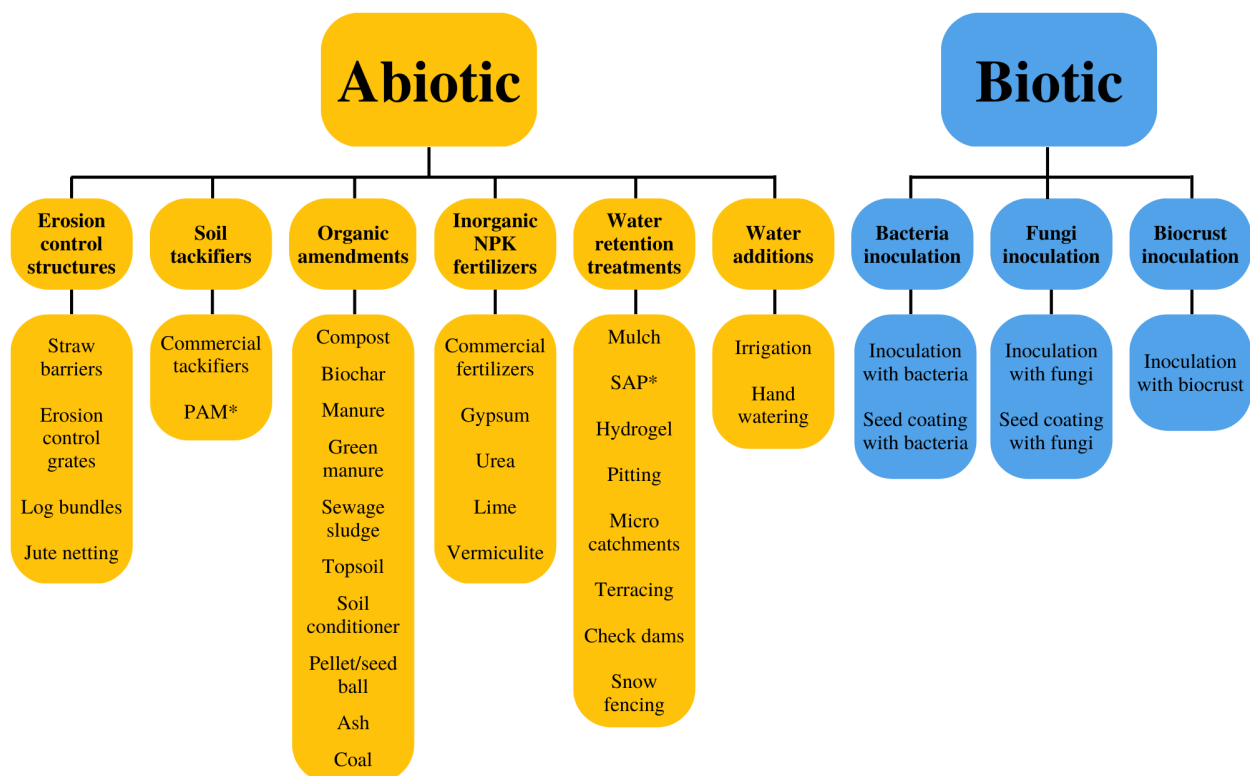


Fig. A1.2. Categorization of treatments analyzed in this meta-analysis. PAM = polyacrylamide. SAP = super absorbent polymer.

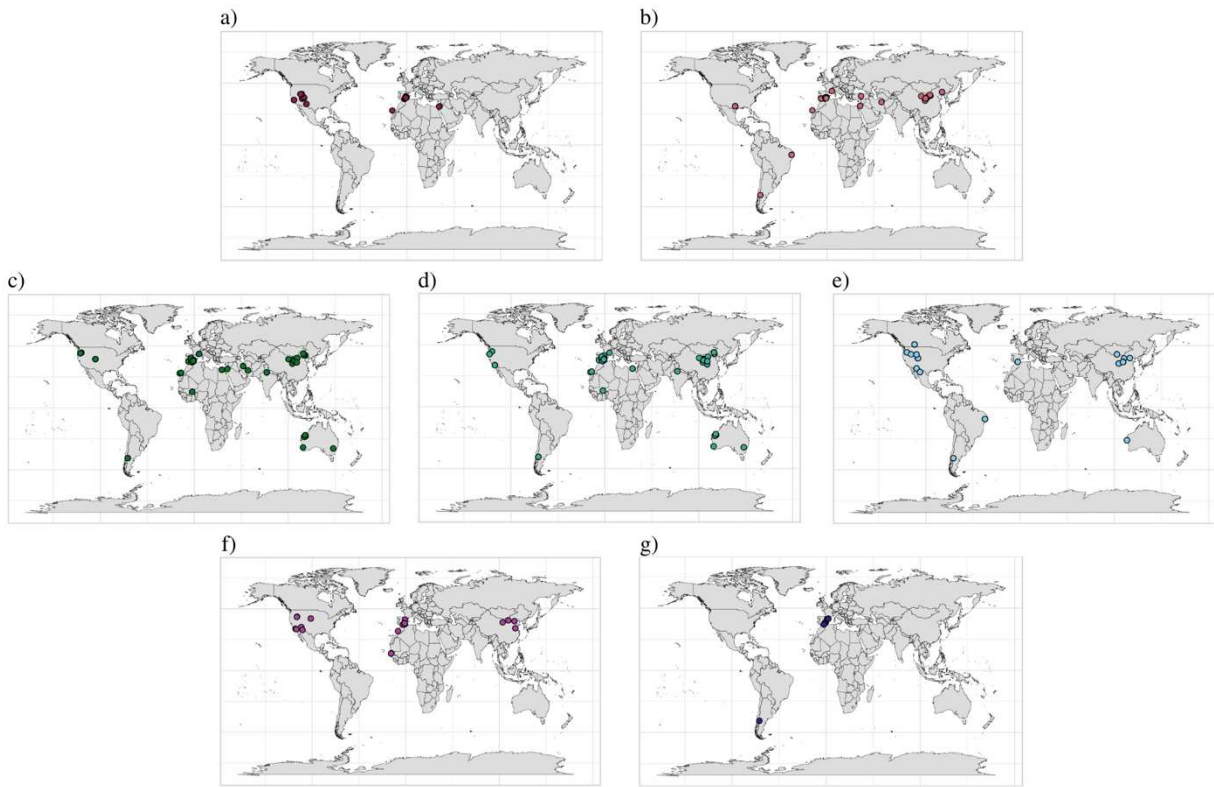


Fig. A1.3. Geographic locations of studies used in this meta-analysis for each soil health metric. Panels a through g correspond to the following soil health metrics, in this order: aggregate stability, bulk density, soil organic carbon, soil nitrogen, soil moisture (%VWC), mycorrhizal colonization, and basal respiration.

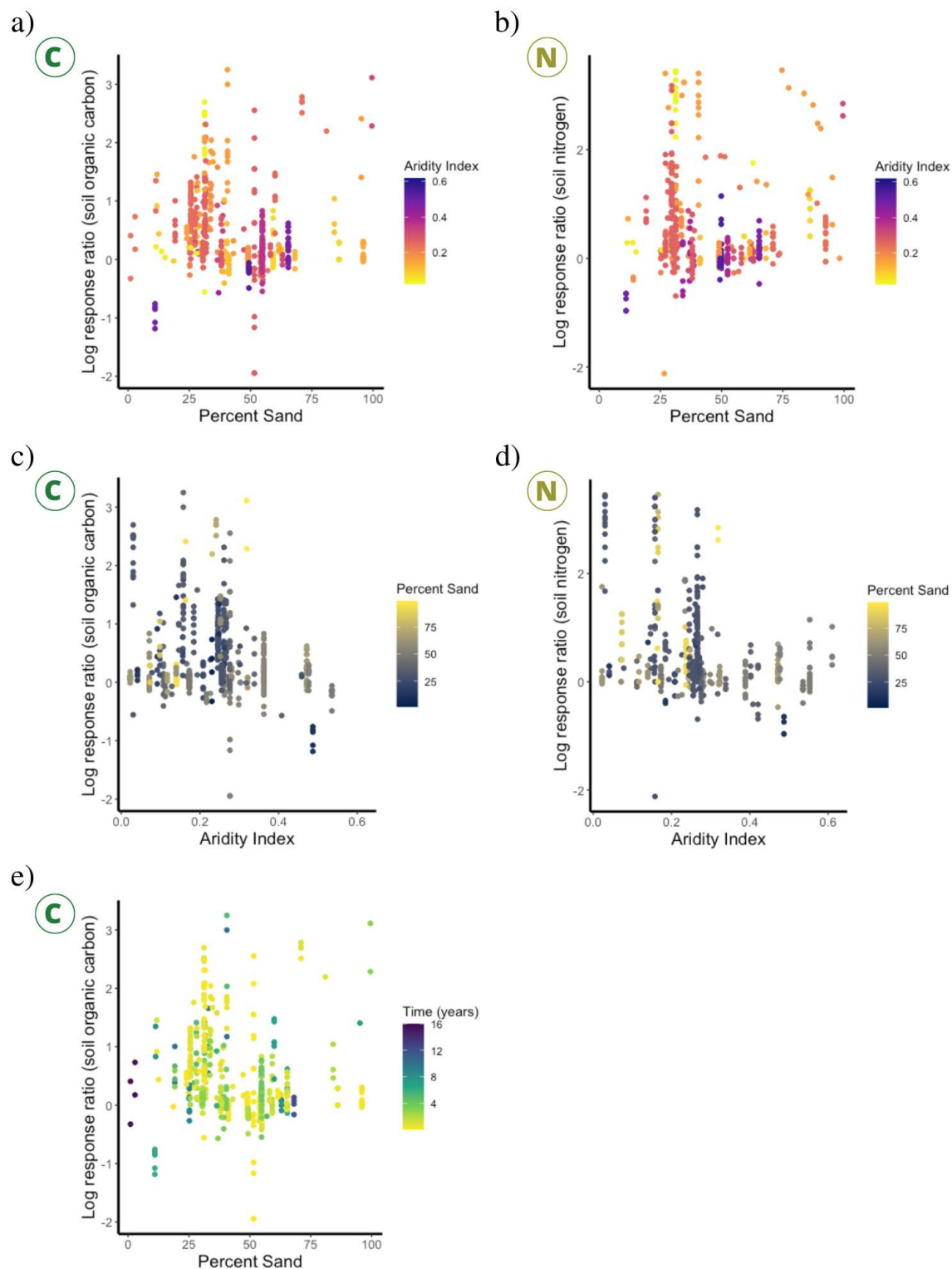


Fig. A1.4. Interactions between Aridity and Percent_Sand, and Time and Percent_Sand, and their influence on the log response ratio (LnRR) for SOC and soil N. Panels a and b depict the relationship between Percent_Sand and the LnRR of SOC and soil N, respectively, with plotted points colored by Aridity_Index. Panels c and d depict the relationship between Aridity_Index

and the LnRR of SOC and soil N, respectively, with plotted points colored by Percent_sSand. Panel e depicts the relationship between Percent_Sand and the LnRR of SOC, with plotted points colored by Time.

Supplementary Methods

After extracting data from publications, we first standardized the units given for all data variables in order for the values to be comparable and used in analysis. For bulk density, all values were converted into g/cm^3 . For volumetric water content, all values were converted into percentages. For SOC and N, all values were converted into g/kg . For mycorrhizal colonization, we used only values that were reported as the percent of root colonized. And for basal respiration, we converted all values to $\text{mg CO}_2/\text{kg/day}$. Studies with values that could not be converted to these units were excluded from analysis. For aggregate stability, in order to have an adequate sample size, we used studies that reported aggregate stability as a 1-6 rating from a slake test, or as a percentage of stable aggregates. While these two units are not identical, all values were later converted into log response ratios to be able to be comparable as unitless measurements of effect size. When calculating effect sizes (log response ratios), we used zero-inflated values by adding 0.00001 (Harrison, 2014) to all values in order to include zero values in the analysis. To calculate within-study variance, we needed standard deviation values for part of the equation. When standard error was given instead of standard deviation, we multiplied the standard error by the square root of the sample size (n) to convert to standard deviation.

Supplementary Results - Database Summary

The majority of studies included in our analysis (65%) had a duration of one year or less, meaning that most data were collected one year or less post treatment application. 27% of studies had a duration between one and five years, while only 4% had a duration of six to ten years, and

3% a duration of over ten years. Majority of studies (69%) did not include a revegetation treatment, while the remaining 31% did. There was more variation in soil depth across studies, with 22% of studies using measurements from the top 0-10 cm of soil, 41% from 10-20 cm, 10% from 20-30 cm, 7% from 30-50 cm, 15% from 60-100 cm, and 4% from 100-120 cm. The two most commonly studied treatment types were organic amendments (494; 36%) and water retention treatments (430; 31%). The next most commonly studied treatment was fungi inoculation, which made up 12% (168) of studies. Other treatment types were inorganic NPK fertilizers (89; 7%), erosion control structures (82; 6%), soil tackifiers (58; 4%), and bacteria inoculation (44; 3%).

Publications included in dataset (n=155):

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APPENDIX 2

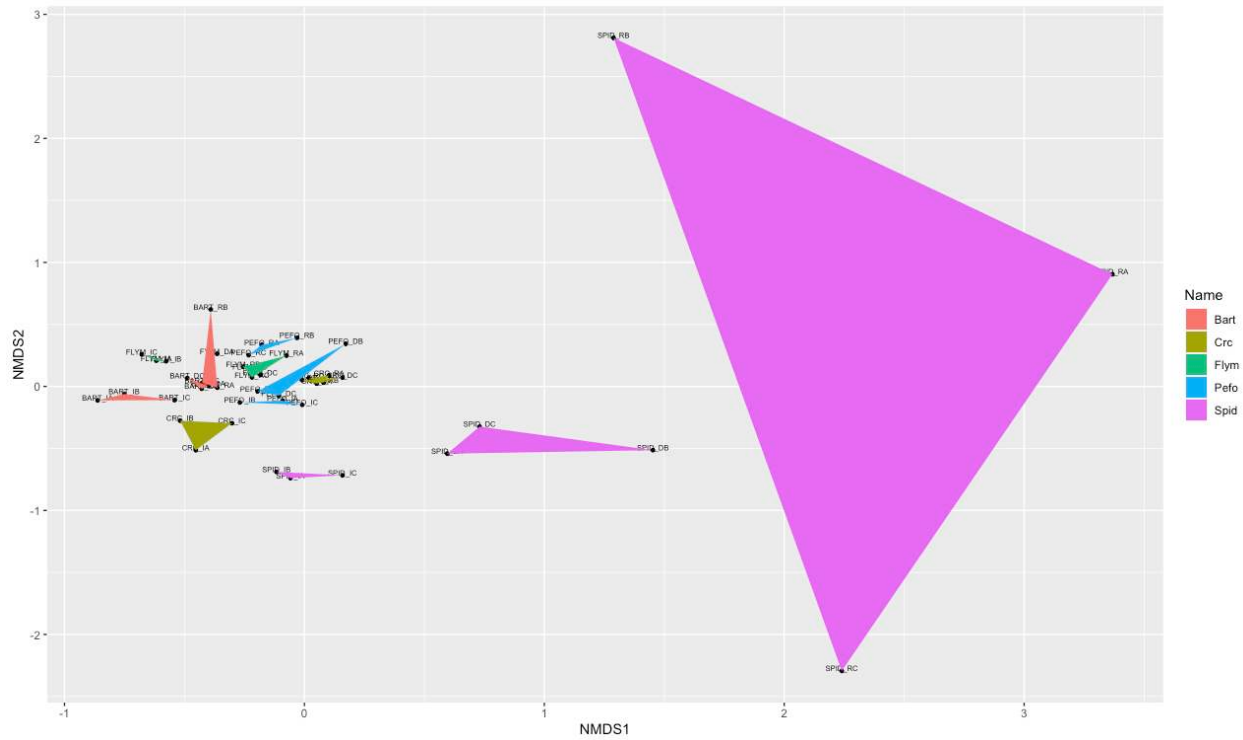


Fig. A2.1. NMDS plot showing intact, degraded, and revegetated plots at each site, including Spiderweb Ranch, highlighting Spiderweb Ranch as an outlier.

Table A2.1. Results from pairwise PERMANOVA tests for differences in microbial community composition between pairs of degraded, intact, and revegetated plots at each site. Sample size for all pairs is $n = 6$. Correlation coefficients (R^2), and p -values (p) are included.

		Degraded vs Intact		Degraded vs Revegetated		Intact vs Revegetated	
		R^2	p	R^2	p	R^2	p
Bacteria/Archaea	CRC	0.506	0.1	0.2	0.5	0.514	0.1
	FLYM	0.43	0.1	0.2	0.5	0.473	0.1
	PEFO	0.291	0.1	0.28	0.2	0.39	0.1

Fungi	BART	0.419	0.1	0.15	1	0.439	0.1
	CRC	0.384	0.1	0.198	0.4	0.376	0.1
	FLYM	0.54	0.1	0.219	0.3	0.564	0.1
	PEFO	0.283	0.1	0.223	0.2	0.332	0.1

Table A2.2. Results from PERMDISP tests for differences in microbial community composition between degraded and intact, and degraded, intact, and revegetated plots. Samples sizes (*n*), correlation coefficients (R^2), and *p*-values (*p*) are included.

	Degraded vs Intact			Degraded vs Intact vs Revegetated		
	<i>n</i>	R^2	<i>p</i>	<i>n</i>	R^2	<i>p</i>
Bacteria/ Archaea	21	N/A	0.541	9	N/A	0.983
Fungi	21	N/A	0.062	12	N/A	0.128

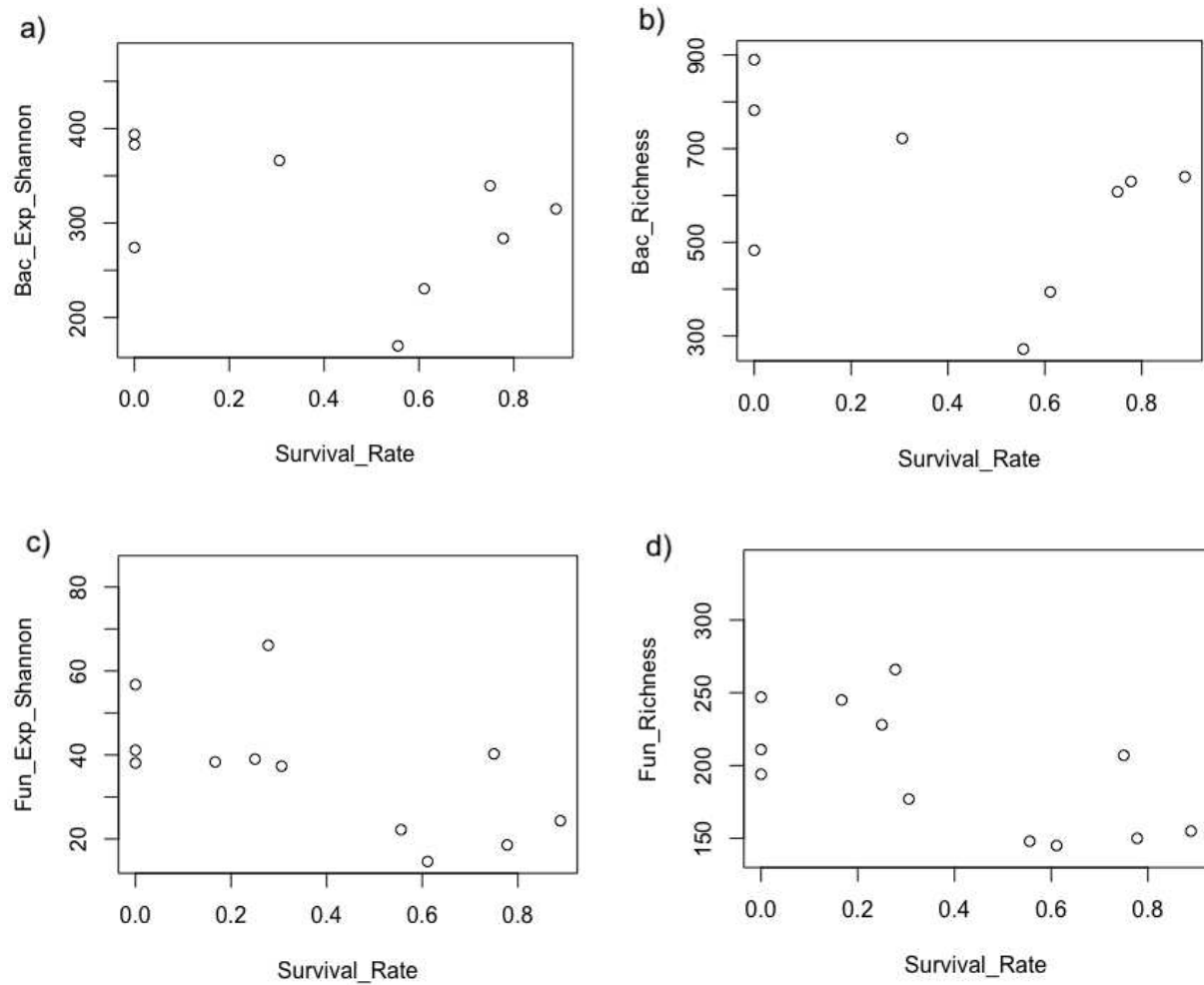


Fig. A2.2. Scatterplots of bacterial/archaeal Shannon Index (a) and species richness (b) versus transplanted seedling survival, and fungal Shannon Index (c) and species richness (d) versus transplanted seedling survival.

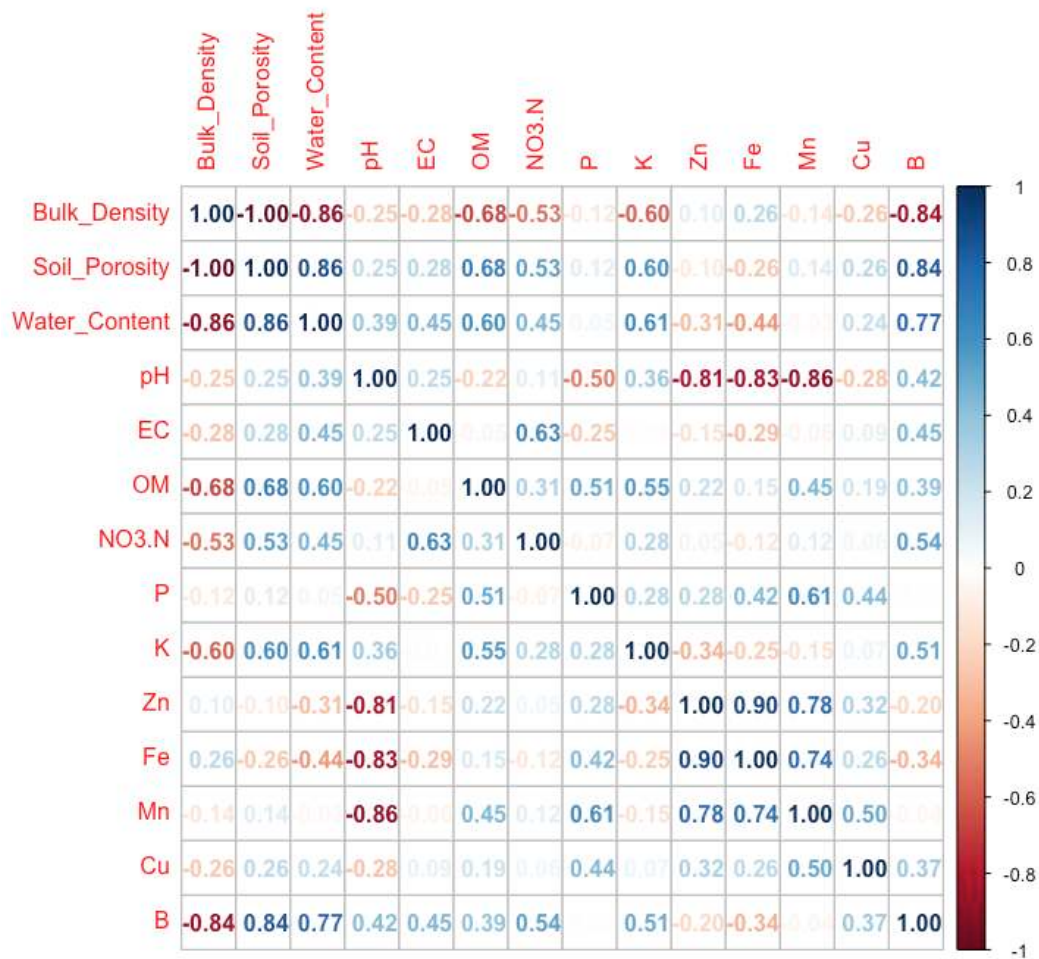


Fig. A2.3. Correlation plot displaying correlation coefficients for soil physical characteristics.