Towards a Predictive Framework for Biocrust Mediation of Vascular Plant Performance and Community Structure

Caroline Ann Havrilla

University of Colorado at Boulder, calouis2@gmail.com

Follow this and additional works at: https://scholar.colorado.edu/ebio_gradetds

Part of the Ecology and Evolutionary Biology Commons, Plant Sciences Commons, and the Soil Science Commons

Recommended Citation
https://scholar.colorado.edu/ebio_gradetds/126

This Dissertation is brought to you for free and open access by Ecology & Evolutionary Biology at CU Scholar. It has been accepted for inclusion in Ecology & Evolutionary Biology Graduate Theses & Dissertations by an authorized administrator of CU Scholar. For more information, please contact cuscholaradmin@colorado.edu.
Towards a Predictive Framework for Biocrust Mediation of
Vascular Plant Performance and Community Structure

By

Caroline A. Havrilla

B.A., Education, Michigan State University, 2010
B.S., Biology, University of Memphis, 2014

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado
In partial fulfillment of the requirement for the degree of
Doctor of Philosophy
Department of Ecology and Evolutionary Biology
2019
This thesis entitled:

Towards a predictive framework for biocrust mediation of vascular plant performance and community structure

Written by Caroline A. Havrilla

has been approved for the Department of Ecology and Evolutionary Biology

__________________________________________________
Dr. Nichole N. Barger, Chair

__________________________________________________
Dr. William D. Bowman

__________________________________________________
Dr. Katharine N. Suding

__________________________________________________
Dr. Timothy R. Seastedt

__________________________________________________
Dr. Daniel F. Doak

Date ________________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above-mentioned discipline.
Havrilla, Caroline A. (Ph.D., Ecology and Evolutionary Biology)
Towards a predictive framework for biocrust mediation of vascular plant performance and community structure
Thesis directed by Prof. Nichole N. Barger

Understanding the key factors that determine community structure is a central goal of ecology. While in plant community ecology there is wide consensus of the primary importance of dispersal limitations and abiotic filters in determining community structure, ecologists are just beginning to understand how biotic interactions restrict or enhance the performance and abundance of certain species within communities. Biological soil crusts (‘biocrusts’) – surface-dwelling soil biotic communities comprised of cyanobacteria, algae, lichens, bryophytes, and fungi – coexist with vascular plants in dryland ecosystems worldwide. Where they occur, biocrusts modify soil resource availability (e.g., water, nutrients) and other soil characteristics that may strongly influence the plants with which they coexist. Yet, general patterns underlying biocrust-plant interaction outcomes have remained uncertain. Using a combination of greenhouse experiments, observational field data, and analytical techniques including meta-analysis, I examine how biocrusts influence dryland plant species and communities. I experimentally demonstrate that, in general, biocrusts inhibit the germination of individual plant species, but enhance plant growth. Using meta-analysis, I quantify the relative importance of key biocrust, plant, and environmental explanatory variables in determining outcomes of plant responses to biocrusts globally. I find that biocrust composition and plant functional traits including lifeform, photosynthetic pathway, and presence of nitrogen-fixing symbionts can be used to predict plant responses to biocrusts. Additionally, I show that biocrusts likely contribute to the biotic resistance of plant communities through inhibition of exotic over native plant
species during recruitment. Collectively, these results suggest that by increasing or decreasing the performance of certain plant functional types within communities, biocrusts may mediate plant community structure and diversity. Finally, I test this assumption using an observational field study. I show that biocrust spatial heterogeneity is positively associated with plant species richness via niche-based processes, suggesting biocrusts may stabilize plant species coexistence at community scale. Across this work, I find that biocrusts can have strong impacts on plant species performance and plant community structure. Generally, this work has implications for understanding the potential of plant-soil interactions to influence plant community assembly and diversity and suggests the importance of biocrusts in supporting plant diversity and invasibility patterns in dryland ecosystems.
DEDICATION

To all of my friends and family who have supported me along the way.
ACKNOWLEDGEMENTS

I am so thankful to my family – David Havrilla, Shann Louis, Tim Louis, Cameron Louis, Linda Louis, Maggie Louis, Linda Cook, Christie Hanes, and Dave Havrilla – for all of their support and encouragement during this process. Thanks to my advisor Nichole Barger for her guidance, feedback, and level-headed wisdom throughout this process, and to my dissertation committee members Drs. Bill Bowman, Katharine Suding, Timothy Seastedt, and Daniel Doak for all of their input on my thesis along the way. Also, a special thanks to my USGS research advisor Miguel Villarreal for all of his guidance and support. I have been fortunate to work with so many amazing collaborators throughout my dissertation including Anita Antoninka, Jayne Belnap, Matthew Bowker, Bala Chaudhary, David Eldridge, Akasha Faist, Scott Ferrenberg, Elisabeth Huber-Sannwald, Sasha Reed, Emilio Rodriguez-Caballero, Yuanming Zhang, the rest of the USGS John Wesley Powell Center Biocrust Working Group, Mark Miller and others at the National Park Service in Moab, and the EBIO Graduate Writing Cooperative. Thank you to my lab members Taylor Chock and Claire Karban, and members of the Bowman lab group including Amy Churchill, Teal Potter, and Chiara Forrester for providing invaluable feedback on grant proposals, manuscript drafts, and presentations throughout my dissertation. I would also like to thank the long list of undergraduate student researchers who assisted me with data collection and organization in the field and lab without whom this thesis would not have been possible. Also, I would like to thank The Nature Conservancy’s Canyonlands Research Center in southeastern Utah and particularly Kristen Redd and the Redd Family for their support during field seasons throughout my dissertation. Finally, a very special thanks to my fellow graduate students in the CU Boulder Department of Ecology and Evolutionary Biology Alex Alexiev, Amy Churchill, Margaret
Habib, Katherine Hernandez, Hannah Holland-Moritz, Melinda Markin, Margaret McCormick, Lauren Shoemaker, Lara Vimercati and others for all of the pie-offs, haunted corn mazes hikes, runs, laughter, and support along the way. Thank you all so much.
# TABLE OF CONTENTS

## CHAPTER 1

Introduction .................................................................................................................. 1

1.1 Overview of Chapters ......................................................................................... 4

## CHAPTER 2

Biocrusts and their disturbance mediate the recruitment of native and exotic grasses
from a hot desert ecosystem ...................................................................................... 8

2.1. Abstract ............................................................................................................. 8

2.2. Introduction ...................................................................................................... 9

2.3. Materials and Methods .................................................................................... 13

   2.3.1. Study site description .................................................................................. 13

   2.3.2. Biocrust and bare soil sample collection for greenhouse experiments .......... 15

   2.3.3. Vascular plant study species ...................................................................... 15

   2.3.4. Seed bank exhaustion, and soil and watering treatments ............................ 16

   2.3.5. Seedling emergence experiment .................................................................. 17

   2.3.6. Seedling survival, growth, and overall performance .................................. 18

   2.3.7. Data analysis .............................................................................................. 19

2.4. Results ............................................................................................................. 19

   2.4.1. Bunchgrass recruitment responses to intact biocrusts ................................. 19

2.5. Discussion ....................................................................................................... 27

   2.5.1. Biocrust effects on native and exotic bunchgrass species recruitment ........... 27

   2.5.3. Biocrusts and their disturbance mediate hot desert bunchgrass recruitment.... 34

2.6. Acknowledgements .......................................................................................... 35

## CHAPTER 3

Species-specificity in biocrust facilitation of plant growth is not driven by differences
in root-associated fungal colonization among species ............................................... 36

3.1. Abstract ............................................................................................................ 36

3.2. Introduction ..................................................................................................... 37
3.3. Materials and Methods ........................................................................................................................................ 40
  3.3.1. Biocrust and bare soil sample collection ........................................................................................................ 40
  3.3.2. Vascular plant study species .......................................................................................................................... 41
  3.3.3. Seed bank exhaustion, mesocosm establishment, and watering treatments ........................................... 42
  3.3.4 Seedling emergence, growth, and leaf chemistry experiments ........................................................................ 43
  3.3.5. Plant root-associated fungi (RAF) quantification .......................................................................................... 44
  3.3.6. Data analysis ................................................................................................................................................ 45

3.4. Results ................................................................................................................................................................. 46
  3.4.1. Effects of biocrust presence on plant RAF colonization .................................................................................. 46
  3.4.2. Biocrust effects on plant species growth and leaf chemistry ........................................................................ 48
  3.4.3. Relationships between root-associated fungi and plant growth responses to biocrusts .............................................................. 50

3.5. Discussion ............................................................................................................................................................. 50
  3.5.1. Root-associated fungi colonization rates do not predict plant growth responses to biocrusts .................. 51
  3.5.2. Biocrusts have facilitative, but species-specific effects on plant species growth and nutrition .................. 53

3.6. Acknowledgements ............................................................................................................................................. 56

CHAPTER 4 ................................................................................................................................................................. 57
When communities collide: a meta-analysis of context-dependency in vascular plant responses to biocrusts ........................................................................................................................................ 57

  4.1. Abstract ............................................................................................................................................................... 57
  4.2. Introduction ........................................................................................................................................................ 58
  4.3. Materials and Methods .................................................................................................................................... 63
    4.3.1. Literature search and database construction ................................................................................................ 63
    4.3.2. Calculation of meta-analysis metrics ........................................................................................................... 66
    4.3.3. Boosted regression tree data exploration .................................................................................................... 67
    4.3.4. Mixed multi-factor meta-analysis .............................................................................................................. 68
4.3. Results .......................................................................................................................... 69
  4.4.1. Database summary .................................................................................................. 69
  4.4.2 BRT data exploration results ................................................................................. 70
  4.4.3. Mixed multi-factor meta-analysis results ............................................................... 71
    4.4.3.1. Biocrust community composition ................................................................. 72
    4.4.3.2. Plant functional group .................................................................................... 73
    4.4.3.3. Plant nativeness ............................................................................................ 76
    4.4.3.4. Soil reference state and other important moderators ...................................... 77
  4.5. Discussion .................................................................................................................. 79
    4.5.1. Biocrust community composition determines plant responses ....................... 80
    4.5.2. Plant species traits and nativeness mediate plant responses to biocrusts .......... 82
      4.5.2.1. Plant functional group: photosynthetic pathway and symbiotic N-fixation influence plant responses to biocrusts ......................................................... 82
      4.5.2.2. Plant nativeness: Biocrust influences on native versus non-native plants shift across plant ontogeny .......................................................................................... 83
    4.5.3. Soil disturbance mediates biocrust impacts on plant performance ................... 85
    4.5.4. Biocrusts: biotic filters and facilitators for plant community assemblages? ....... 86
  4.6. Acknowledgements .................................................................................................... 89

CHAPTER 5 .......................................................................................................................... 90
Biocrusts are positively associated with dryland herbaceous plant diversity at local scales ......................................................................................................................... 90

  5.1. Abstract ...................................................................................................................... 90
  5.2. Introduction ............................................................................................................... 91
  5.3. Materials and methods ............................................................................................ 95
    5.3.1. Study Site ........................................................................................................... 95
    5.3.2. Soil cover and soil heterogeneity metrics ........................................................... 96
    5.3.3. Vascular plant cover and metrics of plant species diversity ............................... 97
      5.3.4.2. Generation of predictive models for plant species richness and Shannon diversity ......................................................................................................................... 99
5.3.4.3. Possible mechanisms driving plant richness and Shannon diversity responses

5.3.4.4. Plant community composition responses to soil cover and soil cover heterogeneity

5.4.2. Relationships between measures of soil cover and heterogeneity and plant diversity metrics

5.4.3. Boosted regression tree (BRT) data exploration

5.4.4. Predictive models of herbaceous plant species richness and Shannon diversity

5.4.5. Species sorting, spatial turnover, and density-richness relationships

5.4.6. Herbaceous plant community composition

5.5. Discussion

5.6. Acknowledgements

CHAPTER 6

Conclusions

References Cited

Appendix 1:

Table A2.1

Figure A2.1

Figure A2.2

Figure A2.3

Appendix 2:

Supplementary Materials for Chapter 3

Table A3.1

Figure A3.1

Figure A3.2
Appendix 3: ................................................................................................................................. 160
Supplementary Materials for Chapter 4 ....................................................................................... 160
  Table A4.1.................................................................................................................................... 160
  Table A4.2.................................................................................................................................... 161
  Figure A4.1................................................................................................................................. 162
Appendix 3.1. ................................................................................................................................. 163
Appendix 3.2. ................................................................................................................................. 168
Appendix 3.3. ................................................................................................................................. 180
Appendix 4: ......................................................................................................................................... 183
Supplementary Materials for Chapter 5 ....................................................................................... 183
  Table A5.1.................................................................................................................................... 183
  Table A5.2.................................................................................................................................... 185
  Table A5.3.................................................................................................................................... 186
  Table A5.4.................................................................................................................................... 189
  Table A5.5.................................................................................................................................... 190
  Table A5.6.................................................................................................................................... 191
  Table 5.7...................................................................................................................................... 192
  Table A5.7.................................................................................................................................... 193
  Figure A5.1................................................................................................................................. 194
  Figure A5.2................................................................................................................................. 195
  Figure A5.3................................................................................................................................. 196
  Figure A5.4................................................................................................................................. 197
  Figure A5.5................................................................................................................................. 198
  Figure A5.6................................................................................................................................. 199
TABLES

Table 2.1. Seedling emergence in biocrust surface and crack microsites........................................23
Table 4.1. Descriptions of the candidate categorical fixed-effect explanatory variables
explored in mixed-effects meta-analyses..............................................................................................65
Table 4.2. Test statistics for categorical fixed effects in meta-regression models for each
plant response analysis..........................................................................................................................74
Table 5.1. Description of environmental predictor variables including soil cover classes
(SCCs), metrics of soil cover heterogeneity, and other plot characteristics.........................98
Table 5.2. Predictive models (GLMMs) for plant richness and Shannon diversity index.......105
Table 5.3. Results for PERMANOVA analysis of Bray-Curtis dissimilarities for
herbaceous plant community structure...............................................................................................111
FIGURES

Figure 2.1. Pictures of biocrust and bare soil surface types .................................................................14
Figure 2.2. Plant overall performance responses to intact biocrusts.....................................................21
Figure 2.3. Plant emergence, survival, and growth responses to intact biocrusts.................................22
Figure 2.4. Plant emergence, survival, and growth responses to biocrust removal .........................26
Figure 3.1. Pictures of greenhouse mesocosms and experimental setup ........................................42
Figure 3.2. Biocrust effects on plant root-associated fungal colonization ........................................46
Figure 3.3. Pictures of root-associated fungi (AMF, DSE) colonizing plant roots .............................47
Figure 3.4. Plant biomass and height responses to biocrust .................................................................48
Figure 3.5. Biocrust effects on plant leaf nitrogen (% N) content .....................................................49
Figure 4.1. Map of locations of study locations incorporated into meta-analyses ..............................70
Figure 4.2. Simplified boosted regression tree (BRT) model results ................................................71
Figure 4.3. Forest plots showing meta-analysis results for plant performance responses
(weighted means ± SE) to biocrusts .....................................................................................................75
Figure 4.4. Forest plots showing meta-analysis results for plant responses (weighted means ± SE) to biocrust presence depending on study control type (SOIL_REFERENCE_STATE) .................................................................78
Figure 4.5. Summary diagram showing significant drivers in plant responses to biocrusts
identified by meta-analyses .................................................................................................................80
Figure 4.6. Conceptual diagram showing how biocrust biotic filtering and facilitation of
plant species could hypothetically constrain a regional plant species pool to modify local plant community composition .................................................................87
Figure 5.1. Conceptual diagram showing hypothesized increase in local plant diversity
with increasing biocrust-mediated soil cover heterogeneity .........................................................94
Figure 5.2. Cross-correlations (Pearson correlation coefficients, r) among plant response
and soil predictor variables in sagebrush and pinyon-juniper plots .................................103
Figure 5.3. Relationships between herbaceous plant species richness and plant Shannon
diversity and soil predictor variables in in best GLMM models of plant
richness and Shannon diversity in sagebrush and pinyon-juniper plots .................................106
Figure 5.4. Indicator species analysis (ISA) results by level of soil cover heterogeneity
(SCD) and biocrust cover in sagebrush and pinyon-juniper plots.........................108
Figure 5.5. Relationships between plant functional group cover and biocrust cover.........109
Figure 5.6. Herbaceous plant species accumulation curves and rarefaction by soil
heterogeneity.................................................................110
CHAPTER 1

Introduction

Understanding the drivers of the distribution, performance, and abundance of species has long been a central goal of ecology (e.g., Callaway, 2007; Oosting, 1948). While there is wide consensus of the primary importance of dispersal limitations and barriers posed by the abiotic environment in predicting species distribution and abundance patterns (e.g., (Cornwell & Ackerly, 2009; Keddy, 1992; Kraft, Adler, et al., 2015), ecologists continue work to understand how local, biotic interactions act to restrict or enhance species performance and generate broader community patterns. Positive (facilitative) and negative (competitive) species interactions can determine key attributes of ecosystems such as the number of species, their distribution, and the range of species traits present within communities (Boulangeat, Gravel, & Thuiller, 2012; Michalet et al., 2006; Wisz et al., 2013). In plant community ecology, the role of plant-plant interactions in determining plant species performance and community composition have been frequently tested (Levine, Adler, & Yelenik, 2004; Noble and Slatyer 1977; Tilman, 2004). In contrast, the importance of soil biotic communities in determining the ecology of plants has been historically less studied, but evidence indicates a strong influence on plant productivity and community structure (Bever et al., 2010; Hortal et al., 2017; Van Der Heijden, Bardgett, & Van Straalen, 2008).

In dryland ecosystems, biological soil crusts (‘biocrusts’) – surface-dwelling soil biotic communities comprised of cyanobacteria, algae, fungi, lichens, and/or bryophytes – are spatially widespread but heterogeneously distributed, occupying ~12% of Earth’s terrestrial
surface (Rodriguez-Caballero et al., 2018). Where they occur, biocrusts provide critical contributions to local soil functioning. For example, relative to soils lacking biocrusts (bare soil), biocrusts increase soil stability (Belnap & Büdel, 2016; Bowker, Belnap, Bala Chaudhary, & Johnson, 2008), modify soil moisture availability (Belnap, 2006; Chamizo et al., 2016; Concostrina-Zubiri, Molla, Velizarova, & Branquinho, 2017; Faist, Herrick, Belnap, Zee, & Barger, 2017), and may increase surface temperature by decreasing soil surface albedo (Couradeau et al., 2016). Further, biocrusts can increase soil nutrient availability directly by fixing atmospheric nitrogen (N; reviewed in Barger, Weber, Garcia-Pichel, Zaady, & Belnap, 2016) and carbon (C; Li, Zhang, Su, & Jia, 2012; Tucker et al., 2017), excreting organic compounds and chelate elements into the soil surface (Harper & Pendleton, 1993), and indirectly by trapping fine, non-local aeolian dust particles that contain bioessential nutrients (e.g., N, P, K, Mg, Cu, Fe, Mn; Delgado-Baquerizo, Castillo-Monroy, Maestre, & Gallardo, 2010; Reynolds, Belnap, Reheis, Lamothe, & Luiszer, 2001).

Given these biologically important soil modifications, biocrusts can have strong positive or negative effects on the performance of vascular plant species with which they coexist (reviewed in Zhang et al., 2016). Plant species often differ in how they interact with soil microbes and how they respond to changes in soil conditions, such as increases in soil moisture or N availability (Bardgett et al., 1999; Veresoglou & Rillig, 2014). Similarly, past work investigating outcomes of biocrust-plant interactions has shown plant responses to biocrusts to be extremely variable depending on the plant species and life stage studied (reviewed in Zhang et al., 2016). Early in the plant life cycle, biocrusts have been shown to have positive (Elbaz 2012; Godínez-Alvarez, Morín, & Rivera-Aguilar, 2012; Hawkes, 2004; Müller, Cooper, & Alsos, 2011), neutral (Godínez-Alvarez et al., 2012) or negative (Morgan,
effects on plant emergence. Similarly, later in the plant life cycle, plant growth can respond positively (Defalco, Detling, Tracy, & Warren, 2001b; Godínez-Alvarez et al., 2012; Harper & Belnap, 2001; Lesica & Shelly, 1992; Zhang & Nie, 2011) or negatively (Boeken & Shachak, 1994; Kidron, 2014; Thiet, Doshas, & Smith, 2014) to biocrusts.

Despite our growing understanding of the importance of biocrusts for plant species, variability in plant responses to biocrusts has generated considerable uncertainty about overall nature of biocrust-plant interactions. To date, ecologists have been unable to generalize the ecological contexts in which biocrusts inhibit or facilitate plant species and the mechanisms underlying these patterns, making it difficult to incorporate biocrusts into ecosystem management frameworks and broader plant community theory. Particularly, although past observations that biocrusts can increase or have neutral effects on the performance of native plant species while inhibiting that of non-native invasive plant species (e.g., Hernandez & Sandquist, 2011; Morgan, 2006), it remains uncertain whether biocrusts generally promote biotic resistance against exotic plant invasion. In addition, while we might predict that through positive and negative effects on plant species performance and biocrust contributions to spatial heterogeneity in soil resource availability that biocrusts might modify niche availability for dryland plant species and thereby influence plant community dynamics, we have much yet to learn about how biocrusts may influence plant community structure.
1.1 Overview of Chapters

My dissertation investigates the role of biocrusts in mediating vascular plant species performance and community structure in dryland ecosystems and seeks to generate a predictive understanding of outcomes of these specialized plant-soil interactions. My research combines experimental mesocosm studies, meta-analytical techniques, and observational field studies to explore the patterns and processes underlying the outcomes of biocrust-plant interactions for plant species and communities. Specifically, I seek to explore how biocrusts, through inhibitive and facilitative effects on plant species, may influence patterns in plant species recruitment, performance, and community diversity and structure in dryland ecosystems.

Specifically, in chapter 2 of this thesis (published as Havrilla & Barger, 2018 in *Ecosphere*), I investigate the potential contributions of biocrusts to biotic resistance against exotic plant invasion. In plant invasion ecology, there has been much focus on quantifying the role of native plant communities in mediating exotic plant invasion through biotic resistance (e.g., Byun, de Blois, & Brisson, 2013; Mitchell et al., 2006). In contrast, there have been far fewer investigations of how resident soil surface biotic communities contribute to biotic resistance which may be similarly important to determining invasibility (Reinhart & Callaway, 2006; Wolfe & Klironomos, 2006). In my second chapter, using a full factorial manipulative greenhouse experiment, I first test whether intact biocrusts from the hot, Chihuahuan Desert offer favorable microhabitats for increased recruitment performance (i.e., emergence, survival, and growth) of native perennial grass species (i.e., *Aristida purpurea* (Nutt.), *Bouteloua eriopoda* (Torr.)) but decrease performance and recruitment of exotic species *Eragrostis lehmanniana* (Nees.) (Lehman lovegrass). Then, I test whether
biocrust removal increases the recruitment success of the exotic species. I demonstrate important effects of intact biocrusts on native and exotic grass species recruitment, and the potential of biocrust disturbance to promote exotic plant performance.

In chapter 3, I explore a potential mechanism underlying species-specificity in plant responses to biocrusts by comparing differences in root-associated fungal (RAF; i.e., arbuscular mycorrhizal fungi (AMF), and dark septate endophytes (DSE)) colonization rates in plants grown in biocrust versus bare soil to differences in plant growth and nutrition responses to biocrusts. Past work suggests biocrusts are niches for specialized free-living fungi (Maier et al., 2016) and labelled isotope studies have demonstrated resource exchange (e.g., $^{15}$N) between biocrusts and plants in communities can likely be attributed to fungal networks (Green, Porras-Alfaro, Sinsabaugh, & L., 2008; Hawkes, 2003; Zhuang, Downing, & Zhang, 2013). Yet, we currently lack a general understanding of whether RAF-mediated resource exchange between biocrusts and plants drives interspecific variation in biocrust facilitation of plant species growth. In my third chapter, I investigate potential linkages between biocrust, RAF, and plant growth responses. Using a full factorial greenhouse mesocosm experiment, I compare growth and elemental uptake responses of five native perennial grass species from a cool desert ecosystem and Zea mays var. indurata (L.) (Hopi blue corn) grown in soil with and without biocrust. Then, I quantify corresponding RAF colonization rates and evaluate whether plant growth responses to biocrusts align with differences in RAF colonization rates between soils with and without biocrust and among plant species.

Chapter 4 was developed to identify overarching trends in existing literature addressing plant responses to biocrusts using ecological synthesis. The high degree of plant
species-specificity in plant responses to biocrusts depending on ecological context has historically made it difficult to predict the outcomes of biocrust-plant interactions, and of yet, what factors determine the direction and magnitude of these effects remain largely unknown. As such, to explore what plant, biocrust, and environmental characteristics mediate the outcomes of biocrust-plant interactions, in chapter 4, I compiled a global dataset encompassing results from 1,004 studies of plant responses to biocrusts from six continents and then conduct multi-factor meta-analysis of plant emergence, survival, growth, cover, and overall performance responses to biocrusts. Specifically, I employ mixed-effects meta-regression to determine the net effects of biocrusts on plant responses, and to determine the relative importance of plant characteristics (e.g., plant functional type, duration, nativeness, root morphology) biocrust community composition, and environmental factors (e.g., regional climate, local disturbance) in mediating these effects.

In chapter 5, to test the hypothesis that variation in plant responses to biocrusts produces community-scale patterns in plant community diversity and structure in situ, I conduct a large-scale observational field study to investigate whether biocrusts increase local plant diversity and community composition by contributing to fine-scale soil cover heterogeneity, often corresponding to spatial soil resource heterogeneity, and thereby niche space for plant taxa with diverse resource requirements as predicted by coexistence theory (Chesson, 2000). Past work has shown positive (Ghiloufi & Chaieb, 2017; Jeffries, Douglas L., Klopatek, 1987; Kleiner & Harper, 1977; Luzuriaga, Sánchez, Maestre, & Escudero, 2012; Scott & Morgan, 2012) or negative (Miller & Damschen, 2017a; Peralta, Sánchez, Luzuriaga, & Escudero, 2016) correlations between biocrusts and local plant diversity, generating uncertainty about the nature of this relationship. Combining results from chapter 4 indicate
biocrust effects on plants differ depending on biocrust community composition and predictions that increased environmental heterogeneity decreases niche overlap among species, I correlative evaluate the effects of biocrust spatial heterogeneity on plant species richness, Shannon diversity index, and community composition. In addition, I quantify the relative importance of niche-type (environmental species sorting; Hutchinson, 1957, 1959) and neutral-type (density-dependence; Hubbell, 2005) processes in generating observed increases in local plant diversity with increasing soil cover diversity mediated by biocrusts.

Finally, in chapter 6, I summarize my key results examining the patterns and processes underlying plant responses to biocrusts. I highlight how biocrust community composition and plant characteristics mediate outcomes of biocrust-plant species interactions and how such interactions may couple with heterogeneity in biocrust spatial structure to contribute to plant community structure at community and ecosystem levels. Finally, I briefly discuss future directions for examining biocrust effects on plant community assembly processes and the implications for understanding these patterns and processes in the context of global change.
CHAPTER 2

Biocrusts and their disturbance mediate the recruitment of native and exotic grasses from a hot desert ecosystem

Caroline A. Havrilla & Nichole N. Barger


2.1. Abstract

In dryland ecosystems, biological soil crusts (‘biocrusts’) coexist in patchy mosaics with vascular plants and can influence plant performance through modifications of soil stability, hydrology, microclimate, and fertility. Biocrusts often have species-specific effects on vascular plant recruitment and hypothesized to promote native over exotic plant establishment. While there is considerable interest in potential contributions of biocrusts to the biotic resistance of plant communities, relatively few studies have investigated this relationship. Particularly, we have a limited understanding of how biocrusts may impact exotic plant recruitment in hot desert ecosystems, and how these relationships may be affected by biocrust disturbance. In a greenhouse setting, we investigated the effects of two biocrust types (cyanobacterial- and lichen-dominated) from the hot, Chihuahuan Desert and their removal on the emergence, survival, growth, and overall recruitment performance of three perennial bunchgrasses: native species Aristida purpurea (Nutt.) and Bouteloua
eriopoda (Torr.), and exotic *Eragrostis lehmanniana* (Nees.). Specifically, we tested two hypotheses: (1) **Intact biocrusts** offer favorable microhabitats for increased performance of native vascular grass species but decrease performance and recruitment of exotic species *Eragrostis lehmanniana*; and (2) **Biocrust removal** increases the recruitment of *E. lehmanniana*. Overall, we found cyanobacterial biocrusts decreased seedling performance, while lichen-dominated biocrusts increased performance. While biocrusts promoted *E. lehmanniana* emergence over that of the two natives, conversely, native species survival and growth responded more positively to biocrusts than the exotic. Biocrust removal increased *E. lehmanniana* recruitment but had mixed effects on the two natives. These results indicate the importance of biocrusts and biocrust disturbance in shaping dryland plant community structure and generate interesting questions about possible contributions of biocrusts to the biotic resistance of plant communities.

### 2.2. Introduction

Understanding the factors that control invasion success a central goal of plant community ecology (Elton 1958; Crawley, 1986; Keane, Crawley, Keane, & Crawley, 2002; Levine et al., 2004; Lowry et al., 2012; Mack et al., 2000). Numerous studies have investigated contributions of biotic resistance, the reduction of plant species invasion success caused by the resident community, in mediating the invasion success of exotic species (Byun et al., 2013; Elton 1958; Levine et al., 2004; Lowry et al., 2012; Mitchell et al., 2006). Much attention has been paid to resident plant communities to biotic resistance to invasion (e.g., Byun et al., 2013; Mitchell et al., 2006). Yet, there have been far fewer investigations of contributions of
resident soil surface communities to biotic resistance which may be similarly important to determining invasibility (Reinhart & Callaway, 2006; Wolfe & Klironomos, 2006).

In dryland ecosystems, biological soil crusts (biocrusts), soil biotic communities comprised of cyanobacteria, lichens, bryophytes, and fungi, coexist with vascular plant species and mediate a suite of critical soil processes. Biocrusts, for example, increase soil structure and stability (Bowker et al., 2008; Zhang et al., 2006) thereby increasing soil resistance to wind and water erosion (Jayne Belnap & Gardner, 1993; Bowker et al., 2008; Eldridge & Leys, 2003). Moreover, biocrusts alter soil surface hydrology (Belnap, 2006), and can increase soil fertility by increasing availability of soil carbon (C; Li et al., 2012), nitrogen (N; reviewed in Barger et al., 2016), phosphorus (P; Zhang et al. 2012), and other mineral nutrients (Harper & Belnap, 2001; Jafari et al., 2004), as well as the abundance and diversity of soil microfauna (Housman et al., 2007; Darby and Neher 2016). As a result of these biologically important soil modifications, biocrusts may impact the performance of the plant species with which they coexist (Zhang et al. 2016; Havrilla et al. Under Review).

Biocrusts may be particularly influential during the recruitment stages of the plant life cycle (i.e., emergence, survival, and growth; reviewed in Zhang et al. 2016; Havrilla et al. Under Review), and therefore may contribute to determining the niche of dryland plant species (Grubb 1977). Past studies have reported biocrusts may have positive (Beyschlag, Wittland, Jentsch, & Steinlein, 2008; Godínez-Alvarez et al., 2012; Rivera-Aguilar, Godínez-Alvarez, Manuell-Cacheux, & Rodríguez-Zaragoza, 2005) neutral (Godínez-Alvarez et al., 2012; Li et al., 2005), or negative (Kidron, 2014; Langhans, Storm, & Schwabe, 2009; Prasse & Bornkamm, 2000) effects on plant species depending on the plant species and life stage studied (Zhang et al. 2016). A recent global meta-analysis of plant responses to biocrusts by
Havrilla et al. (Under Review) suggests plant functional traits and nativeness predict plant species responses to biocrusts. As such, recently there has been considerable interest in the potential of biocrusts to mediate biotic resistance to exotic plant invasion and the consequences of biocrust disturbance to this relationship (Warren and Eldridge 2001; Gelbard & Belnap, 2003; Stohlgren, Otsuki, Villa, Lee, & Belnap, 2001; Zhang et al., 2016). Though, to date there have been relatively few empirical investigations of biocrust mediation of invasibility, and most studies have been limited to assessing the responses of the Mediterranean annual grass Bromus tectorum L. (cheatgrass) to biocrust communities in cool deserts of US with few exceptions (Table A2.1). Thus, we currently have a limited understanding of biocrust contributions to biotic resistance in other systems, particularly in hot desert ecosystems which remain largely unstudied in this context.

Biocrusts influence seedling emergence through a variety of mechanisms that may differ considerably depending on the biome studied. Biocrust community composition and microtopography, which vary largely as a function of regional climate (Belnap, 2003; Bowker et al., 2016), may be particularly important in determining biocrust impacts on seedling emergence. Smooth or rugose biocrusts common in hot deserts may inhibit seed retention or penetration of the soil surface (Clements, Krannitz, & Gillespie, 2009; Li et al., 2005), which may decrease emergence because of seed desiccation or predation by granivores (Morgan, 2006; Stohlgren et al., 2001). Conversely, in cool deserts, biocrusts with rolling or pinnacled microtopography may increase seed capture and retention (Boudell, Link, & Johansen, 2002). Subsequently, these biocrust communities may offer a favorable microhabitat for seed emergence by increasing soil moisture (Kleiner & Harper, 1977) and temperature (Couradeau et al., 2016). Differences in seed traits among native and exotic
plant taxa such as size (Briggs & Morgan, 2010) and external morphology (Zhang & Belnap, 2015) are additionally thought to be important drivers of species-specific effects of biocrusts on seedling emergence (Zhang et al., 2016).

Following emergence, biocrusts may offer favorable soil conditions for seedling establishment and growth (Zhang et al., 2016) by increasing the availability of soil water and nutrients including greater soil organic matter and inorganic N (DeFalco et al., 2001; Pendleton, Pendleton, Howard, & Warren, 2003). Benefits of biocrusts to native plant growth have been shown in a variety of ecosystems including cold (Bliss & Gold, 1999; Breen & Lévesque, 2006; Elmarsdottir, Aradottir, & Trlica, 2003), cool (Harper & Belnap, 2001; Lesica & Shelly, 1992; Zhang & Nie, 2011), and hot desert ecosystems (Defalco et al., 2001; Godínez-Alvarez et al., 2012; Scott & Morgan, 2012). In contrast, past studies have also demonstrated the capacity of exotic plant species growth to benefit from soil resource availability provided by biocrusts. For instance, while numerous studies conducted in the Southwestern US have demonstrated emergence of the problematic, invasive annual grass *B. tectorum* is often hindered by biocrust presence, others have shown that once established, its growth is often increased in the presence of biocrusts (literature reviewed in Table A2.1).

While intact biocrusts play important roles in influencing plant recruitment, biocrust communities are also highly susceptible to physical disturbance (reviewed in Zaady et al., 2016) which may impact the ecological functioning of biocrusts and may thus disrupt relationships between biocrusts and plants. Biocrust disturbance or removal has been shown to increase seedling emergence, survival, and growth of certain plant species (Beyschlag et al., 2008; Hernandez & Sandquist, 2011) perhaps by releasing nutrients contained in biocrusts (Belnap, 2003) or by reducing resource competition between
biocrusts and seedlings (Stohlgren et al., 2001). Exotic plant species in particular may be more capable of benefitting from disturbance than natives (Larsen, 1995), especially in low-resource environments (D’Antonio and Vitousek 1992; Davis, Grime, & Thompson, 2000). For example, in a semiarid California sage scrub community biocrust disturbance resulted in increases in the emergence of exotic over native plant species (Hernandez & Sandquist, 2011). Given such evidence, additional work is needed to investigate biocrust impacts on native and exotic plant recruitment in hot desert ecosystems, and how disturbance may impact invasibility in these low-resource systems.

To address these knowledge gaps, in this greenhouse study we examined the effects of biocrusts and biocrust disturbance on the seedling performance of two native perennial bunchgrass species common in the hot Chihuahuan Desert ecoregion (*Aristida purpurea* (Nutt.) and *Bouteloua eriopoda* (Torr.)), and exotic bunchgrass *Eragrostis lehmanniana* (Nees.). Specifically, we tested two hypotheses: (1) **Intact biocrusts** offer favorable microhabitats for increased performance of native vascular grass species but decrease performance and recruitment of exotic species *E. lehmanniana*; and (2) **Biocrust removal** increases the recruitment of *E. lehmanniana*.

### 2.3. Materials and Methods

#### 2.3.1. Study site description
We collected biocrust samples for this study near the Jornada Experimental Range (JER) of the United States Department of Agriculture and Agricultural Resource Services near Las Cruces, New Mexico, within the hot, Chihuahuan Desert ecoregion. Mean annual precipitation for this area is approximately 253 mm (80-year average; Western Regional Climate Center, 2017), falling mainly during the summer (July-September) and a lesser component in the winter (December-February). Mean annual temperature is 14.6°C (80-year average; Western Regional Climate Center, 2017; https://wrcc.dri.edu/), and droughts are a recurrent climatic phenomenon in this region. Natural vegetation is dominated by perennial grasses and shrubs, with the effective growing season occurring between July and September. Cyanobacteria- and lichen-dominated biocrusts are widespread in this area, occupying a majority of vascular plant interspaces. Biocrust physical microtopography of is characterized as smooth (cyanobacteria-dominated; Fig. 2.1) or rugose (lichen-dominated; Fig. 2.1) as defined in Belnap (2003).

**Figure 2.1.** Photographs of biocrust and bare soil surface types. Pictures of the three intact surface types: (a) bare soil; (b) smooth, cyanobacteria-dominated biocrust; and (c) rugose, lichen-dominated biocrust all collected from the silty site at the Jornada Experimental Range near Las Cruces, New Mexico, USA.
2.3.2. Biocrust and bare soil sample collection for greenhouse experiments

In February 2015, we selected two soil sample collection sites near the JER with contrasting soil textures: one with sandy (sandy site) and one with silty clay loam soils (silty site; Fig. A2.1). The sandy site (32.298309°N, -106.697478°W) is located near the Tortugas Mountain in Las Cruces, NM at an elevation of approximately 1302 m, and is characterized as a Deep Sand ecological site (SoilWeb, 2017). The silty site (32.545232°N, -106.723644°W) is located within JER at an elevation of approximately 1316 m and is characterized as a Clayey ecological site (SoilWeb, 2017). Natural vegetation at both sites is dominated by perennial grasses *Bouteloua eriopoda*, *Aristida purpurea*, *Sporobolus* spp., and shrubs (*Artemisia filifolia* at the sandy site, and *Atriplex canescens* at the silty site). Biocrust communities at both sites are smooth, dominated by light cyanobacteria, or rugose, dominated by lichens including the N-fixing species *Collema tenax*, and other lichen genera including *Psora* (Fig. 2.1). We used cylindrical PVC arenas (12 cm diameter, 5 cm height) to collect biocrust and bare soil samples for the greenhouse experiment from unvegetated interspaces at each site. Bare soils were identified based on a visual absence of cyanobacterial filaments. To prevent biocrust surface breakage during sampling, we wetted soils with deionized water and allowed water to infiltrate for approximately 5 minutes prior to arena placement. At each site, we used this method to collect 24 bare soil samples, 48 lichen-dominated biocrust samples, and 48 cyanobacteria-dominated biocrust samples for a total of 120 soil cores per site (n = 240 total).

2.3.3. Vascular plant study species
Using ecological site descriptions and informal field surveys for the two sites, we selected two common native, C4 perennial bunchgrass species for the study region: *Aristida purpurea* (Nutt.) (purple three awn), and *Bouteloua eriopoda* (Torr.) (black grama). We additionally selected the C4, exotic perennial bunchgrass *Eragrostis lehmanniana* (Nees.) (Lehmann lovegrass) as our third study species. The three species have diverse external seed morphologies: *A. purpurea* has large linear seeds with three awns (~25 mm including awns); *B. eriopoda* has medium linear seeds with short awns (~8 mm including awns); and *E. lehmanniana* has small, round seeds (>2 mm) with no appendages. Seed for all plant study species was purchased from the Native American Seed company (http://www.seedsource.com/) which sources its seed in relatively close geographic proximity to the study location and stored at 4°C until use in the greenhouse experiment. Prior to experimentation, all species were tested for viability on filter paper in petri dishes and showed high (>70%) levels of emergence.

### 2.3.4. Seed bank exhaustion, and soil and watering treatments

Our greenhouse experiments were conducted at the University of Colorado Boulder Ramaley greenhouse. We fixed weed barrier to the bottom of each soil core using waterproof adhesive, and cores were randomly assigned to one of four wet benches in the greenhouse. To exhaust the preexisting seed bank in the soil cores, we watered all soil cores via subirrigation every other day for 20 days. When seedlings emerged, we carefully extracted seedlings from the samples using tweezers and disposed of them. We determined that the seed bank was exhausted after observing 7 consecutive days without seedling emergence.
After exhausting the preexisting seed bank, all soil cores were allowed to dry for 7 days. We then applied one of two disturbance treatments to cyanobacteria- and lichen-dominated biocrust cores to simulate compounded physical biocrust degradation: (1) *Intact* biocrust (control) and (2) *Removed* biocrust (disturbance). Intact cores received no treatment and were left with their cyanobacterial- or lichen-dominated biocrust communities intact. For the removal treatment, we scraped away the top 1 centimeter of the soil surface of each soil sample with a metal spatula. We then compressed the surface of each sample using a ceramic cylinder to mimic compressional disturbance common in disturbed field settings. Following treatment, we added 25 seeds per plant species to each soil treatment for a total of eight replicates per plant species-soil treatment combination. All cores were watered every third day for the duration of the experiment. In drylands, significant plant recruitment generally occurs only during wet periods (Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Muñoz-Rojas, Erickson, Martini, Dixon, & Merritt, 2016; Schwinning, Sala, Loik, & Ehleringer, 2004). As such, watering was an essential part of our experimental design needed to address questions about plant recruitment interactions with biocrusts.

2.3.5. Seedling emergence experiment

We first evaluated the effects of intact biocrusts on seed emergence by measuring seedling emergence on: (i) smooth, cyanobacteria-dominated biocrust; (ii) rugose, lichen-dominated biocrust; and (iii) bare soil using a full factorial greenhouse experiment. Then, we evaluated the effects of biocrust removal on seed emergence. Due to the high number of seeds in the experimental design (~3,600 seeds), monitoring of daily radical emergence was
infeasible. So, we instead took daily, high-resolution photographs of each soil core from a set height using a Canon SX710 HS camera. Images were uploaded daily to a computer yielding one high-resolution image/sample/day for 26 days. Images were then input to Adobe Photoshop CC (Adobe, 2015) for photo-processing and manual scoring and characterization of radical emergence events using a virtual 10 x 10 cm grid overlay coordinate system. We tracked individual seedling emergence over time using this coordinate system at 6 (Day 1 of radical emergence for all species), 16, and 26 days following seeding. In addition to tracking radical emergence, we used this grid method to analyze how biocrust microtopography affected seed fate by recording the microsite (i.e. biocrust surface or crack) of each emerged seedling.

2.3.6. Seedling survival, growth, and overall performance

Biocrust effects on seedling survival and growth were analyzed using the same experimental design as for emergence. Following the emergence experiment (Day 0-26), we selected five seedlings per species per soil core. To control for age differences in seedlings, we randomly selected only seedlings that emerged between Days 6-16. We then thinned out the remaining seedlings in each core by clipping seedlings at their bases and discarding. All soil cores were then watered every three days for an additional month (Day 27-57). To calculate seedling survival, we tracked individual seedling fate for all grass species and recorded the proportion of seedlings that survived during this period. At the end of the growth period, we measured the ending biomass (mg) of each seedling for each species. We
harvested leaves, shoots, and roots from all seedlings at the end of the experiment. Plant materials were then oven dried at 70°C and weighed.

In addition to calculating the effects of biocrust on plant emergence, survival, and growth, net performance for each plant study species was calculated for each surface type as the product of the mean proportion of emerged seeds, proportion of surviving seedlings, and the dry biomass (mg) per seedling (as in Godínez-Alvarez et al., 2012).

2.3.7. Data analysis

To address our first hypothesis, we used two-way ANOVAs to test the effects of intact surface type (i.e. bare soil, cyanobacteria-dominated biocrust, lichen-dominated biocrust), and soil texture (i.e. sandy and silty) on plant response variables (i.e. percent seedling emergence, survival, and growth) of the three species. Pairwise differences in seedling response variables among soil surface types and textures were detected with Tukey’s HSD test with \( \alpha = 0.05 \). To address our second hypothesis, we analyzed the effects of soil surface type, texture, and soil treatment (i.e., intact and removed) on plant response variables. Shapiro-Wilk tests were used to test all plant response variables for normality. When appropriate, plant response variables were square root transformed to meet assumptions of normality. All statistical analyses were performed in R version 3.3.3 (R Core Team, 2017).

2.4. Results

2.4.1. Bunchgrass recruitment responses to intact biocrusts
Seedling overall performance responses to biocrusts – Biocrust effects on overall seedling performance were species-specific and varied by biocrust community type (Fig. 2.2; Fig. A2.2). Native seedling responses to biocrust presence differed between species. Relative to bare soil, *A. purpurea* performance was higher on lichen-dominated biocrust, and unaffected by the presence of cyanobacteria-dominated biocrust (Fig. 2.2). In contrast, *B. eriopoda’s* overall performance was lower on both biocrust community types relative to bare soil (Fig. 2.2). *E. lehmanniana* performance was decreased on cyanobacteria-dominated biocrusts but increased on lichen-dominated biocrusts (Fig. 2.2; Fig. A2.2). Species overall performance, however, was driven by differing responses during plant life stages (Fig. 2.3).

Effects of biocrust type and microtopography on seedling emergence – Biocrust effects on emergence relative to bare soil controls were species-specific (Figure 2.3a), and were affected by biocrust community type, but not soil texture. In contrast with our predictions, *E. lehmanniana* emergences benefitted most consistently from biocrust presence among bunchgrass species with emergence 38% higher (*P* = 0.05; Fig. 2.3a) on cyanobacteria-dominated biocrust and 29% higher (*P* = 0.10; Fig. 2.3a) on lichen-dominated biocrust relative to bare soil, suggesting biocrusts offered favorable microhabitats for emergence in this species. Native grasses, however, had mixed emergence responses to biocrust presence. *A. purpurea* emergence was slightly higher (+ 18%) on lichen biocrust relative to both bare soil and cyanobacteria-dominated biocrust (both *P* = 0.05; Fig. 2.3a) suggesting lichen-dominated biocrusts offered favorable microenvironment for the emergence of this species. However, *B. eriopoda* emergence decreased on both biocrust types with emergence 28% lower (*P* = 0.04; Fig. 2.3a) on cyanobacteria-dominated biocrust, and 21% lower (*P* = 0.04; Fig. 2.3a) on lichen-dominated biocrust compared to bare soil respectively.
Relative germinant occupancy of soil crack and surface microsites also varied by species. On cyanobacteria-dominated biocrust, 44% of *A. purpurea* seedlings occurred in cracks versus 56% on top of the biocrust surface (Table 2.1). This was unexpected given both the large size of *A. purpurea* seeds and the low occurrence of crack area on the soil surface (>5% of surface). On lichen-dominated biocrust, *A. purpurea* germinants occurred in cracks less frequently, but still a surprising 28% of the time (Table 2.1). For the medium, awned species *B. eriopoda*, however, germinants were found less frequently (25% of the time)
within cracks, both cyanobacterial and lichen-dominated biocrusts relative to 75% occurring on the surface. The proportion of germinants found in cracks for small, smooth-seeded *E. lehmanniana* was lower yet with only 21% and 22% of germinants occurring in cracks on cyanobacterial and lichen-dominated biocrusts compared to 79% and 78% occupancy of surface microsites respectively (Table 2.1).
Plant survival and growth responses to biocrusts – Survival of native species responded positively to biocrust whereas *E. lehmanniана* survival decreased on biocrust relative to bare soil (Fig. 3b). *A. purpurea* seedling survival benefitted from the presence of both cyanobacterial- and lichen-dominated biocrust relative to bare soil (+ 25%; *P* = 0.01; Fig. 2.3b). *B. eriopoda* seedling survival was higher with 19% and 38% greater survival on cyanobacterial and lichen biocrust respectively relative to bare soil (*P* = 0.09 and *P* = 0.02; Fig. 2.3b). In contrast to the positive effects of biocrusts on native seedling survival, *E. lehmanniана* seedling survival was 22% lower (*P* = 0.03; Fig. 2.3b) on cyanobacteria-dominated biocrust relative to bare soil, while survival was similar on bare soil and lichen biocrust (Fig. 2.3b).

Native species also experienced greater positive growth responses to biocrusts relative to *E. lehmanniана* (Fig. 2.3c). Plant growth across species, did however, vary by soil texture and surface type. Overall, seedling growth trended higher on sandy versus silty soil (Fig. 2.3c). Native grass seedling biomass was 38% and 48% higher on sandy versus silty soil in *A. purpurea* and *B. eriopoda* respectively, and surface type was only a significant determiner of biomass accumulation on sandy soil (*P* = 0.03; Fig. 2.3c). *E. lehmanniана’s*

**Table 2.1.** Percent of emerged seedlings (± 1 standard error) found in one of two microsite types (biocrust surface, crack) for *A. purpurea*, *B. eriopoda*, and *E. lehmanniана* on intact cyanobacterial and lichen-dominated biocrusts.

<table>
<thead>
<tr>
<th></th>
<th>Cyanobacterial biocrust</th>
<th>Lichen biocrust</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biocrust surface</td>
<td>Crack</td>
<td>Biocrust surface</td>
</tr>
<tr>
<td><em>A. purpurea</em></td>
<td>56.1 ± 4.7</td>
<td>43.9 ± 4.7</td>
</tr>
<tr>
<td><em>B. eriopoda</em></td>
<td>74.8 ± 11.7</td>
<td>25.2 ± 11.7</td>
</tr>
<tr>
<td><em>E. lehmanniана</em></td>
<td>78.6 ± 10.6</td>
<td>21.4 ± 10.6</td>
</tr>
</tbody>
</table>
growth, however, was not influenced by soil texture \((P = 0.44; \text{Fig. 2.3c})\) and was more consistently impacted by surface type between soil textures.

Biocrust surface type had a strong effect on growth in the three species on sandy soil \((P = 0.04; \text{Fig. 2.3c})\). Seedling biomass was lower on cyanobacterial crusts across all species (Fig. 2.3c). Interestingly though, the magnitude of this negative response was greatest in the exotic grass species. In the native species, \textit{A. purpurea}'s mean biomass decreased by a third on cyanobacteria-dominated biocrust relative to bare soil \((P = 0.02; \text{Fig. 2.3c})\), and \textit{B. eriopoda}'s biomass was decreased by half on this surface type \((P = 0.05; \text{Fig. 2.3c})\). \textit{E. lehmanniana} experienced the greatest reduction in biomass on biocrust surfaces with a 69% reduction on cyanobacteria-dominated biocrust on sandy soil \((P = 0.01; \text{Fig. 2.3c})\) and a 54% reduction on silty soil \((P = 0.04; \text{Fig. 2.3c})\) relative to bare soil controls. While plant growth was lower on cyanobacteria-dominated biocrust across all species, lichen biocrust had species-specific effects on growth. While lichen-dominated biocrusts had positive or neutral effects on the growth of the two native grass species (+ 27% in \textit{A. purpurea}; no change in \textit{B. eriopoda}), biocrusts \textit{E. lehmanniana} growth was 33% lower on biocrusts relative to bare soil \((P = 0.06; \text{Fig. 2.3c})\).

2.4.2. Effects of biocrust removal on bunchgrass seedling recruitment

\textit{Overall seedling performance responses to biocrust removal} – Biocrust removal effects on overall seedling performance varied depending on plant species, biocrust type, and soil texture (Fig. 2.2; Fig. A2.3). \textit{E. lehmanniana} performance increased with cyanobacterial biocrust removal relative to intact cyanobacterial biocrust controls on both soil textures, while the two native species had mixed responses to cyanobacterial biocrust removal.
Specifically, *A. purpurea* performance increased with cyanobacterial biocrust removal, whereas *B. eriopoda* performance decreased (Fig. 2.2; Fig. A2.3). Lichen biocrust removal decreased the performance of all bunchgrass species relative to intact lichen biocrust controls, with the magnitude of these decreases differing between silty- and sandy-textured soils (Fig. 2.2; Fig. A2.3). On sandy soils, *E. lehmanniana* performance was least negatively affected among the three species (Fig. 2.2; Fig. A2.3).

**Emergence responses to biocrust removal** – Biocrust removal increased emergence of all grass species, with the magnitude of this increase greatest overall in *E. lehmanniana* (Fig. 2.4a). *E. lehmanniana* emergence increased with both cyanobacteria- (+32%; *P* = 0.05; Fig. 2.4a) and lichen-dominated biocrust removal (69%; *P* = 0.01; Fig. 2.4a) respectively. Cyanobacterial biocrust removal also increased *A. purpurea* emergence by 34% (*P* = 0.02; Fig. 2.4a), whereas lichen biocrust removal only marginally increased emergence in this species (+9%; *P* = 0.09; Fig. 2.4a) compared to intact biocrust controls. *B. eriopoda* emergence also marginally increased with biocrust removal although these results were not statistically significant (*P* = 0.10; Fig. 2.4a). Emergence responses to biocrust removal were not influenced by soil texture (*P* = 0.38).

**Seedling survival and growth responses to biocrust removal** – Biocrust removal effects on seedling survival and growth were also species-specific and differed by biocrust community type, soil texture (Fig. 2.4b-c). Overall, survival of the two native species decreased with biocrust removal treatments, while biocrust removal generally increased *E. lehmanniana* survival (Fig. 2.4b), although the magnitude of species responses to biocrust removal differed depending on soil texture. On sandy soils, *A. purpurea* survival decreased when lichen biocrusts were removed (-13%; *P* = 0.01; Fig. 2.4b) while *B. eriopoda* and *E.
**Figure 2.4.** Plant emergence, survival, and growth responses to biocrust removal. (a) Emergence responses (± 1 SE) of *A. purpurea*, *B. eriopoda*, and *E. lehmanniana* to biocrust removal compared to intact biocrust controls. (b) Survival responses (± 1 SE) of the three species to biocrust removal and community type. (c) Growth (biomass accumulation (mg/seedling)) responses of *A. purpurea*, *B. eriopoda*, and *E. lehmanniana* to biocrust removal on sandy and silty soils compared to intact biocrust controls. Seedling emergence (a) responses to biocrust removal are not split by soil texture class because soil texture did not significantly influence plant emergence responses to biocrust removal. Lowercase letters “a–c” denote statistically significant (α = 0.05) differences between removal treatments and the appropriate intact biocrust control on sandy soil, while lowercase letters “e–g” denote these differences on silty soil.

*lehmanniana* survival was unaffected. On silty soils, however, both native species’ survival decreased 38% with lichen biocrust removal, whereas *E. lehmanniana* survival was slightly increased (+13%; *P* = 0.07; Fig. 2.4b). Removal of cyanobacterial biocrusts had less substantial effects on seedling survival overall. Survival of *A. purpurea* and *B. eriopoda* was unaffected by cyanobacteria-dominated biocrust removal on both soil textures, while *E.
*lehmanniana* survival increased with cyanobacteria-dominated biocrust removal on both sandy and silty soils (+25% each; $P = 0.01$; Fig. 2.4b).

Growth responses of the bunchgrass species to biocrust removal also varied by plant species and biocrust type (Figs 2.2, 2.4c; Fig. A2.3). Cyanobacteria-dominated biocrust removal had variable effects on native species growth depending on soil texture. Cyanobacteria-dominated biocrust removal slightly increased *A. purpurea* growth on sandy soils (+42%; $P = 0.09$; Fig. 2.4c) but was unaffected on silty soils. *B. eriopoda* growth, however, decreased with cyanobacterial biocrust removal both on both sandy (-61%; $P = 0.04$; Fig. 2.4c) and silty soils (-67%; $P = 0.02$; Fig. 2.4c). In contrast, *E. lehmanniana* growth was unaffected by cyanobacterial biocrust removal (Fig. 2.4c). Lichen biocrust removal resulted in greater negative growth responses in the three grasses, which were most negative on silty soils (Fig. 2.4c). Removal of lichen-dominated biocrusts resulted in dramatic growth decreased in the two native grasses. *A. purpurea* growth was decreased 50% on both sandy and silty soils (both $P = 0.01$; Fig. 2.4c), and *B. eriopoda* experienced growth decreases of 58% ($P = 0.01$; Fig. 2.4c) and 84% ($P < 0.001$; Fig. 2.4c) on sandy and silty soils respectively. *E. lehmanniana* growth also decreased 55% ($P = 0.05$; Fig. 2.4c) and 76% ($P < 0.001$; Fig. 2.4c) on sandy and silty soils respectively with lichen biocrust removal.

2.5. Discussion

2.5.1. Biocrust effects on native and exotic bunchgrass species recruitment

Overall, biocrusts had mixed effects on the recruitment of two native vascular plant species but decreased recruitment of *E. lehmanniana*. Overall plant performance was also
dependent on plant species and biocrust type, with overall performance trends by species
driven by both positive and negative responses at different stages of plant recruitment.

*E. lehmanniana* emergence increased on both cyanobacterial and lichen biocrusts
whereas the natives had no response or responded negatively to cyanobacteria biocrusts
(Fig. 2.2; Fig. A2.2). The later result is unexpected given numerous studies have
demonstrated cyanobacterial biocrusts often enhance native seed emergence (St. Clair et al.,
1984; Godínez-Alvarez et al., 2012; Rivera-Aguilar et al., 2005; Su, et al., 2009) by providing
favorable conditions for seedling emergence relative to bare soil (George et al., 2003; Su et
al., 2009). Negative emergence responses to cyanobacterial biocrusts may be partially
explained by water limitations to seeds on cyanobacterial biocrusts relative to bare soil.
Adequate water availability is critical to seed water imbibition during germination, and seed
metabolic activity leading to radical emergence (Fenner and Thompson 2005). Past work
suggests smooth cyanobacterial biocrusts from hot deserts can have higher surface
evaporation and drying compared to bare soil (reviewed in Chamizo et al. 2016). In support
of this assumption, while watering treatments may have decreased water limitations to
seedlings in the greenhouse, we qualitatively observed that cyanobacterial biocrust cores
dried down faster than lichen biocrusts or bare soil. It is additionally possible that the
smooth, cyanobacterial biocrusts in our study were accompanied by some degree of physical
crusting. Physical soil crusting is common in hot desert ecosystems (reviewed in Belnap
2001) and is known to pose barriers to vascular plant recruitment (Awadhwal & Thierstein,
1985; Belnap 2001). Thus, if present, physical crusting may have contributed to decreased
native species emergence.
Lichen biocrusts, in contrast, increased *A. purpurea* and *E. lehmanniana* emergence. This result agrees with empirical work which suggests lichen biocrusts offer favorable microhabitats for increased seedling emergence (Deines, Rosentreter, Eldridge, & Serpe, 2007; Godínez-Alvarez et al., 2012), but conflicts with others that suggest biocrust lichens can obstruct seed contact with, or penetration into, the mineral soil (Zhang & Belnap, 2015), which can expose seeds to over-drying or predation (Schupp et al. 1995). *E. lehmanniana* emergence responded positively to both biocrust types conflict with past work that suggests biocrusts on exotic plant species emergence (in cool deserts: Deines et al., 2007; Eckert, Peterson, Meurisse, & Stephens, 1986; Kaltenecker, Wicklow, & Pellant, 1999; Serpe, Orm, Barkes, & Rosentreter, 2006; mesic ecosystems: Hernandez & Sandquist, 2011; and hot deserts: McLvanie 1942; DeCorte & Abella, 2011; Table A2.1).

Variation in emergence responses to biocrusts among species and the unexpected positive responses to biocrusts in *E. lehmanniana* may be partially explained by differences in species’ external seed morphologies. Past work suggests emergence of large-seeded plant species, especially those with appendages (e.g., awns) are often inhibited by biocrusts (Briggs & Morgan, 2010; Morgan, 2006; Zhang & Belnap, 2015). This mechanism has been hypothesized to drive biocrust inhibition of large-seeded, awned, exotic Mediterranean grasses like *Bromus* spp. in the Southwestern US (Evans and Young 1984; Howell 1998; Hernandez & Sandquist, 2011; Reisner, Grace, Pyke, & Doescher, 2013) and Israel (Prasse & Bornkamm, 2000), and *Shismus* spp. in Australia and Israel (Crisp 1976; Zaady, Gutterman, & Boeken, 1997). Native dryland plant species are often thought to possess seed adaptations that allow seeds to overcome physical barriers posed by biocrusts such as hygroscopic awns for self-burial (Belnap 2001), potentially as a result of coevolutionary relationships between
native plants and biocrusts (Stohlgren et al. 2001). Thus, exotic species lacking such structures may experience greater emergence inhibition by biocrusts than natives (e.g., Deines et al., 2007; Song, Li, & Hui, 2017; Table A2.1). In our study, *A. purpurea*, which has large, awned seeds, germinated frequently within biocrust cracks, and was generally uninhibited by biocrusts (Table 2.1). Thus, we hypothesize the barb-like trichomes on the seed tips of *A. purpurea* allowed for its lodging into biocrust surfaces (Table 2.1). Seed morphology may also partially explain *E. lehmanniana’s* emergence success on biocrusts. Compared to the two natives and large-seeded Mediterranean exotics commonly inhibited by biocrusts (Table A2.1), *E. lehmanniana* has small, smooth seeds which may have facilitated its lodging into small, favorable microsites on biocrust surfaces.

Although biocrusts promoted *E. lehmanniana* emergence over that of the two natives (Fig. 2.3a), we found this positive response was reversed in later plant stages, with biocrusts promoting native species survival and growth over that of the exotic (Fig. 2.3b-c). Native plant survival increased on both cyanobacterial and lichen-dominated biocrusts (Fig. 2.2, Fig. A2.3), a result that is consistent with other studies that have found biocrusts can provide favorable conditions for plant survival (Godínez-Alvarez et al., 2012; Lesica, P., Shelly, 1992; Seghieri, Rajot, & Ehrmann, 1997; Zhang & Nie, 2011; Y. Zhang & Belnap, 2015). Inhibitory and neutral survival responses in *E. lehmanniana* to cyanobacterial and lichen-dominated biocrusts respectively suggest seedlings of this species may be less able to benefit from biocrust-mediated soil resources (e.g., water, nutrients) than the natives, although potential mechanisms driving differences in species survival responses to biocrusts are unclear.

While numerous studies have demonstrated positive plant growth responses to cyanobacterial- and lichen-dominated biocrusts (Godínez-Alvarez et al., 2012; Lesica, P.,
we observed lower seedling growth on cyanobacterial biocrusts in all species relative to bare soils. This result could suggest cyanobacteria-dominated biocrusts in this system may offer inhospitable soil environments for the growth of certain plant species, possibly as a result of decreased soil moisture (Chamizo et al. 2016). As discussed above, this result may also suggest that there was some degree of physical crusting on cyanobacterial biocrusts in our study, which may have decreased seedling growth (Awadhwal & Thierstein 1985; Belnap 2001). In contrast, positive growth responses to lichen biocrusts in *A. purpurea* may be partially explained by enhanced soil nutrient conditions by this biocrust community type relative to bare soil which may increase plant nutrient uptake (St. Clair et al., 1984; Li et al., 2005; Langhans et al., 2009). Neutral and negative growth responses to lichen-dominated biocrusts in *B. eriopoda* and *E. lehmanniana* to lichen biocrusts, however, suggest plant species may differ in their capacity to benefit from biocrust-mediated soil resources (i.e., water, nutrients). Interestingly, negative growth responses in *E. lehmanniana* conflict with evidence from cool desert ecosystems that suggest that, once established, exotic plant species experience increased growth in the presence of biocrusts (Howell 1998; Defalco et al., 2001).

### 2.5.2. Bunchgrass recruitment responses to biocrust removal

Biocrust removal provided greater benefits to the recruitment of exotic *E. lehmanniana* compared to the two native bunchgrass species (Fig. 2.2; Fig. A2.3). In general, positive plant species performance responses to biocrust removal tended to be driven by
increased emergence and survival (Fig. 2.4b-c), while negative performance responses to biocrust removal were driven by decreases in seedling growth (Fig. 2.4c).

Biocrust removal increased the emergence of all grass species in this study (Figure 2.4a), although only significantly so in *E. lehmanniana* and *A. purpurea*. This result is consistent with past studies showing physical disturbance or removal of biocrusts generally increases plant emergence (Beyschlag et al., 2008; Hernandez & Sandquist, 2011; Langhans, et al., 2010; Li, Xiao, Cheng, Luo, & Liu, 2006). Notably, positive emergence responses to biocrust removal were greatest in *E. lehmanniana* (Fig. 2.4a), suggesting biocrust degradation may benefit exotic species recruitment during germination. A variety of mechanisms have been proposed for how biocrust disturbance may benefit seedling emergence (Belnap 2001). For example, biocrust disturbance may reduce competition between seedlings and biocrusts for nutrients, water, space, and light (Belnap, 2001; Serpe et al. 2006). Intact biocrusts may thus contribute to biotic resistance to exotic plant invasion by reducing resource availability to vascular plants (Stohlgren et al. 2001; Belnap 2001). Though biocrust disturbance may also benefit native plant recruitment, exotic plants have been shown to germinate and grow more rapidly under disturbance conditions than native species, especially in nutrient-poor environments (D'Antonio & Vitousek, 1992), which may partially explain this result.

Seedling survival and growth responses to biocrust removal were species-specific and varied by biocrust community type. Cyanobacteria-dominated biocrust removal increased survival of *E. lehmanniana* and *B. eriopoda*, perhaps as a result of decreased competition for soil resources between these species and biocrust organisms following disturbance (Stohlgren et al., 2001; Belnap, 2001). In contrast, removal of lichen-dominated
biocrusts uniformly decreased survival in all grass species, although on sandy soils *E. lehmanniana* was least inhibited (Fig. 2.3b; Fig. A2.3). Decreased seedling growth responses to lichen-dominated biocrust removal may be partially explained by decreased soil services associated with the removal biocrust-dwelling organisms. Lichens and cyanobacteria are known to have high water-holding capacities (Lange, 1980; Mager & Thomas, 2011) as well as C- and N-fixing capabilities (Barger, Herrick, Van Zee, & Belnap, 2006). Moreover, it is again possible that biocrust removal resulted in the formation of physical crusts which form readily when biocrusts are disturbed (Lemos & Lutz, 1957; Belnap, 2001). As such, biocrust removal may have decreased seedling growth by decreasing soil moisture and nutrient availability to seedlings.

Finally, soil texture also played an important role in determining the magnitude of seedling responses to biocrust removal (Figs. 2.2, 2.3b, 2.4b-c). Overall, seedling survival and growth were lower on silty versus sandy soil. *E. lehmanniana*, in particular responded with a ~2.5-fold greater decrease in performance to lichen-dominated biocrust removal on silty versus sandy soil. This effect was mostly driven by decreased growth (Fig. 2.3b). Lower growth on silty soils is unsurprising given the tendency of finely textured dryland soils to have higher evaporative losses and lower water availability than more coarsely textured soils (‘Inverse texture hypothesis’; Noy-Meir, 1973), and for silty soils to have lower plant available water and a higher permanent wilting point compared to sandy soils (Saxton et al. 1986, 2006). In support of this, we observed after equal watering, silty soils tended to dry out faster than sandy soils, forming hardened cement-like surfaces between watering events. This, and plant performance on silty soils again suggests the formation of physical crusting, which are known to form more readily on fine textured (i.e., silty) soils than on coarsely
textures (i.e., sandy) soils (Lemos & Lutz, 1957) that we suspect hindered seedling success. Interestingly, lower performance of *E. lehmanniana* on silty soils also aligns with past field observations that show *E. lehmanniana* can spread to many soil types, but only predominates on sandy textured soils (Cox & Ryule, 1986).

2.5.3. Biocrusts and their disturbance mediate hot desert bunchgrass recruitment

Our results suggest that hot desert biocrust communities and their disturbance contribute to moderating the recruitment success of native and non-native plant species. Biocrusts, particularly cyanobacteria-dominated communities, decreased the overall performance of exotic perennial bunchgrass *E. lehmanniana* while having mixed effects on native bunchgrass species performance. Overall plant performance responses to biocrusts, however, were driven by variability in plant responses at different stages of plant recruitment (i.e., emergence, survival, growth) indicating plant responses to biocrusts may shift over the course of the plant lifecycle. For instance, *E. lehmanniana* emergence was increased by biocrusts. Yet, the native grasses tended to receive greater benefits from biocrust presence during survival and growth stages of recruitment. Our results additionally suggest that biocrust removal, especially that of cyanobacteria-dominated biocrusts, may increase the recruitment success of the exotic bunchgrass *E. lehmanniana* over native species recruitment.

Our results raise interesting questions involving the potential contributions of biocrusts to biotic resistance of hot desert plant communities to invasion and identify a need for empirical field investigations of this relationship. Potential contributions of biocrusts to
biotic resistance may be useful in predicting which communities are susceptible to invasions (Levine & D’Antonio, 1999) and, in a restoration ecology context, designing communities resistant to invasion (Corbin & Antonio, 2004; Seabloom, Harpole, Reichman, & Tilman, 2003). Biocrusts have been identified as critical components of terrestrial ecosystems worldwide (Rodriguez-Caballero et al., 2018). Results from this study add to a growing body of literature that indicate the importance of biocrusts in shaping dryland plant community structure and offer novel information about the manner in which biocrust communities and their disturbance influence hot desert native and exotic bunchgrass recruitment. Thus, we suggest biocrust conservation and restoration be incorporated into dryland management practices, especially those focused on invasive species management.

2.6. Acknowledgements

We would like to thank Akasha Faist, Anita Antoninka, Melinda Markin, and Hannah Cruz for assistance with biocrust sample collection in the field. We would also like to thank Halle Bramer and Natalie Templeman for their assistance with data collection in the greenhouse, and Laura Wegleitner for her help with data processing in the lab. This work was made possible by undergraduate researchers with the generous support of the University of Colorado Boulder Undergraduate Research Opportunities Program (UROP), the USDA-ARS Jornada Experimental Range, and the Strategic Environmental Research and Development Program (SERDP; RC-2329; Department of Defense, Department of Energy, and the Environmental Protection Agency). Caroline Havrilla was supported by a National Science Foundation Graduate Fellowship (Grant DGE 1144083).
CHAPTER 3

Species-specificity in biocrust facilitation of plant growth is not driven by differences in root-associated fungal colonization among species

Caroline A. Havrilla, Alexander D. Leslie, Jacob DiBiase, & Nichole N. Barger


3.1. Abstract

Plant-soil interactions are important drivers of plant productivity and community structure. Biocrusts – soil surface-dwelling biotic communities comprised of cyanobacteria, fungi, bryophytes, and/or lichens - are widespread in drylands globally. Biocrusts are described as “mantles of fertility" and often have facilitative, but species-specific effects on plant productivity. Yet, patterns and mechanisms underlying biocrust facilitation of plant productivity remain unclear. Using mesocosms with bare soil versus biocrust cover we investigated the effects of biocrusts on the emergence, biomass allocation, and leaf chemistry of six grass species and evaluated the potential role of root-associated fungi (RAF) in mediating these relationships. Plant responses to biocrusts were species-specific. Overall, biocrusts decreased seedling emergence but increased plant biomass and leaf N concentrations in Elymus elymoides (Raf.), Bouteloua gracilis (Willd. ex. Kunth), and Zea mays var. indurata (L.). However, plants grown in biocrusts had lower RAF colonization compared
to bare soils. Biocrusts promoted plant growth and increased leaf N. Yet, growth responses to biocrusts were not driven by differences RAF colonization between soil surface types suggesting RAF did not mediate resource exchange between biocrusts and plants in this study. Understanding plant species-specificity in biocrust facilitation of plant growth may have important implications for understanding plant community structure in dryland ecosystems.

3.2. Introduction

Biotic interactions between plant and soil communities play key roles in structuring terrestrial ecosystems by influencing plant growth and primary production, particularly in low resource environments (Bever et al., 2010; Bever, Westover, & Antonovics, 1997; Hoeksema et al., 2010; Van Der Heijden et al., 2008). In dryland ecosystems, plant primary production is largely constrained by low and heterogeneously distributed water and nitrogen (N) availability (Austin et al., 2004; Hooper & Johnson, 1999; Ladwig et al., 2012; Peterjohn & Schlesinger, 1990), and resources are susceptible to loss via evaporation (Kurc & Small, 2004), erosion (Peterjohn & Schlesinger, 1990), and denitrification (Marusenko et al., 2013). As such, plant-soil interactions may play important roles retaining resources and increasing primary productivity in drylands through maintaining resources within biotic pools and facilitating efficient resource exchange (Bardgett & Wardle 2010).

Biological soil crusts (biocrusts) – biotic soil surface-dwelling communities comprised of cyanobacteria, algae, fungi, bryophytes, and/or lichens – are spatially widespread and coexist alongside vascular plants in drylands globally (Rodriguez-Caballero
et al., 2018). Recent synthetic work suggests biocrusts generally facilitate plant species growth, though there is a high degree of species-specificity in these results (Zhang et al., 2016; Havrilla et al., Under Review). Positive plant growth responses to biocrusts may be ascribed to enhanced soil conditions, including greater soil moisture retention (e.g., Chamizo, Rodríguez-Caballero, Cantón, Asensio, & Domingo, 2015), increased soil organic matter and inorganic N content (Defalco, Detling, Tracy, & Warren, 2001b; Ferrenberg, Faist, Howell, & Reed, 2018; Pendleton et al., 2003). Biocrusts have been described as ‘mantles of fertility’ (Schlesinger, Raikes, Hartley, & Cross, 1996), and often enhance soil fertility by increasing availability of soil organic carbon (C; Li et al., 2012; Tucker et al., 2017) and nitrogen (N; Barger et al., 2016; Ferrenberg et al., 2018). As a result, studies have demonstrated increased N tissue content in plants grown in biocrusts relative to bare soil (Defalco et al., 2001; Langhans et al., 2009; Zhang & Nie, 2011), as well as greater concentrations of phosphorus (P; Yan, 2009) and other mineral nutrients (e.g., Concostrina-Zubiri, Huber-Sannwald, Martínez, Flores Flores, & Escudero, 2013; Guo, Zhao, Zuo, Drake, & Zhao, 2008; Harper & Belnap, 2001). Though, we have a limited understanding of what patterns and mechanisms underpin interspecific variation in biocrust facilitation of plant growth, and how resources are transferred between biocrusts and plants.

One possibility is that root associated fungi may mediate resource transfer between biocrusts and plants (Collins et al., 2008; Collins et al., 2014; Green et al., 2008; Rudgers et al., 2018). Root associated fungi (RAF) – including dark septate endophytic fungi (DSE) and arbuscular mycorrhizal (AM) fungi - are widely recognized as important drivers of plant productivity in drylands (Aguilar-Trigueros, Powell, Anderson, Antonovics, & Rillig, 2014; Collins et al., 2008; Collins et al., 2014; Rodriguez, Jr, Arnold, & Redman, 2009). Biocrusts are
niches for specialized free-living fungi and are heavily dominated by DSE, although they also contain AMF in lower abundance (Aanderud et al., 2018; Bates & Garcia-Pichel, 2009; Bates, Nash, & Garcia-Pichel, 2012; Green et al., 2008; Porras-Alfaro, Herrera, Natvig, Lipinski, & Sinsabaugh, 2011). Genomic sequencing studies suggest there is substantial overlap between biocrust and plant rhizosphere fungal communities (Porras-Alfaro et al., 2011; Steven, Gallegos-Graves, Yeager, Belnap, & Kuske, 2014), and labelled isotope studies have demonstrated translocation of $^{15}$N between biocrusts and plants in communities can likely be attributed to fungal networks (Green et al., 2008; Hawkes, 2003; Zhuang et al., 2013). However, whether biocrusts influence plant RAF colonization, and/or differences in biocrust-associated RAF colonization among plant species can mediate species-specificity in plant growth responses to biocrusts remains unclear.

In this study, we investigated the effects of biocrusts from a cool desert ecosystem in western North America on growth and RAF colonization of six grass species. Specifically, we focus on the following questions: (1) Is plant RAF colonization influenced by biocrust presence? and if so; (2) Do differences in RAF colonization rates predict differences in plant growth and nutrition between soils with and without biocrusts? We hypothesize that biocrusts, by increasing soil fertility, promote plant species growth and nutrition (e.g., N content), and that increased growth corresponds to higher colonization rates of RAF in plants grown in biocrust relative to bare soil. To test these hypotheses, we conducted a greenhouse experiment to investigate the effects of biocrusts on the emergence, biomass accumulation, leaf chemistry, and colonization of RAF in grass species grown in biocrust versus bare soil mesocosms.
While past studies have shown biocrusts can facilitate plant species growth, relatively few studies have investigated the patterns and mechanisms underlying interspecific variation in biocrust facilitation of plant growth, and the potential role of fungal linkages between biocrusts and plants in determining plant growth and nutrition. Such an approach can provide broader insights into the patterns and processes underlying biocrust facilitation of plant species performance and may be an important step towards understanding dryland community structure and predicting how drylands will respond to global change. Recent evidence suggests biocrusts may be highly susceptible to ongoing and future climate and land use changes (Ferrenberg, Reed, & Belnap, 2015; Reed et al., 2012; Rodriguez-Caballero et al., 2018). Understanding how changes to biocrust cover in response to global change will influence plant community structure requires improved knowledge of how biocrusts influence plant species and primary production in drylands.

3.3. Materials and Methods

3.3.1. Biocrust and bare soil sample collection

In October 2017, we collected biocrust and bare soil samples \((n = 72\) each) from a cool desert ecosystem site (30-year mean annual temperature = 9.9 °C, 30-year mean annual precipitation = 326 mm; PRISM, (Daly et al., 2008), http://www.prism.oregonstate.edu) located in the Needles District in Canyonlands National Park (38°09’ N, -109.452 W, elevation 1502 m) in southeastern Utah, USA. The site is classified as a Loamy Bottom (Basin Big Sagebrush) ecological site type (USDA NRCS, 2018). Soils in this area are classified as sandy loam, Mido series Aridisols with sodic surfaces (SoilWeb Survey Application,
Vegetation is dominated by perennial grass species *Elymus elymoides* Raf. Swezey spp. *elymoides* (squirreltail), *Hesperostipa comata* Trin & Rupe. Barkworth ssp. *Comata* (needle and thread), *Aristida purpurea* Nutt. (purple three awn), *Bouteloua gracilis* Willd. ex Kunth (blue grama), and *Pleuraphis jamesii* Torr. (James’ galleta), and shrub species *Artemisia tridentata* Nutt. ssp. *tridentata* (basin big mountain sagebrush) and *Atriplex canescens* Pursh. (fourwing saltbrush). Biocrust communities at this site, in the absence of soil disturbance, are co-dominated by cyanobacteria, mosses (e.g., *Syntrichia* spp.), and lichens (e.g., *Collema, Psora* spp.) with pinnacled and/or rolling microtopography (Fig. 3.1). We collected biocrust and bare soil samples (*n* = 72 each) in custom-made PVC arenas (diameter = 11 cm) using the collection methods described in Havrilla and Barger 2018 (chapter 2). Following field sample collection, all soil samples were transported to the University of Colorado Boulder.

### 3.3.2. Vascular plant study species

We selected five native perennial grass species common to the soil collection site in Canyonlands National Park: C3 species *Elymus elymoides* (squirreltail) and *Hesperostipa comata* (needle and thread) and C4 species *Aristida purpurea* (purple three awn), *Bouteloua gracilis* (blue grama), and *Pleuraphis jamesii* (James’ galleta). Given our interest in examining relationships among biocrusts, plant productivity, and RAF colonization, we also included the annual, C4 grass species *Zea mays* var. *indurata* L. (Hopi blue maize) in our study, a cultivated crop species often used as a model plant species for investigations of RAF colonization. Prior to experimentation, in an effort to remove preexisting fungal spores from
seed surfaces, we surface-sterilized seeds of all species by soaking in 4.125% sodium hypochlorite for 10 minutes then rinsing with DI water seven times. We then tested the viability of seed of all plant species on filter paper in petri dishes. All species showed high (>70%) levels of emergence.

3.3.3. Seed bank exhaustion, mesocosm establishment, and watering treatments

This greenhouse experiment was conducted in a University of Colorado Boulder greenhouse. In Spring 2018, we randomly assigned biocrust and bare soil mesocosms to one of two wet benches in the greenhouse (Fig. 3.1). To exhaust the preexisting seed bank in all mesocosms, we watered all cores via subirrigation every other day for 21 days. When seedlings emerged from the seed bank, we carefully extracted seedlings from cores using forceps and disposed of them. We deemed the seed bank was exhausted after observing seven consecutive days without seedling emergence. Soil mesocosms were then allowed to
dry for 7 days. Seeds of the 6 plant study species were sowed on 21 March 2017. In total, we established 144 mesocosms: 72 with bare soil and 72 with mixed cyano-moss-lichen biocrust cover, each with 10 seeds of *E. elymoides, H. comata, A. purpurea, B. gracilis, P. jamesii*, or *Z. mays* planted in monocultures with 12 replicates of each plant species-mesocosm type combination. Seeds were scattered as uniformly as possible over the surface of each soil mesocosm. All mesocosms were then watered via subirrigation every third day for the remainder of the experiment. In drylands, significant plant recruitment generally occurs only in wet periods (Holmgren & Scheffer, 2010; Muñoz-Rojas et al., 2016; Ogle & Reynolds, 2004). As such, watering was an essential part of our experimental design needed to address questions about biocrust effects on plant species performance.

3.3.4 *Seedling emergence, growth, and leaf chemistry experiments*

Mesocosms were maintained in the greenhouse under full sun, natural light conditions, a mean air temperature of 17.6 °C, and the watering regime described above for the duration of the experiment. Following seeding, we monitored daily radical emergence for all plant species for 28 days. We calculated percent emergence as the percent of emerged seedlings per mesocosm during the emergence period. We also calculated emergence time as the number of days from planting to visible radicle emergence. Percent emergence data are summarized in Table A3.1 and Figure A3.1. After the emergence period (Day 1-28) we removed seedlings to maintain two seedlings per mesocosm. We chose seedlings of similar size and age, spaced as evenly apart as possible. Then, we allowed remaining seedlings to grow for an additional 28-day period (Day 29-56). Individual plants were harvested from
soil mesocosms on 15 May 2018. We measured plant biomass by first separating aboveground (shoot) and belowground (root) biomass for each plant. A small (~ 0.50 g wet) subsample of root material was weighed and set aside for staining and fungal analysis as in (Giovannetti & Mosse, 1980). Remaining root and shoot material were dried at 60 °C for 48 hours and then weighed to determine above- (shoot) and below-ground (root) biomass. Shoot biomass was calculated as the dry weight of all above-ground biomass. Root biomass was calculated as:

\[
\text{Root biomass (mg)} = \text{Wet mass of entire root sample} \times \frac{\text{Dry mass of subsample}}{\text{Wet mass of subsample}}
\]

Total biomass (mg) was the sum of all root and shoot biomass (mg). After above ground (shoot) biomass was calculated, a subset of dried leaf biomass for each plant species and soil surface (mesocosm) type combination were randomly chosen for assessment of leaf carbon (% C) and N (% N), and C:N ratios via a combustion method via elemental analyzer (ESC 4010 Analyzer; Costech Analytical Technologies, Valencia, CA).

3.3.5. Plant root-associated fungi (RAF) quantification

To quantify RAF colonization in plants, we first stained root subsamples as described in (Giovannetti & Mosse, 1980). To remove cell contents and cell wall pigments, root subsamples were cleared in boiling 10% KOH solution for 10 minutes, rinsed with DI water, then soaked in 1 % HCL for five minutes. Cleared roots were then placed in boiling 0.05% trypan blue stain for 5 minutes. Stained root sections were then suspended in water and stored in a refrigerator at 4 °C until they were placed on slides. Slides were assembled with
10, 1-cm sections of stained root sections suspended in glycerol, sealed by a cover slip. To quantify RAF colonization rates for all plant species, we used a gridline intersect method (e.g., Brundrett, Bougher, Dell, Grove, & Malajczuk, 1996; Giovannetti & Mosse, 1980; McGonigle et al., 1990). Using 100 intersections on the root sections, we counted the number of root intersections colonized by RAF, noting whether the colonization was AMF or DSE. We then calculated a mean infection percentage (MIP) as the total number of infected roots intersecting gridlines/total number of roots intersecting gridlines x 100 and the percent colonization of AMF and DSE as the number of AMF or DSE/100 respectively.

3.3.6. Data analysis

Plant performance responses (i.e., percent emergence, time to emergence, total biomass, root:shoot ratio, leaf % C and % N, and C:N ratio) and RAF colonization rates (i.e., MIP, % AMF, % DSE) for all plant species were compared between soil surface types (i.e., biocrust versus bare soil) using linear models. The linear modelling approach for plant species responses was determined by: (1) assessing whether data were normally distributed via a Shapiro-Wilk W test, (2) determining whether data were normally distributed via tests of homoscedasticity (graphically), and (3) selecting an appropriate test given the results of normality and homoscedasticity tests. Specifically, when data were normally distributed and homoscedastic, a one-way ANOVA was performed. When data were not normally distributed but homoscedastic, a Kruskal-Wallis test was performed. Finally, when data were heteroscedastic, regardless of normality, a Welch’s ANOVA was performed. We evaluated relationships between plant growth (total biomass, root:shoot ratio) or chemistry measures
(leaf % C and % N, and C:N ratio), RAF colonization rates, germination time, and soil cover type using general linear models (GLM) with maximum likelihood estimation of parameters validated with AICc values. All GLMs were based on Gaussian distributions. All statistical analyses were performed in R version 3.5.1 (R Core Team, 2018).

3.4. Results

3.4.1. Effects of biocrust presence on plant RAF colonization

All grass species formed associations with both AM and DSE fungi (Figs. 3.2, 3.3; Table A3.1), though RAF colonization rates differed between soil surface types. In contrast with our prediction that fungal endophyte infection rates would be greater in plant species grown in biocrust versus bare soils, we found mean infection percentage (MIP) overall was 33.8% lower for grass

![Figure 3.2. Biocrust effect on plant root-associated fungal colonization.](image)

Mean infection percent (MIP) (± 1 SE) (a-b), and percent colonization of AMF (c-d) and DSE (e-f) fungi for plant species grown in biocrust versus bare soil mesocosms. Boxplots in panels a, c, and e show average for all grass species. Barplots in panels b, d, and f show colonization rates for individual grass species (no between-species comparisons are shown). "*" denotes statistically significant (P < 0.05) difference in means between mesocosm type.
species grown in biocrust versus bare soil mesocosms (Wilcoxon $X^2 = 4.90, P = 0.027$; Fig. 3.2a). *E. elymoides*, *H. comata*, *B. gracilis*, and *P. jamesii* had 35.8%, 55.3%, 57.7% and 58.1% lower MIP respectively when grown in biocrust versus bare soil mesocosms (*E. elymoides*, $F = 4.87$, $P = 0.034$; *H. comata*, $F = 3.44$, $P = 0.017$; *B. gracilis*, Wilcoxon $X^2 = 5.04$, $P = 0.025$; *P. jamesii*, $F = 1.47$, $P = 0.024$, Fig. 3.2b; Table A3.1). Differences in total MIP between soil surface types overall were driven by both lower colonization of AMF and DSE for plants grown in biocrust versus bare soil mesocosms (AMF, Welch’s $t = 2.136$, $P = 0.146$; Fig. 3.2c-d; DSE, Welch’s $t = 4.01$, $P = 0.047$; Fig. 3.2e-f; Table A3.1). Specifically, in *E. elymoides* and *B. gracilis*, % AMF

**Figure 3.3. Colonization of root-associated fungi.** Arbuscular mycorrhizal fungi (a-e) and dark septate endophytes (f-g), and other endophytic fungi inhabiting roots of grass species. (a) *A. purpurea* (bare soil) - intracidal and extraradical AMF hypha; (b) *P. jamesii* (bare soil) - AMF extraradical hypha and terminal vesicles in the rhizodermis; (c) *P. jamesii* (bare soil) - AMF intracidal hypha and vesicles in the root cortex; (d) *B. gracilis* (biocrust) - AMF intercidual hypha and extraradical fruiting body; (e) *Z. mays* (biocrust) - AMF extraradical hypha and terminal vesides and fine, melanised intracidal DSE hypha; (f) *Z. mays* (bare soil) - infection and growth of septate, melanised hypha (DSE); (g) *A. purpurea* (biocrust) - microsclerotium-like structure formed by dark septate fungal endophytes. Bar = 100 µm.
colonization was lower in plants grown in biocrust versus bare soil mesocosms respectively (E. elymoides, F = 6.31, P = 0.017; B. gracilis, Welch’s t = 3.05, P = 0.051; Fig. 3.2d). In A. purpurea and Z. mays % DSE colonization was lower for plants grown in biocrust versus bare soil mesocosms respectively (A. purpurea, Wilcox $X^2 = 3.05$, $P = 0.046$; Z. mays, Welch’s $t = 6.15$, $P = 0.019$; Fig. 3.2f; Table A3.1).

3.4.2. Biocrust effects on plant species growth and leaf chemistry

Plant growth and biomass allocation – Plant biomass on biocrusts was 44% higher relative to bare soil (Welch’s $t = 8.94$, $P = 0.004$; Fig. 4a; Table A3.1). This difference was mainly driven by higher biomass responses in E. elymoides and Z. mays which was 28% and 85% percent higher on biocrusts relative to bare soils respectively (E. elymoides, Kruskal-Wallis $X^2 = 4.29$, $P = 0.048$; Z. mays Welch’s $t = 6.28$, $P = 0.019$; Fig. 3.4b; Table A3.1).

Overall, mean plant height did
not differ significantly between biocrust versus bare soil mesocosms (Fig. 3.4c), though height of *E. elymoides* and *Z. mays* was 16.0% and 42.3% greater for plants grown in biocrust versus bare soil respectively (*E. elymoides* $F = 8.07, P = 0.006$; *Z. mays* $F = 8.34, P = 0.006$; Fig. 3.4d; Table A3.1). Effects of biocrusts on plant root to shoot ratios were species-specific, with lower root to shoot ratios in plants grown in biocrust versus bare soil in *E. elymoides* and *A. purpurea* (*E. elymoides*, $F = 1.33, P = 0.067$; *A. purpurea*, $F = 2.457, P = 0.034$; Table S3.1; Fig. A3.2), but no effects in *B. gracilis* and *Z. mays* (Table A3.1; Fig. A3.2). Differences in root to shoot ratios between soil surface types were not evaluated for *H. comata* or *P. jamesii* due to insufficient root sample data for these species.

*Leaf chemistry* - Leaf N concentrations (% N) were higher in plants grown in biocrust versus bare soil (Welch’s $t = 5.00, P = 0.031$; Fig. 3.5a; Table A3.1). This overall response was driven by higher leaf % N in *E. elymoides*, *B. gracilis*, and *Z. mays*, which experienced 32.3%, 21.7%, and 21.7% (*E. elymoides*, $F = 7.23, P = 0.014$; *B. gracilis*, $F = 4.34, P = 0.050$; *Z. mays*, Kruskal-Wallis $X^2 = 1.74, P = 0.095$; Fig. 3.5b; Table A3.1) higher leaf N concentrations on biocrust versus bare soil respectively (Table 3.1, Figure 3.5).
Leaf C concentrations (% C) did not significantly differ among soil surface types overall 
($P > 0.05$, Table A3.1), or within individual plant species (all $P > 0.05$; Fig. 3.4d; Table A3.1).

3.4.3. Relationships between root-associated fungi and plant growth responses to biocrusts

While biocrusts were associated with increased plant biomass and/or concentrations of leaf nitrogen (% N) in some plant species (i.e., *E. elymoides*, *B. gracilis*, and *Z. mays*; Figure 3.3, Fig. 3.4) and lower RAF colonization (i.e., MIP, % AMF, % DSE; Fig. 3.2), GLMs revealed no significant relationships between RAF measures and plant responses overall ($P > 0.05$). The higher plant biomass and leaf nitrogen on biocrusts did not correspond to RAF colonization for plant species overall (all $P > 0.05$), though within individual plant species, increased growth in *E. elymoides* by biocrusts was associated with marginally lower AMF colonization relative to bare soil controls ($F = 4.989, P = 0.061$) and in *B. gracilis*, increased % N was associated with higher MIP ($F = 0.034, P = 0.021$). Lower % AMF colonization in biocrust versus bare soil mesocosms corresponded to decreased C:N ratios in plants grown in biocrusts overall ($F = 1.450, P = 0.041$), though this overall trend was mainly driven by *E. elymoides* which experiences lower C:N ratios in response to lower % AMF on biocrust versus bare soil ($F = 1.642, P = 0.034$).

3.5. Discussion

We found *E. elymoides* and *Z. mays* experienced increased growth on biocrust versus bare soil (Fig. 3.4), and that this increase aligned to greater leaf N content in these species (Fig.
3.5), suggesting positive growth responses to biocrusts may be associated with increased N uptake on biocrust versus bare soil. However, in contrast with our predictions, biocrust facilitation of plant species growth did not correspond to rates RAF colonization in plants, suggesting RAF did not mediate resource exchange between biocrusts and plants in this study. Variation in biocrust facilitation of plant species growth may have important implications for understanding plant distribution and abundance patterns in drylands, though additional work is needed to resolve mechanisms underlying these effects.

3.5.1. Root-associated fungi colonization rates do not predict plant growth responses to biocrusts

In contrast with our prediction that variation in plant species growth responses to biocrust might be partially explained by differences in root-associated fungal abundance (i.e., MIP, % AMF, % DSE) among species between soil surface types, we found that (1) plants grown in biocrusts had lower root-associated fungi colonization compared to plants grown in bare soil (Fig. 3.3), and (2) fungal colonization rates did not correspond to plant growth responses. Lower RAF colonization in plants grown in biocrusts was unexpected given that past work has shown that biocrusts often host greater fungal diversity and abundance compared to soils lacking biocrust under field conditions (reviewed in Maier et al., 2016), particularly in late successional biocrust communities like those in this study (Bates et al., 2012). Moreover, this result conflicts with field studies that have shown that fungal networks can link C and N transfer between biocrusts and plants under field conditions (Aanderud et al., 2018; Collins et al., 2008; Collins et al., 2014; Dettweiler-Robinson, 2016; Hawkes, 2003).
Lower fungal colonization in plants grown in biocrusts could suggest there was lower abundance of RAF in biocrusts versus bare soils, though it is perhaps more likely that plants grown in biocrusts simply formed fewer associations with RAF, despite the likely higher presence of fungi in biocrusts (Maier et al., 2016). This pattern may be attributed in part to possible differences in soil resource availability (i.e., N, organic C, and water) between soil surface types.

Plant-fungal mutualisms depend heavily on abiotic soil conditions (Johnson, Graham, and Smith 1997; Mack & Rudgers 2008; Hoeksema et al., 2010). Lower fungal colonization in plants in the presence of biocrusts may be partially explained by potential differences in soil fertility between soil surface types. Biocrusts can increase fine-scale soil fertility by increasing organic matter, inorganic N, and the availability of other mineral nutrients in soil (Breen and Lévesque 2006; Zhao et al., 2014; Gao et al. 2010; Ferrenberg et al. 2018). Changes in soil fertility can alter how constituents of soil biotic communities interact with plants. One of the best-known examples of this is the tendency of nutritional mutualists such as mycorrhizae to become parasitic under conditions of high soil fertility (Johnson, Graham, and Smith 1997; Mack and Rudgers 2008; Hoeksema et al. 2010). Presumably, higher N availability in biocrust versus bare soil mesocosm may thus have contributed to plants forming fewer associations with RAF in soils containing biocrusts (Fig. 3.5). Similarly, increased soil organic matter by biocrusts may have decreased soil microbial demand for plant C, which in turn may have led to observed decreases in RAF colonization (Fig. 3.5) and increases in plant biomass in the presence of biocrust (Fig. 3.3).

Consistent watering treatments in our study may have additionally contributed to lower RAF colonization in plant species grown in biocrusts versus bare soils (Fig. 3.2) and
differences between results from our greenhouse study versus past field studies in drylands (e.g., Aanderud et al., 2018; Collins et al., 2008). Benefits of plant-fungal mutualisms are generally weakened under high soil water availability (Hoeksema et al., 2010). A recent meta-analysis of plant responses to fungal endophytes by (Dastogeer, 2018) concluded that the effects of fungal endophytes on plant physiology are greater under conditions of low water availability than under well-watered conditions. Thus, increased water availability under greenhouse conditions may explain differences between results of our study compared with evidence suggesting N and C exchange between biocrusts and plants is mediated by fungal networks under field conditions in drylands where precipitation is low and infrequent and the metabolic activities of biocrust and plant are separated in space and time (e.g., Aanderud et al., 2018; Collins et al., 2008; Collins et al., 2014).

3.5.2. Biocrusts have facilitative, but species-specific effects on plant species growth and nutrition

Our finding that biocrusts have species-specific, but facilitative effects on plant growth, biomass allocation, and nutrient content (Figs. 3.4-3.6) is consistent with positive growth responses to biocrusts reported for other plant species (Ferrenberg et al., 2018; Havrilla et al., Under Review; Langhans et al., 2009; Pendleton et al., 2003; Pendleton, Pendleton, Howard, & Warren, 2004; Zhang & Nie, 2011). Studies in cool desert ecosystems in western North America and northwestern China have shown biomass of native plant species to be higher on biocrust-covered soils versus adjacent soils lacking biocrusts (Harper & Belnap, 2001; Zhang & Nie, 2011). Positive plant biomass accumulation responses to biocrusts are
often attributed to increased soil fertility by biocrusts, including greater content of soil organic matter and inorganic N (Defalco et al., 2001; Ferrenberg et al., 2018; Pendleton et al., 2003). That we found lower root to shoot ratios in *E. elymoides* and *A. purpurea* plants grown in biocrust versus bare soil mesocosms (Fig. A3.2) supports our assumption that soil nutrient availability was increased in the presence of biocrusts. Plant allocation of biomass to roots generally decreases with increasing soil nutrient availability as a result of decreased plant requirement for root foraging (Van Wijk, 2011). Our results agree with studies that have demonstrated plants grown in biocrusts tend to have lower root to shoot ratios and/or shorter roots compared to those grown bare soil (e.g., Bliss and Gold 1999; Pendleton et al. 2003; Thiet et al. 2014). Though, species-specificity in biocrust effects on root to shoot ratios agrees with past work showing root to shoot responses to biocrusts are not always positive. For example, a study conducted by Liu and colleagues (2013) in China reported higher root to shoot ratios in plants grown in fixed sand dunes containing biocrusts compared non-fixed dunes, despite increased organic matter and N in soils containing biocrust.

Leaf N is often positively correlated with photosynthesis and plant biomass accumulation (e.g., Evans, 1989). Increased leaf N concentrations (% N) in *E. elymoides*, *B. gracilis*, and *Z. mays* plants grown in biocrusts versus bare soil mesocosms indicate that plants experienced increased N uptake in the presence of biocrusts. Species-specificity in this response suggests plant species may differ in their capacity to take up and/or utilize N from biocrusts possibly as a result of differences in species morphological or physiological traits. Contributions of biocrusts to soil N fertility tend to be greatest in the top several centimeters of the soil surface (Breen & Lévesque, 2006; Gao et al., 2010). Fine-scale variation in biocrust contributions to N availability depending on soil depth may lead to differences in N uptake.
among plant species depending on plant root architecture. For example, studies suggest plants with shallow, and/or ephemeral root structures may benefit more from biocrust presence than deeper-rooted plants (Defalco et al., 2001; Yan 2009; Zhang & Nie 2011). Although we did not measure root depth in the greenhouse, it is possible that differences in rooting depth among plant species resulted in observed differences in leaf N content and C:N ratio responses to biocrusts among grasses.

Given that C3 species have lower water- and N-use efficiency relative to C4 species (Pearcy & Ehleringer, 1984) and biocrusts often increase soil water and nutrient availability relative to soils without biocrust, we might expect that C3 species growth would respond more positively to biocrusts than C4 species. However, we found little support of this. Instead, we found biocrusts facilitated growth and promoted leaf N content in some C3 (i.e., *E. elymoides*) and C4 (i.e., *B. gracilis*, *Z. mays*) species, but not others. This result conflicts with the results of past work showing C3 and C4 grasses often experience different growth responses to the presence of symbiotic soil microorganisms under both greenhouse and field conditions (Hetrick, Wilson, and Todd, 1990; Wilson & Hartnett, 1998). However, our results do align with the results from recent meta-analysis conducted by Havrilla et al. (*Under Review*) showing biocrusts generally facilitate grass species growth regardless of photosynthetic pathway.

Collectively, results from this study highlight that plant growth responses to biocrusts are highly species-specific. Additionally, our results suggest plants in this study acquired soil resources (e.g., N) directly via root absorption rather than via fungal agents. However, this result may have been influenced in part by higher water availability in this greenhouse study.
compared to studies performed under field conditions in drylands where resource availability is more limited. It remains unclear why biocrusts facilitate the growth of some plant species and not others. Future studies should examine what plant functional traits influence plant growth responses to biocrusts under different abiotic soil conditions. Interspecific variation in biocrust facilitation of plant species growth may have important implications for understanding current and future plant distribution and abundance patterns in drylands, particularly in light of expected global declines in biocrust cover in response to global climate change (Ferrenberg et al., 2015; Reed et al., 2012; Rodriguez-Caballero et al., 2018).

3.6. Acknowledgements

This work was made possible by the support of Dr. Mark Miller and other U.S. National Park Service staff in Moab, UT who provided critical assistance with site permitting and access in Canyonlands National Park. We would like to thank Tyler Turk for her assistance with soil sample collection in the field, Lindsey Foust and Luke Lemons for their help with experimental monitoring and data collection in the lab and greenhouse, and Dr. Jane Zelikova for her logistical support on leaf elemental analysis. Undergraduate research assistants who contributed to this work were generously supported by the University of Colorado Research Opportunities Program (UROP) and Biological Sciences Initiative (BSI). This research was also supported by a University of Colorado Boulder Department of Ecology and Evolutionary Biology Maxy Pope Award and by a National Science Foundation (NSF) Graduate Research Fellowship (Grant DGE 1144083).
CHAPTER 4

When communities collide: a meta-analysis of context-dependency in vascular plant responses to biocrusts


4.1. Abstract

Understanding the importance of biotic interactions in driving the distribution and abundance of species is a central goal of plant ecology. Early vascular plants likely colonized land occupied by biocrusts — photoautotrophic, surface-dwelling biotic soil communities comprised of cyanobacteria, bryophytes, lichens, and fungi — suggesting biotic interactions between biocrusts and plants may have been at play for some 2,000 million years. Today, biocrusts coexist with plants in dryland ecosystems worldwide, and have been shown to facilitate or inhibit plant species performance depending on ecological context. Yet, what factors drive the direction and magnitude of these effects remain largely unknown. We conducted a meta-analysis of plant responses to biocrusts using a global data set encompassing 1,004 studies from six continents. Our meta-analysis revealed there is no simple positive or negative effect of biocrusts on plants. Rather, plant responses are driven
by biocrust composition and plant species traits and vary across plant ontogeny. Moss-dominated biocrusts facilitated, while lichen-dominated biocrusts inhibited overall plant performance. Plant responses also varied among plant functional groups: C4 grass species received greater benefits from biocrusts compared to C3 grasses and plants without N-fixing symbionts responded more positively to biocrusts than plants with N-fixing symbionts. Biocrusts decreased germination but facilitated growth of non-native plant species. Our results suggest interspecific variation in plant responses to biocrusts, contingent on biocrust type, plant traits, and ontogeny, can have strong impacts on plant species performance, and may have important implications for understanding plant community assembly processes and ecosystem responses to global change.

4.2. Introduction

Understanding the drivers of species distribution and abundance has long been a central goal of ecology (e.g., Callaway, 2007; Oosting, 1948). While there is wide consensus of the primary importance of dispersal limitations and barriers posed by the abiotic environment in predicting species distribution and abundance patterns (e.g., Cornwell & Ackerly, 2009; Keddy, 1992; Kraft et al., 2015), ecologists continue work to understand how local, biotic interactions restrict or enhance species performance. Positive (facilitative) and negative (competitive) species interactions can determine key attributes of ecosystems such as the number of species, their distribution, and the range of species traits present within communities (Boulangeat et al., 2012; Michalet et al., 2006; Wisz et al., 2013). Accordingly, biotic interactions are increasingly being incorporated into community theory (Brooker et
al., 2008; Bruno, Stachowicz, & Bertness, 2003; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Lortie et al., 2004) and predictions of how communities will respond to global change (Brooker et al., 2008; He, Bertness, & Altieri, 2013; McCluney et al., 2012; Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017; Van Der Putten, Macel, & Visser, 2010). In plant community ecology, the role of plant-plant interactions in determining plant species performance and community composition have been frequently tested (Levine et al., 2004; Noble and Slatyer 1977; Tilman, 2004). In contrast, the importance of soil biotic communities in determining plant species performance has been historically less studied, but evidence indicates a strong influence on plant community structure and productivity (Bever et al., 2010; Hortal et al., 2017; Van Der Heijden et al., 2008).

Biological soil crusts (“biocrusts”) - visible, photoautotrophic, biotic soil surface communities comprised of varying assemblages of cyanobacteria, algae, bryophytes, lichens and fungi - occupy the top few millimeters of the soil surface in dryland ecosystems globally (Belnap, Weber, & Büdel, 2016). Fossil data suggest early biocrusts began their colonization of Earth’s terrestrial surface some 2,500 million years ago (Beraldi-Campesi, 2013), predating the evolution of seed plants by at least 2,000 million years (Kenrick & Crane, 1997). This suggests that, during their colonization of dry land, early vascular plant (hereafter “plant”) communities were likely confronted by biocrusts, and that biotic interactions between biocrusts and plants have likely been playing out for millennia. Today, biocrusts are estimated to cover ~12% of the Earth’s terrestrial surface (Rodriguez-Caballero et al., 2018), and are particularly widespread in dryland ecosystems, which comprise ~45% of global landmass (Prăvălie, 2016). As biocrusts and plants continue to coexist in ecosystems worldwide, we are offered a unique opportunity to study the impacts
of biocrusts in mediating the performance of present-day plant species and communities where biocrusts and plants co-occur.

Abundant evidence suggests biocrusts can be key mediators of plant species performance. Biocrusts occur in patchy mosaics alongside adjacent patches of bare soil and vegetation, creating habitat and soil resource heterogeneity through physical and chemical modifications of the soil environment (Concostrina-Zubiri et al., 2013). Where they occur, biocrusts positively influence soil structure and physical stability (Bowker et al., 2008; Zhang & Belnap, 2015; Zhang et al., 2006). Biocrusts are also key intermediaries of nutrient cycling, accounting for ~15% of global terrestrial carbon (C) and ~40-85% of nitrogen (N) fixation globally (Rodriguez-Caballero et al., 2018). As such, biocrusts enhance soil fertility by increasing the availability of C (Li et al., 2012) and N (Barger et al., 2016) as well as other mineral nutrients (Concostrina-Zubiri et al., 2013; Guo et al., 2008; Harper & Belnap, 2001; Jafari et al., 2004). Biocrusts additionally modify soil microclimate via alteration of soil hydrology (Chamizo et al., 2016; Concostrina-Zubiri et al., 2017; Faist et al., 2017) and surface temperature (Concostrina-Zubiri et al., 2017; Couradeau et al., 2016). Given this wide range of soil modifications, biocrusts can strongly impact the recruitment and performance of plant species with which they coexist (Zhang et al., 2016).

In recent decades, a growing number of individual studies have investigated biocrust effects on plant species performance worldwide (Belnap, 2003; Zhang et al., 2016). Evidence suggests biocrust effects on plant species can be facilitative (Defalco et al., 2001; Godínez-Alvarez et al., 2012; Lesica & Shelly, 1992; Zhang & Nie, 2011), neutral (Godínez-Alvarez et al., 2012; Megill, Walker, Vanier, & Johnson, 2011), or inhibitory (Eldridge, Zaady, & Shachak, 2000; Zhang et al., 2010; Zaady et al., 1997), depending on the ecological context in which
they are studied. Moreover, empirical work has demonstrated biocrusts may affect plant community assembly processes and coexistence *in situ* (Chung & Rudgers, 2016; Luzuriaga et al., 2012) and may increase or decrease plant community diversity (Breen & Lévesque, 2006; Lan et al., 2013; Luzuriaga et al., 2012; Miller & Damschen, 2017; Peralta et al., 2016; Scott & Morgan, 2012). What is less known though is when and where the influence of biocrusts on plants can be generalized as negative or beneficial, and the relative importance of key explanatory variables (e.g., plant traits, climate) in driving interspecific variability in plant responses to biocrusts. As such, context-dependency in plant responses to biocrusts remains poorly understood given the narrow spatiotemporal and taxonomic focus of most individual studies.

Functional traits capture essential aspects of species’ ecophysiology, morphology, and life history strategies, and are thus often important predictors of interspecific variation in outcomes of biotic interactions (Ackerly & Cornwell, 2007; Kraft, Crutsinger, Forrestel, & Emery, 2014; Kraft, Godoy, & Levine, 2015; Lavorel & Garnier, 2002; Lebrija-Trejos et al., 2010; McGill, Enquist, Weiher, & Westoby, 2006). Given the species-specificity of plant responses to biocrusts and the general importance of plant functional traits in determining biotic interactions, we hypothesize that plant functional traits, especially those associated with acquisition of limiting resources (e.g., water, nutrients), may mediate plant responses to biocrusts. These include plant functional groups, which encompass species’ life form, photosynthetic pathway, and presence of N-fixing symbionts, as well as plant duration, and root morphology. Moreover, observations that biocrusts can increase native plant species performance while inhibiting that of non-native species have generated considerable interest in the potential of biocrusts to contribute to the biotic resistance of plant
communities (Briggs & Morgan, 2010; Gelbard & Belnap, 2003; Havrilla & Barger, 2018; Hernandez & Sandquist, 2011; Peterson, 2013; Reisner et al., 2013). Biocrust community composition may also determine effects on plant species given biocrust type largely determines the magnitude of biocrust contributions to soil hydrology, and C and N cycling (Barger et al., 2016; Bowker, Mau, Maestre, Escolar, & Castillo-Monroy, 2011; Sonia Chamizo, Cantón, Miralles, & Domingo, 2012). Finally, as community theory predicts that biotic interactions may differentially influence species performance and trait organization along environmental gradients as resource limitations shift (Cornwell & Ackerly, 2009; He et al., 2013; Maestre et al., 2010) and the importance of niche-based processes increases with increasing abiotic stress (Bruno et al., 2003; Gross, Liancourt, Choler, Suding, & Lavorel, 2010; Liancourt, Callaway, & Michalet, 2005), we posit the magnitude and direction of plant responses to biocrusts may also be mediated by climate and disturbance.

To address these important knowledge gaps concerning the outcomes and drivers of plant responses to biocrusts, we compiled a global database of biocrust-plant interaction literature and employed meta-analytical techniques to synthesize global patterns in existing data. Our specific research objectives were to assess the overall effects of biocrusts on plants, document what ecological factors are most influential in determining the magnitude and direction of these effects and identify remaining knowledge gaps and provide recommendations for future research. Specifically, we tested the propositions that (1) biocrust community composition mediates the direction and strength of plant responses to biocrusts, (2) biocrust effects on plants are not uniformly experienced by all plant types but vary depending on plant characteristics and functional traits, and (3) plant responses to biocrusts shift depending on abiotic environmental conditions (e.g., climate, disturbance).
Results from this meta-analysis are expected to have broad implications for understanding the effects of biocrusts on plant species performance. In turn, this knowledge will allow incorporation of biocrusts into broader plant community theory and ecosystem management practices. Moreover, given that global landcover of biocrust communities is expected to decline 20-40% within the next 65 years in response to climate change and land use intensification (Rodriguez-Caballero et al., 2018), and local biocrust community structure may also shift in response to climate change (Ferrenberg et al., 2015; Reed et al., 2012), we believe it is critical and timely to examine relationships between biocrusts and plant communities to better understand how ecosystems in which they co-occur will respond to global change.

4.3. Materials and Methods

4.3.1. Literature search and database construction

To populate our global dataset we searched the ISI Web of Science database (http://www.webofknowledge.com/) and records from 1940 to 2017 in the Chinese National Knowledge Infrastructure (CNKI) Digital Learning Platform (http://www.cnki.net/) for Chinese records not available in English), using all possible combinations of keywords for biocrust (i.e., [biological soil crust, biocrust, cryptobiotic soil crust, cryptogamic soil crust, and microbiotic soil crust] * plant responses [plant] * [germination, survival, growth, cover, nutrient uptake, phenology, reproduction, and diversity]) to generate the set of records to be considered. We then employed a systematic screening process to retain or exclude articles for this meta-analysis (Fig. A4.1). Eligible
articles were defined as those including any comparison ("study") of the performance of plants grown in the presence of biocrusts to plants that were grown in biocrust-absent controls (i.e., bare soil, biocrust removal, or biocrust disturbance). We retained articles that quantified the impacts of biocrusts on plant performance variables (i.e., germination, survival, growth, cover, nutrient uptake, phenology, and diversity) in observational or experimental settings, omitting studies that considered the effects of plants on biocrust communities. Individual articles often yielded multiple studies: for example, if a study compared multiple responses (e.g., germination and growth) of multiple plant species to biocrust presence, each plant response and species was considered separately, but given a unique numerical identifier to later test for non-independence.

From each study, we collected data on plant response variables in the presence and absence of biocrusts, as well as eight study characteristics (i.e., BIOCRUST_TYPE, CLIMATIC_REGION, PLANT_FUNCTIONAL_GROUP, PLANT_NATIVENESS, PLANT_DURATION, PLANT_ROOT_MORPHOLOGY, SOIL_REFERENCE_STATE, STUDY_LOCATION; Table 4.1) used as candidate explanatory variables (predictors) in our multi-factor meta-analysis. We recorded the mean (X), standard deviation (SD), standard error (SE), and sample size (n) of both the biocrust and biocrust-absent (control) plots for the plant response variables. Data were extracted directly from tables, published supplementary materials, and from digitized figures using “xyscan” version 4.2.1 (http://rhig.physics.yale.edu/~ullrich/software/xyscan/). A detailed description of our data extraction protocol is outlined in Appendix 3.1.
Table 4.1. The eight, candidate categorical fixed-effect explanatory variables explored in our mixed-effects meta-analyses.

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Number of levels</th>
<th>Description of variable levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIOCRUST_TYPE</td>
<td>4</td>
<td>Cyanobacteria, Moss, Lichen, Mixed; Classified by the dominant biocrust taxonomic group in the biocrusted treatment as reported in the study. 'Mixed' biocrusts are communities containing substantial cover of both mosses and lichens.</td>
</tr>
<tr>
<td>CLIMATIC_REGION</td>
<td>5</td>
<td>Hyper-Arid, Arid, Semi-Arid, Dry Sub humid, Other; Ecosystem type is based on aridity index (AI)* in order of greatest to least aridity: Hyper-arid (AI &lt; 0.05); Arid (0.05 &lt; AI &lt; 0.20); Semi-arid (0.20 &lt; AI &lt; 0.50); Dry sub humid (0.50 &lt; AI &lt; 0.65); Other (AI &gt; 0.65).</td>
</tr>
<tr>
<td>PLANT_FUNCTIONAL_GROUP</td>
<td>7</td>
<td>C3 grass, C4 grass, N-fixing forb, Non-N-fixing forb, N-fixing woody plant, Non-N-fixing woody plant, and Community; Plant functional group as designated in herbarium record for plant species. 'Community' designates multiple plant species belonging to multiple plant functional groups.</td>
</tr>
<tr>
<td>PLANT_NATIVENESS</td>
<td>3</td>
<td>Native or Non-Native; Corresponding to the native status of the plant in the study region. Non-Native species include any species not native to the study region.</td>
</tr>
<tr>
<td>PLANT_ROOT_MORPHOLOGY</td>
<td>3</td>
<td>Fibrous, Tap, or Community; Designated based on herbarium records. 'Community' designates multiple plant species with a combination of tap and fibrous root morphologies.</td>
</tr>
<tr>
<td>PLANT_DURATION</td>
<td>3</td>
<td>Annual, Perennial, or Community; As designated in herbarium records. 'Community' designates multiple plant species with a mix of annual and perennial species.</td>
</tr>
<tr>
<td>SOIL_REFERENCE_STATE</td>
<td>4</td>
<td>Bare soil, Biocrust removal, Biocrust disturbance, or Filter paper; Experimental control soil substrate for comparison to biocrusted treatment as recorded in the study. 'Biocrust removal' controls are those in which biocrust organisms have been removed from the soil surface while 'biocrust disturbance' controls are those that have been mechanically disturbed or trampled.</td>
</tr>
<tr>
<td>STUDY_LOCATION</td>
<td>2</td>
<td>Field or Greenhouse; Corresponding to the experimental setting of the study.</td>
</tr>
</tbody>
</table>

* Aridity index (AI) was calculated as the average yearly precipitation divided by average yearly potential evapotranspiration, an aridity index defined by the United Nations Environmental Program (UNEP). The input data used to calculate this dataset are part of the "CRU CL 2.0 Global Climate Dataset" prepared by the Climate Research Unit of the University of East Anglia, UK (New et al. 2002), and distributed through the website: http://www.cru.uea.ac.uk/.
4.3.2. Calculation of meta-analysis metrics

EFFECT SIZE

For each biocrust-present and absent comparison, we calculated an effect size for each plant response variable using mean values. In addition, to investigate biocrust effects on ‘overall plant performance’, we estimated an overall effect size (and within-study variance; see below) for plant performance by averaging the effect sizes of all plant responses reported for each reported plant species. Specifically, the effect size of biocrust presence was calculated as the log response ratio: \( \ln(X_{\text{crust}}/X_{\text{ctrl}}) \), where \( X_{\text{crust}} \) is the mean plant response in the biocrust treatment, and \( X_{\text{ctrl}} \) is the mean plant response in the biocrust-absent control. When positive, this metric indicates that biocrusts have a beneficial influence on the plant response of interest and when negative, a detrimental influence. Log response ratios provide a standardized measure of plant performance with favorable statistical properties for meta-analysis (Hedges, Gurevitch, & Curtis, 1999) and means for comparisons among studies with different plant response metrics.

WITHIN-STUDY VARIANCE

To account for differences in study precision, we weighted our analysis by estimating within-study variance for each study as in Hedges, Gurevitch, & Curtis (1999). Specifically, the within-study variance used in our weighted regressions was calculated as:

\[
\sigma^2 = \left[ \frac{SD_{\text{crust}}^2}{(n_{\text{crust}})(X_{\text{crust}}^2)} \right] + \left[ \frac{SD_{\text{ctrl}}^2}{(n_{\text{ctrl}})(X_{\text{ctrl}}^2)} \right]
\]
where $X_{\text{crust}}$ and $X_{\text{ctrl}}$ are the mean plant response with and without in biocrust, $SD_{\text{crust}}$ and $SD_{\text{ctrl}}$ are the standard deviation of treatment and control means, and $n_{\text{crust}}$ and $n_{\text{ctrl}}$ are the number of replicates with biocrust versus biocrust-absent soil treatments, respectively. If no measure of variance was reported for a study (SD or SE; 20.8% of studies), we used imputation to calculate missing variances in our dataset (Nakagawa, 2015) using Taylors Law, the relationship between mean and variance (for our dataset $(\log(SD_{\text{pooled}}) = (\log(X_{\text{pooled}}) * 0.7998) - 0.5236; R^2 = 0.73)$.

4.3.3. Boosted regression tree data exploration

To explore the relative importance of the candidate explanatory variables in explaining variation among plant response to biocrusts, we performed boosted regression tree (BRT) analyses on candidate variables in each of the five plant response models (Table 4.1; Table A4.1a). Boosted regression tree analysis additively fits and combines multiple trees using a forward stepwise procedure, thus improving accuracy (De’ath, 2007). BRT analysis is ideal for complex data and unidentified distributions (De’ath, 2007), and additionally, can accommodate missing values in predictor variables (De’ath, 2007; Elith, Leathwick, & Hastie, 2008).

We performed BRTs using the ‘gbm.step’ function in the gbm (Ridgeway, 2013) and dismo packages (Hijmans, Phillips, Leathwick, & Elith, 2017) as in (Elith & Leathwick, 2017). This and all subsequent statistical analyses in this study were conducted in the R open-source software environment (version 3.3.3; R Core Development Team, 2017). In each BRT model, we included only those moderators that had sufficient representation in the dataset
and corresponded to meaningful \textit{a priori} hypotheses (Fig. A4.1a); we then weighted each analysis according to the within-study variance. Models were simplified using the ‘gbm.simplify’ function suggested by (Elith & Leathwick, 2017). Simplified BRT models for each analysis included the most influential moderators and ranked them according to their relative contributions (which are scaled to sum to 100 \% within each model—i.e., the moderator explains X \% of the variation explained by the fitted BRT) to the explanation of variation in effect size. Relative variable influences were derived as an average of variable influence in all trees in each BRT model (Friedman & Meulman, 2003). Potential interactions between moderators in final BRT models were explored using the ‘gbm.interaction’ function (Elith & Leathwick, 2017).

4.3.4. Mixed multi-factor meta-analysis

Following the selection of key factors to be retained in each of the five plant variable response models via BRT, meta-analyses were performed by fitting mixed-effects meta-regression models using the \textit{rma.mv} function from the \textit{metafor} package (Viechtbauer & Cheung, 2010) with restricted maximum likelihood estimation of parameters. We first used pure random effects models to estimate the overall weighted mean effect size for each plant response model (i.e. the weighted, overall log response ratios of the plant response variables to biocrust presence; Table 4.2), with each effect size weighted by within-study variance and the residual between-study variance component (‘STUDY_ID’) as a random-effect variable. Then, for each of the five separate analyses, we investigated the relative importance of the categorical fixed-effect moderators (Table 4.1) included in each model (Fig. 4.1, Table A4.1b)
by analyzing a series of mixed-effect multiple meta-regression models, including a global model containing all the fixed factors being considered for that dataset and each of the nested subset models containing one more fixed factor. Every model also contained the random effect STUDY_ID to account for residual between-studies variation. When categorical moderators were significant (Q statistic < 0.05), differences in moderator levels were detected using planned contrasts with the 'linearHypothesis' function from the car package (Fox & Sanford, 2011; Fox, Friendly, & Weisberg, 2013). To explain residual heterogeneity and understand the potential effect of contextual factors on plant responses to biocrusts, we ran a series of separate univariate meta-regression models for each analysis that included single significant moderators. Parameters associated with explanatory variables with non-significant effects are not depicted graphically.

4.3. Results

4.4.1. Database summary

We retained 1,004 usable studies from 75 unique articles in our final database (Appendix 3.2) after our iterative screening process (Fig. A4.1). Of these, most studies focused on biocrust effects on seedling germination (n = 491; 48.9 % of studies), followed by effects on plant cover (n = 231; 23.0 %), growth (n = 159; 15.8 %), and then survival (n = 123; 12.3 %). Our database search did not yield sufficient articles to analyze biocrust effects on plant nutrient uptake, reproduction, or community diversity. Articles included in our database were published between 1942-2017 and studies spanned six continents, with over
a third of studies conducted between 30 and 50 degrees in latitude, being mainly in China (42.4 %) and North America (34.6 %). Studies were also included in lesser numbers from Europe (14.8 %), Australia (5.3 %), South America (2.8 %), and Africa (0.59 %) (Figure 4.1). With these studies, we evaluated the response to biocrusts in a total of 171 plant species occurring in 40 plant families.

**4.4.2 BRT data exploration results**

Across analyses, the candidate variables with the most explanatory power were BIOCRUST_TYPE (overall plant performance and cover), PLANT_FUNCTIONAL_GROUP (germination and growth), and PLANT_DURATION (survival). Overall, BIOCRUST_TYPE, PLANT_FUNCTIONAL_GROUP, PLANT_NATIVENESS, SOIL_REFERENCE_STATE, and CLIMATIC_REGION were most commonly identified as important explanatory variables in simplified BRT models (Fig. 4.2), while PLANT_ROOT_MORPHOLOGY, PLANT_DURATION, and STUDY_LOCATION were unimportant. Following BRT identification, strong moderators...
identified for the five plant models were included in mixed multi-factor meta-analyses (Table A4.1b). Results for the final simplified BRT models are summarized in Figure 4.2 and in additional detail in Appendix 3.3.

### 4.4.3. Mixed multi-factor meta-analysis results

Overall mean effect sizes for plant responses to biocrusts were not statistically different from zero (Overall plant performance: -2.0%. $P = 0.891$; Germination: -5.5%; $P =$
0.530; Survival: -44.2 %; \( P = 0.406 \); Growth: +27.0 %, \( P = 0.074 \); Cover: -0.10 %; \( P = 0.978 \); Figs. 4.3, 4.4, 4.5). However, meta-regression revealed plant germination, survival, growth, and cover responses to biocrusts in the five models were highly context-dependent, and varied significantly depending on biocrust community composition, plant species traits, and disturbance.

4.4.3.1. Biocrust community composition

\textbf{BIOCRUST\_TYPE} was consistently an important predictor of plant responses across plant response models. Biocrust community composition influenced overall plant performance (\( P < 0.001 \); Table 4.2; Fig. 4.3; Fig. 4.5). Lichen biocrust communities reduced average overall plant performance by 16 % (\( P = 0.098 \); Fig. 4.3), while moss biocrusts increased performance by 21 % (\( P = 0.092 \); Fig. 4.3). Biocrust community composition also influenced plant germination (\( P < 0.001 \); Table 4.2). Lichen biocrusts reduced seed germination by 32\% (\( P < 0.001 \); Fig. 4.3), whereas cyanobacterial, moss, and taxonomically mixed biocrusts neutrally affected plant germination responses overall (Fig. 4.3). Plant survival was also influenced by biocrust type (\( P < 0.001 \); Table 4.2; Fig. 4.3). While mean effect size for plant survival was negative across biocrust types, no individual biocrust type’s mean was significantly different from zero (Fig. 4.3). Planned contrasts, however, showed lichen biocrusts had lesser negative effects on plant survival than cyanobacterial or taxonomically mixed biocrusts (Fig. 4.3). \textbf{BIOCRUST\_TYPE} was again significant in determining plant growth (\( P < 0.001 \); Table 4.2; Fig. 4.3), with lichen and mixed biocrust communities increasing plant growth by 47 \% and 71 \% respectively (lichen, \( P = 0.098 \);
mixed, $P = 0.006$; Fig. 4.3). Finally, BIOCRUST_TYPE also predicted plant cover responses ($P < 0.001$; Table 2, Fig. 3) with moss and mixed biocrusts corresponding to plant cover

4.4.3.2. Plant functional group

PLANT_FUNCTIONAL_GROUP was also important for predicting all plant responses across models. Overall plant performance was impacted by plant functional type ($P < 0.001$; Table 2; Fig. 3; Fig. 5). C4 grass performance was increased 55 % by biocrusts ($P < 0.001$; Fig. 3d), while performance of C3 grasses was neutral (Fig. 3d). Among non-grasses, non-N-fixing forbs (plants lacking N-fixing symbionts) and woody plants responded neutrally, whereas performance of N-fixing forbs was decreased 23 % in the presence of biocrusts ($P = 0.056$; Fig. 3). Plant functional type also influenced plant germination responses to biocrusts presence ($P < 0.001$; Table 2; Fig. 4d). Among grasses, germination of C4 species was decreased 25 % ($P < 0.001$, Fig. 4.3), while germination of C3 species was unaffected by biocrusts (Fig. 4.3). Although survival was not significantly different from zero for any functional type, survival among the groups was affected ($P < 0.001$; Table 4.2), with survival of C4 species greater than any other group (Fig. 4.3). PLANT_FUNCTIONAL_GROUP additionally an important predictor of plant growth ($P < 0.001$; Table 4.2). Grasses received the greatest benefit from biocrust presence, with C4 grasses experiencing a 200 % increase ($P < 0.001$; Fig. 4.3), and C3 grasses experiencing a 149 % increase, in growth ($P < 0.001$; Fig. 4.3) compared to biocrust-absent controls. Growth of non-N-fixing woody plants also increased 56 % with biocrust presence ($P = 0.016$; Fig. 4.3), while growth of N-fixing woody plants decreased by 38 % ($P = 0.010$; Fig. 4.3). Biocrust presence decreased the overall growth of
Table 4.2. Test statistics for categorical effects in meta-regression models for each plant response analysis.

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Overall Performance</th>
<th>Germination</th>
<th>Survival</th>
<th>Growth</th>
<th>Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Qe (df_{682}) = 98192.1 P &lt; 0.001</td>
<td>Qe (df_{667}) = 31284.3 P &lt; 0.001</td>
<td>Qe (df_{69}) = 31800.7 P &lt; 0.001</td>
<td>Qe (df_{141}) = 9758.0 P &lt; 0.001</td>
<td>Qe (df_{171}) = 25592.6 P &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Qm (df_{10}) = 4215.6 P &lt; 0.001</td>
<td>Qm (df_{14}) = 1483.2 P &lt; 0.001</td>
<td>Qm (df_{12}) = 2432.2 P &lt; 0.001</td>
<td>Qm (df_{13}) = 11887.7 P &lt; 0.001</td>
<td>Qm (df_{14}) = 19759.8 P &lt; 0.001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Qm</th>
<th>df</th>
<th>P-val</th>
<th>Qm</th>
<th>df</th>
<th>P-val</th>
<th>Qm</th>
<th>df</th>
<th>P-val</th>
<th>Qm</th>
<th>df</th>
<th>P-val</th>
</tr>
</thead>
<tbody>
<tr>
<td>523.40</td>
<td>4</td>
<td>&lt;0.001</td>
<td>1075.2</td>
<td>4</td>
<td>&lt;0.001</td>
<td>100.35</td>
<td>4</td>
<td>&lt;0.001</td>
<td>333.15</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1919.4</td>
<td>7</td>
<td>&lt;0.001</td>
<td>339.15</td>
<td>7</td>
<td>&lt;0.001</td>
<td>351.55</td>
<td>5</td>
<td>&lt;0.001</td>
<td>4956.0</td>
<td>5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>8.00</td>
<td>5</td>
<td>0.157</td>
<td>6.93</td>
<td>5</td>
<td>0.226</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.49</td>
</tr>
<tr>
<td>8.99</td>
<td>2</td>
<td>0.011</td>
<td>25.89</td>
<td>2</td>
<td>&lt;0.001</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>24.53</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1764.1</td>
<td>4</td>
<td>&lt;0.001</td>
<td>9.63</td>
<td>4</td>
<td>0.047</td>
<td>79.91</td>
<td>3</td>
<td>&lt;0.001</td>
<td>6122.4</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>SOIL_REF_STATE</th>
<th>STUDY_LOCATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1764.1</td>
<td>4</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
II. Overall performance

III. Emergence

III. Survival

IV. Growth
plant communities with multiple plant functional types ('Community') by 42 % \( (P = 0.011; \text{ Fig. 4.3}) \). Relationships between biocrusts and plant cover also varied depending on \text{PLANT_FUNCTIONAL_GROUP} \( (P < 0.001; \text{ Table 4.2, Fig. 4.3}) \). Plant cover responses to biocrusts were only statistically distinct from zero for N-fixing woody plants, which decreased 70 % \( (P = 0.011; \text{ Fig. 4.3}) \). However, pairwise contrasts between plant functional types revealed among grasses, C4 cover was 59 % greater than that of C3 species in the presence of biocrusts \( (P < 0.001; \text{ Fig. 4.3}) \). Among non-grasses, cover of non-N-fixing woody plants was approximately one-fold greater than that of N-fixing woody plant species \( (P < 0.001; \text{ Fig. 4.3}) \).

4.4.3.3. Plant nativeness

\text{PLANT_NATIVENESS} was also an important predictor of overall plant performance \( (P = 0.011; \text{ Table 4.2}) \), although pairwise differences between native and non-native species in

**Figure 4.3.** Overall plant performance responses to biocrusts (weighted mean ± SE): (a) overall plant response ('AVG'), and the three important explanatory variables of this model: (b) \text{BIOCRUST_TYPE}, (c) \text{PLANT_NATIVENESS}, and (d) \text{PLANT_FUNCTIONAL_GROUP}. The number of studies in each moderator group level are shown in parentheses. The \( P \)-value in the corner of each graph denotes the statistical significance of the explanatory variable in the plant performance model. Lowercase letters denote statistically significant pairwise differences between moderator levels at \( P < 0.05 \), and "*" and "*" denote the effect size of a given moderator level is statistically different from zero at \( P < 0.05 \) or \( 0.10 > P > 0.05 \) respectively.
the overall dataset were not statistically significant from zero or each other (Fig. 4.3). However, this overall neutral effect was likely driven by opposing native and non-native responses to biocrusts during germination and growth stages of the plant life cycle (Figs. 4.3, 4.5). Germination was influenced by plant nativeness \( (P < 0.001; \text{Table 4.2}) \). The presence of biocrusts reduced germination in non-natives by 10 % \( (P = 0.100; \text{Fig. 4.3}) \), while native species were unaffected (Fig. 4.3c). In contrast, while plant growth responses to biocrusts were also influenced by PLANT_NATIVENESS \( (P < 0.001; \text{Table 4.2}; \text{Fig. 4.3}) \) the direction of biocrust influences on native and non-native species growth were reversed. Non-native species growth increased 51% in the presence of biocrust relative to biocrust-absent controls \( (P = 0.005; \text{Fig. 4.3}) \), whereas the growth of native species growth was not affected.

4.4.3.4. Soil reference state and other important moderators

Plant responses to biocrusts were also moderated by the type of uncrusted soil control used to compare to biocrusted soils (SOIL_REFERENCE_STATE; bare soil, biocrust removal, disturbed biocrust, or filter paper). SOIL_REFERENCE_STATE influenced overall plant performance responses to biocrust presence \( (P < 0.001; \text{Table 4.2}; \text{Figs. 4.4, 4.5}) \), with overall performance 34 % greater in the presence of biocrusts when compared to biocrust-removed controls \( (P = 0.024; \text{Figure 4.4}) \). Plant germination responses to biocrusts were mediated by soil reference type \( (P = 0.045; \text{Table 4.2}; \text{Fig. 4.4}) \) with seedling germination marginally lower on soils with biocrust relative to disturbed biocrust controls \( (-12 \%; P = 0.097; \text{Fig. 4.4}) \). Survival responses also differed by SOIL_REFERENCE_STATE \( (P < 0.001; \text{Table 4.2}) \). Mean effect sizes of biocrusts were negative for all control types, though SOIL_REFERENCE_STATE levels were not different from one another (Fig. 4.4). Plant growth responses to biocrusts
were influenced by SOIL_REFERENCE_STATE ($P < 0.001$; Table 4.2; Fig. 4.4). Only experiments using biocrust removal found an effect different from zero. Among uncrusted surfaces, pairwise contrasts revealed plants benefited most from biocrust presence when compared to biocrust-removed controls (+190%; $P < 0.001$; Fig. 4.4) while biocrust impacts on plant growth were slightly negative when compared to biocrust disturbance controls (-27%; $P = 0.094$; Fig. 4.4). Control type also influenced plant cover responses to biocrusts ($P < 0.001$;
Table 4.2, Fig. 4.4) with biocrust presence corresponding to a more than two-fold increase in plant cover when compared to biocrust removed controls ($P < 0.001$; Fig. 4.4).

Finally, PLANT_DURATION was also an influential explanatory variable in predicting plant survival responses to biocrusts ($P < 0.001$; Table 4.2; Fig. 4.3) with survival of perennial plant species on average decreased 54% by the presence of biocrust ($P = 0.061$; Fig. 4.3), while biocrust effects on annual species were neutral. Importantly, neither CLIMATIC_REGION nor STUDY_LOCATION nor their interactions with other explanatory variables were important in the final overall plant performance model, nor were they important in any of the plant models.

### 4.5. Discussion

Our analysis of 1,004 biocrust-plant studies revealed that there is no simple positive or negative effect of biocrusts on plants (Figs. 4.3-4.5). Rather, our results indicate that the overall neutral responses of plants to biocrusts are driven by interspecific variation in plant responses to biocrusts and trade-offs in biotic interaction outcomes across different stages of plant ontogeny (i.e., germination, survival, growth, cover). As such, results from this meta-analysis provide provisional support for the hypothesis that biocrusts serve, in some cases facilitators and in others, competitors for plant species and suggest these outcomes may be contingent upon biocrust community type, plant functional traits, and disturbance (abiotic stress). Moreover, our results helped us to identify existing knowledge gaps and future research needs (summarized in Table A4.2).
### 4.5.1. Biocrust community composition determines plant responses

Biocrust community composition was consistently an important explanatory factor for understanding variation in overall plant performance, germination,
growth, and cover (Figs. 4.3 b, f, n, r, respectively, Fig. 4.5). While cyanobacterial biocrusts had few effects on plants at any stage, moss biocrusts increased both overall plant performance and cover, while lichen-dominated biocrusts considerably reduced overall plant performance and germination but increased plant growth. One reason for this stark contrast may be driven by water relations. Soil water availability largely determines biotic interactions and the structure of plant assemblages in dryland environments (Chesson et al., 2004; Miranda, Armas, Padilla, & Pugnaire, 2011) and has specifically been shown to mediate biocrust effects on plant community structure (Luzuriaga et al., 2012). Adequate water availability is critical to seed water absorption during germination and subsequent seed metabolic activity and radical emergence (Fenner & Thompson, 2005). Therefore, variability in germination responses among biocrust types can likely be ascribed to differences in community physical structure and impacts on soil water balance. Lichens are often hard and smooth, and can obstruct seed contact with, or penetration into, the mineral soil (Zhang & Belnap, 2015), which can expose seeds to drying or predation on the soil surface (Schupp, 1995; Deines, Rosentreter, Eldridge, & Serpe, 2007; Serpe, Orm, Barkes, & Rosentreter, 2006). In contrast, mosses grow in cushions (sometime loosely) and can capture water, including dew and fog (Pan et al., 2016) and thus promote water infiltration into the soil (Eldridge et al., 2000) and soil water availability (Concostrina-Zubiri et al., 2017). This would enhance water availability to seeds and seedlings, promoting germination and increased plant cover, leading to biocrusts facilitating plant performance.

Despite lichen biocrusts demonstrating some negative effects on some plant life stages, our analysis revealed plant growth generally increased in the presence of lichen and mixed biocrusts. Numerous individual studies have noted the positive effects of lichen-
dominated biocrusts on plant biomass when seed penetration and survival filters are overcome (e.g., Langhans et al., 2009; Pendleton et al., 2003). Plants grown with lichen and mixed biocrusts have been shown to have greater concentrations of N and phosphorus in their tissues than plants grown in the absence of these biocrust types (Ferrenberg et al., 2018). Lichens with N-fixing cyanobacterial photobionts (cyanolichens; e.g., Collema) are associated with high levels of N-fixation (Barger et al., 2016; Rosentreter et al., 2016) and N-fixation may be higher yet in communities containing both cyanolichens and free-living N-fixing cyanobacteria (e.g., Nostoc, Scytonema; Barger et al., 2016).

4.5.2. Plant species traits and nativeness mediate plant responses to biocrusts

4.5.2.1. Plant functional group: photosynthetic pathway and symbiotic N-fixation influence plant responses to biocrusts

Plant functional traits often predict the outcome of positive and negative biotic interactions that may in turn influence community structure (Ackerly & Cornwell, 2007; Kraft et al., 2014; Kraft et al., 2015; Kunstler et al., 2016; Lavorel & Garnier, 2002; Lebrija-Trejos et al., 2010; McGill et al., 2006). In this study, plant functional type, a proxy for multiple key plant functional traits (i.e., life form, photosynthetic pathway, N-fixation, woodiness), mediated plant response to biocrusts across all models (Table 4.2, Fig. 4.3). Overall, C4 species performance, survival, and cover responses to biocrusts were greater than that of C3 species. C3 grasses were only positively affected by biocrusts during growth (Fig. 4.3). In contrast, C4 species, despite a significant decrease in germination, showed an increase in both overall performance and growth by biocrusts. This pattern is similar to studies that have shown C4 species receive greater benefits than C3 species from the presence of soil
microorganisms such as arbuscular mycorrhizal fungi (e.g., Hetrick, Wilson, & Todd, 1990; Hoeksema et al., 2010). Overall, our results conflict with our predictions for C3 and C4 grasses. C3 species have lower water- and N-use efficiency compared to C4 species (Pearcy & Ehleringer, 1984). Thus, we would expect C3 species overall would receive greater benefits from biocrusts, which presumably increase soil water and nutrient availability relative to uncrusted soil. One potential explanation for this pattern is that biocrusts that contain darkly pigmented cyanobacteria (e.g., Nostoc, Scytonema, Tolypothrix) are often associated with elevated soil surface temperature (Couradeau et al., 2016), C4 species may respond more favorably to biocrusts given their greater temperature requirements and tolerances compared to C3 species (Pearcy & Ehleringer, 1984; Sage & Kubien, 2007).

Among non-grasses, plants species lacking bacterial N-fixing symbionts exhibited a more positive response to biocrusts than N-fixing species (Fig. 4.3). This result suggests the benefits of N-fixing symbionts to plants are precluded in the presence of N-fixing biocrusts. Empirical evidence suggests that when soil nutrient limitations are relaxed, net benefits of maintaining N-fixing symbionts are decreased and may in turn lead to decreased performance of N-fixing plant species (Suding et al., 2005; Vitousek, Menge, Reed, & Cleveland, 2013). This pattern was less defined in survival, growth, and cover analyses, perhaps due to relatively low sample size of N-fixing forbs and woody plant species in these analyses, indicating additional studies are needed that directly compare the responses of plant species with and without N-fixing symbionts.

4.5.2.2. Plant nativeness: Biocrust influences on native versus non-native plants shift across plant ontogeny
We might expect that biocrusts, acting as strong facilitators or inhibitors would similarly influence both native and non-native plant species performance in the case of similar traits among native and non-native species. However, since the native plant community has likely coevolved in the presence of biocrusts and may have already experienced historical and ongoing facilitation or filtering, we might expect a divergence in traits of exotics and native plants and a differential response to biocrusts.

Overall, biocrusts inhibited the germination of non-native species. This negative effect is consistent with past reports that biocrusts pose greater inhibition to non-native versus native seeds (Deines et al., 2007; Hernandez & Sandquist, 2011; Song et al., 2017) and may be partially explained by physical interactions between non-native seed morphological traits and biocrusts. Nearly half (48.6 %) of germination studies included in our database addressed biocrust effects on non-native grasses with seeds with large awns (e.g., Bromus, Schismus spp.). Large awns may decrease or prevent contact between the seed and the mineral soil surface and can prevent the seeds from slipping into small cracks found in the biocrusts leaving seeds on the soil surface vulnerable to predation and lacking sufficient moisture to germinate (Belnap, Phillips, & Troxler, 2006; Deines et al., 2007; Morgan, 2006; Zhang & Belnap, 2015). Seed size may also govern plant germination responses to biocrusts. For instance, a study conducted by Morgan (2006) in grasslands of southwestern Australia found the large-seeded non-native grass species Briza maxima showed stronger inhibition by biocrusts than smaller seeded native species. Together, these morphological mechanisms are thought to play an important role in biocrust suppression of germination in awned, large-seeded Bromus species in the western US (Evans & Young 1984; Howell, 1998; Hernandez &
Sandquist, 2011; Peterson, 2013; Reisner et al., 2013) and Israel (Prasse & Bornkamm, 2000), and *Schismus* species in Australia and Israel (Crisp, 1975; Zaady et al., 1997).

In contrast to germination responses, non-native plant species growth increased on average two-fold by biocrusts (Fig. 4.3), indicating potential tradeoffs in non-native plant responses to biocrusts across plant ontogeny. This result is supported by individual studies that have reported increased growth in non-native and invasive plants by biocrusts (Defalco et al., 2001a; Ferrenberg et al., 2018; Pendleton et al., 2003). Most existing studies compare responses of exotic annuals to native perennial plants. As annual plants often have greater relative fitness than native perennials when key resources are not limiting, as often found in biocrusted soils, these results are not surprising (Davis et al., 2000; Van Kleunen, Weber, & Fischer, 2010). These results also suggest intact biocrust communities can act as a barrier exotic grass species invasion by inhibiting germination. However, once established, the exotic annuals may be more able than the native perennials to utilize the resources available in biocrusted soils leading to heightened competitive ability.

4.5.3. *Soil disturbance mediates biocrust impacts on plant performance*

Perhaps the best approach for understanding the importance of biotic interactions in filtering or facilitating plant species is to remove a putative influence and observe the effects. This approach to understanding biocrust-plant interactions exists in studies with two common methodologies: those where biocrusts have been removed (e.g., scraping away the biocrust layer) and those where biocrusts have been disturbed (e.g., trampling biocrusted soil surfaces). Both approaches suggest important interactions among plants and biocrusts,
but we found that the method of eliminating the biocrust had an important influence on outcomes (Table 4.2, Fig. 4.4, Fig. 4.5). In studies where biocrusts were disturbed but not removed, overall plant performance increased compared to controls, while plant performance decreased in plots where biocrusts were removed compared to control plots. This effect was mainly driven by plant growth but was also supported by patterns in germination and cover. These results suggest that upon mechanical disturbance of biocrusts, there may be initial increases in plant performance, indicating potential competition between intact biocrusts and plant communities. Individual studies have shown biocrust disturbance can increase the survival and growth of seedlings (Hernandez & Sandquist, 2011; Langhans, Storm, & Schwabe, 2010; Li et al., 2012), potentially because of temporary nutrient pulses released from biocrusts during biocrust disturbance (Beyschlag et al., 2008) and decomposition (Maestre et al., 2013), altered water infiltration rates via disruption of physical crusting or hydrophobic biocrust organisms (Chamizo, Cantón, Lázaro, Solé-Benet, & Domingo, 2012; Chamizo et al., 2016) or enhancing seed burial.

4.5.4. Biocrusts: biotic filters and facilitators for plant community assemblages?

Biotic interactions can strongly influence plant community assembly outcomes (Boulangeat et al., 2012; HilleRisLambers et al., 2012; Levine et al., 2004; Lortie et al., 2004). Collectively, results from this meta-analysis suggest strong context-dependency in plant responses to biocrusts. Given the potential of biocrusts to have positive, neutral, or negative effects on plant species performance, it is likely that biocrusts influence plant community assembly and composition by promoting the performance of certain plant species while
inhibiting others. As a working hypothesis to be tested further, we advance a few provisional generalizations summarizing the potential role of biocrusts in plant community assembly:

1. **Different biocrusts types differentially facilitate or inhibit potential plant community members.** Specifically, biocrust community composition can determine whether biocrusts facilitate, inhibit, or neutrally affect plant species. For example, moss-dominated biocrusts positively influenced plant performance overall, while lichen-dominated biocrusts negatively impacted plant performance.

2. **Plant traits can be both diminished or enhanced in the presence of biocrusts.** Effects of biocrusts on plants are not uniformly experienced by all members of the plant community. Specifically, C4 grasses responded more positively to biocrusts than C3 grasses and N-fixing species were more negatively affected by biocrusts than non-N-fixing species.

3. **The effect of biocrusts on plants shifts across plant ontogeny and may suggest trait-based tradeoffs that may equalize overall performance of functionally diverse competitors.**

**Figure 4.6.** Conceptual diagram showing hypothesized effects of biocrust biotic filtering and facilitation of vascular plant species that could act upon a regional plant species pool to determine local plant community composition.
Biocrusts reduce germination in non-native plants and C4 grasses but subsequently benefit these two groups in later life stages. Such trade-offs in interaction outcomes across plant ontogeny could be a mechanism that allows inferior competitors to coexist with these two groups which otherwise have adaptations that help to buffer them against environmental fluctuations.

4. **Biocrusts can facilitate or inhibit potential plant community members, depending on abiotic stress levels.** Our results suggest that, compared to a simulated highly disturbed environment, biocrusts are likely to exert a positive influence on potential plant community members, although the magnitude is contingent on biocrust type and plant traits. This observation aligns with ecological hypotheses that increased disturbance and/or abiotic stress increases the importance of niche-based processes once stochastic influences of species dispersal dissipate (e.g., (Ferrenberg et al., 2013; Jiang & Patel, 2008) and competition and facilitation between interacting species begins structuring communities (Bruno et al., 2003; Gross et al., 2010; Liancourt, Callaway, & Michalet, 2005).

Biotic interactions are increasingly being incorporated into plant community theory (Bruno et al., 2003; Lortie et al., 2004; Maestre, Callaway, Valladares, & Lortie, 2009) and predictions into how communities will respond to accelerating environmental change (Brooker et al., 2008; He et al., 2013; McCluney et al., 2012; Van Der Putten, Macel, & Visser, 2010). Given the acute vulnerability of biocrusts to ongoing and future climate change and land use intensification (Ferrenberg et al., 2015; Reed et al., 2012; Rodriguez-Caballero et al., 2018), understanding biocrust contributions to plant community assembly and structure may be particularly important for predicting how communities will respond to global change. We show biocrusts can have strong, context-dependent effects on plant species.
Therefore, we suggest their integration in the development of plant community theory is needed, in a manner akin to ongoing efforts to understand the broader influences of soil microbial communities on plant community structure (Bever et al., 2010; Kardol, Cornips, Van Kempen, Bakx-Schotman, & Van Der Putten, 2007; Van Der Heijden et al., 2008).

### 4.6. Acknowledgements

This work was conducted as part of the “Completing the dryland puzzle: creating a predictive framework for biological soil crust function and response to climate change” Working Group supported by the John Wesley Powell Center for Analysis and Synthesis, funded by the U.S. Geological Survey. We thank the University of Colorado Boulder Undergraduate Research Opportunities Program (UROP), which helped support undergraduate researchers who assisted with data entry for this project. Particularly, we would like to thank CU Boulder undergraduate researchers Emma Brokyl, Whitney Gabbert, and Julius Gayo for their invaluable work on database compilation and organization for this project. CAH was supported by a National Science Foundation Graduate Research Fellowship (DGE-1144083) and by the Department of Ecology and Evolutionary Biology at the University of Colorado Boulder. VBC was supported by a grant from the DePaul University College of Science and Health. JB was supported by the USGS’ Ecosystem and Land Change Sciences program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
CHAPTER 5

Biocrusts are positively associated with dryland herbaceous plant diversity at local scales

Caroline A. Havrilla, Nichole N. Barger, Jacob DiBiase, & Miguel L. Villarreal

5.1. Abstract

Spatial heterogeneity in soil resource availability is often an important driver of differences in plant species diversity among communities. In dryland ecosystems, biological soil crusts ('biocrusts') – surface-dwelling soil biotic communities comprised of cyanobacterial, algae, fungi, lichens, and/or bryophytes – are spatially widespread and contribute to fine-scale soil resource heterogeneity through modification of soil stability, fertility, and microclimate. Biocrusts can have strong, but species-specific effects on vascular plant performance. Yet, we have a limited understanding of how biocrusts, by regulating soil heterogeneity, may influence patterns of plant species richness, diversity, and community structure. We used an observational field survey to explore two main research questions: (1) Does biocrust-associated soil cover heterogeneity increase local plant diversity and community composition; if so (2) Are plant diversity responses to soil cover heterogeneity driven by niche-type (species sorting) or neutral-type (density-dependent) processes? We hypothesized that biocrusts increase local plant diversity by increasing soil heterogeneity, and thereby niche space for plant taxa with diverse resource requirements. We found that soil heterogeneity and biocrust cover were positively associated with local plant diversity, although this relationship was only significant in sagebrush versus pinyon-juniper plots.
Additionally, we found that species sorting, rather than density-richness relationships explained differences in local plant diversity between different soil patch types. Our results suggest biocrusts and biocrust-mediated soil heterogeneity may play important roles in supporting dryland plant biodiversity and may have important implications for predicting how dryland ecosystems will respond to predicted habitat homogenization under global change.

5.2. Introduction

Environmental heterogeneity is an important driver of differences in biological diversity among communities (Wiens 1976; Huston 1994; Turner & Chapin 2005; Stein, Gerstner, & Kreft, 2014). Coexistence theory predicts that spatial heterogeneity in environmental factors that affect fitness such as resource availability can promote coexistence through species-environment sorting (Bolker, Pacala, & Neuhauser, 2003; Chesson, 2000; Freestone, A.L., Inouye, 2006; Melbourne et al., 2007; Williams & Houseman, 2014). In plant communities, plant alpha diversity is often predicted to increase with increasing spatial heterogeneity in soil resource availability at local scales (Kumar, Stohlgren, & Chong, 2006; MacArthur & Levins, 1964; Ricklefs, 1977). The importance of soil heterogeneity in regulating plant diversity has been most frequently tested by experimentally manipulating soil physical properties and nutrient levels in spatially heterogeneous and homogeneous patterns (Reynolds, Mittelbach, Darcy-Hall, Houseman, & Gross, 2007; Stevens & Carson, 2002; Vivian-Smith, 1997; Wijesinghe, John, & Hutchins, 2005). Yet, these studies have generated inconsistent and often negative results. Further, as most studies have been conducted under
controlled conditions, our understanding of how soil heterogeneity may affect plant diversity in natural systems remains limited.

In dryland ecosystems, soil resources are heterogeneously distributed in space and time (e.g., water, nutrients; Burke, Lauenroth, Parton, Ecology, & Jul, 2013; García-Palacios, Maestre, & Gallardo, 2011; Schlesinger et al., 1996). Soil resource heterogeneity in drylands is further modified at finer scales via biotic processes. Specifically, biological soil crusts (‘biocrusts’) – surface-dwelling soil biotic communities comprised of cyanobacteria, algae, fungi, lichens, bryophytes – play critical roles in determining soil resource availability at local scales (Concostrina-Zubiri et al., 2013). For example, relative to bare soil, biocrusts increase soil stability (Belnap & Büdel, 2016; Bowker et al., 2008) and can modify soil moisture availability (Belnap, 2006; Chamizo et al., 2016; Concostrina-Zubiri et al., 2017; Faist et al., 2017) and increase surface temperature (Couradeau et al., 2016). Further, biocrusts can increase soil nutrient availability by fixing atmospheric nitrogen (N; Barger et al., 2016), excreting organic compounds and chelate elements into the soil surface (Harper & Pendleton, 1993), and trapping fine dust particles that are nutrient-rich (e.g., N, P, K, Mg, Cu, Fe, Mn; Delgado-Baquerizo et al., 2010; Martínez et al., 2006; Reynolds et al., 2001). Despite such contributions to soil resource and patch heterogeneity (Bowker et al., 2014), biocrusts have historically been examined as single units within ecosystems rather than as biologically and spatially complex communities (Maestre et al., 2005). Yet, exploring biocrust contributions to fine-scale soil spatial heterogeneity may be fundamental to understanding biocrust roles in ecosystem functioning (Maestre et al., 2005).

Recent evidence suggests biocrust-mediated soil heterogeneity may have important filtering effects on vascular plant assemblages (Havrilla et al., Under Review; Luzuriaga et al.,
2012; Zhang et al., 2016). Plant responses to biocrusts often vary depending on plant species and functional traits (Havrilla et al., *Under Review*) and biocrust community composition and diversity (Luzuriaga et al., 2012). Such variation suggests plant species may differ in their affinity to establish, survive, and grow in patches containing biocrust. If present, such spatial niche dissimilarity could support plant coexistence by reducing plant niche overlap and thereby increase local plant diversity (Hutchinson, 1957,1959). The few field studies that have examined biocrust effects on plant diversity and community composition have generated mixed results whereby biocrusts have been shown to have positive (Ghiloufi & Chaieb, 2017; Jeffries & Klopatek, 1987; Kleiner & Harper, 1977; Luzuriaga et al., 2012; Scott & Morgan, 2012) or negative (Miller & Damschen, 2017; Peralta et al., 2016) associations with plant species richness, thus generating uncertainty about the nature of this relationship. Moreover, the potential of biocrust spatial heterogeneity to influence local plant diversity remains largely unexplored.

To investigate potential relationships between spatial heterogeneity in biocrust cover and herbaceous plant diversity, we conducted an observational field study under natural field conditions in a cool desert ecosystem within the Colorado Plateau of western North America. We hypothesized that biocrusts increase local plant alpha diversity (i.e., species richness, Shannon diversity index) by increasing fine-scale spatial soil heterogeneity and thereby niche space for plants with diverse resource requirements (Fig. 1). Thus, the main goal of this study was to test this hypothesis by investigating the following research questions: (1) Does biocrust presence and/or biocrust-associated soil cover heterogeneity increase local herbaceous plant diversity and community composition; if so (2) Are plant
diversity responses to biocrust-mediated soil cover heterogeneity driven by niche-type (environmental species sorting) or neutral-type (density-dependent) processes? Notably, rather than being conducted under heavily controlled experimental conditions like many soil heterogeneity-plant diversity studies (Reynolds et al., 2007; Stevens & Carson, 2002; Vivian-Smith, 1997; Wijesinghe, John, & Hutchins, 2005; Williams & Houseman, 2014), this study was conducted in an area where human land use, particularly cattle grazing, may contribute patterns in biocrust cover and spatial heterogeneity and plant diversity on the landscape. Such an approach may be valuable for determining whether spatial heterogeneity in biocrust cover contributes to plant diversity patterns in situ.

In addition to being fundamental components of drylands, biocrusts are also highly susceptible to physical disturbance (Zaady et al., 2016; Rodriguez-Caballero et al., 2018) and climate change (Ferrenberg et al., 2015; Reed et al., 2012; Rodriguez-Caballero et al., 2018). Consequentially, in the next several decades, biocrusts are expected to experience significant declines in cover and compositional shifts globally (Rodriguez-Caballero et al., 2018) which could presumably lead to increased soil habitat homogenization. Increasing our

**Figure 5.1** Biocrust-mediated soil cover heterogeneity-plant richness hypothesis. Conceptual diagram showing hypothesized increase in local plant diversity with increasing biocrust-mediated soil cover heterogeneity.
understanding of how biocrusts, by contributing to soil heterogeneity, may drive plant community diversity and structure thus has important implications for predicting how dryland ecosystems will respond to global change.

5.3. Materials and methods

5.3.1. Study Site

The study area is located in Beef Basin in Southeastern Utah, USA within the Colorado Plateau Desert (Lat 37°58'N, Long 109°56'W). The climate is semiarid with a mean annual precipitation of 335 mm, and a mean annual temperature of 11.6 °C (PRISM Climate Group; 30-year average, 1981-2010; Daly et al., 2008). We focused our survey on two ecological site types in the study area: (1) Semidesert Shallow Loam (Black Sagebrush/Indian Ricegrass) dominated by *Artemisia nova* (A. Nelson) and perennial grasses *Achnatherum hymenoides* (Roem. & Shult.), *Pleuraphis jamesii* (Torr.), and *Bouteloua gracilis* (Willd. & Kunth) (hereafter ‘sagebrush’ sites; USDA-NRCS, 2018), and (2) Upland Stony Loam (Pinyon-Utah Juniper Woodland), dominated by *Pinus edulis* (Engelm.) and *Juniperus osteosperma* (Torr.) (hereafter ‘pinyon-juniper’ sites; USDA-NRCS, 2018). Mean site elevation is 1882 m and 1873 m in sagebrush and pinyon-juniper plots respectively, and soils are characterized as Leanto fine sandy loams (Soil Web, 2017). The main land use type of the area is cattle grazing.

On June 2, 2018, we established five, 50-m² observational field sites in each of the two ecological site types (i.e., sagebrush, and pinyon-juniper, n = 10 plots total). Within each site, we established eight, nested subplots (“patches”) to measure cover and composition of biocrusts (0.5-m²) and herbaceous plants (1-m²) for a total of 80 patches within the study
region. Patches were positioned randomly in open areas of plots (i.e., areas not covered by shrub or tree canopies) but at least five meters apart and represented a gradient of biocrust cover. In sagebrush plots, we also assigned a qualitative metric of grazing level (i.e., low, medium, high) to each plot based on ocular estimates of the average observed number of hoofprints present within a five randomly selected 10-m² areas within each sagebrush plot (0-5 = low, 5-10 = medium, > 11 = high).

5.3.2. Soil cover and soil heterogeneity metrics

We used a 0.5-m² quadrat with 100 intersects to measure cover of soil cover classes (SCCs) within all subplots. Descriptions of all SCCs are provided in Table 5.1. Soil data from each subplot were analyzed using a multi-scale approach to describe soil heterogeneity at the subplot, plot, and site level. First, from our soil cover measurements we calculated the percent cover of all SCC’s. Then, using these soil cover data, we used land cover heterogeneity metrics commonly used in larger-scale spatial landscape analyses: Land Cover Richness, Land Cover Diversity (Shannon diversity index) to quantify metrics of fine-scale soil cover heterogeneity at the patch level: (1) Soil cover richness (SCR): the total number of different soil cover classes present within the sampling area; and (2) Soil cover diversity (SCD): calculated using the Shannon-Weaver diversity index \( H = \text{Sum}(p_i); \) Shannon & Weaver, 1949) where \( p_i \) are the proportions of the different SCCs (see Table 5.1) within the sampling area. These metrics were chosen due to their widespread use in spatial landscape analysis and well-documented effectiveness in quantifying environmental spatial patterns (Turner and Gardner 1991; Peng et al., 2010; Plexida, Sfougaris, Ispikoudis, & Papanastasis, 2014).
5.3.3 Vascular plant cover and metrics of plant species diversity

For 1-m² all subplots, we also quantified herbaceous plant community composition. We focused our investigations on the herbaceous plant community (rather than herbaceous and woody because herbaceous plant species, in general, have shallower roots and shorter life spans than woody plants and thus may have greater potential to influenced by local soil resource modifications at the soil surface by biocrusts (Kidron & Aloni, 2018). We used a 1-m² quadrat with 100 intersects to measure percent cover and abundance of herbaceous plant species by dropping a pin flag and recording all plant canopies down to the soil level. Herbaceous plant species identified in our study plots are provided in Table A5.1. Plant species that could not be identified in the field were collected and identified in the herbarium at the University of Colorado Boulder (University of Colorado Boulder Herbarium, Colorado, USA). Fewer than 10% of unknown species specimens encountered could not be identified due to phenological stage or missing flower parts. In these cases, plants were identified to the genus level and treated as individual species. Then, plant census data were used to calculate herbaceous plant richness and Shannon diversity.

5.3.4 Data analyses

5.3.4.1 Effects of soil cover and heterogeneity on plant alpha diversity: Correlation analysis and boosted regression tree data exploration

Soil cover and heterogeneity metrics were used to develop predictive models for plant species richness and Shannon diversity index in sagebrush and pinyon-juniper plots. Before conducting analyses, we tested all variables for normality and homogeneity of
Table 5.1. Environmental predictor variables. Descriptions of all non-vegetation soil cover classes (SCCs), metrics of soil heterogeneity (i.e., SCR, SCD), and other plot characteristics.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil cover classes (SCCs)</td>
<td></td>
</tr>
<tr>
<td>Bare cover (%)</td>
<td>Soil without biocrust organisms present*, without physical crust present</td>
</tr>
<tr>
<td>Physical crust cover (%)</td>
<td>Aggregated soils lacking cyanobacterial filaments*</td>
</tr>
<tr>
<td>Dark biocrust cover (%)</td>
<td>Biocrusts dominated by cyanobacteria, mosses, and lichens – dark in coloration</td>
</tr>
<tr>
<td>Light biocrust cover (%)</td>
<td>Biocrust dominated by cyanobacteria* – light in coloration</td>
</tr>
<tr>
<td>Non-photosynthetic vegetation (NPV) cover (%)</td>
<td>Non-photosynthetic vegetation on the soil surface (e.g., litter, duff, and wood)</td>
</tr>
<tr>
<td>Rock cover (%)</td>
<td>Rock or gravel</td>
</tr>
<tr>
<td>Soil heterogeneity metrics</td>
<td></td>
</tr>
<tr>
<td>Soil cover richness (SCR)</td>
<td>Number of soil cover classes present within spatial extent</td>
</tr>
<tr>
<td>Soil cover diversity (SCD)</td>
<td>Shannon diversity (H) of soil cover classes present within spatial extent</td>
</tr>
<tr>
<td>Other plot characteristics</td>
<td></td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>Depth of soil taken outside top right corner of subplot (cm)</td>
</tr>
<tr>
<td>Plot altitude (m)</td>
<td>Mean plot altitude (m)</td>
</tr>
<tr>
<td>Grazing level</td>
<td>Plot grazing level (i.e., low, medium, high)</td>
</tr>
</tbody>
</table>

Notes: Cover of soil classes determined using quadrat sampling methods in 0.5-m² soil plots. * Whether ground cover was classified as “Bare Soil,” “Physical crust,” or “Light biocrust” was determined by taking a small sample of soil adjacent to the sampling quadrat. Soils that fell apart immediately with no visible cyanobacterial filaments were labelled “Bare Soil,” soils that stuck together, but without visible present cyanobacterial filaments present were labelled “Physical crust,” and soils that stuck together, with visible cyanobacterial filaments present (but without dark pigmentation or accompanying mosses and/or lichens) were labelled “Light Biocrust.”
by examining cross-correlations (Pearson correlation coefficients, $r$) between variables using the *Hmisc* package in R (Harrell, 2019). When the correlation coefficient between two predictor variables was strong (greater than or equal to $|r| \geq 0.65$; Taylor 1990), one of them was discarded for subsequent analyses. After testing variables for normality, heteroscedasticity, and multicollinearity, we used boosted regression tree (BRT) analysis with forward stepwise multiple regression to identify and eliminate non-significant predictor variables from best models using the ‘gbm.step’ function in the *gbm* (Ridgeway, 2013) and *dismo* packages in R (Hijmans et al., 2017) as in Elith & Leathwick (2017).

5.3.4.2. Generation of predictive models for plant species richness and Shannon diversity

Following the selection of key factors to be retained in each of the five plant variable response models via correlation and BRT analyses, we used generalized linear mixed models (GLMMs) to generate predictive models for plant richness and Shannon diversity at the plot level using the ‘glmer’ function in the *lme4* package in R (Bates et al., 2008). Akaike’s Information Criterion adjusted for small sample size ($AIC_c$; Burnham & Anderson, 2002) was used to select the best models from a set of GLMMs developed for plant species richness and Shannon diversity. Data distributions that were strongly skewed were transformed prior to analysis (e.g., log$_{10}$ transformations were performed on plant species richness). We used the ‘r.squaredGLMM’ function in the *MuMIn* package in R (Bartoń, 2018) to calculate marginal and conditional $R^2$ values associated with fixed and random effects in best models. For variables that were found to be significant in best GLMMs, we used univariate regression to explore relationships between independent predictor variables (e.g., biocrust cover, SCD).
and plant response variables (i.e., species richness). Alpha = 0.05 was used to determine significance level in all cases.

5.3.4.3. Possible mechanisms driving plant richness and Shannon diversity responses

To examine possible mechanisms that prompted greater species richness and/or Shannon diversity in patches with higher soil cover heterogeneity (SCD) and levels of biocrust cover, we tested whether species sorting and among patches with low, medium, and high SCD and biocrust cover could explain differences in plot species richness and Shannon diversity (SCD: low = 0.66-0.95, medium = 0.97-1.26, high = 1.27-1.58; biocrust cover: low = 0-33%, medium = 34-66%, high = 67-100%). To identify which plant species were associated with important metrics of soil cover (e.g., biocrust cover, bare soil) and soil cover heterogeneity (SCD) (species sorting), we used indicator value (IndVal) analysis (Dufrêne & Legendre, 1997; McCune, Grace, & Urban 2002) using the ‘multipatt’ function in the *indicspecies* package in R (De Caceres, Jensen, & De Caceres (2016) to test for species affinities for *a priori* defined groups. Species were identified as being sorted when a significant indicator value among soil predictor levels was detected ($P < 0.10$) based on 999 randomizations. Then, we used the ‘beta.multi’ function in the *betapart* package in R (Baselga et al., 2018) to calculate overall species turnover (Simpson's index for dissimilarity) and spatial turnover (Sørensen index for dissimilarity) for SCD patch types (Baselga, 2010). Finally, to examine the relative dominance of niche versus neutral processes in driving plant community richness and Shannon diversity in patches with different levels of soil heterogeneity (Doncaster, 2009), we also tested the strength of density-richness relationships among patches within low, medium, and high SCD.
5.3.4.4. Plant community composition responses to soil cover and soil cover heterogeneity

We explored relationships between soil cover and heterogeneity and plant community composition using a multivariate approach. We used nonparametric permutational multivariate analysis of variance (PERMANOVA) and distance-based tests of homogeneity for multivariate dispersion (PERMDISP) (Anderson 2001, 2006) based on Bray-Curtis dissimilarity matrices to test for differences in group centroids and dispersions (measures of central tendency and variance in multivariate space) at the subplot and plot levels using the ‘adonis’ and ‘betadisper’ functions respectively in the vegan package in R (Oksaken et al., 2018). In sagebrush plots, in addition to testing for the effects of soil cover and heterogeneity, we also tested for potential effects of grazing level on plant community composition. To visualize community patterns in species composition and abundance, we conducted ordinations of relativized plant species abundance data using non-metric multidimensional scaling (NMDS; McCune & Grace 2002) using the ‘metaMDS’ function in the vegan package. All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018).

5.4. Results

5.4.1. Sagebrush and pinyon-juniper plot characteristics: groundcover, grazing, and climate

Herbaceous plant cover was 24.0 % higher in sagebrush versus pinyon-juniper plots, although plant species richness and Shannon diversity index did not vary significantly between plot types (Table A5.2). Soil cover characteristics differed between the two plot types. Overall, sagebrush plots had higher bare soil (+ 4.6 %) and physical crust (+ 6.0 %)
cover, but lower cover of light biocrust (- 9.3 %) and dark biocrust (- 22.7 %) compared to pinyon-juniper plots (Table A5.2). However, soil cover richness (SCR) and soil cover diversity (SCD) did not vary significantly between plot types (Table A5.2). Importantly, there was a substantial drought during the 2018 growing season. Precipitation in the 12 months leading up to our field survey in June 2018 was 58.9% lower than long-term averages (Fig. A5.1) and mean temperature was 1.4 °C higher (+ 11.2%) than long-term averages during this time period (Fig. A5.1). Based on our ocular estimations, grazing level was variable in sagebrush plots ranging from low to high, but was consistently low and/or absent in pinyon-juniper plots likely due to rough surrounding terrain, which presumably made these plots less accessible to cattle.

5.4.2. Relationships between measures of soil cover and heterogeneity and plant diversity metrics

Measures of soil cover and soil cover heterogeneity (e.g., percent cover of SCCs, SCD) were significantly correlated with ecological site type (Table A5.3a). Accordingly, we made the decision to analyze sagebrush and pinyon-juniper plots separately in all subsequent analyses. In sagebrush plots, both plant species richness and plant Shannon diversity were positively correlated with soil heterogeneity (SCD; plant richness, r = 0.42, P = 0.008; plant Shannon diversity, r = 0.40, P = 0.011; Figs. 5.2-5.3, Table A5.3b), and soil depth (plant richness, r = 0.53, P = 0.005; plant Shannon diversity, r = 0.49, P = 0.002; Figs 2-3, Table A3b). Plant Shannon diversity was also positively correlated with dark biocrust cover (r =
In pinyon-juniper plots, plant species richness and Shannon diversity were positively correlated with dark biocrust cover (plant richness, $r = 0.35$, $P = 0.028$; plant Shannon diversity, $r = 0.44$, $P = 0.005$; Figs 5.2-5.3, Table A5.3c) but negatively correlated with physical crust cover (plant richness, $r = -0.33$, $P = 0.011$; plant Shannon diversity, $r = -0.53$, $P = 0.039$; Table A5.3c). Plant richness was also negatively correlated with mean site elevation (m) in pinyon-juniper plots ($r = -0.35$, $P = 0.025$; Fig. 5.2; Table A5.3c).

5.4.3. Boosted regression tree (BRT) data exploration

In sagebrush plots, the candidate variables with the most explanatory power in predicting plant species richness were soil depth, dark biocrust cover, and physical crust cover explaining 24.0 %, 22.7 %, and 17.7 % of variation respectively (Fig. A5.2). In pinyon-juniper plots, plant richness was most
explained by dark and light biocrust cover, which explained 49.0 % and 20.5 % of variation in plant richness respectively (Fig. S2). Plant Shannon diversity in sagebrush plots was most strongly predicted by physical crust cover, soil depth, dark biocrust cover, and soil heterogeneity which explained 25.1 %, 23.4 %, 16.5 %, and 11.6 % of variation respectively (Fig. A5.2). In pinyon-juniper plots, dark and light biocrust cover had the greatest explanatory power, explaining 63.3 % and 14.0 % of variation in plant Shannon diversity respectively (Fig. A5.2). Significant variables identified in BRT models were used to inform GLMM model selection.

5.4.4. Predictive models of herbaceous plant species richness and Shannon diversity

Predictive models (GLMMs) of plant species richness and Shannon diversity were developed separately for the two ecological site types (i.e., sagebrush, pinyon-juniper). In sagebrush plots, the amount of variation explained by the best models (based on AICc) was 48.1 % and 67.4 % for plant richness and Shannon diversity models respectively, whereas in pinyon-juniper plots, models explained only 19.2 % and 22.5 % of variation in plant richness and Shannon diversity respectively (Table 5.2). In sagebrush plots, plant species richness and Shannon diversity models included soil cover heterogeneity (SCD), dark biocrust cover, and soil depth. Univariate regression on significant variables in best GLMMs revealed that in sagebrush plots, plant species richness and Shannon diversity increased with increasing soil cover heterogeneity (SCD; richness, $t = 2.47, P = 0.018$; Shannon diversity, $t = 2.68, P = 0.010$; Table A5.4), dark biocrust cover (richness, $t = 2.56, P = 0.014$; Shannon diversity, $t = 2.01, P = 0.052$; Table A5.4), and soil depth (richness, $t = 3.44, P = 0.001$; Shannon diversity, $t = 3.43$,...
Table 5.2. *Predictive models for plant richness and Shannon diversity index.* GLMM and Wald Type II ChiSquare analysis of deviance test results – significance in fixed effects; for full model Plot and Vegetation type included as random nested effects (1|Plot_ID/Ecological_Site_Type). Species richness (S) models = Poisson, Shannon diversity (H) models = Gaussian. Full model and Sagebrush model also include random effect for grazing level (1|Grazing).

<table>
<thead>
<tr>
<th>Plant response</th>
<th>Predictor</th>
<th>Est</th>
<th>SE</th>
<th>t-value</th>
<th>R²m</th>
<th>R²c</th>
<th>df</th>
<th>X²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model</td>
<td>Dark biocrust cover (%)</td>
<td>0.030</td>
<td>0.009</td>
<td>3.535</td>
<td>0.28</td>
<td>0.45</td>
<td>1</td>
<td>12.494</td>
<td>&lt; 0.001 ***</td>
</tr>
<tr>
<td></td>
<td>Soil heterogeneity (SCD)</td>
<td>-3.973</td>
<td>1.890</td>
<td>-2.102</td>
<td></td>
<td></td>
<td>1</td>
<td>9.195</td>
<td>0.002 **</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.022</td>
<td>0.005</td>
<td>4.046</td>
<td>0.29</td>
<td>0.45</td>
<td>1</td>
<td>16.371</td>
<td>&lt; 0.001 ***</td>
</tr>
<tr>
<td></td>
<td>Soil heterogeneity (SCD)</td>
<td>-2.751</td>
<td>1.246</td>
<td>-2.208</td>
<td></td>
<td></td>
<td>1</td>
<td>4.375</td>
<td>0.036 *</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.022</td>
<td>0.005</td>
<td>4.046</td>
<td>0.29</td>
<td>0.45</td>
<td>1</td>
<td>16.371</td>
<td>&lt; 0.001 ***</td>
</tr>
<tr>
<td></td>
<td>Light biocrust cover (%)</td>
<td>0.025</td>
<td>0.013</td>
<td>1.907</td>
<td></td>
<td></td>
<td>1</td>
<td>3.636</td>
<td>0.057.</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.021</td>
<td>0.008</td>
<td>2.554</td>
<td>0.19</td>
<td>0.19</td>
<td>1</td>
<td>6.523</td>
<td>0.011 *</td>
</tr>
<tr>
<td></td>
<td>Light biocrust cover (%)</td>
<td>0.020</td>
<td>0.006</td>
<td>3.148</td>
<td>0.22</td>
<td>0.22</td>
<td>1</td>
<td>9.912</td>
<td>0.002 **</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.013</td>
<td>0.010</td>
<td>1.290</td>
<td></td>
<td></td>
<td>1</td>
<td>1.665</td>
<td>0.197</td>
</tr>
</tbody>
</table>
Figure 5.3. Soil cover-plant diversity relationships. Relationships between herbaceous plant species richness (a-c) and plant Shannon diversity (d-e) and soil predictor variables in GLMMs (i.e., SCD, dark biocrust cover (%), and soil depth) in best models of plant richness and Shannon diversity in sagebrush and pinyon-juniper plots. Plant species richness data were log transformed. Relationships were significant at alpha < 0.05; $r$ is the correlation coefficient; NS indicates nonsignificant (alpha > 0.05).
In pinyon-juniper plots, best predictive models for plant richness and Shannon diversity included dark biocrust cover and light biocrust cover (Table 2). Univariate regression revealed that in pinyon-juniper plots, plant species richness and Shannon diversity increased with increasing dark biocrust cover (richness, \( t = 1.902, P = 0.065 \); Shannon diversity, \( t = 3.00, P = 0.005 \); Table A5.4). Light biocrust cover was also moderately associated species richness (\( t = 1.71, P = 0.095 \)), but not Shannon diversity (\( P > 0.05 \); Table A5.4).

5.4.5. Species sorting, spatial turnover, and density-richness relationships

Indicator Species Analysis (ISA) identified a substantial number of plant species as being significantly associated with different soil patch types with respect to soil cover heterogeneity (i.e. species sorting; Fig. 5.4; Table A5.5). In sagebrush plots, cactus *Schlerocactus whipplei*, and perennial grasses *Elymus elymoides* and *Achnatherum hymenoides* experienced greater abundance in high SCD patches relative to other patch types (Fig. 5.4; Table A5.5). In pinyon-juniper plots, an unknown annual *Asteraceae* species showed an affinity for low SCD patches and *A. hymenoides* had greater abundance in medium SCD patches (Fig. 5.4; Table A5.5). We also identified six species as sorting with respect to levels of patch biocrust cover. Relative to other patch types, in sagebrush plots, *Plantago patagonia* and *Calochortus nuttallii* were associated with high biocrust patches, while the invasive annual grass *Bromus tectorum* was associated with low biocrust patches (Fig. 5.4; Table A5.5). In pinyon-juniper plots, *Tetraneuris acaulis* var. *acaulis* and *C. nuttallii* showed affinity for high biocrust patches whereas *A. purpurea* was associated with low biocrust
patches (Fig. 5.4; Table A5.5). While we found evidence of species sorting by SCD levels and biocrust cover, analysis of species turnover indicated that communities in patches with high

**Figure 5.4.** *Indicator species analysis: species sorting by biocrust cover and soil cover heterogeneity.* Significant results for indicator species analysis (ISA) by level of soil cover heterogeneity (SCD; a-b) and biocrust cover (c-d) in sagebrush and pinyon-juniper plots at alpha < 0.10. Cactus *Schlerocactus whipplei,* and perennial grasses *Elymus elymoides* and *Achnatherum hymenoides* were associated with areas with high SCD in sagebrush plots (a). In Pinyon-juniper plots, an unknown annual *Asteracea* spp. was associated with areas with low SCD, while *A. hymenoides* was associated with areas of medium SCD (b). Annual forb *P. patagonica* was associated with areas with high biocrust cover in Sagebrush plots (c), while perennial forb *T. acaulis* ssp. *acaulis* was associated areas with high biocrust cover in pinyon-juniper plots (d). Perennial forb *C. nattalii* showed an affinity for areas with high biocrust cover in both sagebrush and pinyon-juniper plots (c-d). Annual grass *B. tectorum* and perennial grass *A. purpurea* showed affinities for areas with low biocrust cover in sagebrush and pinyon-juniper plots respectively. No species were found to be significantly sorting in medium biocrust cover plots.
SCD (heterogeneous) did not differ significantly in their spatial turnover compared to medium or low SCD (homogeneous) patches (all $P > 0.05$, Table A5.6).

We also tested for relationships between biocrust cover and the cover of different plant functional types. Overall, while total plant cover was negatively associated with biocrust cover overall ($r = -0.57; P < 0.001$; Figs 5.2-5.3), this relationship was not consistent across plant functional types. Annual and perennial grass cover decreased with increasing
biocrust cover ($P = 0.001$ and $P < 0.001$; Fig. 5.5a-b). Notably, the annual grass category was almost entirely comprised of the invasive exotic grass species *B. tectorum*, suggesting biocrusts are negatively associated with *B. tectorum* cover. In contrast, we found a small but significant increase in annual forb cover with increasing biocrust cover ($P = 0.034$; Fig. 5.5c). Additionally, perennial forb cover was marginally higher with increasing biocrust cover in pinyon-juniper plots ($P = 0.080$; Fig. 5.5d).

Finally, to examine the relative importance of neutral-based processes driving plant community diversity responses to soil cover heterogeneity, we tested the strength of density-richness relationships among patches with low, medium, and high soil cover.

**Figure 5.6.** *Species accumulation curves and rarefaction by soil heterogeneity.* Species accumulation and rarefaction curves for communities in patches with low, medium, and high soil heterogeneity (SCD). Lines in rarefaction plots (a-c) represent sample-based Coleman rarefaction curves for the sample data set +/- 1 SD over standard density. Boxplots (d-f) represent the species accumulation curves for low, medium, and high SCD respectively. Pink background lines represent lines for Arrhenius models.
heterogeneity (SCD). Overall, density-richness relationships were relatively weak (Fig. A5.3). In sagebrush plots, the density-richness relationship was marginally positive in patches with low heterogeneity (SCD; $R^2 = 0.52; P = 0.067$; Fig. A5.3) but was not significant in medium or high SCD patches (medium, $R^2 = 0.01, P = 0.850$; high, $R^2 = 0.18, P = 0.152$; Fig. A5.3). In pinyon-juniper plots, there were no significant density-richness relationships among SCD patch types (all $P > 0.05$; Fig. A5.3).

### Table 5.3. Herbaceous plant community composition

Results for PERMANOVA analysis of Bray-Curtis dissimilarities for herbaceous plant community structure in sagebrush and pinyon-juniper plots in relation to total biocrust cover (%), soil heterogeneity (SCD), grazing level (sagebrush), and their interactions.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>pseudo-$F$</th>
<th>$R^2$</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sagebrush</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total biocrust cover (%)</td>
<td>1</td>
<td>0.416</td>
<td>0.416</td>
<td>2.240</td>
<td>0.052</td>
<td>0.058</td>
</tr>
<tr>
<td>Soil heterogeneity (SCD)</td>
<td>1</td>
<td>0.334</td>
<td>0.334</td>
<td>1.797</td>
<td>0.042</td>
<td>0.119</td>
</tr>
<tr>
<td>Grazing</td>
<td>1</td>
<td>0.676</td>
<td>0.085</td>
<td>0.459</td>
<td>0.011</td>
<td>0.792</td>
</tr>
<tr>
<td>Total biocrust cover (%) x SCD</td>
<td>1</td>
<td>0.139</td>
<td>0.384</td>
<td>2.064</td>
<td>0.048</td>
<td>0.084</td>
</tr>
<tr>
<td>Total biocrust cover (%) x Grazing</td>
<td>2</td>
<td>0.863</td>
<td>0.384</td>
<td>1.955</td>
<td>0.046</td>
<td>0.094</td>
</tr>
<tr>
<td>SCD x Grazing</td>
<td>2</td>
<td>0.515</td>
<td>0.250</td>
<td>1.343</td>
<td>0.031</td>
<td>0.248</td>
</tr>
<tr>
<td>Total biocrust x SCD x Grazing</td>
<td>2</td>
<td>0.126</td>
<td>0.183</td>
<td>0.983</td>
<td>0.023</td>
<td>0.423</td>
</tr>
<tr>
<td>Residuals</td>
<td>64</td>
<td>10.595</td>
<td>0.186</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td>15.223</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pinyon-juniper</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total biocrust (%)</td>
<td>1</td>
<td>1.317</td>
<td>1.317</td>
<td>2.240</td>
<td>0.123</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Soil heterogeneity (SCD)</td>
<td>1</td>
<td>0.268</td>
<td>0.267</td>
<td>1.797</td>
<td>0.025</td>
<td>0.350</td>
</tr>
<tr>
<td>Residuals</td>
<td>64</td>
<td>9.080</td>
<td>0.245</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td>10.664</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-$F$ = $F$ value by permutation. Bold face indicates statistical significance ($P < 0.05$); $P$-values are based on 9999 permutations (i.e., the lowest possible $P$-value is 0.0001). Significance codes: $< 0.001$ ’****’, $< 0.01$ ‘**’, $< 0.05$ ‘*’, $< 0.1$ ‘.’

5.4.6. *Herbaceous plant community composition*
Because plant community composition is expected to depend on multiple interrelated variables, we used multivariate analyses to test differences in plant community composition among patches types with varying cover of SCCs and soil cover heterogeneity (SCD). PERMANOVA results for each of the two ecological sites types showed that only patch total biocrust cover (%) had a significant effect on plant community composition in both sagebrush and pinyon-juniper plots (Table 5.3, Fig. A5.5). PERMDISP analysis indicated homogeneous dispersion of the total biocrust cover variable in both ecological site types (Table A5.7). Importantly, we explicitly tested for differences in plant community composition among sagebrush plots with different levels of grazing level and found no differences in community composition among grazing levels (Fig. A5.6).

5.5. Discussion

Results from our study suggest that soil spatial heterogeneity mediated by biocrusts may be associated with increased local plant diversity in cool desert ecosystem. Overall, we found that biocrust cover was an important predictor of plant species richness and Shannon diversity in both sagebrush and pinyon-juniper plots, and these metrics of plant alpha diversity were highest in patches with the greatest soil cover heterogeneity (Fig. 5.3), though only in sagebrush plots.

One possible reason explaining this observed increase in local plant alpha diversity with increasing soil cover heterogeneity observed in sagebrush plots might be differences in total plant density among patches. Community theory predicts a strong relationship between
plant species richness and plant density often suggests neutral-type assembly processes (a sampling effect) where stochastic colonization and extinction generate richness patterns that are largely dependent on total plant density (Hubbell, 2001, 2005). However, we found no strong differences between density-richness relationships among patches with different levels of soil cover heterogeneity (Fig. A5.3), and species rarefaction curves suggest that high soil cover diversity (heterogeneous) patches accumulate more species over standardized densities than patches with medium or low heterogeneity (Fig. 5.6). These results were not unexpected given past evidence suggests neutral processes tend to dominate in more benign environments with low abiotic stress, whereas niche processes prevail in determining community assembly and species distribution in harsher environments like drylands (Inouye & Tilman 1995; Chase, 2003, 2007; Trexler, Loftus, & Perry, 2005).

Given there was little evidence of density-dependent drivers of plant alpha diversity among SCD patch types, a second possibility is that species richness increases in more heterogeneous patches as a result of differential species sorting among soil patch types (species sorting; Hutchinson 1957, 1959; Chase & Leibold, 2003) which can generate differences in spatial turnover among patch types. While we found no significant differences in species turnover among SCD patch types (Table A5.6), we did find a substantial number of plant species (24 of 46 total species) experienced species sorting into patches with different levels of soil heterogeneity (Fig. 5.4; Table A5.5). In sagebrush plots, 3 plant species were significantly associated with high SCD patches whereas no species were sorting in low SCD patches (Fig. 5.4; Table A5.5). This result, along with observed increases in local plant diversity in patches with higher soil cover heterogeneity, aligns with theoretical predictions that environmental heterogeneity can increase plant diversity by decreasing species niche
overlap and providing opportunities for the colonization of species with diverse resource requirements (e.g., Chesson, 2000; Tilman, 1986).

Results from our study also suggest biocrust individually contributed to determining observed plant diversity patterns. Total biocrust cover was positively associated with plant richness in both sagebrush and pinyon-juniper plots (Fig. 5.3). This result agrees with past studies that have shown positive correlations between biocrust cover and plant diversity (Ghiloufi & Chaieb, 2017; Jeffries, Douglas, Klopatek, 1987; Kleiner & Harper, 1977; Luzuriaga et al., 2012; Scott & Morgan, 2012). One potential explanation for this pattern is that biocrusts may promote plant species diversity by increasing overall soil resource availability to plants. In drylands, moderate resource availability tends to favor facilitative plant-plant interactions over competition (Maestre et al., 2009) whereas increases or decreases in overall resource availability are predicted to promote increased competitive plant-plant interaction outcomes (McCluney et al., 2012). As such, we might expect that increased soil fertility or soil moisture by biocrusts would increase plant-plant competition which could lead to competitive exclusion and reduced plant species richness (Grime, 1973).

A second possibility is that biocrusts may support increased plant diversity by generating spatial heterogeneity in soil stability, moisture, and fertility (Concostrina-Zubiri et al., 2013) and thereby increasing available soil niche space for plants. Species sorting into patches with high and low biocrust cover (Fig. 5.4, Table A5.5) supports this assumption and suggests plant species may differ in fitness in patches with differing levels of biocrust cover. That perennial forb species C. nuttallii (sego lily) consistently showed greater abundance in high biocrust patches in both ecological site types may suggest that certain plant species have consistent affinities for patches containing biocrusts (Fig. 5.4; Table A5.5). Our results
also suggest that such relationships may translate to cover patterns at the plant functional group level. That we found small but significant increases in annual forb cover with increasing biocrust cover overall and increased perennial forb cover in high biocrust patches in pinyon-juniper plots (Fig. 5.5) could suggest that biocrusts may offer more favorable niches for forb over grass species.

A majority of past work investigating soil heterogeneity-plant diversity relationships has been conducted under highly controlled experimental conditions (Reynolds et al., 2007; Stevens & Carson, 2002; Vivian-Smith, 1997; Wijesinghe, John, & Hutchins, 2005; Williams & Houseman, 2014), presumably because in natural systems, there are few regions where naturally-occurring heterogeneity can be measured in the absence of potentially confounding factors like natural abiotic and/or disturbance gradients. Similarly, in our study, there were several important environmental factors that may have contributed to the observed patterns in local plant alpha diversity across gradients of biocrust cover and soil cover heterogeneity.

First, seasonal cattle grazing is present on the landscape in this study system. In drylands, increased grazing level often leads to decreased plant species richness (Hanke et al., 2014; Herrero-Juregui & Oesterheld, 2018; Milchunas, Sala, & Lauenroth, 2002) and biocrust cover and diversity as a result of physical disturbance via trampling (reviewed in Zaady et al., 2016). As such, we might have predicted that we would consistently find the highest plant richness in undisturbed areas with the greatest intact biocrust cover (e.g., in low-grazing sagebrush plots and ungrazed pinyon-juniper plots). However, we found overall plant species richness was similar in sagebrush and pinyon-juniper plots (Table A5.2), and in sagebrush sites, grazing level was not significantly correlated with plant species richness
or Shannon diversity (Fig. 5.2), and further overall plant community composition did not explicitly vary by grazing level (Fig. A5.6).

Indeed, grazing may have contributed to increased soil cover heterogeneity in sagebrush sites by fragmenting dark biocrust patches and creating diverse mosaics of patches with different biocrust successional levels and bare soil. Empirical evidence suggests small-scale disturbances can increase soil heterogeneity and species coexistence (Questad & Foster, 2008). Past field work on soil heterogeneity-plant diversity relationships has often involved field manipulations that employ patchy disturbance treatments to create heterogeneous soil conditions in comparison to undisturbed conditions (Questad & Foster, 2008; Wilson & Tilman, 2002). In this study, cattle grazing may have contributed to observed differences in soil cover heterogeneity in sagebrush plots that was associated with increased local plant diversity. However, as Concostrina-Zubiri and colleagues (2013) showed grazing negatively impacts biocrust-mediated soil heterogeneity when grazing level is high, it is likely that overgrazing might diminish these effects as predicted by the intermediate disturbance hypothesis (Grime, 1973).

There were several abiotic environmental factors that may have also contributed to observed differences in plant species richness among patch types. Soil depth differed among patches in sagebrush and pinyon-juniper plots and was positively associated with plant species richness in sagebrush plots (Fig. 5.3). This result agrees with past studies that show positive associations between plant species richness with increasing soil depth (e.g., Dornbush & Wilsey, 2010). As plant diversity was positively associated with both SCD and soil depth (Fig. 5.3), we are unable to parse apart the individual effects of soil heterogeneity and soil depth. However, best predictive models (GLMMs) for plant diversity metrics
included soil cover diversity (Table 5.2), biocrust cover, and soil depth, suggesting a significant amount of variation was explained by each factor individually. Nonetheless, to explicitly disentangle the effects of biocrust-mediated soil cover heterogeneity, soil depth, and grazing on local plant diversity, future studies should attempt to quantify these effects in the absence of differences in soil depth and grazing in situ.

In addition, we conducted our study in a single growing season which was marked by a significant drought (Fig. A5.1). Drought acts as a primary abiotic filter on annual plant community assembly in drylands (Luzuriaga et al., 2012) and can strengthen the dominance niche-type processes in determining plant community assembly (e.g., Chase, 2007). As such, future research should explore whether biocrust-plant diversity patterns (particularly in the annual plant community) shift depending interannual variability in precipitation and/or temperature or across time. Finally, given that environmental heterogeneity-species diversity relationships can be highly scale-dependent (e.g., Freestone & Inouye 2006), future work should also evaluate whether biocrust-soil heterogeneity-plant species richness patterns hold across multiple spatial scales.

Results from this study offer provisional support for the hypothesis that biocrusts may play a role in supporting local plant diversity by increasing soil cover heterogeneity and thereby niche space for plant taxa with diverse resource requirements. In the next several decades, biocrusts are expected to experience significant declines and compositional shifts worldwide in response to global change (Ferrenberg et al., 2015; Reed et al., 2012; Rodriguez-Caballero et al., 2018). Consequentially, drylands may experience increased soil habitat homogenization. Increasing our understanding of how biocrusts, by contributing to
soil heterogeneity, may drive plant community diversity and structure thus has important implications for predicting how drylands will respond to global change.

5.6. Acknowledgements

This work was made possible by the support of scientists and staff at the U.S. Geological Survey Southwest Biological Science Center in Moab, Utah who provided intellectual feedback, assistance with site selection for this project. We would also like to thank Cloe Dickson for her assistance with ground data collection in the field, and Rachael Merkt, Lindsey Foust, Christopher Manning, and Adam Berger for their assistance in the lab with data entry and organization. Undergraduate research assistants who contributed to this work in the field and lab were generously supported by University of Colorado Research Opportunities Program (UROP) and Biological Sciences Initiative (BSI) research grants. CAH was supported by a National Science Foundation (NSF) Graduate Research Fellowship (Grant DGE 1144083), an NSF Graduate Research Internship Program grant, and a University of Colorado Boulder Department of Ecology and Evolutionary Biology Maxy Pope Award. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
CHAPTER 6

Conclusions

The primary goal of my dissertation was to advance current understanding of biocrust-plant interactions by generating a better understanding of the general effects and underlying mechanisms of biocrusts on vascular plant species, identifying what plant, biocrust, and environmental characteristics are important for predicting plant responses to biocrusts, and testing whether these relationships generate patterns in plant community diversity and structure in situ. In chapter 2, I examined the effects of biocrusts on the recruitment of two native and one exotic grass species from the hot, Chihuahuan Desert to evaluate whether biocrusts differentially mediate native versus exotic species performance. In chapter 3, I tested whether differences in root-associated fungal colonization among plant species mediates plant species-specificity in biocrust facilitation of plant growth and nutrition. In chapter 4, using meta-analysis, I evaluated global trends in existing biocrust-plant interactions literature to determine the overall effects of biocrusts on plant emergence, survival, growth, and groundcover and quantified the relative importance of biocrust, plant, and environmental factors in determining the magnitude and direction of these effects. Finally, in chapter 5, I examined larger scale relationships between biocrust spatial heterogeneity and local plant diversity and evaluated whether niche- versus neutral-type processes likely contributed to these observed patterns.

In chapter 2, I tested two hypotheses to compare the recruitment responses of native versus invasive exotic grass species to biocrusts. Past work has suggested that biocrusts are often inhibit the recruitment of invasive exotic plant species, particularly invasive annual
grasses, but promote the recruitment of native plant species, potentially as a result of past coevolutionary relationships between native plant and biocrust communities (Stohlgren et al., 2001). However, most past work has focused on quantifying these effects in *Bromus tectorum* in cool deserts of western North America. To test whether biocrusts may promote biotic resistance to invasive species in other systems, in chapter 2, I conducted a full-factorial greenhouse experiment to quantify the recruitment responses two native bunchgrasses (*Aristida purpurea* and *Bouteloua eriopoda*) and exotic bunchgrass *Eragrostis lehmanniana* (Lehman lovegrass) to biocrusts from the hot, Chihuahuan Desert ecoregion. I hypothesized that *intact biocrusts* offer favorable microhabitats for increased performance of native vascular grass species but decrease performance and recruitment of exotic species. In partial support of this hypothesis, I found that while biocrusts promoted *E. lehmanniana* emergence over that of the two natives, conversely, native species survival and growth responded more positively to biocrusts than the exotic. Secondly, I also hypothesized that *biocrust removal* increases the recruitment of *E. lehmanniana* by eliminating potential barriers posed by biocrusts to exotic plant recruitment. I found that biocrust removal increased *E. lehmanniana* recruitment but had mixed effects on the two natives. These results indicate the potential importance of biocrusts and biocrust disturbance in shaping plant community structure and suggest possible contributions of biocrusts to the biotic resistance of dryland plant communities.

In general, perhaps one of the greatest remaining uncertainties in our understanding of biocrust-plant interactions is why some plant species respond positively to biocrusts while others respond neutrally or negatively (Zhang et al., 2016; Havrilla et al. *Under Review*). Biocrusts have often been shown to have facilitative, but species-specific effects on plant
growth (see for example, results of chapter 4 of this dissertation), yet the mechanisms underlying this species-specificity, and more generally, how biocrusts exchange resources with plants, has remained uncertain. In chapter 3, I conducted a greenhouse mesocosm experiment to investigate two primary research questions: (1) Is plant root associated fungal (RAF) colonization influenced by biocrust presence? and if so; (2) do differences in RAF colonization rates predict differences in plant growth and nutrition responses between soils with and without biocrusts? I hypothesized that because biocrusts are niches for free-living fungi including arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) (Maier et al., 2016), plant RAF colonization rates would be higher in plants grown in biocrust versus bare soil. Secondly, I hypothesized that biocrusts, by increasing soil fertility and/or moisture, promote plant species growth and nutrition (e.g., foliar N content), and that increased growth corresponds to higher colonization rates of RAF in plants grown in biocrust relative to bare soil. Instead, I found that RAF colonization rates were lower in plants grown in biocrusts versus bare soil. Lower RAF colonization in plants grown in biocrusts could result from greater C costs of maintaining relationships with symbiotic RAF exceed benefits to plants in soils containing biocrusts which presumably had greater availability of N (Barger et al., 2016; Ferrenberg et al., 2018) and soil organic matter (Li et al. 2012; Tucker, et al. 2017) relative to bare soil. Plants grown in biocrusts did, however, have greater biomass, height, and corresponding N content (% leaf N) compared to plants grown in bare soil, though these results were plant species-specific. Together, these results suggest that plant roots may have taken up biocrust-associated soil resources directly via root absorption rather than through fungal intermediaries.
In chapter 4, to address knowledge gaps concerning the general outcomes of drivers of plant responses to biocrusts, I compiled a global database of 1,004 existing, unique studies of biocrust-plant interactions encompassing and employed meta-analytical techniques to synthesize existing patterns in global data. Specifically, I tested the hypotheses that: (1) biocrust community composition mediates the direction and strength of plant responses to biocrusts; (2) biocrust effects on plants are not uniformly experienced by all plant types but vary depending on plant characteristics and functional traits; and (3) plant responses to biocrusts shift depending on abiotic environmental conditions (e.g., climate, soil disturbance). Meta-analyses revealed there is no simple positive or negative effect of biocrusts on plants. Rather, plant responses are driven by biocrust composition and plant species traits and vary across plant ontogeny. Moss-dominated biocrusts facilitated, while lichen-dominated biocrusts inhibited overall plant performance. Plant responses also varied among plant functional groups: C4 grass species received greater benefits from biocrusts compared to C3 grasses and plants without N-fixing symbionts responded more positively to biocrusts than plants with N-fixing symbionts. Biocrusts decreased germination but facilitated growth of non-native plant species. Importantly, these results suggest interspecific variation in plant responses to biocrusts, contingent on biocrust type, plant traits, and ontogeny, can have strong impacts on plant species performance, and may have important implications for understanding plant community assembly processes.

In chapter 5, I conducted an observational field study in a cool desert ecosystem in the Colorado Plateau ecoregion of southeastern Utah to investigate whether variability in plant responses to biocrusts generates observable patterns in local plant diversity and/or community structure under natural field conditions. While other studies have shown
positive correlations between biocrust presence and plant alpha diversity (Ghiloufi & Chaieb, 2017; Jeffries, Douglas L., Klopatek, 1987; Kleiner & Harper, 1977; Luzuriaga et al., 2012; Scott & Morgan, 2012), I was particularly interested in exploring how biocrust spatial heterogeneity might contribute to these patterns. I addressed two main research questions in chapter 5: First, does biocrust-associated soil cover heterogeneity increase local plant diversity and community composition; if so, are plant diversity responses to soil cover heterogeneity driven by niche-type (environmental species sorting; Hutchinson 1957, 1959) or neutral-type (density-dependent; Hubbell 2005) processes? I found that soil cover heterogeneity and biocrust cover were positively associated with local plant species richness and Shannon diversity. Additionally, I found that species sorting, rather than density-richness relationships explained differences in local plant diversity between different soil patch types. These results suggest biocrust-mediated soil heterogeneity may an important role in supporting dryland plant biodiversity and have important implications for understanding how dryland ecosystems will respond to habitat homogenization under global change.

Together, the research that comprised this dissertation contributes to knowledge of how biocrusts influence vascular plants at multiple scales – from individual plants to plant communities. I found that while plant species responses to biocrusts are variable (chapters 2, 3, 4), there are underlying patterns in these responses and that specific biocrust, plant, and environmental characteristics can be used to generate predictive frameworks of plant responses to biocrusts (chapter 4). Further, I demonstrate that variability in plant responses to biocrusts among plant species, functional types, and native versus exotic species may have the potential to influence plant community invasibility (chapter 2) and may generate broad-
scale plant diversity patterns in situ through fine-scale niche-based processes (i.e., small-scale environmental species sorting into patches with and without biocrusts; chapter 5). All four of my dissertation research chapters highlight the nuanced roles of biocrusts in driving variation in the ecology of plant species and adds to our current understanding of how soil biotic communities contribute to plant species performance and community structure (Bever et al., 2010; Hortal et al., 2017; Van Der Heijden et al., 2008).

This thesis contributes to the field of plant-soil interactions by addressing how plant responses to soil biotic communities differ in different environmental contexts and across plant species and functional types. My work demonstrates the importance of plant traits in determining these responses and highlights the importance of incorporating more detailed measures of variation in biocrust communities (e.g., functional composition, spatial heterogeneity) for generating more accurate predictive frameworks of biocrust contributions to plant productivity and community structure. In addition, this thesis also highlights a continued lack of clear mechanisms associated with the outcomes of biocrust-plant interactions highlights the complexity of these biotic interactions. Building a mechanistic framework of biocrust-plant interactions will be necessary to refine our predictive understanding of how plant species, population, and community respond to biocrusts, and the contributions of these interactions to the function and productivity of dryland ecosystems globally. Further, as biotic interactions play key roles in mediating the responses of populations, communities, and ecosystems to environmental change, understanding these important biotic interactions may be critical for predicting dryland responses to global change drivers.
REFERENCES CITED


Belnap, J., & Büdel, B. (2016). Biological soil crusts as soil stabilizers. In Biological soil
crusts: An organizing principle in drylands (pp. 305-320). Springer, Cham.


Plant and Soil, 429(1–2), 77–90. doi:10.1007/s11104-017-3525-1


Steven, B., Gallegos-Graves, L. V., Yeager, C., Belnap, J., & Kuske, C. R. (2014). Common and


## Appendix 1:
### Supplemental Materials for Chapter 2

<table>
<thead>
<tr>
<th>Study</th>
<th>Desert</th>
<th>Biocrust type</th>
<th>Plant species</th>
<th>Plant response</th>
<th>Net Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cool Deserts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>St. Clair et al. (1984)</td>
<td>Colorado Plateau</td>
<td>Mixed</td>
<td><em>Agropyron elongatum</em> (PG); <em>Psathyrostachys junceus</em> (PG)</td>
<td>Establishment</td>
<td>(+)</td>
</tr>
<tr>
<td>Eckert et al. (1986)</td>
<td>Great Basin</td>
<td>Mixed</td>
<td><em>Agropyron desertorum</em> (PG); <em>Bromus tectorum</em> (AG)</td>
<td>Emergence</td>
<td>(-)</td>
</tr>
<tr>
<td>Howell (1998)</td>
<td>Great Basin</td>
<td>Mixed</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Emergence; Growth</td>
<td>(-); (+)</td>
</tr>
<tr>
<td>Kaltenecker et al. (1999)</td>
<td>Great Basin</td>
<td>Mixed</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Emergence</td>
<td>(-)</td>
</tr>
<tr>
<td>Serpe et al. (2006)</td>
<td>Great Basin</td>
<td>Moss</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Emergence; (-)</td>
<td></td>
</tr>
<tr>
<td>Deines et al. (2007)</td>
<td>Great Basin</td>
<td>Lichen</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Emergence; Establishment</td>
<td>(-); (-)</td>
</tr>
<tr>
<td>Serpe et al. (2008)</td>
<td>Great Basin</td>
<td>Lichen or Mixed</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Root penetration</td>
<td>(+)</td>
</tr>
<tr>
<td>Reisner et al. (2013)</td>
<td>Great Basin</td>
<td>Mixed</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Establishment</td>
<td>(-)</td>
</tr>
<tr>
<td>Ferrenberg et al. (2017)</td>
<td>Colorado Plateau</td>
<td>Moss</td>
<td><em>Bromus tectorum</em> (AG)</td>
<td>Growth</td>
<td>(+)</td>
</tr>
<tr>
<td><strong>Mesic Environments</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hot Deserts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>McIlvaine (1942)</td>
<td>Sonoran</td>
<td>Moss</td>
<td><em>Eragrostis lehmanniana</em> (PG); <em>Panicum antidotale</em> (PG)</td>
<td>Emergence</td>
<td>(-)</td>
</tr>
<tr>
<td>DeFalco et al. (2001)</td>
<td>Mojave</td>
<td>Mixed</td>
<td><em>Bromus tectorum</em> (AG); <em>Bromus madritensis</em> spp. <em>rubens</em> (AG); <em>Schismus barbatus</em> (AG); <em>Erodium cicutarium</em> (AG) <em>Bromus madritensis</em> spp. <em>rubens</em> (AG), <em>Schismus spp.</em> (AG), <em>Brassica tournefortii</em> (AF)</td>
<td>Emergence; Shoot nutrient content</td>
<td>(+); (+)</td>
</tr>
<tr>
<td>DeCorte (2011)</td>
<td>Mojave</td>
<td>Mixed</td>
<td></td>
<td>Emergence</td>
<td>(-)</td>
</tr>
</tbody>
</table>
Table A2.1.  *Biocrust effects on non-native and/or invasive species literature.* Summary of results of prior studies investigating biocrust effects on non-native plant emergence, establishment, and growth in drylands of the United States. Biocrust types based on dominant functional type over of biocrust community (i.e., Lichen, Moss, Mixed [Lichen + Moss]). No study measured responses to cyanobacteria-dominated biocrusts. Abbreviations in the non-native plant study species column denote plant lifeform (i.e., AG = annual grass, PG = perennial grass, AF = annual forb). Net effects are characterized as negative (-) or positive (+) according to reported study results.
Figure A2.1. *Picture of soil collection site.* Photograph of the silty sample collection site at the Jornada Experimental Range near Las Cruces, New Mexico, USA in February 2015.
**Figure A2.2.** *Summary diagram of plant responses to intact biocrusts.* Summary diagram of effects of intact biocrust communities (cyanobacterial and lichen-dominated) on the recruitment (emergence, survival, growth, and overall performance) of *A. purpurea*, *B. eriopoda*, and *E. lehmanniana* seedlings compared to a bare soil control. Emergence and survival are expressed as proportions of seedlings while growth is expressed as the average amount of biomass in mg acquired per seedling during the growth period. Performance was calculated as the product of these three measurements. Green cells denote positive seedling recruitment responses to on intact biocrust compared to bare soil, whereas red cells denote negative responses.
Figure A2.3. Summary diagram of plant responses to biocrust removal. Summary diagram of effects of biocrust removal on the recruitment (emergence, survival, growth, and overall performance) of *A. purpurea*, *B. eriopoda*, and *E. lehmanniana* seedlings compared to intact biocrust controls. Emergence and survival are expressed as proportions of seedlings while growth is expressed as the average amount of biomass in mg acquired per seedling during the growth period. Performance was calculated as the product of these three measurements. Green cells denote positive seedling recruitment responses to biocrust removal compared to intact biocrust controls, whereas red cells denote negative responses.
Table A3.1. *Plant morphological and leaf chemistry responses to biocrust presence.* Means (± SE) of morphological and leaf chemical measures for plant species sown in mesocosms with bare soil vs. biocrust cover. The mesocosm cover-type *P*-value column is from one-way tests between cover types for each given plant response variable; *P*-values in bold type indicate measures that were considered to be statistically significant among cover types (*P* < 0.05) and *P*-values in italicized type indicate measures that were marginally statistically different (0.10 > *P* > 0.05) among cover types. Dashed lines in cells (“---”) denote no statistical test was performed for a given response due to insufficient data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Measure</th>
<th>Bare soil</th>
<th>Biocrust</th>
<th><em>P</em>-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All species</strong></td>
<td>Emergence (%)</td>
<td>51.67 ± 6.38</td>
<td>34.17 ± 5.70</td>
<td>0.051</td>
</tr>
<tr>
<td></td>
<td>Time to emergence (d)</td>
<td>13.68 ± 0.87</td>
<td>17.72 ± 1.33</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>Height (cm)</td>
<td>13.83 ± 0.55</td>
<td>16.24 ± 0.63</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Biomass (mg)</td>
<td>97.65 ± 12.96</td>
<td>183.95 ± 31.55</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Root:shoot ratio</td>
<td>0.87 ± 0.06</td>
<td>0.87 ± 0.07</td>
<td>0.926</td>
</tr>
<tr>
<td></td>
<td>Mean leaf C (%)</td>
<td>38.17 ± 0.94</td>
<td>41.64 ± 1.97</td>
<td>0.116</td>
</tr>
<tr>
<td></td>
<td>Mean leaf N (%)</td>
<td>1.35 ± 0.05</td>
<td>1.77 ± 0.18</td>
<td>0.031</td>
</tr>
<tr>
<td></td>
<td>C:N ratio</td>
<td>30.49 ± 1.46</td>
<td>27.22 ± 1.73</td>
<td>0.146</td>
</tr>
<tr>
<td></td>
<td>MIP</td>
<td>29.37 ± 2.00</td>
<td>24.14 ± 2.25</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>% AMF</td>
<td>28.24 ± 1.70</td>
<td>19.64 ± 2.06</td>
<td>0.096</td>
</tr>
<tr>
<td></td>
<td>% DSE</td>
<td>7.39 ± 1.05</td>
<td>4.51 ± 0.80</td>
<td>0.047</td>
</tr>
<tr>
<td><strong>Native species</strong></td>
<td>Emergence (%)</td>
<td>51.67 ± 6.38</td>
<td>34.17 ± 5.70</td>
<td>0.051</td>
</tr>
<tr>
<td><strong>E. elymoides</strong></td>
<td>Time to emergence (d)</td>
<td>13.68 ± 0.87</td>
<td>17.72 ± 1.33</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>Height (cm)</td>
<td>13.83 ± 0.55</td>
<td>16.24 ± 0.63</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Biomass (mg)</td>
<td>168.75 ± 17.15</td>
<td>215.67 ± 22.09</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
<td>Root:shoot ratio</td>
<td>1.42 ± 0.11</td>
<td>1.16 ± 0.16</td>
<td>0.067</td>
</tr>
<tr>
<td></td>
<td>Mean leaf C (%)</td>
<td>34.02 ± 0.22</td>
<td>34.55 ± 3.09</td>
<td>0.515</td>
</tr>
<tr>
<td></td>
<td>Mean leaf N (%)</td>
<td>1.30 ± 0.08</td>
<td>1.72 ± 0.15</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>C:N ratio</td>
<td>26.81 ± 1.35</td>
<td>19.62 ± 2.41</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>MIP</td>
<td>19.38 ± 2.28</td>
<td>12.44 ± 1.92</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td>% AMF</td>
<td>17.62 ± 1.94</td>
<td>10.89 ± 1.66</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>% DSE</td>
<td>1.76 ± 0.67</td>
<td>1.56 ± 0.71</td>
<td>0.876</td>
</tr>
<tr>
<td><strong>H. comata</strong></td>
<td>Emergence (%)</td>
<td>5.83 ± 1.49</td>
<td>7.50 ± 3.51</td>
<td>0.668</td>
</tr>
<tr>
<td></td>
<td>Time to emergence (d)</td>
<td>18.83 ± 3.36</td>
<td>22.86 ± 2.31</td>
<td>0.333</td>
</tr>
<tr>
<td></td>
<td>Height (cm)</td>
<td>11.17 ± 1.39</td>
<td>12.12 ± 2.68</td>
<td>0.747</td>
</tr>
<tr>
<td></td>
<td>Biomass (mg)</td>
<td>98.41 ± 37.58</td>
<td>102.68 ± 47.40</td>
<td>0.794</td>
</tr>
<tr>
<td></td>
<td>Root:shoot ratio</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>Mean leaf C (%)</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>Mean leaf N (%)</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>C:N ratio</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>MIP</td>
<td>17.17 ± 3.48</td>
<td>7.67 ± 0.88</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>% AMF</td>
<td>12.67 ± 3.93</td>
<td>6.00 ± 1.73</td>
<td>0.294</td>
</tr>
<tr>
<td></td>
<td>% DSE</td>
<td>4.50 ± 1.78</td>
<td>1.67 ± 1.67</td>
<td>0.290</td>
</tr>
<tr>
<td>Species</td>
<td>Emergence (%)</td>
<td>Time to emergence (d)</td>
<td>Height (cm)</td>
<td>Biomass (mg)</td>
</tr>
<tr>
<td>----------</td>
<td>----------------</td>
<td>----------------------</td>
<td>-------------</td>
<td>--------------</td>
</tr>
<tr>
<td>A. purpurea</td>
<td>46.67 ± 6.19</td>
<td>19.48 ± 0.90</td>
<td>5.64 ± 0.46</td>
<td>9.80 ± 1.48</td>
</tr>
<tr>
<td>B. gracilis</td>
<td>64.17 ± 7.83</td>
<td>15.30 ± 0.96</td>
<td>16.40 ± 1.13</td>
<td>43.48 ± 4.77</td>
</tr>
<tr>
<td>P. jamesii</td>
<td>34.17 ± 6.57</td>
<td>19.11 ± 1.54</td>
<td>7.96 ± 0.72</td>
<td>18.06 ± 2.31</td>
</tr>
<tr>
<td>Z. mays</td>
<td>30.00 ± 4.08</td>
<td>16.67 ± 0.95</td>
<td>15.92 ± 0.61</td>
<td>243.70 ± 50.05</td>
</tr>
</tbody>
</table>

Cultivated species:

<table>
<thead>
<tr>
<th>Species</th>
<th>Emergence (%)</th>
<th>Time to emergence (d)</th>
<th>Height (cm)</th>
<th>Biomass (mg)</th>
<th>Root:shoot ratio</th>
<th>Mean leaf C (%)</th>
<th>Mean leaf N (%)</th>
<th>C:N ratio</th>
<th>MIP</th>
<th>% AMF</th>
<th>% DSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Z. mays</td>
<td>30.00 ± 4.08</td>
<td>16.67 ± 0.95</td>
<td>15.92 ± 0.61</td>
<td>243.70 ± 50.05</td>
<td>1.03 ± 0.08</td>
<td>37.65 ± 1.06</td>
<td>1.06 ± 0.11</td>
<td>39.06 ± 4.28</td>
<td>41.12 ± 4.61</td>
<td>31.24 ± 4.44</td>
<td>9.88 ± 2.55</td>
</tr>
</tbody>
</table>

### Notes:
- Values are presented as mean ± standard error.
- Statistical significance levels are indicated where applicable.
Figure A3.1. *Seedling emergence responses to biocrust.* Mean seedling emergence (± 1 standard error [SE]) for seeds sown into biocrust vs. bare soil mesocosms. (a) Average plant emergence response for all species. (b) Individual species emergence responses to biocrust versus bare soil mesocosms. “*” indicates statistically significant ($P < 0.05$) difference in plant species emergence on biocrust relative to bare soil control. *E. elymoides, B. gracilis, and P. jamesii* experienced decreased emergence on biocrust, while emergence in *H. comata, A. purpurea,* and *Z. mays* was unaffected. No between-species comparisons are shown.
Figure A3.2. Biocrust effects on plant root:shoot ratios. Root:shoot ratio for grass species (± 1 SE) grown in biocrust versus bare soil mesocosms showing lower root:shoot ratios in *E. elymoides* and *A. purpurea* for plants grown in biocrusts. Results for *H. comata* and *P. jamesii* are not shown because there were insufficient replicates for root samples of these species. “*" indicates statistically significant (*P < 0.05*) difference in plant root:shoot ratio on biocrust relative to bare soil controls. No between-species comparisons are shown.
Table A4.1. *Candidate and selected predictor variables for meta-analysis.* (a) Summary of which candidate explanatory variables were explored in each of the five separate plant response datasets with boosted regression trees based on a priori hypotheses; and (b) Candidate explanatory variables incorporated in each of the five separate plant response models (meta-analyses) after BRT data exploration and model selection. An “X” indicates inclusion of the candidate explanatory variable in the analysis of a particular dataset. An “X” indicates inclusion of the candidate explanatory variable in the exploration (a) or analysis (b) of a particular plant response dataset/model.

<table>
<thead>
<tr>
<th>(a) Explanatory variables</th>
<th>Overall plant performance ($n = 847$ studies)</th>
<th>Germination ($n = 491$ studies)</th>
<th>Survival ($n = 123$ studies)</th>
<th>Growth ($n = 159$ studies)</th>
<th>Cover ($n = 231$ studies)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIOCRUST_TYPE</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>CLIMATIC_REGION</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_FUNCTIONAL_GROUP</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>PLANT_NATIVENESS</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_ROOT_MORPHOLOGY</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_DURATION</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>SOIL_REFERENCE_STATE</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>STUDY_LOCATION</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b) Explanatory variables</th>
<th>Overall plant performance ($n = 847$ studies)</th>
<th>Germination ($n = 491$ studies)</th>
<th>Survival ($n = 123$ studies)</th>
<th>Growth ($n = 159$ studies)</th>
<th>Cover ($n = 231$ studies)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIOCRUST_TYPE</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>CLIMATIC_REGION</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_FUNCTIONAL_GROUP</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>PLANT_NATIVENESS</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_ROOT_MORPHOLOGY</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>PLANT_DURATION</td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>SOIL_REFERENCE_STATE</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>STUDY_LOCATION</td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
**Table A4.2. Identified knowledge gaps and future research needs.**

<table>
<thead>
<tr>
<th>Knowledge gap or needed research</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biocrust impacts on plant community assembly and diversity</td>
<td>Direct tests of hypotheses pertaining to biocrust mediation of plant community assembly and diversity patterns at multiple spatial scales are needed.</td>
</tr>
<tr>
<td>Studies across the plant lifecycle</td>
<td>Given observed variability in plant responses to biocrusts depending on plant life stage, future studies should track plant responses to biocrusts across the entire plant lifecycle. Additionally, biocrust effects on plant phenology and sexual reproduction should be examined.</td>
</tr>
</tbody>
</table>
| Trait-based approaches | Explicit tests of the interactions between specific plant functional traits, life forms, and strategies and biocrusts are needed. For example:  
  - C3 versus C4 grasses;  
  - Presence and absence of N-fixing symbionts;  
  - Bunchgrasses versus rhizomatous species;  
  - Annuals versus perennials.  
  In addition, obtaining a greater understanding of how seed characteristics influence plant establishment is critical. |
| Mechanisms underlying plant responses to biocrusts | Future work should directly examine mechanisms whereby biocrusts drive plant species and community responses to biocrusts (e.g., water relations, nutrient cycling, fungal networks). |
| Geographic inclusivity | There is need for additional study of plant responses to biocrusts in South America, Australia, and Africa. Moreover, studies of plant responses to biocrusts in arctic and alpine ecosystems are needed. |
| Climate manipulation experiments | Climate change will impact the dynamics and structure of biocrust and plant communities. Future work should address how plant responses to biocrusts may change in a global change context and examine potential feedbacks between biocrust-plant interactions and climate change. |
| Consistent experimental protocols | Finally, we call for a common set of protocols to be adopted by researchers studying this topic to facilitate better comparisons among results. For example, we suggest studies should include:  
  - Biocrust-absent controls and their descriptions  
  - Detailed descriptions of biocrust community composition (e.g., functional group dominance, cover)  
  - Soil texture information  
  - Soil moisture data and experimental watering treatment information |
Figure A4.1. *Pre-meta-analysis iterative study screening process.* PRISMA flow diagram (Moher et al. 2009) showing the iterative screening process used to retain or exclude studies for this meta-analysis.
Appendix 3.1. Supplementary methods: Chapter 4. Further information on data extraction, construction of the data subsets, and candidate statistical models

Hypothesis generation, data extraction, and construction of data subsets:

Our primary goals were to understand the relative importance of multiple explanatory factors for plant response to biocrust presence, and to generate quantitative estimates of the magnitude of effects for those factors. As a first step, we assembled a group of 13 scientists from federal and academic institutions as part of the “Completing the dryland puzzle: creating a predictive framework for biological soil crust function and response to climate change” Working Group at the John Wesley Powell Center for Analysis and Synthesis. The group generated a list of 12 possible plant response variables and 36 candidate explanatory variables that might explain variation in plant responses to biocrusts.

We then performed an extensive literature search of the ISI Web of Science database (http://www.webofknowledge.com/) and the Chinese National Knowledge Infrastructure (CNKI) Digital Learning Platform (http://www.cnki.net/; for Chinese articles not available in English) (1940 – 2017) using all possible combinations of keywords for biocrust (i.e., [biological soil crust, biocrust, cryptobiotic soil crust, cryptogamic soil crust, and microbiotic soil crust] * vascular plant responses [plant] * [germination, survival, growth, cover, nutrient uptake, phenology, reproduction, and diversity]) to generate the set of records to be considered. We used an iterative screening process (Fig. 1) to generate a list of 75 eligible articles containing 1,004 studies. A ‘study’ is defined as a comparison of plant response to biocrust versus a biocrust-absent control. Individual articles often yielded multiple studies: for example, if a given article may have offered data for multiple plant species responses to different biocrust community types (e.g., cyanobacteria-dominated,
lichen-dominated) or multiple plant responses to biocrusts (e.g., germination, growth, survival, cover) each comparison was treated as a separate study.

Following our literature search, from each study we then extracted values for as many of our candidate explanatory variables as possible, the means for plant responses on biocrust ($X_{\text{crust}}$) and biocrust absent controls ($X_{\text{ctrl}}$), replication, and measures of dispersion (i.e., standard error (SE), standard deviation (SD)). For results in papers presented in graphical form only, we estimated means and measures of variation using the digitalizing software program ‘xyscan’ version 4.2.1 (http://rhig.physics.yale.edu/~ullrich/software/xyscan/).

Plant taxonomic information, and explanatory variables for biocrust community composition (BIOCRUST_TYPE), and experimental design characteristics (i.e., STUDY_LOCATION and SOIL_REFERENCE_STATE), were determined based directly on information reported in the papers. However, additional candidate explanatory variables were also created post-hoc, using information from the literature. For example, each plant taxon was classified into a functional group (PLANT_FUNCTIONAL_GROUP) based on its growth form, lift history characteristics, photosynthetic pathway, and symbiotic nitrogen-fixing ability (Akkermans & van Dijk 1981; Allen & Allen 1981; Bond 1983). Plant traits used to designate plant functional group were acquired from Kew Gardens (http://www.kew.org/herbcat), TRY (https://www.try-db.org/de/de.php), and USDA PLANTS (http://plants.usda.gov) databases. PLANT_NATIVENESS and PLANT_DURATION, when not reported by the article, were determined through the USDA’s Plant database for sites in the US and Canada, or Kew Garden’s database for areas outside of North America. PLANT_ROOT_MORPHOLOGY was determined through use of herbarium catalogs at the University of Colorado Boulder and TRY and SEINet (http://swbiodiversity.org/seinet/index.php) databases. If this method
failed to return an herbarium sheet with roots expert knowledge was considered. We also used coordinates and geographic data reported in papers to extract climate data from WorldClim Database version 2.0 (http://www.worldclim.org/) for each study location. WorldClim data were then used to calculate an aridity index (AI) for each study location as the average yearly precipitation divided by average yearly potential evapotranspiration, an aridity index defined by the United Nations Environmental Program (UNEP). The input data used to calculate this dataset are part of the "CRU CL 2.0 Global Climate Dataset" prepared by the Climate Research Unit of the University of East Anglia, UK (New et al. 2002), and distributed through the website: http://www.cru.uea.ac.uk/~timm/grid/CRU_CL_2_0.html. The categorical CLIMATIC_REGION variable was then designated based on AI in order of greatest to least aridity: Hyper-arid (AI < 0.05); Arid (0.05 < AI < 0.20); Semi-arid (0.20 < AI < 0.50); Dry sub humid (0.50 < AI < 0.65); Other (AI > 0.65). While we were additionally interested in incorporating soil texture data for all studies, very few articles reported soil classification data. We attempted to add this information to all records post-hoc using SoilGrids (https://soilgrids.org/), but ultimately decided not to use these data as given their coarse (1 km or 250 m) spatial resolution.

*Construction of data subsets and candidate statistical models*

Given that biocrusts are hypothesized to affect plant species differently at different stages of the plant life cycle (reviewed in Zhang et al. 2016), we first divided studies into separate analysis groups corresponding to plant germination, survival, growth, cover, phenology, reproduction, and diversity responses to biocrusts. We additionally formed a global analysis group encompassing the average plant species responses to biocrusts by
taking the average of all plant responses recorded for a given record. To assure adequate sample size in each analysis group, we performed analyses only on plant response variables that were reported in at least five separate articles. Thus, in the end, we performed analyses on five plant response analysis groups: overall plant performance, germination, survival, growth, and cover. Ultimately, this process resulted in five different data subsets (Overall plant performance: 847 studies from 75 articles, Germination: 491 studies from 44 articles, Survival: 123 studies from 13 articles, Growth: 159 studies from 49 articles, and Cover: 231 studies from 23 articles; see Appendix 3.2 below for a list of the articles used in these analyses), on which separate meta-analyses were conducted using different subsets of candidate explanatory variables (Table 4.1).

Many of the studies from which data were collected did not provide data for one or more of the candidate explanatory variables. As such, data were not available to explore all levels of each explanatory variable (Table 4.1) across the dataset. Additionally, we eliminated some explanatory variables from consideration if they did not align to a clear hypothesis regarding plant responses to biocrust presence. Thus, we focused our analyses on the main effects of eight fixed and one random factors as explanatory variables, corresponding to hypotheses about the effects of biocrust community composition (BIOCRUST_TYPE), plant species traits (i.e., PLANT_FUNCTIONAL_GROUP, PLANT_NATIVENESS, PLANT_DURATION, and PLANT_ROOT_MORPHOLOGY), climate (i.e., CLIMATIC_REGION), and experimental location (i.e., STUDY_LOCATION) and control type (i.e., SOIL_REFERENCE_STATE; See Table 4.1 in main text for a list and explanation of all candidate explanatory predictor levels). We initially considered incorporating two-way interactions among all fixed factors in our analyses for which there were clear hypotheses. However, following examination of our
dataset, we ultimately did not include interactions in any of our analyses since most subsets of the data did not include sufficient replication of all factorial combination of levels of interacting variables, precluding meaningful analysis of most interactions. In addition to fixed effects, we included STUDY_ID as a random effect in all models to account for between-study variation in the data.
Appendix 3.2. Bibliography of data sources considered for use in meta-analysis. Full bibliographic references for resources used for (I) publications included in the final database from which data were analyzed and extracted, and (II) for publications analyzed, but not included in the final database.

(I) Publications included in database (n = 75):


influenced by inoculation of Nostoc kihlmani and Anabaena cylindrica. Rendiconti Lincei, 26(2), 121–131. https://doi.org/10.1007/s12210-014-0351-8


Rivera-Aguilar, V., Godínez-Alvarez, H., Manuell-Cacheux, I., & Rodríguez-Zaragoza, S.


(II) Publications analyzed but not included in final database (n = 53):


Concostrina-Zubiri, L., Martínez, I., Rabasa, S. G., & Escudero, A. (2014). The influence of


Appendix 3.3. Supplementary results for publication bias, sensitivity, and boosted regression tree (BRT) analyses.

Publication bias and sensitivity analyses

We detected publication bias in data subsets evaluating overall plant performance ($P = 0.080$), germination ($P = 0.046$), survival ($P < 0.001$) and cover ($P = 0.001$). No publication bias was detected in the growth data set ($P = 0.675$). We did not detect influential outliers in any of the data subsets. A significant amount of heterogeneity remained for all models ($P < 0.001$ for all). All five plant response data subsets had a sufficient number of studies to explore the potential relationships between biocrust, plant, and study explanatory variables and plant response outcomes.

Boosted regression tree (BRT) data exploration and model selection:

For the overall plant performance response ($N = 847$; Figure 4.2), BIOCRUST_TYPE had the largest influence on effect size, explaining 25.9 % of variation in the plant response, closely followed by Ecosystem_TYPE and STUDY_CONTROL which explained 20.3 % and 20.1 % of variation respectively. The moderators PLANT_FUNCTIONAL_GROUP and PLANT_NATIVENESS also had substantive influences on the overall effect size, explaining 18.2 % and 15.4 % variation in the response respectively. STUDY_TYPE, PLANT_DURATION, and PLANT_ROOT_MORPH were not found to be influential explanatory variables in the overall plant performance model.

For the plant germination model ($N = 491$; Figure 4.2), the moderators PLANT_FUNCTIONAL_GROUP and STUDY_CONTROL had the largest influences on effect size, explaining 24.9 % and 23.9 % of variation in the plant response to biocrust respectively.
BIOCRUST_TYPE and ECOSYSTEM_TYPE also explained 20.2 % and 19.3 % of variation respectively. PLANT_NATIVIVENSS additionally influenced germination effect size, explaining about 11.6 % of variation. STUDY_TYPE, PLANT_DURATION, and PLANT_ROOT_MORPHOLOGY were not found to be influential explanatory variables in the germination model.

In the plant survival model ($N = 123$; Figure 4.2), effect size was most substantially affected by PLANT_DURATION, which explained 32.4 % of variation in plant responses to biocrusts. BIOCROST_TYPE additionally explained 25.4 % of variation, followed by STUDY_CONTROL (24.9 %) and PLANT_FUNCTIONAL_GROUP (17.2 %). STUDY_TYPE, ECOSYSTEM_TYPE, PLANT_NATIVENESS, and PLANT_ROOT_MORPH were not found to be influential explanatory variables in the plant survival model.

In the plant growth model ($N = 159$; Figure 4.2), PLANT_FUNCTIONAL_GROUP had the largest influence on effect size, explaining 38.9 % of variation in the response. BIOCROST_TYPE also explained a substantive 17.7 % of variation. STUDY_CONTROL, STUDY_TYPE, PLANT_NATIVENESS also had lesser, but significant influences on growth effect size, explaining 17.5 %, 15.0 %, and 10.8 % of variation in the response respectively. ECOSYSTEM_TYPE, PLANT_ROOT_MORPH, and PLANT_DURATION were not found to be influential explanatory variables in the plant growth model.

Finally, for the plant cover model ($N = 231$; Figure 4.2), the BIOCROST_TYPE moderator had the greatest (28.2 %) influence on effect size, followed by STUDY_CONTROL (28.1 %) and PLANT_FUNCTIONAL_GROUP (22.2 %). ECOSYSTEM_TYPE additionally explained 21.4 % of variation in plant responses to biocrusts. Assessment of variable interactions in each of the five BRT models revealed that interactions were existent but negligible. STUDY_TYPE,
PLANT_NATIVENESS, PLANT_ROOT_MORPH, and PLANT_DURATON were not found to be influential explanatory variables in the plant cover model.
## Appendix 4: Supplementary Materials for Chapter 5

**Table A5.1. List of herbaceous plant species identified.** List of herbaceous (non-woody) plant species identified within the sagebrush and pinyon-juniper plots.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Scientific name</th>
<th>Common Name</th>
<th>Native/Exotic</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Perennial forbs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ANSE6</td>
<td><em>Astragalus newberryi</em> A. Gray</td>
<td>Newberry's milkvetch</td>
<td>N</td>
<td>Fabaceae</td>
</tr>
<tr>
<td>ASMO7</td>
<td><em>Astragalus mollissimus</em> Torr.</td>
<td>Wooly locoweed</td>
<td>N</td>
<td>Fabaceae</td>
</tr>
<tr>
<td>CANU3</td>
<td><em>Calochortus nuttallii</em> Torr. &amp; A. Gray</td>
<td>Sego lily</td>
<td>N</td>
<td>Liliaceae</td>
</tr>
<tr>
<td>ERIN4</td>
<td><em>Eriogonum inflatum</em> Torr. &amp; Frem</td>
<td>Desert trumpet</td>
<td>N</td>
<td>Polygonaceae</td>
</tr>
<tr>
<td>GUSA2</td>
<td><em>Gutierrezia sarothrae</em> (Pursh) Britt. &amp; Rusby</td>
<td>Broom snakeweed</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>HEMI2</td>
<td><em>Helianthemella microcephala</em> Torr. &amp; A. Gray</td>
<td>Purpledisk helianthella</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>HYFI</td>
<td><em>Hymenopappus filifolius</em> Hook.</td>
<td>Fineleaf hymenopappus</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>IPRO</td>
<td><em>Ipomopsis roseata</em> (Ryd.b) V.E. Grant</td>
<td>Rosy ipomopsis</td>
<td>N</td>
<td>Polemoniaceae</td>
</tr>
<tr>
<td>SPGR2</td>
<td><em>Sphaeralcea grossulariifolia</em> Hook &amp; Arn.</td>
<td>Gooseberryleaf globemallow</td>
<td>N</td>
<td>Malvaceae</td>
</tr>
<tr>
<td>TEACA2</td>
<td><em>Tetraneuris acaulis</em> (Pursh) Greene var. acaulis</td>
<td>Stemless four-nerve daisy</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>XYVE</td>
<td><em>Xylorhiza venusta</em> (M.E. Jones) A. Heller</td>
<td>Charming woodyaster</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>YUAN2</td>
<td><em>Yucca angustissima</em> Englem. ex Trel.</td>
<td>Narrowleaf yucca</td>
<td>N</td>
<td>Agavaceae</td>
</tr>
<tr>
<td><strong>Cacti</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ECCOC</td>
<td><em>Echinocereus coccineus</em> var. coccineus</td>
<td>Scarlet hedgehog cactus</td>
<td>N</td>
<td>Cactaceae</td>
</tr>
<tr>
<td>ESV12</td>
<td><em>Escobaria vivipara</em> (Nutt.) Buxbaum</td>
<td>Spinystar</td>
<td>N</td>
<td>Cactaceae</td>
</tr>
<tr>
<td>OPPO</td>
<td><em>Opuntia polyacantha</em> Haw.</td>
<td>Plains pricklypear</td>
<td>N</td>
<td>Cactaceae</td>
</tr>
<tr>
<td>PESI</td>
<td><em>Pediocactus simpsonii</em> (Engelm.) Britton &amp; Rose</td>
<td>Mountain ball cactus</td>
<td>N</td>
<td>Cactaceae</td>
</tr>
<tr>
<td>SCWH</td>
<td><em>Sclerocactus whipplei</em> (Engelm. &amp; J.M Bigelow) Britton &amp; Rose</td>
<td>Whipple's fishhook cactus</td>
<td>N</td>
<td>Cactaceae</td>
</tr>
<tr>
<td><strong>Annual forbs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALLE7</td>
<td><em>Aliciella leptomeria</em> (A. Gray) J.M. Porter</td>
<td>Sand gilia</td>
<td>N</td>
<td>Polemoniaceae</td>
</tr>
<tr>
<td>COWR2</td>
<td><em>Cordylanthus wrightii</em> A. Gray</td>
<td>Wright's bird's beak</td>
<td>N</td>
<td>Scrophulariaceae</td>
</tr>
<tr>
<td>CRCR3</td>
<td><em>Cryptantha crassisepala</em> (Torr. &amp; A. Gray) Greene</td>
<td>Thicksepal cryptantha</td>
<td>N</td>
<td>Boraginaceae</td>
</tr>
<tr>
<td>DENU2</td>
<td><em>Delphinium nuttallianum</em> Pritz. Ex. Walp.</td>
<td>Twolobe larkspur</td>
<td>N</td>
<td>Ranunculaceae</td>
</tr>
<tr>
<td>GARA2</td>
<td><em>Gayophytum ramosissimum</em> Torr. &amp; A. Gray</td>
<td>Pinyon groundsmoke</td>
<td>N</td>
<td>Onagraceae</td>
</tr>
<tr>
<td>GIIN2</td>
<td><em>Gilia inconspicua</em> (Sm.) Sweet</td>
<td>Shy gilia</td>
<td>N</td>
<td>Polemoniaceae</td>
</tr>
<tr>
<td>Code</td>
<td>Scientific Name</td>
<td>Common Name</td>
<td>Life Form</td>
<td>Family</td>
</tr>
<tr>
<td>-------</td>
<td>-----------------------------------------------------</td>
<td>------------------------</td>
<td>-----------</td>
<td>-----------------</td>
</tr>
<tr>
<td>LAOC3</td>
<td><em>Lappula occidentalis</em> (S. Watson) Greene</td>
<td>Flatspine stickweed</td>
<td>N</td>
<td>Boraginaceae</td>
</tr>
<tr>
<td>LEHA11</td>
<td><em>Leptosiphon harknessii</em> (Curran) J.M. Porter &amp; L.A. Johnson</td>
<td>Harkness' flaxflower</td>
<td>N</td>
<td>Polemoniaceae</td>
</tr>
<tr>
<td>PLPA2</td>
<td><em>Plantago patagonica</em> Jacq.</td>
<td>Wooly plantain</td>
<td>N</td>
<td>Plantaginaceae</td>
</tr>
<tr>
<td>SESEA</td>
<td><em>Senecio serra</em> Hook. Var. <em>admirabilis</em> (Greene) A. Nelson</td>
<td>Tall ragwort</td>
<td>N</td>
<td>Asteraceae</td>
</tr>
<tr>
<td>SIAL2</td>
<td><em>Sisymbrium altissimum</em> L.</td>
<td>Tall tumblemustard</td>
<td>E</td>
<td>Brassicaceae</td>
</tr>
</tbody>
</table>

**Perennial grasses**

<table>
<thead>
<tr>
<th>Code</th>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Life Form</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACHY</td>
<td><em>Achnatherum hymenoides</em> (Roem. &amp; Schult.) Barkworth</td>
<td>Indian ricegrass</td>
<td>N</td>
<td>Poaceae</td>
</tr>
<tr>
<td>ARPU9</td>
<td><em>Aristida purpurea</em> Nutt.</td>
<td>Purple threeawn</td>
<td>N</td>
<td>Poaceae</td>
</tr>
<tr>
<td>BOGR2</td>
<td><em>Bouteloua gracilis</em> (Willd. Ex. Kunth) Lag. ex Griffiths</td>
<td>Blue grama</td>
<td>N</td>
<td>Poaceae</td>
</tr>
<tr>
<td>ELELE</td>
<td><em>Elymus elymoides</em> (Raf.) Swezey ssp. elymoides</td>
<td>Squirreltail</td>
<td>N</td>
<td>Poaceae</td>
</tr>
<tr>
<td>HECOC8</td>
<td><em>Hesperostipa comata</em> (Trin. &amp; Rupr.) Barkworth ssp. comata</td>
<td>Needle and thread</td>
<td></td>
<td>Poaceae</td>
</tr>
<tr>
<td>PLJA</td>
<td><em>Pleuraphis jamesii</em> Torr.</td>
<td>James' galleta</td>
<td>N</td>
<td>Poaceae</td>
</tr>
<tr>
<td>SPCR</td>
<td><em>Sporobolus cryptandrus</em> (Torr.) A. Gray</td>
<td>Sand dropseed</td>
<td>N</td>
<td>Poaceae</td>
</tr>
</tbody>
</table>

**Annual grasses**

<table>
<thead>
<tr>
<th>Code</th>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Life Form</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>BRTE</td>
<td><em>Bromus tectorum</em> L</td>
<td>Cheatgrass</td>
<td>E</td>
<td>Poaceae</td>
</tr>
<tr>
<td>VUOC</td>
<td><em>Vulpia octoflora</em> (Walter) Rydb.</td>
<td>Sixweeks fescue</td>
<td>N</td>
<td>Poaceae</td>
</tr>
</tbody>
</table>
Table A5.2. *Plant response and soil predictor variables.* Means (± SE) of plant responses and soil cover (SCCs) and soil heterogeneity predictors (i.e., SCR, SCD) in sagebrush and pinyon-juniper plots. “*” denotes a statistically significant difference in factor means between sagebrush and pinyon-juniper plots.

<table>
<thead>
<tr>
<th>Ecol. site type</th>
<th>Plant responses</th>
<th>Soil cover and heterogeneity predictor variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cover (%)</td>
<td>Richness (S)</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>45.02 (2.66)</td>
<td>3.58 (0.26)</td>
</tr>
<tr>
<td>Pinyon-juniper</td>
<td>21.00* (3.02)</td>
<td>3.00 (0.20)</td>
</tr>
</tbody>
</table>

*Notes: Soil cover richness (SCR) and soil cover diversity were calculated as the average number of soil cover classes within plots and the Shannon diversity (H) of soil cover classes within plots respectively.*
Table A5.3a. *All plots correlation matrix.* Cross-correlations (Pearson correlation coefficients, \( r \)) among plant response and environmental predictor variables in both sagebrush and pinyon-juniper plots \( (n_{\text{patches}} = 80) \).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Ecol. site type</th>
<th>Plant cover (%)</th>
<th>Plant species richness (S)</th>
<th>Plant Shannon diversity (H)</th>
<th>Dark biocrust cover (%)</th>
<th>Light biocrust cover (%)</th>
<th>Bare soil cover (%)</th>
<th>Phys. soil crust (%)</th>
<th>Soil cover rich. (SCR)</th>
<th>Soil cover diversity (SCD)</th>
<th>Alt</th>
<th>Soil depth (cm)</th>
<th>Grazing intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecological site type</td>
<td>1.00</td>
<td>-0.56</td>
<td>NS</td>
<td>NS</td>
<td>0.56</td>
<td>0.32</td>
<td>0.30</td>
<td>-0.31</td>
<td>0.25</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Plant cover (%)</td>
<td>-0.56</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>0.32</td>
<td>1.00</td>
<td>0.30</td>
<td>-0.31</td>
<td>0.25</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Plant species richness (S)</td>
<td>NS</td>
<td>NS</td>
<td>1.00</td>
<td>0.30</td>
<td>-0.31</td>
<td>-0.34</td>
<td>0.29</td>
<td>1.00</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Plant Shannon diversity (H)</td>
<td>NS</td>
<td>-0.24</td>
<td>0.83</td>
<td>1.00</td>
<td>-0.37</td>
<td>-0.34</td>
<td>0.29</td>
<td>1.00</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Dark biocrust cover (%)</td>
<td>0.56</td>
<td>-0.61</td>
<td>NS</td>
<td>NS</td>
<td>0.32</td>
<td>1.00</td>
<td>0.30</td>
<td>-0.31</td>
<td>0.25</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Light biocrust cover (%)</td>
<td>0.30</td>
<td>-0.30</td>
<td>NS</td>
<td>NS</td>
<td>-0.37</td>
<td>-0.34</td>
<td>0.29</td>
<td>1.00</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Bare soil cover (%)</td>
<td>-0.31</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.50</td>
<td>-0.46</td>
<td>0.29</td>
<td>1.00</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Physical crust cover (%)</td>
<td>-0.25</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.50</td>
<td>-0.46</td>
<td>0.29</td>
<td>1.00</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Soil cover richness (SCR)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Soil cover diversity (SCD)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Alt</td>
<td>-0.56</td>
<td>0.23</td>
<td>NS</td>
<td>NS</td>
<td>-0.35</td>
<td>-0.35</td>
<td>NS</td>
<td>0.54</td>
<td>NS</td>
<td>0.28</td>
<td>1.00</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>0.31</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Grazing level</td>
<td>-0.78</td>
<td>0.51</td>
<td>NS</td>
<td>NS</td>
<td>-0.44</td>
<td>-0.28</td>
<td>NS</td>
<td>0.25</td>
<td>NS</td>
<td>0.49</td>
<td>0.33</td>
<td>1.00</td>
<td>NS</td>
</tr>
</tbody>
</table>

*Notes:* Variables with \( r > \pm 0.70 \) were not included in the same model. Transformed data were used where it was appropriate. Correlations are significant at alpha = 0.05, NS, nonsignificant at alpha > 0.05.
Table A5.3b. **Sagebrush plots correlation matrix.** Cross-correlations (Pearson correlation coefficients, \( r \)) among plant response and environmental predictor variables in sagebrush plots \((n_{\text{patches}} = 40)\).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Plant cover (%)</th>
<th>Plant species richness (S)</th>
<th>Plant Shannon diversity (H)</th>
<th>Dark biocrust cover (%)</th>
<th>Light biocrust cover (%)</th>
<th>Bare soil cover (%)</th>
<th>Phys. soil crust (%)</th>
<th>Soil cover richness (SCR)</th>
<th>Soil cover diversity (SCD)</th>
<th>Altitude (m)</th>
<th>Soil depth (cm)</th>
<th>Grazing level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant cover (%)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant species richness (S)</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Shannon diversity (H)</td>
<td>NS</td>
<td>0.87</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark biocrust cover (%)</td>
<td>NS</td>
<td>0.41</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light biocrust cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.32</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare soil cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.36</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physical crust cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.50</td>
<td>-0.47</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil cover richness (SCR)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil cover diversity (SCD)</td>
<td>-0.32</td>
<td>0.42</td>
<td>0.40</td>
<td>NS</td>
<td>NS</td>
<td>0.42</td>
<td>0.56</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>-0.33</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.40</td>
<td>NS</td>
<td>0.26</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>NS</td>
<td>0.53</td>
<td>0.49</td>
<td>NS</td>
<td>NS</td>
<td>0.37</td>
<td>NS</td>
<td>0.31</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing level</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.33</td>
<td>NS</td>
<td>-0.51</td>
<td>-0.54</td>
<td>NS</td>
<td>-0.32</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Notes:* Variables with \( r > \pm 0.70 \) were not included in the same model. Transformed data were used where it was appropriate. Correlations are significant at alpha = 0.05, NS, nonsignificant at alpha > 0.05
Table A5.3c. *Pinyon-juniper plots correlation matrix.* Cross-correlations (Pearson correlation coefficients, \( r \)) among plant response and environmental predictor variables in pinyon-juniper plots (\( n_{\text{patches}} = 40 \)).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Plant cover (%)</th>
<th>Plant species richness (S)</th>
<th>Plant Shannon diversity (H)</th>
<th>Dark biocrust cover (%)</th>
<th>Light biocrust cover (%)</th>
<th>Bare soil cover (%)</th>
<th>Phys. soil crust (%)</th>
<th>Soil cover richness (SCR)</th>
<th>Soil cover diversity (SCD)</th>
<th>Alt (m)</th>
<th>Soil depth (cm)</th>
<th>Grazing level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant cover (%)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant species richness (S)</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Shannon diversity (H)</td>
<td>NS</td>
<td>0.87</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark biocrust cover (%)</td>
<td>NS</td>
<td>0.41</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light biocrust cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.32</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare soil cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.36</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physical crust cover (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.50</td>
<td>-0.47</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil cover richness (SCR)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil cover diversity (SCD)</td>
<td>-0.32</td>
<td>0.42</td>
<td>0.40</td>
<td>NS</td>
<td>NS</td>
<td>0.42</td>
<td>0.56</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>-0.33</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.40</td>
<td>NS</td>
<td>0.26</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>NS</td>
<td>0.53</td>
<td>0.49</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.37</td>
<td>NS</td>
<td>0.31</td>
<td>NS</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Grazing level</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>-0.33</td>
<td>NS</td>
<td>-0.51</td>
<td>-0.54</td>
<td>NS</td>
<td>-0.32</td>
</tr>
</tbody>
</table>

*Notes:* Variables with \( r > \pm 0.70 \) were not included in the same model. Transformed data were used where it was appropriate. Correlations are significant at alpha = 0.05, NS, nonsignificant at alpha > 0.05
Table A5.4. Univariate ANOVA model results for significant predictor variables from GLMMs. Significance in fixed effects in best predictive models (GLMMs) of plant species richness and Shannon diversity in sagebrush and pinyon-juniper plots.

<table>
<thead>
<tr>
<th>Plant response</th>
<th>Predictor</th>
<th>Est</th>
<th>SE</th>
<th>t-value</th>
<th>R²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sagebrush</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species richness *</td>
<td>0.788</td>
<td>0.319</td>
<td>2.472</td>
<td>0.1</td>
<td>0.018 *</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.019</td>
<td>0.007</td>
<td>2.564</td>
<td>0.1</td>
<td>0.014 *</td>
</tr>
<tr>
<td></td>
<td>Soil depth (cm)</td>
<td>0.078</td>
<td>0.023</td>
<td>3.444</td>
<td>0.2</td>
<td>0.001 ***</td>
</tr>
<tr>
<td></td>
<td>Shannon diversity</td>
<td>1.815</td>
<td>0.678</td>
<td>2.682</td>
<td>0.1</td>
<td>0.010 *</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.032</td>
<td>0.016</td>
<td>2.009</td>
<td>0.1</td>
<td>0.052</td>
</tr>
<tr>
<td></td>
<td>Soil depth (cm)</td>
<td>0.168</td>
<td>0.049</td>
<td>3.429</td>
<td>0.2</td>
<td>0.001 ***</td>
</tr>
<tr>
<td><strong>Pinyon-juniper</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species richness *</td>
<td>0.006</td>
<td>0.003</td>
<td>1.902</td>
<td>0.0</td>
<td>0.065</td>
</tr>
<tr>
<td></td>
<td>Dark biocrust cover (%)</td>
<td>0.009</td>
<td>0.005</td>
<td>1.714</td>
<td>0.0</td>
<td>0.095</td>
</tr>
<tr>
<td></td>
<td>Light biocrust cover (%)</td>
<td>0.020</td>
<td>0.006</td>
<td>3.000</td>
<td>0.1</td>
<td>0.005 **</td>
</tr>
<tr>
<td></td>
<td>Shannon diversity</td>
<td>0.010</td>
<td>0.011</td>
<td>0.858</td>
<td>0.0</td>
<td>0.396</td>
</tr>
</tbody>
</table>

*Species richness (S) data are log\(^{10}\) transformed.

Notes: When predictors were significant in best GLMMs, we performed univariate regression on those variables to understand their influence on plant species richness and Shannon diversity. *Species richness (S) data are log\(^{10}\) transformed.
Table A5.5. *Indicator species analysis: species sorting.* Significant results for indicator species analysis (ISA) in sagebrush and pinyon-juniper plots with alpha < 0.10. ISA was only performed when there were multiple levels for a given grouping factor within community type. Given there were not multiple levels of dark biocrust in sagebrush plots, we performed ISA on levels of total biocrust cover rather than splitting by dark and light cover as in pinyon-juniper plots.

<table>
<thead>
<tr>
<th>Ecological site type</th>
<th>Grouping factor</th>
<th>Level</th>
<th>Species</th>
<th>Plant functional type</th>
<th>IndVal</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagebrush</td>
<td>SCD</td>
<td>High</td>
<td><em>A. hymenoides</em></td>
<td>Perennial grass</td>
<td>0.562</td>
<td>0.054</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High</td>
<td><em>E. elymoides</em></td>
<td>Perennial grass</td>
<td>0.489</td>
<td>0.088</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High</td>
<td><em>S. whipplei</em></td>
<td>Cactus</td>
<td>0.460</td>
<td>0.093</td>
</tr>
<tr>
<td>Bare soil</td>
<td>Low</td>
<td><em>H. comata</em></td>
<td>Perennial grass</td>
<td>0.761</td>
<td>0.092</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td><em>Asteraceae spp.</em></td>
<td>Annual forb</td>
<td>1.000</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td><em>O. polyacantha</em></td>
<td>Cactus</td>
<td>0.891</td>
<td>0.060</td>
<td></td>
</tr>
<tr>
<td>Biocrust</td>
<td>Low</td>
<td><em>B. tectorum</em></td>
<td>Annual grass</td>
<td>0.663</td>
<td>0.077</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td><em>P. patagonica</em></td>
<td>Annual forb</td>
<td>0.705</td>
<td>0.032</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td><em>C. nuttalii</em></td>
<td>Perennial forb</td>
<td>0.613</td>
<td>0.052</td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>Low</td>
<td><em>E. elymoides</em></td>
<td>Perennial grass</td>
<td>0.472</td>
<td>0.068</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td><em>H. comata</em></td>
<td>Perennial grass</td>
<td>0.772</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td><em>B. tectorum</em></td>
<td>Annual grass</td>
<td>0.628</td>
<td>0.096</td>
<td></td>
</tr>
<tr>
<td>Pinyon-juniper</td>
<td>SCD</td>
<td>Low</td>
<td><em>Asteraceae spp.</em></td>
<td>Annual forb</td>
<td>0.414</td>
<td>0.078</td>
</tr>
<tr>
<td></td>
<td>Biocrust</td>
<td>Low</td>
<td><em>A. purpurea</em></td>
<td>Perennial grass</td>
<td>0.378</td>
<td>0.089</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High</td>
<td><em>T. acaulis ssp. acaulis</em></td>
<td>Perennial forb</td>
<td>0.614</td>
<td>0.082</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High</td>
<td><em>C. nuttalii</em></td>
<td>Perennial forb</td>
<td>0.446</td>
<td>0.100</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td><em>B. gracilis</em></td>
<td>Perennial grass</td>
<td>0.632</td>
<td>0.100</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td><em>C. nuttalii</em></td>
<td>Perennial forb</td>
<td>0.504</td>
<td>0.071</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td><em>T. acaulis ssp. acaulis</em></td>
<td>Perennial forb</td>
<td>0.632</td>
<td>0.029</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td><em>Unknown_AF</em></td>
<td>Annual forb</td>
<td>0.534</td>
<td>0.022</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td><em>G. sarothrae</em></td>
<td>Perennial forb</td>
<td>0.643</td>
<td>0.056</td>
<td></td>
</tr>
</tbody>
</table>
**Table A5.6. Species turnover.** Results for species turnover (beta-diversity) between patches with low, medium and high soil heterogeneity (SCD) sagebrush and pinyon-juniper plots. $\beta_{SIM}$ represents the Simpson index of dissimilarity, which indicates spatial species turnover, $\beta_{SOR}$ represents the Sørensen index for dissimilarity, which indicates overall beta-diversity, and $\beta_{SNE}$ indicates the loss or gain of species due to nestedness (Baselga, 2010). $\beta_{SIM}$, $\beta_{SOR}$, and $\beta_{SNE}$ did not vary significantly among patches with different levels of soil heterogeneity (SCD; all pairwise comparisons $P > 0.05$).

<table>
<thead>
<tr>
<th>Soil heterogeneity (SCD)</th>
<th>$\beta_{SIM}$</th>
<th>$\beta_{SOR}$</th>
<th>$\beta_{SNE}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Full</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.72 ± 0.04</td>
<td>0.81 ± 0.02</td>
<td>0.08 ± 0.02</td>
</tr>
<tr>
<td>Medium</td>
<td>0.67 ± 0.05</td>
<td>0.78 ± 0.02</td>
<td>0.11 ± 0.04</td>
</tr>
<tr>
<td>High</td>
<td>0.65 ± 0.06</td>
<td>0.80 ± 0.02</td>
<td>0.14 ± 0.05</td>
</tr>
<tr>
<td><strong>Sagebrush</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.72 ± 0.04</td>
<td>0.81 ± 0.08</td>
<td>0.08 ± 0.02</td>
</tr>
<tr>
<td>Medium</td>
<td>0.67 ± 0.05</td>
<td>0.78 ± 0.02</td>
<td>0.11 ± 0.02</td>
</tr>
<tr>
<td>High</td>
<td>0.61 ± 0.04</td>
<td>0.76 ± 0.01</td>
<td>0.15 ± 0.03</td>
</tr>
<tr>
<td><strong>Pinyon-juniper</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.65 ± 0.02</td>
<td>0.78 ± 0.02</td>
<td>0.12 ± 0.04</td>
</tr>
<tr>
<td>Medium</td>
<td>0.66 ± 0.04</td>
<td>0.76 ± 0.03</td>
<td>0.11 ± 0.03</td>
</tr>
<tr>
<td>High</td>
<td>0.61 ± 0.04</td>
<td>0.80 ± 0.02</td>
<td>0.14 ± 0.05</td>
</tr>
</tbody>
</table>
Table 5.7a. *Sagebrush community dispersion (PERMDISP).* Results for PERMDISP analysis of Bray-Curtis dissimilarities for herbaceous plant community dispersion in sagebrush plots.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>pseudo-F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total biocrust (%)</td>
<td>29</td>
<td>1.138</td>
<td>0.039</td>
<td>11.579</td>
<td>0.115</td>
</tr>
<tr>
<td>Residuals</td>
<td>10</td>
<td>0.034</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark biocrust (%)</td>
<td>31</td>
<td>1.317</td>
<td>0.042</td>
<td>1.535</td>
<td>0.569</td>
</tr>
<tr>
<td>Residuals</td>
<td>8</td>
<td>0.221</td>
<td>0.028</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light biocrust (%)</td>
<td>26</td>
<td>1.196</td>
<td>0.050</td>
<td>2.571</td>
<td>0.157</td>
</tr>
<tr>
<td>Residuals</td>
<td>13</td>
<td>0.233</td>
<td>0.038</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare soil (%)</td>
<td>9</td>
<td>0.520</td>
<td>0.058</td>
<td>1.512</td>
<td>0.190</td>
</tr>
<tr>
<td>Residuals</td>
<td>30</td>
<td>1.145</td>
<td>0.038</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physical crust (%)</td>
<td>20</td>
<td>1.064</td>
<td>0.053</td>
<td>4.686</td>
<td>0.025</td>
</tr>
<tr>
<td>Residuals</td>
<td>19</td>
<td>0.216</td>
<td>0.011</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil heterogeneity (SCD)</td>
<td>18</td>
<td>0.875</td>
<td>0.067</td>
<td>1.257</td>
<td>0.323</td>
</tr>
<tr>
<td>Residuals</td>
<td>21</td>
<td>0.058</td>
<td>0.005</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>4</td>
<td>0.096</td>
<td>0.024</td>
<td>0.663</td>
<td>0.606</td>
</tr>
<tr>
<td>Residuals</td>
<td>35</td>
<td>1.264</td>
<td>0.036</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>58</td>
<td>1.623</td>
<td>0.028</td>
<td>28.881</td>
<td>0.011</td>
</tr>
<tr>
<td>Residuals</td>
<td>21</td>
<td>0.020</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>2</td>
<td>0.083</td>
<td>0.041</td>
<td>1.318</td>
<td>0.284</td>
</tr>
<tr>
<td>Residuals</td>
<td>37</td>
<td>1.159</td>
<td>0.031</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table A5.7b. *Pinyon-juniper community dispersion*. Results for PERMDISP analysis of Bray-Curtis dissimilarities for herbaceous plant community dispersion in pinyon-juniper plots.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>pseudo-F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total biocrust (%)</td>
<td>29</td>
<td>1.733</td>
<td>0.060</td>
<td>6.050</td>
<td>0.248</td>
</tr>
<tr>
<td>Residuals</td>
<td>10</td>
<td>0.010</td>
<td>0.010</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark biocrust (%)</td>
<td>14</td>
<td>1.378</td>
<td>0.098</td>
<td>6.680</td>
<td>0.001</td>
</tr>
<tr>
<td>Residuals</td>
<td>25</td>
<td>0.368</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light biocrust (%)</td>
<td>31</td>
<td>1.118</td>
<td>0.036</td>
<td>1.550</td>
<td>0.539</td>
</tr>
<tr>
<td>Residuals</td>
<td>8</td>
<td>0.186</td>
<td>0.023</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare soil (%)</td>
<td>17</td>
<td>1.214</td>
<td>0.071</td>
<td>2.255</td>
<td>0.067</td>
</tr>
<tr>
<td>Residuals</td>
<td>22</td>
<td>0.697</td>
<td>0.032</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physical crust (%)</td>
<td>22</td>
<td>1.488</td>
<td>0.068</td>
<td>2.043</td>
<td>0.102</td>
</tr>
<tr>
<td>Residuals</td>
<td>17</td>
<td>0.563</td>
<td>0.033</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil heterogeneity (SCD)</td>
<td>30</td>
<td>1.220</td>
<td>0.042</td>
<td>1.567</td>
<td>0.645</td>
</tr>
<tr>
<td>Residuals</td>
<td>9</td>
<td>0.203</td>
<td>0.021</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>4</td>
<td>0.088</td>
<td>0.022</td>
<td>0.542</td>
<td>0.726</td>
</tr>
<tr>
<td>Residuals</td>
<td>35</td>
<td>1.421</td>
<td>0.041</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>35</td>
<td>0.011</td>
<td>0.028</td>
<td>28.881</td>
<td>0.013</td>
</tr>
<tr>
<td>Residuals</td>
<td>5</td>
<td>0.020</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure A5.1. Differences in study site climate from long-term averages. Differences in total monthly precipitation (mm) and temperature (°C) compared with 30-year long-term averages (1981-2010) at Beef Basin, Utah. (PRISM Climate Group, http://prism.oregonstate.edu; Daly et al., 2009) for the 12 months leading up to the time of our field survey (June 2018, *).
Figure A5.2. BRT data exploration. Boosted regression tree (BRT) model results for simplified models of plant species richness (left column) and plant Shannon diversity index (right column) (of 1-m² plots) showing the relative influence (%) of retained ground-based predictor variables in best models.
**Figure A5.3. Plant species richness predicted by plant density.** Regression of plant species richness from sagebrush and pinyon-juniper plots on plant density within patches of low, medium, and high soil cover heterogeneity (SCD). In sagebrush plots, there were marginally significant negative relationships between plant richness and plant density in low and medium SCD patches, with the strength of this density-richness relationship stronger in the low SCD patches. In pinyon-juniper plots, slopes did not vary significantly \((P > 0.05)\) within patches of any SCD level.
**Figure A5.4.** *Species rarefaction by soil cover heterogeneity.* Coleman rarefaction curves for communities in patches with low (homogeneous), medium, and high (heterogeneous) soil cover heterogeneity (SCD). Lines represent sample-based Coleman rarefaction curves for the sample data set +/- 1 SD over standard density.
**Figure A5.5.** *Herbaceous plant community composition by ecological site type and biocrust cover.* Non-metric multidimensional scaling (NMDS) plots showing differences in herbaceous plant community composition based on (a) ecological site type (i.e., sagebrush, pinyon-juniper), and (b) total biocrust cover. Stress = 0.124.
Figure A5.6. Herbaceous plant community composition (sagebrush plots) by grazing level. Non-metric multidimensional scaling (NMDS) plot showing no difference in herbaceous plant community composition in sagebrush plots based on grazing level (i.e., low, medium, high).