

# Compositional resistance and successional reversal after long-term experimental drought in biocrust communities

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## Abstract

The effects of severe drought on the stability of dryland ecosystems are still uncertain and it is unknown whether diversity can buffer changes in systems that are adapted to water-limitation. We investigated the effects of long-term induced drought on the composition and maturity of biological soil crusts (biocrusts), as well as tested the hypothesis that diversity promotes stability using compositional resistance as a measure for ecosystem stability. We surveyed an array of 25 sites in the central Colorado Plateau, USA, that included plots that received ambient precipitation and plots that had experienced eight years of ~35% precipitation reduction. We found that biocrusts can maintain broad compositional integrity after long-term climate disturbance. However, biocrust successional reversal still occurred, with a reduction of later successional constituents and an increase of early successional cyanobacterial cover. Our findings indicate that long-term drought could have major impacts on biocrust community stability.

## Compositional resistance and successional reversal after long-term experimental drought in biocrust communities

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MCRF collected and analyzed the data and wrote the manuscript. MB and AA conceived the project. All authors contributed to the ideas and manuscript editing.

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### **Abstract**

The effects of severe drought on the stability of dryland ecosystems are still uncertain and it is unknown whether diversity can buffer changes in systems that are adapted to water-limitation. We investigated the effects of long-term induced drought on the composition and maturity of biological soil crusts (biocrusts), as well as tested the hypothesis that diversity promotes stability using compositional resistance as a measure for ecosystem stability. We surveyed an array of 25 sites in the central Colorado Plateau, USA, that included plots that received ambient precipitation and plots that had experienced eight years of ~35% precipitation reduction. We found that biocrusts can maintain broad compositional integrity after long-term climate disturbance. However, biocrust successional reversal still occurred, with a reduction of later successional constituents and an increase of early successional cyanobacterial cover. Our findings indicate that long-term drought could have major impacts on biocrust community stability.

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### **Introduction**

For decades we have witnessed the rapid decline of biodiversity across ecosystems due to the synergistic impacts of natural and human-caused disturbances (Stork 2010; Pimm *et al.* 2014). The combined effects of current and future disturbances represent a threat to the stability of ecosystems that can have significant and broad-scale impacts on multiple environmental services that are linked to and supported by biodiversity (Millennium Ecosystem Assessment 2005). The stability of ecosystems in response to disturbance has intrigued ecologists for decades (Odum 1950; Holling 1973; McCann 2000) and considerable research has been devoted to the relationship between diversity and ecosystem stability. The work of MacArthur (1955) and Elton (1958) pioneered the diversity-stability hypothesis, which states that diversity promotes stability. However, later theoretical and applied ecological studies found evidence of positive, negative, neutral, and dynamic effects of diversity on ecosystem stability (Ives & Carpenter 2007; Tilman *et al.* 2012; Isbell *et al.* 2015; Pennekamp *et al.* 2018). These varied findings and lack of consensus correspond to the multifaceted nature of disturbances, species diversity, and stability, coupled with the limitations of what can be measured by ecologists (Donohue *et al.* 2016).

Ecological stability is a broad concept that can be described using three main components in response to a disturbance: temporal variability in a system property, persistence of functions and structure in the face of a change in external conditions (resistance), and rate of recovery from disturbance (resilience) (Pimm 1984; McCann 2000; Donohue *et al.* 2016). Empirical studies of biodiversity-stability have focused primarily on the temporal variability of one major measure of ecosystem function – plant productivity – in order to establish and measure the integrity of a community or ecosystem (Tilman 1996; Pfisterer & Schmid 2002; Vogel *et al.*

. 2012; Isbell *et al.* . 2015; Lepš *et al.* . 2018). But it is also important to assess the ecological resistance as a measure of stability, as pressures of climate change become more frequent, that can help inform policies governing land use and biodiversity conservation (Donohue *et al.* . 2016; Pennekamp *et al.* . 2018).

We focused our study on the Colorado Plateau, a dryland ecoregion of the Southwest United States, where increasing aridity and drought severity are among several expressions of climate change likely to impact these ecosystems and the human societies that depend on their services (Seager *et al.* . 2007; Munson *et al.* . 2011; Cook *et al.* . 2015; Hoover *et al.* . 2015). While responses of dryland ecosystems to the changing climate are still uncertain (Huang *et al.* . 2017), global drylands could exhibit shifts in the distribution, structure, function, and composition of ecosystems; however, geographical and latitudinal variation suggest different outcomes for particular regions (Trenberth *et al.* . 2014; Huang *et al.* . 2017). The cold desert of the Colorado Plateau in southern Utah is one of several dryland regions suffering the combined effects of climate change, changes in land use and invasive species (Munson *et al.* . 2011; Copeland *et al.* . 2017).

One nearly ubiquitous feature of drylands is the presence of a soil surface biocrust community. In these systems, the soil beneath and between the canopy of widely spaced vascular plants is generally dominated by the soil surface community of cyanobacteria, algae, fungi, lichens, bryophytes, and soil microbes collectively known as a biological soil crust (biocrust). This community is a major ecosystem component involved in water balance maintenance, nitrogen fixation, soil stability, wind and water erosion resistance, and dynamic interactions with other biota of dryland ecosystems (Belnap & Gardner 1993; Belnap & Weber 2013; Maestre *et al.* . 2016; Seitz *et al.* . 2017; Havrilla *et al.* . 2019; Eldridge *et al.* . 2020).

Biocrusts often follow a pattern of successional sequence, in which the bare ground is colonized by lightly-pigmented, filamentous cyanobacteria that aggregate the soil particles, making soils suitable for subsequent colonization by nitrogen-fixing, darkly pigmented cyanobacteria, and then by mosses and/or lichens (Read *et al.* . 2016; Weber *et al.* . 2016). Based on the dominance of cyanobacteria versus mosses and/or lichens, biocrusts are often classified into early and late successional stages, respectively, which inform the properties of the community (Lan *et al.* . 2012). Despite being well-adapted to harsh arid conditions, biocrusts and particularly mosses are sensitive to shifts in the timing and magnitude of precipitation and to rising temperatures that shorten the hydration periods in which biocrusts are physiologically active (Reed *et al.* . 2012). Therefore, climate change is a disturbance that can potentially lead to a decrease of the late successional constituents, mosses and lichens, i.e., a reversal of succession (Ferrenberg *et al.* . 2015).

We used a long-term precipitation reduction experiment in the field to investigate the effects of drought on biocrust community composition and successional maturity, and to test the diversity-stability hypothesis using resistance to climate disturbance as one component of ecosystem stability (Pimm 1984). In this context, we defined resistance as the ability of a community to maintain compositional and structural integrity following a disturbance (Sankaran & McNaughton 1999; Connell & Ghedini 2015). Biocrust composition was measured by species presence and abundance, while the successional maturity was considered as the abundances of the functional groups of the community. We hypothesized that: (1) Precipitation reduction would induce a successional reversal in biocrust composition, which would be indicated by a decline in moss and lichen cover and increase in cyanobacterial cover; (2) Higher initial diversity would confer greater compositional resistance, which would be indicated by less extreme changes of community composition to the imposed climate perturbation; and (3) The degree of compositional resistance observed in the biocrust community would be inversely related to the degree of the environmental stress experienced. Testing these hypotheses helped to illuminate the factors controlling community change under a climate change scenario and to move us closer to being able to predict the magnitude of changes in dryland communities.

## Material and methods

### *Precipitation exclusion array*

We conducted our study using an array of 25 paired control and precipitation exclusion sites that were established by the US Geological Survey across Southeastern Utah (central Colorado Plateau) in 2010 to understand the impacts of forecast increased aridity on Colorado Plateau drylands (Hoover *et al.* . 2015,

2017; Winkler *et al.* 2019). Our set of 25 paired plots (with each pair representing one site) are a subset of the 40 sites in the USGS study, which we selected based on presence of well-developed biocrusts. The other 15 sites had insufficient biocrust cover to be suitable for our research (i.e., less than 15% cover of moss and lichen). The ca. 4500-km<sup>2</sup> study region from which the experimental sites were selected spanned a range of plant communities, soil depths and parent materials, soil textures, elevations, climates and an aridity gradient (Table 1, Supporting Information). The climate in the ecoregion is characterized as a cold arid to semi-arid dryland with bimodal precipitation.

At each site, pairs of similar vegetation and soil patches were identified that represented a target plant community and treatments were assigned randomly. Each site consisted of two paired 150 x 200 cm plots: a control and a drought treatment. Control plots received ambient precipitation while drought plots experienced 35% precipitation reduction year-round using passive precipitation removal shelters from 2010 to 2018. These shelters were 230 x 310 cm and sufficiently wide to provide a large buffer around the plots that also received the drought treatment; their slanted roofs were composed of V-shaped plexiglass strips that served as troughs to intercept rainfall and snow (Figure S1.). These strips were connected to a gutter system that directed water away from the plot. Furthermore, vinyl flashing was installed vertically around the plot, below and a few cm above ground, but beneath the shelters to hydrologically isolate them (Hoover *et al.* 2015).

### *Biocrust community survey techniques*

In April of 2018, we used a non-destructive method to survey the paired plots in the 25 selected sites, the cover of individual biocrust bryophyte and lichen species, cyanobacterial community types (i.e., “dark” and “light”; see below) were measured, and other ground cover at the soil surface such as rocks, litter, and scat were noted. Cyanobacterial biocrust cover was not classified taxonomically but categorized as lightly-pigmented vs. darkly-pigmented because of the impossibility of species identification of cyanobacteria in the field; a darker level of pigmentation is indicative of successional development and function (Belnap *et al.* 2008; Lan *et al.* 2017). To collect cover data, we placed ten 25 x 25 cm gridded point intercept quadrats per plot, recording 20 intersections for each (Jonasson 1983). To place the quadrats, each plot was divided into 12 sections of 0.5 x 0.5 m. We placed quadrats in the bottom left corner of the 10 outer sections. Within each gridded quadrat, we aligned a pin flag with each grid intersection and extended it downward to the soil surface, recording the species or ground cover element intercepted. An intersection accounts for 5% cover within that framework. To account for species or cover types that the pin flag did not hit, but were within the quadrat, we searched the quadrat for additional species and estimated a visual percentage of cover to the nearest one percent. When a moss or lichen species was unknown, we assigned a genus or consistent morphospecies name to separate it from other species and take it into account in our diversity estimates. All evaluations were made when biocrust species were dry and inactive. Because our assessment was non-destructive, specimen collection was not possible, and some species were not identified to the species level. For all 10 sections per plot, we calculated the percentage cover of all visible components. We subtracted the cover of non-colonizable soil surface (i.e., plant litter, rock) and recalculated the cover of all major functional groups: bryophytes, lichens, cyanobacteria, and bare ground, as well as the Shannon diversity index (Shannon & Weaver 1949) based on available habitat. We then averaged the values of the 10 cover frames to calculate cover at the plot level. In the absence of a biocrust diversity survey of the plots at the time of installation, we used the diversity data of the control plots as our best available proxy for the initial biocrust diversity, due to the proximity of the plots and similar environmental conditions.

### *Data analysis*

We performed all data analyses using the statistical program R (R Core Team 2016). We checked for normality using the Shapiro-Wilk test and made square root transformations of percentage of cover for bare soil, darkly-pigmented cyanobacterial cover, lichen cover, and moss cover to meet normality assumptions. Data on lightly-pigmented cyanobacterial and late successional cover (the sum of darkly-pigmented cyanobacterial cover, lichen cover, and mosses cover) did not need transformations. To evaluate changes in community successional maturity, we compared the percentage of cover of the biocrust functional groups between control

and treatment using a blocked ANOVA with site as a random effect.

Using the community ecology *vegan* package in R (Oksanen *et al.* 2018), we summarized biocrust community composition with a two-dimensional nonmetric multidimensional scaling (NMDS) ordination using Bray-Curtis distance. This method allowed us to visualize and test the direction and magnitude of community composition changes from control to treatment; we extracted the NMDS coordinates and calculated the difference (treatment minus control) along each axis. We performed a one sample t-test on the values for each axis, the p-values were then combined in a single Fisher's C statistic (Shipley 2000), which follows a chi-squared distribution with 2k degrees of freedom.

To further test for dissimilarities in the communities between the control and drought treatments, we used a dissimilarity index test, called a temporal beta-diversity index (TBI), treating the observations between control and treatment as if they were surveys through time. TBI is calculated as a common pairwise beta diversity index but allows a test of significance at each site, which differs from most beta diversity analyses (Legendre 2019). The dissimilarity index used for community composition for each of the 25 sites was the percentage of difference (Odum 1950), also known as the Bray-Curtis index and equivalent to the Sorensen index, but for species abundances, which tend to be more informative than incidence data (Legendre 2012). Further, the dissimilarity index was partitioned into finer indices of losses (B) and gains (C) of abundances-per-species. The mean of the differences between the B and C statistics is also computed across all sites in a study. The gains versus losses (C – B) difference across all sites were tested for significance using a paired t-test to observe specific patterns obscured in the overall test. All calculations were implemented in the TBI() function, available in the R package *adespatial* (Dray *et al.* 2020). We used the dissimilarity index and its components of losses (B) and gains (C) as indices of community resistance to climate disturbance, where a greater value indicates a greater degree of change in the community. Multiple linear regressions were used to evaluate how much variation of the community resistance was explained by the control Shannon alpha diversity, aridity, and its interaction. To avoid violations of assumptions, the normality of model residuals was verified by the QQ-plot, model linearity was visually evaluated by inspecting the residuals vs fitted values plot, and we identified outliers using the outlierTest function from the *car* package. Finally, plots were made using the *ggplot2* package (Wickham 2016).

## Results

### *Successional reversal in biocrust maturity*

We found that eight years of precipitation reduction had a significant effect on cover and relative abundance of some biocrust functional groups. Overall, percentage bare soil was higher by 13.1% ( $F(1,24) = 3.843$ ,  $p = 0.062$ ), and lightly-pigmented cyanobacterial cover was higher by 17.6% ( $F(1,24) = 5.267$ ,  $p = 0.031$ ) with the precipitation reduction treatment compared with ambient precipitation control plots. In contrast, moss cover was lower by 31.6% ( $F(1,24) = 6.617$ ,  $p = 0.017$ ) and total late successional biocrust cover was lower by 23% ( $F(1,24) = 6.319$ ,  $p = 0.019$ ). No effect was found in the lichen cover ( $F(1,24) = 1.98$ ,  $p = 0.172$ ) or in the darkly-pigmented cyanobacterial cover ( $F(1,24) = 0.872$ ,  $p = 0.36$ ) (Figure 1, Table S5.).

Out of six morphospecies of mosses encountered in our sites, *Syntrichia caninervis* was the dominant species with 10.9% and 7.5% mean cover in control and drought plots, respectively, followed by *Syntrichia ruralis* with 8.8% and 5.4% mean cover, respectively. All the other bryophytes had less than 1% mean cover (Table S6). Lichens showed a richness with 12 morphospecies. The lichens were dominated by *Enchylium coccophorum* with 1.3% and 1.2% of mean cover in control and drought plots, respectively, followed by *Enchylium tenax* with 1% and 0.7% mean cover, respectively (Table S7).

### *Biocrust community resistance to climate disturbance*

The final stress of our two-dimensional NMDS analysis was 0.157, indicating a good representation of the data. Community composition of biocrusts in control and treatment plots did not show clear differences (Figure 2). Neither distance nor direction of change from control to paired treatment plot were consistent among pairs of treated and control plots. We tested the magnitude and direction by using shifts in axis

coordinates on both axis 1 and 2. A one sample t-test in axis 1 did not show a significant difference ( $p = 0.916$ ). The same test for Axis 2 showed a significant shift toward the positive pole of the axis ( $p = 0.012$ ), which correlates with the direction of the aridity gradient. Our combined test of these two results (Fisher's  $C = 9.04$ ,  $p = 0.06$ ) suggested only a mild overall shift in direction and magnitude.

No site had significant TBI indices at the  $p < 0.05$  significance level after correction for 25 simultaneous tests (Supporting Information, Table S1). The overall dissimilarity was partitioned in the component indices, where species abundance losses (B) represented 49.6% of the dissimilarity and the species abundance gains (C) 50.6% (Table S2, Table S3). The mean of the differences between gains and losses was positive but not significant ( $p = 0.905$ , Table S4).

We observed positive linear slopes between control diversity and the percentage difference dissimilarity index ( $R^2 = 0.072$ ,  $p = 0.110$ ), species abundance losses ( $R^2 = 0.095$ ,  $p = 0.078$ ), and species abundance gains ( $R^2 = 0.091$ ,  $p = 0.083$ ), after excluding one outlier in every model. However, multiple regression models showed that neither control plot diversity, aridity, nor their interaction had a significant effect on the overall dissimilarity of the biocrust communities or their components (Table 2, Figure 3).

## Discussion

In this study, we sought to understand the impacts of drought on the community stability of biocrusts. We examined two perspectives on how the central Colorado Plateau's biocrusts might resist change under experimental precipitation reduction, i.e., community successional maturity and species composition. Our results supported our hypothesis that successional reversal or successional slowing would occur, with lower abundance of later successional moss cover and higher abundance of early successional lightly-pigmented cyanobacterial cover. Further, we showed broad compositional resistance with no evidence to support the diversity-stability hypothesis; rather, our results indicated a negative relationship between diversity and compositional resistance with no effect from the aridity gradient.

### *Successional retrogression of biocrusts: a common response to perturbation*

Eight years of reduced precipitation input led to lower late successional biocrust cover and higher lightly-pigmented cyanobacterial cover, which likely expanded into areas previously occupied by mosses (Figure 1). The moss constituent of the biocrust, dominated by *Syntrichia caninervis* in this region, has previously shown pronounced and rapid mortality due to carbon starvation in response to an increased frequency of small summer watering events relative to a lesser frequency of larger hydration events (Coe *et al.* 2012; Reed *et al.* 2012). Because mosses, like all biocrust organisms, lack roots and do not actively regulate water loss (e.g., do not have stomates), their activity and carbon gain are directly tied to the amount of time that soil surfaces are wet (Mishler & Oliver 2009). Furthermore, upon rehydrating, they initially lose more CO<sub>2</sub> to respiration than they gain from photosynthesis (Coe *et al.* 2012). If the biocrusts dry again before equilibrium is reached beyond the compensation point for C fixation, then they experience a net C loss over that hydration event. Repeated short-duration hydration (e.g., small amounts of water added during summer monsoon precipitation) can nearly eliminate mosses in approximately one year (Reed *et al.* 2012). Our results indicated that a similar trajectory may unfold more gradually if the amount of precipitation is decreased across all rain events—with the 35% year-round reductions in this experiment effectively shifting the storm size distribution towards a greater frequency of smaller events. Less precipitation reaching the surface is likely to shorten hydration periods on average, offering less C gain per hydration event, and thus potentially more hydration events that result in net C-losses. *Syntrichia caninervis* did appear to be substantially more resistant to an overall reduction in precipitation than previous evidence on sudden simultaneous shifts in hydration frequency and magnitude. Relative to mosses, lightly-pigmented cyanobacteria (usually *Microcoleus* spp.; Garcia-Pichelet *et al.* 2013) appear much more resistant and able to expand in response to both kinds of precipitation change (Ferrenberg *et al.* 2015). Contrary to our hypothesis lichen cover did not experience the same negative impact as mosses with precipitation reduction despite being a late-successional species.

One of the more common successional sequences observed in biocrusts across dryland ecosystems is early

colonization of lightly-pigmented pigmented, filamentous cyanobacteria, followed by darker pigmented cyanobacteria, followed by lichens and/or mosses (Weber *et al.* 2016). This sequence is not universal but has been widely documented in our study area and many other locations. Thus, our observations are consistent with a significant slowing of succession or even with a reversal of succession. Ferrenberg *et al.* (2015) demonstrated that similar reversals are a common response to climate change and recurrent pulse perturbations, including stressful shifts in watering frequency, experimental warming, and physical trampling. We add long-term experimental precipitation reduction to the perturbations that can induce this response in biocrust successional maturity.

A successional retrogression of the biocrust state points toward cascading effects on multiple dryland ecosystem processes and functions. In comparison to the functions provided by earlier successional biocrust, reduced abundance of late successional biocrust implies a decrease in carbon and nitrogen fixation (Housman *et al.* 2006), soil moisture (Eldridge *et al.* 2020), soil stability (Fickett *et al.* 2019), and increases in soil redistribution, runoff, surface albedo, soil microtopography, and alterations to land-surface energy (Rutherford *et al.* 2017; Xiao & Bowker 2020). Moreover, the elevated bare soil (13.1% higher in droughted plots) implies that not only are the droughted biocrusts less functional, but precipitation reduction may cause an overall lower cover of biocrusts across a wide range of dryland types, consistent with global models predicting an overall decline in biocrust coverage as the climate changes (Rodríguez-Caballero *et al.* 2018).

#### *Biocrusts are compositionally resistant to climate perturbation*

We found a general compositional resistance indicated by the lack of substantial shifts in biocrust species composition in response to the imposed 8 year drought. Our analysis based on the NMDS ordination suggested only weak evidence of compositional shift; the lack of a stronger trend could be due to the heterogeneity of the communities, the variance in successional state among communities, and the often strong random component of the community responses to perturbations (Schmitz 1997). Part of the heterogeneity of the sites involves the long history of disturbances of the Colorado Plateau, like grazing by domestic livestock and wildfire, that are associated with a slow recovery rate due to the low productivity of the system (Schwinning *et al.* 2008). This may have resulted in a landscape where our experimental sites had different initial biocrust states and communities did not start at their maximum potential, having a realistic mosaic of communities of the region. Nonetheless, the weak direction of the compositional shifts correlated with the aridity gradient suggests that drought could slowly drive biocrusts to a species composition characteristic of more arid environments, underlying the common successional retrogression response of community maturity previously shown. This could occur both through alterations to the pace of recovery following disturbance and through unique successional trajectories caused by an altered climate. These minor shifts in biocrust composition, here measured as dissimilarity indices, were partitioned into two components: species gains and species losses. The biocrust species gains and losses indices were on average equivalent, showing that neither of the two processes was dominant in the compositional changes, regardless of the indication given by successional retrogression in which a consistent species loss would be expected as late successional cover decreases. However, we consider that perhaps a longer experimental time period than our eight-year drought could be necessary to shift composition, as biocrust species reach environmental conditions outside their tolerance range.

We expected that diversity would increase biocrust resistance to drought based on our second hypothesis. However, our models showed that the dissimilarity between control and droughted communities was not driven by the control diversity or by site aridity. Although diversity is rarely the primary driver of stability (Worm & Duffy 2003), finding no predictive power of diversity on the compositional resistance was unexpected, and leads us to infer that the degree of the compositional resistance may be driven by other community attributes rather than taxonomic diversity.

Additionally, we found a weak but positive relationship between overall dissimilarity and control plot diversity, suggesting that more diverse biocrusts are slightly less resistant due to greater shifts in composition as they gain and lose species (Figure 3). These results do not support our initial diversity-stability hypothesis; however, resistance, as a component of stability, refers to the difference in a system property from its un-

perturbed condition to a perturbed one. If under undisturbed conditions a property increases with diversity, the post-disturbance relationship is likely to have a less positive slope. Because species-poor systems already have low values of such properties under undisturbed conditions, they may be less affected by disturbance than species-rich systems (Pfisterer & Schmid 2002). Past studies have documented a negative relationship between diversity and resistance in systems with diversity-dependent productivity (Pfisterer & Schmid 2002; Vogel *et al.* 2012). This rationale explains the stronger negative impact of drought on richer biocrust communities, where the change in composition accounts for changes in relative abundance or cover (a productivity proxy), in a system that has shown richness to enhance productivity and functionality (Maestre *et al.* 2012; Bowker *et al.* 2017).

While previous studies have shown aridity to drive biocrust composition and functionality (Bowker & Belnap 2008; Delgado-Baquerizo *et al.* 2016), which could create variations in the strength of biotic interactions (Bowker *et al.* 2010; Maestre *et al.* 2010), we found no support here for the effect of aridity in biocrust compositional resistance. This lack of an aridity effect could also reflect a strong adaptation of the biocrust community to ambient aridity. Similarly, previous work at these same study sites found a surprising lack of interaction between drought and soil attributes in determining plant response (Hoover *et al.* 2015), which led to the suggestion that vegetation communities are adapted to their local soil conditions such that drought responses are similar across contrasting soil types. However, it is also possible that the range of our environmental gradient, our sample size, varied land use history, or the experimental duration, was not broad enough to capture the interaction of aridity and drought on biocrust composition resistance, or that other environmental factors not considered could have a stronger effect on the impacts of global change in our system.

#### *What does the changing climate hold for biocrusts?*

Climate change with its many expressions threatens the stability of ecological systems, yet difficulties arise when predicting different ecological consequences without understanding the impacts arid communities experience under changing conditions. Although biocrusts are generally composed of stress tolerant species, they are still sensitive to physical compression, frequent sub-optimal hydration periods, and hydration periods with high temperatures (Reed *et al.* 2012; Ferrenberg *et al.* 2015; Doherty *et al.* 2018). Ongoing climate perturbations and land use practices that result in soil disturbance will further cause habitat unsuitability and we will witness a strong decline in the cover of biocrusts globally (Rodríguez-Caballero *et al.* 2018). Studies focused on climate disturbances, ours included, indicate not only a decline in biocrust cover in the future, but also the retrogression of the developmental states of these communities. However, we demonstrated that biocrusts could broadly maintain the integrity of their species composition after long-term climatic disturbance, while having noticeable structural shifts with greater impact on mosses.

The diversity of species in biocrusts has been documented to influence productivity and multifunctionality but has not been studied with respect to its influence on community resistance. Although we limited our study to the diversity of lichens and mosses, more diverse communities seem to be more susceptible to experiencing a greater change in their composition. Press perturbations are also driving biocrusts to less functional states, in which the decrease in richness will directly impact the dynamics of the ecosystem. The combined impacts on well-developed and richer biocrust communities calls for urgent conservation actions on standing dryland biodiversity and the mitigation of climate change impacts to assure the preservation of their ecosystem functions and services. In addition, adding knowledge on long-term effects of climate change on the community maturity and composition of Southwest dryland communities will facilitate future climate projections of ecosystem function and feedbacks to the climate system.

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Table 1. Soil and climate characteristics of the rainfall reduction sites used in this study (See supplemental for data description)

| Site ID | Elevation (m) | Aridity Index | Climate | Soil depth and parental material | Soil texture (0-10 cm) |
|---------|---------------|---------------|---------|----------------------------------|------------------------|
| RR-10   | 1263          | 0.1208        | Arid    | Deep Sandstone                   | Sandy Loam             |
| RR-11   | 1264          | 0.1208        | Arid    | Deep Sandstone                   | Sandy Loam             |
| CV-07   | 1335          | 0.1264        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| CV-09   | 1332          | 0.1264        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| NR-41   | 1499          | 0.1269        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| NR-42   | 1499          | 0.1269        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| HQ-01   | 1364          | 0.1284        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| ON-23   | 1520          | 0.1296        | Arid    | Shallow Sandstone                | Loamy Fine Sand        |
| CV-08   | 1334          | 0.1305        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |
| NE-13   | 1526          | 0.1305        | Arid    | Deep Sandstone                   | Loamy Fine Sand        |
| JH-05   | 1377          | 0.1309        | Arid    | Shallow Sandstone                | Loamy Fine Sand        |
| OI-19   | 1741          | 0.1414        | Arid    | Shallow Sandstone                | Fine Sandy Loam        |
| MB-18   | 1788          | 0.1458        | Arid    | Deep Sandstone                   | Fine Sandy Loam        |

| Site ID | Elevation (m) | Aridity Index | Climate   | Soil depth and parental material | Soil texture (0-10 cm) |
|---------|---------------|---------------|-----------|----------------------------------|------------------------|
| IM-43   | 1804          | 0.1460        | Arid      | Shallow Sandstone                | Loamy Fine Sand        |
| GP-44   | 1838          | 0.1543        | Arid      | Deep Sandstone                   | Fine Sandy Loam        |
| DH-17   | 1850          | 0.1558        | Arid      | Deep Sandstone                   | Fine Sandy Loam        |
| BA-24   | 1824          | 0.1770        | Arid      | Shallow Sandstone                | Fine Sandy Loam        |
| OR-16   | 1902          | 0.1799        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| BB-26   | 1919          | 0.1812        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| BB-27   | 1920          | 0.1812        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| BB-28   | 1920          | 0.1812        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| BB-29   | 1919          | 0.1812        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| BB-30   | 1919          | 0.1812        | Arid      | Deep Sandstone                   | Very Fine Sandy Loam   |
| NH-22   | 1953          | 0.2001        | Semi-arid | Deep Sandstone                   | Fine Sandy Loam        |
| BC-31   | 2008          | 0.2110        | Semi-arid | Deep Sandstone                   | Loam                   |

Table 2. Results of the multiple linear regression models used to examine the influence of control plot diversity, aridity and the interaction on Dissimilarity Index and its components. Parameter estimates, standard errors, and *P* values are shown.

|                             | Percentage difference dissimilarity index (D) | Percentage difference dissimilarity index (D) |
|-----------------------------|-----------------------------------------------|-----------------------------------------------|
|                             | F = 0.767 Adj R <sup>2</sup> = -0.005         | F = 0.767 Adj R <sup>2</sup> = -0.005         |
| Model terms                 | Coef                                          | S.E.                                          |
| (Intercept)                 | 0.086                                         | 0.377                                         |
| Control diversity           | 0.270                                         | 0.427                                         |
| Aridity                     | 0.535                                         | 2.700                                         |
| Control diversity * Aridity | -1.149                                        | 3.067                                         |
|                             | N= 24                                         |                                               |

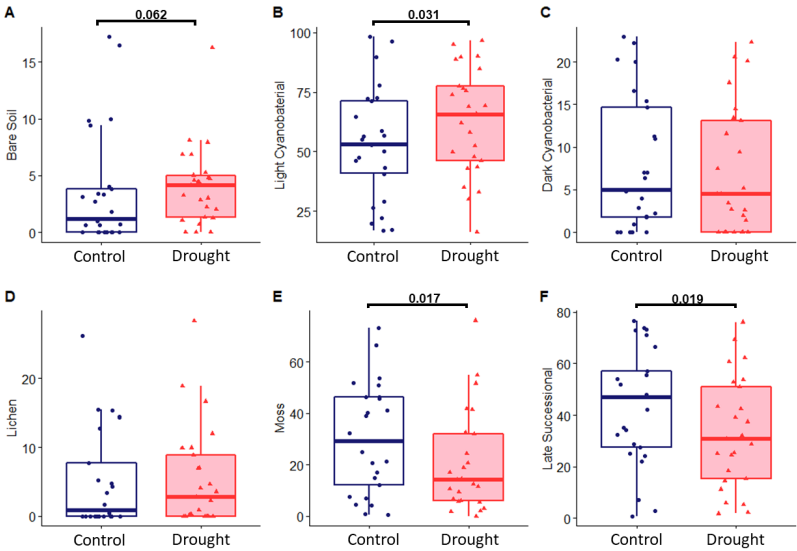


Figure 1. Comparisons of percentage of cover between control and drought treatment plots for the four biocrust functional groups, bare soil and the overall late successional biocrust cover. (A) Bare soil cover. (B) Lightly-pigmented cyanobacterial cover. (C) Darkly-pigmented cyanobacterial cover. (D) Lichen cover. (E) moss cover. (F) Late successional cover (the sum of darkly-pigmented cyanobacterial cover, lichen cover, and mosses cover).  $P$ -values of treatment effects within blocks are indicated when significant.

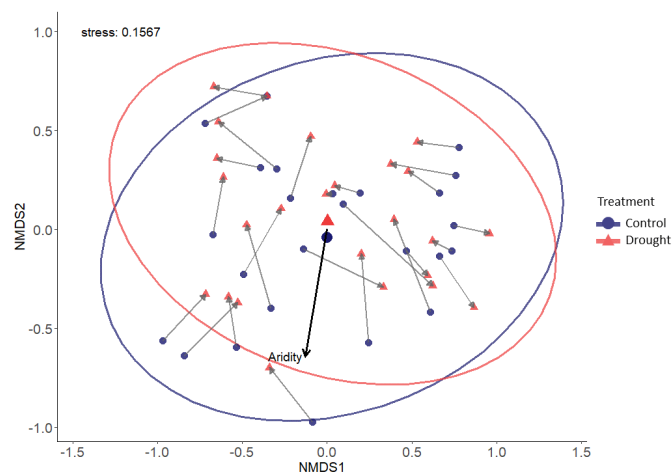


Figure 2. Nonmetric multidimensional scaling (NMDS) ordination plot of community composition. The ordination is based on cover (%) of moss and lichen species, and cyanobacterial community types (“dark” and “light”) from control and drought treatment plots. Grey arrows represent the distance of change between control and drought treatments per site. The black arrow indicates the direction of the maximum correlation of aridity index parameter with the ordination configuration, hence the decreasing aridity.

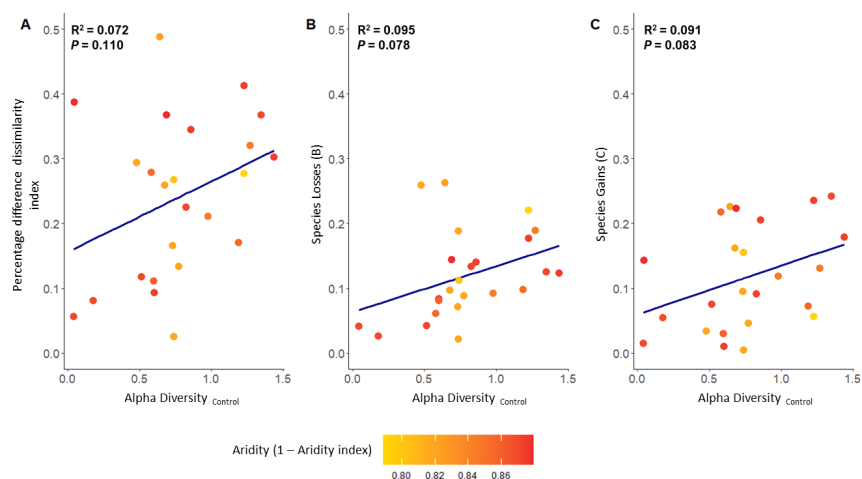


Figure 3. Relationships between control alpha diversity (Shannon index) and community resistance (percentage difference index and its components). The solid lines represent the fitted simple linear model. Each dot represents a site (N=25), and color intensity of dots reflects aridity values (variable not included in linear regression of fitted line for visual purposes).