REGULAR ARTICLE

Soil surface disturbance alters cyanobacterial biocrusts and soil properties in dry grassland and shrubland ecosystems

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Abstract

Aims Biological soil crusts (biocrusts) dominate soil surfaces in drylands, providing services that include soil stabilization and carbon uptake. In this study, we investigated the direct and biocrust-mediated effects of anthropogenic disturbances in two dryland ecosystems.
Methods We applied low intensity soil surface disturbance (twice-yearly footfalls) in grassland and shrubland ecosystems in northern Chihuahuan Desert, USA.
Results After five years of disturbance, biocrust photosynthetic capacity (chlorophyll *a*) declined by 44%. Declines were largest in interspaces between grassland plants. Levels of scytonemin, a biocrust sunscreen pigment, were 38% greater in shrubland than grassland and 44% greater under grass canopy than in interspaces, but decreased only 5% with disturbance. Disturbance

reduced soil surface stability 2 times more in the grassland than shrubland. Disturbance effects on other hydrologic and physical properties were indirectly mediated by the photosynthetic capacity of biocrusts. Disturbance indirectly increased infiltration depth and shallow (2–3 cm) soil moisture in the grassland but reduced surface moisture (<1 cm) in the shrubland.
Conclusions Biocrusts were more sensitive to low intensity soil disturbance in a grassland than shrubland ecosystem. While biocrusts mediated the effects of soil disturbance on dryland soil hydrological and physical properties, the nature of their influence differed between ecosystem types.

Keywords Biocrust · *Bouteloua* · Soil stability · Ecohydrology · *Larrea tridentata* · Sevilleta LTER

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Introduction

In dryland ecosystems, biological soil crusts (biocrusts) often form on soil surfaces between sparse patches of vascular plants, and are known to provide essential ecosystem services (Belnap 2003). For example, biocrusts can stabilize soil surfaces, enhance resistance to water and wind erosion, and increase soil nitrogen and soil aggregate formation (Eldridge and Kinnell 1997; Belnap and Lange 2003; Zhang et al. 2016; Rodriguez-Caballero et al. 2018). They have also been shown to alter local soil physical and hydrologic properties including soil porosity, water infiltration, and run-

off compared to bare dryland soils (Belnap 2006; Chamizo et al. 2012; Kidron 2015).

In regions dominated by biocrusts, trampling of soils by humans, livestock, or vehicular traffic is a primary form of disturbance (Zaady et al. 2016). Surface soil disturbance is predicted to reduce global biocrust surface area by as much as 40% over the next 65 years (Rodriguez-Caballero et al. 2018). Such mechanical disturbances to soil surfaces can directly alter soil properties by increasing soil compaction, reducing pore size, or increasing soil erosion by wind or water (Hamza and Anderson 2005; Drewry et al. 2008; Poesen 2018). However, surface soil disturbance can also *indirectly* alter soil functions by reducing biocrust biomass and altering microbial community structure, which can have cascading effects on soil properties such as soil ammonium and nitrate content (Kuske et al. 2012; Ferrenberg et al. 2015).

Prior studies report divergent results on the magnitude and direction of effects of surface soil disturbance on biocrusts and associated soil hydrology. For example, surface soil disturbance or removal of cyanobacterial-dominated crusts has been shown to increase, decrease, or have no effect on surface water runoff (Kidron et al. 2012; Rodríguez-Caballero et al. 2013; Faist et al. 2017), and to decrease or have no effect on water infiltration (Herrick et al. 2010; Chamizo et al. 2012). Past experiments examining soil hydrological properties suggest that it is often difficult to disentangle the direct effect of physical soil disturbance from the indirect effects on biocrust activity, possibly explaining the equivocal conclusions across studies (Belnap 2006). For example, surface soil disturbances can compact soil and directly reduce water infiltration; however, biocrust cyanobacteria can also decrease infiltration by reducing soil surface porosity and roughness through the formation of extracellular polysaccharide sheaths (Eldridge et al. 2000). One way to address this issue is to statistically separate the physical effects of surface soil disturbance from the biological effects of disrupting biocrust activity by leveraging biocrust bio-indicators such as pigment production. For example, cyanobacteria that are the foundational species of biocrusts produce chlorophyll *a* and key nitrogen-fixing species produce scytonemin, a photoprotective pigment. The concentrations of such pigments can be used as covariates in explaining disturbance effects. In addition, differences among

ecosystems in edaphic properties and biocrust microbial composition (Belnap and Lange 2003; Rossi et al. 2012) suggest that studies that impose the same disturbance on different ecosystem types will accelerate the ability to draw general conclusions about how surface soil disturbance affects biocrusts and associated soil properties.

We report results from experimental surface soil disturbance in two dominant dryland ecosystem types, grassland and shrubland, in the northern Chihuahuan Desert. These ecosystems differ in plant community composition and edaphic properties, but not strongly in biocrust microbial composition (Garcia-Pichel et al. 2013), allowing for direct comparisons of the role of biocrust in mediating disturbance. We imposed low intensity disturbance twice yearly by trampling non-vegetated soil surfaces wearing heavy boots, and tracked surface soil chlorophyll *a* and scytonemin content as indicators of biocrust photosynthetic capacity and potential biological activity (Belnap et al. 2008). Specifically, we addressed the following questions: (1) What are the effects of disturbance on biocrust microbial pigments through time? (2) What are the effects of disturbance on soil physical and hydrological characteristics? (3) Are the effects of disturbance mediated by biocrust activity? (4) For the preceding questions, how do these effects differ between the grassland and shrubland ecosystems? We hypothesized that physical disturbance to the soil surface would suppress indicators of biocrust microbial activity such as chlorophyll *a* and scytonemin (Kuske et al. 2012), and effects would differ between microsites in open interspaces and under plant canopies due to variation in light intensity. We expected that disturbance would directly decrease soil surface stability and increase soil bulk density by compacting soil. These physical effects of disturbance have well-known consequences for soil hydrology such as decreased infiltration, increased runoff, and reduced soil moisture (e.g. Warren et al. 1986). We used structural equation modeling to statistically partition the direct impacts of surface soil disturbance on physical and hydrological properties from the indirect effects mediated by reduced biocrust activity. We expected biocrust-mediated effects to be strongest for properties affected by biocrust microbe extracellular polysaccharides such as surface soil stability, moisture, and infiltration. Finally, we expected that disturbance would have different effects in shrubland and grassland ecosystems due to their different soil textures and dominant vegetation.

Materials and methods

Study site

The surface soil disturbance experiment was located in the Five Points region of the Sevilleta National Wildlife Refuge (NWR) and Long Term Ecological Research site (SEV-LTER) in the southwestern United States. We selected two ecosystems, shrubland and grassland, which differed mainly in dominant vegetation as well as some edaphic characteristics. The shrubland was dominated by Creosotebush (*Larrea tridentata* (DC.) Coville; 5% canopy cover) and black grama grass (*Bouteloua eriopoda* (Torr.) Torr.; 17% cover) (coordinates: 34.34048, −106.73406). The grassland did not have large shrubs and was dominated by a mix of black grama grass (27% cover) and blue grama grass (*Bouteloua gracilis* (Kunth) Lag. ex Griffiths; 6% cover) (coordinates: 34.33516, −106.70551). Previous work showed that these different communities differed strongly in the sensitivity of primary production to drought, with the grassland showing greater sensitivity to changes both in mean and interannual variance in aridity (Rudgers et al. 2018). Both ecosystems had sandy clay loam soils, but the grassland soils had higher sand content and bulk density. In addition, grassland soils had higher Mg, lower Ca, and lower N compared to the shrubland (unpublished data). Biocrusts in both ecosystems were dominated by cyanobacteria (*Microcoleus vaginatus* and *Microcoleus steenstrupii* complex; Garcia-Pichel et al. 2013; Fernandes et al. 2018), and few lichens (*Collema* spp). Previous work at our site determined that biocrust fluxes accounted for <3% of ecosystem gross primary productivity but could contribute up to >10% of observed soil respiration in grassland and shrubland ecosystems (Dettweiler-Robinson et al. 2018).

In May 2013, 20 plots (6 m × 6 m) were established in each ecosystem to study the effects of surface soil disturbance on community and ecosystem dynamics. All plots were spaced ≥20 m apart in all directions and were > 500 m from any access roads to avoid effects of dust. Plots were arranged in a 4 × 5 grid in each ecosystem. The disturbance treatment was assigned to plots in a completely randomized design, and beginning June 2013, disturbance was imposed twice each year (May, Oct) to capture the beginning and end of the growing/monsoon season. To impose the disturbance treatment, we scuffed all non-vegetated surface soil with two footsteps while wearing thickly treaded (heavy) boots (Kuske et al. 2012). As the experiment was located in a protected Wildlife Refuge, human foot traffic was the most relevant form of physical disturbance, but the treatment more generally mimics low-level surface soil disturbance. Control plots were left undisturbed. Twice yearly, we measured biocrust indicators and in 2016 (after 3 years of treatment), we quantified soil hydrological and physical properties.

Biocrust bio-indicators

We determined chlorophyll *a* content of surface soils (<1 cm depth) as an indicator of cyanobacteria photosynthetic capacity. In each plot, we collected samples (1–2 g) from open areas away from nearby plants (interspaces) and from under plant canopies to capture differences associated with microsite as biocrust microbial distribution can be very heterogeneous at a small spatial scale. At the grassland, we collected samples from four randomly chosen interspaces and below the canopies of two unique, randomly chosen *Bouteloua* spp. in each plot. At the shrubland, we collected samples from four interspaces, beneath the canopies of two unique *Bouteloua* sp. individuals, and beneath the canopies of two unique creosotebush individuals. Chlorophyll *a* was extracted from soil surface samples using DMSO, and content assessed using spectrometry via the methods outlined by Castle et al. (2011) and Caesar et al. (2018). Starting Oct 2015, we also analyzed the concentration of scytonemin, a photoprotective compound found in cyanobacterial sheaths, in the DMSO extracts but using the equation for acetone (Garcia-Pichel and Castenholz 1991). Chlorophyll *a* content and scytonemin values were averaged to obtain a single measure of each bioindicator per plot per microsite type per sampling date. Between 2013 and 2018, we made 15 collections on 2013-07-15, 2014-07-05, 2014-10-17, 2015-04-10, 2015-07-18, 2015-10-12, 2016-04-08, 2016-07-01, 2016-10-11, 2017-05-17, 2017-10-14, 2017-12-07, 2018-01-26, 2018-03-08, and 2018-04-28. Most samples were collected prior to the disturbance treatment application; thus the estimate of treatment effects is conservative because it allowed for maximum recovery of biocrusts between disturbances. During the final year (2017–2018), we collected samples approximately every 6 weeks to obtain a finer scale timeline of the chlorophyll *a* response.

Soil physical and hydrological properties

Soil moisture time series Throughout the experimental period, we sampled soil moisture in each plot before treatment re-application (2013-05-04, 2013-06-09, 2013-07-28, 2014-05-28, 2014-10-09, 2015-05-18, 2015-05-23, 2016-10-10, 2017-05-08, 2017-05-08, 2017-10-18, 2018-04-25). In 2013–2014, volumetric soil moisture was measured as the average of 4 capacitance measures to 15 cm depth made with a soil moisture probe (Aquaterr T-300, Costa Mesa, CA, USA) at randomly chosen locations near the center 1 m × 1 m of each plot. Starting in 2015, we began measuring gravimetric soil water content from three 2.5 cm diameter cores (0–15 cm depth) from each plot as the capacitance probe measurements were of insufficient precision. Soils were weighed immediately after collection, dried for 1 week at 105 °C, and then weighed dry.

Infiltration time In June 2016, we made additional one-time measurements of soil physical and hydrological properties. Water infiltration was measured with one double-ring infiltrometer (inner ring: 12 cm tall, 6 cm diameter; outer ring: 12 cm tall, 15 cm diameter) per plot. Rings were inserted 2 cm into the soil, being careful not to disturb the surface structure. Then, rings were completely filled with deionized water (300 ml in the inner ring; 1500 ml in the outer ring). Infiltration time was recorded as the time required for the water to completely infiltrate the soil.

Runoff potential and infiltration depth Runoff potential and infiltration depth were measured following the methods of Brotherson and Rushforth (1983) with some alterations. In each plot, we added approximately 1 L of deionized water onto the plot by pouring it through a perforated disk (8 cm diameter; 2 mm diameter holes) at 1.37 m height above the ground for 60 s. While this did not fully simulate natural rain droplets, the perforated disk allowed the addition of water in a more dispersed manner as opposed to a steady stream. Following the water addition, we measured the major and minor axes of the resulting wet ellipse of soil to the nearest mm. We then calculated the runoff potential of the soil as the surface area wetted, assuming the shape of an ellipse. A soil profile was created using a metal trowel inserted slightly off-center from the center of the wet soil area. Infiltration depth was recorded

as the greatest depth that water reached in the soil profile immediately after the water addition.

Soil moisture by depth Immediately after the water addition, we collected 3 cm diameter soil samples (~10–20 g) from strata along the soil profile at depths 0–1 cm (surface moisture), 1–2 cm, 2–3 cm (soil disturbance depth), and 9–10 cm (grass rooting depth) using a square scoop. Soil samples were processed individually for gravimetric soil water content as described above.

Soil texture After drying soils for gravimetric soil water content, we combined the four samples of soil moisture by depth (~50 g total per plot) to determine soil texture for each plot using the hydrometer method (Bouyoucos 1962).

Soil bulk density and aggregate stability We determined soil bulk density in each plot using a 5.08 cm diam. × 5.08 cm depth core (Robertson et al. 1999). Soil aggregate stability was assessed using the Jornada Experimental Range Soil Stability Test Kit in the field (Herrick et al. 2001). We averaged the stability ratings of two randomly chosen surface soil samples (6–8 mm diameter, 0–4 mm depth) taken from the interspaces of each plot.

Data analysis

Biocrust bio-indicators time series data We analyzed time series data on chlorophyll *a* and scytonemin concentrations using linear mixed effects models with the fixed effects of time (categorical, as there was no linear trend), ecosystem type (grassland or shrubland), soil disturbance treatment (disturbed or control), and microsite of sample collection (interspace or under grass canopy) and their interactions. We included the random effect of plot (nested within ecosystem type and disturbance treatment) to account for the non-independence of repeated measures on the same plot. Residuals were examined to ensure analyses met assumptions of normality of residuals and homogeneity of variances. Because we collected additional samples under the canopy of creosotebush, which was only possible in the shrubland ecosystem, we ran a similar analysis for samples from the shrub canopy, with the fixed effects of disturbance treatment (disturbed or control), time (categorical), and the treatment × time interaction, also including the random effect of plot (nested within treatment). In

addition, because we collected surface soil samples from interspaces on a larger number of dates than we collected under plant canopies, we ran a similar analysis on only the interspace samples with no microsite effect. We examined time series models with an autoregressive-1 (AR1) variance-covariance matrix to account for temporal autocorrelation, implemented in the <nlme> package (Pinheiro et al. 2018) of R (R Core Team 2018). However, there was no evidence for significant temporal autocorrelation in any analysis, based on comparison of the *AICc* value against a model lacking temporal autocorrelation. Thus, the reported models were implemented in the <lme4> package without AR1 autocorrelation (Bates et al. 2015). Post-hoc pairwise comparisons of treatment means for each sampling date were conducted with the package <emmeans> (Searle et al. 1980), using false discovery rate (FDR) correction for multiple comparisons (Benjamini and Hochberg 1995).

Soil moisture time series data Soil moisture was measured differently during 2013–2014 than during 2015–2018. Thus, we analyzed the time series separately. We used a linear mixed effects model with the fixed effects of time (categorical, as there was no linear trend), ecosystem type (grassland or shrubland), soil disturbance treatment (disturbance or control), and their interactions, including the random, repeated effect of plot (nested within ecosystem type and disturbance treatment). Residuals were examined to ensure analyses met assumptions of normality of residuals and homogeneity of variances. Similar to the analysis of bioindicators, there was no evidence for significant temporal autocorrelation, and reported models were implemented in <lme4>. Post-hoc pairwise comparisons of treatment means for each sampling date were conducted with the package <emmeans>, using FDR correction for multiple comparisons.

Soil physical and hydrological properties We examined differences in individual soil properties between ecosystem types and soil disturbance treatments using two-way ANOVA models that included the ecosystem × disturbance interaction. Since these were one-time measures, plot was the unit of replication. Residuals were examined to ensure analyses met assumptions of normality of residuals and homogeneity of variances.

Structural equation modeling To statistically decompose the direct effects of soil disturbance on soil properties from the indirect effects that were mediated by biocrust responses to disturbance, we used structural equation modeling (SEM) (Pugesek et al. 2003). We used the disturbance treatment as the exogenous variable (coded as 1 for disturbance, 0 for control). The general model included direct effects of disturbance on chlorophyll *a* content and soil properties (bulk density, stability, runoff, infiltration time and depth, and soil moisture at depth), and indirect effects of disturbance on soil properties mediated through biocrust chlorophyll *a* content (see Fig. 1 for cartoon of generalized model). We fit each soil property response in separate models. Because models were just-identified, no measure of overall model fit was reported. Analyses were conducted using the <lavaan> package in R (Rosseel 2012).

Results

Soil disturbance reduced levels of biocrust chlorophyll a and microbial sunscreen pigment

Chlorophyll *a* content was, on average, 44% greater in the control plots than in the disturbance treatment (Fig. 2, Table 1). Biocrust chlorophyll *a* did not, on average, significantly differ between the grassland or shrubland ecosystem (estimated mean ± s.e.: grassland = 1.17 ± 0.05 μg/g soil; shrubland 1.16 ± 0.05 μg/ g soil; $P > 0.7$, Table 1). Soil disturbance caused the largest declines in chlorophyll *a* during early spring and summer (Mar-Jul), as indicated by a significant treatment × time interaction (Table 1, Fig. 2). The effect of soil disturbance on chlorophyll *a* was largely consistent across the two ecosystems, as indicated by non-significant ecosystem × treatment interactions (Table 1, $P > 0.1$). However, soil disturbance effects were statistically significant on the largest number of dates for interspace soils in the grassland ecosystem type (Fig. 2a). Treatment effects were generally weaker during the first year of disturbance, when only interspace soils were sampled for chlorophyll *a* content (grassland: Jul 2013 $P = 0.26$, Jul 2014 $P = 0.50$, Oct 2014 $P = 0.0058$; shrubland: Jul 2013 $P = 0.95$, Jul 2014 $P = 0.91$, Oct 2014 $P = 0.65$). The only significant treatment effect prior to 2015 was during fall 2014 at the grassland, when chlorophyll *a* was reduced 49% by disturbance. Biocrust chlorophyll *a* was 24% higher under grass canopies, on average, than in the interspaces between plants (estimated mean ± s.e.: grass canopy
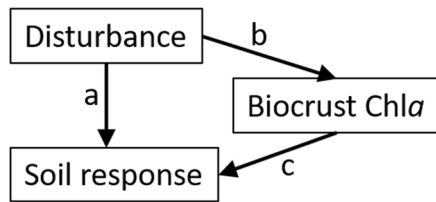
Fig. 1 Diagram of the general form of structural equation model to analyze the direct (path "a") and biocrust (biocrust chlorophyll a) – mediated (paths "b" and "c") effects of disturbance on individual soil responses in each ecosystem

1.32 ± 0.05 μg/g soil, interspace 1.01 ± 0.05 μg/g soil; $P = 0.0367$, Table 1). In the shrubland ecosystem, biocrust chlorophyll a under shrub canopies was not significantly reduced by the disturbance treatment (estimated mean ± s.e.: control 1.12 ± 0.09 μg/g soil, disturbance 1.00 ± 0.09 μg/g soil; $P > 0.25$ for Treatment and Treatment x Time).

On average, soil disturbance reduced scytonemin by 5% (Fig. 3, Table 1). This effect was small relative to microsite differences, in which scytonemin was 44% higher under grass canopy than in interspaces between plants. The strongest differences between grass and interspace microsites occurred in the shrubland, which had, on average, 38% higher scytonemin than the grassland (Fig. 3c, d, Time × Ecosystem × Microsite, $P = $

0.003). In the grassland, interspace scytonemin concentration had an initial, significant drop due to soil disturbance, but then remained at low levels in both disturbance and control plots (Fig. 3a), whereas scytonemin under grass canopies was significantly affected by disturbance only during winter of the final year of treatment (Fig. 3b). In contrast, in the shrubland, disturbance reduced scytonemin in interspace microsites but not under grass canopies, and significant treatment effects occurred near the beginning and at the end of the experiment (Figs. 3c, d and 3). Under creosotebush, which only occurred in the shrubland, scytonemin was significantly reduced 2.5% on average across all dates (estimated mean ± s.e.: control 0.80 ± 0.07 μg/g soil, disturbance 0.78 ± 0.06 μg/g soil; Treatment, $P = 0.022$; Treatment × Time, $P = 0.39$).

Soil disturbance altered some soil hydrological and physical properties

Of the properties measured, soil disturbance only significantly altered soil stability (Table 2). Soil disturbance decreased soil surface stability by ~60% on average across both ecosystems ($F_{1,36} = 56.00$, $P < 0.001$). However, soil disturbance

Table 1 Analysis of Deviance table of statistical results (chi-squared statistic, degrees of freedom, and P value) for repeated measures analysis of the responses of chlorophyll a and scytonemin concentration to Ecosystem Type (grassland, shrubland), Treatment (soil disturbance, control), Location of collection (interspace, under grass canopy), and Time of collection

Effect	Chlorophyll a μg/g soil			Scytonemin μg/g soil		
	X^2	df	P	X^2	df	P
Time	271.61	11	**<0.0001**	130.50	9	**<0.0001**
Ecosystem Type	0.13	1	0.7192	3.41	1	<u>0.0648</u>
Treatment	5.83	1	**0.0158**	3.84	1	**0.0500**
Location	4.36	1	**0.0367**	1.45	1	0.2293
Time × Ecosystem	70.97	11	**0.0000**	62.44	9	**<0.0001**
Time × Treatment	22.33	11	**0.0219**	9.20	9	0.4192
Ecosystem × Treatment	1.73	1	0.1888	0.01	1	0.9051
Time × Location	36.37	11	**0.0001**	70.04	9	**<0.0001**
Ecosystem × Location	2.00	1	0.1575	0.71	1	0.3995
Treatment × Location	0.09	1	0.7580	0.15	1	0.6956
Time × Ecosystem × Treatment	16.90	11	0.1109	4.76	9	0.8545
Time × Ecosystem × Location	29.66	11	**0.0018**	25.39	9	**0.0026**
Time × Treatment × Location	19.15	11	<u>0.0585</u>	8.92	9	0.4444
Ecosystem × Treatment × Location	0.02	1	0.8953	0.14	1	0.7045
Time × Ecosystem × Treatment × Location	11.50	11	0.4025	6.58	9	0.6811

P values <0.05 are bold, <0.1 are underlined

reduced stability more strongly in the grassland eco-system (64% decline) than in the shrubland (48% decline), as indicated by a significant interaction ($F_{1,36} = 7.01$, $P = 0.012$). Overall, the grassland had higher potential for stability to decline because it had 40% greater soil stability than the shrubland ecosystem ($F_{1,36} = 9.66$, $P = 0.004$, Table 2). In contrast to our initial hypothesis, soil bulk density was not significantly affected by the disturbance treatment ($P > 0.05$, Table 2). However, grassland soils had ~10% greater bulk density than shrubland soils ($F_{1,36} = 27.05$, $P < 0.001$, Table 2).

Soil disturbance did not directly alter soil moisture, infiltration, or runoff potential

Soil disturbance did not directly affect soil moisture throughout the experiment (Supplementary

Table S1, Supplementary Fig. S1). Similarly, infiltration rates and depth of infiltration were similar between disturbance and control plots, but differed between ecosystems. Grassland soils had 38% deeper water infiltration after the simulated rain event ($F_{1,36} = 8.73$, $P = 0.006$) and 37% faster infiltration times ($F_{1,36} = 6.25$, $P = 0.004$) than shrubland soils. There were no significant differences between disturbance treatments or ecosystems in water runoff potential or soil moisture at any depth after water addition (all $P > 0.05$, Table 2).

Direct versus indirect responses of soil properties to surface soil disturbance

Structural equation modeling revealed that the direct effects of disturbance on soil properties and the indirect effects mediated by biocrusts differed between
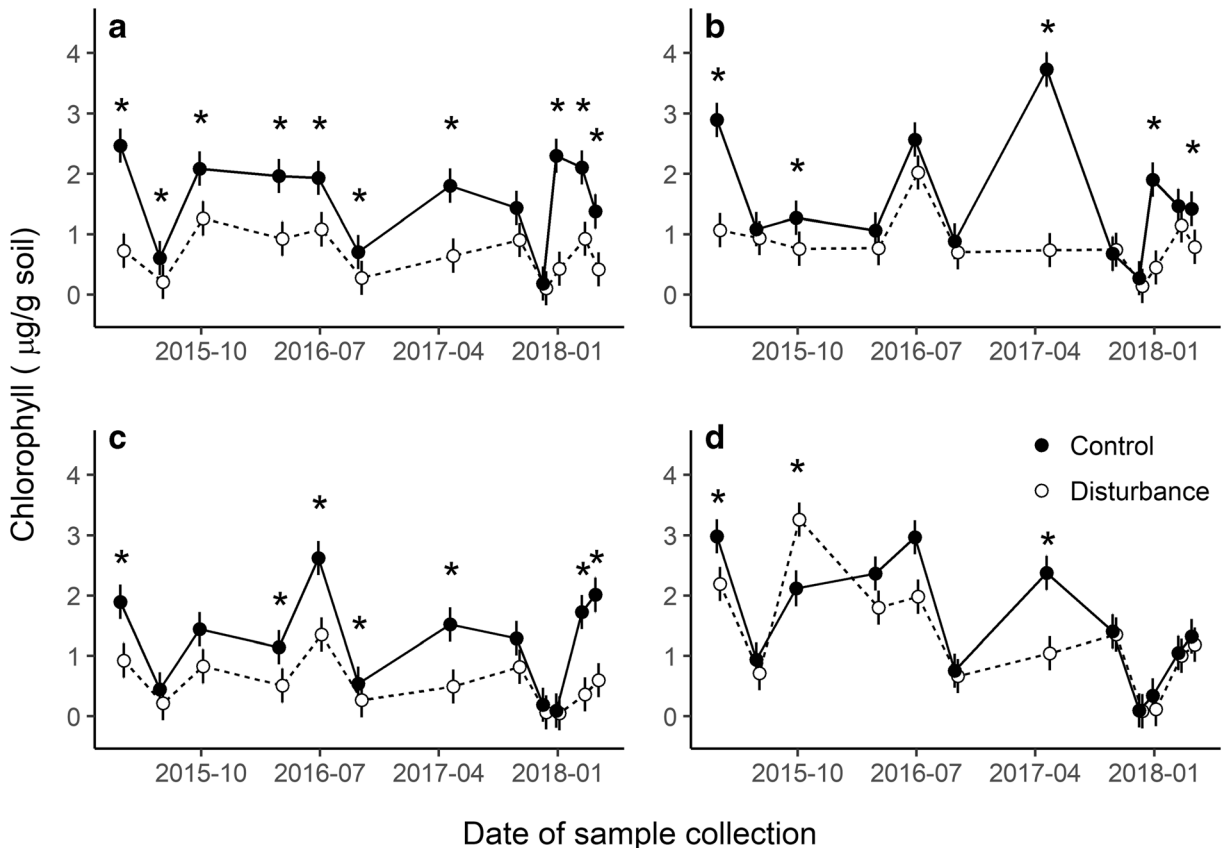

Fig. 2 Estimated marginal mean chlorophyll *a* concentration (µg/ g) on each sampling date for Control and Disturbance treatments. Plots show results for two ecosystem types: Grassland (**a**, **b**) or Shrubland (**c**, **d**) by two microsite locations of collection: Interspace between plants (A, C) or under a Grass Canopy (**b**, **d**). Error bars are standard errors, and asterisks indicate significant differences between treatments using false discovery rate (FDR) correction for multiple pairwise comparisons within the repeated measures analysis
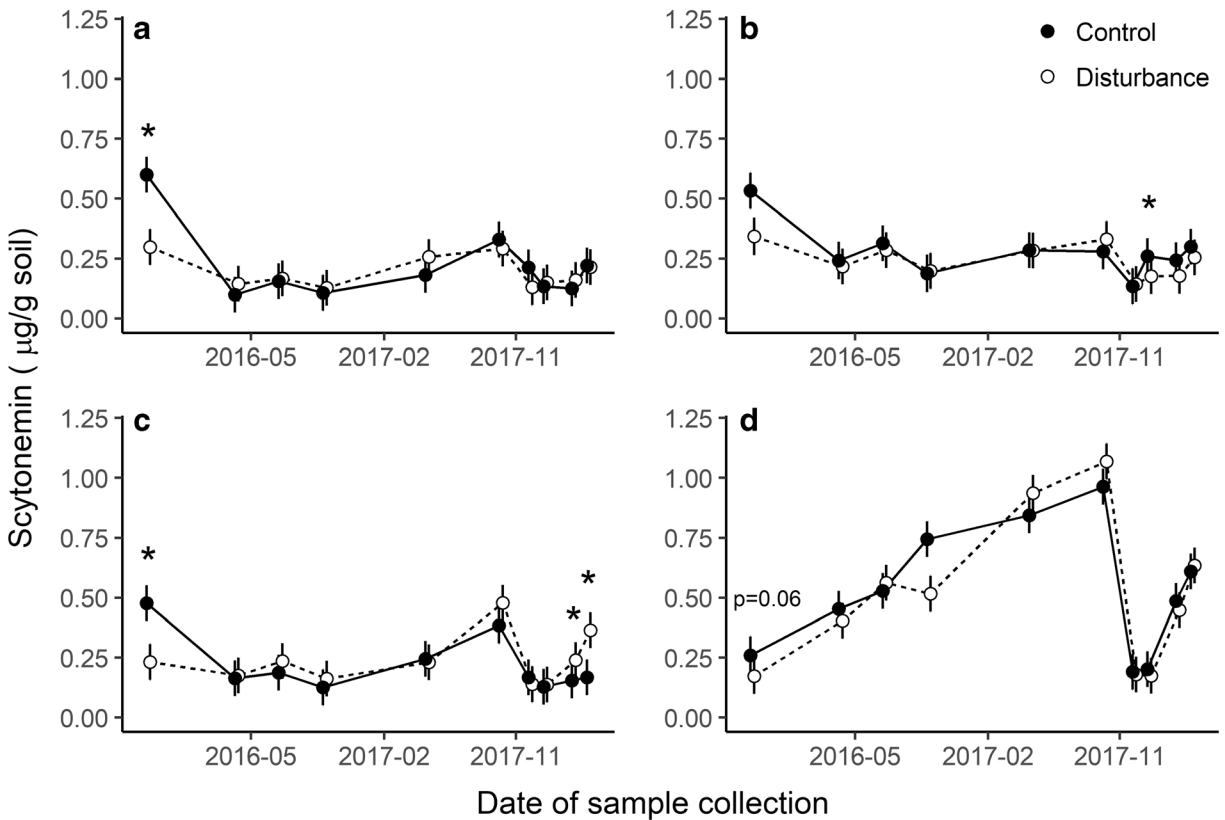
Fig. 3 Estimated marginal mean scytonmenin concentration (μg/g) on each sampling date for Control and Disturbance treatments. Plots show results for two ecosystem types: Grassland (**a**, **b**) or Shrubland (**c**, **d**) by two locations of collection: Interspace between plants (**a**, **c**) or under a Grass Canopy (**b**, **d**). Error bars are standard errors, and asterisks indicate significant differences between treatments using false discovery rate (FDR) correction for multiple pairwise comparisons within the repeated measures analysis

Table 2 Means (SE) and ANOVA statistics (F-statistic with numerator and denominator degrees of freedom, P value) for soil properties measured July 2016

	Grassland Mean (SE)		Shrubland Mean (SE)		Ecosystem Type		Treatment	
	Control	Disturbed	Control	Disturbed	$F_{1,36}$	P	$F_{1,36}$	P
Bulk Density (g/cm^3)	1.36 (0.01)	1.38 (0.02)	1.24 (0.01)	1.25 (0.01)	27.05	**<0.001**	0.50	0.482
Stability	3.45 (0.25)	1.25 (0.13)	2.20 (0.32)	1.15 (0.07)	9.66	***0.004**	56.00	***<0.001**
Infiltration Depth (cm)	3.54 (0.40)	3.45 (0.35)	2.38 (0.26)	2.70 (0.27)	8.73	**0.006**	0.13	0.724
Infiltration Time (s)	766.0 (106.8)	885.9 (153.1)	1513.9 (302.4)	1100.4 (147.8)	6.25	**0.017**	0.58	0.451
Runoff Potential (cm^2)	9727.7 (828.8)	9658.1 (593.2)	9431.3 (534.6)	9614.5 (1159.5)	0.04	0.836	<0.01	0.945
Moisture 0–1 cm (%)	22.47 (0.85)	23.20 (0.92)	23.47 (1.37)	23.41 (1.04)	0.33	0.572	0.10	0.756
Moisture 1–2 cm (%)	16.10 (0.40)	16.17 (0.48)	14.32 (1.03)	16.40 (1.00)	0.97	0.331	1.90	0.176
Moisture 2–3 cm (%)	9.51 (1.67)	10.17 (1.36)	7.32 (1.27)	7.66 (1.61)	2.50	0.123	0.11	0.740
Moisture 9–10 cm (%)	2.13 (0.15)	2.11 (0.20)	2.11 (0.13)	2.06 (0.13)	0.05	0.823	0.01	0.822

Interaction effects were not significant unless noted. P-values <0.05 are bold

*Significant interaction effect ($F_{1,36} = 7.012$, $P = 0.012$)

Table 3 Structural equation modeling statistics

	Grassland Ecosystem					Shrubland Ecosystem				
	R^2	Direct effect	P	Indirect effect	P	R^2	Direct effect	P	Indirect effect	P
Bulk Density (g/cm^3)	0.07	0.30	0.26	−0.16	0.31	0.02	0.23	0.47	−0.13	0.57
Stability	0.78	**−0.94**	**<0.01**	0.06	0.42	0.38	−0.45	<u>0.08</u>	−0.15	0.42
Infiltration Depth (cm)	0.32	−0.43	<u>0.06</u>	**0.39**	**<0.01**	0.09	−0.04	0.90	0.24	0.30
Infiltration Time (s)	0.09	0.34	0.20	−0.18	0.24	0.08	−0.19	0.54	−0.09	0.70
Runoff Potential	0.11	0.22	0.40	−0.23	0.15	0.03	0.22	0.49	−0.19	0.42
Moisture 0–1 cm (%)	0.10	0.34	0.19	−0.20	0.21	0.21	0.48	0.10	**−0.48**	**0.04**
Moisture 1–2 cm (%)	0.02	−0.07	0.80	0.10	0.53	0.10	0.318	0.30	0.01	0.98
Moisture 2–3 cm (%)	0.29	−0.30	0.20	**0.37**	**0.04**	0.06	−0.22	0.48	0.26	0.27
Moisture 9–10 cm (%)	0.05	0.07	0.80	−0.08	0.59	0.10	0.25	0.41	−0.32	0.17

"Direct effect" quantifies the direct effect of surface soil disturbance treatment on the soil property using a standardized coefficient (path "a" in Fig. 3). "Indirect effect" quantifies how the disturbance treatment affects soil properties through changes in biocrust chlorophyll, and is the combined effect of disturbance on chlorophyll multiplied by the effect of chlorophyll on the soil property measured (path "b" * path "c" in Fig. 3). *T*-test of coefficient difference from zero *P*-values (*P*) <0.05 are bold, <0.1 are underlined. For estimates of all fitted coefficients, see Supplementary Table S2

ecosystem types (Table 3, Supplementary Table S2). In the grassland, SEM showed that disturbance directly decreased soil stability, similar to previous ANOVA analyses. In addition, we found significant biocrust-mediated indirect effects on infiltration depth and soil moisture at 2–3 cm in the grassland. Specifically, increasing biocrust chlorophyll *a* content decreased infiltration depth and reduced soil moisture. Combined with the negative effect of disturbance on chlorophyll *a* concentration, this led to a *net positive* indirect effect of disturbance on these soil properties. This contrasted with the statistically non-significant *negative* direct effects of soil disturbance in the grassland. In the shrubland, we found little evidence of direct effects of soil disturbance on soil properties. However, biocrust chlorophyll *a* content was positively associated with soil moisture <1 cm, and combined with the negative effect of soil disturbance on chlorophyll *a*, resulted in a *net negative* biocrust-mediated effect of disturbance on this soil property.

Discussion

Low intensity surface soil disturbance chronically reduced biocrust photosynthetic capacity

Our multi-year experiment revealed that soil disturbance that consisted of only twice yearly heavy footsteps was

sufficient to chronically reduce biocrust chlorophyll *a* in both grassland and shrubland ecosystems of the northern Chihuahuan Desert. The only exception was in microsites under shrub canopies in the shrubland, where disturbance did not reduce chlorophyll *a*. This may be due to a faster recovery of cyanobacteria under shrubs compared to the harsher conditions in interspace and grass canopy microsites. Extensive temporal sampling in this project showed that the greatest reductions were in spring/early summer, prior to the application of the spring disturbance treatment and following the previous year's disturbance treatment after late summer monsoon rains. Past work has observed temporal variation in concentrations of biocrust pigments throughout the year (Bowker et al. 2002; Belnap et al. 2004). At our site, potential biocrust activity, as measured by chlorophyll *a*, was often greater in spring than fall. This resulted in larger differences in chlorophyll *a* content between the disturbed and control plots during the spring sampling period. While we cannot yet pinpoint the underlying drivers of biocrust activity, our work suggests that interactions between natural temporal dynamics of biocrust activity and the temporal dynamics of disturbance could be an important component of successful dryland management.

Despite the edaphic and vegetation differences between shrubland and grassland ecosystems, soil disturbance caused declines in chlorophyll *a* concentration that were of similar magnitude between the two locations. Prior studies that have imposed soil surface

disturbance in other ecosystem types have resulted in chlorophyll *a* decline, though magnitudes varied across ecosystems. For example, a 10-year experiment in cold desert sites of the Colorado Plateau, USA, found that two flat-footsteps per year reduced biocrust chlorophyll *a* by 25–50% (Kuske et al. 2012). In the Negev Desert, chlorophyll *a* levels in scraped biocrust took 6–7 years to fully recover to control levels (Kidron et al. 2008). Together, these results suggests a general pattern in drylands globally: Infrequent soil surface disturbances reduce the photosynthetic capacity of cyanobacteria-dominated biocrusts. Given that cyanobacterial crusts can be carbon sinks due to photosynthesis (Elbert et al. 2012), this widespread consequence of soil disturbance has implications for current understanding of dryland carbon cycling.

Low intensity surface soil disturbance slightly reduced biocrust sunscreen pigment production

In comparison to chlorophyll *a*, scytonemin pigment was less sensitive to soil disturbance (5% decline vs. 44%). Scytonemin also had greater spatiotemporal variability than chlorophyll *a*, differing among microsites, ecosystem types, and sampling dates. This variation may be partially explained by shifts in cyanobacteria community composition, which was outside of the scope of this study, and abiotic variation in ambient UV intensity. Scytonemin protects microbes from UV radiation, and its production is upregulated in response to UV exposure (Karsten et al. 1998). In addition to its importance for UV protection, scytonemin is a primary contributor to soil surface albedo and can increase soil surface temperatures (Couradeau et al. 2016). The positive relationship between scytonemin and temperature saturates at high concentrations of scytonemin; therefore, fluctuations in concentration at the low end of scytonemin production, such as in our focal ecosystems, have a stronger influence on soil surface temperature than variability at the high end of scytonemin production (Couradeau et al. 2016). The relationship between albedo and temperature has also been shown to create a positive feedback loop in dryland biocrust soils (Rutherford et al. 2017). Our results suggest that physical disturbance could increase soil albedo and reduce soil surface temperature by reducing scytonemin, which could have cascading effects on soil microbial activity and ecosystem functioning (Maestre et al. 2012).

Surface soil disturbance reduced surface soil stability, but had few direct effects on other soil properties

Contrary to our initial hypotheses, experimental soil disturbance reduced surface soil stability (by 60%), but did not have strong direct effects on other measured soil physical or hydrological properties. Some prior evidence supports our findings that low-intensity surface soil disturbance has minimal effects on soil physical and hydrological properties. Past experimental work has shown that foot traffic <10 passes did not have significant effects on dryland soil compaction or bulk density in a blackbrush shrubland (Lei 2004). Similarly, experimental surface soil disturbance had little effect beyond surface penetration resistance in sandy soils of Aladag Natural Park in Turkey (Yaşar Korkanç 2014). Our results suggest that disturbance via trampling may alter soil properties at different thresholds, and that biological indicators, such as pigment concentrations discussed above, are more sensitive than soil properties to the negative impacts of surface soil disturbance. Future work including a broader range of dryland ecosystems as well as a gradient of disturbance magnitude would further elucidate this hypothesis. However, our results also revealed that biocrust activity potential was a key component of indirect effects on dryland soil properties.

Biocrust activity potential mediated indirect effects of soil disturbance

Our work suggests that in northern Chihuahuan Desert grassland and shrubland ecosystems, the direct effects of footfall disturbance on soil properties are minimal. Rather, effects on soil hydrology appear to be mediated indirectly by live biocrusts, sometimes in the opposite direction of the potential direct effects. These indirect effects differed between grassland and shrubland ecosystem types. Soil disturbance indirectly increased soil moisture and infiltration in the grassland but decreased it in the shrubland. These effects arose from complex relationships between soil properties and biocrust chlorophyll *a* concentration in the two ecosystems. In the grassland ecosystem, soil moisture at 2–3 cm depth and infiltration depth both *decreased* with greater chlorophyll *a* concentration. In the shrubland ecosystem, soil moisture at <1 cm depth instead *increased* with greater chlorophyll *a* concentration. Our analysis highlights the utility and importance of disentangling these multiple factors that regulate

dryland soil ecosystem services. Similarly, Eldridge et al. (2010) showed that the effect of rabbit disturbance on water infiltration was largely mediated by biocrust cover, and that direct effects of disturbance were small (Eldridge et al. 2010).

The role of biocrusts in soil hydrology can depend on the dominant organisms of the biocrust community, the underlying soil texture, and the regional climate (Warren 2003; Belnap 2006). In particular, it has been hypothesized that *in sandy soils*, cyanobacteria sheaths swell upon wetting to block macropore space on the soil surface, thus reducing infiltration relative to non-biocrusted soils of the same texture. Whereas *in soils with finer texture* that have slower natural infiltration, cyanobacteria sheaths instead increase aggregate stability and macropore space, which increases infiltration (Warren 2003). Our results aligned with this hypothesis: chlorophyll *a* was associated with decreased infiltration and soil moisture in the grassland ecosystem, which had a sandier soil texture. In contrast, chlorophyll *a* was associated with greater soil moisture in the shrubland ecosystem, which had finer textured soil. Our results suggest understanding heterogeneity in the vertical distribution of microbial biomass or cyanobacteria sheaths in the soil could be crucial to understanding how soil disturbance differentially alters soil hydrology in dryland ecosystem types. Future work that quantifies microbial biomass and cyanobacteria abundance at different soil depths in combination with larger scale water addition treatments could shed light on the depth-specific moisture effects observed in our study.

Biocrust responses as early warning signals of anthropogenic disturbances

Biocrust community or activity responses to disturbance may serve as early warning signals (Scheffer et al. 2009) against future declines in ecosystem functions and services. In addition, biocrust preservation and rehabilitation could be crucial for restoring those functions (Rodriguez-Caballero et al. 2018). In our study, biocrust responses had greater sensitivity to disturbance and responded at lower thresholds of disturbance than soil properties. Future efforts toward the conservation of dryland ecosystem function should consider manipulating disturbance magnitude to identify the threshold at which surface disturbance impedes all facets of soil functioning. Higher levels of disturbance likely scales with increasingly detrimental effects on soil properties,

but this relationship could have nonlinear thresholds that depend on edaphic contexts. We suggest that the role of biocrusts in mediating the effects of disturbance and other external perturbations likely extend beyond physically proximate responses, such as soil properties, and cascade to other key community and ecosystem services such as primary production (Zhang et al. 2016) and terrestrial food web stability (Neher et al. 2009).

Conclusion

Our work suggests that the biological components of dryland surface soils are sensitive to infrequent, low-intensity disturbances, and may serve as early warning signals for ecosystem function decline. Experimental soil disturbance directly reduced soil surface stability, whereas effects on soil moisture dynamics were mediated indirectly by the activity of biocrusts and differed between grassland and shrubland ecosystems. Our work highlights the importance of disentangling direct and indirect effects in ecological study, as well as understanding the biotic and abiotic contexts that mediate the impact of external forcing in ecological systems. As anthropogenic disturbance regimes intensify in drylands throughout the globe, our work demonstrates that it is critical to evaluate its cascading effects on ecosystem services.

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