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Effects of disturbance on soil microbial abundance in biological soil crusts on the Loess Plateau, China

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ABSTRACT

Biological soil crusts (biocrusts) are important surface cover in drylands, but they are vulnerable to disturbance. To date, research has mostly specialized in changes in the soil microorganisms between disturbed and undisturbed biocrusts, and it is unclear whether disturbance intensity drives the soil microorganisms in biocrusts toward distinct responses. Thus, we investigated the changes in biocrust characteristics, soil properties and microbial abundance at six simulated grazing disturbance gradients (based on the coverage of the broken biocrusts) in the Loess Plateau region of China. The results showed that moderate disturbance, in which the biocrust coverage experienced a 20–30% breakage, was beneficial for improving the abundances of bacteria, actinomycetes and total microorganisms, but severe disturbance (i.e., 40–50% disturbance) may result in a significant reduction in abundance. The increased fungal abundance with the disturbance gradients was related to the aerobic feature of fungi. Additionally, a varied proportion of actinomycetes and bacterial abundance was found under disturbance. Disturbance induced the alteration of soil aeration, moisture and nutrient status (total N or ratio of C/N) that driving the changes of microbial abundance. These results will be meaningful for evaluating the ecosystem services of biocrusts under a disturbance event in dryland ecosystems.

1. Introduction

Biological soil crusts (biocrusts) include the microscopic (algae, cyanobacteria, bacteria, and fungi) and macroscopic (lichen, moss, and microarthropod) organisms that occur on the soil surface (Belnap et al., 2016). In dryland settings, where vascular plants are sparse, biocrust communities create a continuous living skin on the terrestrial surface and significantly increase the biodiversity in these regions (Belnap et al., 2003). More importantly, biocrusts perform critical ecological roles in these regions, such as improving carbon and nitrogen accumulation (Belnap, 2002; Billings et al., 2003), stabilizing the soil surface (Eldridge, 2003; Gao et al., 2017), altering soil aeration (Belnap et al., 2003), influencing soil hydrology (Bowker et al., 2008), and promoting plant growth and microbial activity (Gryndler et al., 2005).

However, biocrusts are susceptible to surface disturbance. Disturbance can profoundly impact biocrust coverage, species composition, and ecosystem function (Zaady et al., 2016). Some studies have confirmed that disturbance may decrease the abundance and alter the species composition of biocrusts. For example, in northwestern, Australia, Daryanto and Eldridge (2010) found that the biocrust cover on the plowed treatments was about four times less than that on the unplowed treatments. The results from Oregon, USA, showed that grazed sites had lower lichen richness than ungrazed sites (Root and McCune, 2012). Moreover, Eldridge et al. (2000) demonstrated that grazing caused significant shifts in biocrust composition by increasing the cyanobacteria at the expense of lichens.

Changes in biocrust coverage and species composition can drive a shift in the ecosystem functions of biocrusts. A study from southern Africa indicated that the soil nitrification rate of biocrusts was 2 times less in grazed sites than in ungrazed sites (Aranibar et al., 2008). Another study in semiarid grasslands in southern Botswana suggested that biocrust removal and burial under sand reduced the organic carbon content by almost 50% compared with well-developed biocrusts (Thomas, 2012). Moreover, research from semiarid Mediterranean grassland revealed that rabbit disturbance resulted in a 30% increase in soil infiltration compared to that of undisturbed biocrusts (Eldridge

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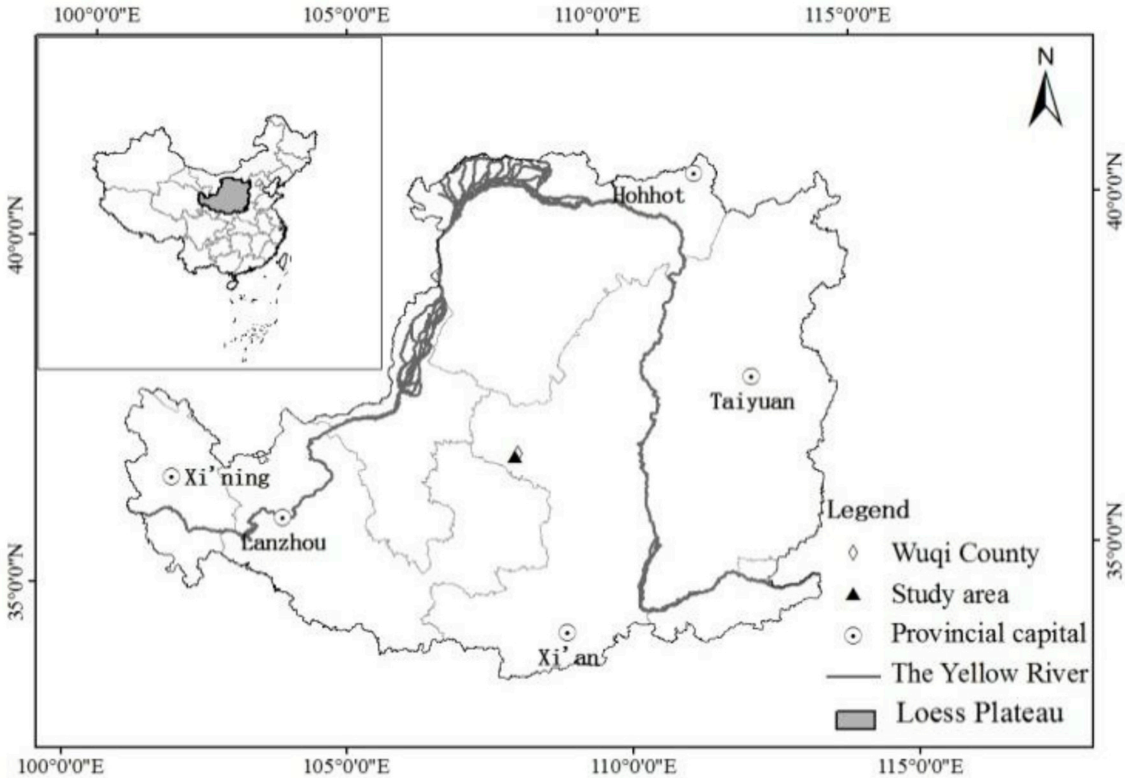

Fig. 1. Location of the study area.

et al., 2010). However, while the severity of environmental disturbances depends on their relative intensities, previous studies have specifically compared the variations in coverage, species composition and ecosystem functions of biocrusts between disturbed and undisturbed sites, and knowledge on the effects of disturbance intensity on biocrusts is still quite limited.

As a major inhabitant in biocrust communities, soil microorganisms play a vital role in biogeochemical cycles (Sofi et al., 2016), soil stability (Cotrufo et al., 2013; Ahrens et al., 2015), plant growth (Hartnett and Wilson, 2002) and ecological processes (Schulz et al., 2013). To date, many studies have suggested that biocrust coverage and composition strongly affect microbial abundance and diversity. Bian et al. (2011) found that soils with biocrusts were 25% greater than bare soils in microbial abundance in the Loess Plateau region, China. Hu et al. (2017) demonstrated that moss-dominated biocrusts (late-successional biocrusts) increased soil microbial numbers by 20% more than early successional cyanobacteria. Further, cyanobacteria create a stable environment for promoting the growth of microorganisms by secreting exopolysaccharides and forming filaments (Housman et al., 2006; Zhang et al., 2009).

Simultaneously, changes in biocrust coverage, species composition and ecological function under disturbance may also influence soil microorganisms. Zhao et al. (2011) and Liu et al. (2014) demonstrated that the soil stability structure in biocrusts was destroyed and the microbial biomass notably decreased. Research from a desert in northern Oman showed that when disturbance by oil pollution decreased the cyanobacteria biomass by half, the microbial abundance was reduced by 14% (Abed and Al-Kindi., 2016). As an indicator of environmental change, soil microorganisms are sensitive to surface disturbances, and determining their abundance and community structure in biocrusts may be the first step toward detecting environment disturbance. Thus, research on the impacts of disturbance on soil microorganisms has important implication for revealing the mechanisms between disturbance regimes and biocrust dynamics.

The Loess Plateau of China is one of the most severely eroded regions in the world. The natural recovery of the biocrusts alongside the grass and shrubs was observed within a few years after the implementation of the "Grain for Green" ecological project. The average biocrust coverage in this region is as high as 70% (Zhao et al., 2006). A few studies have examined the influences of disturbance on biocrusts in the region. Shi et al. (2017) found that soil infiltration increased by 12.55% when the biocrusts coverage experienced a 50% breakage. Wang et al. (2017) observed that the total N and available N decreased half a year after a disturbance.

In this study, we measured the soil microbial abundance using the dilution plate counting method. This method can directly reflect the response of soil microbial abundance to disturbance in a timely manner, even though the total microbial population detected by the method is low. The objectives of this study were to (1) evaluate changes in the biocrust characteristics and soil properties under different disturbance intensities, (2) analyze the responses of microbial abundance in the biocrusts to the disturbance intensities, and (3) determine the critical factors driving the microbial abundance in biocrusts under disturbance.

2. Materials and methods

We conducted a large-scale field sampling campaign to evaluate disturbance effects on the microbial communities of biocrusts. The soils at the collected plots were assumed to have similar soil properties. Thus, two slopes from south-north were used to build our plots, with a semisunward aspect of 315° and a sunward aspect of 297° (both of the slopes were approximately 25°), which represented almost parallel background values of soil properties. The plant and biocrust coverage on the semisunward aspect were 8.5% and 66.4%, respectively, and on the sunward aspect, they were 12.1% and 52.9%, respectively.

2.1. Study region

The study was conducted in Wuqi County of northwestern Shaanxi Province (Fig. 1). This area represents a typical district of the Loess Plateau in China (36°53′31″ N 108°13′28″ E; elevation range 1233–1809 m), where the topography varies locally in a complex of loessial hills and gullies. There is a typical warm temperate monsoon climate in the region, with an average annual temperature of 7.80 °C. The mean annual precipitation ranges from 400 to 450 mm (Fu et al., 2011). The region experiences an annual average of 2400 h of sunshine. The soils in the region are predominantly typical loessial soil. The dominant vegetation includes *Stipa* Spp., *Lespedeza* Spp. and *Artemisia* Spp.

The natural recovery of the biocrusts has been observed for more than ten years since the implementation of the "Grain for Green" ecological project in the region. The biocrusts have developed stably and are less original disturbance. Cyanobacteria are mostly distributed on south-facing slopes and always appear in the first year after cropland is abandoned (Yang, 2013). The dominant common cyanobacteria species are *Phormidium calceola, Phormidium tenue* and *Nostoc* spp. Lichens can be most often be found ten years after abandonment, and the dominant lichen species were *Fulgensia fulgens, Psora decipiens* and *Endocarpon pusillum*. Moss generally formed in the fourth year after cropping cessation, and their coverage may reach 80% on north-facing slopes in the region. The dominate moss species usually were *Didymodon tectorum, Bryum argenteum,* and *Didymodon vinealis* (Zhao et al., 2006).

2.2. Experimental design and disturbance operation

1) Experimental design

Five gradients of disturbance intensity were set up to explore the disturbance effects on the soil microorganisms of biocrust soil. The five gradients were set as G1 (10 ± 5)%, G2 (20 ± 5)%, G3 (30 ± 5)%, G4 (40 ± 5)%, and G5 (50 ± 5)%. The numbers between the brackets represent the practical disturbance percentage, which was counted on the basis of the coverage of the damaged biocrusts. Well-developed biocrusts without additional disturbance were built as a control (G0). Four replicates per combination of treatments were established, resulting in a total of 24 experimental plots (3.0 × 6.0 m in size).

2) Disturbance operation

In July 2015, 24 experimental plots were established by using sheet iron on the slopes. The collected plots were less original disturbance because tillage and grazing has been forbidden for 18 years. The experimental plots (18 m^2) were randomly arranged on two slopes in a south-north direction. A minimum separation distance between the plots of 5 m was ensured to minimize the risk of sampling non-independent areas.

Simulated grazing disturbance was conducted by a homemade tool the shape of a goat's hoof. The disturbance intensity was approximately 30 kg based on the average weight of an adult goat. The manpower strength was repeatedly calibrated by an electronic scale to ensure the consistency of the disturbance intensity. We randomly disturbed the soil surface on the basis of the coverage of the biocrusts. After disturbance, the components of the soil surface, including the biocrust taxa, vegetation, bare soil and litter, were investigated by using a 25 cm × 25 cm quadrat (Belnap et al., 2001). To maintain the level of disturbance, the disturbance was conducted approximately every two months based on the biocrust recovery.

2.3. Sample collection and preparation

Soil samples were collected on 19, July 2016 (one year after disturbance) from the 24 plots in the five disturbance gradients and the control. In each plot, samples of the biocrust layer and the 0–2 cm and 2–5 cm soil beneath the biocrusts were collected. Five subsamples per plot were randomly selected to assure the sample representativeness. Then, the five subsamples from the same depth were thoroughly mixed to obtain one composite sample. After field sampling, the samples were immediately transported to the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in Yangling City, Shaanxi Province. A portion of the fresh samples was frozen at −4 °C for quantifying the microbial abundance. The rest of the samples were air-dried and sieved (1 and 0.25 mm mesh) to measure other soil properties.

2.4. Measurement and methodology

2.4.1. Biocrust coverage

The coverage of cyanobacteria, lichen, moss, bare soil, recovered cyanobacteria, litter and vegetation was measured by using a 25 cm × 25 cm quadrat (Belnap et al., 2001).

2.4.2. Soil moisture and temperature

To determine the effects of disturbance on the soil environment, we measured the soil moisture (volumetric water content) and temperature by soil moisture and temperature sensors (ECH_2O 5TM probe, Decagon Devices Inc., Pullman, WA, USA) every 10 min in every disturbance gradient. The soil moisture and temperature data were collected from 11 to 19 July 2016 (including the day of sampling) in our study. We averaged all the soil moisture and temperature values of the collection times to remove data variability in a short period. The soil moisture was measured in the 0–5 cm soil layer (including the biocrust layer), and the soil temperature was measured in the biocrust layer and the 0–5 cm soil layer.

2.4.3. Organic matter, total N, available P and soil pH

The concentrations of soil organic matter and total N were measured using the Walkley Black and Kjeldahl methods (Nelson and Sommers, 1982), respectively. The available P was measured from $NaHCO_3$ 0.5 mol L^{-1} soil extracts according to Olsen et al. (1954). The soil pH was measured with an automatic acid-based titrator (Metrohm 702) in a soil: water w/w ratio of 1: 2.5.

2.4.4. Soil microbial abundance

The microbial abundance was measured using the dilution plate counting method (Long et al., 2003). The abundances of the bacteria, fungi and actinomycetes were extracted using a beef extract peptone culture medium, a Bengal red culture medium and a Gao culture medium (starch medium), respectively.

2.5. Statistical analyses

To test the first hypothesis (i.e., changes in biocrust characteristics and soil properties with disturbance gradients), we determined the differences among the disturbance gradients studied on the coverage (cyanobacteria, lichen, moss, bare soil, recovered cyanobacteria, vegetation and litter), soil moisture and temperature, and soil properties (organic matter, total N, available P and soil pH) with differences determined by conducting a one-way analysis of variance (ANOVA) and a least significant difference (LSD) multiple comparison ($P < 0.05$). The above data were collected to predict variations in microbial abundance. The data were tested for normality with a Kolmogorov-Smirnov test and for equality of variance using Levene's test.

To test the second hypothesis (i.e., whether there are variations in the microbial abundance and species proportions of the biocrusts among the disturbance gradients), the differences in microbial abundance (bacteria, fungi, actinomycetes and total microorganisms) were conducted using the same ANOVA and LSD analysis approach. To visualize the differences in species proportions among the disturbance gradients, we calculated the percent variation to verify the disturbance effects on their proportion

Table 1
Changes in characteristics of the sampling plots in response to disturbance intensity (mean ± SD).

Disturbance gradient (%)	Cyanobacterial coverage (%)	Moss coverage (%)	Lichen coverage (%)	Bare soil coverage (%)	Recovered cyanobacterial coverage (%)	Vegetation coverage (%)	Litter coverage (%)
G0	37.48 ± 9.36a	17.26 ± 2.68a	2.00 ± 0.68a	4.39 ± 3.04a	0.00a	13.50 ± 5.89a	12.90 ± 3.86a
G1	35.31 ± 8.26 ab	16.21 ± 1.75a	2.00 ± 0.75a	10.03 ± 3.21b	2.33 ± 4.14b	14.19 ± 3.13a	10.78 ± 3.05a
G2	34.15 ± 5.06b	13.29 ± 1.72b	1.50 ± 0.72a	20.60 ± 7.73c	4.19 ± 3.36b	15.37 ± 6.64a	10.73 ± 4.83a
G3	29.48 ± 3.59c	9.01 ± 0.87b	2.00 ± 0.87a	24.05 ± 6.58c	8.94 ± 4.21c	13.33 ± 5.44a	12.89 ± 3.03a
G4	22.50 ± 4.70d	5.98 ± 1.28c	0.60 ± 0.28a	33.42 ± 9.77d	7.91 ± 2.01c	10.32 ± 2.99a	12.19 ± 2.80a
G5	13.35 ± 5.36e	5.11 ± 1.59c	0.90 ± 0.20a	42.20 ± 4.03e	9.38 ± 2.57c	10.10 ± 4.85a	12.17 ± 3.76a

Note: Different lowercase letters indicate significant differences among disturbance intensities. The disturbance gradients were set as G1 (10 ± 5)%, G2 (20 ± 5)%, G3 (30 ± 5)%, G4 (40 ± 5)%, and G5 (50 ± 5)% based on the coverage of the broken biocrusts. The number between the brackets represents the practical coverage of the broken biocrusts. G0: no disturbance (the control).

of the microbial composition. Finally, to test our third hypothesis (assess the most important drivers of microbial abundance among the disturbance gradients), we estimated the effects of the biocrust characteristics and soil properties on the microbial abundance using regression tree analysis by SYSTAT 13.1. All statistical analyses were carried out using SPSS statistical software ver. 18 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Effects of disturbance on the biocrust characteristics and soil properties

Disturbance had the largest influence on the biocrust coverage (Table 1). The cyanobacterial and moss coverage decreased along with the increment of the disturbance gradients. Specifically, the cyanobacterial coverage decreased from 37% to 13%, and the moss coverage declined by 1–12% among the disturbance treatments compared to the control (G0). Lichen was found in the study, but its coverage had little change among the treatments. However, the bare soil coverage rose to 42% from 4%, and the recovered cyanobacterial coverage increased by 2–9% during disturbance compared with the that in the undisturbed biocrusts. There were no significant differences in vegetation and litter coverage in any of the observed plots.

The soil moisture was altered by disturbance (the variations ranged from 17.01 to 21.99%) in the 0–5 cm soil layer (including the biocrust layer) and showed a reduction in G1, G2 and G3, while G5 showed an increase in soil moisture compared to G0. No significant difference was found in soil moisture between G4 and the plot with no disturbance. However, there were small changes in the soil temperature under disturbance relative to G0 in the observed plots in the biocrust layer and the 0–5 cm soil layer (Table 2).

Table 2
Soil moisture and temperature under different disturbance gradients (mean ± SD).

Disturbance gradient (%)	Soil moisture (%) in the 0–5 cm soil layer (including the biocrust)	Soil temperature (°C) in the biocrust layer	Soil temperature (°C) in the 0–5 cm soil layer
G0	19.45 ± 1.43a	22.71 ± 2.60a	22.63 ± 1.70a
G1	18.04 ± 2.56b	22.74 ± 3.19a	22.60 ± 2.59a
G2	17.24 ± 1.55b	22.77 ± 2.12a	22.56 ± 3.13a
G3	17.01 ± 2.01b	22.66 ± 3.33a	22.43 ± 2.67a
G4	19.74 ± 2.18a	22.55 ± 2.68a	22.30 ± 4.01a
G5	21.99 ± 1.46c	22.43 ± 3.23a	22.51 ± 2.43a

Note: The data for soil moisture and soil temperature were collected from 11 to 19 July 2016 in our study. Different lowercase letters indicate significant differences among disturbance intensities within the same depth. The disturbance gradients were set as G1 (10 ± 5)%, G2 (20 ± 5)%, G3 (30 ± 5)%, G4 (40 ± 5)%, and G5 (50 ± 5)% based on the coverage of the broken biocrusts. The number between the brackets represents the practical coverage of the broken biocrusts. G0: no disturbance (the control).

After one year of disturbance, the organic matter was not greatly altered by disturbance. No significant differences were found in organic matter in the determined three soil layers. A higher total N was observed at G2 and G3, which was 8.8% and 10.2% higher than that at G0, respectively, but the total N was 12.9% less at G4 than that with no disturbance in the biocrust layer. The ratio of C/N at G2 and G3 decreased by 7.6% and 5.8%, respectively, while it increased by 14.2% and 11.8% in G4 and G5, respectively, compared with G0 in the biocrust layer. There were no significant differences in the total N and the ratios of C/N in the 0–2 cm and the 2–5 cm soil layers among the treatments (Table 3).

Significant variation in available P was observed under disturbance. A higher content was found in G2 and G3, and it was 9.6% and 29.5% greater, respectively, than G0 in the biocrust layer. There was no significant difference in available P in the 0–2 cm and the 2–5 cm soil layers. The soil pH varied over a range (8.05–9.17) in all of the measured plots. There was no obvious difference in soil pH in the biocrust layer. It increased by 6.3% and 7.4% in G2 and G3, respectively, in the 0–2 cm soil layer, and it was 4.3% higher in G5 than G0.

3.2. Effect of disturbance on soil microbial abundance

3.2.1. Bacterial, fungi and actinomycetes abundance

The microbial abundance was greatly altered by disturbance, which was connected with the disturbance gradients in all of the detected soil layers (Fig. 2). Disturbance depleted the bacterial abundance by 20–73% compared to G0. There was a significant reduction in bacterial abundance in G1, G4 and G5, but there was no significant difference in G2 and G3 compared with G0 in the biocrust layer. In the 0–2 cm soil layer, the bacterial abundance was 92%, 106% and 49% higher at G1, G2 and G3, respectively, while it was 4.2 times less than that at G5 compared with the plots with no disturbance. Thirty-eight and 33% declines in bacterial abundance at G4 and G5 were detected in the 2–5 cm soil layer, but there was no distinct difference in the treatments other than at G0 (Fig. 2).

The fungal abundance dramatically increased with the increments of the disturbance gradients (Fig. 2). The fungal abundance was 16–115 times greater under disturbance than that at G0 in the biocrust layer. Similarly, in the 0–2 cm soil layer, the fungal abundance was 13–34 times higher under disturbance compared with the control, and disturbance resulted in 5–16 times of increases with the disturbance gradients compared to G0 in the 2–5 cm soil layer.

The actinomycetes abundance also showed statistical variation under disturbance (Fig. 2). It increased by 125% and 123% in G2 and G3, respectively, but it dropped by 88% at G4 compared with the control in the biocrust layer. No significant differences were found among the G0, G1 and G5 treatments. Additionally, G1 and G3 resulted in 47% and 57% increases in actinomycetes abundance, respectively, while G2, G4 and G5 numerically decreased the actinomycetes abundance compared to G0 in the 0–2 cm soil layer. Ultimately, the

Table 3
Soil properties (mean ± SD) among the disturbance gradients and soil layers collected from the field after one year.

Soil layer	Disturbance gradient (%)	Organic matter (g kg^{-1})	Total N (g kg^{-1})	C/N	Available P (mg kg^{-1})	pH
Biocrust layer	G0	30.51 ± 2.83a	1.47 ± 0.16a	11.98 ± 4.17a	10.32 ± 3.33a	8.15 ± 0.04a
	G1	28.87 ± 4.83a	1.37 ± 0.04a	12.17 ± 5.75a	9.45 ± 1.44a	8.27 ± 0.05a
	G2	29.09 ± 4.56a	1.60 ± 0.27b	11.07 ± 2.57b	11.31 ± 2.63b	8.48 ± 0.02a
	G3	28.69 ± 6.73a	1.62 ± 0.31b	11.29 ± 4.58b	13.36 ± 2.88c	8.30 ± 0.03a
	G4	27.32 ± 3.96a	1.28 ± 0.03c	13.68 ± 2.77c	9.61 ± 3.25a	8.05 ± 0.02a
	G5	28.56 ± 5.01a	1.35 ± 0.13a	13.27 ± 4.03c	10.01 ± 2.63 ab	8.21 ± 0.16a
0–2 cm	G0	12.37 ± 1.35a	0.79 ± 0.04a	9.04 ± 1.57a	4.16 ± 1.61a	8.54 ± 0.01a
	G1	11.82 ± 1.43a	0.73 ± 0.04a	9.35 ± 1.25a	4.05 ± 0.84a	8.64 ± 0.14a
	G2	11.43 ± 1.63a	0.72 ± 0.12a	9.17 ± 0.95a	4.75 ± 0.94a	9.08 ± 0.06c
	G3	12.55 ± 1.24a	0.81 ± 0.11a	8.95 ± 4.43a	4.68 ± 0.66a	9.17 ± 0.24c
	G4	12.56 ± 1.08a	0.76 ± 0.06a	9.54 ± 2.73a	4.56 ± 0.74a	8.86 ± 0.29b
	G5	11.45 ± 0.97a	0.71 ± 0.05a	9.31 ± 1.68a	3.94 ± 0.71a	8.97 ± 0.10bc
2–5 cm	G0	10.46 ± 1.65a	0.64 ± 0.02a	9.44 ± 1.28a	2.70 ± 0.76a	8.71 ± 0.08a
	G1	10.87 ± 1.92a	0.65 ± 0.03a	9.66 ± 3.63a	2.77 ± 0.77a	8.64 ± 0.08a
	G2	11.11 ± 1.74a	0.65 ± 0.02a	9.87 ± 3.14a	3.01 ± 0.24a	8.71 ± 0.07a
	G3	10.29 ± 1.10a	0.61 ± 0.09a	9.74 ± 1.16a	2.77 ± 1.04a	8.82 ± 0.15a
	G4	10.09 ± 1.68a	0.60 ± 0.08a	9.71 ± 1.04a	2.45 ± 1.36a	8.62 ± 0.06a
	G5	10.29 ± 2.01a	0.62 ± 0.02a	9.58 ± 3.08a	1.98 ± 0.90a	9.08 ± 0.02b

Note: Different lowercase letters indicate significant differences among the disturbance intensities within the same depth. The disturbance levels were set as G1 (10 ± 5)%, G2 (20 ± 5)%, G3 (30 ± 5)%, G4 (40 ± 5)%, and G5 (50 ± 5)% based on the coverage of the broken biocrusts. The number between the brackets represents the practical coverage of the broken biocrusts. G0: no disturbance (the control).

actinomycetes abundance indicated a visual decrease in the 2–5 cm soil layer with the increase in the disturbance gradients.

3.2.2. Total microbial abundance

Total microbial abundance decreased by 59%, 73% and 28% in G1, G4 and G5, respectively, but it showed little alteration in G2 and G3 compared with the control in the biocrust layer. In the 0–2 cm soil layer, G1 and G3 showed relatively higher abundances of total microorganisms, resulting in 60% and 55% increases, respectively, in total microbial abundance compared to G0. However, the total microbial abundance showed a 52% and 61% reduction in G4 and G5. Moreover, the total microbial abundance in the 2–5 cm soil layer particularly declined in G3, G4 and G5 compared with that in G0, and the lowest abundance of total microorganisms was detected at G4 in the study (Fig. 3).

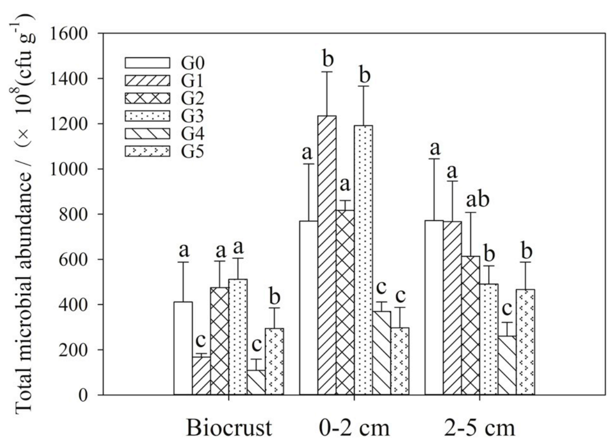

Fig. 3. Effects of disturbance on the total microbial abundance. Different lowercase letters indicate significant differences among the disturbance gradients within the same depth ($P < 0.05$).

3.2.3. Species proportions of soil microbial abundance

The proportion of soil bacteria, fungi and actinomycetes abundance was altered by disturbance (Fig. 4). Compared with the control in the biocrust layer, an increasing proportion of actinomyces abundance was found, except in G4. There were increasing proportions of actinomyces abundances of 42.5%, 32.4%, 19.5% and 15.9% in G1, G2, G3 and G5, respectively, following the reduced proportion of bacterial abundance under disturbance. There was no significant difference in the proportion of bacterial and actinomyces abundance in G1 and G3 than in G0, while there was a declining proportion of actinomyces abundance in G2, G4 and G5 in the 0–2 cm soil layer. Furthermore, in the 2–5 cm soil layer, there was an elevated proportion of bacterial abundance, following a reduction in the proportion of actinomyces abundance, with the increment of disturbance gradients. However, there was little change in

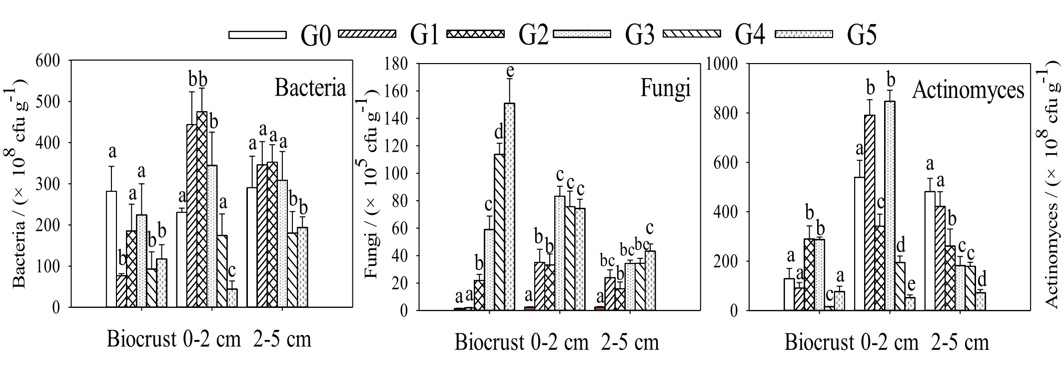

Fig. 2. Effects of disturbance on soil microbial abundance. Different lowercase letters indicate significant differences among the disturbance gradients within the same depth ($P < 0.05$).

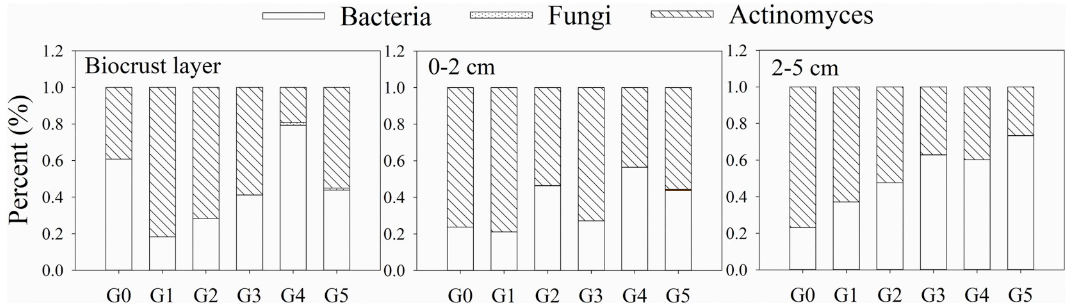

Fig. 4. Varied proportion in microbial abundance under disturbance in the biocrust layer and the 0–2 cm and 2–5 cm soil layers.

the fungal proportion in all of the observed soil layers.

3.3. Predicting soil microbial abundance cover with biocrust characteristics and soil properties

We collected the average values of the biocrust characteristics, soil properties and microbial abundances in the three soil layer to evaluate the key factors for driving the shifts in the abundances of bacteria, fungi, actinomycetes and total microorganisms using a regression tree analysis. When all the biocrust characteristics and soil properties were combined, the results explained 56.4% of the variance in soil moisture on the bacterial abundance (Fig. 5). Regarding the fungal abundance, 71.3% of the variation in the biocrust characteristics and soil properties was explained. The bare soil coverage was the most influential factor driving the changes in fungal abundance (Fig. 6).

The regression tree analysis predicted 67.7% of the variance in actinomycetes abundance, the first node splitting explained 53.0%, indicating that bare soil coverage was the main factor that determined the variation in actinomycetes abundance, and total N explained 14.7% of the variance in the second node splitting for predicting the alteration of actinomycetes abundance (Fig. 7). Furthermore, the most important explanatory variables of total microbial abundance were bare soil coverage in the first node splitting (explanatory variable of 53.5%) and the ratio of C/N in the second node splitting (explanatory variable of 18.6%) for driving the changes in total microbial abundance (Fig. 8).

4. Discussion

Previous research has suggested that disturbance has profound effects on biocrust characteristics, soil properties and soil microorganisms (Dojani et al., 2011; Kuske et al., 2012); however, these impacts are variable depending on the magnitude and severity of the disturbance and the characteristics of the site (Belnap and Eldridge, 2003; Lake, 2000). Our study using field experiments demonstrated that annual trampling disturbance, a large reduction in biocrust coverage and

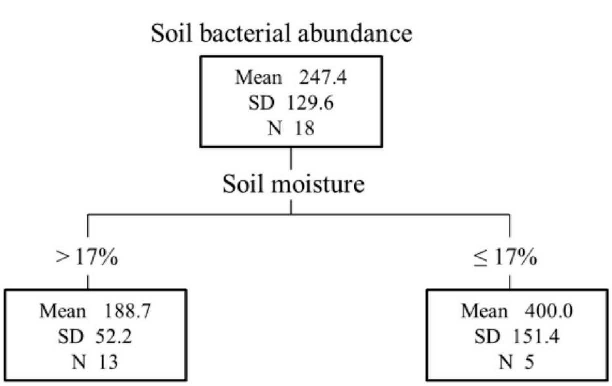

Fig. 5. Regression tree analysis of the biocrust characteristics and soil properties predicting soil bacterial abundance.

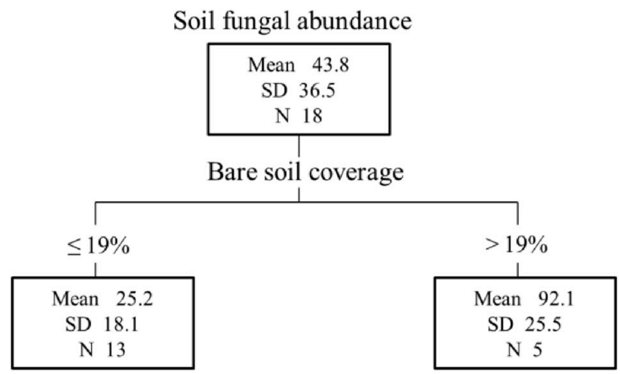

Fig. 6. Regression tree analysis of the biocrust characteristics and soil properties predicting soil fungal abundance.

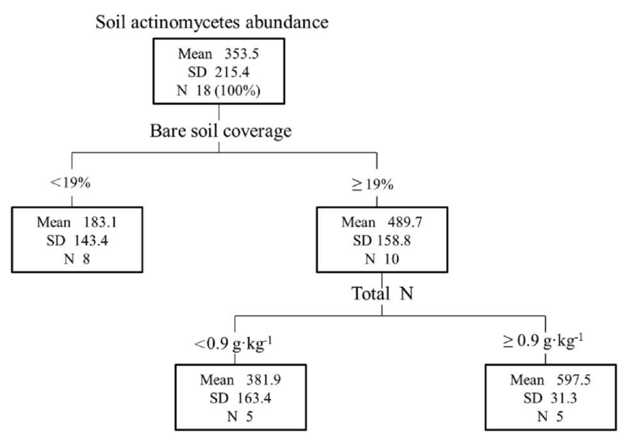

Fig. 7. Regression tree analysis of the biocrust characteristics and soil properties predicting soil actinomycetes abundance.

biomass, or a combination of alteration in ecological services of the biocrusts markedly impact microbial abundance and species proportions in the Loess Plateau region, China. These results demonstrated that the effects of disturbance on the biocrusts were predominantly related to the disturbance intensity.

4.1. Disturbance in the biocrust characteristics

In line with previous findings, the biocrust coverage (cyanobacteria and moss) were reduced by disturbance; they notably decreased with the disturbance gradients in the present study. These results have been shown in multiple studies, which indicated that biocrust cover and biomass decline with increased disturbance intensity (Zaady et al., 2016; Williams et al., 2008). Despite the loss of biocrust integrity, the soil aeration (presented by the bare soil coverage) was improved by the open biocrust surface, which increased with disturbance intensity. In

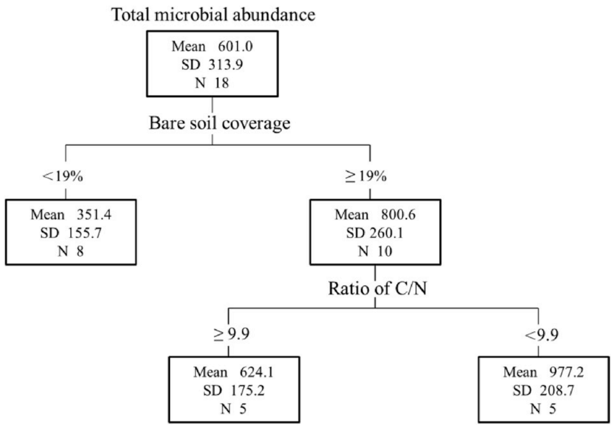

Fig. 8. Regression tree analysis of the biocrust characteristics and soil properties predicting the total microbial abundance in soils.

addition, cyanobacteria are thought to act as pioneers in the stabilization processes of soils and may rapidly recover after disturbance (Zaady et al., 2016); thus, an increase in cyanobacteria (a raised cover of recovered cyanobacteria) in the study region was occurring (Table 1), bringing with it the new succession and construction of biocrusts.

4.2. Disturbance-induced effects on the ecosystem services of biocrusts related to the disturbance gradients

Disturbance-induced effects on biocrust cover and species composition can indirectly influence a number of key ecosystem processes, such as soil infiltration, soil fertility, and so on (Zaady et al., 2016). In this study, there was a fluctuation in soil moisture (volumetric water content), with declining volumetric water content at moderate disturbances (G2 or G3) but increasing content in severe disturbance (G4 or G5). In agreement with our findings, Eldridge et al. (2010) and Shi et al. (2017) found that disturbance impacts soil infiltration, which was attributed to disruption to the compact biocrust surface. The results demonstrated that biocrust disturbance affected soil infiltration that was related to the disturbance gradients (Table 2).

Additionally, soil fertility, such as total N and available P, had a shift that was dependent on the disturbance gradients (Table 3). These results may be primarily due to the alteration of the biocrust taxa. Disturbance induced successional shifts in the biocrust communities (Bowker et al., 2011). In the study, disturbance almost resulted in the loss of moss (a later successional stage) and the relative increase of earlier successional cyanobacteria (Table 2), which enhance the ecological role of biocrusts through their contributions to N-cycling (Belnap et al., 2016; Zhao et al., 2010). The results in our study showed that the cyanobacteria coverage (sum of the well-developed cyanobacteria and recovered cyanobacteria) increased by 2–3% under moderate disturbance and decreased by 18–39% under severe disturbance. Thus, varied cyanobacteria coverage may impact the availability of soil nitrogen (elevated content under moderate disturbance and reduced content under severe disturbance).

The available P indicated a similar alteration with the nitrogen level. Gao et al. (2018) demonstrated that biocrusts in the earlier successional stage (cyanobacteria) had a lower ratio of C/P than that in the later successional stage (moss). Wang and Yu (2008) found that P availability is often dependent on the reduction of the ratio of C/P. A likely explanation for the increased available P (G2 or G3) is that the disturbance induced successional shifts between the moss and cyanobacteria, which then affected the content of available P.

4.3. Variations in microbial abundance and species proportions of the biocrusts along with the disturbance gradients

Disturbance drove significant changes in the coverage, composition and ecofunction of the biocrusts. Such alterations resulted in the response in microbial abundance. In our analysis of maximal contrasts, moderate disturbance was favorable for improvements in the abundance of bacteria, actinomycetes and total microorganisms. Some examples have demonstrated that small-scale and low-intensity (such as moderate intensity) disturbance events may lead to positive ecosystem outcomes (Li et al., 2005; Jeschke and Kiehl, 2008). By allowing the exploitation of random opportunities, it may be possible for more species to coexist after a disturbance event (Chesson and Warner, 1981).

Furthermore, the fungal abundance dramatically increased with the disturbance gradients in all of the measured soil layers (Figs. 2 and 3); the results may be due to the fungal physiological properties in ecosystems, as fungi prefer to live in aerated environments (Tabacchioni et al., 2000). A fluctuation in the proportion of bacterial and actinomycetes abundance was also detected in the study (Fig. 4), which in turn affected the ecosystem function and processes.

As an important population in biocrusts, soil microorganisms perform crucial roles in biocrusts, which is connected with the species composition. Bacteria are the most common genera in microbial communities, and they are thought to act as pioneers in the stabilization processes of the soils in biocrusts (Maier et al., 2016). Fungi can play a key role in mediating the nutrient exchange between biocrusts and plant vegetation in dryland ecosystems, which is described by the fungal loop hypothesis (Maier et al., 2016). Actinomycetes are the major decomposing members and resolve more complex litters and refractory organics (Holtkamp et al., 2008). Therefore, changes in microbial abundance and species proportions can modify the nutrient cycling and energy flow in ecosystems, as they mediate decomposition and the subsequent mineralization rates. Moreover, microbial abundance is sensitive and presents a rapid response to environmental disturbance. Their alterations may have potential implication for predicting ecosystem processes and improving the way we view the mechanisms between the ecosystem services of biocrusts and disturbance regimes.

4.4. Key factors driving the variation in microbial abundance

Microbial processes are often dependent on environmental factors, such as aeration, moisture and nutrient availability (Solomon et al., 2007). Based on the regression tree analysis, soil moisture was the main factor driving the changes in bacterial abundance (Fig. 5). This agrees with Grube et al. (2012), who found the presence of bacteria possibly correlates with fluctuating water conditions. Further, moderate disturbance (G2 or G3), which resulted in the 17.0% volumetric water content in the soils (Table 2), resulted in an increase in bacteria abundance (Fig. 2). The degree of soil moisture associated with our study (volumetric water content of 16.0% was appropriate for the improvement in bacterial abundance) is known to have favorable effects on bacterial abundance (unpublished data, Zhao et al.), which was close to the soil moisture level of the moderate disturbance.

In addition, fungal abundance was significantly connected with bare soil coverage (Fig. 6). Indeed, disturbance can modify soil aeration (Dec et al., 2009). Disturbance resulted in an increase in soil porosity by breaking the compact surface of the biocrust. Under aerobic conditions, aerobic microorganisms (such as fungi) are more abundant (Amann and Ludwig, 2000). Furthermore, alterations in both soil aeration and nutrient status induced the variations in actinomycetes and total microbial abundance (Figs. 7 and 8). Cyanobacteria coverage recurred and increased under moderate disturbance, bringing more nitrogen fixation to the biocrust surface (Belnap et al., 2003; Zhao et al., 2010), which may dramatically promote actinomycetes abundance in poor environments. Moreover, the reduced ratio of C/N caused elevated total microbial abundance under moderate disturbance. Research has demonstrated that a reduction in the ratio of C/N is favorable to microbial development due to the lowered nutrient competition between plants and microorganisms (Huang et al., 1999; Doran, 1994).

The dilution plate counting method was used to measure the microbial abundance in the study. This method may actually favor microbial determination by directly detecting microbial abundance and allowing researchers to get experimental data in a timely manner (Kalam et al., 2004; Yao and Huang, 2006). Clearly, advanced techniques have been employed by several researchers to meet their objectives. Muńoz-Rojas et al. (2018) explored the cyanobacteria effects on the regeneration of native species existence by using 16S rDNA profiling as well as culturing in western Australia. Castillo-Monroy et al. (2011) characterized bacterial abundance using a culture-based technique and community richness using a PCR-DGGE technique to verify the relationships between biocrusts, microbial diversity and abundance and ecosystem functioning in a semiarid Mediterranean environment.

However, the objective of this study was to demonstrate the disturbance effects on the microbial responses of biocrusts, which in turn predicted the ecosystem processes in drylands. In fact, disturbance in ecosystems may initially change the microbial abundance. Long-term disturbances are thought to have further influences on the speed with community structure and species composition. This study by the dilution plate counting method successfully made clear the specific responses of soil microorganisms to different disturbance intensities. This research has important implications for indicating the succession of soil health and ecosystem processes in dryland landscapes.

It is worth indicating that the disturbance in our study only simulated grazing disturbance, and there were many practical problems have not been referred to, such as the lack of trampling by sheep, the absence of animal gnawing and the lack of animal excrements, which can cause more complex effects on the soil microbial abundance of biocrusts. Furthermore, our data were collected after a year of disturbance. Long-term studies are needed to reveal the more complicated impact of disturbance on soil microorganisms.

5. Conclusion

Our results demonstrated that changes in biocrust characteristics, soil properties and microbial abundance were connected with disturbance intensity. Moderate levels of disturbance (G2 or G3) did not drive a large reduction in biocrust coverage and soil nutrients, but they seem to create a more favorable soil environment (modest soil aeration and moisture) and relatively improve the nutrient status, which resulted in elevated microbial abundance (bacteria, actinomycetes and total microorganisms), while the severe disturbance (G4 or G5) significantly reduced the biocrust coverage and microbial abundance. The fungal abundance increased along with the disturbance gradients, and this response may be accounted for by its own aerobic feature. Additionally, disturbance resulted in a varied proportion of actinomycetes and bacteria. These shifts may have long-term impacts on the nutrient cycles and soil properties of biocrusts, which may further affect system functioning and ecosystem processes. These results will be meaningful for evaluating the ecosystem services of biocrusts under a disturbance event in drylands.

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