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REGULAR ARTICLE

Moderate disturbance increases the PLFA diversity and biomass of the microbial community in biocrusts in the Loess Plateau region of China

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Abstract
Aims Biological soil crusts (biocrusts) play key roles in dryland ecosystems. Examining the effects of different intensities of disturbance on biocrusts and exploring appropriate disturbance levels can provide important information about ecosystem processes and services in drylands.
Methods Five disturbance intensities ranging from 10% to 50% based on the percentage of broken biocrusts were implemented to examine the effects of simulated goat trampling on microbial communities; microbial community structure was measured with the phospholipid fatty acid method.
Results The effects of disturbance on the biocrusts were closely related to disturbance intensity. Surprisingly, moderate disturbance had a weak effect on total biocrust coverage but increased cyanobacterial coverage by 2 ~ 3%. Consequently, there was an increase in total N, a reduction in the C/N ratio and improvements in soil moisture, and these effects led to 13 ~ 21% and 5 ~ 6% increases in microbial biomass and diversity, respectively, compared with those in undisturbed biocrusts. However, high-intensity disturbance substantially reduced biocrust coverage and microbial abundance.
Conclusions The study supports the intermediate disturbance hypothesis and suggests that moderate disturbance has positive effects on the microbial communities of biocrusts. These findings provide vital information for the ecological management of drylands.

Keywords Biocrusts · Disturbance · Microorganism · Intermediate disturbance hypothesis · Dryland

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Introduction

Drylands cover 35% of Earth's land surface and are characterized by sparse vegetation cover (Belnap 2006). In the open spaces devoid of plants, biological soil crusts (biocrusts), which consist mostly of cyanobacteria, algae, lichens, mosses, archaea, microfungi and other microorganisms that grow in close association within the uppermost millimeters of the soil surface, dominate the ground cover (Belnap et al. 2016). These diverse communities contribute to critical ecosystem functions in dryland regions by improving soil fertility (Elbert et al. 2012), increasing soil stability (Bowker et al. 2004), altering related hydrological

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processes (Eldridge et al. 2010) and promoting microbial activity (Maier et al. 2014), among other activities.

Disturbance is a key driver that affects species composition and community structure of ecosystems and modifies substrate availability and ecosystem processes (Pickett and White 1985). As a type of living surface cover in drylands, biocrusts are highly vulnerable to physical disturbance, which often causes significant changes in biocrust species composition (Belnap et al. 2006) and ecological function (Pickett et al. 1989; Gomez et al. 2012). In the northern Negev region of Israel, Golodets and Boeken (2006) found that the biocrust coverage in a grazed shrubland was 30% lower than that in an ungrazed shrubland. A study from the Gurbantünggüt Desert in China, Wu et al. (2012) demonstrated that the coverage of early-successional cyanobacterial crusts increased (by 5 ~ 30%) at the expense of later-successional lichen (10 ~ 55%) and moss (8 ~ 16%) crusts due to grazing. Additionally, in southern Utah, USA, Neff et al. (2005) suggested that disturbance resulted in a 60 ~ 70% depletion in the soil C and N content associated with biocrusts in comparison with those in undisturbed areas.

Although some studies suggested that disturbance simplifies biocrust species and reduces soil nutrients, disturbance promotes the soil hydrological processes of biocrusts to some extent. By simulating sheep trampling in Australia, Eldridge (1998) found that moderately trampled biocrusts had no significant effects on soil erosion and may enhance soil infiltration. A study involving simulated agricultural disturbance in Israel showed that infiltration rates in disturbed plots significantly increased in comparison with those in control biocrust plots (Zaady et al. 2013). However, most studies focused on the effects of disturbance on biocrusts by comparing disturbed and undisturbed treatments. Research examining the effects of different disturbance intensities on biocrusts is still lacking.

Disturbance simultaneously acts as a filter and management tool to affect community assembly and species establishment in an ecosystem (Hobbs et al. 2006). Although disturbance disrupts population structure and changes substrate availability or the physical environment (Neff et al. 2005; Golodets and Boeken 2006; Wu et al. 2012), an appropriate level of disturbance can steer an ecosystem toward dynamic equilibrium. The famous intermediate disturbance hypothesis (IDH) was put forward by Connell in 1978, and the IDH presented that the relationship between species diversity and richness and disturbance is hump-shaped such that moderate levels of disturbance are associated with maximal biological diversity and abundance in terrestrial ecosystems. Roxburgh et al. (2004) later suggested that intermediate disturbance can promote the coexistence of species in ecological communities, and Catford et al. (2012) found that the IDH is a useful framework for managing community diversity in grassland ecosystems.

In drylands, some researchers have also noted that disturbance of moderate intensity can lead to positive ecosystem outcomes, and they suggested that the occurrence of disturbance events of moderate intensity may promote the successful coexistence of biocrust organisms and higher plants in some nutrient-poor environments (Beyschlag et al. 2008; Jeschke and Kiehl 2008; Li et al. 2005). Thus, the influence of disturbance on biocrusts clearly depends on the severity and intensity of the disturbance. Examining the variability in biocrust responses following disturbances of differing intensity may provide additional insights into disturbance effects and their causal processes in drylands.

Soil microorganisms inhabiting biocrusts play many key ecological roles in the regulation of soil stability, nutrient cycling, and ecosystem productivity (Garcia-Pichel and Pringault 2001; Gundlapally and Garcia-Pichel 2006; Steven et al. 2013), and these communities are always the first to respond to environmental change (Zhang et al. 2018). Disturbance-induced changes in biocrusts can cause a rapid response in microbial communities (Collins et al. 2008). Therefore, studying the response of microbes to disturbance would enable us to predict how ecosystems will respond to environmental changes under varying disturbance regimes. Moreover, increased recognition of disturbance-driven changes in the microbial communities of biocrusts will be vital for predicting and managing the ecosystem services on which humans rely in drylands.

Our study was carried out on the Loess Plateau in China. The enforcement of the "Grain for Green" ecological project resulted in the natural recovery of biocrusts as well as shrubs and grasses within a couple of years, with the biocrust coverage as high as 70% (Zhao et al. 2006). However, most biocrusts are on slopes. The presence of biocrusts decreases precipitation infiltration and increases runoff. Consequently, the Loess Plateau in China has become one of the most severely eroded regions in the world. Perhaps appropriate disturbance of biocrusts in the region will be beneficial to the ecological management.

To date, a few studies conducted in this region examined the effects of disturbance on the ecological function of biocrusts. For example, Shi et al. (2017) found that the soil infiltration rate of biocrusts increased by 13% in response to a moderate disturbance. Wang et al. (2017) and Yang et al. (2018) observed that disturbance reduced the total N and organic C contents in biocrusts, respectively. For the microbial study, we found that disturbance significantly affected the microbial abundance in biocrusts and that bacteria and actinomycetes were the most abundant groups under moderate disturbance (Bao et al. 2019). However, the study used the dilution plate counting method to measure the abundance of microbes. This method detects only approximately 1% of the total microbial population in soil samples. As a result, changes in microbial communities remain poorly understood.

Here, we examined the effects of simulated trampling disturbance using artificial goat hooves at five disturbance intensities on the microbial communities in intact biocrusts with the phospholipid fatty acid (PLFA) method. We hypothesized that the microbial communities in the biocrusts would change with varying disturbance intensities, and we expected that microbial biomass and community diversity would reach their optimal values under a moderate disturbance intensity. Thus, our three objectives were to (1) examine how disturbance impacts the microbial communities in biocrusts; (2) evaluate whether changes in disturbance intensity impact the microbial communities of biocrusts; and (3) determine the critical factor driving changes in biocrust microbial communities following disturbance.

Materials and methods

Study region

This study was conducted in Wuqi County in the northwestern portion of Shaanxi Province (Fig. 1), specifically, in abandoned farmland in the Loess Plateau region of China (36°53′31″ N, 108°13′28″ E). The mean altitude of this region ranges from 1233 m to 1809 m; the area has a typical warm temperate monsoon climate, with an annual average temperature of 7.8 °C. Annually, the region experiences an average of 2400 h of sunshine per year, and the mean annual precipitation ranges from 400 mm to 450 mm (Fu et al. 2011). The soil in the region is classified as a typical loessial soil, and the

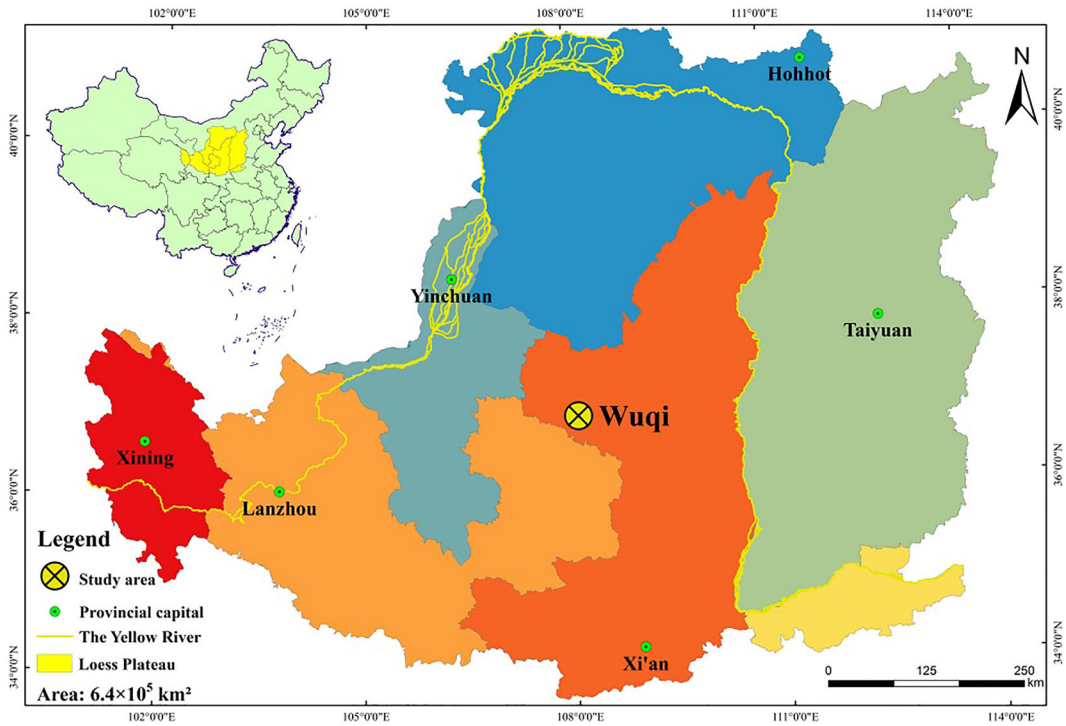

Fig. 1 Study area location

vegetation is dominated by *Artemisia* spp., *Stipa* spp. and *Lespedeza* spp.

In this region, cyanobacteria and mosses dominate the major biocrust communities. Cyanobacteria are mostly distributed on south-facing slopes. The common cyanobacterial species include *Phormidium calciola*, *Phormidium tenue* and *Nostoc* spp. *Nostoc* spp., as core ecological engineers, contribute to soil nitrogen inputs (Büdel et al. 2016). Moss coverage and density increase as the number of years since abandonment increases. *Didymodon tectorum*, *Bryum argenteum* and *Didymodon vinealis* are usually the dominant moss species (Zhao et al. 2006). Lichens are mostly found ten years after cropland abandonment, and their coverage seldom reaches 10% (Wang et al. 2016).

Experimental design

In this study, we conducted a large-scale field survey on the Loess Plateau in China. As a critical component of this investigation, biocrusts distributed over a large area were essential, and to the extent possible, it was ensured that these biocrusts experienced no additional disturbance. Moreover, the soils in the collection areas were assumed to have similar background properties. Consequently, we selected two slopes, one with a sunward aspect of 297° and one with a semisunward aspect of 315° (both slopes at approximately 25°) from south to north, on which to establish the experimental plots. The two slopes had very similar soil properties (Supplemental Table S1). The natural recovery of the biocrusts in this region has been observed for more than 10 years since the implementation of the "Grain for Green" project (tillage and grazing have been prohibited for 18 years). The biocrusts have developed stably and are seldom disturbed. We used a 25 × 25 cm quadrat (Belnap et al. 2001) to survey the percent coverages of vascular plants and biocrusts on the two slopes, and the average coverages of vascular plants and biocrusts on the slope with a sunward aspect were 12% and 53%, respectively, whereas those on the slope with a semisunward aspect were 9% and 66%, respectively.

In July 2015, five trampling levels were randomly implemented on the two slopes to explore the disturbance effects on the biocrust systems. The five intensities were set as L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%) and L5 (50 ± 5%).The numbers in parentheses indicating the actual disturbance percentages calculated based on the coverage of broken biocrusts. Well-developed biocrusts without additional trampling were built as a control (L0). Four replicates of each level were carried out in this study. Consequently, twenty-four plots using sheet iron were established in a south-north direction on the two slopes (3.0 × 6.0 m in size). The plots were separated by 5 m to minimize the risk of sampling nonindependent areas. The coverage and composition of the sampling sites prior to disturbance are shown in Supplementary Table S2.

Disturbance simulation

Disturbance was simulated using a homemade tool shaped like a goat's hooves (Supplemental Fig. S1). The area of each hoof was 6.25 cm^2, and the feet were 40 cm apart. The overall height of the tool was approximately 60 cm. The tool was designed according to the body characteristics of adult goats in the Loess Plateau region. The simulated trampling intensity was approximately 30 kg of pressure; this value was selected based on the average weight of adult goats. Thus, the weight distributed to each of the four feet was approximately 7.5 kg. Before the disturbance was implemented, a scale was used to calibrate the overall human force-based strength required to achieve the 30 kg weight. Then, we attempted to maintain as constant a pressure as possible to implement the different levels of disturbance according to the actual coverage of broken biocrusts in the experimental plots. Preliminary investigations showed that broken biocrusts start to recover in two months; therefore, to maintain the disturbance level, we performed trampling every two months.

Evaluation of the trampling disturbance intensities

Five disturbance intensities ranging from 10% to 50% was evaluated by the percentage of broken biocrust coverage. The disturbance frequency on biocrusts in each plot was calculated according to the target disturbance intensity. Therefore, the frequencies using the stimulated goat hooves for the five intensities were 360, 540, 720, 900 and 1080 times, respectively. The maximum disturbance level was set to 50% based on the fundamental function of biocrusts in soil and water conservation in our study region. Then 20 ~ 30% (L2 and L3) broken biocrusts was defined as moderate disturbance. The disturbance levels that were lower and higher than these were light (L1) and severe disturbances (L4 and L5), respectively. However, the

determination of disturbance severity varies with the characteristics of the study region, climatic conditions and disturbance type. The effects of the different disturbance intensities on the biocrust characteristics and soil properties one year after disturbance can be found in Supplementary Tables S3, S4 and S5.

Sample collection and preparation

Soil samples were collected from the various disturbed biocrusts on July 19, 2016, after the plots had been subjected to the disturbance treatments for 1 year. Five 10 × 10 cm samples were randomly collected from each plot, and we avoided edge effects on the samples to the greatest extent possible. The samples of the biocrust layer were first collected using a scoop, and the thickness of the biocrusts ranged from 4 to 10 mm. Then, we measured to depths of 2 cm and 3 cm by a ruler to collect samples 0–2 cm and 2–5 cm beneath the biocrusts. After sampling, the collected pits were filled and coated by biocrusts for the long-term experiment, and the five samples from the same depth were thoroughly mixed to obtain one composite sample. Immediately after collection, the samples were transported to the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in Yangling city, Shaanxi Province. Part of each fresh sample was stored at −80 °C for further microbial analysis, and the remainder of each sample was air dried for the measurement of soil physicochemical properties.

Measurement of microbial community structure

Microbial PLFAs were extracted from each soil sample according to the methods described by Frostegård et al. (1993). PLFA abundances were quantified using an Agilent 7890 gas chromatograph combined with a flame ionization detector (Agilent Technologies, Santa Clara, CA, USA) and converted to nmol PLFAs g^{-1} of organic matter using conventional nomenclature. The measuring system was controlled by using Agilent ChemStation and MIDI Sherlock software (version 4.5; Microbial ID, Inc., Newark, NJ, USA). An Agilent Ultra 2 column (25 m length × 200 μm internal diameter (ID) × 0.33 μm film thickness) was used, and hydrogen was utilized as the carrier gas. The fatty acid terminology that was used was consistent with that delineated by Ratledge and Wilkinson (1988). Specific lipids were used as indicators of bacteria (B), fungi (F), and gram-positive (G+) and gram-negative bacteria (G-) (Fanin et al. 2018; Zelles 1999). Total microbial biomass was calculated as the sum of all microbial PLFAs, including those of bacteria, fungi, actinomycetes, G+, G-, anaerobic bacteria, arbuscular mycorrhizal fungi (AMF), and methanogens.

The PLFA method is often used to measure the living cells of soil microorganisms because phospholipids are a component of all living cells and decompose rapidly after cell death (Bardgett and McAkister 1999), but the detected microbial composition is limited compared with that detected via molecular techniques. However, the phospholipid profile can be used as a "fingerprint" of the soil microbial community (White et al. 1979). More importantly, the method used in this study successfully revealed the responses of microbial community structure to different disturbance intensities. Nevertheless, more advanced molecular techniques need to be used in studies of microbial communities.

The Shannon index was used to analyze microbial diversity and was calculated according to the following equation (Garland and Mills 1991):

$$\text{Shannon index}: H = -\sum P_i \ln P_i$$

where $P_i = N_i / N$, P_i is the relative abundance of each fatty acid among the total PLFAs and N is the number of detected fatty acids.

Statistical analyses

We tested the data for normality using the Kolmogorov-Smirnov test and for equality with Levene's test. For the data that were nonnormally distributed, such as the microbial indices (bacterial, fungal, G+, G-, and total microbial PLFAs; B/F PLFA and G+/G- PLFA ratios; and the Shannon index), we logarithmically transformed the data to meet the assumptions of parametric statistical tests. Then, the microbial PLFAs (bacterial, fungal, G+, G- and total microbial biomass), B/F and G+/G- ratios and Shannon index were also analyzed using the same analysis of variance (ANOVA) and least significant difference (LSD) approach to analyze the significance of the differences in disturbance level for the biocrust layer and the soil layers at depths of 0–2 cm and 2–5 cm.

To identify the most important drivers of the microbial communities among the different disturbance intensities, we assessed the effects of biocrust characteristics and soil properties on the microbial communities with

redundancy analysis (RDA) using Canoco 4.5. Furthermore, we used path analysis to evaluate how disturbance intensity affected the microbial communities. The path coefficients were calculated with SPSS statistical software version 18, and Microsoft Visio 2010 was used to draw the path diagram.

Results

Effects of disturbance intensity on the soil microbial community

Microbial PLFA biomass

Unimodal relationships between bacterial, fungal, G+, G- and total microbial PLFAs and disturbance intensity were found, with maximum biomass detected at the L2 or L3 disturbance intensity. Additionally, disturbance greatly influenced the microbial PLFAs in the biocrust layer and 0–2 cm beneath the biocrusts. No significant differences in microbial PLFAs were found in the 2–5 cm soil layer (Fig. 2).

Specifically, bacterial PLFAs in the biocrust layer were not significantly different in L2 and L3 plots compared to plots with no disturbance, while they were markedly lower at L1, L4 and L5. The bacterial PLFAs in the 0–2 cm soil layer increased by 33% and 57% at L2 and L3, respectively, compared to L0. No significant differences from the control were found at L1, L4 and L5. Fungal PLFAs were 55% and 61% higher in the biocrust layer at L2 and L3 than at L0. There were no notable differences from L0 for the L1, L4 and L5 treatments. An 18% increase in fungal PLFAs at L3 and 52% and 31% decreases in fungal PLFAs at G1 and G5, respectively, were detected in the 0–2 cm soil layer.

The G+ PLFAs in the biocrust layer were more abundant (25%) at L2 but less abundant at L1 and L4 (29% and 28%, respectively) compared with L0, and there were no significant differences at L3 and L5 compared with L0. In the 0–2 cm soil layer, except for L1 and L5, disturbance increased the G+ PLFAs by 56 ~ 89% compared to those at L0, and the G+ PLFAs reached the maximum content in the L2 and L3 treatments. The G- PLFAs in the biocrust layer increased by 16% at L3 but decreased significantly in the other treatments compared with L0. Similarly, in the 0–2 cm soil layer, the G- PLFAs were 1.6 times greater at L3 than at L0 and deceased by 51% at L1 compared to L0.

These changes were accompanied by increases in total microbial PLFAs in the biocrust layer of 21% and 13% at L2 and L3, respectively, compared to the control with no disturbance, while there were 21% and 24% decreases at L1 and L4, respectively. No significant differences were found between L5 and L0. The highest total microbial PLFAs content occurred in the L3 treatment. The total microbial PLFAs content increased by 25% in comparison to that at L0 and was 12% greater at L2 than at L0 in the 0–2 cm soil layer. However, the L1 and L5 treatments resulted in 40% and 24% decreases, respectively, in total microbial PLFAs in comparison with that observed at L0.

Ratio of bacterial to fungal PLFAs (B/F PLFA ratio)

We found that the B/F PLFA ratio in the L3-treated biocrust layer was significantly lower (by 30%) than that in the control. Similarly, at a soil depth of 0–2 cm, the L3 treatment also substantially decreased the B/F PLFA ratio, whereas the L4 treatment significantly increased the B/F PLFA ratio. No significant differences in the B/F PLFA ratio were found among the treatments at a soil depth of 2–5 cm (Fig. 3).

Ratio of G+ to G- bacterial PLFAs (G+/G- PLFA ratio)

In our study, the L4 and L5 treatments markedly increased the G+/G- PLFA ratio in the biocrust layer to values that were 60% and 32% higher than that in the control, respectively. However, no significant differences in this ratio in the biocrust layer were found between the moderately disturbed (L2 and L3 treatments) plots and L0-treated plots. Accordingly, the G+/G- PLFA ratio at a soil depth of 0–2 cm showed no notable changes at L2 and L3, but it increased by 67%, 75% and 33% at L1, L4 and L5, respectively. However, no significant differences in this ratio at a soil depth of 2–5 cm were detected among the treatments (Fig. 4).

Microbial diversity (Shannon index)

The Shannon index was used to analyze soil microbial diversity after the different disturbance treatments were applied (Table 1). The number of PLFA markers in each microbial group was used to calculate the Shannon index in the study. Thus, the calculated difference was quite small, on the order of 1/100th. In the study, L2 and

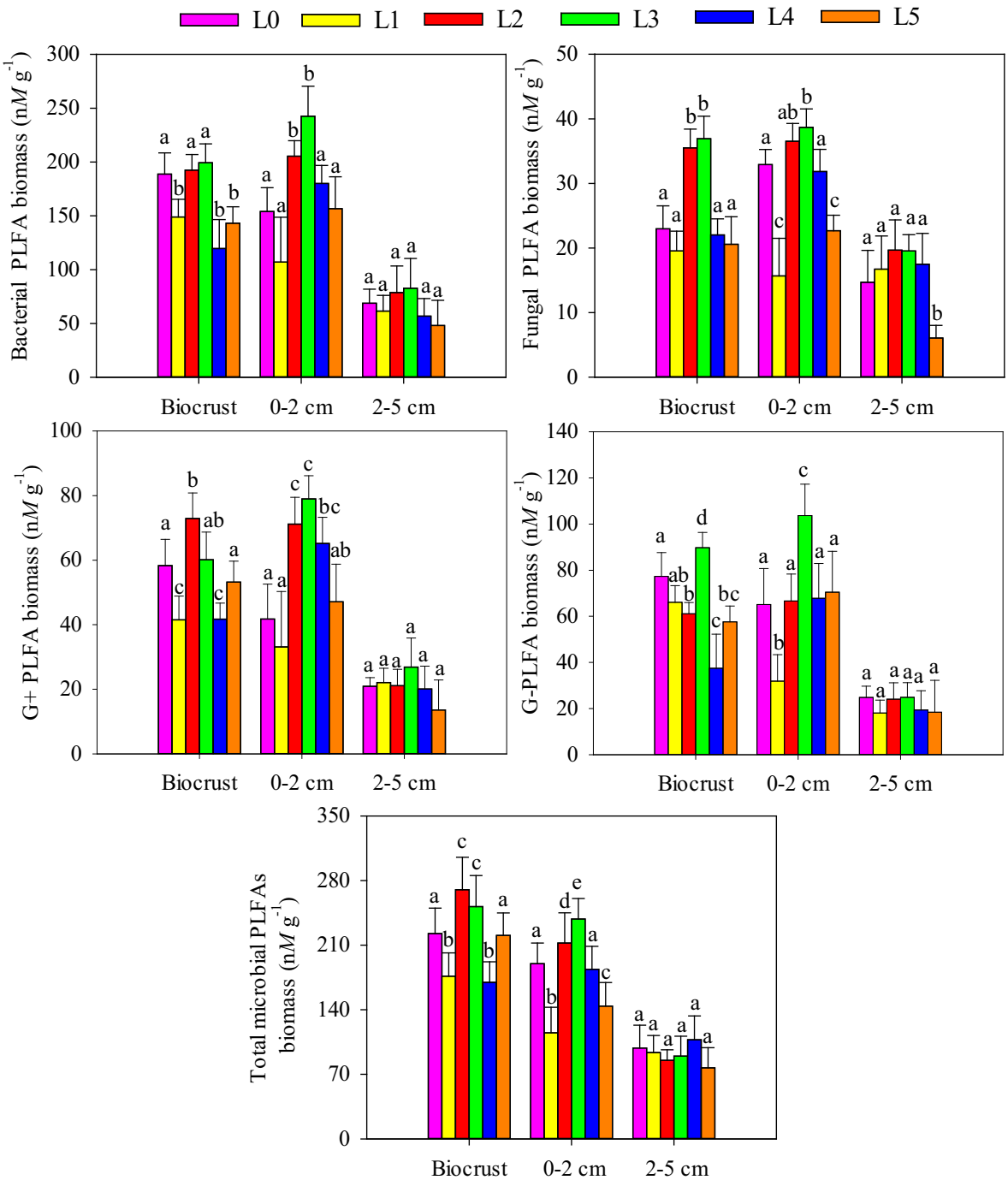

Fig. 2 Responses of soil microbial PLFA biomass to disturbance at different intensity levels. Bars correspond to averages and standard errors of $n = 12$ samples per treatment. Different lowercase letters indicate significant differences between disturbance intensities at the same depth. The disturbance levels, L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%) and L5 (50 ± 5%), were based on the coverage of broken biocrusts. The numbers in parentheses represent the measured coverage of broken biocrusts. L0: no disturbance (control)

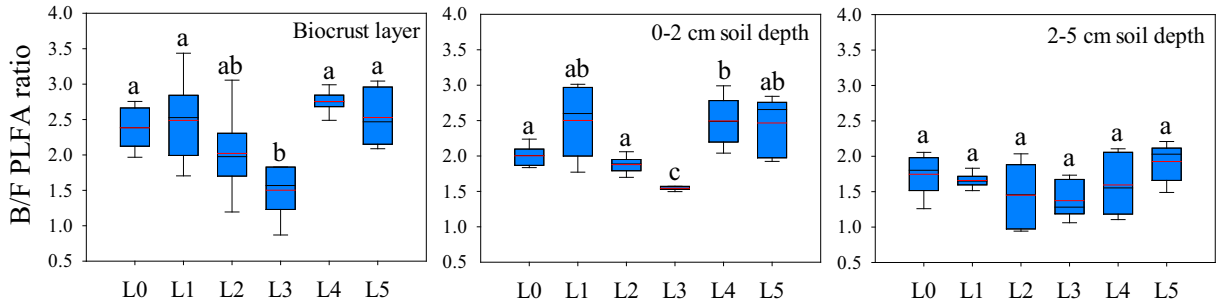

Fig. 3 Influences of disturbance intensity on the ratio of bacterial to fungal PLFAs. Values are means ± standard error ($n = 12$). Different lowercase letters indicate significant differences between disturbance intensities at the same depth. The red line indicates the mean value of the B/F PLFA ratio. The disturbance levels, L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%) and L5 (50 ± 5%), were based on the coverage of broken biocrusts. The numbers in parentheses represent the measured coverage of broken biocrusts. L0: no disturbance (control)

L3 notably increased the Shannon index values in the biocrust layer (5 ~ 6%), whereas L4 and L5 significantly decreased the Shannon index values in this layer (2 ~ 11%). At a soil depth of 0–2 cm, all disturbance treatments increased the Shannon index values, and the highest Shannon index value was found at L3 (25% higher than that found at L0). At a soil depth of 2–5 cm, the L5 disturbance treatment induced a 26% reduction in the Shannon index value compared with that observed at L0, and the Shannon index values obtained with all other treatments notably increased compared with that in the L0-treated soils.

Relationships between the biocrust characteristics, soil properties and microbial communities

The RDA performed in our study identified the effects of different biocrust characteristics and soil properties on the microbial communities (Fig. 5). The two axes explained 72.1% of the total variance, indicating that soil moisture, bare soil coverage, total N, the C/N ratio and total cyanobacterial coverage were the most influential factors driving the observed changes in the microbial communities.

On the basis of the RDA (Fig. 5), path analysis (Fig. 6) was used to estimate how disturbance intensity affected the microbial community. In this study, total microbial PLFAs, the B/F and G+/G- ratios and the Shannon index responded similarly to the different disturbance intensities. Thus, we used total microbial PLFAs to analyze the effects of disturbance intensity on the soil properties and microbial communities.

The results of the path analysis explained 94.6% of the total variance. A path coefficient of 0.405 was obtained for the direct effect of bare soil coverage on total microbial PLFAs, indicating that disturbance intensity greatly affected total microbial PLFAs ($P = 0.002$). Additionally, bare soil coverage had notable

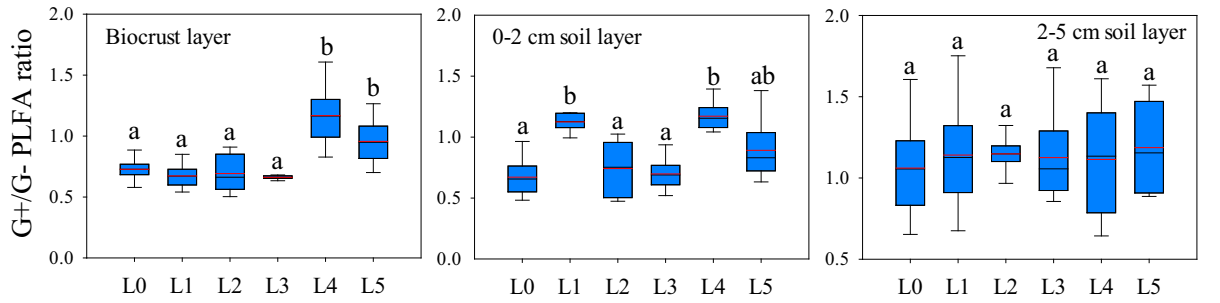

Fig. 4 The ratio of gram-positive to gram-negative bacterial PLFAs (G+/G- PLFA ratio) after disturbance at different intensity levels. Values are means ± standard error ($n = 12$). Different lowercase letters indicate significant differences between disturbance intensities at the same depth. The red line indicates the mean value of the G+/G- PLFA ratio. The disturbance levels, L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%) and L5 (50 ± 5%), were based on the coverage of broken biocrusts. The numbers in parentheses represent the measured coverage of broken biocrusts. L0: no disturbance (control)

Table 1 Shannon index values of the microbial communities in different soil layers after disturbance at different intensity levels (mean ± SE)

Disturbance level/ soil layer	Biocrust layer	0–2 cm	2–5 cm
L0	0.9409 ± 0.0012a	0.8315 ± 0.0040a	0.8728 ± 0.0010a
L1	0.9448 ± 0.0005a	0.9606 ± 0.0010c	0.9528 ± 0.0016c
L2	0.9988 ± 0.0014b	0.9600 ± 0.0011c	0.9494 ± 0.0009c
L3	0.9887 ± 0.0006b	1.0389 ± 0.0007e	0.9336 ± 0.0014c
L4	0.8376 ± 0.0009d	0.9762 ± 0.0012d	0.9314 ± 0.0035c
L5	0.9189 ± 0.0023c	0.9534 ± 0.0005b	0.6473 ± 0.0009b

Note: Values correspond to averages and standard errors of n = 12 samples per treatment. Different lowercase letters indicate significant differences between disturbance intensities at the same depth. The disturbance levels, L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%) and L5 (50 ± 5%), were based on the coverage of broken biocrusts. The numbers in parentheses represent the measured coverage of broken biocrusts. L0: no disturbance (control)

effects on total cyanobacterial coverage (path coefficient = 0.512; $P = 0.004$) and soil moisture (path coefficient = 0.418; $P < 0.001$) but had little effect on total N and the C/N ratio. Path coefficients of 0.101 ($P = 0.209$) and − 0.132 ($P = 0.247$) described the direct effect of disturbance intensity on total N and the C/N ratio, respectively.

Furthermore, the indirect effects of soil moisture under disturbance significantly affected total microbial PLFAs, and a path coefficient of 0.506 ($P < 0.001$) was found for the alteration of total microbial PLFAs. Although cyanobacterial coverage had only a slight effect on total microbial PLFAs, with a path coefficient of only 0.203 ($P = 0.351$) between these two variables, it altered total N and the C/N ratio under disturbance and further notably altered total microbial PLFAs. Path coefficients of 0.437 and − 0.412 were observed for the relationships of total N ($P = 0.001$) and the C/N ratio ($P < 0.001$) with total microbial PLFAs, respectively (Fig. 6).

Discussion

Changes in disturbance intensity within an ecosystem are likely to affect the biotic community, resource availability or soil properties (Neff et al. 2005; Hobbs et al. 2006; Wu et al. 2012). In this study, we confirmed that distinct disturbance intensities had varying effects on biocrust microbial communities in the Loess Plateau region of China. Importantly, we found that the moderate disturbance was beneficial to the increases of microbial biomass and community diversity of biocrust taxa.

Moderate disturbance enhances the diversity of microbial community structure in biocrusts

As expected, we found that biocrust microbial PLFA biomass and Shannon index of community diversity significantly increased under moderate disturbance compared to undisturbed biocrusts (Fig. 2). In turn, increases in microbial communities can promote the development of soil fertility and ecosystem services in dryland regions (Maier et al. 2016). Additionally, we characterized the ratios of bacterial to fungal (B/F) PLFAs and G+ to G- (G+/G-) PLFAs in the biocrusts to reveal the responses of microbial community structure to different disturbance practices, and we found that moderate disturbance exerted greater effects on microbial community structure than did no disturbance, light disturbance and severe disturbance (Figs. 3, 4). Vries et al. (2006) found that a lower B/F PLFA ratio was associated with increased microbial abundance and more balanced microbial numbers, and the G+/G- PLFA ratio, which decreases with increasing ecosystem productivity, can serve as a useful indicator of relative C availability and energy limitation in natural ecosystems (Fanin et al. 2018). The results also suggest that moderate disturbance increased microbial community structure in the biocrusts by reducing the B/F PLFA and G+/G- PLFA ratios.

In the high-stress ecological environments of drylands, the microbial communities that develop might influence the overall environment and nutrients and hence further influence ecosystem processes that are crucial for ecosystem functioning and services (Han et al. 2007). Furthermore, ecosystem stability and

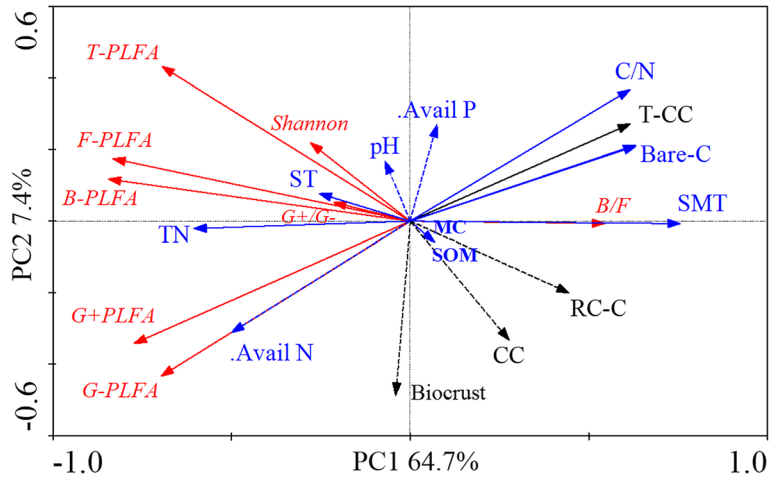

Fig. 5 Relationships between the microbial community variables (red arrows), soil properties (blue arrows) and biocrust characteristics (black arrows) identified with RDA. CC: cyanobacterial coverage; MC: moss coverage; Bare-C: bare soil coverage; RC-C: recovered cyanobacterial coverage; T-CC: developed cyanobacterial coverage + recovered cyanobacterial coverage; Biocrust: total biocrust coverage; SMT: soil moisture; ST: soil temperature; SOM: soil organic matter; TN: total N; Avail P: available P; Avail N: available N; B-PLFA: bacterial PLFA biomass; F-PLFA: fungal PLFA biomass; G + PLFA: gram-positive bacterial PLFA biomass; G-PLFA: gram-negative bacterial PLFA biomass; B/F: ratio of bacterial to fungal PLFAs; G+/G-: ratio of gram-positive to gram-negative bacterial PLFAs; and Shannon: microbial diversity index. The blue and black arrows with dashed lines correspond to the factors with a noncritical impact on the microbial community, and the blue and black arrows with solid lines indicate the key factors impacting the microbial community

development often depend on population dynamics and species abundance and composition, and greater microbial abundance and diversity will lead to stronger equilibrium and stability (Tilman and Downing 1994). Consequently, the increases in biocrust microbial communities under moderate disturbance can enhance substrate availability and strengthen biological community resistance to environmental stress in dryland regions (Belnap et al. 2003).

However, severe disturbance (L4 or L5) notably decreased the microbial biomass and community diversity in the biocrusts (Fig. 2; Table 1). Jentsch (2009) suggested that severe disturbance might destroy microbial biomass and lead to species loss. The light disturbance treatment (L1) also reduced microbial biomass in our study. Rodríguez-Verdugo et al. (2019) demonstrated that low-intensity disturbance results in the loss of microbial biomass because microbial species are prone to competitive exclusion under a competition regime.

The microbial biomass in the biocrust layer was generally greater than that at a depth of 0–2 cm beneath the biocrusts. However, the PLFA biomasses of soil bacteria, fungi, G+, and G- were greater at soil depths of 0–2 cm than in the biocrust layer (Fig. 2). The reason for this observation could be that cyanobacteria were among the dominant taxa in the biocrusts in our study. Most cyanobacterial biocrusts can mediate chlorophyll synthesis, but strong sunlight in summer might inhibit chlorophyll synthesis by cyanobacteria and negatively impact the growth of microorganisms (Zhao et al. 2010). The exposed environment and intense sunlight may have reduced the living cells of microorganisms and then decreased microbial PLFA biomass. Thus, in this study, the microbial biomass in the biocrust layer was lower than that in the subsoil at the time of sampling. Another likely explanation for our finding is that soil microorganisms moved deeper into the soil to avoid strong sunlight due to microbial tropism (Yurkov and Gemerden 1993; Garcia-Pichel and Pringault 2001).

How disturbance regimes drive changes in the microbial communities in biocrusts

Disturbance-driven changes in the ecological services provided by biocrusts (such as soil infiltration and soil nutrient status) might cause alterations in microbial communities (Fraterrigo and Rusak 2008; Zaady et al. 2016). Based on our RDA results, shifts in biocrust composition (cyanobacteria) and soil properties (soil moisture, total N and the C/N ratio) were critical drivers of the observed changes in the microbial communities (Fig. 5).

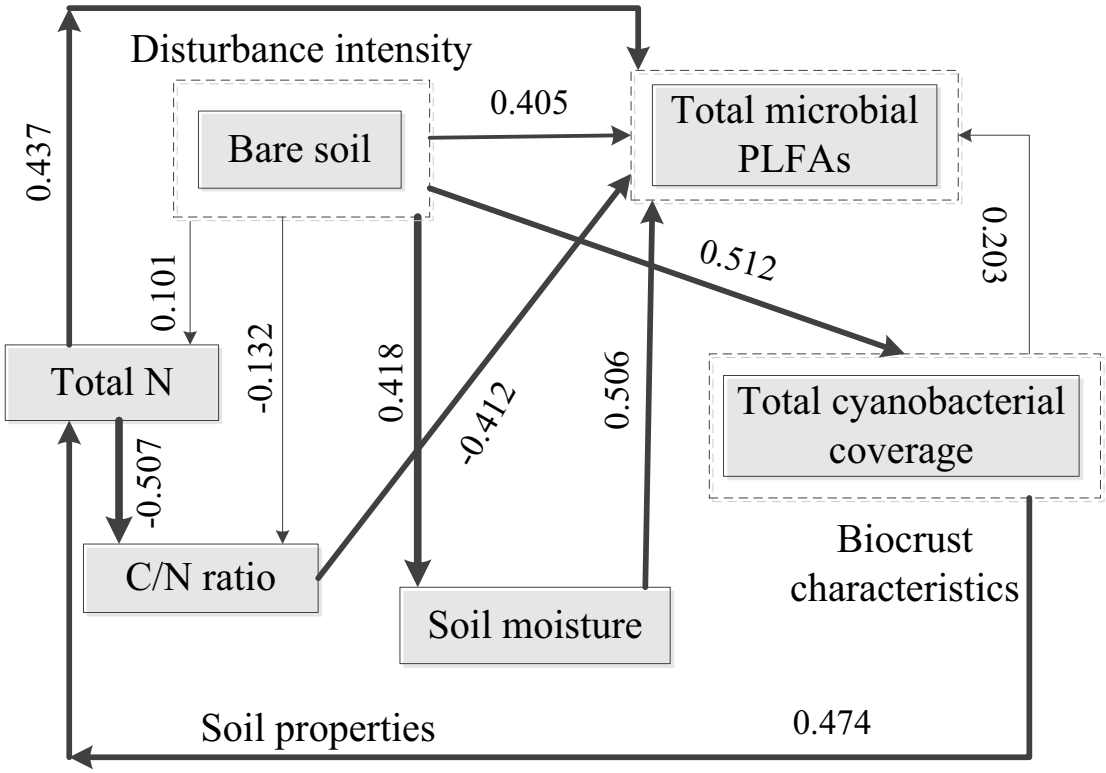

Fig. 6 Path analysis demonstrating how disturbance intensity affects microbial biomass. Bare soil coverage was the quantitative characteristic of disturbance intensity used in the study. The dashed-outline boxes and associated text correspond to the category of measured variables. Rectangles indicate the measured variables. Single-headed arrows represent hypothetical causal relationships between disturbance intensity, biocrust characteristics, soil properties and microbial diversity. Adjacent path coefficients (equivalent to correlation coefficients or regression weights) reflect the degree of the relationship, and arrow width is proportional to the coefficient value

Naturally, disturbance can increase soil infiltration by disrupting the compact biocrust surface (Eldridge et al. 2010). In this study, soil moisture was notably higher in the L5 treatment than in the control (Supplemental Table S4). Shi et al. (2017) found that 50% broken biocrust coverage substantially increased soil infiltration. In contrast, the soil moisture in the moderate disturbance was significantly lower than that in the plots with no disturbance. A possible explanation for the reduced soil moisture is partial loss from evaporation due to the open biocrust surface caused by disturbance (Eldridge and Rosentreter 1999). Another possible reason is our choice of sampling season and depths. Additional research is necessary to confirm the reason. However, suitable moisture benefits the biological processes and metabolic rates of microbes (Baldrian et al. 2010). A 16% soil moisture (volumetric water content), which is similar to the soil volumetric water content (17%) under moderate disturbance (Supplemental Table S4), is appropriate for increasing microbial abundance (unpublished data, Zhao et al.).

Changes in soil nutrients alter the growth of microorganisms, and improvements in nutrient resources could result in greater niche availability, which would in turn decrease the effects of species competition on microbial biomass (Mårtensson and Olsson 2012). In our study, moderate disturbance increased the total N content in biocrusts (Supplemental Table S5). The results of the path analysis (Fig. 6) demonstrated that the changes in total N might have primarily been due to the impact of cyanobacteria.

Generally, early-successional cyanobacterial biocrusts fix less nitrogen than do later-successional lichen or moss biocrusts (Barger et al. 2016). However, in this study, moderate disturbance, which was associated with no significant changes in total biocrust coverage and a slight alteration in lichen and moss coverage, increased the coverage (2 ~ 3%) of cyanobacterial biocrusts (Supplemental Table S3, Fig. 7). Cyanobacteria are able to recover rapidly and might benefit from the open spaces that appear following disturbance (Concostrina-Zubiri et al. 2014),

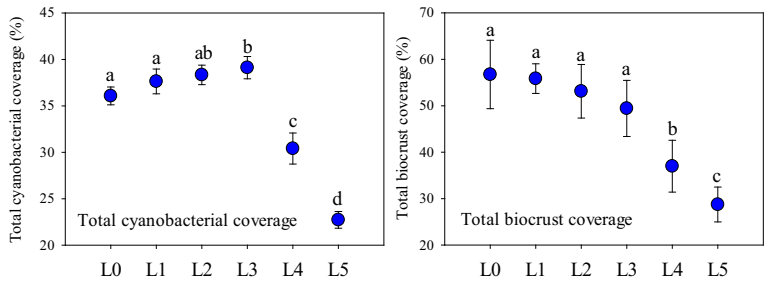

Fig. 7 Total cyanobacterial and biocrust coverage (mean ± SE) after disturbance at different intensity levels. Values are means ± standard error ($n = 40$). Total cyanobacterial coverage: developed cyanobacterial coverage + recovered cyanobacterial coverage; Total biocrust coverage: developed cyanobacterial coverage + moss coverage + lichen coverage + recovered cyanobacterial coverage. The disturbance levels were set at L1 (10 ± 5%), L2 (20 ± 5%), L3 (30 ± 5%), L4 (40 ± 5%), and L5 (50 ± 5%) based on the coverage of broken biocrusts. The number between brackets represents the measured coverage of broken biocrusts. L0: no disturbance (the control)

enhancing the ecological role of biocrusts via their contribution to N cycling (Belnap et al. 2003). Thus, the increase in cyanobacterial coverage might have enhanced the total N content in soils. Additionally, *Nostoc commune*, as a crucial cyanobacterial species in biocrusts, plays a key role in biocrusts via its contribution to N fixation; thus, an increase in its frequency and number of occurrences under moderate disturbance may be a critical factor driving the increase in soil N (Wang 2017). Regardless, distinct declines in total N after severe disturbance (L4 and L5) were detected due to a large decline in biocrust coverage.

Although the coverage of cyanobacterial biocrusts increased significantly under moderate disturbance, cyanobacterial biomass (chlorophyll a) decreased linearly with increasing disturbance (Supplemental Table S3). The reason for the mismatch between coverage and biomass (chlorophyll a) data for the cyanobacterial biocrusts may be that chlorophyll a was lower one year after disturbance. In addition, sampling and chlorophyll a measurement errors may also explain this mismatch.

Furthermore, the C/N ratio showed a significant reduction (6 ~ 8%) after moderate disturbance and a notable increase (8 ~ 11%) after severe disturbance (Supplemental Table S5). Changes in the C/N ratio might drive changes in the microbial communities in soils (Doran 1994). A reduction in the C/N ratio after moderate disturbance is favorable to microbial development because such a reduction reflects a decrease in nutrient competition between plants and microorganisms (Huang et al. 1999).

Additionally, there were no significant differences in available N under moderate disturbance compared to no disturbance, while available N markedly decreased in the light (L1) and severe disturbance (L4 and L5) treatments. This result may primarily be attributed to the alteration of biocrust coverage (a pattern very similar to the changes in biocrust coverage, Fig. 7). Distinct declines in available N under severe disturbance were detected based on the large reduction in biocrust coverage. Simultaneously, a higher available P content was found in the L3 treatment (Supplemental Table S5). Gao et al. (2018) demonstrated that biocrusts of earlier-successional cyanobacteria had a lower C/P ratio than those of later-successional mosses. Wang and Yu (2008) found that P availability is often dependent on a reduction in the C/P ratio. Reducing the size of patches of moss biocrusts and increasing the discontinuous and sparse patches of cyanobacteria may increase the available P content (Bowker et al. 2011). Furthermore, no significant differences in available P were found between other disturbance intensities and the control. Long-term research needs to be conducted to explore whether changes in available nutrients drive changes in the microbial communities.

Microbial performance in the biocrusts under the disturbance regimes is in line with the intermediate disturbance hypothesis

Our findings were consistent with the IDH (Connell 1978), an ecological hypothesis that has not been widely tested in biocrust taxa. Microbial communities often perform important ecosystem roles in biocrust formation and development and regulate nutritional availability and primary productivity. Members of the developed microbial community may themselves strongly influence the overall environment and nutrients of biocrusts and hence further influence ecosystem processes. Our ability to predict the effects of disturbance on soil

microorganisms may be the first step toward predicting ecosystem responses to environmental changes. Such effort has potential implications for improving the way we view the succession of soil health and ecosystem processes, which are important for ecosystem functioning and services in dryland ecosystems.

Moreover, as a model system for ecosystem studies, biocrusts respond rapidly to stressors and can serve as useful tools for predicting ecosystem processes (Bowker et al. 2014). For the development of dryland ecosystems, optimal biocrust systems can be achieved by disturbance at a moderate intensity rather than by completely eliminating disturbance activities (Concostrina-Zubiri et al. 2017), and the application of appropriate disturbance levels might steer a system toward positive development (Zaady et al. 2016). However, the increases in microbial PLFA biomass and community diversity observed in this study represented a short-term burst (a single year) of ecosystem productivity in response to biocrust disturbance. Will the effects of moderate disturbance always benefit ecosystems? Are different aspects such as food, habitat space, and time of activity sufficient to support biodiversity under disturbance? Whether other ecological functions of biocrusts benefit from such interference? Further research is necessary to ascertain the long-term effects of disturbance intensity on microbial communities and other ecosystem services in biocrusts.

In this study, the disturbance treatments were applied by simulating trampling disturbance; however, there are some practical concerns related to the absence of actual grazing in this study, such as the lack of trampling by goats and animal gnawing and excrement, which can exert complex effects on the soil microorganisms in biocrusts and could not be addressed in this study. Practical grazing at varying intensities need to be conducted to examine the changes of biocrust composition and functions. Additionally, later-successional lichens and mosses may recover after a year of disturbance, while the changes in recovered lichens and mosses may be unobservable. Long-term investigations need to be conducted to explore the recovery of these species.

Conclusions

Our results demonstrated that disturbance intensity was a vital factor driving the observed changes in biocrust microbial communities. As expected, we found that moderate disturbance levels did not markedly reduce biocrust coverage, increased cyanobacterial coverage and subsequently created favorable conditions with respect to soil moisture and nutrient status (increased total N and reduced C/N ratio). These effects consequently increased the microbial PLFAs and community diversity of biocrust associates. However, the low and high disturbance intensities exerted negative effects on the microbial communities in the biocrust systems. Our study supports the IDH and suggests that moderate disturbance has a positive effect on functional responses from a microbial perspective, but this conclusion may not apply to all ecosystem functions. Long-term research is needed to examine the effects of disturbance intensity (especially moderate disturbance) on the microbial communities of and other important roles played by biocrusts.

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