RESEARCH ARTICLE

WILEY

Dryland nitrogen deposition induces microbiome-driven increases in biocrust respiration and losses of soil carbon

Weiqiang Dou[1] | Bo Xiao[1,2,3] | Manuel Delgado-Baquerizo[4] | Daniel Revillini[4] | Giora J. Kidron[5]

[1]Key Laboratory of Arable Land Conservation in North China, Ministry of Agriculture and Rural Affairs/College of Land Science and Technology, China Agricultural University, Beijing, China

[2]State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, China

[3]Breeding Base for State Key Laboratory of Land Degradation and Ecological Restoration in Northwestern China/Key Laboratory of Restoration and Reconstruction of Degraded Ecosystems in Northwestern China of Ministry of Education, Ningxia University, Yinchuan, China

[4]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Seville, Spain

[5]Institute of Earth Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel

Correspondence
Bo Xiao, College of Land Science and Technology, China Agricultural University, No. 2, Yuanmingyuan West Road, Haidian District, Beijing 100193, China.
Email: xiaobo@cau.edu.cn

Abstract

Biocrusts are a dominant component in drylands worldwide and play critical roles in supporting soil microbial diversity and carbon (C) stocks. Nitrogen (N) fertilization associated with human activities threatens drylands, which are often considered N-limited ecosystems. Here, we conducted a field experiment in two contrasting soil types (loess vs. sand) to investigate the impacts of low (30 kg N ha^{-1} year^{-1}) and high (90 kg N ha^{-1} year^{-1}) fertilization on moss-biocrust dominated traits, soil nutrients, microbial taxonomic richness, soil C stocks and respiration rates (R_s). We showed that 5 months of N addition resulted in reductions in soil organic C content by 91% and increased both soil microbial richness and diversity. Our results further showed that relative to controls, low levels of N addition increased biocrust R_s by 52% through increased moss biomass and density (38% and 73%) and microbial taxonomic richness and diversity (18% and 23%), while no significant changes in biocrust R_s were observed after high levels of N addition. Considering multiple environmental factors simultaneously, we show that N fertilization indirectly promoted soil respiration and C losses via increases in microbial richness and diversity, which are critical drivers of soil function. Our work provides solid evidence that N deposition, even at low levels of N addition, can result in rapid losses of C in dryland soils. Our findings suggest that to maintain healthy dryland ecosystems and promote C, we must mitigate future land degradation and minimize anthropogenic N deposition.

KEYWORDS
biological soil crust, C cycling, global change, land degradation, soil health

1 | INTRODUCTION

Global anthropogenic nitrogen (N) inputs have increased $\sim$13-fold from 1860 to 2005 due to the burning of fossil fuels and overuse of fertilizers in agriculture (Davidson, 2009; Galloway et al., 2008), which has severely impacted the health and functioning of terrestrial ecosystems. Drylands represent an important, but often overlooked, component of terrestrial ecosystems, occupying approximately 41% of the planet's terrestrial surface (Schimel, 2010). However, dryland degradation resulting from intensified human activities and global climate change has become an environmental issue of great concern globally. Drylands are especially at risk from excessive N inputs, as these ecosystems are naturally limited by N availability (Dias et al., 2020; Zhou, Ke, et al., 2020). Specifically, increased N deposition can not only influence vegetation growth and soil N cycling (Zhou, Tao, et al., 2020) but also have important impacts on the soil microbiome and the capacity of drylands to sequester soil carbon (C) (Devaraju et al., 2016). Beyond the role of soil C and C sequestration in the context of climate change, soil C is essential to support critical soil processes such as nutrient cycling and maintain the biodiversity of the soil microbiome (Maestre et al., 2015). Quantifying the impacts of N deposition on soil C sequestration is thus critical for predicting dryland soil health and functioning under global change.

Biocrusts are a globally distributed and dominant component of drylands. Formed by the combination of mosses, lichens, algae, fungi, and bacteria together with topsoil particles (Guan et al., 2021), biocrusts are essential for supporting the biodiversity and function of the soil microbiome (Delgado-Baquerizo et al., 2018; Delgado-Baquerizo, Maestre, Eldridge, et al., 2016), and help to maintain soil stability, water regulation and C sequestration (Eldridge et al., 2023). However, the performance of biocrusts and associated soil microbiomes in supporting C sequestration may be altered by increased N inputs associated with fertilization (Dias et al., 2020; Zhou, Ke, et al., 2020). Microbial diversity contains the machinery that carries out complex soil processes such as nutrient cycling and organic matter decomposition, which requires the cooperation of thousands of soil organisms to connect hundreds of metabolic pathways. The diversity of microbial communities has been shown to support multiple ecosystem functions in global drylands (Delgado-Baquerizo, Maestre, Reich, et al., 2016). Under natural low-N conditions, dryland microbes are in a historic state of equilibrium with the environment and decompose organic matter at the pace dictated by water and nutrient limitations. However, because microbial communities are adapted to N limitation in drylands, we posit that additions of N via deposition and fertilization will accelerate microbial-driven decomposition, resulting in greater soil respiration rates (R_s) and reductions in soil C stocks. Understanding the interactions between microbial diversity and N in driving soil C and R_s is essential to accurately assess the soil C balance of biocrusts found in globally important dryland ecosystems.

Here, we conducted a five-month field experiment to investigate the impacts of low (30 kg ha^{-1} year^{-1}) and high (90 kg ha^{-1} year^{-1}) N fertilization on soil microbial taxonomic richness and diversity, respiration, and C stocks in two contrasting soils (loess and sand) in ecosystems dominated by biocrust-forming mosses located on the northern Loess Plateau of China. After N addition, we continuously measured biocrust R_s and soil temperature and moisture for 5 months. We collected paired soil and biocrust samples to characterize biocrusts and to measure nutrient contents, microbial taxonomic richness, and diversity. In this study, we proposed the following research questions: (i) What are the responses of biocrust characteristics and their R_s to exogenous N addition? (ii) How does N addition affect soil properties and microbial taxonomic richness and diversity? (iii) What are the underlying mechanisms affecting biocrust R_s after N addition? The answers to these questions will improve our understanding of biocrust health and soil C balance in drylands and further provide insights into the structural and functional changes in fragile dryland ecosystems, induced by an increase in anthropogenic N deposition.

2 | MATERIALS AND METHODS

2.1 | Site description

The Liudaogou watershed at Shenmu in Shaanxi Province, China was chosen as our study site (6.9 km^2) in (Figure 1a,b). The mean annual temperature and rainfall amount are 8.4°C and 454 mm, respectively. The mean monthly temperatures in summer and winter are −9.7 and 23.7°C, respectively, and 70%–80% of rainfall occurs in summer and autumn. Therefore, the climate of the area is typical of semiarid temperate continental monsoon habitats. The watershed has two types of soil, including loess (86.5%) and sand (13.5%) (Gao et al., 2017). The loess was composed of 35.9% sand, 61.5% silt, and 2.6% clay; and the sand was composed of 90.2% sand, 9.1% silt, and 0.7% clay.

Since the 21st century, the "Grain for Green" project has been carried out in the region, with a large number of native shrubs planted to prevent soil erosion (Xiao et al., 2019). After two decades, the vegetation cover extensively increased and now reaches $\sim$30%. As a result, sparse vegetation provides favorable interspace habitats with stabilized soil surfaces for biocrust development, which covers $\sim$30% and up to >70% of the soil surface (Li, Xiao, et al., 2021). These particular biocrusts are usually moss-dominated, composed mostly of *Didymodon constrictus* (Mitt.) Saito., *Didymodon vinealis* Brid., and *Bryum argenteum* Hedw.

2.2 | Experimental design

A randomized experiment was designed with two levels of N additions, low (30 kg N ha^{-1} year^{-1}) and high (90 kg N ha^{-1} year^{-1}), and a control with zero N addition on the two types of soils (loess and sand). Correspondingly, we had six treatments in total, and each plot had four replicates. Accordingly, a total of 24 plots (1 × 1 m each) were built on the loess and sand soils (Figure 1c,d). All the plots were located on level land (slope <5°), and they were at least 5 m away from the nearest shrub to avoid root respiration. The plots were also
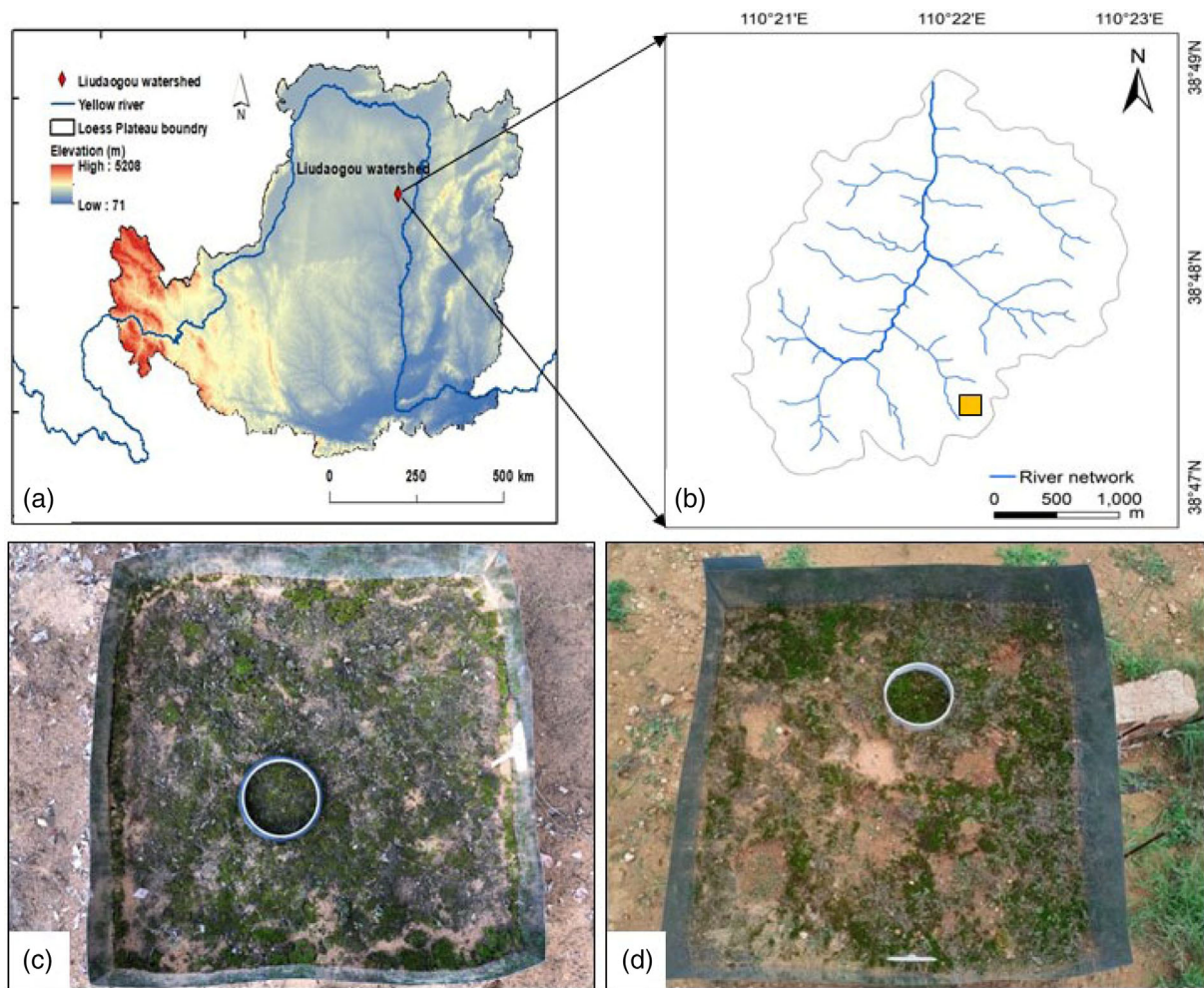
FIGURE 1 Experimental sites and biocrust plot monitoring design. (a) Locations of the Chinese Loess Plateau and Liudaogou watershed; (b) Experimental plot in Liudaogou watershed; (c) Biocrusts on sand; and (d) Biocrusts on loess. [Colour figure can be viewed at wileyonlinelibrary.com]

spaced at least 5 m from each other to minimize the effects of mutual disturbance.

At the beginning of every month (June to November 2021), NH_4NO_3 was dissolved in 1 L of water (low and high levels of N concentration were 0.72 and 2.14 g NH_4NO_3 m^{-2}, respectively) and evenly distributed across each plot using a handheld sprayer. Control plots with zero N addition received 1 L of water without NH_4NO_3. Throughout the experiment, N addition was performed five times, leading to a total amount of N addition for the low and high N treatment levels of 3.6 and 10.7 g NH_4NO_3 m^{-2}, respectively.

2.3 | Measurements of biocrust R_s and microbial relative abundance and diversity

To avoid measurement errors caused by soil disturbance, one soil respiration collar (12 cm high and 20 cm inner diameter) was fitted in the soil of each plot prior to the respiration measurements. Biocrust R_s was measured daily in each plot during July and October 2021 using

an Li-8100A automated soil CO_2 flux system (Li-COR, Inc. in USA) between 9:00 and 11:00 a.m. Each measurement lasted for a total of 180 s and included a 30 s pre-purge, a 30 s post-purge, a 90 s measurement time, and a 30 s dead band. During the measurement periods, 25% of the days had rainfall events (the total amount was 58.5 mm and the maximum individual rainfall was 11.5 mm), and among these rainfall events slight (individual rainfall amount <2 mm) and moderate or heavy rainfall (individual rainfall amount >5 mm) accounted for 69% and 12% (Figure S3), respectively. Thus, the biocrusts were inactive (dormant phase due to draught) for about 75% of the time during our measurements.

We also collected soil and biocrust samples (0–5 cm) from each plot at the end of the experiment in November to measure microbial taxonomic richness and diversity. The samples (preserved at −20°C until processing) were used for high-throughout sequencing. DNA was extracted using a QIAquick PCR purification kit (Qiagen), and the concentration and purity of the extracted DNA were tested using a NanoDrop One (Thermo Fisher Scientific; USA). The V4 region of the bacterial 16S *rRNA* gene was amplified with primers 515F

(GTGCCAGCMGCCGCGGTAA) and 907R (CCGTCAATTCMTTTR AGTTT), and the ITS1 region of the fungal *rRNA* gene was amplified with primers ITS5-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC). The constructed amplicon libraries were sequenced by PE250 using the Illumina Nova 6000 platform, and all measurements were performed by Magigene Biotechnology Co. Ltd. in Shenzhen, China. Raw paired-end reads were merged using FLASH, and demultiplexed sequences were based on the unique barcode in each sample. Processing and analysis of these joined reads were conducted using QIIME2 software (Han et al., 2020; Wang et al., 2022).

2.4 | Measurements of soil and biocrust properties

Some studies have indicated that N addition is also likely to affect soil temperature and moisture through changes in vegetation cover (Zhou et al., 2014). Thus, the soil temperature and moisture content were measured at a 5 cm depth in each plot with PT1000 and EC-5 sensors (METER Group, Inc. in USA), and the results logged every 10 min were saved on the CR1000 data logger. Meteorological factors (air temperature and rainfall) were measured with the HMP155 sensor (Vaisala, Finland) and TE525MM rain gauge (Texas Electronics, Inc. in USA), respectively.

Additionally, we measured biocrust cover and thickness using the grid method and digital vernier calipers at the end of the N addition experiment (November 2021), respectively (Dou et al., 2022). Moreover, we collected samples of both soil (0–5 cm) and biocrusts (0–2 cm) from each plot. The moss plants within the biocrust layer were separated from the soil by washing with water, passing through a 2 mm sieve, dried at 65°C for 24 h, and weighed to measure moss biomass. Following moss counting, the moss density was measured (Xiao et al., 2019). Extractions of nitrate (NO_3^--N) and ammonium (NH_4^+-N) were made from the soil using 2 mol L^{-1} KCl (Wang et al., 2015), and the filtered extracts were then analyzed using a continuous flow analyzer. The soil organic C (SOC) content was determined by the Walkley-Black potassium dichromate oxidation method (Walkley & Black, 1934), and the total N (TN) content was determined by the Kjeldahl method (Pocknee & Sumner, 1997). Samples of the total phosphorus (TP) and available phosphorus (AP) were determined photometrically using the malachite-green method based on digestion by perchloric acid and extraction by 0.05 mol $NaHCO_3$, respectively (Zhou, Tao, et al., 2020).

2.5 | Data analysis

Differences in biocrust R_s, soil properties (temperature, moisture, SOC, TN, TP, NH_4^+-N, NO_3^--N, and AP), biocrust characteristics (thickness, cover, moss biomass, and moss density), and microbial taxonomic richness (Ace) and diversity (Shannon) indices (calculated using the "Vegan" package in R 4.1.1) among treatments were tested with one-way ANOVA. Meanwhile, the interaction impacts of N addition and soil type on biocrust R_s, soil properties, and biocrust characteristics were evaluated by a two-way ANOVA. Moreover, structural equation

modeling was carried out with Amos 24.0 to understand the relationships among N addition, environmental conditions, soil nutrients, microbial taxonomic richness, and diversity indices, biocrust properties, and biocrust R_s. Before performing structural equation modeling, principal component analysis (PCA) was used to decrease the number of variables and integrate them along principal components (PC1). The components ultimately included were: environmental conditions (soil temperature and moisture), soil nutrients (SOC, TN, TP, NO_3^--N, NH_4^+-N, and AP), microbial taxonomic richness, and diversity indices (Ace index of bacteria, Ace index of fungi, Shannon index of bacteria, and Shannon index of fungi), and biocrust properties (biocrust cover, biocrust thickness, moss biomass, and moss density).

3 | RESULTS

3.1 | Testing the efficiency of N fertilization in controlling N availability

The experimental N addition resulted in expected increases in N and P availability (Figure S1). The contents of TN, TP, NO_3^--N, NH_4^+-N, and AP significantly increased after N addition (Figure S1A–E). Specifically, the contents of TN, NO_3^--N, and NH_4^+-N after low and high levels of N addition were 4.0–4.5, 4.2–4.8, and 3.8–6.3 times and 13.2–14.8, 12.9–16.0, and 17.2–20.8 times higher than those of the control, respectively (Figure S1A,C,D). Meanwhile, the contents of TP and AP were 3%–16%, 7%–24%, 180%–420%, and 22%–87% higher than those of the control after low and high levels of N addition, respectively (Figure S1B,E). Both N addition and soil type had a significant ($p < 0.001$) impact on N availability (Table 1).

3.2 | Impacts of N addition on moss-dominated biocrust characteristics

As listed in Table 1 and Figure 2, significant ($p < 0.001$) changes in moss biomass and density occurred after N addition. After low levels of N addition, moss biomass was increased by 26.3%–50.0% relative to the controls, while under high N addition, moss biomass was increased by 25.0% in the loess and decreased by 35.7% in sand (Figure 2c). Moreover, moss density increased by 58.4%–88.1% after low levels of N addition but decreased by 34.1%–41.3% after high levels of N addition in both soils (Figure 2d). The results of the two-way ANOVA in Table 1 show that the influence of both N addition and soil type on moss biomass and density was statistically significant ($p < 0.001$; Table 1). Additionally, the sand had higher ($p < 0.001$) biocrust thickness, moss biomass, and moss density than the loess (Figure 2).

3.3 | Impacts of N addition on SOC content and soil respiration

Our results provide solid evidence for rapid decreases in SOC in response to fertilization. Particularly, the SOC content was decreased

TABLE 1 A two-way ANOVA of soil type and nitrogen (N) addition on biocrust respiration rate (R_s), soil properties, and biocrust characteristics.

Measurements	Soil type		N addition		Soil type × N addition	
	F	p*	F	p	F	p
Biocrust R_s	57.27	<0.001	45.78	<0.001	0.28	0.14
Soil temperature	6.84	0.32	0.07	0.13	0.36	0.32
Soil moisture	456.49	<0.001	0.76	0.08	0.47	0.25
SOC	464.11	<0.001	481.02	<0.001	18.13	<0.001
TN	53.42	<0.001	3556.69	<0.001	15.10	<0.001
TP	7.81	0.002	7.71	0.005	0.20	0.08
NO_3^--N	142.24	<0.001	8591.21	<0.001	19.73	<0.001
NH_4^+-N	172.25	<0.001	4684.71	<0.001	127.86	<0.001
AP	9.85	0.008	6.78	0.006	3.15	0.34
Biocrust cover	6.61	0.29	4.28	0.15	0.22	0.12
Biocrust thickness	70.13	<0.001	5.65	0.12	1.33	0.21
Moss biomass	1466.57	<0.001	65.73	<0.001	60.24	<0.001
Moss density	123.53	<0.001	97.09	<0.001	17.54	<0.001

Abbreviations: AP, available phosphorus; NH_4^+-N, ammonium; NO_3^--N, nitrate; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.
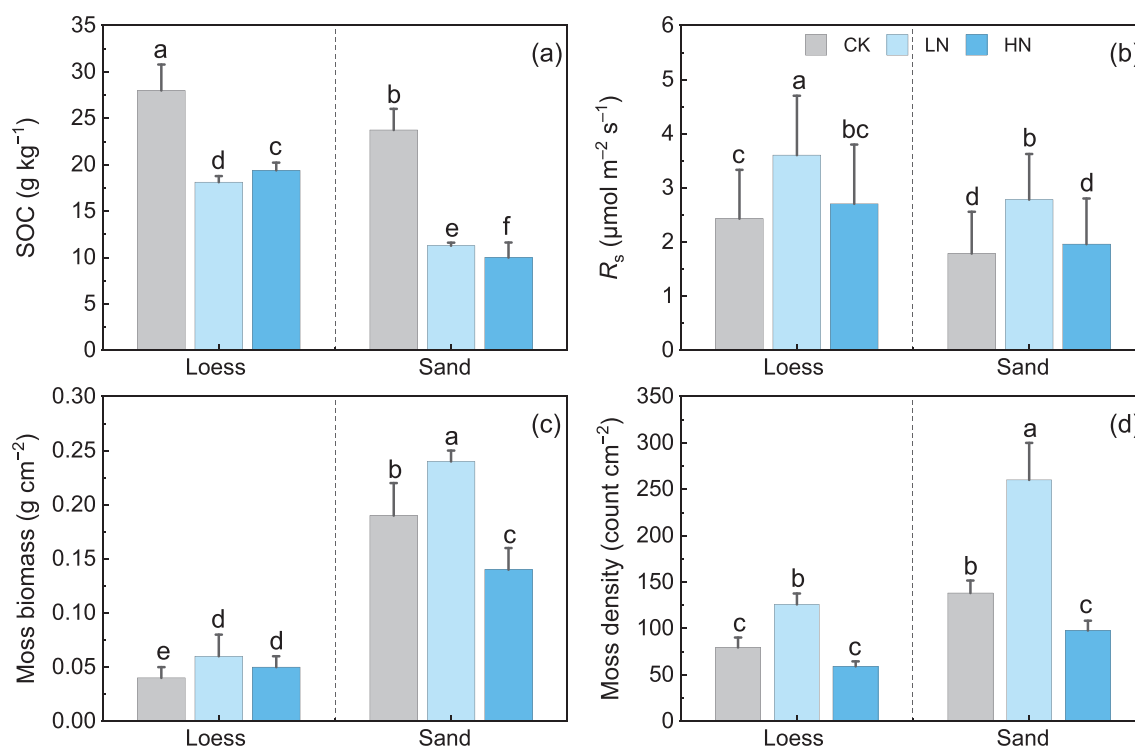*$p < 0.05$ represent a significant influence.

FIGURE 2 Differences in soil organic carbon (SOC) content (a), respiration rates (R_s) (b), moss biomass (c), and moss density (d) among treatments with both levels of N addition and two types of soil. CK, control; HN, high level of N addition; LN, low level of N addition. Different lowercase letters represent significant differences among treatments at 0.05 level of probability. [Colour figure can be viewed at wileyonlinelibrary.com]

by 44.4%–54.8% and 110.6%–137.4% after low or high levels of N addition, respectively (Figure 2a). Moreover, the biocrust R_s was increased by 48.3%–55.7% ($p < 0.001$) after low levels of N addition compared with the control (Figure 2b). However, the biocrust R_s was not significantly ($p = 0.45$) different from that of CK after a high level of N addition (Figure 2b). Moreover, whether before and after N addition, the biocrust R_s was higher in the loess than in the sand, which had 1.3–1.4 times higher R_s than the sand (Figure 2b). Soil

temperature and moisture did not differ between plots at either level of N addition (Figure S2C,D). However, the temperature and moisture of loess were significantly higher than those of sand, both before and after N addition (Figure S2C,D). Finally, there were no observed interaction effects of N addition and soil type on biocrust R_s, temperature, and moisture ($p = 0.14$–0.32) (Table 1). The variation in biocrust R_s with time was similar after both levels of N addition, indicating a gradual decrease over time (Figure S3B,C).

3.4 | Changes in the microbial community in biocrusts following N addition

Bacterial communities (whether on loess soil or aeolian sand, with and without N addition) consisted primarily of *Acidobacteria*, *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, *Chloroflexi*, and *Planctomycetes*, and the fungal communities were dominated by *Ascomycota*, *Basidiomycota*, *Mortierellomycota*, and *Chytridiomycota* (Figure S4). Importantly, we found that N addition enhanced bacterial and fungal richness, and diversity. Compared to the controls, the taxonomic richness of bacteria and fungi increased by 9.4%–31.5% and 3.9%–24.4% after low and high levels of N addition, respectively (Figure S4). Correspondingly, after low and high levels of N addition, the Ace index of bacteria and fungi was increased by 5.2%–28.8% and 3.6%–26.1% (Figure 3a,c), and the Shannon index of bacteria and fungi was

increased by 5.2%–41.3% and 4.6%–36.4%, respectively (Figure 3b,d). Among them, *Acidobacteria*, *Actinobacteria*, and *Proteobacteria* were the most common bacterial communities under both levels of N addition, and their combined relative abundance exceeded 65% (Figure S4). Similarly, *Ascomycota* and *Basidiomycota* were the most common fungal communities, and their relative abundances reached ~50% (Figure S4).

3.5 | Microbial diversity drives the indirect impacts of N fertilization on biocrust R_s

As listed in Figure S5, the relative abundances of *Actinobacteria* (bacteria), *Ascomycota*, and *Basidiomycota* (fungi) were positively correlated with biocrust R_s after N addition. Furthermore, structural equation modeling indicated that the impacts of N input on soil nutrients and microbial activities (e.g., richness and community diversity) drive changes in biocrust R_s (Figure 4). More specifically, N addition indirectly influenced biocrust R_s by increasing microbial relative richness and diversity, and N addition and microbial activities together explained 81%–96% of the overall variation in biocrust R_s (Figure 4). Additionally, the standardized total effects of soil nutrients and microbial activities on biocrust R_s after N addition were −0.10 to −0.60 and 0.89 to 0.92 (Figure S6), respectively, indicating that biocrust R_s was primarily modulated by changes in microbial activities (Figure S6).
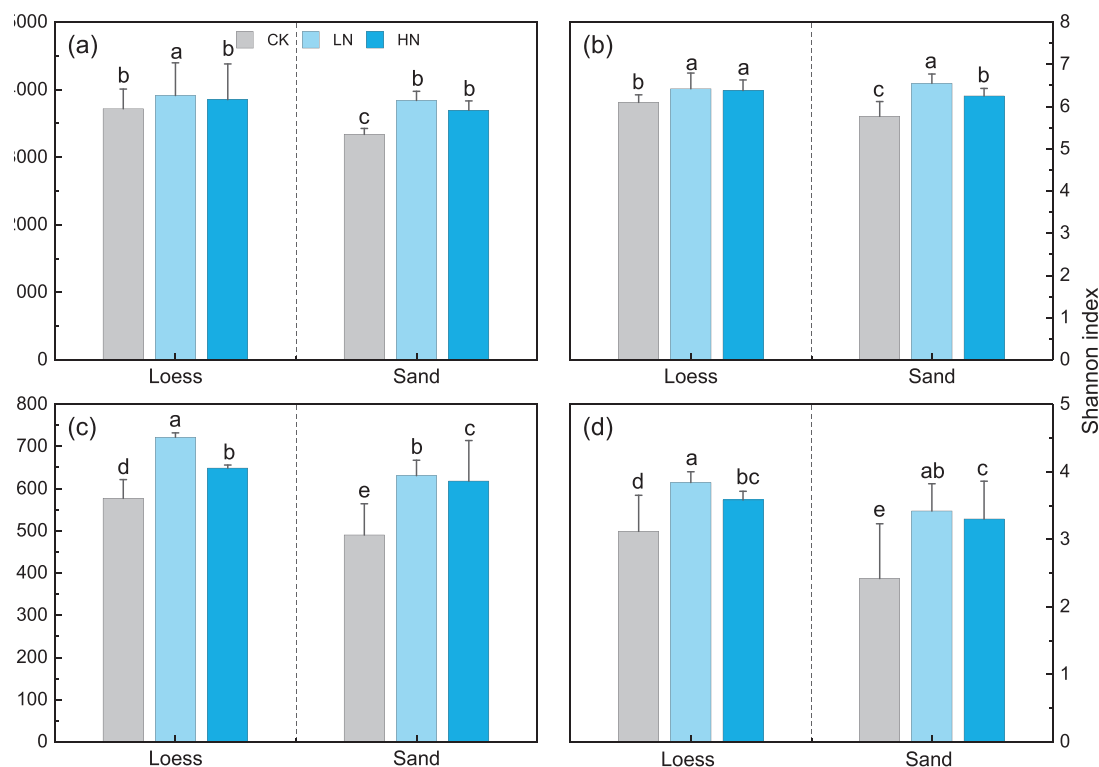

FIGURE 3 Differences in the taxonomic richness and diversity of microbes after two levels of N addition on two types of soils. (a and b) represent Ace and Shannon indices of the bacteria, respectively; (c and d) represent Ace and Shannon indices of the fungi, respectively. Different lowercase letters represent significant differences among treatments at 0.05 level of probability. [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Structural equation model showing the correlation pathways of N addition, environmental conditions, soil nutrients, microbial diversity, and biocrust properties on biocrust respiration rate (R_s). (a) R_s on loess; (b) R_s on sand. AP, available phosphorus; BC, biocrust coverage; BT, biocrust thickness; MB, moss biomass; MD, moss density; NH_4^+-N, ammonium; NO_3^--N, nitrate; Shannon-B, shannon index of bacteria; Shannon-F, shannon index of fungi; SOC, soil organic carbon; ST, soil temperature; SWC, soil water content; TN, total N; TP, total phosphorus. Red and blue arrows represent positive and negative impacts, respectively; solid and dashed arrows represent significant and insignificant impacts, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]
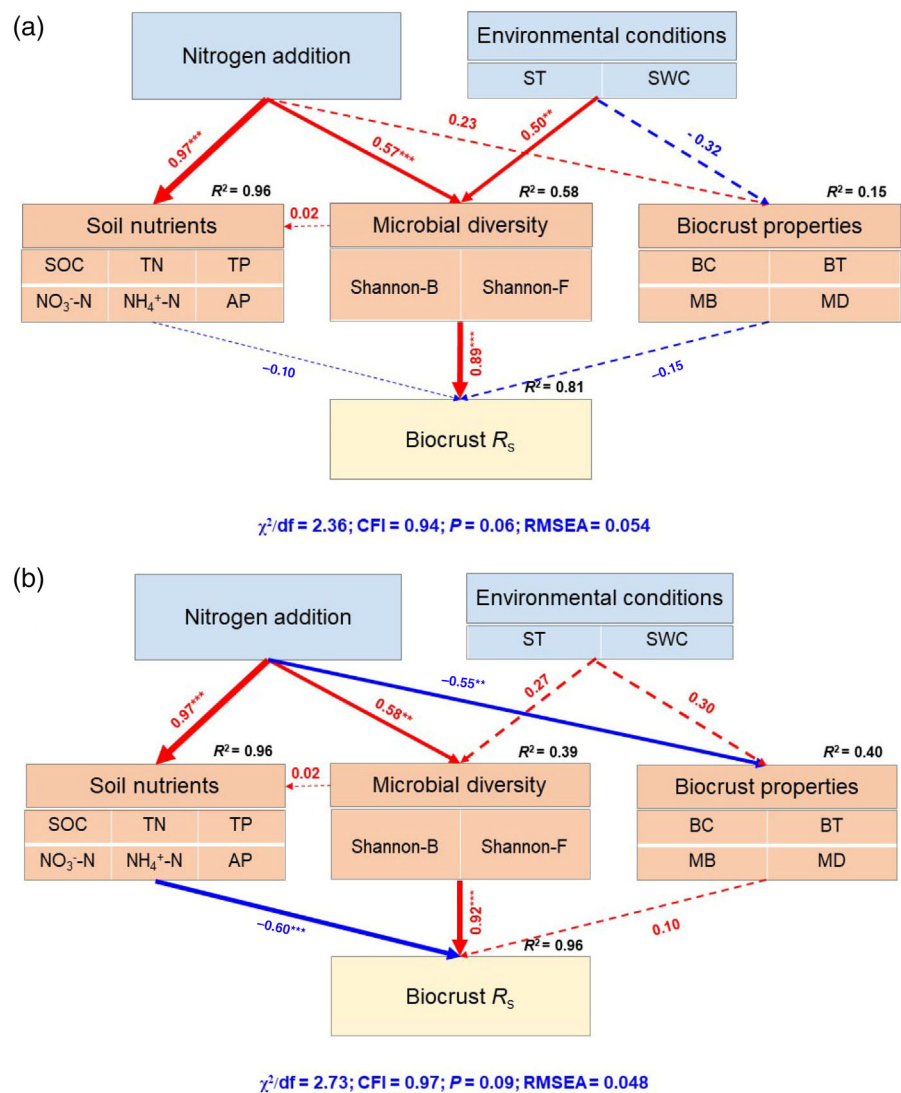
4 | DISCUSSION

Our study of dryland biocrusts from two distinct soil types showed that N fertilization significantly increased soil R_s and reduced SOC content. Fertilization with N also promoted the richness and diversity of soil bacteria and fungi. Importantly, we showed that low levels of N addition significantly increased soil R_s via increases in moss biomass and density, as well as shifts in microbial richness and increases in diversity. These results suggest that even modest future increases in N deposition may limit our ability to promote C sequestration in dryland ecosystems, which cover >40% of Earth's terrestrial surface. Coupled with global land-use changes and increasing land degradation, our findings further cement the need for immediate actions to minimize anthropogenic impacts on the landscape and to mitigate climate change.

4.1 | Influences of N addition on soil nutrients and microbial communities

Our results showed that N addition enhanced the levels of TN, NH_4^+-N, NO_3^--N, and AP. Obviously, an increase in the

contents of available N was triggered by the direct addition of NH_4^+-N and NO_3^--N (Ye et al., 2018). Furthermore, since N addition stimulates phosphatase activity and enhances microbial decomposition of SOC (Ren et al., 2016), this accelerates the conversion process of soil P (Chen et al., 2020). Thus, we can conclude that atmospheric N deposition can have a significant influence on the ecological functioning of biocrusts by triggering concurrent or subsequent shifts in multiple soil nutrient levels in drylands.

The microbial communities in biocrusts analyzed in our study were mostly *Acidobacteria*, *Proteobacteria*, *Actinobacteria*, *Ascomycota*, and *Basidiomycota*. Despite the regional, climatic, and methodological differences in previous studies, the microbial communities in biocrusts reported were generally consistent with our results, including microbiomes from other dryland habitats such as the Sonoran Desert (Soule et al., 2009), Colorado Plateau (Bates et al., 2012), and Mojave Desert in the United States (Mueller et al., 2015); the Gurbantunggut Desert (Zhang et al., 2011), Tengger Desert (Zhang et al., 2012), and the Loess Plateau in China (Xiao & Veste, 2017), as well as the Tabernas Desert in Spain (Maier et al., 2014).

We also discovered that N addition promoted the richness and diversity of bacterial and fungal communities in biocrusts. N-induced soil nutrient variations may be the underlying mechanism driving changes in the microbial community (Wang et al., 2018). Previous studies have shown that the richness and diversity of specific phyla in microbial communities increased with increasing soil nutrients (e.g., SOC, TN, and AP) after N addition (Guo et al., 2017). However, structural equation modeling indicated that microbial richness and diversity in our study were decoupled from other soil nutrients after N addition, where the addition of N directly affected microbial richness and diversity rather than indirectly through other nutrients. This response is likely driven by a complicated interaction between resource availability and the response of microorganisms following N addition (Clark & Tilman, 2008). Locally adapted soil microbes may be highly sensitive to exogenous inputs of nutrients that are typically under chronic nutrient (particularly N) stress in drylands. Multiple dynamics arise when organisms, in this case both biocrusts and soil microbes, undergo drastic resource availability changes; the alleviation of biocrust N-limitation can alter their relationships with associated soil bacteria and fungi in a manner that optimizes new resource requirements (Daniel et al., 2016). For instance, N addition led to increased biocrust biomass, increased microbial taxonomic richness and diversity, and greater TP and AP in our study; this could be a result of complex plant-microbial interactions designed to increase P allocation to biocrust mosses after prior N limitations were removed. Importantly, soil microbes are also nutrient-limited themselves and can utilize nutrients directly as needed when they are added to soil (Mueller et al., 2015). These results provide interesting areas for future research in the field.

4.2 | Changes in biocrust R_s following N addition and their underlying mechanisms

Numerous studies have demonstrated that N deposition influences soil C dynamics by regulating soil respiration, which in turn affects global climate change (Xing et al., 2022). Our study observed a marked enhancement in the biocrust R_s at low levels of N addition. Owing to the severe water and wind erosion on the northern Loess Plateau, N becomes a dominant restricting factor for vegetation development and microbial activity. As we hypothesized, low N addition influenced the biocrust R_s primarily by enhancing microbial activity. N addition enhanced soil microbial richness and diversity, which subsequently resulted in an enhanced biocrust R_s (Yuan et al., 2020). Similar results have been reported in some recent studies in other ecosystems around the world. As listed in Table 2, low or moderate N addition in grassland and forest ecosystems stimulates soil respiration mainly by stimulating plant growth and improving microbial activity (Wilcots et al., 2022; Xing et al., 2022).

Surprisingly, high levels of N addition had no remarkable influence on biocrust R_s. Some previous studies have also reported that high levels of N addition had no influence or even a negative impact on soil respiration (Peng et al., 2020). Usually, excessive N inputs can reduce

soil pH and acidify the soil, thereby affecting the microbial community (Wilcots et al., 2022). For instance, excessive N input can induce shifts in the microbial community, which usually results in a reduction in SOC decomposition and increased C use efficiency, ultimately reducing soil respiration (Xing et al., 2022). Therefore, we conclude that the changes in biocrust R_s after N addition may be regulated mainly by microbial activity.

We also observed higher biocrust R_s in loess than in sand. Structural equation modeling indicated that greater biocrust R_s was primarily regulated through the positive direct effects of N addition and N-induced changes to microbial activity in the loess, while the lower biocrust R_s in sand was regulated by the negative impact of N-induced changes to soil nutrients and a moderately positive impact of microbial activity. Thus, with N addition to the sand, the negative impact of soil nutrients (mainly SOC) is likely to counterbalance the positive impact of microbial activity. Overall, there was a much greater sensitivity of sand to N addition, highlighting the necessity for further investigation of the possible influence of soil type on N deposition and subsequently on C cycling in drylands.

4.3 | Losses of SOC after N addition and the potential mechanisms

Our results showed that N addition reduced the SOC content of biocrust-covered soils, and even more importantly, low levels of N addition enhanced moss biomass and density, which seemed to contradict the reduction of SOC content. Actually, SOC accumulation is the result of a balance between photosynthetic fixation and respiration losses (Kheirfam, 2020). An increase in moss biomass and density may lead to an increase in photosynthetic C sequestration, but this would only happen for active biocrusts after rehydration (not dormant phase) (Wu et al., 2015). Moreover, for C sequestration and growth, sufficient wetness duration is required (Kidron et al., 2009; Wilske et al., 2008). In drylands, the photosynthetic C sequestration and growth of biocrusts mostly occur after moderate or heavy rainfall events (Kidron et al., 2012). Although only a few such rain pulses may occur (>5 mm of rainfall only three times), as recorded during our research, they will result in a growth boast of the biocrusts (Hui et al., 2021; Kidron et al., 2012; Su et al., 2013; Zheng et al., 2018), especially following N addition, as recorded during the current research. Yet, the high temperatures coupled with consecutive low-depth rains (which while not being sufficiently long to result in C sequestration were capable of moistening the subsurface) resulted in high R_s, mainly attributed to the subsurface microbial population. In this regard it is worth mentioning Wilske et al. (2008) findings from the Negev, that clearly showed that low-depth rain events were actually ineffective to induce the restoration of biocrust physiological activity (Wilske et al., 2008). This may lead to a reduced accumulation of photosynthetically sequestered C in biocrusts.

Moreover, following the close link between subsurface moisture content and biocrust biomass (Kidron & Benenson, 2014), and subsequently between biocrust biomass and subsurface biomass

TABLE 2 Impacts of N addition on soil respiration in different regions and ecosystems around the world.

Location	Annula precipitation (mm)	Ecosystem type	N addition (g N m^{-2} year^{-1})	Response of soil respiration to N addition	Reference
Loess Plateau, China	454	Dryland	0, 3, 9	Stimulating by 48.3%–55.7%	This study
Heilongjiang, China	500	Boreal forest	0, 2, 5, 10	Increasing by 8.0% in short-term (1 a) but inhibiting by 21.0% in long-term (10 a)	Xing et al. (2022)
Svartberget, Sweden	600	Forest	0, 0.3, 0.6, 1.2, 5	No significant impact	Forsmark et al. (2020)
Henan, China	619	Grassland	10	Stimulating by 5.1%	Zhang et al. (2022)
Shaanxi, China	620	Farmland	0, 1, 2, 4, 8, 16, 32, 64	Nonlinearly decreasing	Li, Niu, et al. (2021)
Kahramnmaraş Plateau, Turkey	750	Grassland	0, 5, 10, 15, 20, 25, 30	Increasing by 97.0%–129.0%	Babur et al. (2021)
Minnesota, United States	750	Grassland	0, 1, 5, 10	Increasing first but then decreasing	Wilcots et al. (2022)
Zhejiang, China	1420	Moso bamboo forest	0, 3, 6, 9	Increasing by 7.0%–145.8%	Li et al. (2022)
Hunan, China	1422	Subtropical forest	0, 5, 15, 30	Inhibiting by 36.2%–39.0%	Yan et al. (2020)

(Grishkan & Kidron, 2017), elevated moss biomass and density also imply an increase in respiration, whether of the biocrusts or by the subsurface microorganisms (Dou et al., 2022; Miralles et al., 2018; Yu et al., 2012), which was confirmed by the significantly elevated R_s of the biocrusts after low level of N addition. One may note that the growth period during the current research was characterized by low precipitation (only 58 mm), which coupled with the high temperatures resulted in relatively dry crust conditions, granting an advantage to microorganism activity at the subsurface. Proportionally, this in turn will result in higher respiration relative to C sequestration, that is, to relatively high consumption of SOC. As a whole, although moss biomass and density were elevated after a low level of N addition, the accumulation of photosynthetically sequestered C in biocrusts may be insufficient to offset the C content losses from biocrust respiration, due to the divergent responses of photosynthetic C sequestration and soil respiration to soil water, which in turn showed a loss of SOC content.

Notably, we conducted a short-term simulated N addition experiment, in which we set a higher N addition gradient than the local natural N deposition rate. Such a high level of short-term N addition above the natural background may change the adaptive mechanisms of biocrusts to long-term natural N deposition (Guo et al., 2017). As a result of short-term mitigation of N limitation in biocrusts (increasing total and available nitrogen), N deposition may facilitate the rapid decomposition and transformation of existing organic substrates (e.g., SOC) by soil microorganisms (increasing microbial abundance and diversity), which in turn led to a decrease in SOC content. However, long-term results may be quite different. For example, along with the gradual adaptation of biocrusts to N additions (especially low level of N addition, which may not cause fundamental changes in biocrust physiological activity and soil properties (Zhang et al., 2020); the

abundance and diversity of soil microbial community may also gradually shift from a short-term rapid increase to a relatively stable state (Guo et al., 2017), similarly to the microbial thermal adaptation mechanism after prolonged warming (Dacal et al., 2020). Therefore, in the long term, the SOC content of biocrust-covered soils after a low level of N addition may undergo a directional reversal due to N adaptation by soil microorganisms; however, this still needs to be further investigated.

4.4 | Uncertainties and implications of biocrust R_s responses to N addition

Although our study demonstrates a remarkable influence of short-term N addition on biocrust R_s, several uncertainties still exist and need to be further considered. For example, our results showed that biocrust R_s was mainly regulated by soil nutrients and microbial activity after N addition, but their interactive effects were not further analyzed. A recent study investigated the complex interactions between soil nutrients and microbial activity, and it estimated that their combined effect contributes up to 10% to biocrust R_s (Wang et al., 2022). Obviously, the combined effect of soil nutrients and microbial activity is essential for a more accurate understanding of biocrust R_s variation; however, the interactions between soil nutrients and microbial activities were not significant in our study. Consequently, this combined effect on biocrust R_s after intensified N deposition deserves more comprehensive study in the future.

More importantly, although the stimulating function of short-term N addition on biocrust R_s was supported by several past investigations (Gao et al., 2014), it is notable that the influence of N input on R_s is a prolonged and complicated process (Zhang et al., 2022). With longer

N addition, the accumulation of N leads to soil acidification, and the richness and diversity of microbes begin to decline (Xing et al., 2022). Taken together, these results emphasize the importance of the duration of N addition on biocrust R_s, and additional long-term studies are necessary to more accurately predict dryland soil C dynamics under global change.

5 | CONCLUSIONS

We performed a simulated N deposition experiment to identify the responses of biocrusts, microbial communities, and R_s and to determine the explanatory mechanisms in drylands. The results indicated that low N input had a positive effect on biocrust health, increasing moss biomass and density, while high N input had a negative impact. Moreover, the taxonomic richness of bacteria and fungi was significantly enhanced by low N addition, resulting in a 48%–56% increase in biocrust R_s, while high N input did not have a remarkable influence on biocrust R_s. Soil type does matter for biocrust R_s after N addition. In the loess, N addition and its induced soil temperature and moisture changes indirectly stimulated biocrust R_s by increasing microbial richness and diversity in biocrusts, whereas in the sand, N addition regulated biocrust R_s mainly by decreasing soil nutrients. Our study provides an important perspective on the responses and mechanisms of biocrust health and their R_s to N deposition in the Loess Plateau of China and other similar drylands. We highlight that the health and R_s of biocrusts are highly dependent on the N addition level and soil type, which is of great concern in scenarios where global atmospheric N deposition is likely to rise in the future, as this could diminish the ability of biocrusts to participate in the C cycle and could further lead to soil degradation in drylands.

ORCID

Bo Xiao https://orcid.org/0000-0002-9544-4207
Giora J. Kidron https://orcid.org/0000-0003-0406-3052

REFERENCES

Babur, E., Uslu, O. S., Battaglia, M. L., Mumtaz, M. Z., Danish, S., Fahad, S., Diatta, A. A., Datta, R., & Ozlu, E. (2021). Nitrogen fertilizer effects on microbial respiration, microbial biomass, and carbon sequestration in a mediterranean grassland ecosystem. *International Journal of Environmental Research*, *15*(4), 655–665. https://doi.org/10.1007/s41742-021-00336-y

Bates, S. T., Nash, T. H., & Garcia-Pichel, F. (2012). Patterns of diversity for fungal assemblages of biological soil crusts from the southwestern United States. *Mycologia*, *104*(2), 353–361. https://doi.org/10.3852/11-232

Chen, Z. F., Xiong, P. F., Zhou, J. J., Yang, Q., Wang, Z., & Xu, B. C. (2020). Grassland productivity and diversity changes in responses to N and P addition depend primarily on tall clonal and annual species in semiarid loess plateau. *Ecological Engineering*, *145*, 105727. https://doi.org/10.1016/j.ecoleng.2020.105727

Clark, C. M., & Tilman, D. (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, *451*(7179), 712–715. https://doi.org/10.1038/nature06503

Dacal, M., Garcia-Palacios, P., Asensio, S., Cano-Diaz, C., Gozalo, B., Ochoa, V., & Maestre, F. T. (2020). Contrasting mechanisms underlie short- and longer-term soil respiration responses to experimental warming in a dryland ecosystem. *Global Change Biology*, *26*(9), 5254–5266. https://doi.org/10.1111/gcb.15209

Daniel, R., Catherine, A. G., & Nancy, C. J. (2016). The role of locally adapted mycorrhizas and rhizobacteria in plant-soil feedback systems. *Functional Ecology*, *30*(7), 1086–1098. https://doi.org/10.1111/1365-2435.12668

Davidson, E. A. (2009). The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nature Geoscience*, *2*(9), 659–662. https://doi.org/10.1038/NGEO608

Delgado-Baquerizo, M., Maestre, F. T., Eldridge, D. J., Bowker, M. A., Jeffries, T. C., & Singh, B. K. (2018). Biocrust-forming mosses mitigate the impact of aridity on soil microbial communities in drylands: Observational evidence from three continents. *New Phytologist*, *220*(3), 824–835. https://doi.org/10.1111/nph.15120

Delgado-Baquerizo, M., Maestre, F. T., Eldridge, D. J., Bowker, M. A., Ochoa, V., Gozalo, B., Berdugo, M., Val, J., & Singh, B. K. (2016). Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands. *New Phytologist*, *209*(4), 1540–1552. https://doi.org/10.1111/nph.13688

Delgado-Baquerizo, M., Maestre, F. T., Reich, P. B., Jeffries, T. C., Gaitan, J. J., Encinar, D., Berdugo, M., Campbell, C. D., & Singh, B. K. (2016). Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nature Communications*, *7*, 10541. https://doi.org/10.1038/ncomms10541

Devaraju, N., Bala, G., Caldeira, K., & Nemani, R. (2016). A model based investigation of the relative importance of CO_2-fertilization, climate warming, nitrogen deposition and land use change on the global terrestrial carbon uptake in the historical period. *Climate Dynamics*, 47(2), 173–190. https://doi.org/10.1007/s00382-015-2830-8

Dias, T., Crous, C. J., Ochoa-Hueso, R., Manrique, E., Martins-Loucao, M. A., & Cruz, C. (2020). Nitrogen inputs may improve soil biocrusts multifunctionality in dryland ecosystems. *Soil Biology and Biochemistry*, 149, 107947. https://doi.org/10.1016/j.soilbio.2020.107947

Dou, W. Q., Xiao, B., Wang, Y. F., & Kidron, G. J. (2022). Contributions of three types of biocrusts to soil carbon stock and annual efflux in a small watershed of northern Chinese loess plateau. *Applied Soil Ecology*, 179, 104596. https://doi.org/10.1016/j.apsoil.2022.104596

Eldridge, D. J., Guirado, E., Reich, P. B., Ochoa-Hueso, R., Berdugo, M., Saez-Sandino, T., Blanco-Pastor, J. L., Tedersoo, L., Plaza, C., Ding, J. Y., Sun, W., Mamet, S., Cui, H. Y., He, J. Z., Hu, H. W., Sokoya, B., Abades, S., Alfaro, F., Bamigboye, A. R., ... Delgado-Baquerizo, M. (2023). The global contribution of soil mosses to ecosystem services. *Nature Geoscience*, 16, 430–438. https://doi.org/10.1038/s41561-023-01170-x

Forsmark, B., Nordin, A., Maaroufi, N. I., Lundmark, T., & Gundale, M. J. (2020). Low and high nitrogen deposition rates in northern coniferous forests have different impacts on aboveground litter production, soil respiration, and soil carbon stocks. *Ecosystems*, 23(7), 1423–1436. https://doi.org/10.1007/s10021-020-00478-8

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z. C., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., & Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, 320(5878), 889–892. https://doi.org/10.1126/science.1136674

Gao, L. Q., Bowker, M. A., Xu, M. X., Sun, H., Tuo, D. F., & Zhao, Y. G. (2017). Biological soil crusts decrease erodibility by modifying inherent soil properties on the loess plateau, China. *Soil Biology and Biochemistry*, 105, 49–58. https://doi.org/10.1016/j.soilbio.2016.11.009

Gao, Q., Hasselquist, N. J., Palmroth, S., Zheng, Z. M., & You, W. H. (2014). Short-term response of soil respiration to nitrogen fertilization in a subtropical evergreen forest. *Soil Biology and Biochemistry*, 76, 297–300. https://doi.org/10.1016/j.soilbio.2014.04.020

Grishkan, I., & Kidron, G. J. (2017). Vertical divergence of cultural microfungal communities at the Hallamish dunefield, western Negev desert, Israel. *Geomicrobiology Journal*, 34, 706–721. https://doi.org/10.1080/01490451.2016.1243597

Guan, C., Zhang, P., Zhao, C. M., & Li, X. R. (2021). Effects of warming and rainfall pulses on soil respiration in a biological soil crust-dominated desert ecosystem. *Geoderma*, 381, 114683. https://doi.org/10.1016/j.geoderma.2020.114683

Guo, P., Jia, J. L., Han, T. W., Xie, J. X., Wu, P. F., Du, Y. H., & Qu, K. Y. (2017). Nonlinear responses of forest soil microbial communities and activities after short and long-term gradient nitrogen additions. *Applied Soil Ecology*, 121, 60–64. https://doi.org/10.1016/j.apsoil.2017.09.018

Han, Q., Ma, Q., Chen, Y., Tian, B., Xu, L. X., Bai, Y., Chen, W. F., & Li, X. (2020). Variation in rhizosphere microbial communities and its association with the symbiotic efficiency of rhizobia in soybean. *ISME Journal*, 14(8), 1915–1928. https://doi.org/10.1038/s41396-020-0648-9

Hui, R., Li, X. R., Zhao, R. M., Tan, H. J., & Jia, R. L. (2021). Physiological response of moss/cyanobacteria crusts along a precipitation gradient from semi-arid to arid desert in China. *Plant and Soil*, 468(2), 97–113. https://doi.org/10.1007/s11104-021-05117-2

Kheirfam, H. (2020). Increasing soil potential for carbon sequestration using microbes from biological soil crusts. *Journal of Arid Environments*, 172, 104022. https://doi.org/10.1016/j.jaridenv.2019.104022

Kidron, G. J., Barinova, S., & Vonshak, A. (2012). The effects of heavy winter rains and rare summer rains on biological soil crusts in the Negev Desert. *Catena*, 95, 6–11. https://doi.org/10.1016/j.catena.2012.02.021

Kidron, G. J., & Benenson, I. (2014). Biocrusts serve as biomarkers for the upper 30 cm soil water content. *Journal of Hydrology*, 509, 398–405. https://doi.org/10.1016/j.jhydrol.2013.11.041

Kidron, G. J., Vonshak, A., & Abeliovich, A. (2009). Microbiotic crusts as biomarkers for surface stability and wetness duration in the Negev Desert. *Earth Surface Processes and Landforms*, 34, 1594–1604. https://doi.org/10.1002/esp.1843

Li, K. Y., Niu, M. G., Bai, W. M., Yang, Z. L., & Li, G. Y. (2021). Water-dominated negative effects of nitrogen enrichment on soil respiration in a temperate steppe. *Applied Soil Ecology*, 165, 104023. https://doi.org/10.1016/j.apsoil.2021.104023

Li, Q., Ma, Q. H., Gao, J. P., Zhang, J. B., Li, Y. F., Shi, M., Peng, C. H., & Song, X. Z. (2022). Stumps increased soil respiration in a subtropical Moso bamboo (*Phyllostachys edulis*) plantation under nitrogen addition. *Agricultural and Forest Meteorology*, 323, 109047. https://doi.org/10.1016/j.agrformet.2022.109047

Li, S. L., Xiao, B., Sun, F. H., & Kidron, G. J. (2021). Moss-dominated biocrusts enhance water vapor sorption capacity of surface soil and increase non-rainfall water deposition in drylands. *Geoderma*, 388, 114930. https://doi.org/10.1016/j.geoderma.2021.114930

Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J., Ochoa, V., Gozalo, B., Quero, J. L., Garcia-Gomez, M., Gallardo, A., Ulrich, W., Bowker, M. A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitan, J., Gutierrez, J. R., Huber-Sannwald, E., Jankju, M., ... Singh, B. K. (2015). Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Sciences of the United States of America*, 112(51), 15684–15689. https://doi.org/10.1073/pnas.1516684112

Maier, S., Schmidt, T. S. B., Zheng, L. J., Peer, T., Wagner, V., & Grube, M. (2014). Analyses of dryland biological soil crusts highlight lichens as an important regulator of microbial communities. *Biodiversity and Conservation*, 23(7), 1735–1755. https://doi.org/10.1007/s10531-014-0719-1

Miralles, I., de Guevara, M. L., Chamizo, S., Rodriguez-Caballero, E., Ortega, R., van Wesemael, B., & Canton, Y. (2018). Soil CO_2 exchange controlled by the interaction of biocrust successional stage and environmental variables in two semiarid ecosystems. *Soil Biology and Biochemistry*, 124, 11–23. https://doi.org/10.1016/j.soilbio.2018.05.020

Mueller, R. C., Belnap, J., & Kuske, C. R. (2015). Soil bacterial and fungal community responses to nitrogen addition across soil depth and microhabitat in an arid shrubland. *Frontiers in Microbiology*, 6, 891. https://doi.org/10.3389/fmicb.2015.00891

Peng, Y., Song, S. Y., Li, Z. Y., Li, S., Chen, G. T., Hu, H. L., Xie, J. L., Chen, G., Xiao, Y. L., Liu, L., Tang, Y., & Tu, L. H. (2020). Influences of of nitrogen addition and aboveground litter-input manipulations on soil respiration and biochemical properties in a subtropical forest. *Soil Biology and Biochemistry*, 142, 107694. https://doi.org/10.1016/j.soilbio.2019.107694

Pocknee, S., & Sumner, M. E. (1997). Cation and nitrogen contents of organic matter determine its soil liming potential. *Soil Science Society of America Journal*, 61(1), 86–92. https://doi.org/10.2136/sssaj1997.03615995006100010014x

Ren, F., Yang, X. X., Zhou, H. K., Zhu, W. Y., Zhang, Z. H., Chen, L. T., Cao, G. M., & He, J. S. (2016). Contrasting effects of nitrogen and phosphorus addition on soil respiration in an alpine grassland on the Qinghai-Tibetan plateau. *Scientific Reports*, 6, 39895. https://doi.org/10.1038/srep39895

Schimel, D. S. (2010). Drylands in the earth system. *Science*, 327(5964), 418–419. https://doi.org/10.1126/science.1184946

Soule, T., Anderson, I. J., Johnson, S. L., Bates, S. T., & Garcia-Pichel, F. (2009). Archaeal populations in biological soil crusts from arid lands in North America. *Journal of Arid Environments*, 41(10), 2069–2074. https://doi.org/10.1016/j.soilbio.2009.07.023

Su, Y. G., Wu, L., Zhou, Z. B., Liu, Y. B., & Zhang, Y. M. (2013). Carbon flux in deserts depends on soil cover type: A case study in the Gurbantunggute desert, North China. *Soil Biology and Biochemistry*, *58*, 332–340. https://doi.org/10.1016/j.soilbio.2012.12.006

Walkley, A., & Black, I. A. (1934). An examination of the Degtjareff method fordetermining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science*, *37*, 29–38. https://doi.org/10.1097/00010694-193401000-00003

Wang, C., Liu, D. W., & Bai, E. (2018). Decreasing soil microbial diversity is associated with decreasing microbial biomass under nitrogen addition. *Soil Biology and Biochemistry*, *120*, 126–133. https://doi.org/10.1016/j.soilbio.2018.02.003

Wang, J., Bao, J. T., Su, J. Q., Li, X. R., Chen, G. X., & Ma, X. F. (2015). Impact of inorganic nitrogen additions on microbes in biological soil crusts. *Soil Biology and Biochemistry*, *88*, 303–313. https://doi.org/10.1016/j.soilbio.2015.06.004

Wang, Y., Hong, Y., Tian, Y. L., Tian, G. Q., Zhang, J. H., Wu, H. W., Bai, Y., & Qian, J. M. (2022). Changes in bacterial community composition and soil properties altered the response of soil respiration to rain addition in desert biological soil crusts. *Geoderma*, *409*, 115635. https://doi.org/10.1016/j.geoderma.2021.115635

Wilcots, M. E., Schroeder, K. M., DeLancey, L. C., Kjaer, S. J., Hobbie, S. E., Seabloom, E. W., & Borer, E. T. (2022). Realistic rates of nitrogen addition increase carbon flux rates but do not change soil carbon stocks in a temperate grassland. *Global Change Biology*, *28*, 4819–4831. https://doi.org/10.1111/gcb.16272

Wilske, B., Burgheimer, J., Karnieli, A., Zaady, E., Andreae, M. O., Yakir, D., & Kesselmeir, J. (2008). The CO$_2$ exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev Desert, Israel. *Biogeosciences Discussions*, *5*, 1969–2001. https://doi.org/10.5194/BG-5-1411-2008

Wu, L., Zhang, Y. M., Zhang, J., & Downing, A. (2015). Precipitation intensity is the primary driver of moss crust-derived CO$_2$ exchange: Implications for soil C balance in a temperate desert of northwestern China. *European Journal of Soil Biology*, *67*, 27–34. https://doi.org/10.1016/j.ejsobi.2015.01.003

Xiao, B., Sun, F. H., Hu, K. L., & Kidron, G. J. (2019). Biocrusts reduce surface soil infiltrability and impede soil water infiltration under tension and ponding conditions in dryland ecosystem. *Journal of Hydrology*, *568*, 792–802. https://doi.org/10.1016/j.jhydrol.2018.11.051

Xiao, B., & Veste, M. (2017). Moss-dominated biocrusts increase soil microbial abundance and community diversity and improve soil fertility in semi-arid climates on the loess plateau of China. *Applied Soil Ecology*, *117*, 165–177. https://doi.org/10.1016/j.apsoil.2017.05.005

Xing, A. J., Du, E. Z., Shen, H. H., Xu, L. C., Zhao, M. Y., Liu, X. Y., & Fang, J. Y. (2022). High-level nitrogen additions accelerate soil respiration reduction over time in a boreal forest. *Ecology Letters*, *25*(8), 1869–1878. https://doi.org/10.1111/ele.14065

Yan, W. D., Chen, X. Y., Peng, Y. Y., Zhu, F., Zhen, W., & Zhang, X. Y. (2020). Response of soil respiration to nitrogen addition in two subtropical forest types. *Pedosphere*, *30*(4), 478–486. https://doi.org/10.1016/S1002-0160(17)60471-5

Ye, C. L., Chen, D. M., Hall, S. J., Pan, S., Yan, X. B., Bai, T. S., Guo, H., Zhang, Y., Bai, Y. F., & Hu, S. J. (2018). Reconciling multiple impacts of nitrogen enrichment on soil carbon: Plant, microbial and geochemical controls. *Ecology Letters*, *21*(8), 1162–1173. https://doi.org/10.1111/ele.13083

Yu, J., Kidron, G. J., Pen-Mouratov, S., Wasserstrom, H., Barnes, G., & Steinberger, Y. (2012). Do development stages of biological soil crusts determine activity and functional diversity in a sand-dune ecosystem? *Soil Biology and Biochemistry*, *51*, 66–72. https://doi.org/10.1016/j.soilbio.1012.04.007

Yuan, X. B., Niu, D. C., Weber-Grullon, L., & Fu, H. (2020). Nitrogen deposition enhances plant-microbe interactions in a semiarid grassland: The role of soil physicochemical properties. *Geoderma*, *373*, 114446. https://doi.org/10.1016/j.geoderma.2020.114446

Zhang, B. C., Zhang, Y. M., Downing, A., & Niu, Y. L. (2011). Distribution and composition of cyanobacteria and microalgae associated with biological soil crusts in the Gurbantunggut Desert, China. *Arid Land Research and Management*, *25*(3), 275–293. https://doi.org/10.1080/15324982.2011.565858

Zhang, J. J., Ru, J. Y., Song, J., Li, H., Li, X. M., Ma, Y. F., Li, Z., Hao, Y. F., Chi, Z. S., Hui, D. F., & Wan, S. Q. (2022). Increased precipitation and nitrogen addition accelerate the temporal increase in soil respiration during 8-year old-field grassland succession. *Global Change Biology*, *28*(12), 3944–3959. https://doi.org/10.1111/gcb.16159

Zhang, K. P., Ni, Y. Y., Liu, X. J., & Chu, H. Y. (2020). Microbes changed their carbon use strategy to regulate the priming effect in an 11-year nitrogen addition experiment in grassland. *Science of the Total Environment*, *727*, 138645. https://doi.org/10.1016/j.scitotenv.2020.138645

Zhang, W., Zhang, G. S., Liu, G. X., Dong, Z. B., Chen, T., Zhang, M. X., Dyson, P. J., & An, L. Z. (2012). Bacterial diversity and distribution in the southeast edge of the Tengger Desert and their correlation with soil enzyme activities. *Journal of Environmental Sciences*, *24*(11), 2004–2011. https://doi.org/10.1016/S1001-0742(11)61037-1

Zheng, J. L., Peng, C. R., Li, H., Li, S. S., Huang, S., Hu, Y., Zhang, J. L., & Li, D. H. (2018). The role of non-rainfall water on physiological activation in desert biological soil crusts. *Journal of Hydrology*, *556*, 790–799. https://doi.org/10.1016/j.jhydrol.2017.12.003

Zhou, L. Y., Zhou, X. H., Zhang, B. C., Lu, M., Luo, Y. Q., Liu, L. L., & Li, B. (2014). Different responses of soil respiration and its components to nitrogen addition among biomes: A meta-analysis. *Global Change Biology*, *20*(7), 2332–2343. https://doi.org/10.1111/gcb.12490

Zhou, X. B., Tao, Y., Yin, B. F., Tucker, C., & Zhang, Y. M. (2020). Nitrogen pools in soil covered by biological soil crusts of different successional stages in a temperate desert in Central Asia. *Geoderma*, *366*, 114166. https://doi.org/10.1016/j.geoderma.2019.114166

Zhou, X. J., Ke, T., Li, S. X., Deng, S. Q., An, X. L., Ma, X., De Philippis, R., & Chen, L. Z. (2020). Induced biological soil crusts and soil properties varied between slope aspect, slope gradient and plant canopy in the Hobq desert of China. *Catena*, *190*, 104559. https://doi.org/10.1016/j.catena.2020.104559

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Dou, W., Xiao, B., Delgado-Baquerizo, M., Revillini, D., & Kidron, G. J. (2023). Dryland nitrogen deposition induces microbiome-driven increases in biocrust respiration and losses of soil carbon. *Land Degradation & Development*, 1–12. https://doi.org/10.1002/ldr.4942