Biocrusts modulate carbon losses under warming across global drylands: A bayesian meta-analysis

Jingyao Sun [a], Kailiang Yu [b], Ning Chen [c,d], Seth M. Munson [e], Xinrong Li [a,*], Rongliang Jia [a]

[a] Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, 730000, China
[b] High Meadows Environmental Institute, Princeton University, Princeton, NJ, 08544, USA
[c] State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, College of Ecology, Lanzhou University, No.222, Tianshui South Road, Lanzhou, Gansu, 730000, China
[d] Yuzhong Mountain Ecosystem Observation and Research Station, Lanzhou University, No.222, Tianshui South Road, Lanzhou, Gansu, 730000, China
[e] U.S. Geological Survey, Southwest Biological Science Center, 2255 N. Gemini Dr., Flagstaff, AZ, 86001, USA

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ABSTRACT

Biocrusts are critical biological components of drylands and play an important role in soil carbon (C) cycling. However, the effect of biocrusts on soil CO_2 exchange across global gradients of temperature and moisture is poorly understood. Moreover, their response to climate change remains highly uncertain. Bayesian hierarchical meta-analyses were performed on 47 published studies to quantify the impact of biocrusts on net soil exchange (NSE) of carbon- the difference between respiration and photosynthesis. Meta-analyses were also used on 23 studies to examine the effects of experimental warming on NSE in biocrusts. Meta-regressions further explored the thermal and wetness sensitivities of biocrust NSE and potential adaptation of biocrust responses to climate change. The development of biocrusts in dryland soils significantly increased NSE by 66.5 [22.2, 112.2] g C $m^{-2}yr^{-1}$, despite seasonal fluctuations, indicating a net loss of carbon to the atmosphere. Experimental warming, on average, increased biocrust NSE by 22.9 [-0.1, 40.8] g C $m^{-2}yr^{-1}$ per °C. However, across the spatial climate gradient, aridity limited the effects of warming, while high temperature decreased the thermal sensitivity of biocrust NSE, thus supporting the thermal adaptation of biocrusts. These results emphasize the critical role of biocrusts in modulating soil carbon exchange in response to climate warming across drylands, with particularly high thermal sensitivity in cool and moist regions. This highlights the need to incorporate biocrusts into global carbon budgets and models for a comprehensive understanding of their impact on the carbon cycle.

1. Introduction

Drylands occupy over 45% of the Earth's terrestrial landscape and are among the most vulnerable to climate change (Maestre et al., 2021; Schimel 2010; Song et al., 2019). Soil CO_2 efflux in drylands is a major ecosystem process of returning fixed C to the atmosphere and plays a critical role in the global C cycle (Arevalo et al., 2010; Tian et al., 2022; Trumbore 2006). Soil CO_2 efflux has high temporal and spatial variation in drylands because of high fluctuations in temperature, pulses of precipitation, and strong soil spatial heterogeneity characterized by vegetation patches and interspaced biocrust patches (Maestre and Cortina 2003; Noy-Meir 1973; Tucker and Reed 2016). Biocrusts, which consist of photoautotrophs such as lichens, mosses, and cyanobacteria, and various heterotrophic microbes, are among the most representative

biotic components of dryland regions (Li et al., 2016; Weber et al., 2022). The poikilohydric metabolism (i.e., carbon uptake and respiration) of biocrusts is activated by rainfall pulses. Their unique metabolism coupled with their global abundance in drylands highlights their crucial role in the soil-atmosphere interfaces of dryland C cycling. (Castillo-Monroy et al., 2011; Xiao et al., 2016). However, it remains poorly understood how biocrusts influence the soil C budget in arid regions across spatial environmental gradients and in a rapidly changing climate (Elbert et al., 2012, Porada et al., 2013).

Biocrusts influence soil CO_2 efflux through multiple pathways. Biocrust respiration can be responsible for a large proportion of total ecosystem C emissions, while biocrusts also fix atmospheric C by photosynthesis (Castillo-Monroy et al., 2011; Elbert et al., 2012). A laboratory study indicated that the gross photosynthesis of biocrust

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tended to be maximized at moderate temperatures and water levels, but respiration tended to increase linearly, thus suggesting a net increase in biocrust respiration under climate warming (Grote et al., 2010). Moreover, biocrusts also indirectly influence the metabolism and respiration of soil microbes by altering soil environmental conditions such as soil temperature, moisture, porosity and stability (Eldridge et al., 2020; Guan et al., 2022). For example, biocrusts, especially moss, can prolong the soil moisture residence time, which buffers environmental variation and thus facilitates soil microbial activity (Li et al., 2012). This prolonged moisture may originate from increased soil albedo and water-holding capacity, which varies in different seasons and biocrust types (Wu et al., 2012; Xiao and Bowker 2020). Altogether, it has been reported that net soil exchange (NSE), or CO_2 loss through respiration minus gross CO_2 uptake through photosynthesis (Darrouzet-Nardi et al., 2015), is usually higher in soil dominated by well-developed biocrusts (i.e., mosses) than in soil with undeveloped biocrusts or bare soil (Miralles et al., 2018); and higher in summer than in spring and autumn, and lowest in winter (Guan et al., 2022). Currently, a synthesis study quantifying the NSE of biocrusts and the potential roles of biocrust type and seasonality is lacking. Thus, our understanding of biocrust CO_2 efflux remains highly uncertain across space or under climate warming.

Climate warming could directly accelerate C emissions by increasing biochemical reactions and enzyme kinetics, thus reducing soil carbon storage and causing a positive climate-carbon cycle feedback (Bradford et al., 2019; Frey et al., 2013; Koven et al., 2017). However, the magnitude of climate-carbon feedback remains uncertain. Over the long-term, the temperature sensitivity of soil respiration was found to decrease because of the depleted labile soil organic carbon (SOC) (Frey et al., 2013; Haaf et al., 2021). Studies have also emphasized the role of thermal adaptation of soil microbial respiration to elevated temperature, which can limit the rate of carbon losses under future warming (Bradford et al., 2009, 2010, 2019). For instance, an incubation study that controlled for substrate depletion and microbial biomass using soil samples from 110 global drylands found that soil microbial mass-specific respiration rates were lower in sites with higher mean annual temperatures across three assayed temperatures than in other sites, thus supporting thermal adaptation of soil microbial respiration (Dacal et al., 2019). A recent warming experiment indicated that relatively low soil moisture could also suppress the thermal response of microbial respiration (Li et al., 2022). This result suggests that the reduced climate-carbon cycle feedback by thermal adaptation could be suppressed further by enhanced aridity in drylands because water-stressed communities tend to reallocate metabolic resources toward survival instead of adapting to elevated temperatures (Schimel and Balser 2007). Therefore, a moisture gradient may act together with a thermal gradient to affect the temperature sensitivity of NSE. Moreover, if the effects of biocrusts on soil properties and hydrothermal conditions (Eldridge et al., 2020; Li et al., 2012) are considered, the spatial variation in biocrust NSE in drylands could be even more differentiated and complex. To our knowledge, few studies have addressed the thermal adaptation of NSE in biocrusts across spatial gradient of drylands. Addressing this potential effect and the underlying drivers would be helpful in elucidating future carbon cycling under warming.

In this study, we synthesized data collected from 37 sites across global drylands. We used 47 studies from these sites to study the influence of biocrusts on NSE (objective 1) and 23 studies to examine the effects of climate warming on the NSE of biocrusts (objective 2). Moreover, we evaluated whether each effect varied across spatial temperature and water availability gradients. To ensure an adequate data volume and statistical validity, the data were collected at both seasonal and annual scales with both monotypic and mixed types of biocrusts. Bayesian models specialized in hierarchal structure were used for this meta-analysis. We hypothesize that biocrusts play important roles in influencing NSE and feedback between warming and the C cycle, and this influence varies across temperature and water availability gradients.

2. Methods

2.1. Data compilation and analysis

The publications used in this meta-analysis were retrieved through Web of Science, Science Direct, and the China National Knowledge Infrastructure (CNKI), combining two groups of keywords. Group 1 was related to the research subject, i.e., "biological soil crust", "biocrust", "poikilohydric", "microbiotic crust", "cryptogam", "moss", "bryophyte", "lichen", "algae", "algal", "cyanobacteria", and "cyanobacterial"; Group 2 was related to the NSE, i.e., "carbon budget", "carbon balance", "net soil exchange", "soil respiration", "carbon dioxide efflux", "carbon dioxide exchange", and "carbon dioxide flux". In total, 962 peer-reviewed publications were collected and then filtered by three criteria for inclusion: (1) the key indicator measured related to NSE, which equals CO_2 loss (respiration) minus gross CO_2 uptake (photosynthesis); (2) the indicator was evaluated based on field experiments in drylands rather than laboratory work; and (3) studies were conducted at annual or seasonal scales. Studies at the daily scale were excluded because daily-scale NSE reflects short-term environmental fluctuations and the goal was to understand more general and long-term trends in carbon balance. The NSE data included in studies were summarized and converted to μmol m^{-2}s^{-1} for compatibility, which spanned at least two months or at least one growing season, representative of long-term variation. Finally, the publications were classified into two groups, with 312 records and 47 studies for objective 1 and 283 records and 23 studies for objective 2. The studies for objective 2 implemented experimental warming treatments in paired study units with biocrust soil and bare soil.

All observations collected in our literature search took place at 37 sites across 5 continents (no studies were included in South America and Antarctica) (Fig. 1). We extracted the mean values ($\overline{Y}$), standard deviation (s.d.) and sample size (n) of NSE measurements in the control and treatment groups as response variables. For objective 1, the biocrust soil served as treatment and bare soil as control. For objective 2, the treatment was experimental warming, mostly implemented with an open top chamber, and the degree of warming (WD, °C) was also recorded. The seasonal/annual mean temperature (MT, °C) and precipitation were extracted from each publication. Precipitation was averaged by month for consistency as the mean precipitation (MP, mm per month). Missing climate records were derived from the WorldClim (http://www.worldclim.org) database using site latitude and longitude. In addition, NSE is closely dependent on substrate availability (Haaf et al., 2021); thus, we also collected total soil organic carbon (SOC) as a covariate to evaluate the influence of substrate. Missing records of SOC and other key soil properties were derived from the SoilGrids (Poggio et al., 2021) database using site latitude and longitude (see appendix Table S1). The MT and MP were combined to calculate the De Martonne wetness index (WI) to reflect the aridity of each observation as follows:

$$WI = \frac{MP \cdot 12}{MT + 10}$$

The mean difference (MD) method was used as effect size of the raw measurement unit (μmol m^{-2}s^{-1}) for objectives 1 and 2 as follows:

$$MD = \overline{Y_T} - \overline{Y_C}$$

with a variance of:

$$Var(MD) = \frac{s.d._T^2}{n_T} + \frac{s.d._C^2}{n_C}$$

where subscripts T and C indicate the treatment and control, respectively. The NSE data was also grouped by biocrust type, including cyanobacteria (Cyan), lichen (Lichen), moss (Moss) and mixed crusts (Mixed). To avoid data hidden in the figure, we used PlotDigitizer (version 2.6.9) to capture all values.
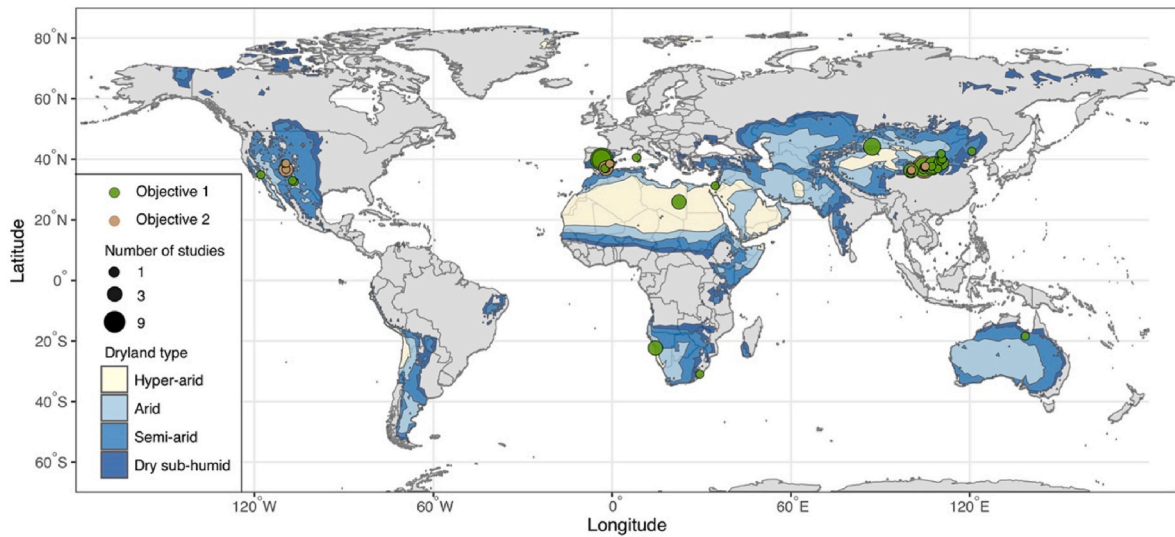
Fig. 1. Map of the distribution of global drylands and study sites used in the meta-analysis. Circle size is proportional to the number of studies from each site. The green and yellow circles indicate different study objectives of the influence of biocrusts on NSE (objective 1) and the effects of climate warming on CO_2 efflux of biocrust soil (objective 2), respectively.

2.2. Statistical analysis

To evaluate the influence of biocrusts and the effect of warming on NSE from hierarchical data with different biocrust types, temporal scales of measurement, and case studies, a Bayesian meta-analysis was conducted for our dataset. Bayesian models have the advantage of flexibility in combining the data at both seasonal and annual scales that have mixed hierarchical structure. The meta-analysis was built on linear mixed-effect equations (Fig. 2 a). MD_{ijk} indicates the mean difference of NSE for each observation. θ_{ij} reflects the mean effect size for biocrust type i and season j, which equals the overall effect $\bar{\theta}$ plus biocrust type

bias $\delta_{(t)i}$ (including mixed biocrusts) plus seasonal bias $\delta_{(s)j}$. Because the mean of four seasons equals the annual value, we set the seasonal bias $\delta_{(s)j} = 0$ for annual data, by which data at different temporal scales can be combined. All the biases δ follow a normal distribution with zero mean, and the bias $\delta_{(n)k}$ follows a normal distribution with variance τ^2 that reflects heterogeneity among observations. ϵ indicates the error, which follows the *s.d.* of each observation. For both study objects, we focus on three key parameters: overall effect $\bar{\theta}$, biocrust effect $\bar{\theta} + \delta_{(t)i}$, and independent seasonal effect $\bar{\theta} + \delta_{(s)j}$. Bayesian models use the highest density intervals (HDI) to reflect the *a posteriori* distribution for
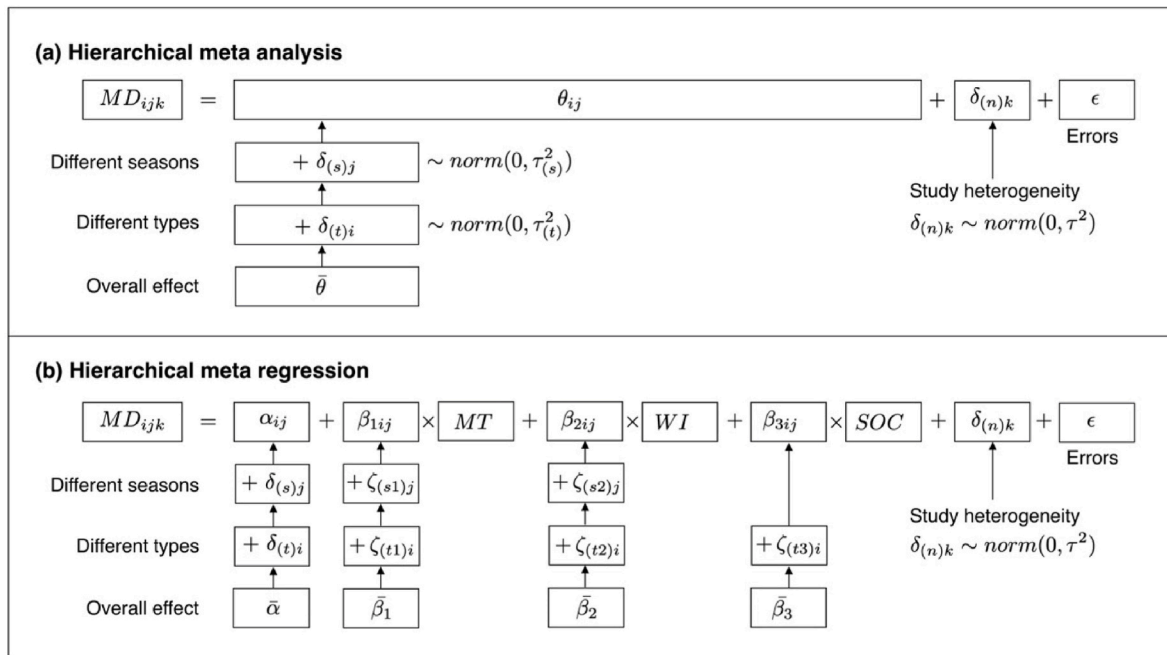

Fig. 2. Schematic of hierarchical Bayesian meta-analysis (a) and meta regression (b) used in the study. MD_{ijk} indicates the mean difference of NSE for each observation. θ_{ij} reflects the mean effect size for biocrust type i and season j, which equals the overall effect $\bar{\theta}$ plus biocrust type bias $\delta_{(t)i}$ (including mixed biocrusts) plus seasonal bias $\delta_{(s)j}$. All the biases δ follow a normal distribution with zero mean, and the bias $\delta_{(n)k}$ follows a normal distribution with variance τ^2 that reflects heterogeneity among observations. ϵ indicates the error. In meta regression, the θ_{ij} is replaced by linear combination of MT and WI and covariate SOC, with intercept α_{ij} and slope β_{ij}. The β_{1ij} and β_{2ij} equals to overall effect $\bar{\beta}$ plus type bias $\zeta_{(s)j}$ and seasonal bias $\zeta_{(s)j}$, while β_{3ij} is independent to seasons.

each parameter and is compared to 0 to calculate Bayesian significance.

Preliminary parallel analysis indicated that the main spatial variation among the study sites was explained by factors related to temperature, water, and SOC (Fig. S1). Thus, we focused on the MT and WI with covariate SOC because of not only the seasonality involved in the collected NSE and data availability but also their representation of geographic variation. As such, we used multiple meta-regressions to evaluate the influences of MT and WI on effect size with covariate SOC, replacing θ_{ij} by their linear combinations with intercept α_{ij} and slope β_{ij} (Fig. 2 b). The slope β_{1ij} and β_{2ij} equals to overall effect $\overline{\beta}$ plus type bias $\zeta_{(s)j}$ and seasonal bias $\zeta_{(s)j}$, while β_{3ij} is independent to seasons. Moreover, we also conducted a simple meta-regression with predictor MD for objective 2 to evaluate the linear temperature sensitivity. The regression intercept and slope of MT, WI and MD followed identical hierarchical structures in the meta-analysis, while the slope of SOC was only nested in biocrust types. For meta regression, we focused on three different parameters: overall slope $\overline{\beta}$, slope of biocrust types $\overline{\beta} + \zeta_{(t)i}$, and slope of different seasons $\overline{\beta} + \zeta_{(s)j}$.

The noninformative priors were adopted in our analyses. That is, the overall effect $\overline{\theta}$ and corresponding components for intercept $\overline{\alpha}$ and slope $\overline{\beta}$ were set to a normal distribution (norm (0, 1.0e4)). Heterogeneity τ_t, τ_s, τ and corresponding components for intercept and slope followed a gamma distribution (gamma (1.0e-4,1.0e-4)). The Bayesian models were developed with Gibbs sampling using the "R2jags" package (Su and Yajima 2021) on the R platform (version 4.2.0). The model stability and accuracy was evaluated by autocorrelation and potential scale reduction factor of 10 Monte Carlo Markov chains with 10,000 iterations.

3. Results

In this study, data were classified by biocrust type and recorded season. For objective 1, mosses, lichens, cyanobacteria and unclassified biocrusts accounted for 30.1%, 22.8%, 30.8% and 16.3% of the total 312 records, respectively. Among which, spring, summer, autumn and winter and annual scale represented 18.2%, 22.1%, 19.6%, 13.5% and 26.7% of records, respectively. For objective 2, mosses, lichens, cyanobacteria and unclassified biocrusts accounted for 28.6%, 24.7%, 26.1% and 20.5% of the total 283 records, respectively. While spring, summer, autumn and winter and annual scale represented 14.5%, 23.0%, 17.7%, 16.3% and 28.6% of records, respectively.

3.1. The influence of biocrusts on NSE

From the meta-analyses at the global and annual scales, the presence of biocrusts increased the NSE by 0.176 µmol m^{-2}s^{-1} with lower and upper intevals of HDI of [0.0597, 0.297], equal to 66.5 [22.2, 112.2] g C m^{-2}yr^{-1} ($P = 0.007$) (Fig. 3 a). On average, mosses had a greater impact on carbon emissions, as they increased NSE relative to bare soil by ~0.222 µmol m^{-2}s^{-1}, than lichens that increased NSE by ~0.171 µmol m^{-2}s^{-1} and cyanobacteria that increased NSE by ~0.143 µmol m^{-2}s^{-1}. The MD for biocrusts in summer (0.261 µmol m^{-2}s^{-1}) was higher than in autumn (0.160 µmol m^{-2}s^{-1}) and spring (0.147 µmol m^{-2}s^{-1}), with MD lowest in the winter (0.073 µmol m^{-2}s^{-1}). It should be noted that the real difference between the groups might be larger than our results because the shrinkage effect of the hierarchical model could have concentrated them to the upper-class mean. The influence of biocrusts on NSE did not change with increasing mean temperature, MT ($P = 0.15$) (Fig. 4a), but did increase with an increasing wetness index, WI (slope = 0.0201, $P < 0.001$) (Fig. 4b). There was no influence of different biocrust types or seasons on NSE as temperature increased (Fig. 4c). However, all biocrust types positively influenced NSE responses to an increasing wetness index similarly, and these increases in NSE mainly occurred in spring, summer and autumn, with slopes of 0.0160 ($P = 0.005$), 0.0273 ($P < 0.001$), and 0.0107 ($P = 0.019$), respectively (Fig. 4d). The overall influence of the biocrusts on NSE increased with higher SOC (slope = 0.0167, $P < 0.001$) (Fig. 4e).

3.2. The effect of warming on biocrust NSE

Warming significantly increased the biocrust NSE by 0.132 [−0.0419, 0.297] µmol m^{-2}s^{-1} ($P = 0.0420$; Fig. 3b), with 0.0606 [0.006, 0.115] µmol m^{-2}s^{-1} per °C increase (Fig. 3c). This effect occurred for cyanobacteria (0.0694 µmol m^{-2}s^{-1} °C^{-1}) and moss (0.0576 µmol m^{-2}s^{-1} °C^{-1}) but not for lichen ($P = 0.073$), and the effect occurred in spring (0.0689 µmol m^{-2}s^{-1} °C^{-1}), summer (0.0617 µmol m^{-2}s^{-1} °C^{-1}) and autumn (0.0555 µmol m^{-2}s^{-1} °C^{-1}) but not in winter ($P = 0.093$).

The effect of warming on biocrust NSE decreased along the MT gradient (slope = −0.0119, $P < 0.001$; Fig. 5a) and increased along the wetness index gradient (slope = 0.00802, $P = 0.009$; Fig. 5b). The decreased warming sensitivity along the MT gradient was stronger for moss (slope = −0.0136, $P < 0.001$) than for cyanobacteria (slope = −0.0119, $P = 0.002$) and lichen (slope = −0.0109, $P = 0.008$), and stronger in spring (slope = −0.0176, $P = 0.003$) and winter (slope = −0.0126, $P = 0.007$) than in summer (slope = −0.0108, $P = 0.014$) and
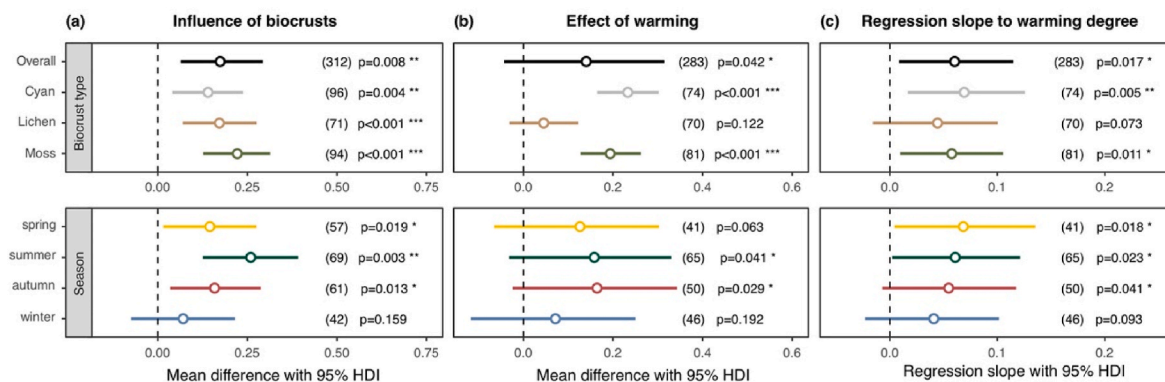

Fig. 3. Influence of biocrusts on NSE (a). Effect of warming on biocrust NSE (b). Regression slope of increased NSE relative to warming degree (c). Bars represent the mean difference (MD) and slope with 95% highest density intervals. MD and slopes above the dashed lines mark larger treatment effect (MD > 0) and positive relationships between warming degree and effect of warming. The upper panels show the effects of biocrust type: cyanobacteria (Cyan), lichen (Lichen), and moss (Moss). The effect of mixed crusts (Mixed) is omitted because the overall effect is more for statistical informational purposes (black bars). The bottom panels reflect the values in different seasons, independent of biocrust type. Although the values and their significances were evaluated from the complete dataset, the number in parentheses denotes the sample size for each group. The *P* value indicates the significance of the difference between 0 and MD with significance codes: *** indicates *P* < 0.001, ** indicates *P* < 0.01, and × indicates *P* < 0.05.
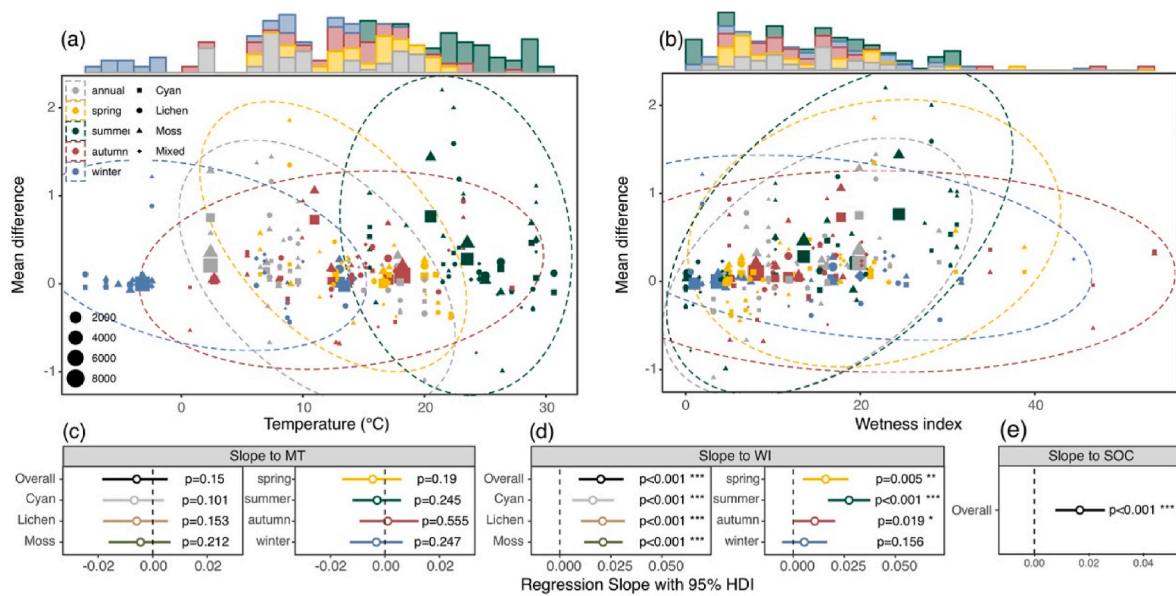
Fig. 4. Change in the effect size of biocrusts (mean difference between biocrust and bare soil) on NSE along the gradient of mean temperature (MT) (a) and wetness index (WI) (b). Each observation is shown by biocrust type, which is represented by different shapes, and has a different regression weight, which is proportional to the point size. Seasons of observation are shown by different colors, with the dashed ellipses delineating the distribution of observations by season, and the histograms reflecting the density of observations by season. The regression slopes of effect size relative to MT, WI, and soil organic carbon (SOC) are shown in the bottom panels (c–e). The left panels show the mean slope by cyanobacteria (Cyan), lichen (Lichen), and moss (Moss). The overall effect, which includes mixed crusts, is also shown. The right panels reflect the slope under different seasons, independent of biocrust type. Bars represent regression slopes with 95% highest density intervals. The *P value* indicates the significance of the difference between 0 and MD with significance codes: *** indicates $P < 0.001$, ** indicates $P < 0.01$, and × indicates $P < 0.05$.
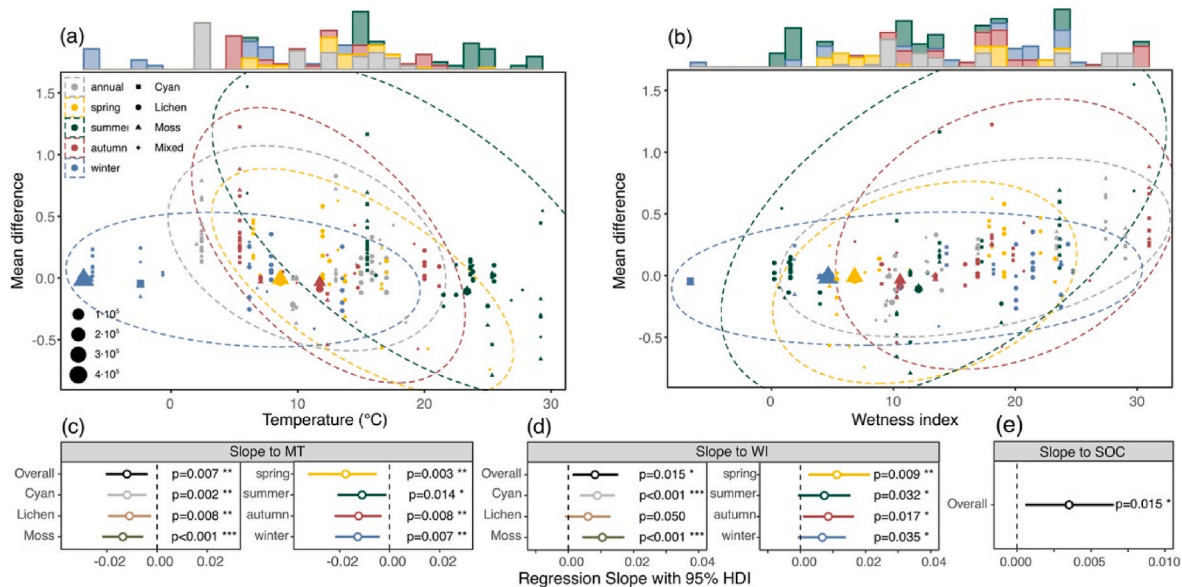

Fig. 5. Change in effect size of biocrusts under warming treatment (mean difference between warming treatment and control) along the gradient of mean temperature (MT) (a) and wetness index (WI) (b). Each observation is shown by biocrust type, which is represented by different shapes, and has a different regression weight, which is proportional to the point size. Seasons of observation are shown by different colors, with the dashed ellipses delineating the distribution of observations by season, and the histograms reflecting the distribution of observations by season. The regression slopes of effect size relative to MT, WI, and soil organic carbon (SOC) are listed in the bottom panel (c–e). The left panels show the mean slope by cyanobacteria (Cyan), lichen (Lichen), and moss (Moss). The overall effect, which includes mixed crusts, is also shown. The right panels reflect the slope under different seasons, independent of biocrust type. Bars represent regression slopes with 95% highest density intervals. The *P value* indicates the significance of the difference between 0 and MD with significance codes: *** indicates $P < 0.001$, ** indicates $P < 0.01$, and × indicates $P < 0.05$.

autumn (slope $= -0.0122$, $P = 0.008$) (Fig. 5c). The effect of warming on biocrust NSE increased with WI (slope $= 0.00802$, $P = 0.009$) and was significant for all crust types except for lichen ($P = 0.05$) (Fig. 5 d). The positive relationship was strong in spring (slope $= 0.0110$, $P = 0.009$) and autumn (slope $= 0.00838$, $P = 0.017$), followed by in summer (slope $= 0.00722$, $P = 0.032$) and winter (slope $= 0.00652$, $P = 0.035$). The covariate SOC was significant, and positively related to warming effects on biocrust NSE with a slope of 0.00343 ($P = 0.015$).

4. Discussion

4.1. Association between biocrusts and NSE

Our results indicated that NSE in soils with biocrusts was on average 66.5 [22.2, 112.2] g C m^{-2}yr^{-1} higher than bare soil without biocrusts. When weighted by the total biocrust area on the terrestrial surface (17.9 million km^2), the presence of biocrusts therefore contributes net carbon emissions up to 1.19 [0.39, 2.01] Pg yr^{-1}, corresponding to approximately 2% of the net primary production by terrestrial vegetation (Elbert et al., 2012; Rodriguez-Caballero et al., 2018). This is a very high proportion, which is likely due to experimental bias because most experimental designs used intact, dense and well-grown biocrusts in well-protected environments (fencing) and avoid interference of vegetation, litter, or soil gaps that can encroach into biocrusts in many natural settings. We also found that the increased NSE differed from cyanobacteria- to lichen- to moss-dominated biocrusts. This is partly because mosses with primary stem and leaf differentiaton have higher metabolic levels than symbiotic lichens, followed by prokaryotic cyanobacteria with the lowest metabolism (Weber et al., 2016). Previous studies also find that developed biocrusts maintain soil moisture for a longer period of time which also facilitates soil respiration (Xiao et al., 2016).

Biocrusts have long been regarded as C sinks in arid regions because of their net photoautotrophic ability (Elbert et al., 2012). Rodriguez-Caballero et al. (2018) synthesized global data and estimated an annual terrestrial biocrust net primary productivity of ~ 0.58 Pg yr^{-1} of C. Studies summarized by Porada et al. (2013) found that lichens and bryophytes can contribute to net carbon uptake by 0.07–316 g C m^{-2}yr^{-1}. However, results from our study that account for carbon losses suggest that biocrusts can negatively affect carbon storage. Relatively high biocrust NSE could be associated with the indirect influence of biocrusts on soil respiration, which has been found to be strong compared to their direct respiration (García-Palacios et al., 2018, Jun et al., 2014). Indeed, it has been reported that microbes living under the biocrust layer generally tend to be more abundant and diverse with higher respiration rates than those in bare soil (Garcia-Pichel et al., 2003; Zhao et al., 2019). Therefore, combining the direct metabolism of biocrusts and their indirect activation of other soil microbes, we suggest that the biocrusts in drylands can act more as C sources than as C sinks.

The climate regime plays a leading role in shaping the general pattern of biocrust distribution and processes (Fischer and Subbotina 2014; Rodriguez-Caballero et al., 2018; Sun and Li 2022). Our results demonstrate that climate shapes the association between biocrusts and carbon efflux in multiple ways. First, we found a nonsignificant negative relationship between the MT and the mean difference on NSE. It is likely that the activities of soil organisms are triggered by precipitation pulses and thus the non-significant temperature effects could be because of the generally low soil water availability in drylands under hot conditions. A result from the Tengger Desert in northern China generally supports this explanation: cumulative C release of mosses, mixed and cyanobacteria biocrusts are significantly higher in summer than in autumn when biocrusts are under wet conditions. In contrast, cumulative C release is lower in summer than in autumn when biocrusts are under dry conditions (Zhao et al., 2016). However, the conventional understanding of soil respiration is its positive relationship with temperature (Grote et al., 2010), counterintuitively different to our result. Notably, the relationship was evaluated within each season, rather than across all seasons. Indeed, the influence of biocrusts on NSE in summer was higher than their influence in winter. This result means that temperature may have played different roles in influencing biocrusts.

The leading activator for soil biological activity in drylands is water. Thus, we expected a higher influence of biocrusts on NSE under moist conditions. We found that a higher wetness index directly increased biocrust NSE and enhanced biocrust CO$_2$ efflux from warming treatments. It is well known that biocrusts can significantly prolong the soil moisture residence time in topsoil, thereby increasing soil respiration (Li et al., 2012). Our results also demonstrate that moss-dominated soil had a higher NSE increase than lichen- and cyanobacteria-dominated soil. Mosses have a more advanced hydraulic conductivity system, which also provides mosses a stronger metabolic capability and higher respiration rate than other biocrust organisms (Michel et al., 2015). Moreover, the vertical and multilayer structure could help mosses absorb more water and maintain activity longer than other flat biocrusts, such as gelatinous or crustose lichens (Kidron and Benenson 2014). We also found a higher influence of biocrusts on NSE and a higher effect of WT on this influence in summer than in the other seasons with a nonsignificant influence in winter, emphasizing the role of temperature in soil respiration.

4.2. Effect of warming on the NSE of biocrusts

Since soil CO$_2$ efflux is a major source of C loss to the atmosphere, the increased NSE from warming-induced effects is expected to generate a positive climate-carbon feedback (Crowther and Bradford 2013; Frey et al., 2013). Our results from biocrusts also indicated a positive climate-carbon feedback. On average, we found that warming could enhance biocrust NSE by ~ 22.9 g C m^{-2} per °C increase. The NSE of lichen-dominated soil was more insensitive to warming than that of cyanobacteria- and moss-dominated soil. It is possible that the soil in lichen dominated crust is relatively dry due to weak water-holding capacity, which impedes the soil activity (Li et al., 2012). However, over a longer period of warming, shifts away from late successional lichen- and moss-dominated to early successional cyanobacteria-dominated biocrust communities may occur (Ferrenberg et al., 2015). Therefore, accounting for extensive species turnover of biocrusts under climate change (Escolar et al., 2012; Rodriguez-Caballero et al., 2018), the pattern of C feedback in drylands will profoundly change.

We found a negative relationship between the effects of warming on the biocrust NSE and MT. That is, the biocrust NSE in hot regions tended to be less temperature sensitive than those in cold regions. A study from southeastern Utah, USA, reported that respiration of soil dominated by late successional biocrusts in drylands shows negative temperature sensitivity at high temperatures and concluded that extremely high temperatures dampen or impair the overall activity of biocrusts, thus resulting in less sensitivity to additional warming (Tucker and Reed 2016). However, it is not likely that organisms that have long been living in hot deserts would be impaired by the high temperature that they regularly experience (Bradford et al., 2019; Dacal et al., 2019). Alternatively, thermal adaptation through which biocrusts and microbes long-adapted to hot places is more likely to explain the lower sensitivity of biocrust NSE to additional warming. Indeed, many current empirical studies commonly based on laboratory incubation of soil samples from different geographical locations have found that soil microbial respiration have adapted to different thermal regimes and thus respond to temperature fluctuations to different extents (Bradford et al., 2010, 2019; Dacal et al., 2019). Our results demonstrate that the temperature sensitivity of NSE in biocrusts decreased along the spatial temperature gradient, which supports thermal adaptation by biocrust. However, the underlying mechanisms – individual physiology and/or shifts in microbial community composition are challenging to disentangle because respiration is commonly measured at the community scale (Bradford et al., 2019; Dacal et al., 2019).

Addressing the influence of WI, we also found a promoting role of WI on the warming-induced effect of increasing NSE. This mediation by WI emphasizes the water-limited characteristics of soil activities in drylands. A previous study indicated that low soil moisture is able to reduce the thermal adaptation of microbial respiration (Li et al., 2022). As such, the NSE is expected to reach a lower temperature sensitivity under relatively wet conditions. It is difficult to disentangle either contribution at this point, but it is certain that they independently explain the performance and potential of the response of NSE to warming. Furthermore, we also found a weak response of the NSE increase in lichen-dominated

soil on spatial WI gradient (Fig. 5 b) because lichens are less water-dependent than other biocrust types and even decline under wet conditions (Belnap et al., 2004; Eldridge et al., 2020). Moreover, lichens are less capable to keep soil moisture, thus, indirectly weaken the soil activities (Guan et al., 2022). Because mosses have stronger preference for moisture than lichens, and they are all considered to be more abundant in late successional dryland biocrust communities (Maestre et al., 2021). Therefore, the large temperature sensitivity in a moist region could be magnified by the development of moss, in contrast, but under dry conditions could be dampened by the development of lichen.

4.3. Implications for climate warming on spatial gradients of temperature and water

We found that spatial temperature and water gradients influenced biocrust NSE and its response to climate warming. It is well known that high temperatures are a common environmental stress in most drylands. Therefore, it is reasonable to consider that a thermal adaptation can contribute to the potential carbon balance of soil (Bradford et al., 2019; Maestre et al., 2021). Hence, biocrusts could maintain respiration at relatively low and favorable temperatures and decrease their physiological potential at stressful high temperatures (Bradford et al., 2019). Overall, NSE is determined by the amount of soil moisture and temperature due to their control of biochemical reactions and enzyme kinetics (Gong et al., 2018; Grote et al., 2010). Climate models generally predict hotter conditions in drylands, although the precipitation forecasts are different regionally (IPCC 2021). Given no changes in precipitation, warming alone would lead to declining surface water availability and potentially have a large impact on the soil CO_2 efflux (Ladrón de Guevara and Maestre 2022). At the same time, the temperature sensitivity of biocrust NSE is high at cool and moist places, where the biocrusts are abundant and developed (Escolar et al., 2012). Therefore, the ecological role of biocrusts in C cycling can be profound and prominent in these regions.

5. Conclusion

We found that the C emissions of biocrust soil were significantly higher than that of bare soil by 66.5 [22.2, 112.2] g C m^{-2} per year. Although experimental bias may exaggerate this value, our result emphasizes the function of biocrusts as a C source rather than an expected sink in drylands. These influences of biocrusts were regulated by temperature and water, and secondarily by soil organic carbon. Under warming treatments, the biocrust NSE presented a positive thermal sensitivity of 22.9 [−0.1, 40.8] g C m^{-2} per °C and was thus expected to decrease soil carbon storage. Along the spatial temperature gradient, thermal adaptation was highly likely to cause a negative relationship between thermal sensitivity and temperature. Our results highlight the importance of biocrusts as a modulator of soil carbon exchange responses to climate warming in drylands, especially in relatively cool and moist regions. As such, we highly recommend that biocrusts need to be explicitly included in analyses and models when evaluating carbon cycling in drylands and responses to climate change.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that support the findings of this study are available in the Additional files of this article

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