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Climate and soil texture collaboratively shape important components of biocrust soil carbon cycling globally

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Purpose: Biocrusts play an important role in regulating the carbon (C) cycle of terrestrial ecosystems. However, there have been few systematic assessments of the important components of the soil C cycling under biocrust cover.
Materials and methods: Hence, we conducted a meta-analysis of soil organic C (SOC), microbial biomass C (MBC), and soil respiration (R_s) under biocrust cover using 437 independent observations from 89 studies throughout the world over the past 40 years (1980–2020) to systematically assess the effects of biocrusts on key components of C cycling in terrestrial ecosystems.
Results and discussion: Our results showed that biocrust cover increased SOC, MBC, and R_s by 98%, 176%, and 35%, respectively, compared to uncrusted soil. The effects of biocrust on important components of soil C cycling depended on biocrust type, climatic condition, and soil texture. The positive effects of moss crusts on SOC (129%), R_s (45%), and MBC (197%) were all stronger than those of cyanobacterial crusts (33%–131%). Elevation, annual potential evapotranspiration, and soil particle composition were identified as the main drivers of variation in SOC, MBC, and R_s under biocrust cover.
Conclusion: Our study systematically assessed the effects of biocrust cover on important components of soil C cycling in terrestrial ecosystems globally, which is important for accurately predicting the contribution of biocrusts to the terrestrial ecosystem C balance in future climate change.

KEYWORDS
biological soil crust, microbial biomass carbon, soil organic carbon, soil respiration, terrestrial ecosystems

1 Introduction

Soils are the largest organic carbon (C) pool in terrestrial ecosystems (Jobbagy and Jackson, 2000), with a storage of approximately 3,300 Pg (Tarnocai et al., 2009; German et al., 2011), which is considered an important source of atmospheric CO_2 (Raich et al., 2002). Thus, small changes in soil C pools may significantly affect atmospheric CO_2 concentrations, potentially exacerbating or mitigating global climate change (Schlesinger and Andrews, 2000; Poeplau et al., 2011). Biocrusts are formed by cryptogams such as cyanobacteria, lichens, mosses, and soil microorganisms bonded to surface soil particles (Johnson et al., 2012), which occupy ~12% of the Earth's land surface (Rodriguez-Caballero et al., 2018), and cover >40% in drylands (Bowker et al., 2014). As engineers of terrestrial ecosystems, biocrusts have a variety of ecological functions, such as stabilizing the soil surface to reduce soil erosion (Tamm et al., 2017), regulating water and nutrient cycling (Eldridge et al., 2020), increasing C and nitrogen (N) sequestration (Yao et al., 2019; Dou et al., 2023), altering the structure of soil microbial communities and enzyme activities (Miralles et al., 2013), and influencing the growth and development of vascular plants (Grote et al., 2010; Zhou et al., 2020). More importantly, biocrusts can influence important components in terrestrial C cycle (such as soil organic C (SOC), microbial biomass C (MBC) and respiration rate (R_s)), through photosynthesis and respiration (Dou et al., 2022; Dou et al., 2024a). However, our understanding of biocrust effects on important components of the terrestrial C cycle under different climates and soil conditions remains limited. These significant knowledge gaps constrain our ability to accurately assess the role of biocrusts in the global C cycle.

SOC is recognized as one of the important indicators of terrestrial C sequestration (Miralles et al., 2018). Its fractions and transformation processes directly govern the key mechanisms of C storage, flux, and feedback within the C cycle, thereby playing a crucial role in soil C dynamics (Lehmann and Kleber, 2015). Numerous studies have shown that biocrusts can increase SOC (Mager and Thomas, 2011; Miralles et al., 2013; Xiao et al., 2019). However, it has also been shown that biocrusts are C source and that has a negative impact on SOC (Su et al., 2013). This may be due to variations in water availability across study areas, which affect the balance between photosynthesis and respiration in biocrusts. Additionally, biocrusts have a significant effect on R_s (Zhao et al., 2014; Wu et al., 2015). Most plot-scale studies have shown that biocrusts promote R_s by stimulating microbial and enzyme activities (Yao et al., 2020; Dou et al., 2024b). A bayesian meta-analysis of global drylands indicated that biocrusts increase soil CO_2 efflux (Sun F. H. et al., 2024). However, a few studies have shown that the presence of biocrusts forms a barrier at the soil-atmosphere interface, which increases the resistance to atmospheric diffusion of soil CO_2 and thus reduces R_s (Guan et al., 2022). This discrepancy may be explained by differences in soil texture across study areas. Although these plot- and regional-scale studies have shown significant effects of biocrusts on SOC and R_s, a global-scale comprehensive analysis of datasets is essential to further understand the important role of biocrusts in regulating the terrestrial C cycle, which will lead to the formulation of rational policies for climate change mitigation.

Biocrusts also have a significant impact on MBC content in terrestrial ecosystems (Dou et al., 2024a). Soil microorganisms mediate the amount and chemical composition of soil organic matter (SOM) through decomposition, respiration, growth, and death (Min et al., 2021). Thereby, they play a central role in regulating soil C transformation and fixation (Bradford et al., 2016; Wang B. et al., 2021), participating in key processes of the terrestrial C cycle. As a key component of the SOC pool, MBC represents the C content of the soil microbial community and serves as a reflection for its size (de Vries et al., 2018; Patoine et al., 2022). Numerous studies have shown that biocrusts can significantly increase MBC by increasing soil microbial abundance and diversity (Christensen, 2001; Chen et al., 2016). However, the magnitude of this effect across different biocrust types remains unclear. Some studies have shown that MBC content is significantly higher under moss crusts than under cyanobacterial crusts (Dou et al., 2024a; Qi et al., 2025), while a meta-analysis focusing on northern temperate ecosystems revealed a unique contribution of lichen crusts to MBC that surpasses other biocrust types (Tian et al., 2024). Therefore, exploring the changes of MBC under the biocrust cover can help us to better understand the role of microorganisms in soil C cycling under biocrust cover and to improve global C cycle models.

The drivers of important components affecting terrestrial C cycling under biocrust cover have been extensively studied at small scales, such as biocrust type, soil moisture, temperature, nutrients, and microbial abundance and diversity (Yao et al., 2006; Bastida et al., 2014; Xiao and Bowker, 2020). Soil moisture is recognized as one of the most important factors influencing the C cycle with biocrust cover (Escolar et al., 2015). Increased soil moisture typically enhances photosynthesis (Guan et al., 2019), R_s (Dou et al., 2024b), and microbial activity of biocrusts (Zhou et al., 2020), thereby influencing the soil C cycle. Conversely, drought stress due to soil water limitation significantly reduces SOC, MBC and R_s (Castillo-Monroy et al., 2011; Elbert et al., 2012). Soil temperature also influences key components of the C cycle by regulating microbial and enzyme activities (German et al., 2011). Differences in biocrust types can also significantly impact the soil C cycle. Moss crusts generally exhibit higher SOC content and R_s (Lange, 2003; Miralles et al., 2018), while cyanobacterial or lichen crusts have relatively lower SOC content and R_s (Garcia-Pichel and Belnap, 1996; Lange, 2003). This may be closely related to the differences in biomass and water-holding capacity among the different crust types. While the factors influencing important components of soil C cycling under biocrust cover have been widely studied, most research has focused on specific locations. Variations in environmental factors such as elevation, climate, and soil texture across different study sites have led to spatial heterogeneity, which in turn has prevented the identification of key environmental factors affecting the relationship between soil C indicators and biocrusts globally. This may impede an in-depth understanding of global soil C cycling. Consequently, it is particularly necessary to explore the drivers of changes in important components of soil C cycling under biocrust cover at the global scale, which is essential for accurately predicting the impacts of climate change on the terrestrial C cycle in the future.

We hypothesize that biocrusts significantly influence important components of the soil C cycle on a global scale, with the strength of these effects mainly depending on biocrust type, climate, and soil texture. To verify these hypotheses, we retrieved data from 89 published papers covering 56 sites from the Web of Science (WOS) and China National Knowledge Infrastructure (CNKI) over the past 40 years (1980–2020). We conducted a meta-analysis of SOC, MBC, and R_s of biocrust cover under different regions and climates in terrestrial ecosystems around the world. The meta-analysis provides a comprehensive and systematic overview of the integrated impacts of biocrust cover on important components of the terrestrial C cycle. Specifically, the objectives of our study were: (i) to evaluate the responses of important components of soil C cycling (SOC, MBC, and R_s) to biocrust cover globally; and (ii) to

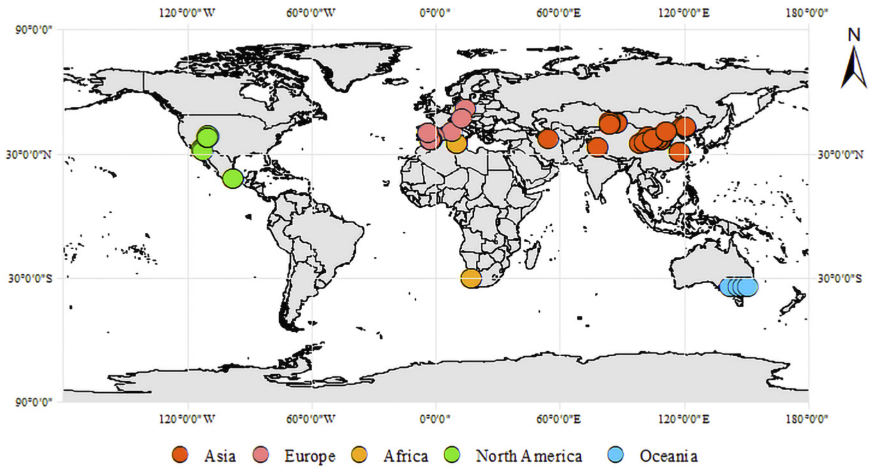

FIGURE 1
Global distribution of 56 research sites in our meta-analysis.

determine the environmental factors (including soil and climatic parameters) that modulate the effects of biocrust cover on important components of soil C cycling in terrestrial ecosystems at the global scale.

2 Materials and methods

2.1 Data acquisition and compilation

We extracted paired comparative data of biocrusts and uncrusted soil from peer-reviewed research papers published over the past 40 years (1 January 1980 to 31 December 2020), which were collected from WOS and CNKI through the following search criteria: TS = (soil respiration OR organic C OR microbial biomass C OR C cycle) AND (biological soil crusts OR cryptophyte OR biological crusts), and TS = (biological crusts OR biological soil crusts OR biocrusts). These two databases cover most of the peer-reviewed articles in English and Chinese, which enables us to conduct a more comprehensive meta-analysis. All collected data were checked manually to meet the following criteria: i) must be considered both biocrusts and uncrusted soil, uncrusted soil could be bare land, bare sand, bare soil, or soil with biocrusts removed; ii) at least one aspect of indicators in the soil C cycle (i.e., SOC, MBC, or R_s) must be studied; iii) repeated experimental design (at least three replicates) must be conducted in field, rather than greenhouse and laboratory culture experiments due to the great variances caused by artificial environments; iv) the sample mean, standard deviation, standard error, and sample size are directly provided or can be obtained indirectly from tables or figures; and v) if data of biocrusts and uncrusted soil from several different sites are reported in a study, each site was considered as an independent study. The detailed retrieval process is shown in Supplementary Figure S1.

We obtained our qualified studies based on the above requirements. Data were extracted directly from the main-text or supplementary documents wherever possible. For the remaining studies, we used Getdata Graph Digitizer software to extract our data. For each available indicator, we collected mean value, standard deviation, standard error, and sample size. If both standard deviation and standard error are missing, we estimated the standard deviation as 1/10 of the mean (Mo et al., 2020). Our final datasets include three dependent variables (SOC, MBC, and R_s). Additionally, we compiled metadata of explanatory variables. This information includes experimental site (latitude and longitude), climatic environment (e.g., elevation, mean annual precipitation (MAP), mean annual temperature (MAT), annual potential evaporation (APE), and climate type), biocrust type, and soil properties (e.g., soil texture, bulk density, and pH). If they are missing, according to the corresponding geographic coordinates, we obtained soil texture, bulk density, and pH from the Harmonized World Soil Database (http://www.fao.org/soils/).

2.2 Data description

We obtained a total of 89 peer-reviewed studies, from 56 locations in five continents of Asia, Europe, North America, Africa, and Australia (Figure 1). Most of these data came from Asia, especially China which accounts for 50% (28:56) of the total number of research sites (Supplementary Figure S2E). Most of these measurements focused on SOC (n = 250), followed by MBC (n = 127), and R_s (n = 60). The explanatory variables were classified based on the assembly data. Firstly, biocrust types were classified as cyanobacterial crust, lichen crust, moss crust, and mixed crust (cyanobacteria-lichen or cyanobacteria-moss), mainly based on the description in the article. Moss crust obviously receives more attention (40%) (Supplementary Figure S2A) than cyanobacterial crust, lichen crust, and mixed crust. Secondly, the climate was divided into four categories according to the description of the regional climate: arid (MAP <200 mm), semiarid (200 mm < MAP <400 mm), subhumid (400 mm < MAP <800 mm), and humid (MAP >800 mm). Thirdly, soil texture is classified as sand, sandy loam, clay loam, and loam based on the definitions by the USDA (http://www.nrcs.usda.gov/). Most of these studies were conducted on loam (58%) or sandy loam (25%) soils (Supplementary Figure S2C) in arid (44%) and semiarid (48%)

climates (Supplementary Figure S2B), and most of the soils were alkaline (77%) (Supplementary Figure S2D). Lastly, soil depth was divided into 4 layers, which are 0–2 cm, 2–5 cm, 5–10 cm, and >10 cm. We also collected continuous variables for climate and soil properties to explain the effects of biocrusts on SOC, MBC, and R_s globally, and these explanatory variables included APE, MAT, MAP, and elevation (climate factors) and sand, silt, clay, pH, and bulk density (soil properties).

2.3 Data analysis

If some studies reported the data of SOM rather than SOC, we used a coefficient of 1.724 to convert SOM to SOC (Mo et al., 2020). If only standard error was reported, we calculated standard deviation from standard error through Equation 1

$$SD = SE \times \sqrt{N} \tag{1}$$

Where SD is the standard deviation, SE is the standard error, and N is the sample size.

To quantify the effects of biocrust cover on the important components in the soil C cycle, we used the natural logarithm of response ratio (lnRR) for each variable (SOC, MBC, R_s, and soil chemical properties) between biocrusts and uncrusts in the meta-analysis (Hedges et al., 1999). The lnRR and its variance ($V_{\ln RR}$) and total standard deviation (S_p) were calculated through Equations 2–4.

$$\ln RR = \ln \frac{X_T}{X_C} \tag{2}$$

$$V_{\ln RR} = \frac{S_T^2}{n_T X_T^2} + \frac{S_C^2}{n_C X_C^2} \tag{3}$$

$$S_p = \sqrt{\frac{(n_T - 1)S_T^2 + (n_C - 1)S_C^2}{n_T + n_C - 2}} \tag{4}$$

Where $\{X_i, S_i, \text{and } n_i\}$ denotes the mean, standard deviation, and number of replicates, respectively; the subindices T and C refer to treatment and control variables of biocrusts and uncrusts, respectively; and S_p is the pooled standard deviation.

Additionally, we performed our analysis of biocrust effects in three stages, each stage informed by the results of the previous stage. Firstly, we performed a separate multilevel random effect meta-analysis for each response variable because we aimed to examine the reasons for the changes in each key indicators in the soil C cycle. A multilevel meta-analysis was used to account for variable dependencies arising when individual studies reported two or more results for the same category, such as a study with two kinds of biocrusts and a control, multi-year observations at the same site, or multiple soil layers within the same study. Secondly, a random effect meta-regression and random forest importance analysis were carried out to assess the relationship between the effect sizes of SOC, MBC and R_s and the climates and soil properties under biocrust cover, and to identify the key drivers of variation in these components under biocrust cover. Lastly, according to the main control factors found in the second stage, we used structural equation modeling to reveal the pathways through which environmental factors influence changes in SOC, MBC, and R_s under biocrust cover.

For the analysis, we assumed a random effects model in which the effective mean and variance of n studies were calculated through Equations 5–11.

$$M = V_{\mathrm{M}} \left(\sum_{i=1}^{n} W_{\mathrm{i}} \mathrm{Y}_{\mathrm{i}} \right) \tag{5}$$

$$V_{\mathrm{M}} = \frac{1}{\sum_{i=1}^{n} W_{\mathrm{i}}} \tag{6}$$

$$W_{\mathrm{i}} = \frac{1}{V_{\mathrm{Y_i}} + T^2} \tag{7}$$

$$T^2 = \frac{Q - df}{C} \tag{8}$$

$$Q = \sum_{i=1}^{n} W_{\mathrm{i}} Y_{\mathrm{i}}^2 - \frac{\left(\sum_{i=1}^{n} W_{\mathrm{i}} \mathrm{Y}_{\mathrm{i}}\right)^2}{\sum_{i=1}^{n} W_{\mathrm{i}}} \tag{9}$$

$$df = n - 1 \tag{10}$$

$$C = \sum_{i=1}^{n} W_{\mathrm{i}} - \frac{\sum_{i=1}^{n} W_{\mathrm{i}}^2}{\sum_{i=1}^{n} W_{\mathrm{i}}} \tag{11}$$

Where M is the effective mean of n studies; V_{M} is the variance of n studies; W_{i} is the weight assigned to each study i; V_{Yi} is the within-study variance of study i; T^2 is the variance between studies; Q is the observed weighted sum of squares; df are the degrees of freedom; and C is a normalization factor. Confidence intervals are given by Equations 12–14:

$$LL_{\mathrm{M}} = M - 1.96SD_{\mathrm{M}} \tag{12}$$

$$UL_{\mathrm{M}} = M + 1.96SD_{\mathrm{M}} \tag{13}$$

$$SD_{\mathrm{M}} = \sqrt{V_{\mathrm{M}}} \tag{14}$$

where LL_{M} and UL_{M} refer to the lower and upper limit of 95% confidence interval of M, respectively; and SD_{M} refers to the standard deviation of n studies.

A treatment was considered to be a significant increase (>0) or decrease (<0) compared to the control ($P < 0.05$) when the 95% confidence interval of the response variable did not overlap with zero. The treatment of biocrusts covering was considered not significantly different from control of uncrusts ($P > 0.05$) if the 95% confidence interval overlapped with zero (Aloe and Weiss, 2015). The effect size was converted back to response ratio from lnRR to make it easier for interpretation. In addition to the p-value of the Q statistic, T^2 and Q -df in Equation 8, and I^2 statistics were used to evaluate heterogeneity. The I^2 statistic estimates the amount of variability in effect size that can be attributed to heterogeneity among true effects, that is, genuine heterogeneity. Finally, we assessed publication bias using the Kendall rank correlation test (Dieleman and Janssens, 2011). A statistically significant correlation

TABLE 1 **Kendall rank correlation test for publication bias.**

Variables	P^a
SOC	0.5669
MBC	0.1136
R_s	0.0582

$^a P > 0.05$ indicates that there is not deviation in the publication of the literature, otherwise, it indicates that there is a publication bias. SOC, soil organic carbon; MBC, microbial biomass carbon; R_s, Soil respiration.

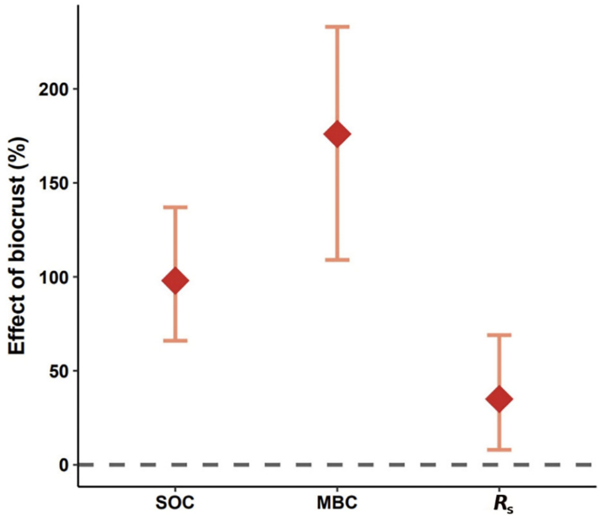

FIGURE 2
Total effects of biocrust cover on soil organic carbon (SOC), microbial biomass carbon (MBC), and soil respiration (R_s).

($P < 0.05$) was considered indicative of publication bias. Our results indicated no significant publication bias for most variables analyzed (Table 1).

The "metafor" package (Viechtbauer, 2010) and "forestplot" package in R ver R 4.1.1 (https://www.r-project.org/) were employed for meta-analysis. Random forest importance analyses were performed using the "randomForest" package (4.7–1.1) in R 4.1.1. Structural equation models were constructed using IBM Amos 24.0.

3 Results

3.1 Response of SOC to biocrust cover

Biocrust cover significantly increased the SOC content at a global scale (Figure 2). The SOC content increased by 98% overall under biocrust cover compared to uncrusts (Figure 2). These effects were highly dependent on the biocrust type, climate type, soil depth, and soil texture (Figure 3). Specifically, well-developed lichen (150%) and moss crusts (129%) showed higher SOC increases than cyanobacterial crusts (88%) (Figure 3A). Biocrusts increased SOC content by 110% and 100% in arid and humid climate regions, respectively (Figure 3D). The effects of biocrusts on SOC content showed significant surface aggregation, meaning that the effects decreased with increasing soil depth. The largest increase in SOC content occurred in the surface layer (173%, 0–2 cm, Figure 3G). Additionally, the biocrust cover increased the SOC content of the sandy soil by 208% (Figure 3J).

3.2 Response of R_s to biocrust cover

R_s was also significantly stimulated by the biocrust cover (Figure 2). Compared to the uncrusts, biocrust cover increased R_s by 35% (Figure 2). R_s varied significantly with biocrust type, climate type, and soil texture (Figure 3). Specifically, moss crusts stimulated R_s the most (45%), followed by cyanobacterial crusts (33%) (Figure 3C). Notably, unlike the higher SOC content, lichen crusts did not contribute the highest to R_s (10%; Figure 3C). A similar pattern was observed across soil textures, biocrusts on loam soil increasing R_s more (82%) than those on sand (45%) (Figure 3L). In contrast, the high SOC content increase under biocrusts in arid climatic regions corresponded to higher R_s (60%; Figure 3F).

3.3 Response of MBC to biocrust cover

The biocrust cover also increased the MBC content at a global scale (Figure 2). Compared with uncrusts, biocrust cover significantly increased MBC content by 176% (Figure 2). Specifically, lichen and mixed crusts contributed to MBC by 205% and 285%, respectively, while cyanobacterial crusts contributed relatively poorly (131%) (Figure 3B). The contribution of biocrust cover to MBC content was significantly higher in the arid climate region (361%) than in the semiarid (103%) and humid climate regions (188%) (Figure 3E). It is noteworthy that the content of MBC under biocrust cover showed an increasing and then decreasing trend with soil depth, with the largest increase in MBC at 2–5 cm (231%) and 5–10 cm (245%) depths (Figure 3H), which differed from the trend of SOC changes. Furthermore, the effect of biocrusts on MBC content was most pronounced in clay loam soil (280%) (Figure 3K).

3.4 Effect of biocrusts on SOC, R_s, and MBC under different environmental factors

The results of the random forest analysis indicated that the responses of SOC, MBC, and R_s to biocrust cover at the global scale were determined by elevation, soil properties (soil particle composition, bulk density, and pH), and climatic conditions (Figure 4). Linear regression analysis revealed that the effect size of biocrust on SOC content was mainly affected by elevation, and the relationship between them was significantly negative (Figure 5A). The effect size of biocrust on MBC significantly and linearly correlated with MAP, APE, pH, and elevation (Figures 5F–I). The effect size of biocrust on R_s was influenced by APE, pH, and soil particle composition (Figures 5K,L,N,O). Our findings were further supported by the results of structural equation models that elevation was the key factor influencing variations in SOC content, while MBC was influenced by APE, and R_s was mainly influenced by particle composition (clay, silt, and sand) (Figure 6).

4 Discussion

4.1 Effects of biocrusts on SOC

Our meta-analysis showed that biocrust cover significantly increased SOC content by 98% at the global scale, which is consistent with many previous studies (Elbert et al., 2012; Gypser et al., 2015). Well-developed moss and lichen crusts had significantly higher SOC content than the early-development cyanobacterial crusts. These differences in SOC content are likely due to the distinct traits of each biocrust type. Generally, well-developed biocrusts (e.g., lichen or moss crusts) have a higher chlorophyll

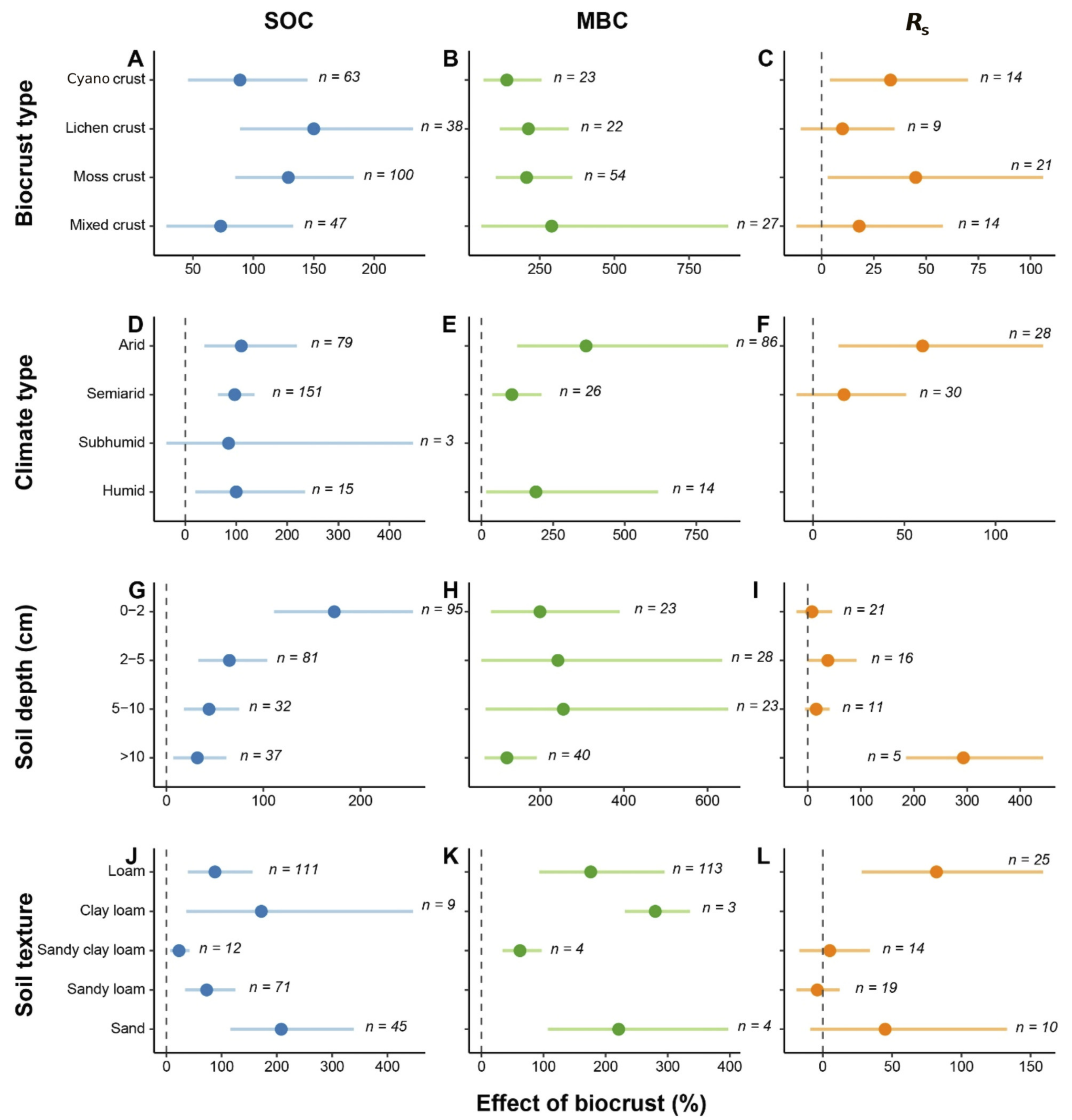

FIGURE 3
Effects of biocrust types **(A-C)**, climatic conditions **(D-F)**, soil depths **(G-I)**, and soil textures **(J-L)** on SOC **(A, D, G, J)**, MBC **(B, E, H, K)**, and R_s **(C, F, I, L)**. A response ratio greater than 1 indicates that the effect of the treatment group is higher than that of the control group. In other words, a higher response ratio means a positive effect of biocrusts covering on SOC, MBC, and R_s. Mixed crusts are cyanobacteria-lichen crusts or cyanobacteria-moss crusts or lichen-moss crusts. *n* is the sample size.

content (Castle et al., 2011; Zaady et al., 2014) and roughness (Dumig et al., 2014), which allow for greater C fixation. Notably, we found that lichen crusts had a higher positive effect on SOC than moss crusts, which seems to contradict most of the previous findings. Indeed, the developmental succession of biocrusts does not exactly follow the succession from cyanobacteria-lichen-moss (Kidron and Xiao, 2024). Both lichens and mosses can be considered well-developed biocrusts. However, lichens may be better suited for large-scale distribution in global drylands than mosses, which have higher survival needs in microenvironments (e.g., more favorable temperatures and sufficient water) (Xu et al., 2022). The wider distribution of lichen crusts in global drylands may therefore result in a greater overall SOC content compared to moss crusts, and a previous meta-analysis supported our findings (Xu et al., 2022).

The content of SOC by biocrusts was higher in sandy soil of arid regions than in clay loam soils of humid regions, which seems to

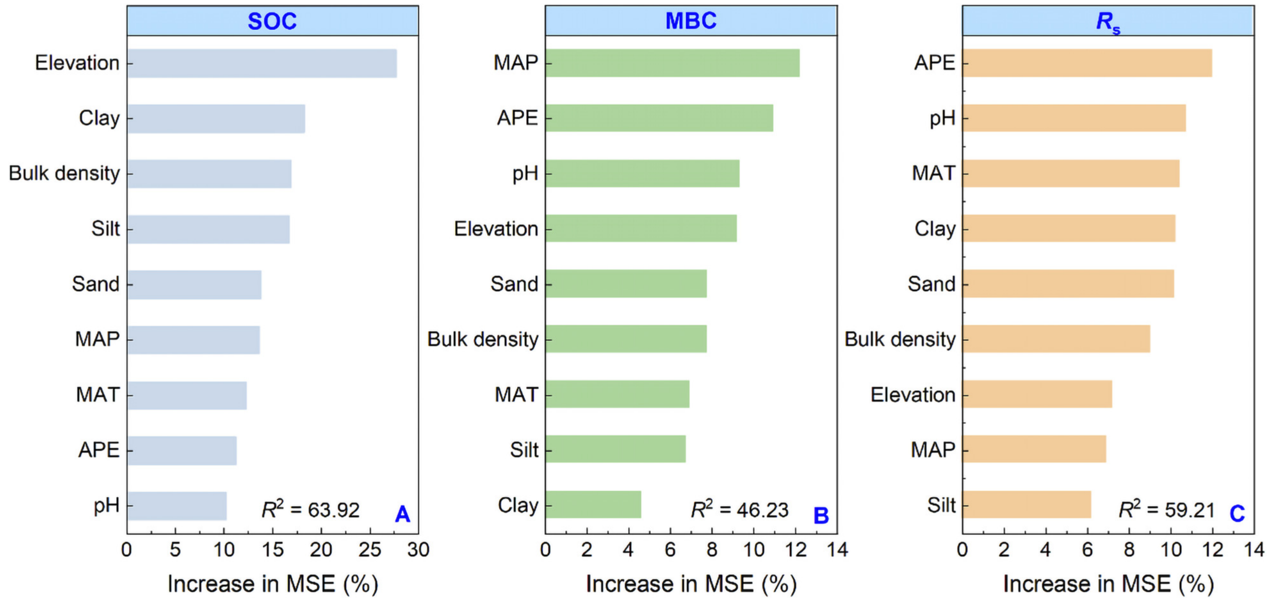

FIGURE 4
Randomized forest importance analysis of the influence effects of environmental factors on SOC, MBC, and R_s under biocrust cover. MAP = Mean annual precipitation; MAT = Mean annual temperature; APE = Annual potential evaporation.

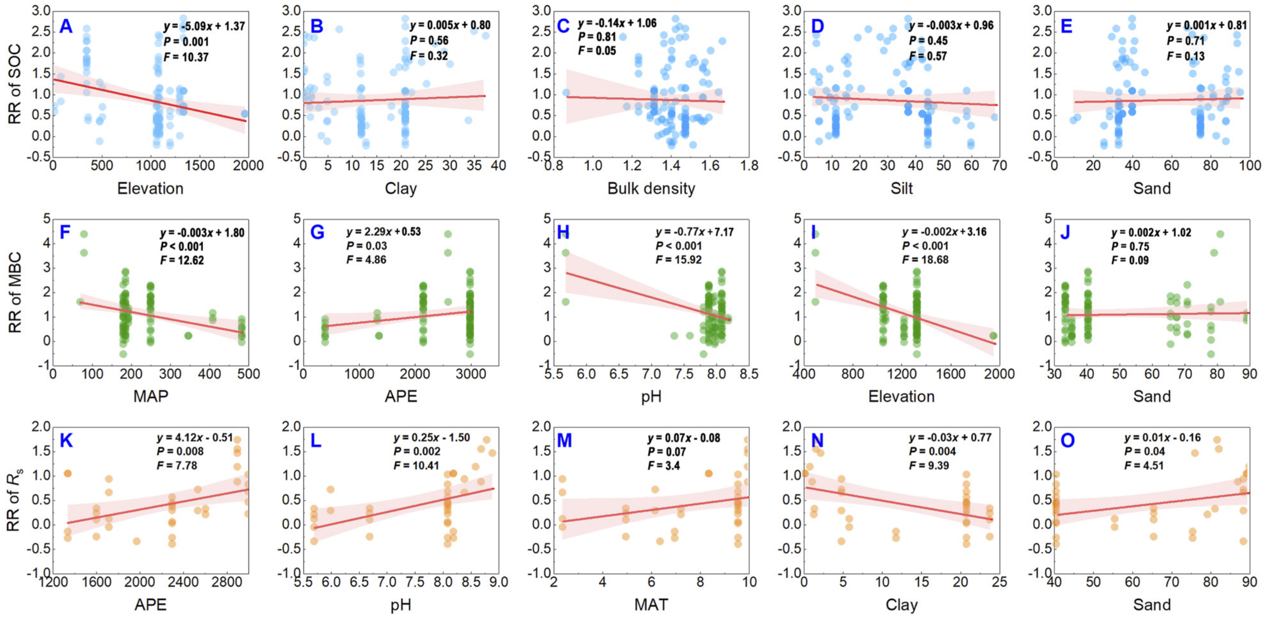

FIGURE 5
Linear correlation analysis between response ratios of SOC **(A-E)**, MBC **(F-J)**, and R_s **(K-O)** and environmental factors under biocrust cover. Shaded areas in the figure refer to 95% confidence intervals. MAP, Mean annual precipitation; MAT, Mean annual temperature; APE, Annual potential evaporation.

contradict our previous understanding. It is generally accepted that biocrusts have a higher photosynthetic C sequestration capacity in humid regions due to less frequent moisture limitation (Feng et al., 2014), while biocrusts in arid regions typically have lower photosynthetic C fixation rates due to chronic water stress. However, soil properties directly influence the formation, transformation, and migration of soil C (Liao et al., 2025). SOC background values differ between arid and humid regions due to factors such as soil parent material (Bowker et al., 2011; Gruba and Socha, 2019). In humid regions, the high species diversity caused by sufficient precipitation and suitable temperatures leads to a greater transfer of photosynthetically fixed C from the vascular plants to the soils (Cox et al., 2000; Bangroo et al., 2017), increasing SOC background values. Compared to the uncrusts, the C photosynthetically fixed by biocrusts can only cause small fluctuations in the SOC. Conversely, in arid regions, the sparse

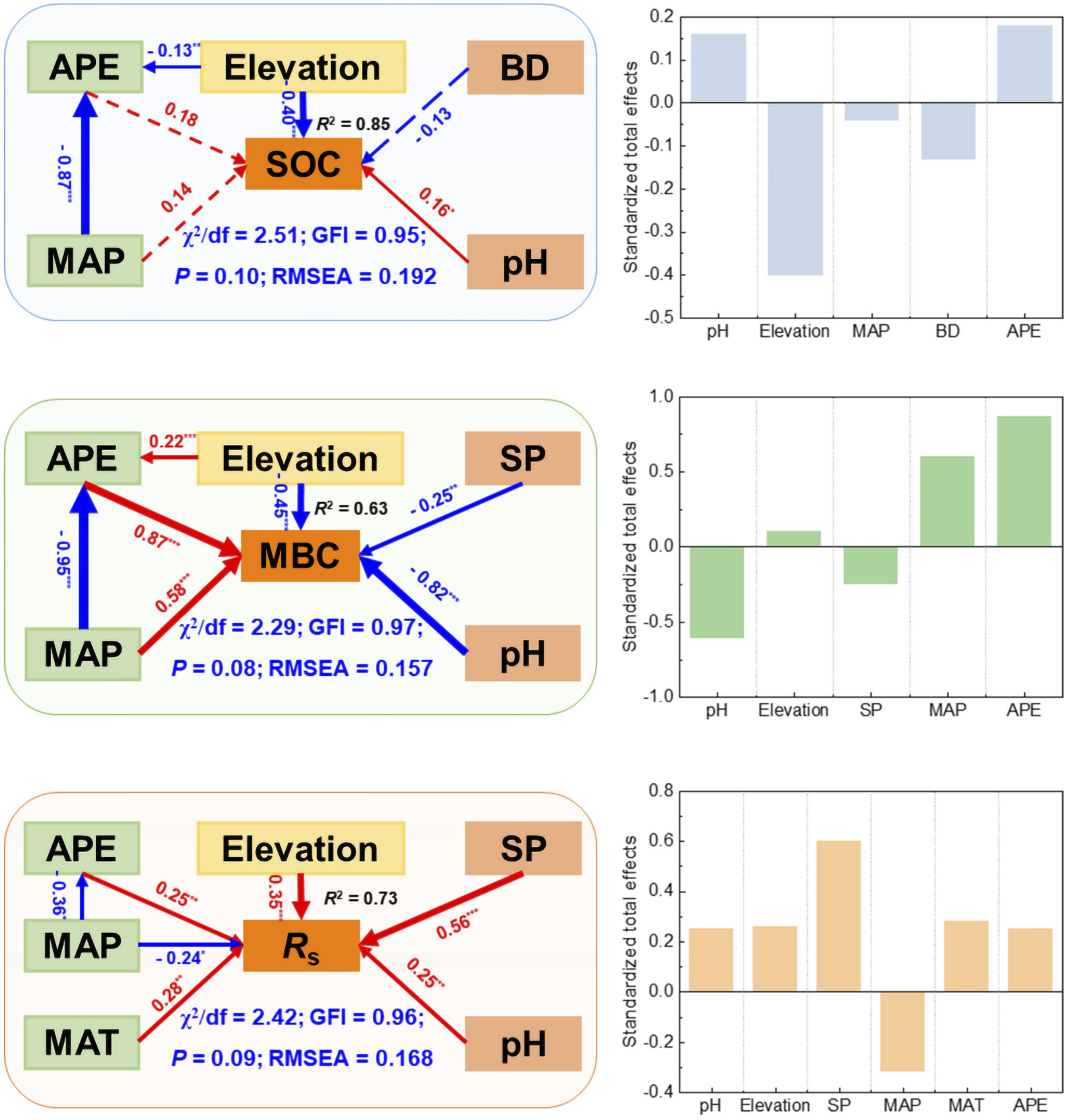

FIGURE 6
Structural equation models showed the pathways of environmental factors affecting SOC, MBC, and R_s under biocrust cover. MAP = Mean annual precipitation; MAT = Mean annual temperature; APE = Annual potential evaporation; SP = Soil particles. The red and blue solid arrows indicate significant positive and negative effect ($P < 0.05$) paths, respectively. The dashed arrows indicate in significant ($P > 0.05$) paths. The values associated with the arrows represent the magnitude of path coefficient, and the width of arrows indicates the strength of the relationship. R^2 associated with response variables indicate the proportion of variation explained by relationships with other variables.

distribution of vascular plants due to limited precipitation and high-temperature stress leads to lower SOC background values (Austin et al., 2004; Ladron de Guevara et al., 2014). Consequently, biocrust cover significantly increased SOC content in drylands relative to uncrusts. The difference in SOC between sandy and clay loam soils may also be largely attributed to differences in soil parent material.

The results of random forest importance analysis, linear regression analysis, and structural equation models all showed that elevation was the most important environmental factor influencing changes in SOC content of biocrusts at the global scale. Many previous studies have shown that SOC content tends to increase with elevation (Feng et al., 2014; Bangroo et al., 2017), which was mainly attributed to lower temperatures and greater humidity in higher elevations, resulting in an inhibition of the SOC rate of microbial decomposition and mineralization (Andersson and Nilsson, 2001; Freeman et al., 2004), thereby facilitating the accumulation of SOC. However, our results showed a significant negative correlation between SOC content under biocrusts and elevation. It is widely believed that biodiversity shows a clear downward trend with increasing elevation gradient (Gruba et al., 2019). Temperature limitation at high elevations may have led to a decrease in biocrust biomass, which is closely related to the rate of photosynthetic C sequestration (Dou et al., 2024c). Consequently, an increase in elevation gradient affects the content of SOC mainly by influencing the biocrust traits. In conclusion, our study emphasizes the positive effects of biocrusts on SOC content at the global scale, but the content of SOC depends on the combined effects of biocrust type, soil parent material, and climatic factors.

4.2 Effects of biocrusts on R_s

Previous studies have shown that biocrusts significantly stimulate R_s, thereby increasing C emissions in terrestrial ecosystems (Liu et al., 2017; Yao et al., 2019), which is consistent with our results. Generally, biocrusts may increase R_s through the following three ways: (i) Biocrusts significantly increase the surface SOC content, which provides abundant food resources for soil microbes, and thus accelerates the mineralization and decomposition of organic C (Bastida et al., 2014; Wang et al., 2021a), which in turn enhances heterotrophic respiration. (ii) Biocrusts have a high surface water-holding capacity (Xiao et al., 2019), which hinders the infiltration of soil moisture into the deeper layers, prolonging the stimulatory effect of moisture on R_s (Eldridge et al., 2020). (iii) Biocrusts significantly increase the abundance and diversity of microbes (Liu et al., 2014), as well as increase soil temperature and stimulate soil enzyme activity (Xiao and Bowker, 2020), which further accelerate the decomposition and mineralization of SOC by microbes, thereby increasing R_s. Therefore, the significant increase in R_s under biocrust cover can be attributed to their combined positive effects on SOC content, enzyme activity, and surface soil moisture.

Our results also showed that the effects of moss crusts on R_s were significantly higher than those of lichen crusts, which seems to contradict our finding that lichen crusts had a greater effect on SOC than moss crusts (i.e., changes in soil respiration could not be explained by the mechanism (i) described above). Most of the previous studies that measured R_s of biocrust considered both above and below ground as a whole (Escolar et al., 2015; Yao et al., 2019; Yao et al., 2020), which measured ecosystem respiration (Dou et al., 2024c), that is, it included both soil and plant respirations in the above ground. Since the aboveground portion of the lichen crusts lacks distinct plant cover, its R_s is mainly contributed by microbe-dominated heterotrophic respiration (Liu et al., 2013; Dou et al., 2022). In contrast to lichen crusts, moss crusts include both heterotrophic respiration from belowground microbes and autotrophic respiration from aboveground moss plants (Dou et al., 2024c). Therefore, moss crusts contribute more to R_s compared to lichen crusts.

Furthermore, our structural equation model showed that soil particle composition significantly affected R_s. Moderate soil porosity maintains soil aeration, which meets the oxygen requirements for microbial heterotrophic respiration (Nuñez et al., 2025), thereby significantly influencing R_s. Soil particle composition also affects R_s by influencing soil water retention capacity. Our study indicates that the R_s of biocrusts was significantly higher on loam than on sand soils (Figure 3L). This may be due to the finer particles and relatively smaller pores in loam soils compared to sandy soils (Sun J. Y. et al., 2024), which impede infiltration of rainfall into deeper soils, thereby increasing the water-holding capacity of surface soils (Xiao et al., 2019), and thus prolonging the stimulatory effect of soil moisture on the R_s. In contrast, the sandy soils with fewer fine particles have larger soil voids, which increase the infiltration of soil moisture into the deeper soil layers, thereby reducing R_s (Sun et al., 2021). More importantly, we found that high SOC content in lichens corresponds to low R_s, a pattern also seen in sandy soils compared to loam soils. Consequently, lichen crusts in drylands may play an important positive role in mitigating climate change.

4.3 Effects of biocrusts on MBC

Our results showed that biocrust cover significantly increased MBC at the global scale. The content of MBC is directly dependent on microbial abundance (Huang et al., 2022). Numerous previous studies have shown that biocrust cover significantly increases microbial abundance and diversity compared to bare soil by improving the soil microenvironment (e.g., water, heat, and nutrient status) (Garcia-Pichel et al., 2003; Wang et al., 2022). Therefore, the increase of microbial abundance under biocrust cover explains the enhancement of MBC content. We also found that the enhancement of MBC by biocrusts depends on biocrust type, climatic conditions, and soil texture. Lichen and mixed crusts had significantly higher positive effects on MBC than cyanobacterial crusts. Generally, increased soil water availability and nutrient effectiveness significantly enhance the abundance of microbes as biocrusts develop (Housman et al., 2006; Dou et al., 2022), which further accelerates the decomposition and mineralization of SOM (Kuzyakov et al., 2019), leading to an increase in MBC content. The relative improvement of the soil microhabitat by biocrusts is more pronounced in arid regions than in semiarid regions, corresponding to a greater relative increase in MBC (Wang et al., 2015; Li et al., 2019). Furthermore, loam soils have a larger specific surface area compared to sandy soils, providing more living space for microorganisms and thereby increasing their abundance (Sun J. Y. et al., 2024). Consequently, different environmental conditions lead to differences in soil microbial abundance, which in turn affect MBC content.

The changes in MBC under biocrust cover at the global scale were mainly driven by APE. Higher APE values typically indicate strong evapotranspiration pressure, higher temperatures, and increased solar radiation. Under conditions of adequate moisture, higher temperatures generally promote microbial diversity and abundance (Wang et al., 2021b), which in turn facilitates the accumulation of MBC. Furthermore, in arid environments with high evapotranspiration demands, microbes in biocrusts secrete large amounts of extracellular polymeric substances, enhancing the water retention capacity of the crust, reducing water loss, and providing a stable microenvironment for microbes, thus promoting their survival and metabolic activity (Adessi et al., 2018).

4.4 Limitations and future studies

Although this study is important for understanding the role of biocrusts in soil C cycling at a global scale, there are still some limitations. The uneven distribution of data presents a challenge for this study. Most of the existing research is concentrated in Asia (especially China), Europe, and the Americas, which may affect the generalizability of our findings, particularly in regions with fewer studies, such as Africa and Oceania. To overcome this limitation, future experimental studies should be expanded more in regions such as Africa and Oceania, to better understand the responses of important C cycling components to biocrust cover on a global scale. This will contribute to a more comprehensive understanding of the role of biocrusts in the global C cycle. Moreover, we explored the effects of biocrusts on three important components (SOC, MBC, and R_s) of the soil C cycle. Although these indicators are representative, they do not fully cover the entire soil C cycle. Therefore, future research should incorporate additional C cycle related indicators, such as biocrust biomass, microbial necromass C, nutrients, and enzyme activity, to provide a more comprehensive understanding of the effect of biocrusts on soil C cycle.

Furthermore, our study did not include a zonal analysis of biocrust effects on important components of the soil C cycle. With the intensification of climate change, regional differences in global C cycling are likely to become more pronounced. The impact of biocrusts on the important components of the C cycle may show varying response patterns due to differences in regional climates, soil types, and ecosystem types. Therefore, a key direction for future research is to explore the zonal patterns of biocrust soil C effects, particularly under future climate change. Systematically quantifying the continuous variation of biocrust C effects along environmental gradients is crucial for improving global C cycle models and developing regional C management strategies.

5 Conclusion

Our meta-analysis highlights the significant impact of biocrust cover on important components (SOC, MBC, and R_s) of the soil C cycle at a global scale. Biocrusts enhanced SOC, increased MBC, and significantly stimulated R_s. The effects are primarily influenced by biocrust type, climatic conditions, and soil texture. the spatial and temporal variabilities of SOC, MBC, and R_s under biocrust cover were mainly driven by elevation, APE, and soil particle composition. In conclusion, this study emphasizes the effects of biocrusts on important components of the soil C cycle (SOC, MBC, and R_s) at a global scale, which is essential for understanding the key role of biocrusts in the global C cycle and accurately predicting the contribution of biocrusts to the terrestrial ecosystem C balance in future climate change.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

XW: Writing – review and editing, Formal Analysis, Writing – original draft, Conceptualization, Investigation, Methodology. XY: Investigation, Software, Resources, Writing – review and editing, Funding acquisition, Supervision, Conceptualization, Writing – original draft, Project administration, Visualization, Data curation, Validation, Methodology, Formal Analysis. WD: Writing – original draft, Funding acquisition, Investigation, Resources, Visualization, Formal Analysis, Software, Validation, Data curation, Conceptualization, Project administration, Writing – review and editing, Supervision, Methodology.

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Conflict of interest

The reviewer CB declared a shared affiliation with the author WD to the handling editor at the time of review.

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