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Advancing studies on global biocrust distribution

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Abstract: Biological soil crusts (biocrusts hereafter) cover a substantial proportion of the dryland ecosystem and play crucial roles in ecological processes such as biogeochemical cycles, water distribution, and soil erosion. Consequently, studying the spatial distribution of biocrusts holds great significance for drylands, especially on a global scale, but it remains limited. This study aimed to simulate global-scale investigations of biocrust distribution by introducing three major approaches: spectral characterization indices, dynamic vegetation models, and geospatial models, while discussing their applicability. We then summarized the present understanding of the factors influencing biocrust distribution. Finally, to further advance this field, we proposed several potential research topics and directions, including the development of a standardized biocrust database, enhancement of non-vascular vegetation dynamic models, integration of multi-sensor monitoring, extensive use of machine learning, and a focus on regional research co-development. This work will significantly contribute to mapping the biocrust distribution and thereby advance our understanding of dryland ecosystem management and restoration.

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Key words: biological soil crusts; distribution; drylands; global scales; regional scales

1. Introduction

Biological soil crusts (biocrusts hereafter) are continuous biotic complexes that live in the topsoil, which are formed by different proportions of photosynthetic autotrophic (e.g. cyanobacteria, algae, lichens, mosses) and heterotrophic (e.g. bacteria, fungi, archaea) organisms colloidal with soil particles, usually with a thickness of a few millimeters to a few centimeters (Weber et al., 2022). Biocrusts occupy a wide range of ecological niches in mid latitudes, polar and alpine regions, covering approximately 11% of the global land area (Porada et al., 2019). In particular, biocrusts are well-adapted to water-limited, nutrient-poor, and hostile environments, such as arid and semi-arid areas characterized by low ratios of precipitation to potential evaporation (0.05-0.5 $\mathrm{mm\ mm^{-1}}$) (Pravalie, 2016; Read et al., 2014; Weber et al., 2016).

As vital components of dryland ecosystems, biocrusts fulfill many essential ecological functions. They contribute to stabilizing the soil surface, improving soil permeability, and enhancing water-holding capacity within the upper few centimeters of soil (Sun et al., 2023; Shi et al., 2023; Gao et al., 2017). By participating in various biogeochemical cycles, biocrusts were estimated to contribute to 15% of terrestrial net primary productivity and 40-85% of biological nitrogen fixation (Elbert et al., 2012; Rodriguez-Caballero et al., 2018). They also impact ecohydrological processes by altering soil microclimate and redistributing soil water (Kidron et al., 2022; Tucker et al., 2017). Moreover, biocrusts influence seed capture and soil seed banks (Kropfl et al., 2022), thereby mediating plant growth and community assembly (Havrilla and Barger, 2018; Song et al., 2022). The extent and magnitude of these ecological functions and services depend on the spatial distribution of biocrusts. Therefore, it is crucial to understand their distribution.

Despite the significance of biocrusts, previous studies have primarily focused on their contributions to carbon and nitrogen cycling across various habitats and climates (Hu et al., 2019; Morillas and Gallardo, 2015), as well as interspecific interactions and biocrust biodiversity (Machado De Lima et al., 2021; Munoz-Martin et al., 2019), rather than their spatial distribution. Countries like China, the United States, Spain, Australia, and Israel, most of which have extensive dryland areas, have attempted to make breakthroughs on this issue (Fig. 1a). However, other dryland countries and regions, such as central and southern Africa, where the biocrust distribution has been reported, still suffer from a paucity of studies and data on biocrusts (Fig. 1b). This geographical imbalance in biocrust distribution studies has resulted

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删除了: A group of ecologists, including Fernando Maestre (Maestre et al., 2021), David Eldridge(Eldridge and Delgado-Baquerizo, 2019; Eldridge et al., 2023), Matthew Bowker (Qiu et al., 2023), Emilio Rodríguez-Caballero (Rodriguez-Caballero et al., 2018) and others, have actively promoted progress in the field (Fig. 1a).

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in most knowledge remaining at local to regional scales, with very limited discoveries on a global scale.

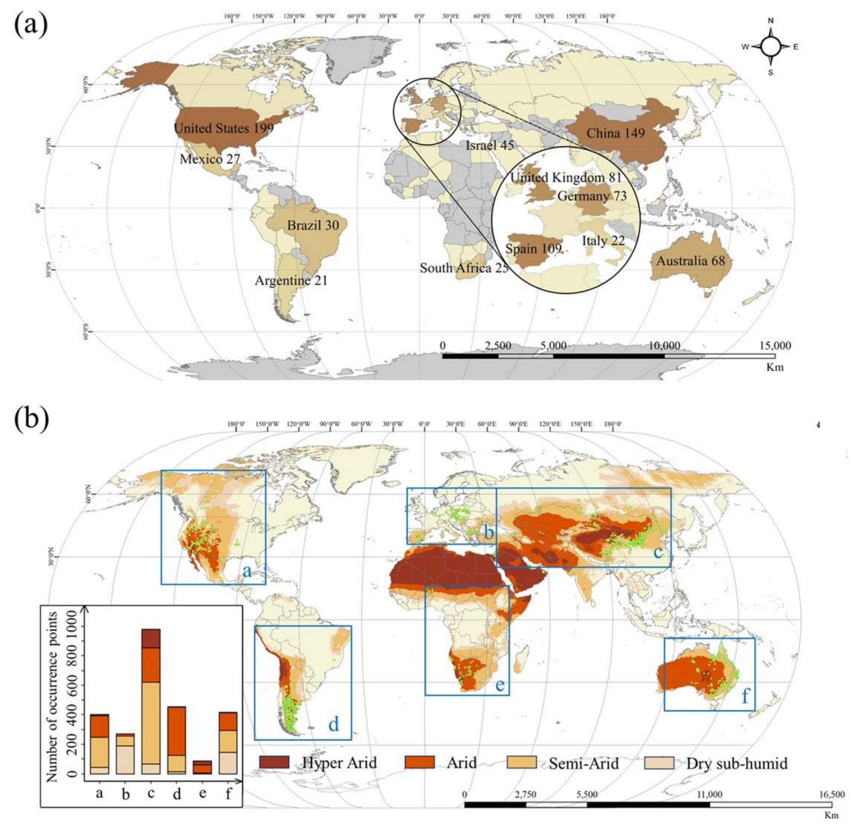
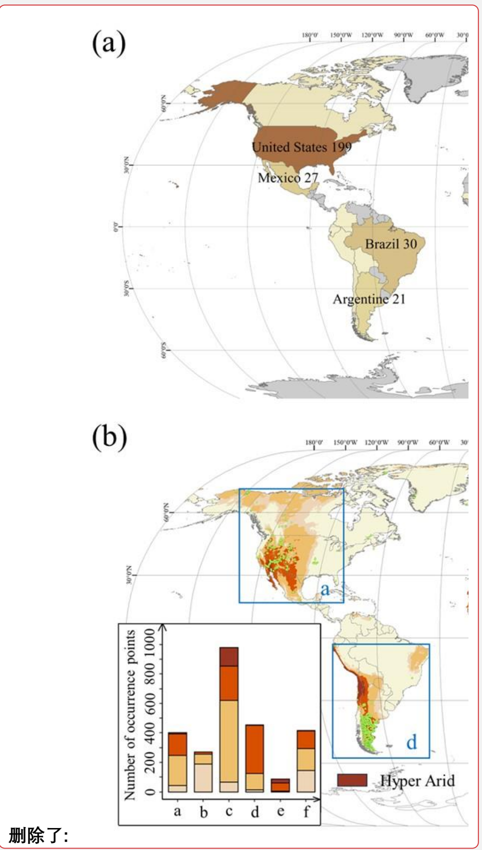


Fig. **1** Literature review of biocrust distribution studies. (a) Map of hotspot countries for biocrust distribution research. Numbers are the countries of the authors of published articles from 1990 to 2022, and the top 12 countries are shown; The database is Web of Science, TS = ("biogenic crust*" OR "biological crust*" OR "biological soil crust*" OR "biocrust*" OR "microphytic crust*" OR "microbiotic crust*" OR "cyanobacterial*" OR "algal*" OR "lichen*" OR "moss*" OR "biotic crust*") AND ("mapping*" OR "distribution*" OR "spatial pattern*") AND (“dryland” OR “hyper*arid*” OR “arid*” OR “semi*arid*” OR “dry subhumid*”), with research interests in Environmental Sciences/Ecology and a total of 700 papers. (b) Global biocrust data distribution, based on field surveys and literature compilation. The bar chart counts the number of entries for biocrust records (presence/absence or cover) for six continents



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删除了: (a) Representative authors associated frameworks for biocrusts distribution studies (1990 to 2022). The time series is the average time of the year of publication, e.g., if the number of articles is 2 in 2004 and 8 in 2019, the node in this figure shows the year as (2004 x 2 + 2019 x 8)/10 = 2016.…

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(regions). Datasets have been collected and expanded from the published database (Chen et al., 2020; Rodriguez-Caballero et al., 2018) to 3848 items (unpublished).

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In this study, we aimed to sort out and advance the understanding of biocrust distribution from three perspectives: the applicability and comparison of research methods (section 2), clarification of factors influencing biocrust distribution (section 3), and challenges and strategies for future studies on biocrust distribution (section 4). This work is expected to deepen our understanding of dryland ecosystem processes and provide a scientific basis for conserving dryland ecosystems and their responses to global change.

2. Research Methods

Three methods are commonly used to study biocrust distribution: spectral characterization, vegetation dynamic modeling, and geospatial modeling. This section provides an overview of these methods, including their basic principles, case studies, adaptability, and limitations.

2.1 Spectral characterization index

With advances in remote sensing and geo-information technology, spectroscopy offers a feasible method of characterizing distribution features from a physical point of view. Differences in absorption or reflection of specific wavelengths by different ground covers can effectively identify soil surface objects (Rodriguez-Caballero et al., 2015). By identifying biocrust-specific bands from reflectance spectral images (Karnieli et al., 1999), it is possible to construct a presence-absence map of biocrust distribution (Fig. 2a).

Currently, spectral characterization indices have been widely applied in many areas of drylands. For example, cyanobacterial biocrusts are widely distributed in the Sahara region of Africa (Beaugendre et al., 2017) and the Negev Desert of Israel(Panigada et al., 2019), where the study invented the Biocrust Index (CI) based on remotely sensed imagery to access the characteristics of localized changes in biocrust distribution over 31 years (Karnieli, 1997; Noy et al., 2021). Sun et al. (2024) developed the fraction biocrust cover index (FBCI) based on radiative transfer and mapped biocrust distribution over a desert area at 10 m resolution, showing well-matched results between the model and field observations (RMSE of 0.0774, systematic deviation of -4.05%). In the Gurbantunggut Desert, a study constructed the Biological Soil Crust Index (BSCI) with lichen biocrust as the dominant group and mapped the

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distribution of biocrusts with high accuracy (accuracy of 94.7%, kappa coefficient of 0.82) (Chen et al., 2005), spatially, biocrusts cover 28.7% of the area, with a high and uniform cover in the southern part of the desert and a scattered distribution in other regions (Zhang et al., 2007). In the Loess Plateau, red-green-blue (RGB) image-based biocrust monitoring showed that variability in biocrusts cover decreased logarithmically with increasing plot size until a critical size of $1m^2$, after which biocrusts cover remained approximately constant (Wang et al., 2022a).

For the spectral characterization method, it is critical to determine the threshold of spectral bands that represent biocrusts. For instance, at an aerosol optical depth of 0.2, the BSCI ranges from 4.13 to 6.23 and narrows to 4.58-5.69 with increasingly poor atmospheric conditions. Overly strict or loose threshold ranges can easily lead to biocrust omission or misidentification. To improve the accuracy of biocrust identification, some researchers have utilized the hyperspectral sensor's continuous waveband capabilities and created the Continuum Removal Crust Identification Algorithm (CRCIA) (Chamizo et al., 2012b; Weber et al., 2008). Baxter et al. (2021) innovatively applied the random forest algorithm to spectral feature classification, achieving an accuracy of 78.5% in biocrusts recognition. Additionally, two other indices, the Sandy Land Ratio Crust Index (SRCI) and the Desert Ratio Crust Index (DRCI), were introduced to account for differences between sandy land (vegetation cover FVC <20%) and desert environments, improving mapping accuracy by approximately 6% (Wang et al., 2022b).

The spectral characterization method is easy to use and, thus, facilitates access to continuous long-term dynamics of biocrusts distribution. However, mosses and vascular plants are generally mixed up in this method because their reflectance characteristics are similar across all wavelengths, especially when mosses are wet, which makes them indistinguishable (Fang et al., 2015). Therefore, the spectral characterization method mainly applies to situations where biocrust cover is greater than 30% and plant cover is less than 10% (Beaugendre et al., 2017). It should be noted that the existing indexes mostly correspond to biocrust cover consisting of specific dominant groups in specific environments, which cannot be directly extrapolated to areas with highly heterogeneous environments (Table 1). Wetting or disturbance may also lead to large fluctuations in the reflectance of different land types, interfering with biocrust

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distribution monitoring (Rodriguez-Caballero et al., 2015; Weber and Hill, 2016).

2.2 Dynamic global vegetation models (DGVMs)

Dynamic global vegetation models are another major method for estimating vegetation cover (Deng et al., 2022). These models mainly focus on simulating the biogeochemical processes (e.g., carbon and water cycles) and the metabolic and hydrological processes of organisms (Fig. 2b) (Lenton et al., 2016; Porada et al., 2017). DGVMs have significant advantages in mapping biocrust distribution because their assumptions have clear biological implications (Cuddington et al., 2013). Porada et al. (2013) focused on CO_2 diffusion rates and photosynthetic processes under dynamic water content saturation in dryland biocrusts. By parameterizing long-term climate data and disturbance intervals and averaging simulation results for the past 20 years for each grid point, they estimated that biocrusts cover 11% of the global terrestrial land surface (Fig. 3a) (Porada et al., 2019). Specifically, the light and dark cyanobacteria were widely distributed in deserts, savannas, grasslands, and Mediterranean woodlands at low latitudes, with their presence increasing to some extent with increasing dryness. In contrast, mosses were mainly distributed in middle and high latitudes and polar regions.

Dynamic vegetation models can be combined with cross-scale remotely sensed data to quantify the geographic distribution and biogeochemical effects of plants, replacing traditional measurements. However, the uneven distribution density of biocrust data points along the aridity gradient or a small amount of data may lead to poor prediction of global-scale distributions (Quillet et al., 2010). So far, non-vascular vegetation has not received enough attention, and only the Lichen and Bryophyte Model (LiBry) used in the above case is uniquely suited to emulating biocrust distribution (Porada et al., 2019; Porada et al., 2013). The LiBry model includes variations in biocrust cover strategy under disturbance and its growth, but it relies heavily on subjective experience and model parameterization, which is still immature compared to dynamic models of vascular vegetation.

2.3 Geospatial models

Directly relating vegetation presence or cover to environmental data, instead of indirectly via biological processes, is another important way to obtain biocrust distribution (Beaugendre et al., 2017; Fischer and Subbotina, 2014; Skidmore et al., 2011). Classic statistical models can serve this purpose. However, they still require comprehensive expert knowledge of how environmental factors affect biocrusts (Pearce et al., 2001), which is hard to obtain and prone to bias. Geospatial models, which integrate machine learning tools with field survey data and remote sensing data, hold the most promise (Fig. 2c) (Crego et al., 2022). They are also known as species distribution models or ecological niche models (Brown and Anderson, 2014; Jiménez-Valverde et al., 2008; Soberon and Nakamura, 2009). At the global scale, there has been only one study that predicted biocrust distribution patterns using geospatial modeling (Rodriguez-Caballero et al., 2018), which found that biocrust covers 12.2% of the global land surface area, which is about 1.79×10^7 km^2 (Fig. 3b).

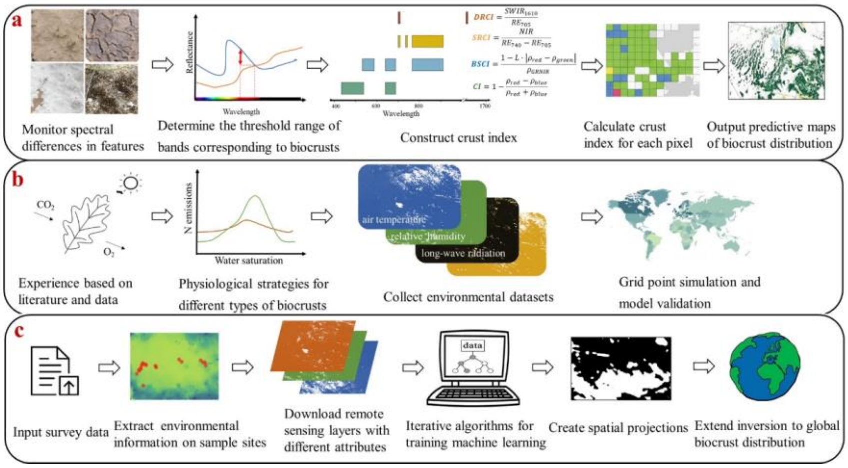
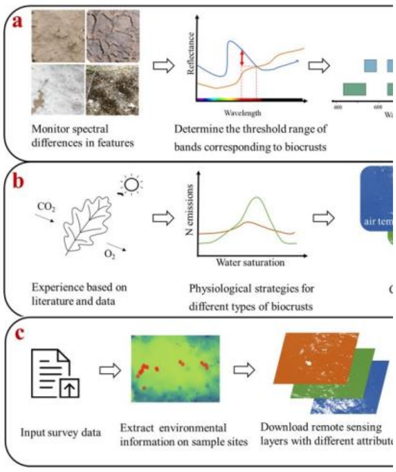


Fig. 2 Summary of three major approaches to studying biocrust distribution. Illuminations of applying spectral characterization method **(a)**, dynamic vegetation model **(b),** and geospatial model **(c)** in biocrusts distribution study. See the main text for a more detailed introduction to these methods.

Compared with the result of the dynamic vegetation model, the simulation accuracy (R^2~0.8) and mapping resolution (0.5° ×0.5°) of the geospatial model were improved. Biocrust distribution is generally consistent in the large deserts of Asia, western America,



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Europe, and Oceania, while some semi-arid regions, such as the northern and southern margins of the African Sahara Desert, South Asia, and central North America, have significantly higher biocrust cover in the projection by Rodriguez-Caballero et al. (2018). We estimate that this may be because geospatial modeling focuses more on the influence of climate, as the Mediterranean climate and tropical desert climate in the Sahara Desert, as well as the tropical desert climate of northwestern South Asia, are suitable for biocrust survival. Additionally, the large number and high cover of biocrust training sets in central North America could have contributed to the generally high predicted cover in machine learning.

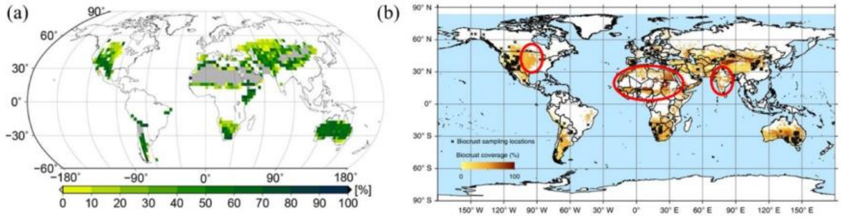

Fig. 3 Maps of global biocrusts distribution. (a) Prediction based on vegetation dynamic model (Porada et al., 2019). (b) Prediction based on geospatial model (Rodriguez-Caballero et al., 2018). Permissions have been obtained from the relevant sources.

As black-boxes, geospatial models are largely non-interpretable and, thus, less capable of capturing the key mechanisms behind phenomena, which may limit their applications. Under this methodological framework, only the direct effects of various environmental indicators are considered. For example, it focuses on the direct effect of precipitation on biocrust distribution while ignoring the indirect effects, such as interactions among shrubs, grasses, and biocrusts (Wang et al., 2024). In addition, to avoid confounding model predictions, the inclusion of environmental factors should be based on their relevance to biocrusts, and expert knowledge should still be needed to a certain degree (Mäkinen et al., 2022). Not only natural conditions such as climate, topography, and soil, but also data on human activities such as afforestation, trampling, and population density need to be considered as environmental indicators in the model. It should be noted that the superimposition of environmental layers of different resolutions may cause deviations in results to some extent, which is unavoidable (Zhao et al., 2024). Despite the above limitations of geospatial modeling, with sufficient computing power, observation data of biocrust distribution, and suitable environmental information, geospatial models are supposed to be relatively optimal solutions for predicting biocrust distribution (Table 1).

Table 1 Comparison among the three main types of methods to predict biocrust distribution

	Spectral characteristic index	**Vegetation dynamics model**	**Geospatial model**
Principle	Differences in wavelength reflectance of surface features	Differences in the physiological processes of different biocrust types	Remote sensing information-driven and survey data-based machine learning framework
Advantages	Convenience and ease of use	Clear ecological significance	Machine training simulation, without subjective interference
Disadvantages	Reflectivity is affected by climate change, disturbances； Mosses and vascular plants have similar reflectance characteristics； The results only show the presence or absence of biocrusts without coverage	Experience-based promotion with significant human intervention； Experiments need to be supported by big data	A large amount of computing power； Adequate number of sample points to support accuracy
Applicable scales	Regional scale (Desert and sandy land with <20% vegetation cover)	Regional scale Global scale	Regional scale Global scale

3. Influencing Factors of Biocrust Distribution

It is of great importance to clarify the environmental variables associated with biocrust distribution. On the one hand, it helps to frame the range of data selection before modeling, and on the other hand, it aids in identifying patterns of biocrust distribution in the context of dynamic changes and various types of environmental information, thereby facilitating the prediction of distributed evolution on longer time scales. Numerous modelling studies (Kidron and Xiao, 2023; Li et al., 2023; Rodriguez-Caballero et al., 2018) have demonstrated that, on the global scale, biocrust distribution is mainly influenced by water conditions, temperature, soil properties, fire, and disturbance (Bowker et al., 2016).

Water conditions. In general, total precipitation (Fig. 4b) is considered to be critical in determining the distribution of biocrusts (Eldridge and Tozer, 1997). Increased precipitation can lead to higher levels of lichen and moss cover, while algal cover may initially increase and then decrease (Budel et al., 2009; Marsh et al., 2006; Zhao et al., 2014). It should be noted that precipitation can also promote the growth of vascular plants, and continuous high cover of vascular plants and litterfall will limit the space available to biocrusts (Bowker et al., 2005). In addition to the total amount of precipitation, the seasonality and frequency of precipitation cannot be ignored (Budel et al., 2009). Winter precipitation and/or smaller rain events benefit biocrusts, especially when mean annual precipitation is less than 500 mm. Meanwhile, a high frequency of precipitation can lead to the dominance of biocrusts over vascular plants (Chamizo et al., 2016; Jia et al., 2019). Experimental evidence shows that precipitation events of 5 mm are able to maintain normal physiological and ecological functions of the biocrust on the Colorado Plateau, USA, while ever lower precipitation events of 1.2 mm can rapidly kill moss biocrust (Reed et al., 2012). Non-precipitation water input is another important water resource type. The Namib Desert receives little rainfall, but lichens and moss biocrusts can reach a relatively high cover (~70%) (Budel et al., 2009). This is because local water vapor tends to condense into fog or dew, which facilitates the survival of three-dimensional species (such as leafy lichens) by trapping air moisture (Eldridge et al., 2020; Kidron, 2019; Li et al., 2021). Similarly, lichen biocrusts are widely distributed in the western U.S. along the Mexican coast due to the high air humidity (dew formation for almost 1/3 of the year) (Mccune et al., 2022; Miranda‐González and Mccune, 2020).

Temperature. Relatively high soil temperature can create an environment of high evaporation that impedes biocrusts colonization (Garcia-Pichel et al., 2013). Regarding air temperature, warming by 4°C could alter biocrust community structure, resulting in a sharp decrease in moss biocrust cover and an increase in cyanobacterial biocrust cover. This effect becomes even more significant when warming interacts with time and precipitation treatments (Ferrenberg et al., 2015). Recent studies have shown that historical and future temperature changes also affect biocrust distribution. For example, the climate legacy over the last 20,000 years could indirectly affect the distribution and relative species richness of biocrusts by altering vegetation cover and soil pH (Eldridge and Delgado-Baquerizo, 2019). Additionally, under future scenarios of increased temperature and aridity, biocrust cover is predicted to decrease by approximately 25% by the end of the century, with communities shifting towards early cyanobacterial biocrusts (Rodríguez-Caballero et al., 2022).

Soil properties. It was commonly believed that finer soils benefit biocrust growth (Belnap et al., 2014; Williams et al., 2013). However, some scientists have challenged this notion (Fig. 4c). For example, Kidron (2018) argued that soils with high dust or fine grains are not a necessary condition for biocrust distribution. Qiu et al. (2023) suggested that soils with small amounts of gravel (0.04-22.34% content, 0.58% being optimal) are more favorable for biocrusts. Another study has shown that the soil parent material determines the degree of surface weathering and the water-holding capacity of the soil, thus indirectly influencing the distribution of biocrusts (Bowker and Belnap, 2008). Gypsum or calcareous soils tend to develop mosses and lichens (Elbert et al., 2012), while sandy soils tend to develop cyanobacteria (Root and Mccune, 2012).

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Fire. The grassland is a major life form in dryland ecosystems, making it crucial to explore the effects of fire events on biocrust distribution (Palmer et al., 2022). Fire-induced soil warming can alter the resource allocation and dynamic growth mechanisms between biocrusts and vascular plants (Mccann et al., 2021), potentially leading to a reduction in species richness and cover of biocrusts, especially cyanobacteria, and algae (Abella et al., 2020; Palmer et al., 2020). (Condon and Pyke, 2018) showed that moss cover increases with time after the fire, with no significant change in lichen cover.

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Disturbance. Activities such as grazing, agricultural practices, and land development can significantly impact biocrust distribution. Studies have demonstrated that grazing intensity can lead to substantial changes in biocrust cover. For instance, in Patagonian rangelands, biocrust cover decreased by 85%, 89%, and 98% under light, medium, and heavy grazing, respectively

(Velasco Ayuso et al., 2019). In the Loess Plateau, total biocrust cover remained almost unchanged under light grazing (< 30.00 goat dung / m^2), but there were variations in community structure, with an increase in cyanobacteria biocrusts (23.1%) and a decrease in moss biocrusts (42.2%) due to reduction in vascular plant cover (Ma et al., 2023). Tillage practices can disrupt the soil surface, leading to a reduction in biocrust cover (6% on average) and diversity, with lichens struggling to survive in tilled fields compared to mosses (Durham et al., 2018). Additionally, late-successional biocrusts exhibit higher tolerance compared to pre-successional biocrusts. Moss biocrusts, for instance, can maintain soil microbial biomass and nematode abundance better under trampling disturbance compared to cyanobacteria and lichen biocrusts (Yang et al., 2018). However, contrary to this view, it has been observed that cyanobacterial biocrusts increased in cover from 81% to 99% after trampling, while lichen and moss biocrusts decreased from 1.5% and 18% to less than 0.5%. Furthermore, mining activities can significantly reduce the photosynthetic potential of biocrusts, particularly affecting the recovery of cyanobacterial biocrusts (Gabay et al., 2022).

Other factors. On a global scale, biocrust distribution is also closely linked to biogeographic isolation. Strong spatial heterogeneity, accompanied by spatial distance, can create barriers to the dispersal of propagules (spores, fungal bodies), which indirectly impedes colonization of the biocrusts (Garcia-Pichel et al., 2013). In addition, factors such as vascular plant cover, topography, and solar radiation also influence biocrust distribution. Albert to a lesser extent than the factors mentioned above. For further insights, readers are encouraged to consult Chapter 10 of *Biological Soil Crusts: An Organizing Principle in Drylands*, which provides an overview of the control and distribution patterns of biocrusts from micro to global scales (Bowker et al., 2016).

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To sum up, climate is the most important factor influencing global biocrust distribution, especially in drylands where water is precious to the organisms. However, exploration of the roles of climatic factors such as rainfall seasonality and atmospheric drought still needs much further effort (Wright and Collins, 2024), especially in the context of global climate change. Although more attention has been paid to the physical properties of soils, the roles of their chemical properties, such as the nitrogen (N) and phosphorus (P) content, need to be taken more

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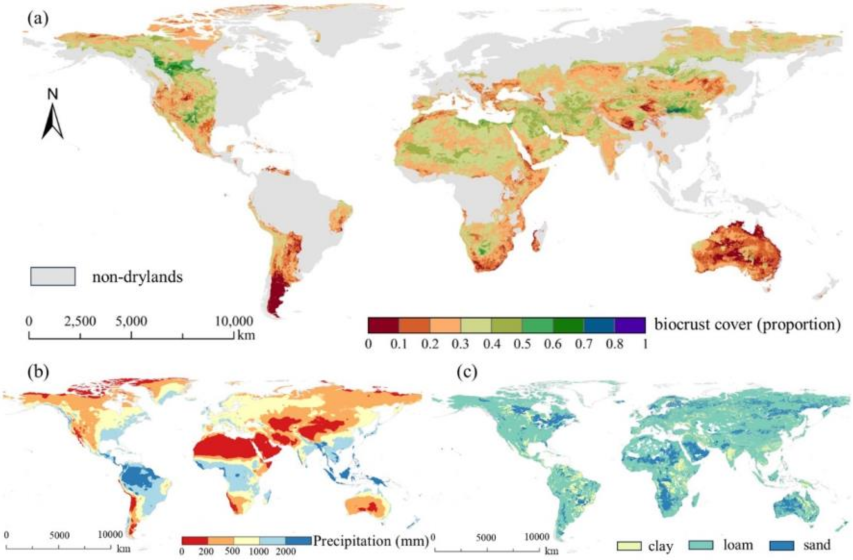
seriously. Fire and disturbance are usually ignored. However, due to the trend towards warmer and drier environments, as well as increasing population and the need to sustain livelihoods, their influences on biocrust distribution may become more important. As one of the basic processes on a global scale, biogeographic isolation or changes in land use should be paid more attention to. With the increasing number of biocrust data points, we can expect this aspect will see a surge in research.

Fig. 4 Biocrust distribution and its critical influencing factors. (a) Biocrust cover map and its influencing factors. (a) Global biocrust distribution, by random forest modelling. Based on a global biocrust database constructed by Chen et al., we expanded the biocrust data to 3848 entries through literature compilation and field surveys and fitted them with four types of remotely sensed environmental data, including climate, land use, soil properties, and elevation, to finally predict the suitable areas for the biocrust distribution and quantify the biocrust cover. (b) Global average annual precipitation (1970-2020), data from the WorldClim database (version 2.1). (c) Global soil texture distribution, data from HWSD (Harmonized World Soil Database, version 1.2). Precipitation and soil texture were taken as examples of environmental factors.



4. Challenges and Perspectives

Biocrusts play a crucial role in dryland ecosystems, making it essential to understand their current status and distribution dynamics. For influencing factors (Chapter 3), traditional observational studies and controlled experiments offer multiple perspectives of foundational knowledge. For assessing biocrust distribution patterns (Chapter 2), the methods shift from traditional approaches to spectral index, vegetation dynamics, and geospatial models that span multiple subjects like ecology, biology, geology, and computer science. However, high-precision biocrust distribution data across geographic units remain scarce, and current research methods are still limited. To further advance studies of biocrust distribution, we propose the following aspects for consideration.

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5.1 Building standardized biocrusts database

Currently, biocrust data are fragmented, low in volume, and derived from narrow sources, largely limiting spatial prediction from points to broader areas. Thus, we suggest that a global effort to build a standardized and specialized biocrusts database. This database should include consistent data items (such as main types and cover of biocrusts, latitude, longitude, and cover) and adhere to uniform inclusion criteria. Such a database is an important infrastructure for mapping global biocrust distribution, serving as the benchmark for training and validating spectral characteristics, DGVM, and geospatial models (Engel et al., 2023). Given the difficulty of conducting field surveys worldwide, compilating biocrust data from the published literature or other sources would be a primary approach (Fig. 4(a)). To date, several published studies have assembled 900 ~ 1,000 data on biocrust presence or absence from the literature (including 584 data on biocrust cover) (Chen et al., 2020; Eldridge et al., 2020; Havrilla et al., 2019; Rodriguez-Caballero et al., 2018). However, compiling from literature largely comes to its limitations and is still far from building a standardized and specialized biocrusts database. While open databases are not specialized to biocrusts, some of them may provide valuable additions (Fig. 5). For instance, the biodiversity and specimen datasets such as GBIF and the Atlas of Living Australia (Belbin and Williams, 2015; García-Roselló et al., 2015) contain a large amount of information on species, including mosses and lichens (Table 2), potentially offering hundreds or even thousands of entries of biocrusts occurrence or cover. Similarly, global, national, and regional plant flora can significantly contribute to building the standardized and specialized biocrusts database. For example, sPlot includes ~2 million vegetation plot data (Sabatini et al., 2021), and the European Vegetation Archive (*EVA*) also holds 1.6 million entries over the globe or Europe (Chytrý et al., 2016). Regional datasets like the Environmental Monitoring of Arid and Semiarid Regions (*MARAS)* have surveyed 426 sites (up to September 2020) and provided regular access to 624.50 km^2 of rangeland vegetation spatial patterns, species diversity, soil functional indices, climatic data, and landscape photographs in the Patagonia region of Argentina and Chile (Oliva et al., 2020). Concerns about land use products are also necessary. Global land use maps, based on the PROBA-V sensor, which contain spatial information for the Moss & Lichen layer, have an annual update frequency and a resolution of 100 m. Additionally, an increasing number of amateurs contribute significantly to global species information entries through species identification apps, which are user-friendly and widely accessible. The citizen science project *iNaturalist* is a very good example (Wolf et al., 2022). Furthermore, when collecting and collating data from non-academic sources, the combination of web crawlers and text analysis can help in obtaining biocrusts data and addressing key ecological issues.

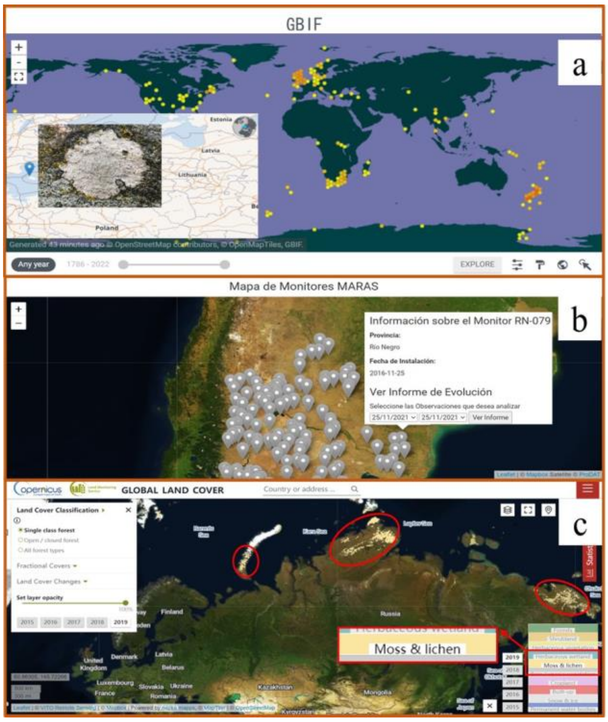

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Fig. 5 Potential approaches to building a standardized biocrusts database. (a) Distribution of lichens in the GBIF database with an example photo, (b) environmental monitors distribution map of MARAS database, (c) distribution of "mosses and lichens" in the PROBAV_LC100 database (light yellow area) in northern Asia, for instance.

Table 2 References for biocrusts database expansion channels

Data type	Data source	Extend	Biocrust type	Georeferenced records	Presence	Coverage	Link
Biodiversity data	the Global Biodiversity Information Facility(GBIF)	Worldwide	Cyanobacteria	~780000	√	- -	https://www.gbif.org/
			Lichen	~19000			
			Moss	~90000			
	Atlas of Living Australia(ALA)	Australia	Cyanobacteria	~53000	√	- -	https://www.ala.org.au/
			Lichen	~12000			
			Moss	~20000			
	Chinese Virtual Herbarium	China	Moss and lichen	--	√	- -	https://www.cvh.ac.cn/
	Global Plants on JSTOR	Worldwide	Lichen	~2000	√	- -	https://plants.jstor.org/
			Moss	~480			
Citizen Science	iNaturalist	Worldwide	All	--	√	- -	https://www.inaturalist.org/
Survey data	MARAS	Argentina and Chile	All	426	√	√	https://springernature.figshare.com/collections/The_MARAS_dataset_vegetation_and_soil_characteristics_of_dryland_rangelands_across_Patagonia/4789113
	sPlot	Worldwide	Lichen	6801	√	√	https://www.idiv.de/en/splot.html
			Moss	11001	√	√	
	GrassPlot	Worldwide	Non-vascular plants	6623	√	√	https://edgg.org/databases/GrassPlot/
	Vegbank	Canada and the United States	Moss and lichen	~15000	√	√	http://vegbank.org/
	BLM_AIM	The United States	Moss and lichen	5200	√	√	https://gbp-blm-egis.hub.arcgis.com/pages/aim
	TERN AEKOS	Australia	All	~300			http://www.aekos.org.au/
Landcover data	PROBAV_LC100	Worldwide	Moss and lichen	--			https://land.copernicus.eu/global/products/lc

5.2 Improving non-vascular vegetation dynamic models

There are only two DGVMs applicable to non-vascular organisms – LiBry and ECHAM6-HAM2-BIOCRUST (Rodriguez-Caballero et al., 2022). Despite their utility, these models still require performance improvements. Future directions for enhancing these models could include incorporating spatial self-organization of non-vascular organisms (Gassmann et al., 2000), the effects of fire (Thonicke et al., 2001), vegetation-environment feedback processes (Quillet et al., 2010), functional traits (Boulangeat et al., 2012), intraspecific-interspecific interactions (Boulangeat et al., 2014) and seasonal dynamics. Moreover, the physical properties, photosynthetic capacity, and carbon and nitrogen allocation of biocrusts change along environmental gradients in complex and context-dependent ways. These factors should be incorporated into DGVMs (Fatichi et al., 2019). Spatial-explicit DGVMs may be one key to effectively improving the accuracy of simulations in future studies, although they are data-intensive. Also, biocrusts are significantly influenced by hydrological processes and, in turn, affect these processes (Chen et al., 2018; Whitney et al., 2017). However, ecohydrological models, which focus on hydrological processes, are rarely connected to global biocrust distribution predictions. (Jia et al., 2019) attempted to incorporate biocrusts cover as a system state variable in an ecohydrological model, investigating biocrusts cover under varying rainfall gradients. By feeding ecohydrological models with global environmental data, particularly hydrological variables, these models could offer a new approach to predicting biocrust distribution on a global scale.

5.3 Integrated application of high-quality sensors

The spectral characterization method lies in the differences in spectral reflectance of biocrusts and other land types at various wavelengths. Consequently, the accuracy of the results is contingent on the quality of the sensors used. Previous studies often employed a single sensor with fixed band intervals for distinguishing biocrusts, potentially missing critical spectral features of different land types (Chamizo et al., 2012a). If the biocrusts index can be constructed by combining and comparing the full-band spectral data from multiple terrestrial sensors and infrared cameras, and other devices, the errors will be reduced to a certain extent, thus improving the classification accuracy (Wang et al., 2022b). In addition, the unique advantages of hyperspectral data, which include large data volumes and narrow bands, allow for the development of new biocrust discrimination standards when combined with observational data. If further estimation of biocrust cover can be achieved on this basis, it will be a significant contribution to the study of large-scale biocrust distribution (Rodríguez-Caballero et al., 2017). To date, high-resolution sensors have proven successful in monitoring lichens and mosses (Blanco-Sacristan et al., 2021), and the release of such products is something important to look out for in the future.

5.4 Making full use of machine learning

Machine learning can be combined with remote sensing products to uncover complex features from big data, enabling the prediction of global biocrust distribution (Collier et al., 2022). This data-driven approach has powerful predictive capabilities, especially for mapping species distribution, and can largely avoid the errors of missing or misidentifying biocrusts caused by traditional methods (relying on field measurements to determine threshold ranges) (Wang et al., 2022b). In remote sensing image classification, mature machine learning algorithms include support vector machines, single decision trees, random forests, artificial neural networks, etc. (Yu et al., 2020). Ensemble models combining multiple algorithms have been widely used in the field of species distribution but have seen relatively few applications in biocrust prediction. In the future, using machine learning to identify parameters for dynamic models of biocrusts may be one of the most promising methods to predict biocrust distribution (Perry et al., 2022).

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5.5 Regional research synergy development

Research on biocrust distribution has shown significant spatial and climatic imbalances. The study areas that have been conducted are relatively concentrated in countries such as China, the United States, Spain, Australia, and Israel. Although there are large areas of dryland distributed in Africa (other than South Africa), central Asia, central South America, and northern North America, research on biocrusts in these regions is scarce. These unbalanced regional research efforts constrain the advancement of studies on global biocrust distribution. Therefore, how to coordinate and promote the common progress of regional research is an urgent issue at present. Climatically, in addition to the drylands, the cold zones may be another important area to explore biocrust distribution (Pushkareva et al., 2016). On the Tibetan Plateau,

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studies have investigated the spatial variation of different types of biocrust communities across climatic gradients and their effects on soil temperature features and freezing duration (Ming et al., 2022; Wei et al., 2022). These findings highlight the need for more studies on biocrust distribution in the alpine areas.

5. Conclusion

Biocrusts are of great significance to the ecohydrological processes, soil material cycling, landscape shaping, and biodiversity conservation in drylands. To date, numerous studies have tried to fill the knowledge gap in biocrust distribution at the regional scale. However, global-scale research remains scarce, and mapping accuracy is still insufficient, directly leading to ambiguities in ecological function assessment and prediction. Therefore, advancing global-scale biocrust distribution research requires a more comprehensive consideration of the applicability of previous methods and a broader knowledge base to help select environmental indicators. For future work in this field, we advocate for closer cooperation among scientists to build a global standardized database incorporating multiple sources of biocrust data. This effort should primarily focus on expanding biocrust data items in understudied regions where biocrusts have been reported, thereby creating a larger, multi-habitat training set. Meanwhile, modern learning tools, such as deep learning, should be broadly applied to high-quality sensor image segmentation, data classification, and model parameter tuning. Finally, long-term monitoring and simulation are necessary to better understand the dynamics of ecological restoration in drylands and the response of biocrusts to environmental changes.

Author contribution

Siqing Wang co-conceived the idea, collected data on the biological soil crust, wrote the first draft, prepared the figures, and revised the manuscript. Li Ma, Liping Yang, Yali Ma, and Yafeng Zhang collected data on biological soil crust and revised the manuscript. Changming Zhao co-conceived the idea. Ning Chen co-conceived the idea, collected data on the biological soil crust, revised the manuscript, and provided support for funding.

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Competing interests

All authors declare no conflict of interest.

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