Running title: Global biocrusts distribution

Advancing studies on global biocrusts distribution

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Abstract: Biological soil crusts (biocrusts hereafter) cover a substantial proportion of 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, which is still lacking, especially in a global scale. This study aimed to stimulate global-scale investigations of biocrusts distribution by introducing three major approaches: spectral characterization indices, dynamic vegetation models, and geospatial models, while discussing their applicability. Then, we summarized present understandings of biocrusts distribution. Finally, to further advance this field, we proposed several potential research topics and aspects, including building standardized database of biocrusts, enhancing non-vascular vegetation dynamic models, integrating multi-sensor monitoring, making full use of machine learning, and focusing on regional research co-development. This work is supposed to significantly contribute to mapping biocrusts distribution, and thereby to advance our understandings of dryland ecosystem management and restoration.

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

1. Introduction

Biological soil crusts (biocrusts hereafter) are continuous complexes that live in the topsoil,

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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) . They are able to occupy a wide ecological niche in the water-limited, nutrient-poor and hostile environments, especially in arid and semi-arid areas characterized by low ratios of precipitation to potential evaporation (0.05-0.5 mm/mm) (Read *et al.*, 2014; Pravalie, 2016; Weber *et al.*, 2016), covering approximately 11% of the global land area (Porada *et al.*, 2019).

As vital components of dryland ecosystems, biocrusts fulfill essential ecological functions. They contribute to stabilizing the soil surface and improving soil permeability and water-holding capacity within the upper top centimeters (Gao *et al.*, 2017; Shi *et al.*, 2023; Sun *et al.*, 2023). By participating in a suite of biogeochemical cycles, biocrusts contributed 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 (Tucker *et al.*, 2017; Kidron *et al.*, 2022). Moreover, biocrusts influence seed capture and soil seed banks (KrÖPfl *et al.*, 2022), thereby mediating plant growth and community assembly (Havrilla & 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 carbon and nitrogen mechanisms (Morillas & Gallardo, 2015; Hu *et al.*, 2019), interspecific interactions and biocrusts biodiversity (Munoz-Martin *et al.*, 2019; Machado de Lima *et al.*, 2021), rather than their spatial distribution, particularly at the global scale. Consequently, a systematic and accurate assessment of biocrusts' ecological roles remains challenging. In this study, we firstly sorted out the main research methods for studying biocrusts distribution (section 1), then reviewed the existing knowledge (section 2), and finally proposed strategies to advance the study of large-scale biocrusts distribution (section 3). This work is expected to deepen our understandings of dryland ecosystem processes, and to provide a scientific basis for dryland ecosystem conservation and their responses to global change.

2. Research Methods

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In the study of biocrusts distribution, three methods are commonly used: spectral characterization, vegetation dynamic modeling, and geospatial modeling. This section provides an overview of these methods, including their basic principles, adaptability, and limitations.

2.1 Spectral characterization index

The first is spectral characterization method. Advances in remote sensing and geo-information technologies have made spectroscopy one of the most powerful approaches for determining the distribution features. Differences in absorption or reflection of specific wavelengths of different ground covers can effectively identify soil surface objects (Rodriguez-Caballero *et al.*, 2015). By identifying biocrust-specific bands from the reflectance spectral images (Karnieli *et al.*, 1999), it is possible to construct a presence-absence map of biocrusts distribution (Fig. **1a**).

The crust index (CI) and biological soil crust index (BSCI) are two of spectral characterization indexes and have been successfully applied in Negev Desert (cyanobacteria-dominated) (Karnieli, 1997; Noy *et al.*, 2021) and Gurbantunggut Desert (lichen-dominated) (Chen *et al.*, 2005). For such indicators, 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 biocrusts omission or misidentification. In order to improve the accuracy of biocrusts identification, some researchers took advantage of the hyperspectral sensor's continuous waveband, and created Continuum Removal Crust Identification Algorithm (CRCIA) (Weber *et al.*, 2008; Chamizo *et al.*, 2012). Baxter *et al.* (2021) innovatively applied the random forest algorithm to spectral feature classification, and achieved an accuracy of 78.5% in biocrusts recognition. Another two indexes, i.e., the sandy land ratio crust index (SRCI) and the desert ratio crust index (DRCI), were also introduced by taking into account the differences between sandy land (vegetation cover FVC <20%) and desert environments, which could improve the accuracy of the mapping by ~6% (Wang *et al.*, 2022).

The spectral characterization method is easy to use, and thus, facilitates the access to continuous long-term dynamics of biocrusts distribution. However, mosses and vascular plants

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are generally mixed up in this case because their reflectance characteristics are close to each other in all wavelengths especially when mosses are wet, which makes them indistinguishable (Fang *et al.*, 2015). Therefore, spectral characterization method is mainly applicable to situations where biocrusts cover is >30% and plants cover is <10% (Beaugendre *et al.*, 2017). It should be noted that, the existing indexes mostly correspond to biocrusts cover consisting of specific dominant groups in specific environments, which cannot be directly extrapolated to areas with high heterogeneous environments (Table 1). Wetting or disturbance may also lead to large fluctuations in reflectance of different land types and interfere with biocrusts distribution monitoring (Rodriguez-Caballero *et al.*, 2015; Weber & Hill, 2016) .

2.2 Dynamic global vegetation models (DGVMs)

Dynamic global vegetation model is another major method to obtain vegetation cover (Deng *et al.*, 2022). Dynamic global vegetation model mainly focuses on simulating the biogeochemical processes (e.g. carbon, water cycles), metabolic and hydrological processes of organisms (Lenton *et al.*, 2016; Porada *et al.*, 2017). The method possesses significant advantages to map global biocrusts distribution because its assumptions have clear biological implications (Cuddington *et al.*, 2013). To use DGVMs, the following procedures need to be taken. The first step is building model framework, simulating important and interesting processes such as biocrusts growth and death, nutrient cycle, and water cycle (Porada *et al.*, 2013). So far, there is only one dynamic global vegetation model targeting at biocrusts - the Lichen and Bryophyte Model (LiBry) (Fig. **1b**) (Porada *et al.*, 2013, 2019). The second step is parameterization. Generally, literature and open databases are used to assign physiological strategies for different types of biocrust, such as photosynthesis, respiration and nitrogen emission under the influence of temperature, precipitation, radiation, biological water saturation, etc. The third step is importing environmental data into the model to obtain the biocrusts cover at grid points over a specific study region. At last, the results are tuned and validated against observation data of biocrusts distribution (obtained by literature comparison and local field observations), and thereby biocrusts distribution map is produced. Such simulation models heavily relies on the differences in the physicochemical properties of metabolic activity of organisms (Quillet *et al.*, 2010). Inevitably, this kind of study requires large observation data and extensive human intervention, yet the accuracy of the study cannot be well guaranteed at present (Table 1).

2.3 Geospatial models

Directly relating vegetation presence or cover to environmental data instead of indirectly via biological processes in DGVMs is another important way to obtain biocrust's distribution (Skidmore *et al.*, 2011; Fischer & Subbotina, 2014; Beaugendre *et al.*, 2017). Classic statistical models can serve for this purpose. However, they still require comprehensive expert knowledge of how environmental factors affect biocrusts (Pearce *et al.*, 2001), which is hard to get and prone to be biased. Geospatial models which integrating machine learning tools with field survey data and remote sensing data is supposed to hold the most promise (Crego *et al.*, 2022). Geospatial model is also known as species distribution model or ecological niche model (Jiménez-Valverde *et al.*, 2008; Soberon & Nakamura, 2009; Brown & Anderson, 2014). The procedures of how to use geospatial modelling are illustrated in Figure 1c (Rodriguez-Caballero *et al.*, 2018): 1) extracting environmental data for the sites where biocrusts observation data are reported, 2) importing the extracted environmental data into the machine learning framework and obtaining the relationship between biocrusts distribution and environmental variables through a specific algorithm (e.g., decision tree algorithms, Bayesian algorithms, artificial neural networks, etc.), 3) simulating biocrusts distribution by extrapolating to the whole study region using the constructed relationships. Nevertheless, geospatial models are black-boxes and largely non-interpretable, and thus, less capable of capturing key mechanisms behind phenomenon, which may limit its applications. One should note that, to avoid confounding model predictions, inclusion of environmental factors should be based on relevance of environmental factors to biocrusts, and still need expert knowledge to a certain degree (Mäkinen *et al.*, 2022). Supplied with sufficient computing power and observation data of biocrust distribution, and suitable environmental, geospatial models are supposed to able to predict biocrust distribution accurately. Therefore, geospatial modelling is considered to be one of the most proper methods available (Table 1).

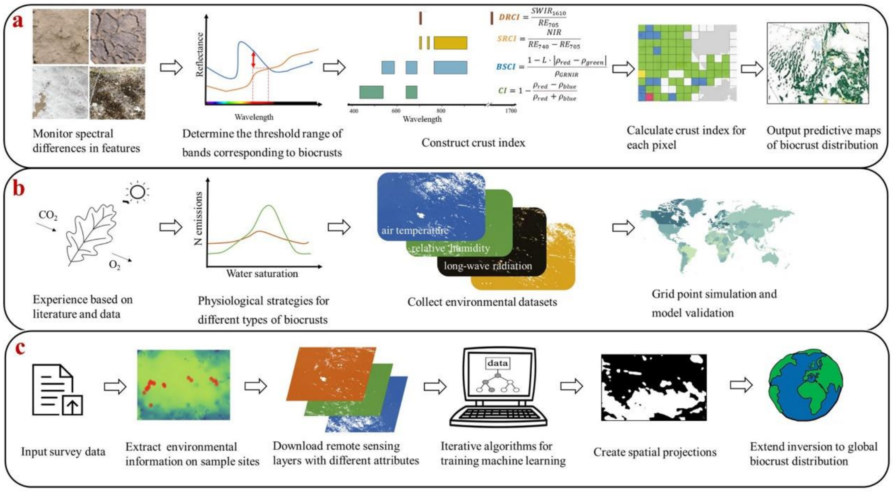

Fig. 1 Illuminations of applying spectral characterization method **(a)**, vegetation dynamics model **(b)** and geospatial model **(c)** in biocrusts distribution study. See main text for more detailed introduction to these methods.

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

	Spectral characteristic index	**Vegetation dynamics model**	**Geospatial model**
Principle	Differences in wavelength reflectance of surface features	Differences in the physiological processes of different biocrusts 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	Experience-based promotion with significant human intervention； Experiments need to be supported by big data	Large amount of computing power； Adequate number of sample points to support accuracy

	of biocrusts, without coverage		
Applicable scales	Regional scale (Desert and sandy land with <20% vegetation cover)	Regional scale Global scale	Regional scale Global scale

3. What have we known?

Since 1990, studies on the distribution of biocrusts has been continuously increasing. Biocrusts spatial distribution has gradually received attention from all over the world, in particular the countries with extensive dryland areas such as China, United States, Spain, United Kingdom, Germany, Australia and Israel. A group of ecologists, represented by Fernando Maestre, David Eldridge, Matthew Bowker, Emilio Rodríguez-Caballero and others, have been have been actively involved in the field (Fig. **2**).

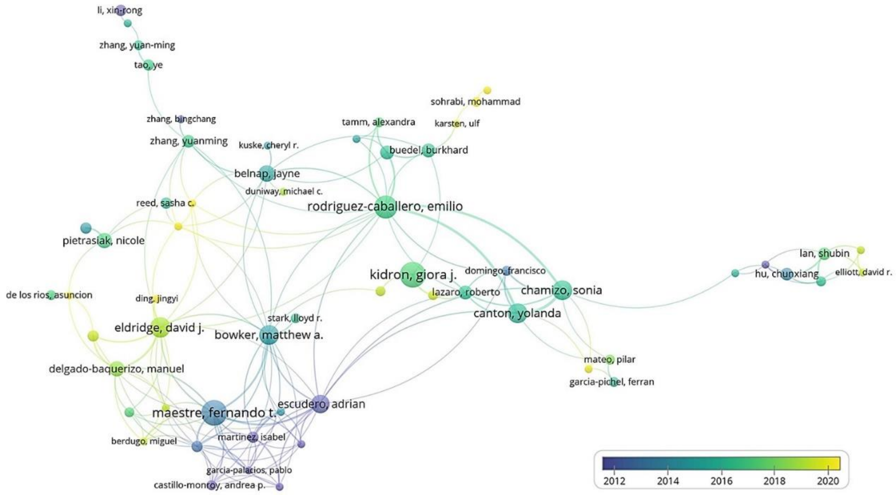

Fig. **2** Representative authors associated frameworks for biocrusts distribution studies (1990 to 2022). The time series is the average time of the year of publication, e.g., if the number of articles is 2 in 2004 and 8 in 2019, the node in this figure shows the year as (2004 x 2 + 2019 x 8)/10 = 2016.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

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"arid*" OR "semi*arid*" OR "dry subhumid*"), with research interests in Environmental Sciences/Ecology and a total of 700 papers.

3.1 Local-regional scales

At local-regional scales, numerous studies have provided valuable insights into the distribution patterns of biocrusts in different regions around the world. In the Mojave Desert, biocrusts distribution was closely related to geological age, surface stability, topography, and dust transport (Miller *et al.*, 2004), lichen, moss, and dark algal crusts patchily distributed on its northeastern slopes, averaging 8% cover, though in some bar and shrub zones, the cover could be as high as 16% (Pietrasiak *et al.*, 2014). In the Colorado Plateau, highly heterogeneous soil matrix determined the fragmented biocrusts distribution of different types and the wide disparity in relative abundance and cover (Reynolds *et al.*, 2006; Steven *et al.*, 2013). Collier *et al.* (2022) trained drone imagery in the Hawaiian region using timely data collected by cameras and then successfully mapped watershed-scale biocrusts distribution, predicting cover of ~15-23%. In the Gurbantunggut Desert, biocrusts cover 28.7% of the area, with a high and uniform biocrusts cover in the southern part of the desert and a scattered distribution of biocrusts in other areas (Chen *et al.*, 2005; Zhang *et al.*, 2007). Does plot size have an effect on the variation in biocrusts cover? RGB image-based biocrusts monitoring on the Loess Plateau 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.*, 2022). In Qatar, 26% of the country is covered by biocrusts, with cyanobacterial biocrusts cover showing a decreasing trend from north-east to south-west (Richer *et al.*, 2012). In the northern Negev, the distribution of biocrusts is well developed, by simulating the spectral characteristics of the different components of biocrusts after seasonal precipitation, especially the chlorophyll absorption characteristics, it was found that the greening of the biocrusts was obvious, which could provide a basis for the subsequent tracking of their distribution (Panigada *et al.*, 2019). At the Sinai Peninsula (Egypt) – Negev desert (Israel) border, the distribution dynamics of cyanobacterial biocrusts over a 31-year period has now been obtained from the crust index (Noy *et al.*, 2021). Filamentous cyanobacteria grow in the African Sahara (Issa *et al.*, 1999), where statistical models of combined environmental indicators showed biocrusts cover of 1 ~ 48% and 0 ~ 65% in Banizoumbou and Tamou respectively (Beaugendre *et al.*, 2017). Recent research predicted that under future scenarios of reduced precipitation, increased temperature and aridity in southwest Africa, the biocrusts cover will decrease ~25% by the end of the century and the communities may shift towards early cyanobacterial biocrusts (Rodríguez-Caballero *et al.*, 2022).

3.2 Global scale

To date, there are only two global-scale studies of biocrusts distribution. 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 and disturbance intervals and averaging simulation results for the past 20 years for each grid point, they estimated that biocrusts cover 11% of global terrestrial land surface (Porada *et al.*, 2019). Their results also showed that the light and dark cyanobacteria were widely distributed in deserts, savannas, grasslands and Mediterranean woodlands at low latitudes, and increase to some extent with increasing dryness, while mosses were mostly distributed in middle and high latitudes and polar regions (Fig. **3a**). Rodriguez-Caballero *et al.* (2018) fitted biocrusts presence-only data to the bioclimate, soil properties, land use data, and then extrapolated to a continuous global distribution of biocrusts using the Maxent model. This work assessed the total area covered by biocrusts to be 1.79×10^7 km^2, 12.2% of global drylands, in other words, biocrusts cover was 1.2% larger compared to the area predicted by Porada et al., (2019) (Fig. **3b**). After comparing two maps of global biocrusts distribution, biocrust distribution is generally consistent in the large deserts of Asia, western America, Europe and Oceania, while some semi-arid regions, such as the northern and southern margins of African Sahara Desert, South Asia and central North America, have significantly higher biocrusts cover in the latter projection of Rodriguez-Caballero *et al.* (2018).

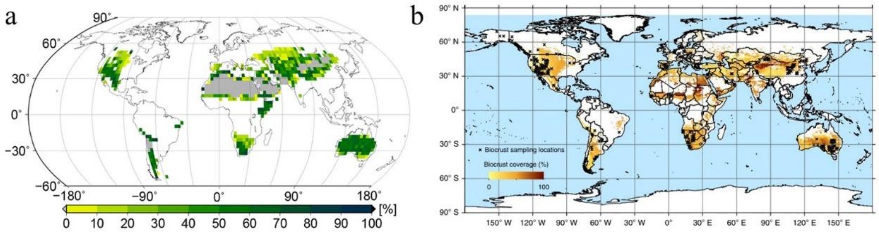

Fig. 3 Maps of the results of global biocrusts distribution. a, prediction based on vegetation dynamic model (Porada *et al.*, 2019). b, prediction based on geospatial model (Rodriguez-Caballero *et al.*, 2018).

3.3 Influencing factors of biocrusts distribution

What factors influence the global distribution of biocrusts? In general, precipitation is considered to be critical in determining the distribution of biocrusts (Eldridge & Tozer, 1997). Increased precipitation could lead to higher levels of lichen and moss, while algal cover may first increase and then decrease (Marsh *et al.*, 2006; Budel *et al.*, 2009; Zhao *et al.*, 2014). It should to be noted that, precipitation can also promote the growth of vascular plants, and the continuous and 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 most (Chamizo *et al.*, 2016; Jia *et al.*, 2019). Whereas, it has been experimentally proven that short-term and frequent light rain events killed moss biocrusts in the Colorado Plateau, USA (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 vapour tends to condense into fog or dew, which facilitates the survival of three-dimensional species (such as leafy lichens) by trapping air moisture (Kidron, 2019; Eldridge *et al.*, 2020; Li *et al.*, 2021). The relatively high soil temperature also creates an environment of high evaporation that impedes biocrusts colonization (Garcia-Pichel *et al.*, 2013). In addition to the effects of the current climate, researches began to study the effects of climate change in the dryland on the structure of biocrusts communities (Ferrenberg *et al.*, 2015), including climatic legacy effects. Changes in temperature and precipitation over the last 20,000 years have been found to indirectly affect the distribution and relative species richness of biocrusts through changing vegetation cover and soil pH (Eldridge & Delgado-Baquerizo, 2019).

The distribution of biocrusts at global scale is also correlated with biogeographic isolation, soil texture and disturbance (Rodriguez-Caballero *et al.*, 2018; Sosa-Quintero *et al.*, 2022).

Strong spatial heterogeneity accompanied with spatial distance can set up barriers to the dispersal of propagules (spores, fungal bodies) (Garcia-Pichel *et al.*, 2013). For a long time, it was commonly believed that finer soils benefit biocrusts growth (Williams *et al.*, 2013; Belnap *et al.*, 2014). However, this has been challenged by some scientists. For example, Kidron (2018) believed that soils with high dust or fine grains were not a necessary condition for biocrusts distribution. Another study had shown that the soil parent material determines the degree of surface weathering and the water-holding capacity of the soil, thus indirectly changing the distribution of biocrusts (Bowker & Belnap, 2008). Gypsum or calcareous soils tend to develop mosses and lichens (Elbert *et al.*, 2012), sandy soils tend to develop cyanobacteria (Root & McCune, 2012). As grassland is one major lifeform in dryland ecosystems, it is of great significance to explore the effects of fire events on biocrusts distribution (Palmer *et al.*, 2022). Fire-induced soil warming will alter the resource allocation and dynamic growth mechanisms between biocrusts and vascular plants (McCann *et al.*, 2021), which may cause a reduction in species richness and cover of biocrusts, especially cyanobacteria and algae (Abella *et al.*, 2020; Brianne *et al.*, 2020). Condon and Pyke (2018) showed that moss cover increases with time after fire, with no significant change in lichen cover. Finally, the intensification of human disturbance, the continued development of land and the intensification of livestock trampling generally harm biocrusts (Rodríguez-Caballero *et al.*, 2022). The effects of soil stability (Stovall *et al.*, 2022), soil fertility (Bowker *et al.*, 2006), vegetation cover (Seitz *et al.*, 2017), topography (Su *et al.*, 2020) and solar radiation (Durham *et al.*, 2018) on the distribution of biocrusts are relatively pronounced at local, landscape and smaller scales, see *Controls on distribution patterns of biological soil crusts at micro- to global Scales* for details (Bowker *et al.*, 2016).

4. Challenges and perspectives

Biocrusts are very important for dryland ecosystems, and thus, biocrust distribution gradually becomes a hot spot since the turn of the century. The methods are shifting from traditional observational and controlled experiments to combining methods across ecology, biology, geology and computer science disciplines. However, high-precision biocrusts distribution data across geographic units are still lacking, and research methods are still limited.

To further advance studies of biocrusts distribution, we raise the following aspects.

4.1 Building standardized biocrusts database

Standardized and specialized biocrusts database consisting of the same data items (main types and cover of biocrusts, latitude, longitude and cover, etc.) and using the same inclusion criteria, which is an important infrastructure for mapping global biocrusts distribution, serving as the benchmark to train and validate spectral characteristics, DGVM, and geospatial models (Engel *et al.*, 2023). Due to the difficulty of conducting field surveys worldwide, compilating biocrusts data from the published literatures or other channels is the major approach (Fig. 4). Several studies had been conducted to collect data from literatures, obtained 900-1000 sample points of biocrusts presence and 584 sample points of biocrusts cover in global dryland (Rodriguez-Caballero *et al.*, 2018; Havrilla *et al.*, 2019; Chen *et al.*, 2020; Eldridge *et al.*, 2020). However, compiling from literatures largely comes to its limitation and is still far from building a standardized and specialized biocrusts database. While open databases are not specialized to biocrusts, some of them may be important additions. For example, the biodiversity and specimen datasets such as GBIF and the Atlas of Living Australia (Belbin & Williams, 2015; García-Roselló *et al.*, 2015), which contain a large amount of information on species, of course including mosses and lichens (Table 2), which can contain hundreds or even thousands of entries of biocrusts occurrence or cover. Similarly, global, national and regional plant flora may significantly contribute to building the standardized and specialized biocrusts database. For example, sPlot includes ~2 millions of vegetation plot data (Sabatini *et al.*, 2021), and the European Vegetation Archive (*EVA*) also possesses 1.6 million entries over globe or Europe (Chytrý *et al.*, 2016). Regional datasets like Environmental Monitoring of arid and Semiarid Regions (*MARAS)* surveyed 426 sites (up to September 2020), and provided regular access to 624.50 km^2 of rangeland vegetation spatial patterns, species diversity data, soil functional indices, climatic data and landscape photographs in Patagonia region straddling Argentina and Chile (Oliva *et al.*, 2020). In addition to above channels, an increasing number of amateurs are getting involved in science through species identification apps with clean, easy-to-use apps, contributing significantly to global species information entries. The citizen science project *iNaturalist* is a very good example (Wolf *et al.*, 2022). Furthermore, when collecting and collating data from the non-academic sources, the combination of web crawlers and text analysis can help in obtaining biocrusts data and solving key ecological issues. In addition, high resolution sensors have been found to be 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.

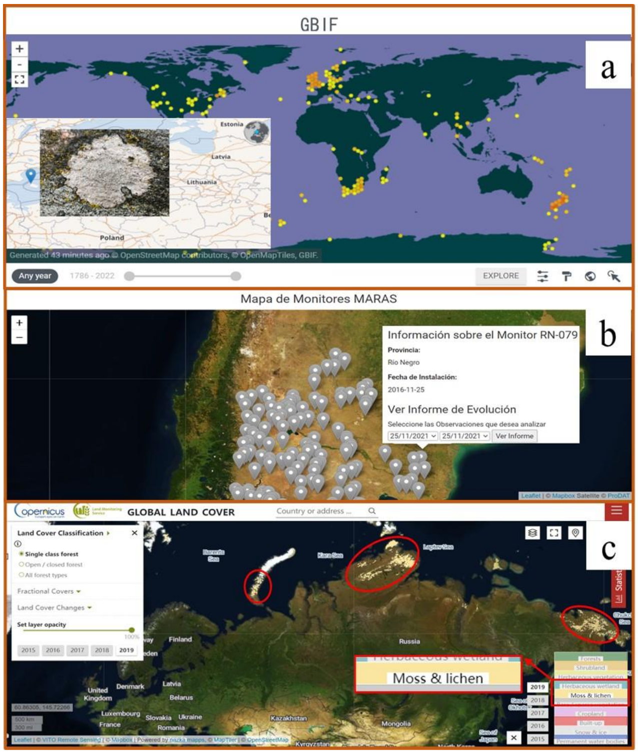

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Fig. 4 Potential approaches to build standardized biocrusts database. (a) Distribution of lichens in the GBIF database with an example photo, (b) environmental monitors distribution map of MARAS database, (c) distribution of "mosses and lichens" in 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

4.2 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). Their performances still need to be improved. Considering 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 in current and/or new DGVMs can be future directions. In addition, how the physical properties, photosynthetic capacity, carbon and nitrogen allocation of biocrusts change along environmental gradient are complex and context-dependent, which 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, but are data-consuming. Also, biocrusts are significantly influenced by hydrological processes and vice versa (Whitney *et al.*, 2017; Chen *et al.*, 2018), while ecohydrological models based on hydrological processes are rarely connected to global biocrusts distribution predictions. Jia *et al.* (2019) tried to incorporate biocrusts cover as a system state variable in an ecohydrological model and investigated biocrusts cover under rainfall gradient. If fed with global data of environmental variables (mainly hydrological relevant ones), ecohydrological models may be a new approach to predicting biocrusts distribution at global scales.

4.3 Integrated application of high-quality sensors

Spectral characterization method lies on the differences in spectral reflectance of biocrusts and other land types at different wavelengths, and thus, the accuracy of the results depends on the quality of the sensors. However, previous studies have often used a single sensor with constant band intervals for distinguishing biocrusts, which may result in missed spectral feature identification of land types (Chamizo *et al.*, 2012). 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. In addition, the unique advantages of hyperspectral data with large data volume and narrow band allow it to be used to combine with observation data to co-develop new biocrusts discrimination standard. If further estimation of biocrusts cover can be achieved on this basis, it will be an important contribution to the study of large scale biocrusts distribution (Rodríguez-Caballero *et al.*, 2017).

4.4 Making full use of machine learning

Machine learning can be combined with remote sensing products to find complex features from big data to predict global biocrust distribution (Collier *et al.*, 2022). This data-driven approach has powerful predictive capabilities, especially for mapping species distribution, and can largely circumvent the mistakes of missing or misidentifying biocrusts caused by traditional methods (relying on field measurements to determine threshold ranges) (Wang *et al.*, 2022). In the remote sensing image classification problem, 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 relatively few applications exist in field of biocrusts prediction (Rodriguez-Caballero *et al.*, 2018). In the future, using machine learning to find parameters for dynamic models of biocrusts, which may be one of the most promising method to predict biocrusts distribution (Perry *et al.*, 2022).

4.5 Regional research synergy development

Spatially, the study areas that have been conducted are relatively concentrated in countries such as China, USA, 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 are scarce. Unbalanced regional research efforts are one of the constraints to advancing studies of global biocrusts distribution. Therefore, how to coordinate and promote the common progress of regional research is an urgent issue at present. In addition to the drylands, the cold zones may be another important area to explore biocrusts distribution (Pushkareva *et al.*, 2016). On the Tibetan Plateau, studies have investigated the spatial variation of different types of biocrusts communities across climatic gradients and their effects on soil temperature features and freezing duration (Ming *et al.*, 2022; Wei *et al.*, 2022). This urges the studies of biocrusts distribution in the alpine areas.

To sum up, as biocrusts being one of key organizing principles in drylands where environmental stress and climate change become increasingly severe, it is essential to explore the global distribution of biocrusts. This study summarized three major methods of predicting biocrust distribution, sorted out the current knowledge of biocrust distribution, and made suggestions for advancing this field. The research will be an important cornerstone of related work that help conserve and restore critical areas of global drylands, and thereby for the healthy development of natural-human society.

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