

1 **Running title:** Global biocrust distribution

2 **Advancing studies on global biocrust distribution**

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18

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

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

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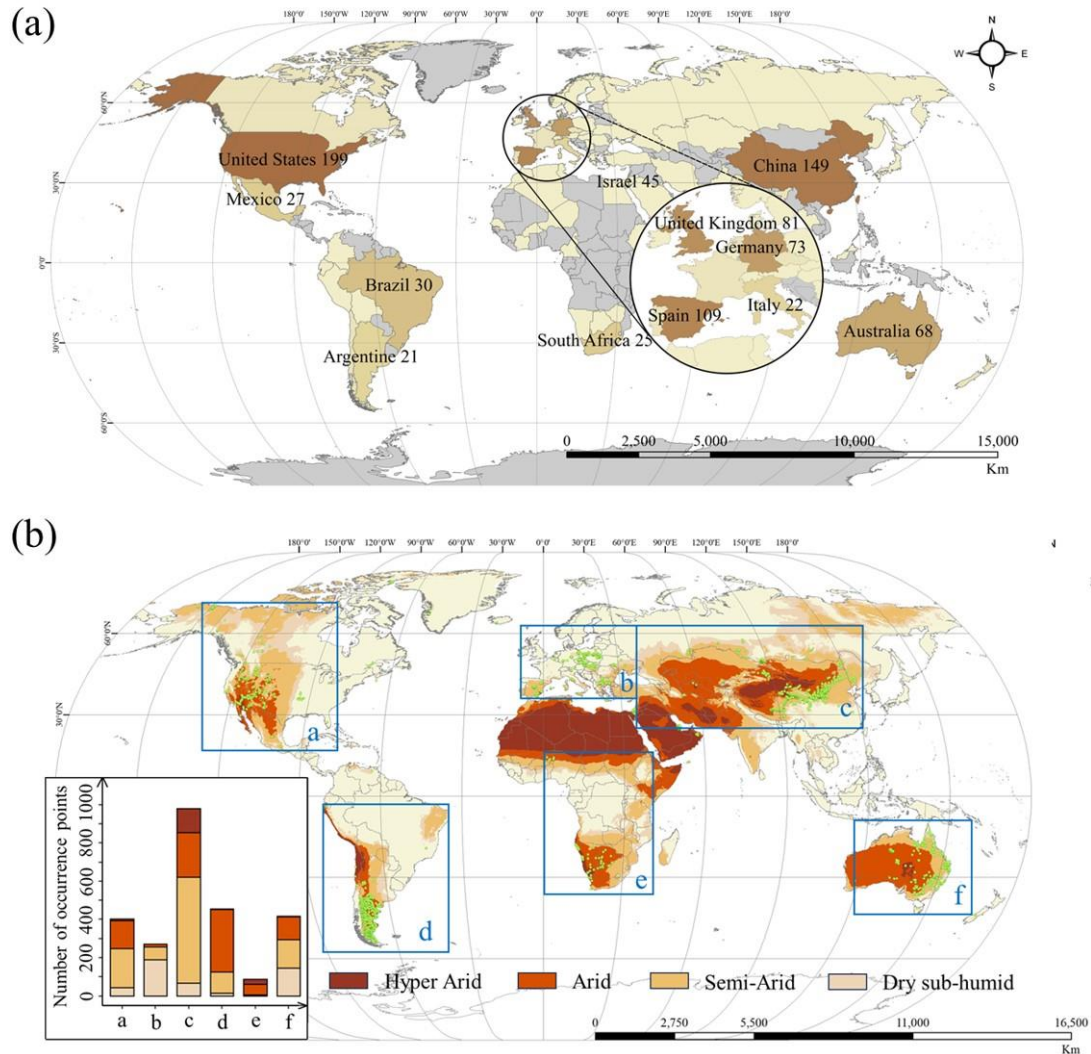
34 **1. Introduction**

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

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

56 Despite the significance of biocrusts, previous studies have primarily focused on their  
57 contributions to carbon and nitrogen cycling across various habitats and climates (Hu et al.,  
58 2019; Morillas and Gallardo, 2015), as well as interspecific interactions and biocrust  
59 biodiversity (Machado De Lima et al., 2021; Munoz-Martin et al., 2019), rather than their  
60 spatial distribution. Countries like China, the United States, Spain, Australia, and Israel, most  
61 of which have extensive dryland areas, have attempted to make breakthroughs on this issue  
62 (Fig. 1a). However, other dryland countries and regions, such as central and southern Africa,  
63 where the biocrust distribution has been reported, still suffer from a paucity of studies and data

64 on biocrusts (Fig. 1b). This geographical imbalance in biocrust distribution studies has resulted  
 65 in most knowledge remaining at local to regional scales, with very limited discoveries on a  
 66 global scale.



67  
 68 **Fig. 1** Literature review of biocrust distribution studies. (a) Map of hotspot countries for  
 69 biocrust distribution research. Numbers are the countries of the authors of published articles  
 70 from 1990 to 2022, and the top 12 countries are shown; The database is Web of Science, TS =  
 71 ("biogenic crust\*" OR "biological crust\*" OR "biological soil crust\*" OR "biocrust\*" OR  
 72 "microphytic crust\*" OR "microbiotic crust\*" OR "cyanobacterial\*" OR "algal\*" OR "lichen\*" OR  
 73 "moss\*" OR "biotic crust\*") AND ("mapping\*" OR "distribution\*" OR "spatial pattern\*")  
 74 AND ("dryland" OR "hyper\*arid\*" OR "arid\*" OR "semi\*arid\*" OR "dry subhumid\*"), with  
 75 research interests in Environmental Sciences/Ecology and a total of 700 papers. (b) Global  
 76 biocrust data distribution, based on field surveys and literature compilation. The bar chart

77 counts the number of entries for biocrust records (presence/absence or cover) for six continents  
78 (regions). Datasets have been collected and expanded from the published database (Chen et al.,  
79 2020; Rodriguez-Caballero et al., 2018) to 3848 items (unpublished).

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

## 86 **2. Research Methods**

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

### 90 **2.1 Spectral characterization index**

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

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

106 Biological Soil Crust Index (BSCI) with lichen biocrust as the dominant group and mapped the  
107 distribution of biocrusts with high accuracy (accuracy of 94.7%, kappa coefficient of 0.82)  
108 (Chen et al., 2005), spatially, biocrusts cover 28.7% of the area, with a high and uniform cover  
109 in the southern part of the desert and a scattered distribution in other regions (Zhang et al.,  
110 2007). In the Loess Plateau, red-green-blue (RGB) image-based biocrust monitoring showed  
111 that variability in biocrusts cover decreased logarithmically with increasing plot size until a  
112 critical size of 1m<sup>2</sup>, after which biocrusts cover remained approximately constant (Wang et al.,  
113 2022a).

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

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

135 to large fluctuations in the reflectance of different land types, interfering with biocrust  
136 distribution monitoring (Rodriguez-Caballero et al., 2015; Weber and Hill, 2016).

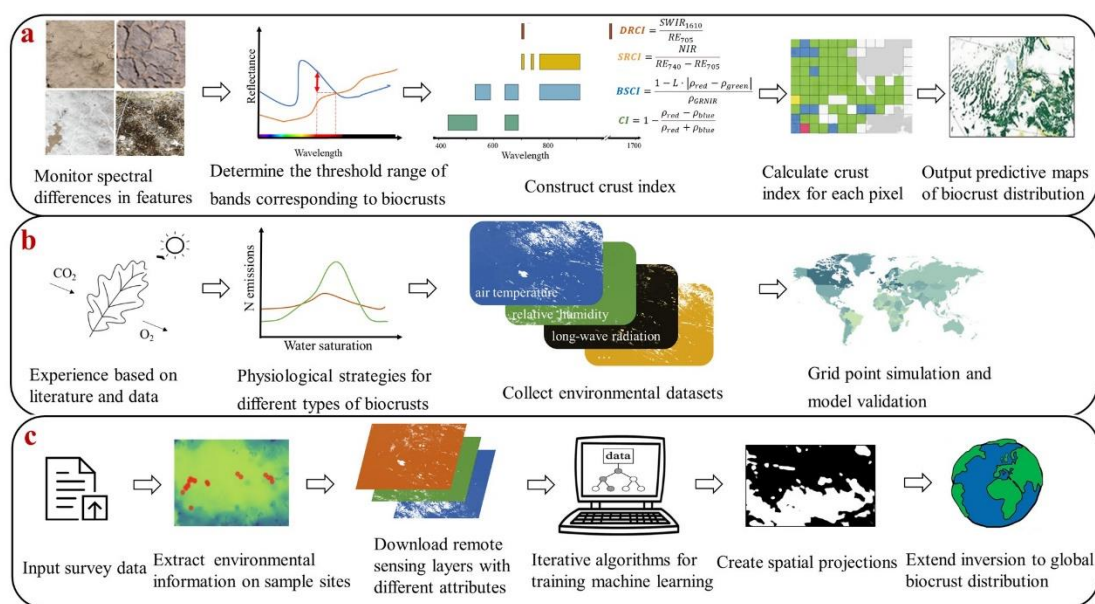
## 137 **2.2 Dynamic global vegetation models (DGVMs)**

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

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

## 162 **2.3 Geospatial models**

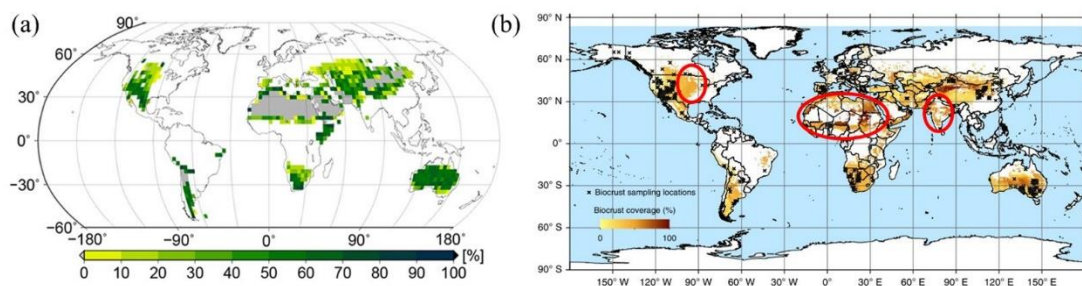
163 Directly relating vegetation presence or cover to environmental data, instead of indirectly  
 164 via biological processes, is another important way to obtain biocrust distribution (Beaugendre  
 165 et al., 2017; Fischer and Subbotina, 2014; Skidmore et al., 2011). Classic statistical models can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



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

179 Compared with the result of the dynamic vegetation model, the simulation accuracy  
 180 ( $R^2 \sim 0.8$ ) and mapping resolution ( $0.5^\circ \times 0.5^\circ$ ) of the geospatial model were improved.  
 181 Biocrust distribution is generally consistent in the large deserts of Asia, western America,

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



190

191 **Fig. 3** Maps of global biocrusts distribution. (a) Prediction based on vegetation dynamic model  
192 (Porada et al., 2019). (b) Prediction based on geospatial model (Rodriguez-Caballero et al.,  
193 2018). Permissions have been obtained from the relevant sources Porada et al., (2019) and  
194 Rodriguez-Caballero et al., (2018).

195 As black-boxes, geospatial models are largely non-interpretable and, thus, less capable of  
196 capturing the key mechanisms behind phenomena, which may limit their applications. Under  
197 this methodological framework, only the direct effects of various environmental indicators are  
198 considered. For example, it focuses on the direct effect of precipitation on biocrust distribution  
199 while ignoring the indirect effects, such as interactions among shrubs, grasses, and biocrusts  
200 (Wang et al., 2024). In addition, to avoid confounding model predictions, the inclusion of  
201 environmental factors should be based on their relevance to biocrusts, and expert knowledge  
202 should still be needed to a certain degree (Mäkinen et al., 2022). Not only natural conditions  
203 such as climate, topography, and soil, but also data on human activities such as afforestation,  
204 trampling, and population density need to be considered as environmental indicators in the  
205 model. It should be noted that the superimposition of environmental layers of different  
206 resolutions may cause deviations in results to some extent, which is unavoidable (Zhao et al.,



207 2024). Despite the above limitations of geospatial modeling, with sufficient computing power,  
 208 observation data of biocrust distribution, and suitable environmental information, geospatial  
 209 models are supposed to be relatively optimal solutions for predicting biocrust distribution  
 210 (Table 1).

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

	<b>Spectral characteristic index</b>	<b>Vegetation dynamics model</b>	<b>Geospatial model</b>
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

212

213 **3. Influencing Factors of Biocrust Distribution**

214 It is of great importance to clarify the environmental variables associated with biocrust  
 215 distribution. On the one hand, it helps to frame the range of data selection before modeling, and  
 216 on the other hand, it aids in identifying patterns of biocrust distribution in the context of

217 dynamic changes and various types of environmental information, thereby facilitating the  
218 prediction of distributed evolution on longer time scales. Numerous modelling studies (Kidron  
219 and Xiao, 2023; Li et al., 2023; Rodriguez-Caballero et al., 2018) have demonstrated that, on  
220 the global scale, biocrust distribution is mainly influenced by water conditions, temperature,  
221 soil properties, fire, and disturbance (Bowker et al., 2016).

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

243 *Temperature.* Relatively high soil temperature can create an environment of high  
244 evaporation that impedes biocrusts colonization (Garcia-Pichel et al., 2013). Regarding air  
245 temperature, warming by 4°C could alter biocrust community structure, resulting in a sharp

246 decrease in moss biocrust cover and an increase in cyanobacterial biocrust cover. This effect  
247 becomes even more significant when warming interacts with time and precipitation treatments  
248 (Ferrenberg et al., 2015). Recent studies have shown that historical and future temperature  
249 changes also affect biocrust distribution. For example, the climate legacy over the last 20,000  
250 years could indirectly affect the distribution and relative species richness of biocrusts by  
251 altering vegetation cover and soil pH (Eldridge and Delgado-Baquerizo, 2019). Additionally,  
252 under future scenarios of increased temperature and aridity, biocrust cover is predicted to  
253 decrease by approximately 25% by the end of the century, with communities shifting towards  
254 early cyanobacterial biocrusts (Rodríguez-Caballero et al., 2022).

255 *Soil properties.* It was commonly believed that finer soils benefit biocrust growth (Belnap  
256 et al., 2014; Williams et al., 2013). However, some scientists have challenged this notion (Fig.  
257 4c). For example, Kidron (2018) argued that soils with high dust or fine grains are not a  
258 necessary condition for biocrust distribution. Qiu et al. (2023) suggested that soils with small  
259 amounts of gravel (0.04-22.34% content, 0.58% being optimal) are more favorable for biocrusts.  
260 Another study has shown that the soil parent material determines the degree of surface  
261 weathering and the water-holding capacity of the soil, thus indirectly influencing the  
262 distribution of biocrusts (Bowker and Belnap, 2008). Gypsum or calcareous soils tend to  
263 develop mosses and lichens (Elbert et al., 2012), while sandy soils tend to develop  
264 cyanobacteria (Root and Mccune, 2012).

265 *Fire.* The grassland is a major life form in dryland ecosystems, making it crucial to explore  
266 the effects of fire events on biocrust distribution (Palmer et al., 2022). Fire-induced soil  
267 warming can alter the resource allocation and dynamic growth mechanisms between biocrusts  
268 and vascular plants (Mccann et al., 2021), potentially leading to a reduction in species richness  
269 and cover of biocrusts, especially cyanobacteria, and algae (Abella et al., 2020; Palmer et al.,  
270 2020). (Condon and Pyke, 2018) showed that moss cover increases with time after the fire, with  
271 no significant change in lichen cover.

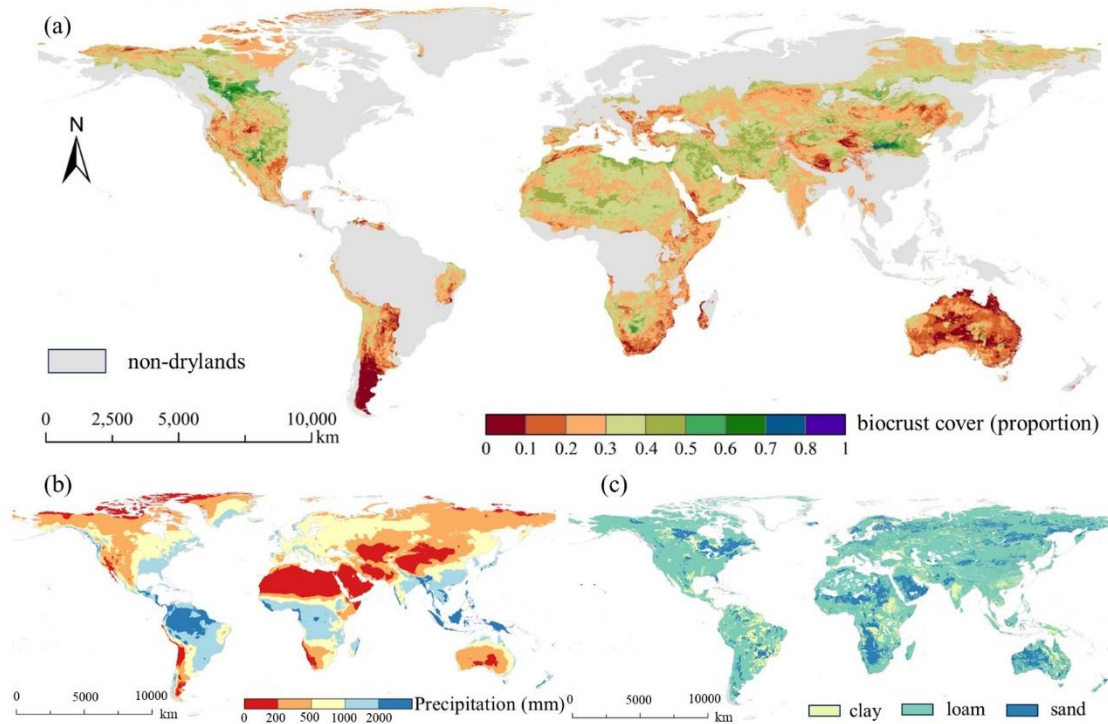
272 *Disturbance.* Activities such as grazing, agricultural practices, and land development can  
273 significantly impact biocrust distribution. Studies have demonstrated that grazing intensity can  
274 lead to substantial changes in biocrust cover. For instance, in Patagonian rangelands, biocrust

275 cover decreased by 85%, 89%, and 98% under light, medium, and heavy grazing, respectively  
276 (Velasco Ayuso et al., 2019). In the Loess Plateau, total biocrust cover remained almost  
277 unchanged under light grazing ( $< 30.00$  goat dung /  $m^2$ ), but there were variations in community  
278 structure, with an increase in cyanobacteria biocrusts (23.1%) and a decrease in moss biocrusts  
279 (42.2%) due to reduction in vascular plant cover (Ma et al., 2023). Tillage practices can disrupt  
280 the soil surface, leading to a reduction in biocrust cover ( 6% on average) and diversity, with  
281 lichens struggling to survive in tilled fields compared to mosses (Durham et al., 2018).  
282 Additionally, late-successional biocrusts exhibit higher tolerance compared to pre-successional  
283 biocrusts. Moss biocrusts, for instance, can maintain soil microbial biomass and nematode  
284 abundance better under trampling disturbance compared to cyanobacteria and lichen biocrusts  
285 (Yang et al., 2018). However, contrary to this view, it has been observed that cyanobacterial  
286 biocrusts increased in cover from 81% to 99% after trampling, while lichen and moss biocrusts  
287 decreased from 1.5% and 18% to less than 0.5%. Furthermore, mining activities can  
288 significantly reduce the photosynthetic potential of biocrusts, particularly affecting the recovery  
289 of cyanobacterial biocrusts (Gabay et al., 2022).

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

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

304 chemical properties, such as the nitrogen (N) and phosphorus (P) content, need to be taken more  
 305 seriously. Fire and disturbance are usually ignored. However, due to the trend towards warmer  
 306 and drier environments, as well as increasing population and the need to sustain livelihoods,  
 307 their influences on biocrust distribution may become more important. As one of the basic  
 308 processes on a global scale, biogeographic isolation or changes in land use should be paid more  
 309 attention to. With the increasing number of biocrust data points, we can expect this aspect will



310 see a surge in research.

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

321 **4. Challenges and Perspectives**

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

### 331 **5.1 Building standardized biocrusts database**

332 Currently, biocrust data are fragmented, low in volume, and derived from narrow sources,  
333 largely limiting spatial prediction from points to broader areas. Thus, we suggest that a global  
334 effort to build a standardized and specialized biocrusts database. This database should include  
335 consistent data items (such as main types and cover of biocrusts, latitude, longitude, and cover)  
336 and adhere to uniform inclusion criteria. Such a database is an important infrastructure for  
337 mapping global biocrust distribution, serving as the benchmark for training and validating  
338 spectral characteristics, DGVM, and geospatial models (Engel et al., 2023). Given the difficulty  
339 of conducting field surveys worldwide, compiling biocrust data from the published literature  
340 or other sources would be a primary approach (Fig. 4(a)). To date, several published studies  
341 have assembled 900 ~ 1,000 data on biocrust presence or absence from the literature (including  
342 584 data on biocrust cover) (Chen et al., 2020; Eldridge et al., 2020; Havrilla et al., 2019;  
343 Rodriguez-Caballero et al., 2018). However, compiling from literature largely comes to its  
344 limitations and is still far from building a standardized and specialized biocrusts database.  
345 While open databases are not specialized to biocrusts, some of them may provide valuable  
346 additions (Fig. 5). For instance, the biodiversity and specimen datasets such as GBIF and the  
347 Atlas of Living Australia (Belbin and Williams, 2015; García-Roselló et al., 2015) contain a  
348 large amount of information on species, including mosses and lichens (Table 2), potentially  
349 offering hundreds or even thousands of entries of biocrusts occurrence or cover. Similarly,  
350 global, national, and regional plant flora can significantly contribute to building the

351 standardized and specialized biocrusts database. For example, sPlot includes ~2 million  
352 vegetation plot data (Sabatini et al., 2021), and the European Vegetation Archive (*EVA*) also  
353 holds 1.6 million entries over the globe or Europe (Chytrý et al., 2016). Regional datasets like  
354 the Environmental Monitoring of Arid and Semiarid Regions (*MARAS*) have surveyed 426 sites  
355 (up to September 2020) and provided regular access to 624.50 km<sup>2</sup> of rangeland vegetation  
356 spatial patterns, species diversity, soil functional indices, climatic data, and landscape  
357 photographs in the Patagonia region of Argentina and Chile (Oliva et al., 2020). Concerns about  
358 land use products are also necessary. Global land use maps, based on the PROBA-V sensor,  
359 which contain spatial information for the Moss & Lichen layer, have an annual update  
360 frequency and a resolution of 100 m. Additionally, an increasing number of amateurs contribute  
361 significantly to global species information entries through species identification apps, which  
362 are user-friendly and widely accessible. The citizen science project *iNaturalist* is a very good  
363 example (Wolf et al., 2022). Furthermore, when collecting and collating data from non-  
364 academic sources, the combination of web crawlers and text analysis can help in obtaining  
365 biocrusts data and addressing key ecological issues.



366

367 **Fig. 5** Potential approaches to building a standardized biocrusts database. (a) Distribution of  
 368 lichens in the GBIF database with an example photo, (b) environmental monitors distribution  
 369 map of MARAS database, (c) distribution of "mosses and lichens" in the PROBAV\_LC100  
 370 database (light yellow area) in northern Asia, for instance.

371

**Table 2** References for biocrusts database expansion channels



372

## 373 5.2 Improving non-vascular vegetation dynamic models

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

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

### 393 **5.3 Integrated application of high-quality sensors**

394           The spectral characterization method lies in the differences in spectral reflectance of  
395 biocrusts and other land types at various wavelengths. Consequently, the accuracy of the results  
396 is contingent on the quality of the sensors used. Previous studies often employed a single sensor  
397 with fixed band intervals for distinguishing biocrusts, potentially missing critical spectral  
398 features of different land types (Chamizo et al., 2012a). If the biocrusts index can be constructed  
399 by combining and comparing the full-band spectral data from multiple terrestrial sensors and  
400 infrared cameras, and other devices, the errors will be reduced to a certain extent, thus  
401 improving the classification accuracy (Wang et al., 2022b). In addition, the unique advantages  
402 of hyperspectral data, which include large data volumes and narrow bands, allow for the

403 development of new biocrust discrimination standards when combined with observational data.  
404 If further estimation of biocrust cover can be achieved on this basis, it will be a significant  
405 contribution to the study of large-scale biocrust distribution (Rodríguez-Caballero et al., 2017).  
406 To date, high-resolution sensors have proven successful in monitoring lichens and mosses  
407 (Blanco-Sacristan et al., 2021), and the release of such products is something important to look  
408 out for in the future.

#### 409 **5.4 Making full use of machine learning**

410 Machine learning can be combined with remote sensing products to uncover complex  
411 features from big data, enabling the prediction of global biocrust distribution (Collier et al.,  
412 2022). This data-driven approach has powerful predictive capabilities, especially for mapping  
413 species distribution, and can largely avoid the errors of missing or misidentifying biocrusts  
414 caused by traditional methods (relying on field measurements to determine threshold ranges)  
415 (Wang et al., 2022b). In remote sensing image classification, mature machine learning  
416 algorithms include support vector machines, single decision trees, random forests, artificial  
417 neural networks, etc. (Yu et al., 2020). Ensemble models combining multiple algorithms have  
418 been widely used in the field of species distribution but have seen relatively few applications  
419 in biocrust prediction. In the future, using machine learning to identify parameters for dynamic  
420 models of biocrusts may be one of the most promising methods to predict biocrust distribution  
421 (Perry et al., 2022).

#### 422 **5.5 Regional research synergy development**

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

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

## 436 **5. Conclusion**

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

452

## 453 **Author contribution**

454 Siqing Wang co-conceived the idea, collected data on the biological soil crust, wrote the first  
455 draft, prepared the figures, and revised the manuscript. Li Ma, Liping Yang, Yali Ma, and  
456 Yafeng Zhang collected data on biological soil crust and revised the manuscript. Changming  
457 Zhao co-conceived the idea. Ning Chen co-conceived the idea, collected data on the biological  
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459

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466

#### 467 **Competing interests**

468 All authors declare no conflict of interest.

469

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