

1 **Running title:** Global biocrust distribution

2 **Advancing studies on global biocrust distribution**

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

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

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### 33 1. Introduction

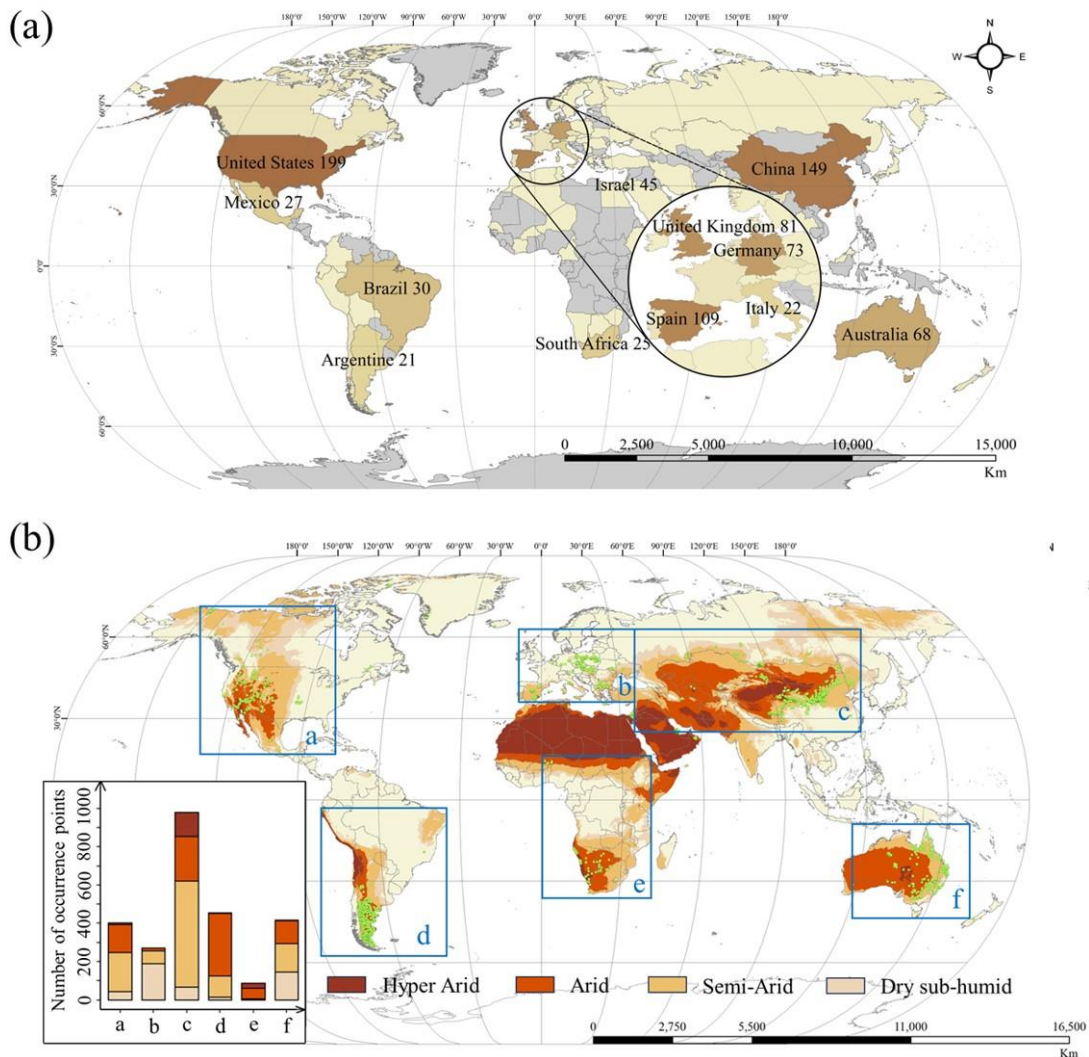
34 Biological soil crusts (biocrusts hereafter) are continuous biotic complexes that live in the

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

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

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

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



66  
 67 Fig. 1 Literature review of biocrust distribution studies. (a) Map of hotspot countries for  
 68 biocrust distribution research. Numbers are the countries of the authors of published articles  
 69 from 1990 to 2022, and the top 12 countries are shown; The database is Web of Science, TS =  
 70 ("biogenic crust\*" OR "biological crust\*" OR "biological soil crust\*" OR "biocrust\*" OR  
 71 "microphytic crust\*" OR "microbiotic crust\*" OR "cyanobacterial\*" OR "algal\*" OR "lichen\*" OR  
 72 "moss\*" OR "biotic crust\*") AND ("mapping\*" OR "distribution\*" OR "spatial pattern\*")  
 73 AND ("dryland" OR "hyper\*arid\*" OR "arid\*" OR "semi\*arid\*" OR "dry subhumid\*"), with  
 74 research interests in Environmental Sciences/Ecology and a total of 700 papers. (b) Global  
 75 biocrust data distribution, based on field surveys and literature compilation. The bar chart  
 76 counts the number of entries for biocrust records (presence/absence or cover) for six continents

77 (regions). Datasets have been collected and expanded from the published database (Chen et al.,  
78 2020; Rodriguez-Caballero et al., 2018) to 3848 items (unpublished).

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

## 85 **2. Research Methods**

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

### 89 **2.1 Spectral characterization index**

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

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

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

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

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

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

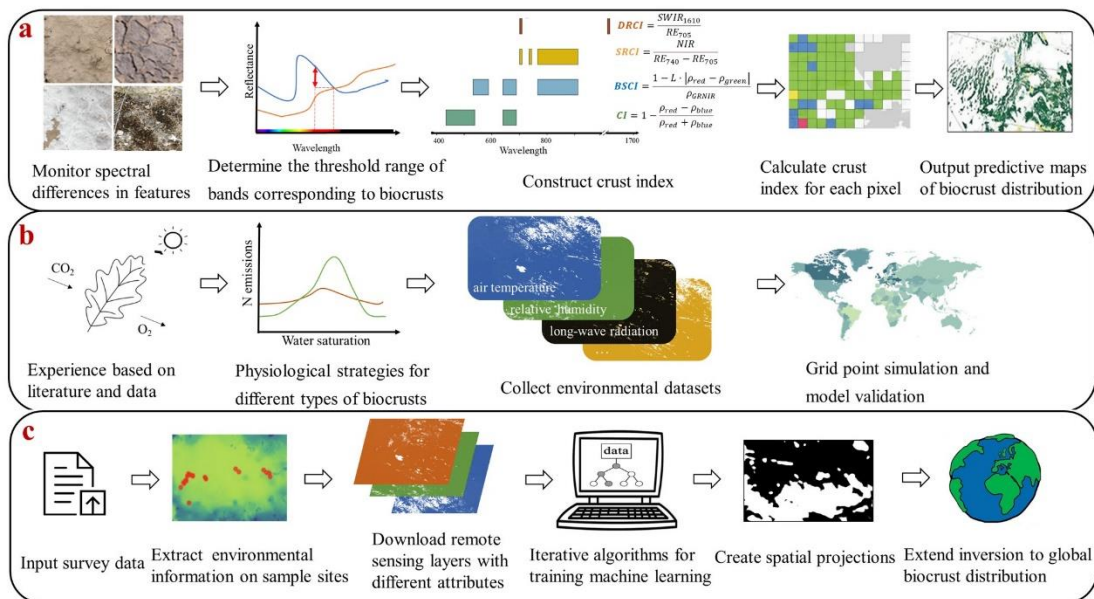
## 136 **2.2 Dynamic global vegetation models (DGVMs)**

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

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

## 161 **2.3 Geospatial models**

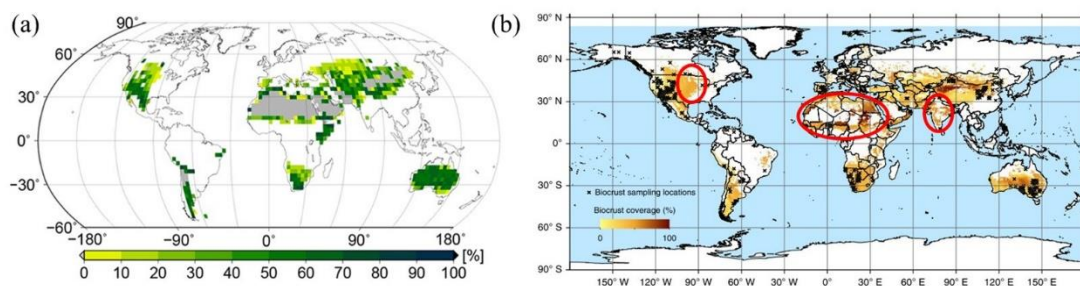
162 Directly relating vegetation presence or cover to environmental data, instead of indirectly  
 163 via biological processes, is another important way to obtain biocrust distribution (Beaugendre  
 164 et al., 2017; Fischer and Subbotina, 2014; Skidmore et al., 2011). Classic statistical models can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



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

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

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



189

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

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



206 observation data of biocrust distribution, and suitable environmental information, geospatial  
 207 models are supposed to be relatively optimal solutions for predicting biocrust distribution  
 208 (Table 1).

209 **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

210

### 211 **3. Influencing Factors of Biocrust Distribution**

212 It is of great importance to clarify the environmental variables associated with biocrust  
 213 distribution. On the one hand, it helps to frame the range of data selection before modeling, and  
 214 on the other hand, it aids in identifying patterns of biocrust distribution in the context of  
 215 dynamic changes and various types of environmental information, thereby facilitating the

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

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

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

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

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

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

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

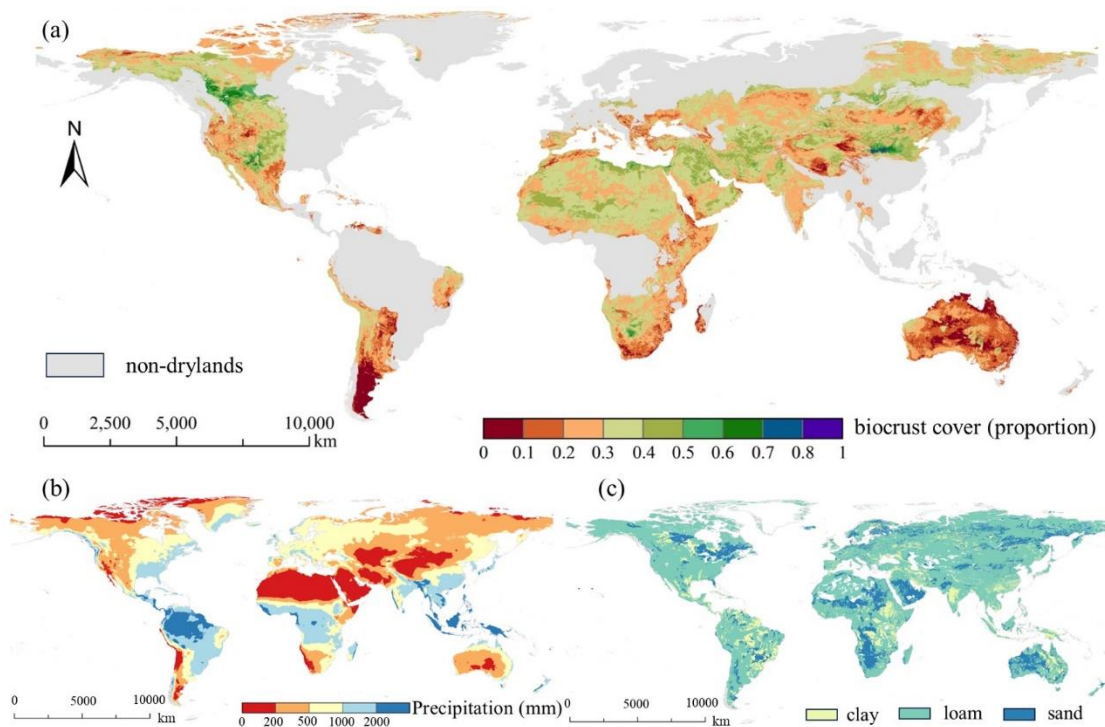
274 (Velasco Ayuso et al., 2019). In the Loess Plateau, total biocrust cover remained almost  
275 unchanged under light grazing ( $< 30.00$  goat dung /  $m^2$ ), but there were variations in community  
276 structure, with an increase in cyanobacteria biocrusts (23.1%) and a decrease in moss biocrusts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

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

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

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

309 Fig. 4 Biocrust distribution and its critical influencing factors. (a) Biocrust cover map and its



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

#### 319 4. Challenges and Perspectives

320 Biocrusts play a crucial role in dryland ecosystems, making it essential to understand their

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

### 329 **5.1 Building standardized biocrusts database**

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

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



364

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

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



370

## 371 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>	
	TERN AEKOS	Australia	All	~300			<a href="http://www.aekos.org.au/">http://www.aekos.org.au/</a>	
	Landcover data	PROBAV_LC100	Worldwide	Moss and lichen	--			<a href="https://land.copernicus.eu/global/products/lc">https://land.copernicus.eu/global/products/lc</a>

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

### 391 **5.3 Integrated application of high-quality sensors**

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

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

#### 407 **5.4 Making full use of machine learning**

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

#### 420 **5.5 Regional research synergy development**

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

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

## 434 **5. Conclusion**

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

450

## 451 **Author contribution**

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

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464

#### 465 **Competing interests**

466 All authors declare no conflict of interest.

467

#### 468 **Reference**

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