Mapping biocrust distribution in China’s drylands under changing climate

Dexun Qiu a,b,c, Matthew A. Bowker d,e, Bo Xiao a,b,c,* , Yunge Zhao b , Xiaobing Zhou f , Xinrong Li g

a Key Laboratory of Arable Land Conservation (North China), Ministry of Agriculture and Rural Affairs/College of Land Science and Technology, China Agricultural University, Beijing 100193, China
b State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University/Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China
c Breeding Base for State Key Laboratory of Land Degradation and Ecological Restoration in Northwestern China/Key Laboratory of Restoration and Reconstruction of Degraded Ecosystems in Northwestern China of Ministry of Education, Ningxia University, Yinchuan 750021, China
d School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA
e Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA
f State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China
g Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resource Research, Chinese Academy of Sciences, Lanzhou 730000, China

HIGHLIGHTS

• We provided the first biocrust distribution map in China’s drylands (250 × 250 m).
• Biocrust distribution depends on soil properties, aridity stress, and altitude.
• Biocrusts currently cover 13.9% of China’s drylands (5.7% of total area).
• Climate change will lead to a 5.5%–9.0% reduction in biocrust cover by 2050.
• Elevated temperature and increased precipitation drive biocrust cover loss.

GRAPHICAL ABSTRACT

ABSTRACT

Biological soil crusts (biocrusts) are widely distributed in global drylands and have multiple significant roles in regulating dryland soil and ecosystem multifunctionality. However, maps of their distribution over large spatial scales are uncommon and sometimes unreliable, because our current remote sensing technology is unable to efficiently discriminate between biocrusts and vascular plants or even bare soil across different ecosystem and soil types. The lack of biocrust spatial data may limit our ability to detect risks to dryland function or key tipping points.

* Corresponding author at: College of Land Science and Technology, China Agricultural University, No. 2, Yuanmingyuan West Road, Haidian District, Beijing 100193, China.
E-mail address: xiaobo@cau.edu.cn (B. Xiao).

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1. Introduction

Dryland biomes, characterized by a precipitation-to-evapotranspiration ratio below 0.65, cover 41% (~60 million km²) of the land surface of our world and support >1/3 of the global population (MEA, 2005; Schimel, 2010). In drylands, the water demand exceeds available supply due to infrequent precipitation and intense evapotranspiration (Praválek, 2016). The vascular plant communities therefore cannot fully cover dryland surfaces (especially in hyper-arid and arid deserts), limiting ecosystem primary production and nutrient cycling (MEA, 2005). These water-limited regions, mainly consisting of deserts and temperate grasslands, are facing severe risks of land degradation and desertification as well as habitat loss (Feng and Fu, 2013; Gober, 2010; Bai et al., 2008). Many dryland ecosystems are currently experiencing degradation (Li et al., 2021; Mariano et al., 2018), and this trend is likely to accelerate due to increasing global warming and population growth (Huang et al., 2016). Some researchers have predicted that drylands will possibly expand significantly by the end of the 21st century (IPCC, 2013), though not all agree that drylands are poised to expand (Berg and McColl, 2021). In any case, preventing further degradation is crucial for maintaining stability and multifunctionality of dryland ecosystem and thus should be a priority.

Because vascular plant cover is sparse in drylands, a large area of exposed soil provides a suitable niche for biocrust colonization (Frenenberg et al., 2015). Biocrusts are a cohesive layer in the uppermost millimeters of soil, engineered by diverse communities of photoautotrophic (e.g., cyanobacteria, algae, lichens, bryophytes) and heterotrophic (e.g., bacteria, fungi, archaea) organisms (Weber et al., 2022). Although these inconspicuous communities have been neglected for quite a long time, biocrusts are known to play multiple critical roles in stabilizing soil against erosion (Gao et al., 2017), regulating ecohydrological (Li et al., 2022) and biogochemical cycles (Elbert et al., 2012), and improving biodiversity (Antoninka et al., 2020) in dryland ecosystems. For example, biocrusts are estimated to prevent the emission of ~0.7 Pg atmospheric dust (which would increase global emissions by 60%) (Rodriguez-Caballero et al., 2022) and are also responsible for approximately 25% of the N-fixed on the global land surface (Rodriguez-Caballero et al., 2018). However, such assessments of biocrust function at large spatial scales is highly dependent on the reliable mapping of biocrust distribution, which is still absent or lacking local to regional validation at present.

Ground-based survey techniques (e.g., estimation of cover in quadrats) is commonly used to indicate biocrust occurrence or measure cover in field investigations at small spatial scales such as plot, slope, or micro watersheds at most (Bu et al., 2013; Biedel et al., 2014; Kidron et al., 2000). These methods have the advantage that the data-collectors can have high confidence in their observations, but the disadvantage that they are incapable of directly mapping biocrust distribution at large spatial scales. Another approach to map biocrust cover at larger scales is remote-sensing, including both satellite and drone-collected data. These approaches identify and map biocrust cover using biocrust-specific multispectral or hyperspectral characteristics through proximal reflectance spectroscopy and remote sensing (Rozenstein and Adamowski, 2017). However, remote sensing of biocrusts presents its own challenges because most techniques are only suitable for a particular type of biocrust, rather than collectively documenting all types, and the presence of a vascular plant canopy makes accurate data collection difficult (Chen et al., 2005; Wang et al., 2022). It can be challenging to distinguish between biocrusts and vascular plants when biocrusts are hydrated, and between biocrusts and bare soil when biocrusts are dry (Rozenstein and Adamowski, 2017). Moreover, a proportion of biocrusts cover is distributed under the canopy of shrubs and grasses, and these biocrusts are even harder to identify and separate in remote-sensing. This is because the presence of shrubs and grasses can obscure biocrusts from satellite or aerial imagery and lead to spectral confusion in remote sensing data (Smith et al., 2019; Swe et al., 2023), making it difficult to accurately quantify biocrust cover beneath vegetation canopies. Today, it is still challenging to reliably map regional or global biocrust distribution, and this problem could persist.

Under these circumstances, spatial prediction modeling provides a feasible option to geographically project the biocrust distribution using occurrence locations and related soil and environmental data. One commonly used type of spatial prediction modeling is ecological niche models (ENMs) or species distribution models (SDMs), such as the maximum entropy (MaxEnt) modeling approach (Phillips et al., 2006). MaxEnt is a general-purpose machine learning method for estimating a target probability distribution by finding the probability distribution of maximum entropy, and it has several advantages such as its flexibility of variable processing and ability in dealing with presence-only data of biota (e.g., a species or community type) and small sample size (Phillips et al., 2006). However, the reliability of the results from such ecological niche models is highly dependent on the spatial scale (Renner and Warton, 2013), the number and evenness of the occurrence locations (Wisz et al., 2008), the resolution and quality of environmental data (Hernandez et al., 2006), and also the user’s experience. It is important to note that while MaxEnt modeling can provide insights into the environmental conditions that are suitable for biocrust growth, it cannot directly predict biocrust cover. The random forest algorithm (Breiman, 2001) is a powerful machine learning approach that has been widely applied in ecological modeling. It is particularly well-suited for modeling complex ecological systems that involve numerous interacting factors (Cutler et al., 2007), making it ideal for predicting biocrust cover. However, this approach requires sufficient and high-quality training data to ensure the modeling accuracy. It should be also noted that models can be only a complementary approach but never a substitution for direct observations. Moreover, the absence of field validation is a common limitation in large-scale modeling, which may reduce the reliability of prediction results from the model.

China’s drylands cover 3.92 million km² of area and accounts for 40.8% of the land surface (Li et al., 2016), providing vast and diverse habitats for the colonization of various biocrust types such as moss, lichen, and cyanobacterial biocrusts. These habitats span a range of

Climate change

Dryland
ecosystems, from desert to grassland, across hyper-arid, arid, semi-arid, and dry sub-humid climates. Since the late 1990s, a series of studies have been conducted in China’s drylands investigating the biocrust structure, function, and management (Li, 2012). However, similarly to most other drylands around the world, a high resolution and reliable map of biocrust distribution in China’s drylands is still absent. Moreover, the impact of climate change on the distribution and cover of biocrusts in China’s drylands has not yet been investigated. Here, we utilized spatial prediction modeling to indirectly estimate the current distribution and coverage of biocrusts in China’s drylands, as well as their changes in response to a changing climate. The aim of this study is to (1) generate high resolution biocrust distribution maps for China’s drylands; (2) investigate the response of biocrust cover to climate change; and (3) identify the environmental controllers that influence biocrust distribution pattern and cover. This study provides a valuable tool for monitoring and understanding the ecological role of biocrusts in large scale, aiding in the identification of risks and the development of effective conservation strategies in dryland ecosystems.

2. Materials and methods

Based on observations and spatial prediction modeling, we designed a methodological framework for mapping high resolution biocrust distribution in China’s drylands (Fig. 1).

2.1. Collection of biocrust occurrence locations


The following search terms were used: (TS = (‘biological crust’ or ‘biocrust’ or ‘moss crust’ or ‘lichen crust’ or ‘cyanobacterial crust’ or ‘algal crust’ or ‘microbial crust’ or ‘microbiotic crust’ or ‘cryptobiotic crust’ or ‘cryptogamic crust’)) AND (TS = (‘soil’)) AND (CU = (‘China’ or ‘Chinese’)).

From the above dataset, we extracted the biocrust occurrence

Fig. 1. Methodological framework for mapping high resolution biocrust distribution in China’s drylands.
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Drought severity and water utilization efficiency.

Precipitation, DI provides a more comprehensive insight into regional aridity index (AI), defined as the ratio of potential evapotranspiration to the region, while a lower value indicates a wetter climate. In contrast to transpiration. A higher value of DI corresponds to a more arid climate of that DI is defined as $\frac{Veg}{NDVI}$, land use/cover (LUC), and altitude. It is worth noting the coldest month [MTCO]), 2 vegetation parameters (vegetation type [Veg] and NDVI), land use/cover product of China from 1990 to 2021 (https://doi.org/10.5066/P9CBDT). Nine bioclimatic variables were obtained from China Scientific Data (http://www.scicb.cn/en/c/00001), which were calculated based on an interpolated dataset of 1-km resolution climate variables across China, averaged over 30 years from 1981 to 2010 (Wei et al., 2022). Vegetation data including vegetation type (Veg) and normalized difference vegetation index (NDVI) were obtained from National Cryosphere Desert Data Center (http://www.nccdc.ac.cn) and NASA EOSDIS Land Processes DAAC (https://lands楔eodasp.eosdis.nasa.gov), respectively. Data on land use/cover (LUC) were taken from Landsat-derived annual land cover product of China from 1990 to 2021 (https://doi.org/10.5281/zenodo.4417810) (Yang and Huang, 2021). Terrain information including altitude, aspect, and slope was obtained from 30-m digital elevation model in Geospatial Data Cloud (https://www.gscloud.cn).

All the environmental data were resampled to 250 × 250 m grid cells using ESRI ArcGIS 10.8 (Redlands, California, US). We next limited the extent of our data layer to China’s drylands through mask extraction. Prior to model calibration, we calculated the Pearson’s correlation coefficient ($r$) among 33 variables as shown in Fig. S3 using ENMTools 1.4.3 (https://purl.oclc.org/enm-tools). To avoid the potential for overfitting due to multicollinearity among environmental variables, we implemented a criterion where one variable was excluded from each highly correlated pair ($|r| > 0.8$) while retaining the variable that was most ecologically relevant for species distribution (Lemke et al., 2011). At last, a total of 21 environmental variables were included in the final model (Table S1), including 11 soil properties (bulk density [BD], silt, sand, coarse fragment content [CF]), total potassium [TK], total potassium density [TKD], total nitrogen [TN], total nitrogen density [TND], total phosphorus [TP], total phosphorus density [TPD], soil type [ST]), 6 bioclimatic variables (maximum temperature [Tmax], minimum temperature [Tmin], drought index [DI], growing degree days of daily temperature $> 0$ °C [GDD0], moisture index [MI], mean temperature of the coldest month [MTCO]), 2 vegetation parameters (vegetation type [Veg] and NDVI), land use/cover (LUC), and altitude. It is worth noting that DI is defined as $1 - \frac{\text{actual evapotranspiration}}{\text{potential evapotranspiration}}$. A higher value of DI corresponds to a more arid climate of the region, while a lower value indicates a wetter climate. The geographic distribution data was randomly divided into 75 % training and 25 % testing datasets. A total of 232 different models (eight beta-multiplier settings × 29 feature class combinations) were built. We then evaluated the performances of the 232 models based on the corrected Akaike Information Criterion (AICC) (Warren and Seifert, 2011). Normally, the models with AICc differences (ΔAICc) between 0 and 2 are considered to be the best candidate models, balancing likelihood and parsimony (Moreno-Amat et al., 2015). In this study, we screened the models with low-omission rate (i.e., $<5$ %) and ΔAICc < 2 as candidate models, and then we selected the model with the lowest ΔAICc value from them.

Based on optimized parameters, we built the species distribution models for biocrusts and their different types (i.e., moss, lichen, and cyanobacterial). The corresponding occurrence points and the above-mentioned 21 environmental variables data were input into each model. The number of repetitions (with replicated Bootstrap runs) was set to 10, and the maximum iterations were set to 1000. After model runs, the obtained mean logistic output was converted to raster using Conversion Tools in ArcGIS 10.8. Subsequently, we reclassified suitability ranging between 0 (unsuitable) and 1 (perfectly suitable) into four levels with the Natural Breaks (Jenks) method. In our case, the break values in the different models were nearly identical; therefore, the four break values were set to 0.1, 0.3, 0.6, and 1.0 uniformly from small to large. Specifically, China’s drylands were divided into high suitability habitat (suitability ≥ 0.6), medium suitability habitat (0.3 < suitability ≤ 0.6), low suitable habitat (0.1 < suitability ≤ 0.3), and unsuitability habitat (suitability ≤ 0.1), for biocrusts and their different types. The proportion and area of potential suitable habitats was then calculated with ArcGIS 10.8. We defined the grid cells with suitability values above the MTSPS (maximum test sensitivity plus specificity) threshold as the area where biocrusts currently exist (Figs. S4–S5) (Liu et al., 2005).

The area under the ROC (receiver operating characteristic) curves, i.e., AUC value, ranging between 0 and 1, was used to evaluate the modeling performance (Figs. S6–S7) (Elith et al., 2008). Normally, the closer the AUC value is to 1, the higher the prediction accuracy of the model. Modeling is considered as failed when the AUC value is < 0.6 (Phillips et al., 2006). The importance of the factors included in the model was evaluated using relative contributions and AUC values (on the data sets retained by the jackknife test). In our case, variables that meet both of the following two criteria at the same time were identified as dominant variables: (1) AUC > 0.75 when used in isolation; and (2) relative contribution rate ranks top five among all variables. Additionally, we analyzed the response curves to explore how predicted suitability responds to changes in the corresponding environmental variables. Based on the above processes, we obtained the range and optimal value of the dominant environmental variables for the area where biocrusts occur.
2.4. Biocrust cover estimation

We estimated the current biocrust cover using the random forest modeling approach in R 4.0.3 with the `randomForest` package (Breiman, 2001). First, we extracted the values of 21 environmental variables (described in Table S1) at each point where biocrust cover value was recorded. These values were combined with the known biocrust cover data to generate a dataset for model training. Next, we used ‘VSURF’ (Variable Selection Using Random Forests) (Genuer et al., 2015) package in R 4.0.3 to evaluate the importance of the variables and determine the best subset of variables for predicting biocrust cover. To train and evaluate the random forest models, we split the dataset into a training set (60 % of the data) and a test set (40 % of the data). We used grid search to identify the optimal hyperparameters including ntree (the number of decision trees), mtry (the number of input variables used at each split of the decision tree), and node size (the number of samples assigned to each leaf node of the decision tree model) for each model. We considered node sizes of 1–5 with three values of 100–1500, and a fixed mtry value set as the square root of the number of input variables during hyperparameter tuning (Hijmans et al., 2005). To ensure the model generalizes well and avoids overfitting to the training data, we used 5-fold cross-validation. Specifically, four folds were used in the training procedure, and the remaining fold was used to validate the performance of the trained model. Using the optimized hyperparameters, we trained the random forest model on the training dataset and evaluated its performance on the test dataset using three metrics: root mean squared error (RMSE), mean absolute error (MAE), and R². The results indicate a good fit, with R² values approaching 0.7 (Table S2). Finally, we used the trained models to predict the biocrust cover in areas that were previously classified as biocrust suitable habitat (with suitability > 0.1).

2.5. Biocrust cover change under future climate scenarios

To determine the impact of climate change on biocrust cover, we estimated and compared the biocrust cover for historical reference period (1970–2000 average) and the year 2050 (2041–2060 average). We utilized the three representative concentration pathways (RCPs) from the Fifth Assessment Report of the IPCC. These RCPs (RCP2.6, 4.5, and 8.5) represent different levels of radiative forcing (+2.6, +4.5, and +8.5 W m⁻²) during the year 2100 and corresponding mean CO₂ concentrations (490, 630, and 1313 ppm) projected by the Coupled Model Inter-comparison Project (CMIP5) (IPCC, 2013). For each RCP, we considered three General Circulation Models: the Beijing Climate Center Climate System Model (BCC-CSM1-1), the Community Climate System Model (CCSM4), and the Hadley Global Environment Model 2 (HadGEM2-AO). We obtained 19 bioclimatic variables at a spatial resolution of 30 s from the WorldClim database (http://worldclim.org) (Probst et al., 2019). As described in the Materials and methods section ‘Selection of environmental factors’, we performed a correlation analysis and included 7 bioclimatic variables (|r| < 0.8) in our model. These variables consist of mean diurnal range (MDR), mean temperature of warmest quarter (MTWQ), mean temperature of coldest quarter (MTCQ), precipitation seasonality (PS), precipitation of driest quarter (PDQ), precipitation of warmest quarter (PWQ), and precipitation of coldest quarter (PCQ). Altitude and 11 soil properties were assumed to be constant over that time. Based on recent research, it is expected that there will be limited alterations to the land use patterns in arid regions over the next few decades (Rodriguez-Caballero et al., 2018). Thus, land use/cover and vegetation changes were not considered in this section. All input layers were resampled to 250 × 250 m cells, and the study area was limited to China’s drylands. Using the suitability values derived from MaxEnt modeling (described in the Materials and methods section ‘Biocrust distribution prediction’), we determined the mean suitability and identified the biocrust suitable habitat (with suitability > 0.1) for both the historical reference period and each RCP scenario. Future biocrust cover was determined by taking the average of the results obtained by three general circulation models for each RCP scenario using the random forest modeling approach (described in the Materials and methods section ‘Biocrust cover estimation’). The input predictors and model performances were shown in Table S3.

3. Results

3.1. Biocrust cover and distribution in China’s drylands

As presented in Fig. 2a, 24.0 % (9.4 × 10⁶ km²) of the China’s dryland is potentially suitable for biocrust (any type) colonization. The potentially suitable habitat for moss-, lichen-, and cyanobacterial-dominated biocrusts accounts for 16%–21% of the drylands, amounting to an area of approximately 6.1 × 10⁵–8.3 × 10⁵ km² (Fig. 2b–d). Moreover, we estimated that the current cover of biocrust encompasses 5.4 × 10⁵ km², accounting for 13.9 % of China’s drylands (Fig. 3a and Table 1). For moss, lichen and cyanobacterial biocrusts, current cover area is 2.2 × 10⁵–4.2 × 10⁵ km², accounting for 5.7%–10.7% of China’s drylands (Fig. 2b–d and Table 1). A strong positive correlation (r ≥ 0.77) exists between biocrust cover and habitat suitability (per pixel), as shown in Table S5.

Biocrust occurrences are mostly distributed in the Loess Plateau, the Gurbantunggut Desert, the Tengger Desert, and the Mu Us Sandy Land. In these regions, suitable habitat encompasses 53.5 %, 47.6 %, 21.3 %, and 41.7 %, respectively, corresponding to 3.4, 2.3, 0.9, and 1.8 × 10⁶ km² in area (Fig. S8). Currently, biocrusts in the Gurbantunggut Desert cover an area of 1.3 × 10⁶ km², or 27.1 % of that region, and the areas with higher biocrust cover are mainly distributed in the central and southern parts (Fig. S9a and Table S4). The Loess Plateau has a biocrust cover area of 2.1 × 10⁶ km², accounting for 33.0 % of the region, and the areas with higher biocrust cover are primarily concentrated in the northwestern portion (Fig. S9b and Table S4). In the Tengger Desert, biocrusts cover over 14.5 % of the region and 6.2 × 10⁵ km² area. The areas with higher biocrust cover are primarily located in the western and southeastern margins of the desert (Fig. S9c and Table S4). In the Mu Us Sandy Land, biocrusts mostly cover the eastern part, with some scattered distribution in the southwest and southeast of the region (Fig. S9d). In this region, the total current range of biocrusts occupies 1.1 × 10⁶ km², or 26.4 % of the total region (Table S4).

3.2. Environmental factors determining biocrust distribution and cover

Five environmental factors, including soil type, total nitrogen, drought index, coarse fragment content, and altitude, in decreasing order of importance, influence the distribution of biocrusts (Fig. S10 and Table S6). According to the response curves in Fig. 4 and Table S7, lower contents of gravel (0.04 %–22.34 %) and total nitrogen (0.01–2.11 g kg⁻¹) in soil are beneficial for biocrust growth, and their optimum contents are 0.58 % and 0.37 g kg⁻¹, respectively. Moreover, biocrusts are distributed in areas with a drought index of 0.28–0.76 (optimum = 0.54) and altitude of 208–4524 m (optimum = 469 m). A variety of soil types, classified according to the first level FAO soil classes (Jahn et al., 2006), including anthrosols, calcisols, cambisols, fluvisols, gleysoils, gypsisols, kastanozems, regosols, and solonchaks are suitable for biocrust growth, but arenosols are the most favorable type of soil. Soil type, drought index, and total nitrogen are three common factors which affect the occurrence of all types of biocrusts. For example, the suitability of biocrusts initially increases and then decreases as the drought index and total nitrogen levels increase, regardless of biocrust type. However, the environmental factors are not always identical for the different types of biocrusts, and some biocrust types respond differently than others to the same key environmental factor. For example, the most favorable soil types are calcisols for moss-dominated biocrusts, gypsisols for lichen-dominated biocrusts, and arenosols for cyanobacterial-dominated biocrusts. Furthermore, it seems that lichen
biocrusts are more suited to growing in arid areas (optimum drought index = 0.74) than other types of biocrusts (Fig. S11 and Table S7). In terms of biocrust cover, climate factors generally have a greater impact than other environmental factors. The predictors of biocrust cover ranked in order of importance are drought index, growing degree days of daily temperature $>0^\circ C$, mean temperature of the coldest month, total nitrogen, altitude, and soil type. Notably, the drought index is a common factor that affects the cover of all types of biocrusts (Table S8).

Table 1
Predicted area and cover of all biocrusts, moss biocrusts, lichen biocrusts, and cyanobacterial biocrusts in China’s drylands.

<table>
<thead>
<tr>
<th>Biocrust type</th>
<th>Area ($\times 10^5$ km$^2$)</th>
<th>Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All biocrusts</td>
<td>5.4</td>
<td>13.9</td>
</tr>
<tr>
<td>Moss biocrusts</td>
<td>3.1</td>
<td>7.8</td>
</tr>
<tr>
<td>Lichen biocrusts</td>
<td>2.2</td>
<td>5.7</td>
</tr>
<tr>
<td>Cyanobacterial biocrusts</td>
<td>4.2</td>
<td>10.7</td>
</tr>
</tbody>
</table>
3.3. Responses of biocrust cover to changing climate

As compared to the historical reference period (1970–2000 average), the synergistic contributions of climate change according to RCP2.6, 4.5, and 8.5 by the year 2050 are expected to cause a decrease in the area potentially suitable for biocrust distribution by $0.4 \times 10^5 - 1.0 \times 10^5 \text{ km}^2$ and a decrease in the biocrust covered area by $0.3 \times 10^5 - 0.5 \times 10^5 \text{ km}^2$ (Table S9), corresponding to relative reductions of 4.0 %–9.9 % and 5.5 %–9.0 %, respectively (Fig. 5 and Table 2). The impact of climate change on biocrust cover is expected to exhibit variation based on the specific types of biocrusts present. For example, lichen biocrusts are highly susceptible to the impacts of climate change, with projected reductions in their coverage ranging from 1.8 % to 19.0 %. Moss biocrusts are expected to experience a relative reduction in coverage ranging from 0.3 %

![Fig. 4. Impact of the dominant environmental variables on biocrust habitat suitability. Suitability varies between 0 (unsuitable) and 1 (perfectly suitable).](image)

![Fig. 5. Cover change of biocrusts in China’s drylands by the year 2050 expected under future climate conditions. Climate change scenarios are calculated based on the three representative concentration pathways: RCP2.6 (a), RCP4.5 (b), and RCP8.5 (c). Green color indicates a decrease and red color indicates an increase in biocrust cover.](image)
to 6.4 %. In contrast, cyanobacterial biocrusts are comparatively less adversely affected by climate change, with a decrease of <0.6 %. It is noteworthy that the cover of cyanobacterial biocrusts is expected to increase by 5.1 % and 0.3 % under RCP4.5 and RCP8.5 scenarios, respectively (Fig. 6 and Table 2). Moreover, our results indicate that the cover of moss and lichen biocrusts may experience the most significant decline in the RCP4.5 scenario. Biocrust cover loss is mainly driven by a combination of the increased temperature and precipitation during both warm and cold seasons (Table S10).

4. Discussion

4.1. Estimated biocrust distribution from regional- to global-scale and our improvement

Despite the great importance of biocrusts and their functions in dryland ecosystems, studies of large-scale biocrust distribution are scarce. In theory, biocrust distribution can be mapped at regional and landscape scales based on remote sensing information combined with ground surveys, but the heterogeneous and mixed structure of dryland ecosystems poses a challenge for such mapping efforts using remotely-sensed imagery (Smith et al., 2019). Therefore, spatial prediction modeling becomes an attractive method for mapping biocrust cover over large spatial scales. In this study, we utilized the MaxEnt and random forest modeling approaches to develop the first version of high-resolution biocrust distribution grids (250 × 250 m) for China’s drylands. We believe that our estimates of biocrust distribution and cover can help fill significant gaps in the data on biocrusts in China. Additionally, our study serves as a vital supplement to the existing limited regional map of biocrusts (Table S11). However, further research and comparisons with alternative methods would be required to validate the accuracy and robustness of the findings.

Actually, a recent study applied MaxEnt and multiple regression models at the global scale and estimated that biocrusts currently cover around 12 % (17.9 million km\(^2\)) of terrestrial surface on Earth, or 30 % of global drylands (Rodriguez-Caballero et al., 2018). For various reasons, it was still valuable to produce a regional scale model for China. However, the number of biocrust occurrence points collected from the literature for China is only 76 in the global model (Rodriguez-Caballero et al., 2018), indicating a relatively small sample size for this large nation. Many available locations reported in non-English literature (especially Chinese) have not been included in previous modeling. This oversight possibly introduced inaccuracies and biases into the model’s predictions, as it failed to capture the full extent of biocrust occurrences in China. We were also able to include more environmental predictors, including a greater number of soil properties, and map our outputs at a much finer resolution more appropriate for regional rather than global uses because there is a wider variety of high quality and high-resolution data available at regional (e.g., national) scales than at global scales. Finally, MaxEnt models are spatial-scale sensitive and the model

<table>
<thead>
<tr>
<th>Biocrust type</th>
<th>Historical reference period</th>
<th>RCP2.6</th>
<th>RCP4.5</th>
<th>RCP8.5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area  (10(^5) km(^2))</td>
<td>Cover  (%)</td>
<td>Area  (10(^5) km(^2))</td>
<td>Cover  (%)</td>
</tr>
<tr>
<td>All biocrusts</td>
<td>5.9</td>
<td>15</td>
<td>5.6</td>
<td>14.2</td>
</tr>
<tr>
<td>Moss biocrusts</td>
<td>3.6</td>
<td>9.2</td>
<td>3.5</td>
<td>8.9</td>
</tr>
<tr>
<td>Lichen biocrusts</td>
<td>3.0</td>
<td>7.7</td>
<td>3.0</td>
<td>7.6</td>
</tr>
<tr>
<td>Cyanobacterial biocrusts</td>
<td>4.2</td>
<td>10.7</td>
<td>4.2</td>
<td>10.6</td>
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Fig. 6. Cover change of moss- (a, d, g), lichen- (b, e, h), and cyanobacterial- (c, f, i) dominated biocrusts in China’s drylands by the year 2050 expected under future climate conditions. Climate change scenarios are calculated based on the three representative concentration pathways: RCP2.6 (a-c), RCP4.5 (d-f), and RCP8.5 (g-i). Green color indicates a decrease and red color indicates an increase in biocrust cover.
performance can vary depending on the size of the study area (Connor et al., 2019). Upscaling or downscaling the model’s output may result in misleading results, thus it is not advisable to extract a regional biocrust map from a global-scale map and therefore a regional model for China’s drylands is necessary. In our study, we collected 379 occurrence locations of biocrusts in China’s drylands from both English and Chinese journals. Each occurrence location was meticulously inspected and the non-biocrust locations were removed according to the explanation of biocrust habitat and functional characteristics (Weber et al., 2022). Additionally, we collected the most comprehensive set of environmental variables (33 in total) compared to similar efforts with a much higher resolution ($250 \times 250$ m) than typically used.

Our model suggests that biocrusts occupy 13.9 % of China’s drylands. It is noteworthy that our estimation of biocrust cover in China’s drylands is lower than the corresponding estimate extracted from the global biocrust cover map (Rodriguez-Caballero et al., 2018). One disparity is evident when comparing the two biocrust maps: our map indicates that there is almost no biocrusts in the Taklimakan Desert (the world’s second largest mobile desert), while the global map shows widespread biocrust cover throughout the desert. The discrepancy could arise from differences in input data and their spatial resolution between the two models. For example, the differences in the number of biocrust locations, as well as the differences in the number, source, and resolution of environmental data, can all introduce high variability into the modeling results, thereby impacting modeling performance. Additionally, the differences in modeling techniques, such as algorithm choices and parameter assignments, could also affect modeling results. Thus, developing additional regional- or national-scale models would be needed to better understand if global-scale models are systematically overestimating biocrust distribution and cover. Crucially, both models indicate that biocrusts are a major part of Chinese dryland ecosystems.

4.2. Regional variation of biocrust cover in China’s drylands and the cause analysis

In this study, we separately mapped biocrust distribution in four typical regions of China’s drylands, and the results are reasonable and agree well with our experiences. For instance, the Loess Plateau has the highest biocrust cover (33.0 %), because the implementation of the Grain-for-Green Program (GFGP) and its elimination of many cropping and grazing practices resulted in the quick colonization of biocrusts in this region (Bao et al., 2020). However, there is almost no biocrust cover in the southeastern Loess Plateau where the land use is mainly constituted by cropland. As the largest fixed and semi-fixed desert in China, the Gurbantunggut Desert is characterized by a predominant cover of lichen-dominated biocrusts (Zhang et al., 2007). In this region, our estimation of biocrust cover is 27.1 %, which is consistent with previous estimates of ~30 % based on remote sensing (Wang et al., 2022; Zhang et al., 2007). We obtained a much higher biocrust cover (26.4 %) in the Mu Us Sandy Land in contrast to previous estimation (<7 %) based on remote sensing (Wang et al., 2022). On the one hand, the increase in vegetation cover resulting from the region’s increased humidity and ecological protection in the area (Gao et al., 2022) may lead to underestimation of biocrust cover by remote sensing. On the other hand, extensive human activities have severely impacted the surface of the Mu Us Sandy Land and fragmented the distribution of biocrusts (Wang et al., 2022). These impacts are difficult to incorporate into the model, which may result in an overestimation of the biocrust cover by spatial prediction modeling. In the Tengger Desert, the overall cover of biocrusts was only 14.5 %, and perhaps the active dunes and frequent sand moving activities are not able to provide a suitable microhabitat for biocrust colonization; indeed most biocrust data in that region originates from dunes that have been stabilized due to human interventions.

4.3. Responses of biocrust distribution to environmental factors and climate change

Among the considered environmental factors, we showed that soil type is the most important factor affecting biocrust distribution. It has been reported that the dominant species of biocrusts is mostly affected by soil type (Bowker et al., 2006). For example, gypsum-rich soil is usually covered with more lichen crusts (Zedda et al., 2011), while the biocrusts growing in calcareous soil are usually dominated by moss (Büdel, 2001; Zedda et al., 2011). Moreover, we also found that the suitable habitats for biocrusts are usually distributed in areas with low content of coarse fragments and total nitrogen, perhaps because that the low coarse fragment content indicates a well-structured soil pore system (Lai et al., 2022) and low level of nitrogen means less vascular plant cover (Büdel, 2001); both could be beneficial for biocrust development. Furthermore, climate (e.g., precipitation, temperature, and evapotranspiration) has been considered as a critical driver globally or regionally affecting biocrust distribution (Bellnap et al., 2004; Bellnap et al., 2007; Kidron et al., 2000; Zedda et al., 2011), and lower mean temperature and amounts of precipitation present a favorable environment for biocrust prevalence (Rodriguez-Caballero et al., 2018). However, in this study we found that the suitability of biocrust habitats sharply dropped once the drought index exceeded 0.74, because extreme drought tends to reduce soil water availability and impact the photosynthesis and respiration, nutrient absorption, and community structure of biocrusts (Bellnap et al., 2007). In some dry sub-humid regions with lower DI, the amount of annual precipitation (400–600 mm) is possible to support some specific forest or shrubland ecosystems, potentially limiting the ecological niche available for biocrusts. Even though, the vascular plants in these regions are mostly sparse and distributed in patches due to the insufficient water availability, and thus the open spaces among the vascular plants are available for biocrust colonization and development (Weber et al., 2022). Lastly, our results showed that the most favorable habitat of biocrusts has an altitude of ~500 m. This specific altitude should be further studied and discussed, because it may have resulted from the clustered distribution of the sampling points which could be a source of bias.

The simulation results indicate that biocrusts are expected to be greatly influenced by climate change. The elevated temperature can potentially intensify evaporation and reduce dew formation (Maestre et al., 2013; Ouyang and Hu, 2017), posing a detrimental impact on the growth of biocrust. Furthermore, augmented precipitation may disrupt the carbon balance of biocrust, leading to the death of biocrust organisms and consequent decline in their coverage (Reed et al., 2012). We believe that further research is essential to validate these mechanisms and explore the influence of additional climatic factors that were not explicitly accounted for in the current model, such as non-rainfall water inputs like dew and dripping fog condensation. These forms of water substantially contribute to the overall water availability in arid and semi-arid environments, thus possibly playing a critical role in sustaining biocrust communities (Cheng et al., 2022). For example, under extreme conditions (e.g., prolonged dry spells) non-rainfall water deposition may determine the survival or demise of biocrusts (Ouyang and Hu, 2017).

4.4. Limitations and uncertainties

Our study provides valuable insights into the distribution of biocrusts in drylands. However, we must acknowledge that some uncertainties may exist in our estimation. One such limitation is that the occurrence locations were not verified in the field, which may cause biased model training and ultimate simulation. Moreover, the specific types of biocrusts were not identified in some locations, which possibly leads to an underestimation of their cover. We expect that the increasing number of biocrust occurrence locations and the filling of sampling gaps will partly improve or even completely fix such problems in the future.
During our data processing, one critical step was to resample all environmental data to a 250 × 250 m grid. Although this step provided a uniform spatial resolution, it is essential to acknowledge that resampling cannot enhance data quality by generating fine-scale details; instead of that, it may lead to data smoothing and the potential loss of fine-scale variability. Therefore, there may still be some limitations in terms of the precision of the environmental data in our modeling, and this could impact the accuracy of the simulation results. Actually, such a problem exists in most spatial modeling and estimations, and we all should be aware of it and take care of it when handling the results.

Additionally, the selected environmental factors and their dataset quality, as well as the ‘scale-dependence’ of the predicted probabilities in the MaxEnt model (Remer and Warton, 2013), may also affect the reliability of our estimation. For example, our model included a range of environmental variables that influence biocrust distribution, but some other factors (such as non-rainfall water deposition as we explained above) may also be important but were not considered due to the absence of available data. The inclusion of additional comprehensive datasets in our model could possibly enhance the reliability of our prediction.

It is noteworthy that we utilized a distinct bioclimatic dataset to evaluate the specific impacts of climate change on biocrusts, which differs from the dataset employed in estimating their current distribution and cover. As a consequence, the changes in biocrust cover under various future climate scenarios are presented as values relative to a historical reference period, rather than accurately reflecting the magnitude of change compared to the current predicted outcomes. Moreover, while projected future changes in land use and vegetation within arid regions are expected to be relatively minor, not considering their potential influence on biocrusts may introduce a degree of uncertainty or bias into our assessments.

4.5. Implications of biocrust distribution for dryland preservation and management

Biocrusts are key players in biogeochemical cycling, with their role in nitrogen fixation being essential for the sequestration of carbon by plants (Elbert et al., 2012). Biocrusts can also increase soil organic matter and carbon stocks (Dou et al., 2022), enhancing soil fertility and productivity of dryland ecosystems. Combining the biocrust distribution data with carbon and nitrogen flux observation data, we can better understand the impact of biocrusts on regional and global carbon and nitrogen cycles, which is essential for mitigating climate change. In addition to their biogeochemical functions, biocrusts play a vital role in reducing soil erosion (Gao et al., 2017) and controlling dust cycling (Rodriguez-Caballero et al., 2022). By identifying the areas where biocrusts are present and how much cover they have, we can estimate the potential reduction in soil erosion and aeolian dust achieved through biocrust cover. The map can be hopefully combined with soil erosion models such as the Universal Soil Loss Equation (USLE) to predict soil erosion rates more accurately (Bowker et al., 2008). With climate change, the decline in biocrust cover has the potential to negatively affect human and ecosystem well-being. It is of great importance to integrate biocrusts into Earth system models to comprehensively capture their significant effects on global or regional-scale processes.

Understanding the spatial distribution patterns and abundance of biocrusts in large scale allows us to identify areas where biocrusts are particularly vulnerable or where they play a crucial role in ecosystem functions. Consequently, it enables us to develop targeted strategies for their preservation and restoration, thereby enhancing their ecological functions. Moreover, the biocrust distribution map can inform land management practices, as it helps in identifying areas where disturbances, such as off-road vehicle use, grazing or infrastructure development, may have detrimental effects on these fragile communities. With this information, we can develop effective approaches that mitigate potential damage and promote sustainable land use practices, ensuring the long-term viability of biocrusts in dryland ecosystems. We hope that our study contributes to the preservation of these important organisms and the ecosystem services they provide, and promotes sustainable management practices in drylands.

5. Conclusions

This study developed the first version of high resolution (250 × 250 m) map of biocrust distribution in China’s drylands through spatial prediction modeling, based on available occurrences of biocrusts and high-resolution soil and environmental data. Our findings show that biocrusts currently occupy 13.9 % of China’s drylands (5.7 % of the country’s total area.). Additionally, we found that moss-, lichen-, and cyanobacterial-dominated biocrusts each cover 5.7 % to 10.7 % of the region. Most of the China’s biocrusts are situated in the northwestern Loess Plateau, central and southern areas of the Gurbantunggut Desert, eastern Mu Us Sandy Land, and western and southeastern margins of the Tengger Desert. By 2050, climate change is projected to result in a decline of biocrust cover by approximately 5.5 % to 9.0 %. Lichen biocrusts are particularly vulnerable to the impacts of climate change, with estimated cover reductions reaching up to 19.0 %. The loss of biocrust cover is primarily attributed to the combined effects of rising temperatures and increasing precipitation. Our estimate of biocrust distribution and cover fills significant gaps in the available data on biocrusts in China. This comprehensive dataset can be widely applied to support dryland ecosystem management and conservation efforts, biogeochemical and hydrological modeling, soil erosion prevention, and climate change mitigation strategies.

CRediT authorship contribution statement

Dexun Qiu: Data collection, Methodology, Writing – original draft. Matthew A. Bowker: Critical review of the manuscript. Bo Xiao: Conceptualization, Data collection, Methodology, Writing – review & editing, Supervision, Funding acquisition. Yunge Zhao: Review and editing of the final manuscript. Xiaobing Zhou: Review and editing of the final manuscript. Xinrong Li: Review and editing of the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used to build Maxent model and random forest model in this study are listed in the Supplementary information. The datasets generated during the current study are available from the corresponding authors upon request.

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Appendix A. Supplementary data

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References


