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Determination of the representative elementary area (REA) of biocrusts: A case study from the Hilly Loess Plateau region, China

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ABSTRACT

Biological soil crusts (biocrusts) are mixed communities of cyanobacteria, lichens and mosses in different ratios, contributing to important ecological functions in arid and semiarid regions worldwide. Biocrusts are spatially variable, and the variability in biocrust composition and coverage is scale-dependent. The following question can then be asked: What is the appropriate spatial scale for observing ecological functions? Without clarifying this issue, we cannot fully understand the ecological functions of biocrusts. The key to answering this question is to determine a threshold area, or representative elementary area (REA). Accordingly, we analyzed red–green–blue (RGB) images of 90 biocrust plots (2.0 m × 2.0 m) from nine revegetated grasslands in the Hilly Loess Plateau region of China. The variability in biocrust composition and coverage across the plot sizes was studied by gradually expanding the plot size from 0.01 m^2 to 4.00 m^2. The results showed that as the plot sizes increased from 0.01 m^2 to 4.00 m^2, the number of biocrust types logarithmically increased. Biocrust patches of a particular type (such as moss, cyanobacteria or lichen) were often characteristic of a plot size of 0.01 m^2, whereas plot sizes larger than 0.25 m^2 supported mixed biocrusts of multiple patch types. The variability in coverage of mixed biocrusts logarithmically decreased with increasing plot sizes. The coverage of mixed biocrusts maintained an approximately constant value after a certain critical plot size was reached (1.00 m^2 in this study). Our data indicated that REAs of mixed biocrusts exist at the slope scale. The REAs of mixed biocrusts were 0.5–1.0 m^2, 1.5–2.5 m^2 and 3.0–3.8 m^2, with alpha (α) values of 0.1, 0.05 and 0.01, respectively. The size of the REAs on the north-facing slope was larger than that on the south-facing slope, and the patch density of biocrusts had an important influence on the REAs. The results of this study could provide a method for determining the REAs of mixed biocrusts and guide surveys and experimental layouts.

1. Introduction

Biological soil crusts (biocrusts) are complex communities of microscopic (cyanobacteria, algae, fungi, and bacteria) and macroscopic (lichens and mosses) organisms that occur directly on or within the very top few centimeters of the soil surface (Belnap et al., 2016). Being ubiquitous living cover types in arid and semiarid regions, biocrusts are often distributed in the open spaces between vascular plants, covering 60%–70% of the soil surface and playing key ecological functional roles, such as improving soil nutrients, regulating soil water infiltration and availability, increasing soil stability and thus reducing erosion (Belnap et al., 2009; Bowker et al., 2008; Eldridge et al., 2000; Zhao and Xu, 2013). Exploring the ecological functions of biocrusts is a major topic in arid and semiarid regions, especially since the beginning of this century.

Many related studies have indicated that the ecological functions of biocrusts depend on their community compositions and vary dramatically among different compositions (Chamizo et al., 2012; Pietrasiak et al., 2013; Zhao et al., 2014). Generally, lichen- and moss-dominated

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crusts (lichen/moss crust hereafter) show a stronger effect than cyanobacterial crusts on soil stability and nitrogen and carbon input (Pietrasiak et al., 2013). Several studies have demonstrated that the infiltration rate of biocrusts is often different among different biocrustal types; specifically, moss crust shows a significantly higher infiltration rate than that of cyanobacterial crust (Belnap et al., 2012; Chamizo et al., 2012). In addition, Zhao et al. (2014) found that the resistance of moss crust to raindrop erosivity is much higher than that of cyanobacterial crust. While cyanobacterial crust can reduce soil erosion by 92%, moss crust completely prevents soil loss (Zhao and Xu, 2013). Those studies mentioned above indicated that the ecological functions of biocrusts were composition dependent.

However, biocrusts are usually mixed assemblages of cyanobacterial, lichen and moss species in varying proportions under field conditions (Büdel et al., 2009). Bowker et al. (2006) demonstrated that the driving factors for the composition of biocrusts vary with spatial scales, which also indicates that the community compositions of biocrusts change dramatically across spatial scales. In general, biocrust is usually composed of a particular organism, such as cyanobacteria, moss or lichen (termed pure biocrust in this study) at the centimeter or smaller scale (Grondin and Johansen, 1993; Wheeler et al., 1993). In contrast, biocrust becomes a mixed community of cyanobacteria, mosses and/or lichens (termed mixed biocrusts in this study) and is not evenly distributed on soil surfaces at the decimeter scale (Bowker et al., 2006). At the meter scale, the mixed biocrusts are patchily distributed in the interspaces among vascular plants (Bowker et al., 2006; Wang et al., 2016). In other words, biocrusts are a mixed community composed of multiple types on the soil surface (Bowker et al., 2016). Thus, their ecological functions should be a combination of multiple types of biocrust (Bowker et al., 2014; Chamizo et al., 2016; Rodríguez-Caballero et al., 2019). In addition, it is important to assess the ecological functions of mixed biocrusts to understand the contribution of biocrusts to the ecosystem.

In many scientific studies, such as ecological studies, spatial scale is a critical influencing factor at all study stages, including sampling, field recording, site description and results analysis (Critchley and Poulton, 1998). Mixed biocrusts are an assemblage of different biocrust types, such as cyanobacteria, moss and lichen in various ratios, and some ecological functions, such as infiltration, are the synthesis of the function of each particular biocrust type. It is difficult to estimate the ecological functions of mixed biocrusts by measuring a particular type because most of the ecological functions of biocrusts depend not only on the type but also on the coverage. Therefore, selecting a suitable sampling area or plot size is a key element in determining the ecological functions of mixed biocrusts. Several studies have reported that the sampling area (also known as the minimum area or optimal plot size in the literature) ranges from 0.01 m^2 to 4.00 m^2 in bryophyte and lichen communities based on the authors' experience (Barkman, 1989; Berg et al., 2016; Bricaud and Roux, 2000; Ellenberg and Mueller-Dombois, 1974). However, the selected areas were mostly based on empirical values and were primarily used to investigate the community composition of those organisms. Then, two questions were raised: (1) Can the area represent the spatial distribution characteristics of mixed biocrusts for a given study site? (2) Is the area suitable for determining the ecological functions of mixed biocrusts? The uncertainty in the answers hinders the study of the ecological functions of mixed biocrusts.

Currently, many studies on the ecological functions of biocrusts have mainly focused on pure biocrust. However, the effect of biocrusts on soil and water loss processes is one of its most important ecological functions and is mostly related to mixed biocrusts in arid and semiarid regions (Eldridge et al., 2020). Soil and water loss processes occur at a wide range of scales, and the nature of the process is scale-dependent (Blöschl and Sivapalan, 1995; Chen et al., 2016). Thus, determination of an appropriate plot size that can represent the effectiveness of mixed biocrusts on soil and water loss is a key step in assessing the effect of biocrusts on soil and water loss at the slope scale.

A representative elementary area (REA) was first used by Wood et al. (1988) to explore the hydrological responses to the scale effect at the catchment scale, and the study pointed out that an REA exists in the context of catchment hydrological responses. At present, the REA is widely used to characterize land surface properties (such as topography, soil hydraulic properties, and vegetation spatial patterns) relevant to soil and water loss processes (Chen et al., 2016). Generally, the REA characterizes a threshold area in which the statistical distribution of surface properties is similar to the entire surface that they represent (Chen et al., 2016). In addition, a few studies defined the smallest discernible area that can represent the statistical distribution pattern of pores in the porous material as the REA (Cosenza et al., 2019; VandenBygaart and Protz, 1999). The definition and use of the REA in previous studies provide ideas and experience for investigating the ecological functions of mixed biocrusts at a larger scale. Nevertheless, there are still some questions, such as whether there is an REA for mixed biocrusts. The method for determining the REA of mixed biocrusts and the factors governing the REA should be investigated.

Generally, sampling methods for multiple scales are based on nested sampling designs, the counting box method and the gliding box method (Cheng, 1999; Grau et al., 2006; Hirave et al., 2021). One of the advantages of using the gliding box method is large sample size which usually leads to better statistical results (Grau et al., 2006). Because the gliding box method essentially constructs samples by gliding a box of a certain line size over the grid map in all possible directions, an "upscaling" partitioning process begins with a minimum line size box, which is steadily enlarged to a specific size smaller than the map size (Cheng, 1999). This method can clearly display the spatial variability of mosaic patterns, and is effectively applied for determining the REA (Grau et al., 2006). Therefore, in the current study, we adopted this approach and probed the spatial distribution characteristics of mixed biocrusts across multiple plot sizes. We hypothesized that the REA was applicable and that the gliding box method could be used to determine the REA according to the variability in the spatial distribution characteristics of mixed biocrusts.

Biocrusts have occurred extensively on the open soil surface of revegetated grasslands since the implementation of the "Grain for Green" project, which aimed to reduce soil and water loss by transforming croplands on steep slopes (≥25°) into grasslands and woodlands in the Hilly Loess Plateau region, China. The average coverage of biocrusts in the revegetated grasslands in this region can reach 60%–70% (Zhao and Xu, 2013). To date, many studies have been conducted on the ecological functions of pure biocrust (Gao et al., 2020; Zhao and Xu, 2013). However, the ecological functions of mixed biocrusts are still unclear. Determining the REA of mixed biocrusts is important in such studies. Therefore, three aims were addressed in this study: (1) to quantitatively determine the spatial distribution characteristics of mixed biocrusts; (2) to assess whether there is an REA for mixed biocrusts and the size of the REA; and (3) to determine the governing factors of the REA of mixed biocrusts if such an REA exists. This study may provide important guidance for the surveys and experimental layouts of mixed biocrusts.

2. Materials and methods

2.1. Study region

This study was conducted in Wuqi County (36°53′32″N, 108°13′26″E), Shaanxi Province, which is located in the typical Hilly Loess Plateau region of China, where the "Grain for Green" project was implemented at the end of the 1990s (Fig. 1A). The topography varies locally in a complex of loessal hills and gullies. The approximate mean altitude ranges from 1233 m to 1809 m. The annual precipitation of this region is approximately 480 mm, 60%–70% of which falls in the summer monsoon period (from July to September). The potential annual evaporation is 2300 mm, which is an average of five times higher than the

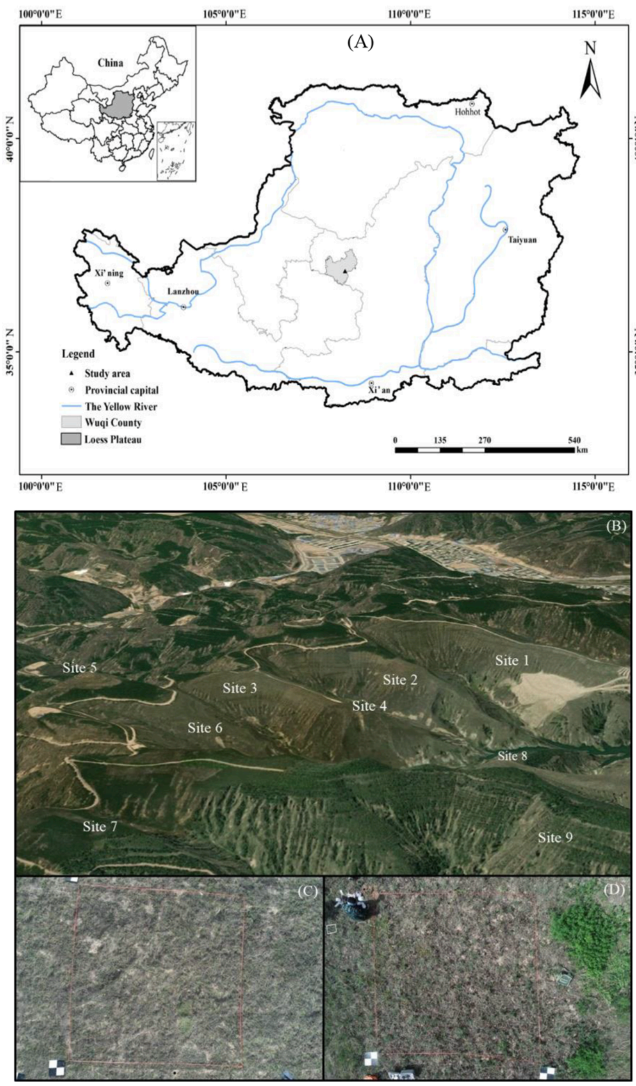

Fig. 1. Schematic diagram of (A) the study area, (B) research sites, (C) the picture of the sunny slope (site 1) and (D) the picture of the shady slope (site 7).

precipitation amount. The mean annual air temperature is approximately 7.8 °C. The region experiences an annual average sunshine duration of 2400 h (Fu et al., 2011). The soil in this region is predominantly typical loessal soil.

In this region, the common herb species are *Artemisia gmelinii*, *Lespedeza davurica*, *Stipa bungeana*, *Potentilla reptans*, *Artemisia kanashiroi*, and *Poa sphondylodes* (Feng et al., 2012). The biocrust community is dominated by cyanobacteria and mosses, and their coverage ranges from 40% to 70% (Bao et al., 2020). On south-facing slopes, the biocrust is characterized by a high density of cyanobacteria and a low density of moss, whereas on north-facing slopes, the crust is characterized by a high-density cover of moss and low-density cover of cyanobacteria. The common cyanobacterial species include *Phormidium calciola*, *Phormidium tenue* and *Nostoc* spp. (Yang et al., 2013). *Didymodon tectorum*, *Bryum argenteum* and *Didymodon vinealis* are usually the dominant moss species (Zhao et al., 2014). Lichens are mostly found ten years after cropland abandonment, and the coverage of lichens in the study area is usually less than 10% (Wang et al., 2016).

2.2. Field survey

From October 10 to 29, 2018, we conducted a large-scale field investigation on the Loess Plateau in China to clarify the distribution characteristics of biocrusts in the whole Loess Plateau and to ensure the representativeness of the sampling sites. Then, we selected nine revegetated grasslands with biocrusts developed over 20 years as the research sites (Fig. 1B). Bowker et al. (2006) distinguished different microaspect according to the orientation of the site, i.e., north–northwest (NNW) to south-south-east (SSE). Thus, we had selected three slope aspects. The aspects of the sites were sunny or south-facing slope (SSE, including sites 1, 2 and 9) (Fig. 1C), semishady slope (ENE or WSW, including sites 3, 5 and 6) and shady or north-facing slope (NNW, including sites 4, 7 and 8) (Fig. 1D). We expressed the slope aspects as degrees from North: 0–180°. Thus, the sunny slope, semishady slope and shady slope were expressed as degrees from North 0–45°, North 45–135° and North 135–180°, respectively. The slope gradients ranged from 15° to 25°. Three replicates were set for each slope aspect in this study. The distance between each site was over one kilometer. The percent coverage of vascular plants was estimated by multiple people (Wang et al., 2017), and the biocrustal coverage was measured by 25 cm × 25 cm quadrat (Belnap et al., 2001). The surface composition of the research sites is presented in Table 1.

Nine 10 cm × 10 cm soil samples were randomly collected from each site, and we avoided edge effects on the samples to the greatest extent possible. The samples of the biocrust layer were first collected using a spade, and the thickness of the biocrusts ranged from 4 mm to 10 mm. Then, we measured to depths of 2 cm and 3 cm with a ruler to collect samples 0–2 cm and 2–5 cm beneath the biocrust layer. The nine samples from the same depth were thoroughly mixed to obtain one composite sample. After collection, the samples were immediately transported to the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in Yangling city, Shaanxi Province. All samples were air dried for the measurement of soil physicochemical properties. The soil properties of the research sites are shown in Table 2.

The community characteristics of biocrusts were investigated using a quadrat of 2.0 m × 2.0 m (4.00 m^2) to ensure that their composition and coverage could be adequately characterized. Ten sampling plots with a size of 2.0 m × 2.0 m were arranged along an "S" shape on each slope, and the sampling points were established every 5 m. The aboveground vegetation was removed from the sampling plots. The sampling plot was divided into sixteen quadrats with a size of 0.5 m × 0.5 m as the unit of every shot (Fig. 2). A quadrat unit was located through the acquisition of megapixel (3035 × 3035) digital red–green–blue (RGB) pictures by a camera (SONY 5100, JPN). Every sixteen pictures were combined into one image measuring 2.0 m × 2.0 m in size according to the orientation and order. There were ten 2.0 m × 2.0 m images for one site, and each slope aspect had 30 images. In total, 90 images were collected from nine revegetated grasslands. All images were transported to the laboratory for analysis to obtain the coverages of soil surface compositions. The patches of cyanobacteria, moss, lichen and bare soil were delineated and filled with different colors using ArcGIS 10.2 (Environmental Systems Research Institute, USA) through manual visual interpretation (Fig. 2). In the image-interpretation process, several criteria were applied in relation to the minimum patch size. For the biocrusts, individual patches were outlined in a minimum area of approximately 4.00 cm^2 (approximately 1 cm in diameter) where lichen patches could be identified. For bare soil, the applied criterion of the minimum patch size was approximately established at 25.00 cm^2 (approximately 2–3 cm in diameter). One image was displayed for each slope aspect (Fig. 2).

2.3. Determination of the REA of mixed biocrusts

The image was interpreted to produce color metric that could be calculated by computer programming (https://www.compuphase.com/cmetric.htm). The 2.0 m × 2.0 m image was represented by a matrix of 1034 × 1034 pixels. Each pixel represented an area of approximately 4 mm^2. The image was split into 400 grid units (Fig. 2). Each unit contained 50 × 50 pixels, each of which was assigned attribute values, k, representing different patch types. The program used the gliding box

Table 1
Surface characteristics of the research sites.

Slope aspects	Cyanobacterial coverage (%)	Moss coverage (%)	Lichen coverage (%)	Bare soil coverage (%)	Litter coverage (%)	Plant root coverage (%)	Biocrust thickness (mm)
Sunny	47.3 ± 5.4a	10.6 ± 4.6b	3.2 ± 1.3a	4.5 ± 1.5a	16.6 ± 8.0b	17.8 ± 3.3a	5.0 ± 0.2a
Semishady	27.9 ± 6.9b	15.1 ± 6.1b	5.5 ± 1.4a	5.4 ± 3.2a	30.7 ± 7.3a	15.4 ± 5.1a	5.4 ± 0.1a
Shady	15.8 ± 4.6c	29.2 ± 6.7a	3.1 ± 1.2a	6.6 ± 5.4a	24.4 ± 6.9a	20.9 ± 5.5a	5.4 ± 0.2a

Values correspond to the average and standard errors of n = 3 samples per slope. Different letters indicate significant differences among different slope aspects.

Table 2
Soil properties of the research sites.

Soil properties/Soil layer/Slope aspects		Biocrust layer			0–2 cm			2–5 cm		
		Sunny	Semishady	Shady	Sunny	Semishady	Shady	Sunny	Semishady	Shady
Particle size	Clay (%)	8.04 ± 0.33	8.48 ± 0.53	8.66 ± 0.33	9.94 ± 0.54	9.41 ± 0.98	9.31 ± 0.88	10.39 ± 1.08	9.46 ± 0.87	9.93 ± 0.98
	Silt (%)	59.91 ± 0.90	63.18 ± 2.77	63.29 ± 3.77	64.54 ± 1.55	64.49 ± 2.88	64.40 ± 2.78	65.25 ± 2.35	64.24 ± 2.37	64.74 ± 2.36
	Sand (%)	32.05 ± 1.16	28.34 ± 3.21	28.05 ± 3.91	25.52 ± 1.78	26.10 ± 3.74	26.29 ± 3.64	24.36 ± 3.41	26.30 ± 3.12	25.33 ± 3.27
Organic matter ($g \cdot kg^{-1}$)		20.16 ± 4.98	20.65 ± 2.13	23.45 ± 3.13	10.75 ± 1.81	12.98 ± 3.08	11.98 ± 2.98	9.12 ± 1.79	9.61 ± 2.41	9.81 ± 2.31
Total N ($g \cdot kg^{-1}$)		1.67 ± 0.16	1.65 ± 0.18	1.75 ± 0.26	0.74 ± 0.10	0.76 ± 0.14	0.78 ± 0.13	0.53 ± 0.07	0.59 ± 0.05	0.60 ± 0.06
Total P ($g \cdot kg^{-1}$)		0.58 ± 0.01	0.56 ± 0.04	0.55 ± 0.04	0.55 ± 0.01	0.51 ± 0.04	0.52 ± 0.03	0.54 ± 0.01	0.49 ± 0.04	0.50 ± 0.03
Soil pH		8.39 ± 0.12	8.34 ± 0.14	8.30 ± 0.23	8.54 ± 0.14	8.60 ± 0.18	8.66 ± 0.13	8.60 ± 0.12	8.62 ± 0.11	8.64 ± 0.13

Values correspond to the average and standard errors of n = 3 samples per slope. Different letters indicate significant differences among different slope aspects.

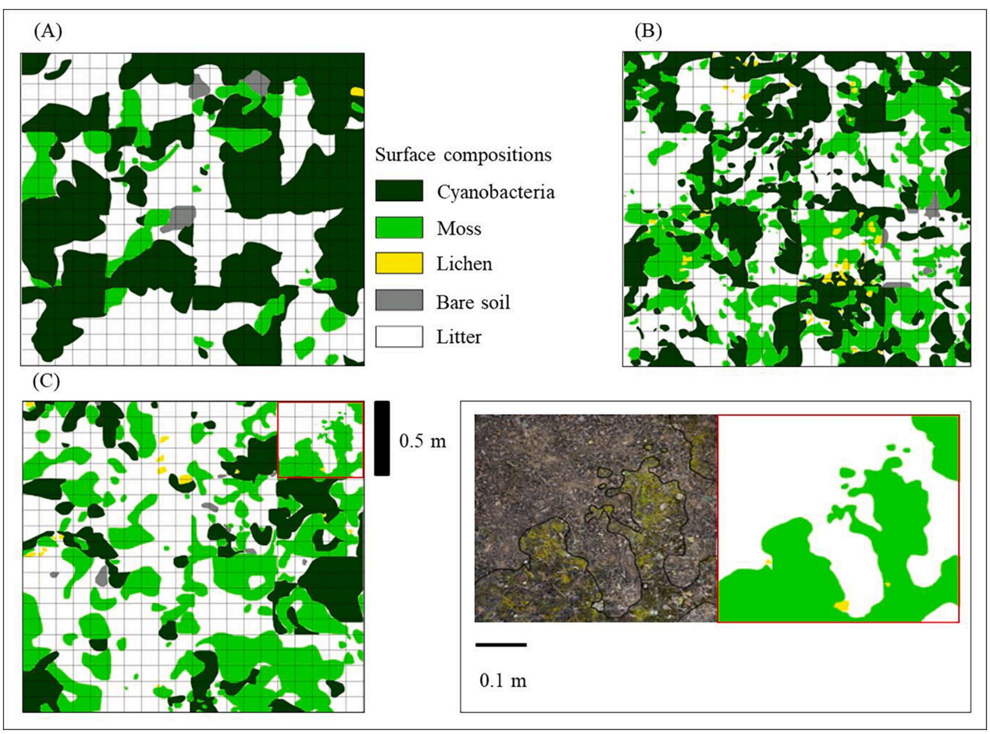

Fig. 2. Soil surface compositions image of (A) the sunny slope, (B) the semishady slope and (C) the shady slope. The insert shows an enlargement from the shady slope of the base image and the picture of the results.

method to calculate the coverage of each patch type. An "up-scaling" partitioning process began with a minimum box size of 0.1 m, which was incrementally increased by 0.1 m or 50 pixels over the image in all possible directions. At each increment the area within the expanded box was grouped together to produce boxes of 4, 9, 16 …400 (i^2) units, corresponding to plot sizes of 0.04 m^2, 0.09 m^2, 0.16 m^2… 4.00 m^2, respectively (Table S1). A diagram of an "up-scaling" partitioning process is shown in the Supplementary Materials (Fig. S1). The specific procedure was as follows: the size of the 0.1 m × 0.1 m box was set in the lower left corner of the image, and the pixels of each color present in the area were then counted. Furthermore, by gliding the box to the right or up by 0.1 m, the pixels of each color were counted again after each movement. Therefore, the number of pixels of each color was used to traverse the entire image and encompassed the all this plot size. Finally, for each plot size, the number of pixels belonging to each patch type (k) was recorded.

The data points of the number of patch types and coverage of patches could be obtained at different plot sizes by Eq. (1). At the plot size of 4.00 m^2, there was only one data point.

$$n = [20\text{-}(i\text{-}1)]^2 \quad i = 1, 2, 3\cdots\cdots20 \tag{1}$$

where n is the number of data points at the i-th plot size.

The number of colors appearing on each plot size was counted, and the value was the number of patch types. The average number ($\overline{x_i}$) of patch types at each plot size was calculated.

The coverages of each patch type were calculated by the following equations:

$$\text{Coverage} = \frac{M_k}{S_i} \quad k = 1,2,3,4,5 \tag{2}$$

$$S_i = 50 \times 50 \times i^2 \tag{3}$$

where M_k is the number of pixels with k patch types, and S_i is the total number of pixels at the i-th plot size.

The community characteristics of mixed biocrusts included the community composition and coverage of different types. The REA is considered to be reached when the values of community characteristics of mixed biocrusts do not change with increasing plot size. Measurements of any mixed biocrusts at the slope scale should be representative of this slope as a whole. In this study, an REA was therefore determined with the following algorithm. 1) The number of biocrust types was considered a criterion for judging the REA. 2) The REA was attained when the coverage of mixed biocrusts did not evolve significantly with increasing plot size. In the study region, mixed biocrusts are dominated by cyanobacteria and moss, and they can be found at a small plot size. However, their coverages are spatially variable. With reference to this algorithm, the REA of mixed biocrusts could be obtained by calculating the error of their coverage. Thus, the root mean square error (RMSE) of those coverage responses within each plot size was calculated; the relationship between RMSE and plot sizes was thus obtained. We used alpha values (α) of 0.1, 0.05 and 0.01 in the RMSE values to determine different levels of statistical significance.

The Shannon index is one of the landscape diversity indices used to measure landscape structural complexity (Garland and Mills, 1991). It was calculated by the following equation:

$$\text{Shannon index}: H = -\sum_{k=1}^{m} P_k \ln P_k \tag{4}$$

where P_k is the coverage proportion in the image of each patch type k, and m is the number of patch types in the image.

Patch density is often used to describe the fragmentation of landscape structure in space (Gustafson, 2019). Patch density was given by

$$Patch\ density = \frac{N}{A} \tag{5}$$

where N is the total number of biocrust patches in the image and A is the image area (Gustafson, 2019).

2.4. Data analyses

The number of patch types and coverages at different plot sizes were computed by using an application written in C#. The diversity index and the patch density were calculated with Fragstats 4.0 (http://www.umass.edu/landeco/research/fragstats/fragstats.html). We tested the data for normality using the Kolmogorov-Smirnov test and for equality with Levene's test. The community characteristics of mixed biocrusts, diversity index and patch density were analyzed using analysis of variance (ANOVA) and the least significant difference ($\alpha = 0.05$) approach to analyze the significance of the differences among different slope aspects using SPSS 18.0 (SPSS, USA). The REAs were analyzed using the same approach to determine the significance of the differences among the different slope aspects.

To identify the governing factors that affect the size of the REAs among the different slope aspects, we assessed the effects of the community characteristics (coverage of different types of biocrusts), the diversity index and the patch density of biocrusts on the REAs with Spearman correlation analysis using SPSS 18.0. Moreover, we constructed a structural equation modeling (SEM) to test the direct and indirect effects of community characteristics based on different slope aspects on REAs. We added slope variables expressed as degrees from North (0–180°) to the SEM. The priori structural equation modeling of factors influencing the REAs of mixed biocrusts is shown in the Supplementary Materials (Fig. S2). According to our knowledge, community characteristics (coverage of different types of biocrusts), the diversity index and the patch density were controlled by slope aspects, while slope aspects did not directly affect the REAs. In particular, we related the variation in REAs to the coverage of different types of biocrusts, diversity index and patch density. We hypothesized that patch density and diversity index would be correlated and that patch density would also be affected by the coverage of different types of biocrusts. In the model, slope aspects, coverage of different types of biocrusts, patch density and diversity index were assigned as endogenous variables, and REAs were regarded as response variables. The degree of fit between the observed and predicted models among variables was assessed with the chi-square test (χ^2), root mean square error of approximation (RMSEA), comparative fit index (CFI) and Akaike information criterion (AIC) (Bentler 2006). As satisfactory goodness of fit is often not found at first, our model was tested iteratively and modified by exploring some suggestions arising from the use of modification indices (e.g., removing a variable from the model) until the fit with the data was satisfactory (Bollen and Stine, 1992). The SEM was processed using Amos 21.0 (SPSS, USA). The path diagram was drawn by Microsoft Visio 2010.

3. Results

3.1. Surface distribution characteristics of different slope aspects

The surface distribution characteristics differed significantly among the three slope aspects (Table 3). The cyanobacterial coverage of the sunny slope was higher than that of the semishady and shady slopes by 70.8% and 142.7%, respectively. The coverage of moss on the shady slope was 4.7 and 1.7 times higher than that on the sunny and semishady slopes, respectively. There was no significant difference among the three slope aspects in lichen coverage, which was less than 1%. The coverage of bare soil was significantly higher on the shady slope than on the sunny and semishady slopes, but their coverage was less than 5%. The litter coverage was 14.8% and 12.1% lower than that on the sunny and shady slopes, respectively, compared with the semishady slope.

The diversity index of the shady slope was 25.7% and 16.5% higher than that of the sunny and semishady slopes, respectively. The patch density on the semishady slope was 3.2 and 1.7 times higher than that on the sunny and shady slopes, respectively.

3.2. Community characteristics of mixed biocrusts across plot sizes

The relationship between the number of biocrust types and the plot sizes was logarithmic (Fig. 3). At the smallest plot size of 0.01 m^2, there was mostly pure biocrust (cyanobacteria, moss or lichen) on the sunny and shady slopes, while there were mixed biocrusts on the semishady slope. The number of biocrust types increased rapidly in the early

Table 3
Surface composition characteristics of different slope aspects.

Characteristics/Slope aspects	Sunny	Semishady	Shady
Cyanobacterial coverage (%)	47.03 ± 1.42a	27.54 ± 7.08b	19.38 ± 0.11c
Moss coverage (%)	6.24 ± 0.46c	17.94 ± 2.01b	29.74 ± 0.59a
Lichen coverage (%)	0.03 ± 0.02a	0.29 ± 0.24a	0.23 ± 0.03a
Bare soil coverage (%)	0.59 ± 0.28b	0.10 ± 0.09b	3.09 ± 0.12a
Litter coverage (%)	46.11 ± 1.26b	54.13 ± 8.61a	47.56 ± 0.76b
Diversity index	0.92 ± 0.04c	0.99 ± 0.05b	1.15 ± 0.01a
Patch density	13.67 ± 2.36c	43.33 ± 15.17a	25.00 ± 8.38b

Values correspond to the average and standard errors of n = 30 samples per slope. Different letters indicate significant differences among different slope aspects.

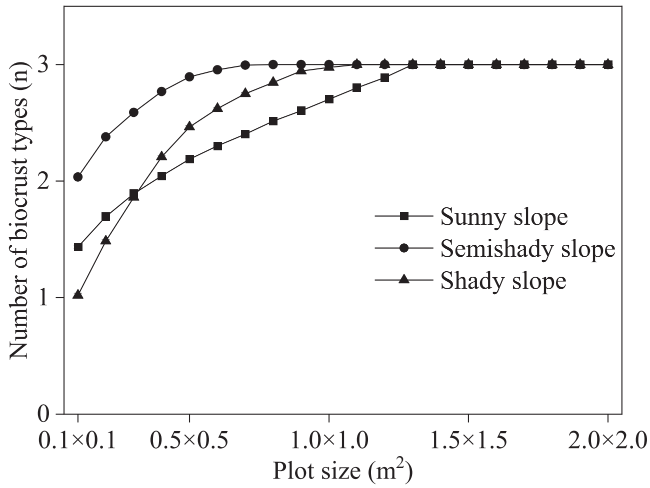

Fig. 3. Biocrust type dynamics across the plot sizes.

expansion of the plot sizes. At a plot size of 0.25 m^2, there were two types of biocrusts dominated by cyanobacteria and moss. Then, the number of biocrust types gradually tended to a constant value and no longer changed by approximately 1.00 m^2 for any of the slopes, indicating that all three types (cyanobacteria, moss and lichen) of biocrusts were included.

The variability in the coverage of pure biocrust across the plot sizes is shown in Fig. 4. All figures showed that the coverages of cyanobacteria, moss and lichen were a decreasing function of the plot size and converged to a constant value. In addition, the RMSE of cyanobacterial,

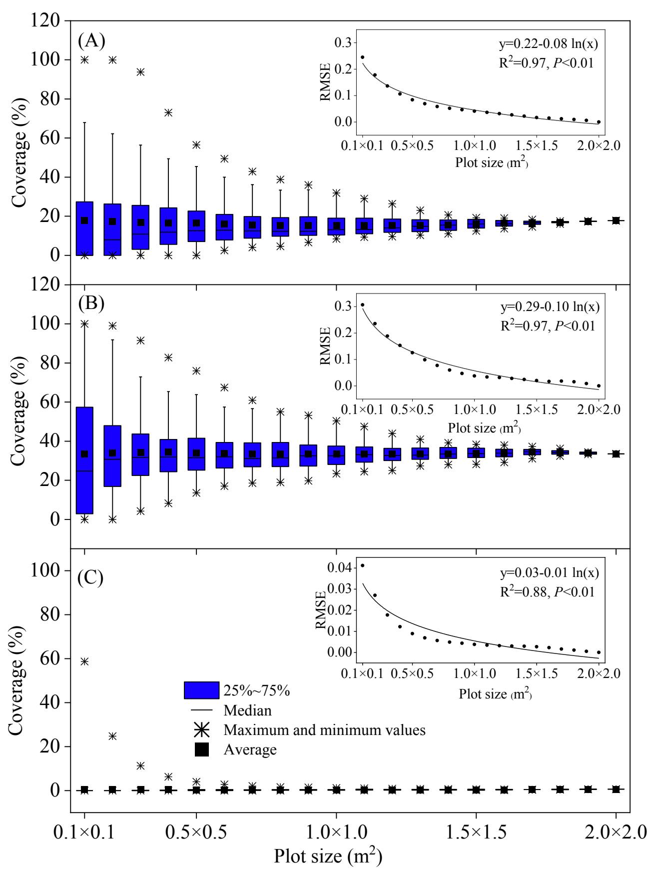

Fig. 4. Variability in the coverage of (A) cyanobacteria, (B) moss and (C) lichen across the plot sizes. The insert shows the RMSE of the coverage of (A) cyanobacteria, (B) moss and (C) lichen across the plot sizes.

moss and lichen coverage decreased logarithmically as the plot sizes increased from 0.01 m^2 to 4.00 m^2 (Fig. 4). The variability in coverage of mixed biocrusts showed a similar pattern (Fig. 5). After a certain critical plot size (1.00 m^2 in this study), the coverage values remained approximately constant. This size could be interpreted as the REA. The area required to reach a constant value of biocrustal coverage was larger on the shady slope than on the sunny and semishady slopes (Fig. 5). The results revealed that the variability in coverage of mixed biocrusts gradually decreased as the plot size increased.

3.3. REAs of mixed biocrusts

According to the logarithmic relationship between RMSE values and plot sizes, the REAs of mixed biocrusts on nine sites of revegetated grasslands were calculated. The REAs of mixed biocrusts at different α values were analyzed (Table 4). The size of the REAs of mixed biocrusts increased significantly with the reduction in the α value. When α values were 0.1, 0.05, and 0.01, the REAs were 0.39–0.83 m^2, 1.04–2.24 m^2 and 2.28–3.75 m^2, respectively, and the average values were 0.52 m^2, 1.38 m^2 and 2.90 m^2, respectively. Under the same α values, the average and median values of the REAs did not differ significantly (Table 4). As the α values decreased, the standard deviation of the REAs increased from 0.23 to 0.60, and the coefficient of variation of the REAs decreased from 0.44 to 0.21.

The size of the REAs of mixed biocrusts differed significantly among different slope aspects with the reduction in the α value (Fig. 6). The highest REAs occurred on the shady slope, i.e., 0.88, 2.03 and 3.64 m^2 for $\alpha = 0.1$, 0.05 and 0.01, respectively. The lowest REAs occurred on the semishady slope, i.e., 0.40, 1.21 and 2.97 m^2 for $\alpha = 0.1$, 0.05 and 0.01, respectively. There were no significant differences in the REAs of mixed biocrusts between the sunny and semishady slopes.

3.4. Factors influencing the REAs of mixed biocrusts

According to the Spearman correlation analysis assessing the effects of community characteristics (coverage of different types of biocrusts), diversity index, patch density and slope aspects on the REAs, several interesting relationships can be observed from Table 5. Slope aspects were positively correlated with cyanobacterial coverage ($r = 0.92$, $P = 0.00$) and were negatively correlated with moss coverage ($r = -0.93$, $P = 0.00$), lichen coverage ($r = -0.67$, $P = 0.00$) and the diversity index ($r = -0.72$, $P = 0.00$). Although a negative relationship existed between cyanobacterial coverage and the diversity index ($r = -0.72$, $P = 0.00$), moss coverage was positively correlated with the diversity index ($r = 0.80$, $P = 0.00$). REAs were strongly positively correlated with the diversity index ($r = 0.49$, $P = 0.01$) and were negatively correlated with the patch density ($r = -0.57$, $P = 0.00$) (Table 5).

The SEM was established to explicate the effects of community characteristics and slope aspects on REAs ($\chi^2 = 0.94$, $P = 0.33$, CFI = 1.00, RMSEA = 0.00, AIC = 38.94, excellent fit). Slope aspects, cyanobacterial coverage, the patch density and the diversity index together explained 56% of the REAs (Fig. 7). Among them, the direct effect of patch density on the REAs was the primary effect, with a path coefficient of −0.63 ($P = 0.00$), followed closely by that of the diversity index, with a path coefficient of 0.25 ($P = 0.19$). Meanwhile, cyanobacterial coverage had a minor effect, with a path coefficient of −0.21 ($P = 0.28$). Moreover, slope aspects had notable effects on the diversity index (path coefficient = −0.75, $P = 0.00$) and cyanobacterial coverage (path coefficient = 0.75, $P = 0.00$) but had little effect on the patch density (path coefficient = 0.05, $P = 0.90$). Patch density was also strongly affected by the diversity index and cyanobacterial coverage, with path coefficients of −0.65 ($P = 0.08$) and −0.73 ($P = 0.00$), respectively (Fig. 7).

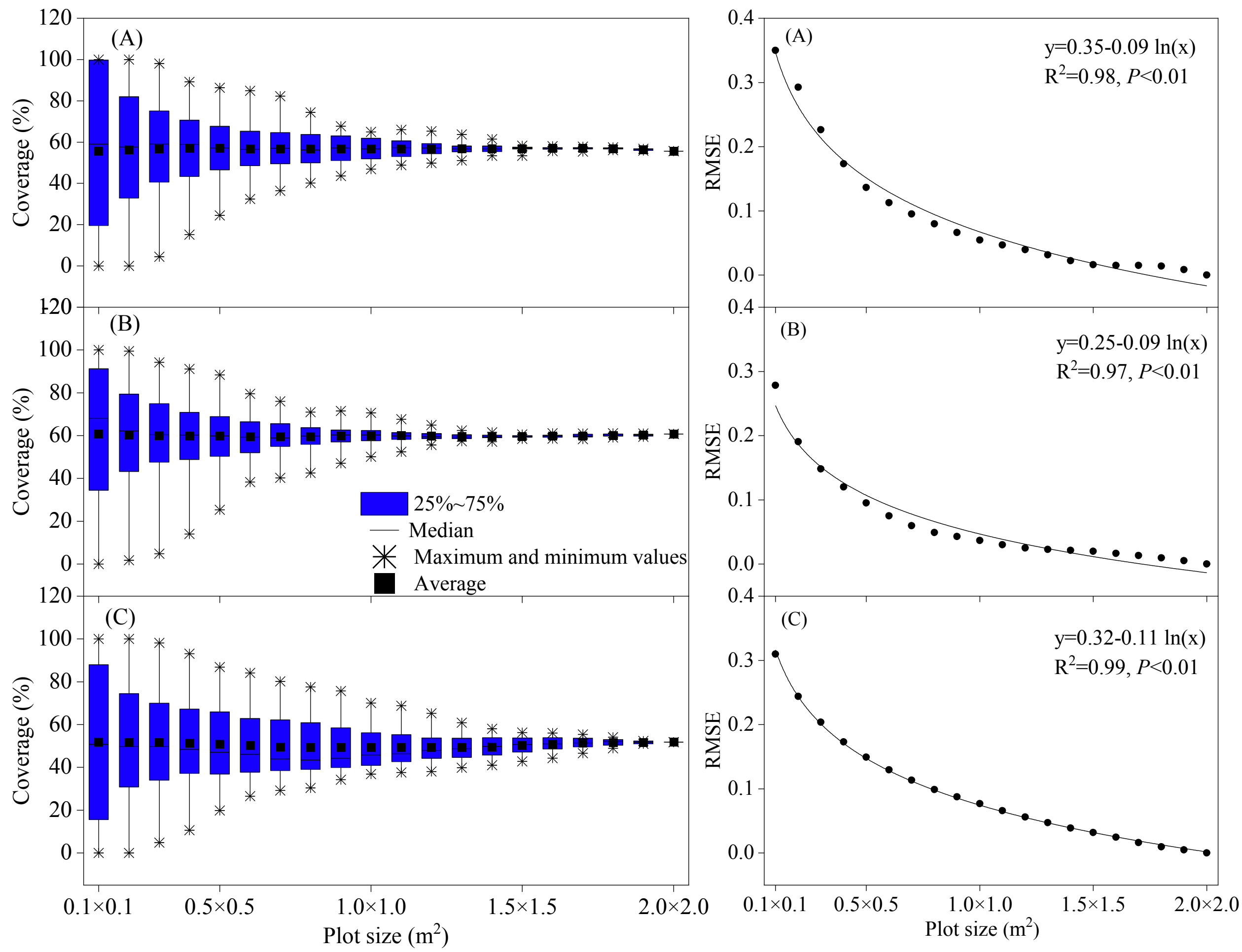

Fig. 5. Variability in coverage of mixed biocrusts on the left and the RMSE of biocrustal coverage on the right across the plot sizes on (A) the sunny slope, (B) the semishady slope and (C) the shady slope.

Table 4
Descriptive statistics of the REAs of mixed biocrusts at different *α* values which refer to significant levels of difference.

α value	REAs (m²)						
	Average	Median	Standard deviation	Max	Min	Range	Coefficient of variation
0.1	0.52	0.50	0.23	0.83	0.39	0.44	0.44
0.05	1.38	1.42	0.50	2.24	1.04	1.21	0.36
0.01	2.90	3.02	0.60	3.75	2.28	1.47	0.21

4. Discussion

4.1. Mixed biocrusts had an REA at the slope scale

Revegetated grasslands show a distributed mosaic pattern of vascular plants and biocrusts (Wang et al., 2016). Biocrusts are assemblages of cyanobacteria, moss and lichen, and they too are distributed in a patchy mosaic pattern on the soil surface in between plants (Bowker et al., 2016). Kutiel et al. (1998) concluded that the presence of microenvironments (light gradient, humidities, pH gradients, micronutrients) within a slope contributes significantly to the potential spatial heterogeneity of biocrusts. Microtopographical features create more suitable microhabitats necessary for the establishment of certain organisms (Grondin and Johansen, 1993; Wheeler et al., 1993). Thus, the mixed biocrusts appear to exhibit a patterned distribution based on the spatial scales investigated in the study (Bowker et al., 2006).

The coverage of mixed biocrusts was obtained through field investigation and image interpretation in the laboratory. Here, we evaluated the accuracy of the biocrust patch segmentation of the image, and the results showed that the error of biocrustal coverage between the image interpretation and the investigation of 25 cm × 25 cm quadrat (Belnap et al., 2001) was within 5% (Tables 1 and 3). This evaluation confirmed the accuracy of biocrust composition and coverage obtained by image interpretation. Both the field data and the image data were measured with error. Neither was the pure “truth”. The fact that they agreed with each other to a strong degree provided reciprocal validation, supporting that both approaches were close to correct.

In our study system, the number of biocrust types increased logarithmically as the plot size increased from 0.01 m^2 to 4.00 m^2, and biocrust types no longer changed by approximately 1.00 m^2 (Fig. 3). This function was quite similar to the species-area curve in the plant community (Plotkin et al., 2000), which indicated that community composition had reached a stable state. Likewise, the variability in coverage of mixed biocrusts gradually decreased as the plot size increased. In small-sized plots, the biocrustal coverage ranged from 0% to 100%, demonstrating that the accuracy of biocrustal coverage was

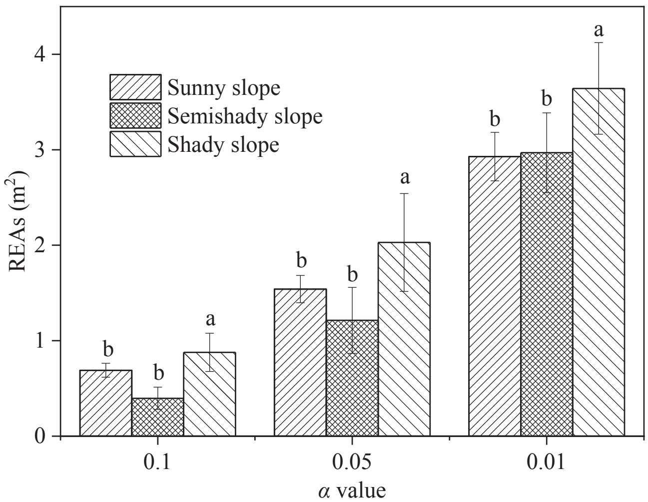

Fig. 6. REAs of mixed biocrusts on different slope aspects. Different letters indicate significant differences among different slope aspects.

low. The coverage values remained approximately constant above a certain plot size (approximately 1.00 m^2) (Figs. 4 and 5). This pattern showed that the spatial variability of community characteristics of mixed biocrusts is low (Bowker et al., 2006). There was a threshold area at which community characteristics of mixed biocrusts were similar to those of the entire image that they represented. This pattern is strictly analogous to the concept of the REA in mosaic patterns (Cosenza et al., 2019; VandenBygaart and Protz, 1999). For example, the characteristic size REA of mineral maps is considered to be reached when the mean values of the surface clay fraction are very close to that of the whole map or did not evolve significantly (relative error values between 5% and 10%) compared with the box size (Cosenza et al., 2019). Additionally, in mosaics of images from thin soil sections, the REA is obtained at the area where the measurements made on a parameter in three successive areas of measurements do not change by ±10% relative to the next greater area of measurement (VandenBygaart and Protz, 1999). The results of this study were similar to those of previous studies. Therefore, mixed biocrusts existed an REA at slope scale.

4.2. The REAs of mixed biocrusts and their underlying influences

The threshold area should reflect the community characteristics, including the species composition and coverage per species (Barkman, 1989). However, lichen crust is especially rare, with less than 10% coverage in this region (Wang et al., 2016). The lichen coverage in our study extracted from all images of 4.00 m^2 was less than 1%. According to the authors' observations, lichen crust had a scattered distribution on the slope. Perhaps the investigation of lichen species biodiversity should be conducted in this larger area. Another study maintained that the threshold area depends on the homogeneity of the plant segments caused by the more dominant species in the community (Ellenberg and Mueller-Dombois, 1974). Cyanobacteria and moss dominate the major biocrust communities in this region, and they also play important ecological roles (Gao et al., 2020; Zhao et al., 2010). Therefore, we should pay attention to the community characteristics of mixed biocrusts composed of cyanobacteria and moss. Regarding community composition, a plot size of 0.25 m^2 corresponded to the REA. Based on the variability in coverage of mixed biocrusts, the REAs were further determined. Generally, the size of REAs is affected by the precision (Wang and Guo, 2016). We simplified the size of the REAs, which were 0.5–1.0 m^2, 1.5–2.5 m^2 and 3.0–3.8 m^2 when $\alpha = 0.1$, 0.05 and 0.01, respectively. The results were in accordance with previous empirical values (Barkman, 1989; Berg et al., 2016; Bricaud and Roux, 2000; Ellenberg and Mueller-Dombois, 1974).

Results of the SEM showed that slope aspects, patch density, diversity index and cyanobacterial coverage jointly affected the REAs of mixed biocrusts (Fig. 7). Because the main biocrust types in the sample sites were cyanobacterial and moss crust, the cyanobacterial coverage had a negative correlation with the moss coverage ($r = -0.89$, $P = 0.00$) (Table 5). Thus, cyanobacterial coverage was used to characterize the coverage of biocrusts. In fact, the patch density, the diversity index and cyanobacterial coverage are controlled by environmental factors (i.e., climate and biotic factors) (Rodríguez-Caballero et al., 2019). Biocrust and vegetation composition, abundance and distribution are mainly controlled by environmental factors (Bowker et al., 2016). Environmental factors based on slope aspects affected the distribution characteristics of mixed biocrusts and, thereby, the size of the REAs.

The direct effect of the patch density on the REAs had a large negative value, and the path coefficient was −0.63 ($P = 0.00$) (Fig. 7). This phenomenon was mainly observed on the semishady slope. The semishady slope had moderate hydrothermal conditions, which had less restrictive effects on cyanobacteria and moss. Thus, their coverage was equivalent (Table 3). These taxa do not need to compete with vegetation for water and light resources (Rodríguez-Caballero et al., 2019) and could multiply more easily on bare soil, which results in a decline in the

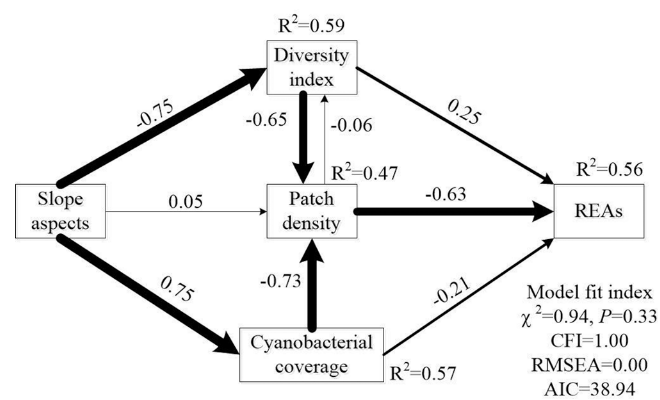

Fig. 7. A structural equation modeling (SEM) demonstrating the direct and indirect effects of community characteristics and slope aspects on the REAs. Rectangles represent measured variables. Single headed arrows represent hypothetical causal relationships tested by the model. Adjacent path coefficients (equivalent to correlation coefficients or regression weights) estimate the strength of the relationship, and arrow width is proportional to the coefficient.

Table 5
Spearman correlations between the REAs and surface composition characteristics.

Variables	Slope aspects	Cyanobacterial coverage	Moss coverage	Lichen coverage	Diversity index	Patch density	REAs
Slope aspects	1.00	0.92**	−0.93**	−0.67**	−0.72**	−0.15	−0.30
Cyanobacterial coverage		1.00	−0.89**	−0.65**	−0.55**	−0.19	−0.19
Moss coverage			1.00	0.46*	0.80**	0.12	0.24
Lichen coverage				1.00	0.09	0.50**	−0.09
Diversity index					1.00	−0.21	0.49**
Patch density						1.00	−0.57**

Note:* and **indicate significant differences at P less than 0.05 and P less than 0.01, respectively.

diversity of surface composition. Cyanobacterial and moss crusts were mostly small-sized patches, and they were evenly distributed on the surface (Fig. 2B). Therefore, the patch density of biocrusts on semishady slopes was greater than that on shady slopes (north-facing slopes) and sunny slopes (south-facing slopes). Meanwhile, the heterogeneity in the biocrust distribution characteristics of the semishady slope was lower than that of the shady slope (Fig. 2). Therefore, the REAs of semishady slopes were smaller than those of the shady or north-facing slopes. Hu et al. (2010) found that when winter wheat areas are sampled in regions where the planting structure is broken and the patch density is extremely high, the threshold area is often small, in accordance with our results.

The diversity index had a direct positive effect on the REAs, and the path coefficient was 0.25 ($P = 0.19$) (Fig. 7). The more complex the landscape and the greater the diversity are, the larger the threshold area of the community is (DeMalach et al., 2019). The shady slope or north-facing slope was characterized as shadier habitats that have higher humidity with low radiation, light and temperature. Surface compositions were abundant and the diversity index was high on the north-facing slope. Moss and vegetation are the dominant surface components in these favorable areas (Gao et al., 2020; Zhao et al., 2010). The vegetation canopy has a shading effect on the moss crust, which is mostly distributed under the plant canopy in the form of mosaic or cluster patches (Li et al., 2005). Zaady et al. (2021) demonstrated that north-facing slopes (heterogeneous slopes) have higher biodiversity than south-facing slopes (homogeneous slopes), in agreement with our results. Another study suggested that more heterogeneous soil surface properties may require a larger threshold area for analysis (Ferreira et al., 2015). Hence, the REAs of mixed biocrusts on the north-facing slope were larger than those on the south-facing slope.

In our study region, cyanobacterial crusts were mainly distributed on sunny or south-facing slopes (Table 3) because of the high solar radiation and drought environmental conditions (Rodríguez-Caballero et al., 2019). The smoothly cyanobacterial crusts are primarily distributed in contiguous patches, resulting in lower fragmentation and heterogeneity (Belnap et al., 2012; Chamizo et al., 2012), and a consequent decrease in the size of the sampling area (Golivets and Bihun, 2016).

Results of the SEM demonstrated that the patch density was an important factor affecting the REAs. Metzger and Muller (1996) also found that the origins of patches may be the main factor that establishes landscape mosaic diversity. Moreover, the diversity index may reflect the uniformity of each patch type in the area distribution, and cannot reflect community distribution characteristics when disturbance factors are taken into account (Metzger and Muller, 1996). The patch density directly reflects the spatial distribution characteristics of landscape mosaics (Gustafson, 2019). Thus, to determine the REAs of mixed biocrusts, the patch density is the primary factor to consider.

The physical and chemical properties of soil from different slope aspects did not show significant differences (Table 2), which may be because the age of the revegetated grasslands we sampled in the study was the same (20 years). A study from the same region suggested that the soil physical and chemical properties of revegetated grasslands became stable approximately 20 years after cropland was abandoned (Jiao et al., 2005). Therefore, soil properties were not the reasons for the difference in biocrust distribution characteristics on different slope aspects in this study.

4.3. The process of determining the REAs

This study provided a method for determining the REAs of mixed biocrusts. Therefore, assuming that an REA can be achieved, it may be more efficient to spend time collecting precise data from fewer sites than to collect more generalized data from a larger site. However, the REAs may increase with the sampling precision and vary with the variation in environmental factors caused by topography. Thus, we suggest the following when selecting an REA to study the ecological functions of mixed biocrusts.

First, the REAs on the north-facing slope were larger than those on the south-facing slope in the absence of disturbance. The higher the diversity was, the larger the REAs of mixed biocrusts were. However, when the patch density of biocrusts was extensively large and the coverage and patch size of biocrusts were small, smaller REAs could be selected.

Second, we speculated that research on the ecological functions of mixed biocrusts has different requirements for REAs. The influence of biocrusts on the soil and water loss processes at the slope scale was related not only to composition and coverage but also to topography, soil physical and chemical properties, disturbance, surface roughness and distribution pattern (Gao et al., 2020; Gao et al., 2017; Ji et al., 2021; Shi et al., 2017). Analyzing the influence and mechanism of mixed biocrusts on the soil and water loss processes and quantitatively evaluating their soil erosion effects at the slope scale are the basis for clarifying soil and water loss in catchments and regions, and they have important practical value for the sustainable management of ecosystems in arid and semiarid regions. Therefore, in consideration of time savings, labor savings and accuracy, it may be effective to measure the soil and water loss processes of mixed biocrusts through REAs. If studies only focus on the distribution characteristics and water infiltration of cyanobacteria and moss dominated mixed biocrusts, an REA of 0.5–1.0 m^2 may be sufficient. Soil and water loss processes are accompanied by soil migration, transport and deposition (Belnap et al., 2009; Zhao and Xu, 2013). These processes may need to be carried out in relatively larger REAs, such as 3.0–3.8 m^2.

Third, the contribution of mixed biocrusts to soil carbon and nitrogen nutrients at the slope scale is mainly related to their composition and coverage (Pietrasiak et al., 2013), and it may not be necessary to determine REAs. Their estimation method may be similar to the estimation method of soil carbon and nitrogen storage in grassland ecosystems. The soil organic carbon and total nitrogen stocks of grassland ecosystems are calculated separately for each soil layer by multiplying the area of each grassland ecosystem by its respective soil organic carbon and total nitrogen concentrations with bulk density, and the soil organic carbon and total nitrogen reserves of the entire grassland ecosystem are then calculated by weighting (Peichl et al., 2012). Total phosphorus is mainly affected by soil parent material (Liu et al., 2010). Although the soil available ammonium, nitrate nitrogen and phosphorus contents are related to the composition of biocrusts, they are mainly controlled by total nutrients and environmental factors, such as temperature, moisture and pH (Zhou et al., 2020). As a consequence of these interacting factors, the soil available nutrient contents of mixed biocrusts may be measured on the REAs, while soil total phosphorus cannot (unpublished data, Zhao et al.).

Under field experimental conditions, it is universally important to consider the spatial scale when investigating and studying the ecological functions of mixed biocrusts (Critchley and Poulton, 1998). REAs could be used in experimental layouts and functional studies of mixed biocrusts on slopes. They build a bridge for analyzing the relationship in ecological functions between pure biocrust and mixed biocrusts, especially in soil and water loss processes. Investigating the scale dependence of soil and water loss processes under stationary land surface properties could serve as a basis for understanding the mechanisms regulating the scaling laws (Chen et al., 2016).

The influencing factors underlying the distribution of biocrusts in space can be described as biogeographic, climatic, edaphic, topographic, and biotic (Bowker et al., 2016). The size of the REAs may vary with those factors. Thus, these factors need to be considered to explore the REAs of mixed biocrusts. Assessing the effects of those factors on REAs is the aim of our next study. The results of this study are especially applicable to the Hilly Loess Plateau Region, China, and the REAs of mixed biocrusts may be different in other regions. Therefore, the spatial heterogeneity of biocrust distribution caused by environmental factors should be considered when determining the threshold area of the community. This study only provides a method, and the results cannot be extended to other regions.

5. Conclusions

To the best of our knowledge, this is the first study to propose the use of an REA to characterize the spatial variability of mixed biocrusts at the slope scale. The spatial variability of mixed biocrusts logarithmically decreased with plot size. Our data indicated that the REAs of mixed biocrusts existed at the slope scale. The REAs could be determined by identifying the biocrust community characteristics in the RGB image by the gliding box method. The higher the sampling precision was, the larger the REAs were. When determining the REAs of mixed biocrusts, the spatial heterogeneity of biocrust distribution due to environmental factors should be considered. The size of the REAs on the north-facing slope was larger than that on the south-facing slope, and the patch density of biocrusts was the main influencing factor. These results provide guidance for surveys and experimental layouts in the future. Future studies are needed to study the REAs of mixed biocrusts under different biogeographic, climatic, edaphic, topographic, biotic conditions and disturbance intensities.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115502.

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