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Effect of crevice density on biological soil crust development on rock cut slope in mountainous regions, Sichuan, China

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Abstract

Background The rock cut slope (RCS) could cause damage to regional ecological functions and landscapes and requires recovery. Biological soil crusts (BSCs) are pioneer and dominant colonizers during the initial recovery stage. To accelerate the natural recovery of RCS, the development process and influencing agents of BSC should be revealed. Thus, the area index of crevices (I_R), BSC coverage (COV) and biomass (BM), soil weight (SW), and major soil nutrients [organic carbon (OC), total nitrogen (TN) and total phosphorus (TP)] content, collected from 164 quadrats on 13 RCSs in the mountainous area of west Sichuan Province, China, were measured, to explore the effect of crevice of RCS on BSC development.

Results Soil OC, TN and TP on RCSs ranged from 18.61 to 123.03 g kg^{-1}, 0.96 to 6.02 g kg^{-1} and 0.52 to 2.46 g kg^{-1}, respectively, and were approximately to or higher than those on natural slopes. The OC, TN and TP contents in soils elevated unsystematically with recovery time of RCSs. BSCs on RCS distributed along crevices generally and firstly. During the first 13 years of natural recovery, COV, BM and SW ranged from 6.5 to 28.2%, 14.43 to 67.25 g m^{-2}, and 127.69 to 1277.74 g m^{-2}, respectively. COV, BM and SW increased linearly with I_R on RCSs. The positive correlation between COV and BM and I_R was insignificantly impacted by bedrock, slope aspect and altitude within the recovery time less than 13 years. COV and BM on RCSs increased significantly when the recovery time is more than 27 years.

Conclusions Crevice on RCSs could be a major environmental factor which is conducive to BSC development and soil accumulation through creating a space for water and soil particle. Furthermore, with the increase of recovery time of RCSs, BSCs may grow and reach a stable state with the promotion of soil nutrients, plant growth and microbial activity. These results provide a development process of BSC that from inside to outside the crevices on RCSs. In the areas with stable rock strata and a low risk of geological disasters, purposeful improvement in crevice density on RCS may effectively accelerate BSC development.

Keywords Rock cut slope, Crevice density, Natural recovery, Biological soil crust, Soil organic carbon, Soil total nitrogen, Soil total phosphorus

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Introduction

Rock cut slope (RCS), which is created by anthropogenic activity (e.g., mining and transportation construction) in mountainous areas, is a type of steep and bare artificial rock face (Chen et al. 2022; Huang 2005; Li et al. 2018a; Yan et al. 2022; Yang et al. 2016; Yuan et al. 2006; Zhao et al. 2020). As an extremely degraded ecosystem, the formation of RCSs not only impairs regional ecological functions as a result of soil and water loss aggravation, landscape fragmentation and the potential risk of natural disaster increments, but also threatens regional biodiversity and sustainable development (Chen et al. 2022; Lai et al. 2022; Lee et al. 2013; Li et al. 2018a, 2022; Liu et al. 2014). To restore ecosystems on RCSs, numerous artificial restoration techniques using artificial soil and metal mesh, such as vegetation concrete foundation spraying, external-soil spray seeding and hydraulic covering, have been adopted (Chen et al. 2022; Lai et al. 2022; Li et al. 2018a; Xu et al. 2015; Yan et al. 2022). These techniques can rapidly create a simple "soil–vegetation" system on RCS (Chen et al. 2022; Huang et al. 2022; Li et al. 2018a; Yang et al. 2016; Zhao et al. 2020). However, the restoration expense using these techniques might be as high as hundreds of RMB yuan per square meter in China (Xu et al. 2015). Thus, the high costs hamper the application of artificial restoration techniques, especially in remote and mountainous areas. Although natural recovery (passive restoration) is convenient and inexpensive, it is a relatively slow process which may take decades or even centuries (Cullen et al. 1998; Pereira et al. 2021, 2022; Tonello et al. 2022). How to restore the ecosystems of RCSs economically and effectively in alpine regions needs to be further studied.

Biological soil crusts (BSCs), which are complex or hybrid of fine soil, bryophytes, lichens, fungi, cyanobacteria and microorganisms, are important components of land cover and are generally categorized into three different successional stages, i.e., cyanobacterial crust, lichen crust and bryophyte crust (Belnap et al. 2001, 2016; Belnap 2010; Deng et al. 2020; Hu et al. 2002; Lan et al. 2012, 2015; Xiao et al. 2019a). BSCs are early and fast pioneer colonizers of degraded and harsh environments, especially in strongly disturbed areas where vascular plant development is less likely to occur (Bowker 2007; Bu et al. 2013). BSCs are widely considered as important ecosystem restorers (Bowker 2007; Bowker et al. 2010; Karimi et al. 2022; Lu et al.2022a) due to the functional roles which BSCs play in natural ecosystems (Concostrina et al. 2019), such as soil microorganism activity and diversity improvement (Tian et al. 2022a; Wang et al. 2022a, b), soil water storage (Chamizo et al. 2013; Gong et al. 2022; Lu et al. 2022b; Belnap et al. 2016), soil fertility improvement (Belnap et al. 2016; Bowker 2007; Chamizo et al. 2012; Deng et al. 2020; Elbert et al. 2009; Gao et al. 2018; Giora et al. 2015; Karimi et al. 2022; Nyenda et al. 2019; Tian et al. 2022b; Wang et al. 2022b; Zhang et al. 2005a; Zhang et al. 2022; Zubiri et al. 2022), soil stability and physical structure enhancement (Gall et al. 2022; Hu et al. 2002; Karimi1 et al. 2022; Mager and Thomas 2011), soil erosion alleviation (Chamizo et al. 2013, 2019; Gall et al. 2022; Guo et al. 2022; Kheirfam and Roohi 2022), and facilitating or inhibiting vascular plant establishment and growth (Belnap et al. 2016; Caroline et al. 2019; Havrilla et al. 2019; Xiao et al. 2019a). Microorganisms play a key role in the most of the functional roles of BSCs (Bilen and Turan 2022), e.g., segregating organic acids so as to contribute to mineral bio-weathering (e.g., releasing and solubilizing P and metal elements) (Al-Maliki and Breesam 2020; Bilen and Turan 2022; Moore et al. 2022; Tian et al. 2022b; Zhu 1995), and regulating soil microbial activity and diversity (Castillo-Monroy et al. 2011; Zubiri et al. 2022), and fixing nutrients (C, N and P) and accelerating the mineralization of organic matters to improve soil fertility and quality and maintain soil nutrients cycling (Hayat et al. 2010; Hyvrinenm et al. 2002; Karimi et al. 2022; Kleber et al. 2021; Margolis et al. 2022; Sokol et al. 2022; Tian et al. 2022a, b; Turan et al. 2019; Wang et al. 2022a, b). In addition to fixing nutrients, microbes also break down organic matters or plant litter in soils, in turn affecting the soil fertility (Albornoz et al. 2022; He et al. 2022; Liu et al. 2022; Sokol et al. 2022; Tian et al. 2022a, b; Tonello et al. 2022; Turan et al. 2019; Wang et al. 2022a, b). Meanwhile, the metal cation released by microorganisms within BSCs also could fix nutrients form water and dust into soils (Hafsteinsdóttir et al. 2015; Netherway et al. 2019; Rasool et al. 2022; Tauqeer et al. 2022). Therefore, BSCs are usually regarded as promising and economic tools for ecological restoration engineering, particularly for degraded ecosystems in alpine regions, which are fragile ecosystems (Bu et al. 2015a, b; Deng et al. 2020; Lu et al. 2022a). A number of studies were conducted to identify the process and influencing agents of BSC development to exploit the ecological restoration functions and efficiency of BSCs. Even for extremely degraded ecosystems, BSCs can develop naturally from cyanobacterial crusts, and lichen crusts to bryophyte crusts over several years or decades (Belnap et al. 2001, 2016; Concostrina-Zubiri et al. 2019; Deng et al. 2020; Xiao et al. 2019a). Although BSCs can tolerate harsh environments, their growth and development are largely controlled by environmental factors such as soil water (Bu et al. 2015b; Chen et al. 2005; Lucieer et al. 2014; Zhang et al. 2005b), air humidity (Oishi 2019; Karger et al. 2012), precipitation (Langhans et al. 2010; Peng et al. 2022; Zaady et al. 2007; Zhang et al. 2005b), soil nutrients (Bu et al. 2015b; Tian et al. 2021;

Zhang et al. 2002, 2021), vascular plants (Peng et al. 2022; Zhang et al. 2002) and microtopography (Ji et al. 2018; Li et al. 2018a; Lucieer et al. 2014; Zhu 1995), soil microorganism (Karimi et al. 2022; Margolis et al. 2022), dusts or sediments (Peer et al. 2022; Reynolds et al. 2001), as well as human activities and inoculation (Chaudhary et al. 2020; Chen et al. 2009; Deng et al. 2020; Karimi et al. 2022; Tian et al. 2022a). Microtopography, as an important environmental factor, also affects BSCs type (Chen et al. 2005), distribution (Ji et al. 2018; Zhang et al.2002; Zhang et al. 2005b; Zhu 1995) and physiological characteristics (Lucieer et al. 2014). In recent years, the application of BSCs on ecological restoration has been highly anticipated. However, the properties of and interaction between mosses and soils within BSCs on RCS are rarely reported (Concostrina-Zubiri et al. 2019).

Crevices (including grooves and cracks), as the main microtopographic features, have been found to exert an important ecological significance for plant growth in arid regions and on RCSs by providing space and nutrients for vascular plant roots (Liu et al. 2019; Sehhati et al. 2015; Yuan et al. 2006; Zhu 2011). Topography (e.g., slope, aspect and latitude) of RCS and soil properties influenced the species composition of BSCs (Concostrina-Zubiri 2019). However, the effect of crevices on BSC development on rock cut slopes is unknown.

To provide scientific basis and guidance for the utilization of BSCs on RCSs, here, the crevice density, coverage and biomass of BSCs and the weight, organic carbon (OC), total nitrogen (TN) and total phosphorus (TP) contents of soils in 164 quadrats on 13 RCSs and the OC, TN and TP contents of soils sampled from 10 natural slopes in the mountainous area of West Sichuan, Southwest China, were measured and analyzed to explore (1) the variation in major nutrients of soils which naturally restored on RCSs; (2) the effect of crevice density on BSCs development on rock cut slopes; (3) the effect of the formation age of crevices on BSC development on RCSs.

Materials and methods

Study regions and sampling sites

This study was conducted on the eastern slope of the Jiajinshan Mountainous Range (31°43.36′–30°51.63′N, 102°40.96′–102°46.05′E) (Fig. 1d) and the northern section of the Jiudinshan Mountainous Range (30°11.86′–31°21.83′N, 103°46.25′–104°03.85′E) (Fig. 1e) in the mountainous regions of West Sichuan, Southwest China (Fig. 1).

The eastern slope of the Jiajinshan Mountainous Range (SR1) is located in Baoxin, Ya'an (Fig. 1c, d). The terrain of Baoxin is relatively high in the north and low in the south, with the highest elevation of more than 5000 m a.s.l. A subtropical monsoon climate prevails in Baoxin with a mean annual temperature of 15.3 °C and mean annual precipitation of 1000 mm. Rain mainly falls during the summer. With elevation increasing from ~ 1500 m to more than 4100 m, the following vegetation successively occurs, viz. subtropical evergreen broad-leaved

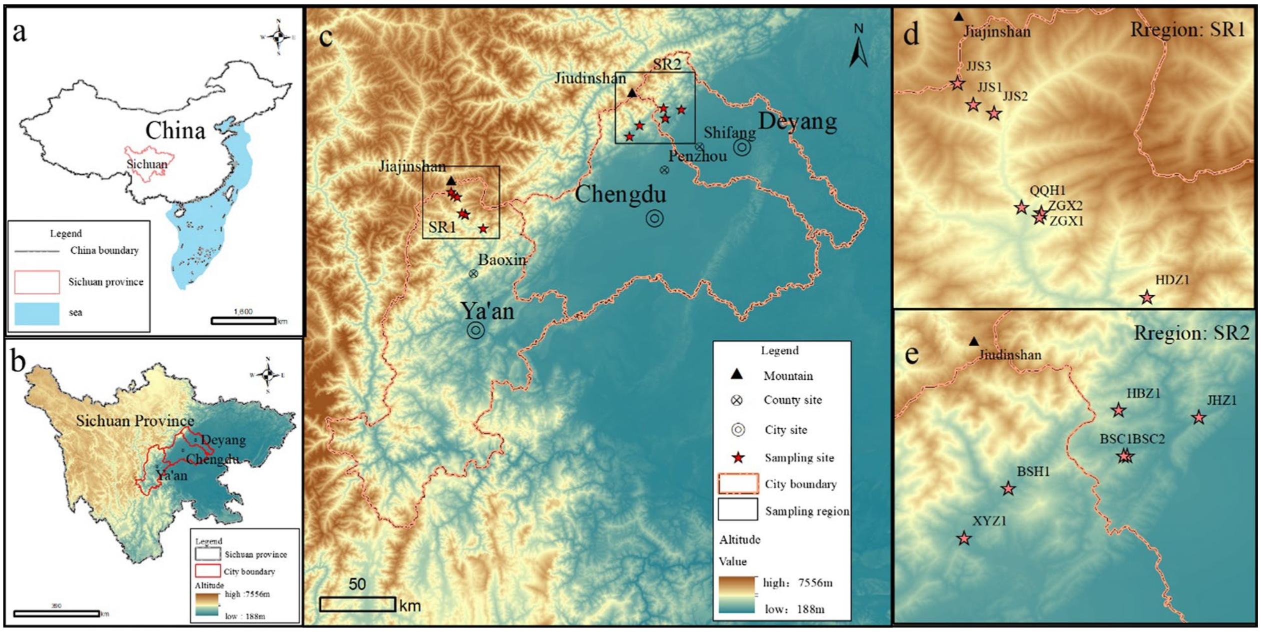

Fig. 1 Study regions and sampling sites lying in mountainous regions of west Sichuan, China

forest, evergreen and deciduous broad-leaved mixed forest, needles and broad-leaved mixed forest, coniferous forest, shrubs, subalpine meadow and alpine talus.

Jiudinshan Mountain lies in the northwestern Sichuan Basin. On the eastern slope of the northern section of the Jiudinshan Mountainous Range (SR2) (Fig. 1c, e), the elevation of many peaks exceeds 3000 m. A subtropical monsoon climate prevailed in SR2, with a mean annual temperature of 15.9 °C and a mean annual precipitation of 1000 mm or higher, accompanied by an air relative humidity greater than 83%. The rainfall in SR2 was also concentrated in summer and increased from southeast (the foot of mountain) to northwest (the summit of mountain). Along the elevation gradient in SR2, the vegetation types of evergreen broad-leaved forest, evergreen broad-leaved forest and deciduous broad-leaved mixed forest, subalpine coniferous forests and subalpine meadow vary successively.

Collection of BSC samples

In May and August of 2018, 164 quadrats on rock cut slopes at 13 sampling sites (7 in SR1 and 6 in SR2) were selected to explore the development process and the effect of crevice density on the development of BSCs (Table 1). Eight to 19 quadrats (20 cm × 20 cm) were randomly set up at each sampling site. To exclude the disturbance of the other environmental factors, all sampling slopes should have the following characteristics: (1) no collapse or falling stone; (2) no perennial running water; (3) no adverse slope; and (4) an area without obvious microrelief except for crevices. Furthermore, bryophyte crust coverage accounted for more than 95% of the total coverage of BSCs at the sampling sites (Fig. 2). The longitude, latitude, elevation, slope gradient and aspect at each site were measured using a handheld GPS receiver and a geological compass. The formation age (FA) of each RCS was obtained by inquiring local reports via newspaper or website or asking local transportation authorities and residents. The FA was also regarded as the formation age of the crevices at the sampling sites.

To analyze the coverage of BSCs (COV, %), images of each quadrat were taken using close-range photogrammetry, before sampling (Ji et al. 2018; Li et al. 2018a, b; Lucieer et al. 2014). Then, the soil and BSCs in the crevices within each quadrat were collected into plastic bags using a knife and a tweezer (Ji et al. 2018).

Mixed soil samples on natural slopes near the sampling sites were collected as references (CK). Each mixed soil sample (approximately 1 kg) is composed of soil collected from 5 to 10 random points on each natural slope (Li et al. 2018a, b; Yuan et al. 2006). In total, 6 mixed soil samples were collected in SR1, while 4 mixed soil samples were collected from coniferous forests in SR2.

Determination of soil properties

The soil weight (SW, g m^{-2}) in each quadrat was measured by the weighting method (Bao 2000). The OC, TP and TN contents in soils were measured by the potassium dichromate oxidation heating method, UV spectrophotometry and semimicro-Kjeldahl method, respectively (Bao 2000; Greene and Tongway 1989).

Table 1 Environment characteristics of sampling sites in mountainous regions of west Sichuan, China

Region	Site	Number of quadrats	FA (years)	Elevation (m)	Gradient (°)	Aspect (°)	Bed rock	CK	Neighboring vegetation
SR1	JJS3	8	2.5	4116	81	155	Sandstone	JJS3	Subalpine meadow
	ZGX1	10	4	2640	71	137	Limestone	QQH1, ZGX2 and ZGX1	Mixed broadleaf and coniferous forests
	ZGX2	14	4	2430	85	310	Limestone	QQH1, ZGX2 and ZGX1	Abandoned farmland
	QQH1	13	13	2164	80	65	Limestone	QQH1, ZGX2 and ZGX1	Abandoned farmland
	JJS1	12	8	3448	90	70	Sandstone	JJS1	Subalpine meadow
	JJS2	12	8	3187	80	50	Sandstone	JJS2	Coniferous forest
	HDZ1	12	27	2353	75	315	Limestone	QQH1, ZGX2 and ZGX1	Mixed broadleaf and coniferous forests
SR2	XYZ1	19	2.5	1043	88	135	Sandstone	XYZ1	Artificial fir forest
	JHZ1	15	1.5	1110	65	100	Sandstone	BSC1	Artificial fir forest
	BSC1	11	1.5	949	70	35	Limestone	BSC1	Artificial fir forest
	BSC2	14	1.5	1003	64	5	Sandstone	BSC2	Artificial fir forest
	HBZ1	9	5	1285	82	0	Limestone	BSC1	Artificial fir forest
	BSH1	15	> 60	1143	90	135	Sandstone	BSH1	Artificial fir forest

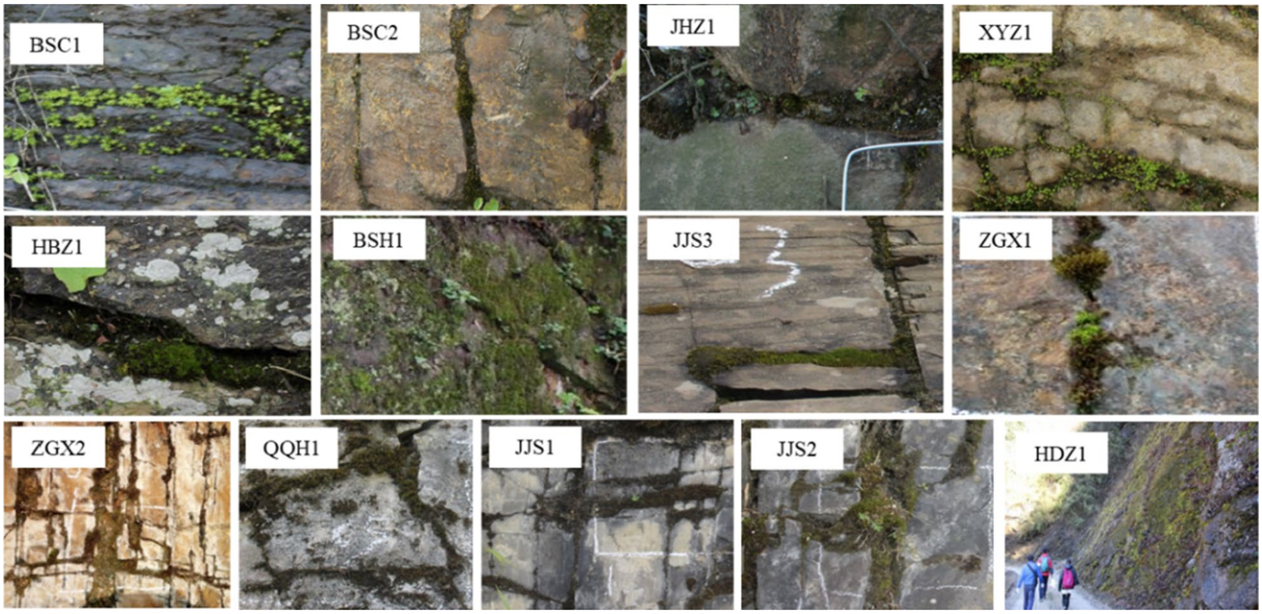

Fig. 2 BSCs development and crevices at selected sampling sites on 13 rock cut slopes

Measurement of BSC biomass and coverage

The biomass of BSCs (BM, g m^{-2}) was the dry weight of bryophytes, lichens, fungi, and cyanobacteria at the sampling sites, measured by the weighting method (Tu et al. 2021). Coverage of BSCs (COV, %) was estimated using close-range photogrammetry (Ji et al. 2018; Lucieer et al. 2014). The main steps to estimate the COV successively are listed as follows: (1) identifying the region with and without BSCs in images of quadrats using multiple software (i.e., ArcGIS, Photoshop and ENVI); (2) calculating the area of the region with and without BSCs in each quadrat using ArcGIS; and (3) estimating the percentage of the region with BSCs in each quadrat as COV. The COV value was obtained using Eq. (1):

$$\mathrm{COV} = 100 \times N_{\mathrm{m}}/(N_{\mathrm{m}} + N_{\mathrm{p}}), \tag{1}$$

where N_m and N_p are the area of the region with and without BSCs within each quadrat, respectively.

Crevice density determination

The crevice density of each quadrat was expressed by the area index of the crevices (I_R, %) of each quadrat, and estimated using Eq. (2) (Sehhati et al. 2015):

$$I_{\mathrm{R}} = I_{\mathrm{s}}/S_{\mathrm{q}} \times 100, \tag{2}$$

where I_S and S_q are the total area of the crevices (mm^2) and the area of each quadrat (40,000 mm^2), respectively.

The area occupied by the crevices in each quadrat was measured on-site using an electronic Vernier caliper (the accuracy was 0.01 mm). The I_S value was measured using the following steps: (1) dividing crevices into multiple regular subzones; (2) measuring the length and width of regular subzones and calculating the area of each regular subzone; and (3) estimating the I_S value at each quadrat using the following Eq. (3):

$$I_{\mathrm{s}} = \sum_{i}^{n} S_i, \tag{3}$$

where n is the total number of subzones in each quadrat and S_i is the area of the ith subzone (mm^2).

Data processing

Linear regression analysis was used to define the correlation among soil weight, BSCs and I_R. The differences in soil and BSC parameters at different sampling sites were calculated using analysis of variance (ANOVA) with the least significant difference (LSD). Pearson correlation matrix analysis (CMA) was used to define the relationships among BSC and soil properties. Linear regression analysis, ANOVA and CMA were performed using SPSS. A level of $P < 0.05$ was considered to be significant.

Results

Crevice density

The averaged I_R values at the sampling sites varied between 0 and 19.8% (Fig. 3). The averaged I_R values decreased in the order of ZGX1 (19.8%) > ZGX2

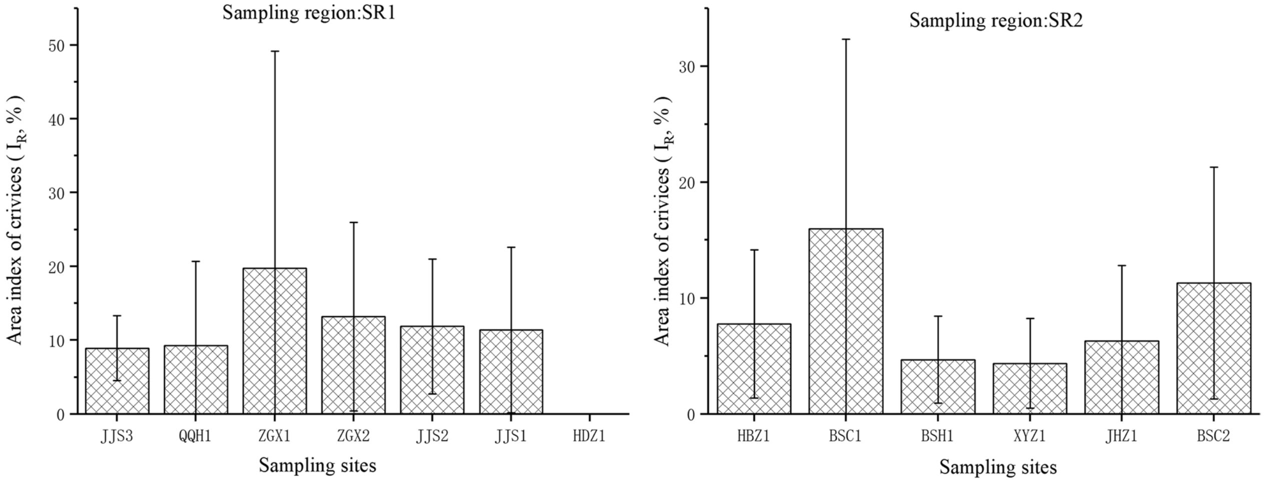

Fig. 3 Averaged area index values and standard deviations of crevices at each sampling site

(13.2%) > JJS2 (11.9%) > JJS1 (11.4%) > QQH1 (9.3%) > JJS3 (8.9%) > HDZ1 (0%) in SR1 and BSC1 (16.0%) > BSC2 (11.3%) > HBZ1 (7.8%) > JHZ1 (6.3%) > BSH1 (4.7%) > XYZ1 (4.4%) in SR2.

BSCs distribution

Regardless of the altitude and bedrock type, BSCs on rock cut slopes were distributed generally and first along crevices, except at sites BSH1 and HDZ1 (FA > 27 years) (Fig. 2). In addition, at site QQH1 (FA = 13 years), star-shaped BSCs appeared scattered in the non-crevices area. Some crevices at sites JJS3, BSC1, ZGX1 and HBZ1 (FA < 5a) were not fully filled with BSCs. For sampling sites with FA values over 27 years, BSCs appeared on nearly the whole rock surface, including the flat surface.

Coverage and biomass of BSCs

The averaged COV and BM values of each sampling site ranged from 6.5 to 69.0%, and 14.43 g m^{-2} to 261.79 g m^{-2}, respectively. Significant differences were found in the mean COV and BM among different sampling sites in the same region (Table 2). In a similar environment (e.g., altitude, bedrock, slope aspect, and gradient), the averaged COV and BM increased significantly with elevated FA (Table 2). In the region SR1, the averaged COV and BM at the youngest site JJS3 (FA = 2.5 years) were significantly lower than those at the other sites, while the averaged COV and BM at the oldest site HDZ1 (FA = 27 years) were the highest and were significantly higher than those at the other sites. In region SR2, the averaged COV and BM at the oldest site BSH1 (FA > 60 years) were significantly higher than those at the other sites (FA < 5 years), while the difference in averaged COV and BM at the sites except BSH1 was insignificant (Table 2).

Table 2 COV and BM on 13 RCSs in study regions of west Sichuan, China

Region: SR1					Region: SR2				
Site	FA (years)	Number of quadrats	BM (g m^{-2})	COV (%)	Site	FA (years)	Number of quadrats	BM (g m^{-2})	COV (%)
JJS3	2.5	8	18.40 ± 18.12c	6.5 ± 4.1c	BSC1	1.5	19	18.20 ± 23.28b	10.3 ± 11.3b
ZGX1	4	10	51.07 ± 62.71bc	20.2 ± 24.0bc	HBZ1	5	15	34.82 ± 25.42b	7.7 ± 5.4b
ZGX2	4	14	49.12 ± 44.48bc	21.1 ± 19.3bc	BSC2	1.5	11	24.08 ± 15.42b	6.5 ± 3.2b
JJS2	8	12	66.40 ± 56.94b	14.6 ± 12.1bc	JHZ1	1.5	14	24.42 ± 30.86b	6.9 ± 7.1b
JJS1	8	12	28.53 ± 21.23bc	13.8 ± 11.2bc	XYZ1	2.5	9	14.43 ± 13.07b	15.7 ± 12.8b
QQH1	13	13	67.25 ± 40.77b	28.2 ± 12.1b	BSH1	> 60	15	68.13 ± 83.24a	38.1 ± 23.9a
HDZ1	27	12	261.79 ± 250.52a	69.0 ± 14.6a					

FA, BM, and COV represent formation age of RCSs, biomass and coverage of BSCs, respectively; BM and COV data are expressed in mean ± standard deviation. Within the same study region, different lowercase letters represent the significant difference ($P < 0.05$) in biomass or coverage among various sites

Soil distribution and weight at sampling sites

Despite the steepness of the RCSs, a small amount of soils might be found along crevices or caves on RCSs (Yuan et al. 2006; Zhu 2011). In our study, the average SW varied significantly at 13 sites (Table 3). The average SW at each site fluctuated between 127.69 and 1277.74 g m^{-2} and insignificantly increased with FA (Table 3). The average SW on rock cut slopes was highest at site ZGX1 (1277.74 g m^{-2}) and lowest at site HDZ1 (231.27 g m^{-2}) in region SR1, while it was highest at site JHZ1 (309.63 g m^{-2}) and lowest at site HBZ1 (127.69 g m^{-2}) in region SR2.

At the sampling sites, soils were distributed along crevices or covered by BSCs (Fig. 2).

Soil OC, TN, and TP contents

The average TN content of soils at all sampling sites fluctuated between 0.96 and 6.02 g kg^{-1} (Table 4). The average TN content of soils at site HDZ1 was significantly lower than that on the natural slope in SR1. Compared with the younger sites in region SR2, the older sites had higher average TN contents of soils (e.g., HBZ1 > BSC1, BSH1 > XYZ1 > JHZ1, YSX2 > YSX3, MLC2 > MLC1), while the average TN contents of soils at various ages of rock cut slopes were different in region SR1 (e.g., QQH1 > ZGX2 > HDZ1). No sampling site had a significantly lower average TN content of soils than those on the natural slope (CK), except at sites HDZ1 and JHZ1.

The average OC content of soils at the sampling sites was the highest at site HBZ1 (123.03 g kg^{-1}) and the lowest at site JHZ1 (18.61 g kg^{-1}). The average OC contents of soils at sites JHZ1, XYZ1 and ZGX1 were significantly lower than those on natural slopes (Table 4). No sampling site had a significantly lower average OM content of soils than those on the natural slope, except at sites ZGX1, JHZ1 and XYZ1.

Table 3 SW with BSCs at sampling sites in mountainous regions of west Sichuan, China

Region	Sites	FA (years)	SW (g m^{-2})	Region	Sites	FA (years)	SW (g m^{-2})
SR1	JJS3	2.5	263.90 ± 201.25b	SR2	BSC1	1.5	240.38 ± 242.98a
	ZGX1	4	1277.74 ± 1614.65a		HBZ1	5	127.69 ± 96.34a
	ZGX2	4	348.94 ± 401.49b		BSC2	1.5	230.27 ± 172.66a
	JJS2	8	613.80 ± 625.71b		JHZ1	1.5	374.27 ± 529.07a
	JJS1	8	425.03 ± 499.94b		XYZ1	2.5	183.27 ± 152.34a
	QQH1	13	250.49 ± 270.31b		BSH1	> 60	266.30 ± 229.80a
	HDZ1	27	231.27 ± 193.26b				

FA and SW represent formation age of RCSs and soil weight, respectively; SW data are expressed in mean ± standard deviation. Within the same region, different lowercase letters represent the significantly different ($P < 0.05$) in soil weight

Table 4 The soil organic carbon, total nitrogen and total phosphorus contents at sampling sites

Regions	Site	FA (years)	TN (g kg^{-1})		OC (g kg^{-1})		TP (g kg^{-1})	
			RS	CK	RS	CK	RS	CK
SR1	JJS3	2.5	1.46 ± 0.46Ba	1.28 ± 0.14a	42.30 ± 32.92Ba	42.30 ± 3.88a	0.85 ± 0.09BCa	0.89 ± 0.03a
	ZGX1	4	2.10 ± 0.99Ba	2.75 ± 0.42a	36.00 ± 11.11Bb	68.87 ± 11.06a	2.46 ± 0.36Aa	0.86 ± 0.16b
	ZGX2	4	2.37 ± 3.39Ba	2.75 ± 0.42a	68.66 ± 47.54Ba	68.87 ± 11.06a	1.19 ± 0.32Ba	0.86 ± 0.16a
	QQH1	13	6.02 ± 1.67Aa	2.75 ± 0.42b	74.67 ± 23.29Ba	68.87 ± 11.06a	2.31 ± 1.11Aa	0.86 ± 0.16b
	JJS2	8	2.22 ± 1.15Ba	0.97 ± 0.11b	56.36 ± 11.43Ba	13.56 ± 4.39b	0.97 ± 0.19BCa	0.99 ± 0.03a
	JJS1	8	2.13 ± 1.03Ba	1.03 ± 0.03b	38.85 ± 20.43Bab	22.04 ± 1.21b	0.87 ± 0.39BCa	0.98 ± 0.03a
	HDZ1	27	1.56 ± 1.02Bb	2.75 ± 0.42a	102.96 ± 43.13Aa	68.87 ± 11.06b	0.44 ± 0.19Cb	0.86 ± 0.16a
SR2	BSC1	1.5	2.42 ± 1.19Ba	3.00 ± 0.19a	90.50 ± 32.13Ba	55.74 ± 4.73b	0.55 ± 0.15Ba	0.42 ± 0.02a
	HBZ1	5	4.03 ± 1.80Aa	3.00 ± 0.19a	123.03 ± 20.44Aa	55.74 ± 4.73b	0.82 ± 0.18Aa	0.42 ± 0.02b
	BSC2	1.5	2.15 ± 0.65Ba	2.97 ± 0.21a	47.29 ± 23.57Ca	53.38 ± 4.01a	0.69 ± 0.19ABa	0.43 ± 0.42b
	JHZ1	1.5	0.96 ± 0.39Cb	3.00 ± 0.19a	18.61 ± 6.82Db	55.74 ± 4.73a	0.52 ± 0.06Ba	0.42 ± 0.02b
	XYZ1	2.5	2.23 ± 1.07Ba	2.53 ± 0.45a	37.23 ± 18.07DCb	46.56 ± 2.37a	0.76 ± 0.25Aa	0.61 ± 0.07b
	BSH1	> 60	3.48 ± 1.94ABa	2.92 ± 0.19a	73.81 ± 18.87Ba	45.92 ± 0.69b	0.85 ± 0.33A	0.66 ± 0.08

FA represents formation age of RCSs; RS and CK represent soils sampled on RCSs and natural slopes, respectively. The date of TN, OC, and TP are expressed in mean ± standard deviation. Within the same region, different lowercase letters represent the significantly different ($P < 0.05$) in major soil nutrients between RS and CK, and different capital letters represent the significantly different ($P < 0.05$) in major soil nutrients among different sites in the same region

The average TP content of soils at the sampling sites ranged from 0.52 to 2.46 g kg^{-1} (Table 4). No sampling site had a significantly lower average TP content of soils than those on the natural slope, except at site HDZ1.

Discussion

Effect of crevice density on BSCs development on RCS

Development of BSC coverage and biomass controlled by crevice density

Positively significant relationships were observed among COV, BM and I_R at the sampling sites with FA of less than 13 years (Figs. 4, 5). At sites XYZ1, HBZ1, JHZ1, BSC2, ZGX1, ZGX2, JJS1 and JJS2, COV had a significantly positive correlation with I_R ($P < 0.05$) (Fig. 4). At sites XYZ1, JHZ1, BSC2, ZGX1, ZGX2, JJS1, QQH1 and JJS2, BM linearly and significantly increased with I_R ($P < 0.05$) (Fig. 5). COV and BM linearly and significantly increased with increasing I_R, despite the bedrock, aspect and altitude of the sampling sites within an age of 13 years (Fig. 6).

Significant correlations between I_R, COV and BM are not significantly impacted by bedrock, slope aspect and altitude at sampling sites within an age of less than 13 years, revealing that crevice density might be the main environmental factor which controls the formation and development of BSCs on newly formed RCSs (FA < 13 years) (Fig. 6).

Despite strong erosion occurring on newly formed RCSs, the crevices can trap soil grains in runoff derived from adjacent ecosystems, airborne particles, and the cells of cyanobacteria or microalgae, which is critical for BSC formation at the initial stage (Lu et al. 2022a; Peer et al. 2022; Reynolds et al. 2001; Yuan et al. 2006; Zhao et al. 2020; Zhu 2011). In other words, the crevices on RCSs could provide a refuge for “seed” and “food” of BSCs, and push the attachment and development of BSCs (Sehhati et al. 2015; Yuan et al. 2006; Zhu 2011). Although BSCs are drought-tolerant fast pioneer colonizers, numerous studies showed that water plays an important role in the development of BSCs (Bu et al. 2015b; Chen et al. 2009; Langhans et al. 2010; Lucieer et al. 2014; Oishi 2019; Peng et al. 2022; Wu et al. 2022; Zaady et al. 2007; Zhang et al. 2005b). Accordingly, the

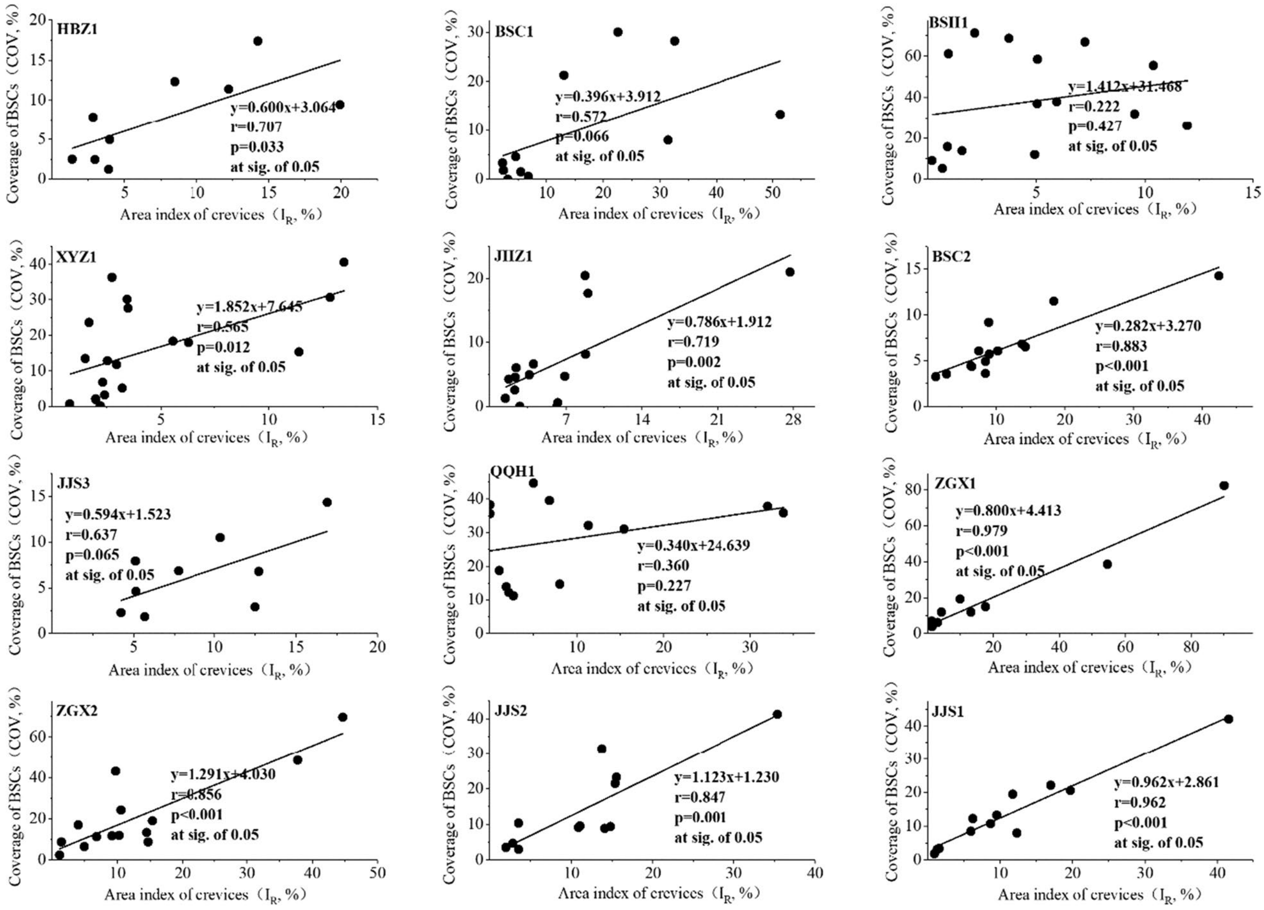

Fig. 4 Plots of BSC coverage and area index of crevices at 13 sampling sites

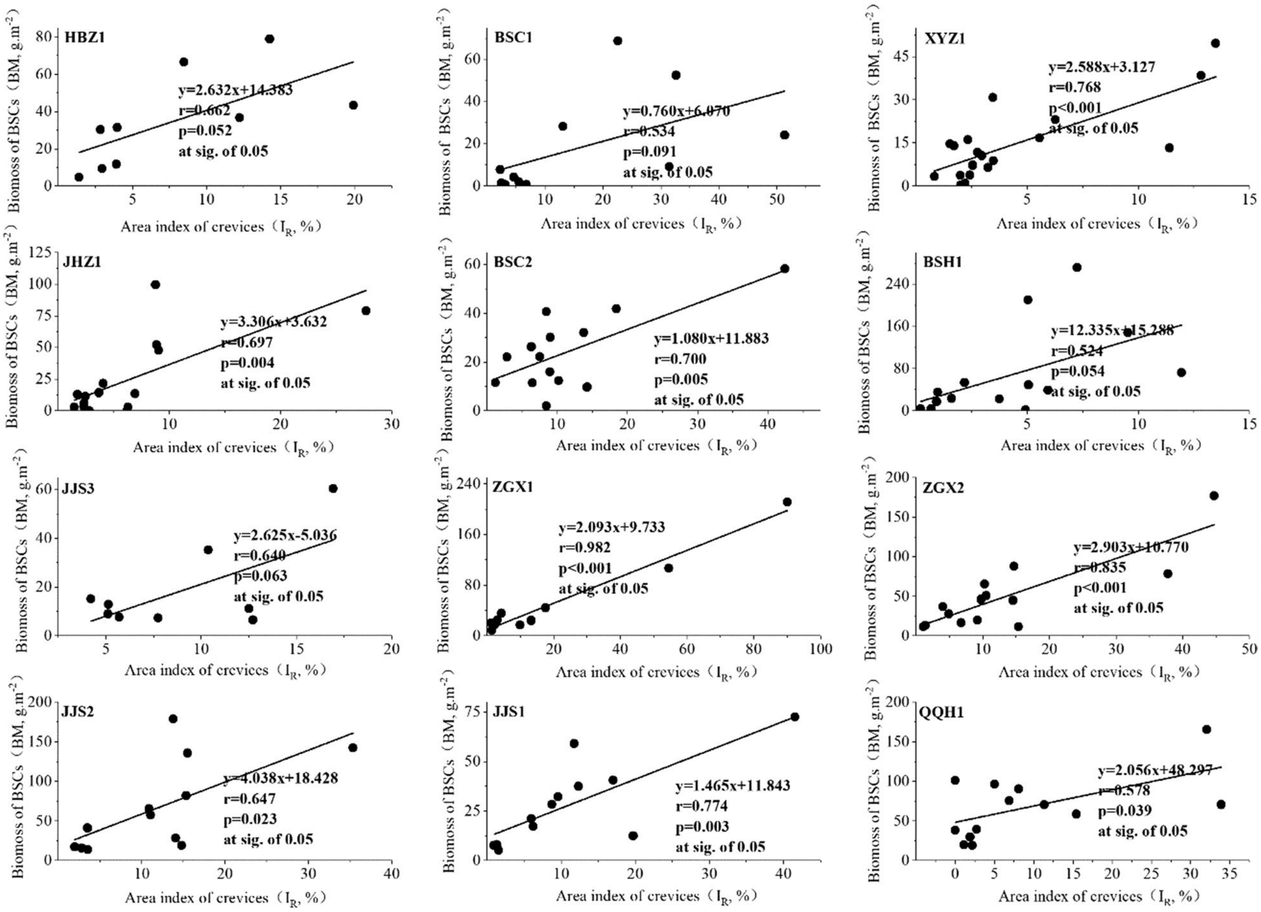

Fig. 5 Plots of BSC biomass and area index of crevices at 13 sampling sites

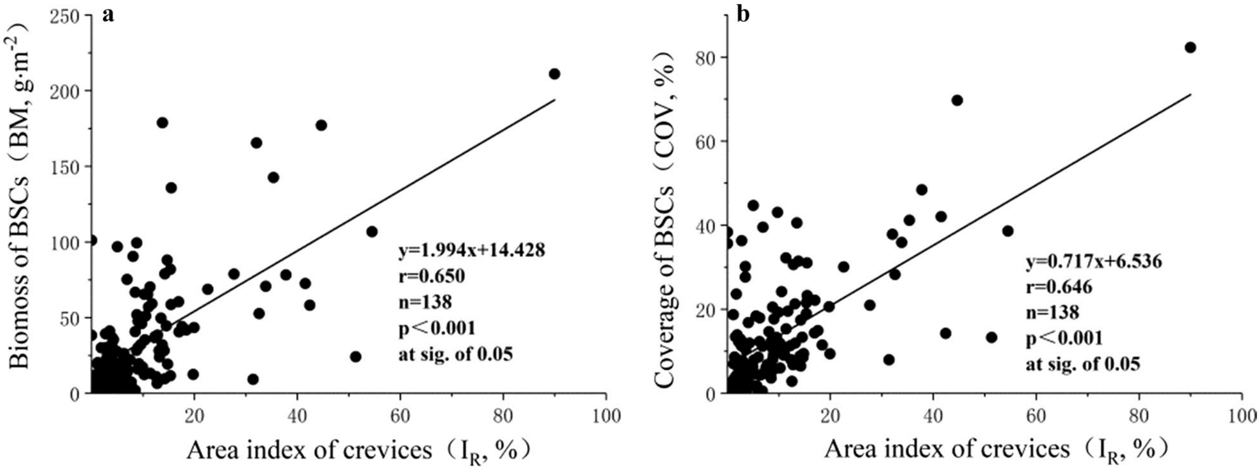

Fig. 6 Relationships between I_R and BM (**a**) and COV (**b**) on RCSs. The data in Fig. 6 all come from the rock cut slopes with formation age of less than 13 years

water-holding environment caused by the crevices relative to the smooth surfaces on the newly formed RCSs is beneficial for BSC growth. The facade conditions of RCSs are harsh, which leads to fast runoff and intense solar evaporation (Yan et al. 2022; Yuan et al. 2006; Zhao et al. 2020). Without room for adequate water conservation, water availability dominantly constrains the growth of many plants on rock faces (Cullen et al. 1998; Yuan et al. 2006; Zhao et al. 2020; Zhu 2011). Fortunately, the concave spaces on RSCs, e.g., the crevices or caves, can store water to support the growth of some organisms (Fitzsimons and Michael 2017; He et al. 2019). Furthermore, the soils trapped by the crevices can also store more water to support BSC growth than relatively flat rock surfaces (Lucieer et al. 2014).

Similarly, although nutrient elements, e.g., the C, N and P, of BSCs may come from the atmosphere, runoff and airborne dusts, the crevices, compared with the relatively flat surfaces on RCSs, could create more favorable conditions, e.g., fertile and fine earths and microorganisms, for BSCs to utilize nutrients on RCSs to facilitate BSC development (Karimi et al. 2022; Margolis et al. 2022; Peer et al. 2022; Turan et al. 2019; Wang et al. 2022b; Wu et al. 2022). Meanwhile, the existence of crevices on RCSs may increase the time of contact between BSCs and water or runoff with nutrients by reducing and blocking runoff (Fitzsimons and Michael 2017). BSCs can take advantage of nutrient elements in the atmosphere (e.g., C and N) by photosynthesis and microorganisms, as well as the capture of runoff nutrients and rainfall nutrients (Bilen and Turan 2022; Mager 2010; Sokol et al. 2022; Tian et al. 2021; Turan et al. 2019; Zhang et al. 2021). BSCs without true root systems have different nutrient utilization modes from many vascular plants (Belnap et al. 2001; Belnap 2010). Generally, BSCs can benefit from nutrients, e.g., N and P derived from water, by absorbing runoff or rainfall through their capillary systems, such as gaps between leaves, between leaves and stems, between rhizomes, and between verrucous projections on the surfaces of leaves or stems (Li et al. 2009; Proctor 1981). The high cation exchange capacity of BSCs can also absorb and accumulate nutrients from the runoff with a very low nutrient content (Buescher et al. 1990). Crevices, relative to relatively smooth rock surfaces, can trap rainfall or runoff in concave spaces and increase the stay time of nutrients. Furthermore, the moisture would be evaporated in grooves less than on a relatively smooth surface of rock (Fitzsimons and Michael 2017). This could also increase the duration that BSCs absorb nutrients and moisture to increase the effectiveness of nutrients and water for BSC growth. Soil microorganisms and enzymes play a key ecological role in nutrient cycling in ecosystems and can promote BSC utilization of nutrients (Deng et al. 2020; Karimi et al. 2022; Margolis et al. 2022; Tian et al. 2022a, b; Wang et al. 2022a, b; Zhang et al. 2021) and BSC growth (Zhao et al. 2020). Bryophytes and nitrogen-fixing microorganisms such as cyanobacteria and rhizobium that contain nitrogen-fixing enzymes form symbiotic nitrogen-fixing systems and have the ability to fix N_2, thus providing nitrogen for BSC development (Hayat et al. 2010; Hyvrinenm et al. 2002; Karimi et al. 2022; Palmqvist et al. 1998; Sokol et al. 2022; Turan et al. 2019). N_2O in the atmosphere can be directly absorbed by BSCs under the catalysis of nitrogenase (Mozen and Burris 1954; Takeshi et al. 1987). Additionally, nutrients, such as P and N, which are the main synthetic elements of amino acids and nucleic acids, in soils may also promote the growth and division of bryophytes in BSCs (Deng et al. 2020; Tian et al. 2022a, b).

Overall, the crevices on RCSs could create more favorable conditions, e.g., water, soil, active and diverse microorganisms, and higher efficiency in nutrient use, and thus definitely facilitate BSC formation or succession.

Effect of crevice density on soil accumulation

The soils accompanied by BSCs were mostly distributed along and coexisted in the crevices. At some younger sampling sites, soils may have been deposited in crevices which were not fully filled with BSCs (Fig. 2). Meanwhile, a positive correlation between SW and I_R occurred at most sampling sites (Fig. 7), which implied that the crevices might be conducive to soil accumulation in the early stage of BSCs growth at the sampling sites.

Two channels might promote soil accumulation along the crevices or explain why the crevices might be conducive to soil accumulation.

It is difficult to sustain soil grains on younger RCSs, which are highly vulnerable due to extremely dramatic runoff and wind erosion (Chen et al. 2022; Cullen et al. 1998; Huang 2005; Li et al. 2018a; Yan et al. 2022; Yuan et al. 2006). However, compared with the relatively flat surfaces of RCSs, the crevices had more sunken spaces that could reduce external forces to provide a refuge for trapping weathering products, soils, and dust deposits carried by runoff and wind (Peer et al. 2022; Reynolds et al. 2001; Sehhati et al. 2015; Yuan et al. 2006; Zhu 2011).

BSCs distributed along crevices are also crucial for soil accumulation and formation (Belnap et al. 2001; Belnap 2010; Bowker et al. 2010; Bu et al. 2015a; Tu et al. 2021; Zhu 1995). Our results showed that SW increased significantly with the coverage and biomass of BSCs, which were dominantly distributed in and around the crevices (Fig. 8). The organic acids secreted by BSCs can promote rock weathering to accelerate soil formation (Meng et al. 2019; Zhu 1995). More importantly, BSCs may

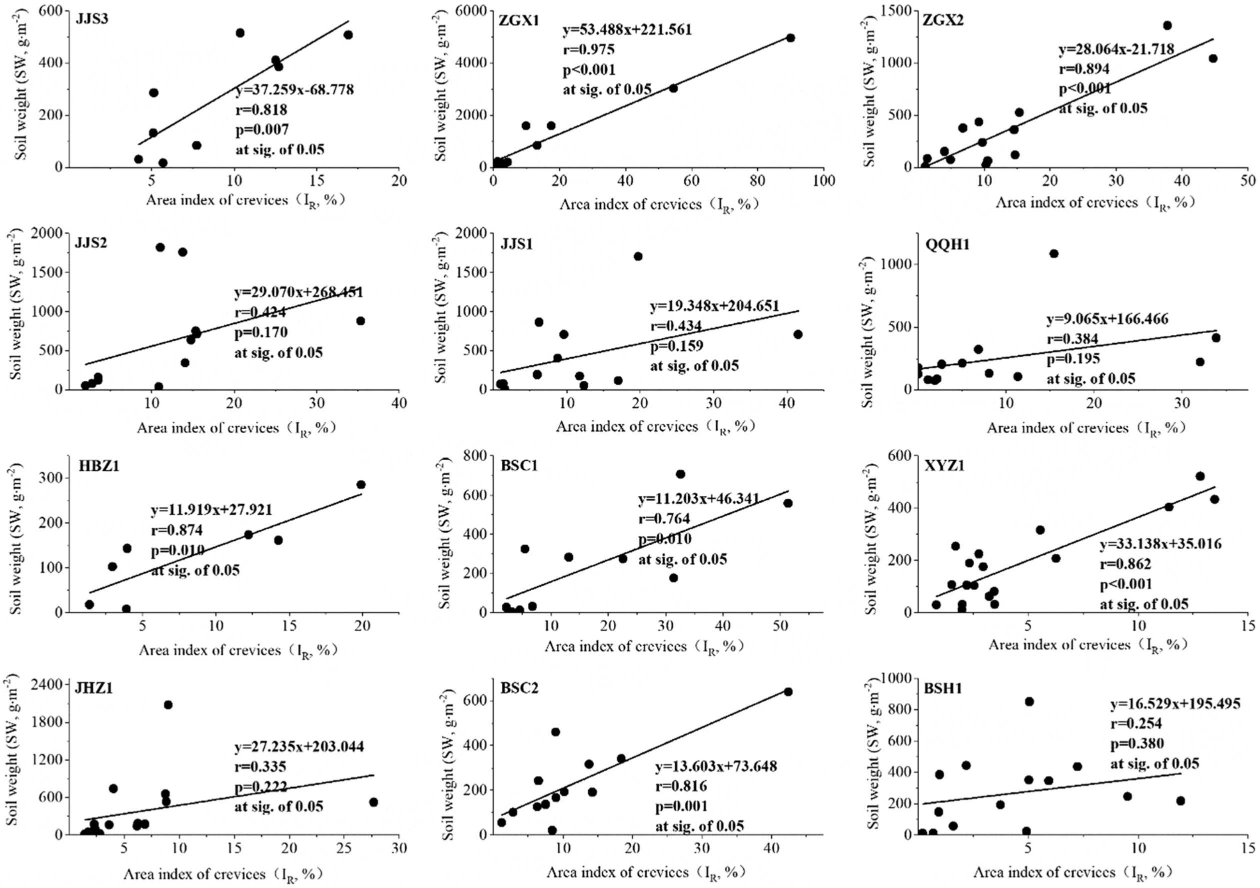

Fig. 7 Relationships between soil weight and area index of crevices at 13 sampling sites

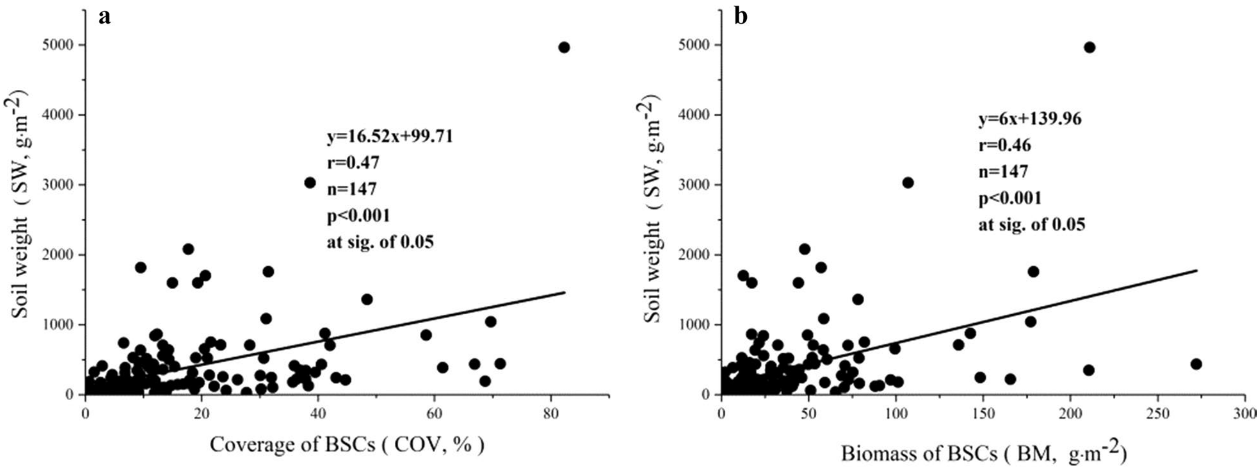

Fig. 8 Relationship between SW and COV (**a**) and BM (**b**) at different sampling sites

capture dust and fine soils in the surrounding environment (Belnap et al. 2001; Belnap 2010; Lu et al. 2022a; Peer et al. 2022; Wu et al. 2005; Zubiri et al. 2022). Additionally, BSC development should be beneficial for soil accumulation against water and wind erosion (Gall et al. 2022; Guo et al. 2022; Kheirfam and Roohi 2022; Lu et al. 2022a). Polysaccharides secreted by BSCs can enhance the adherence of soil particles to each other, which in turn increases the soil stability and forms a dense layer for the surface to protect the soil from external forces (Mager and Thomas 2011; Margolis et al. 2022; Lu et al. 2022a; Nyenda et al. 2019; Zhang et al. 2002). The bryophytes in BSCs could bond the fine soils to increase the stability of soils on RCSs (Belnap et al. 2001, 2016; Belnap 2010; Deng et al. 2020; Lucieer et al. 2014).

In all, the crevices on RCS might be conducive to soil accumulation by promoting BSCs growth and providing a refuge for trapping weathering products, soils, and dust deposits.

Effect of crevice density on major soil nutrient contents

The OC, TN and TP contents are usually considered as important indicators of soil fertility and quality (Li et al. 2018a; Lucieer et al. 2014; Nyenda et al. 2019; Yuan et al. 2006). Although most sampling sites formed only in 1.5–4 years, the OC, TN and TP contents of soil in or around crevices exceeded 18.61 g kg^{-1}, 0.96 g kg^{-1} and 0.52 g kg^{-1}, respectively, which were approximate to or even higher than those on natural slopes (CK) (Table 4).

The crevices might be beneficial to preserve and offer the nutrients in soils at newly formed rock cut slopes via three pathways. First, in the early stage of natural recovery, the soil materials trapped by the crevices mainly came from the natural, mature and fertile soils lying at the top and upper positions of the rock cut slope (Table 4) (Wu et al. 2022; Yuan et al. 2006; Zhu 2011). Second, water-dissolved N, P and C can be storage in soils in crevices through the process of absorption of soil particles, capture within soil pores and runoff evaporation (He et al. 2019; Fitzsimons and Michael 2017; Wu et al. 2022). Third, with BSC development along the crevices, major nutrients of soils may concentrate along the crevices greatly with respect to BSCs, particularly dominated by bryophytes (Chamizo et al. 2012; Deng et al. 2020; Dong et al. 2019; Elbert et al. 2009; Gao et al. 2018; Hyvrinenm et al. 2002; Karimi et al. 2022; Kleber et al. 2021; Nyenda et al. 2019; Sokol et al. 2022; Tian et al. 2022a, b; Wang et al. 2022a, b; Zhang et al. 2005a, 2022, 2012; Zubiri et al. 2022). Furthermore, BSCs are rich in microorganisms, e.g., Chloroflexi, cyanobacteria, CO dehydrogenases and rhizobium (Belnap et al. 2001; Belnap 2010; Hyvrinenm et al. 2002; Margolis et al. 2022; Sokol et al. 2022; Tian et al. 2022a, b; Wang et al. 2022a; Zhang et al. 2022; Zhu 1995), which can fix atmospheric nitrogen and carbon into soils through the biogeochemical cycle or by producing organics such as extracellular polysaccharides and amino acids, thus increasing the content of soil OC and TN (Al-Maliki and Breesam 2020; Elbert et al. 2009; Karimi et al. 2022; Mager and Thomas 2011; Moore et al. 2022; Nyenda et al. 2019; Sokol et al. 2022; Tian et al. 2022a, b; Turan et al. 2019). The amount of C and N fixed by BSCs accounts for ~ 6% of the annual C fixed by terrestrial plants and ~ 40% of the total N fixed by organisms (Elbert et al. 2009; Wu et al. 2001). Soil P might also be greatly enriched by BSCs via precipitation, runoff, dust (fine-textured sediments) and dew, which are typically enriched in P (Parzych and Trojanowski 2006; Peer et al. 2022; Reynolds et al. 2001; Wu et al. 2001; Zhang et al. 2012; Zubiri et al. 2022). In addition, organic acids segregated by BSCs could contribute to mineral bio-weathering, thus solubilizing P compounds (Sokol et al. 2022; Zubiri et al. 2022). Nutrients released from the litter of BSCs are the most relevant sources of humus formation, and could improve soil major nutrients (He et al. 2022; Liu et al. 2022; Sokol et al. 2022; Tian et al. 2022b; Tonello et al. 2022; Turan et al. 2019). It has been found that BSCs can boost surface soil fertility, especially in terms of the TN, TP and OC contents of soils in deserts and mine dust (Deng et al. 2020; Gao et al. 2018; Karimi et al. 2022; Lucieer et al. 2014; Mager and Thomas 2011; Nyenda et al. 2019; Tian et al. 2022b; Wang et al. 2022a, b; Wu et al. 2001; Zhang et al. 2012; Zubiri et al. 2022).

In general, the mature and fertile soils lying at the top and upper positions of the rock cut slope and BSCs growth could ensure high soil fertility.

Effect of recovery time on BSC development at the rock cut slope

BSC coverage and biomass increase with FA

In the early stage of natural recovery on RCS, plant development was restricted by abiotic factors (Yuan et al. 2006). In our study, BSCs development was restricted in crevices in the early stage of natural recovery (Figs. 2, 4), while under a similar I_R, the coverage of BSCs increased with FA (Fig. 9), revealing that BSC development might be affected by both microrelief (e.g., crevices) and FA in the early stage of natural recovery.

BSCs might preferentially develop from or along the crevices and subsequently enlarge or even fully cover RCSs with FA. The recovery time might be beneficial to BSC development because the tillering, reproduction and growth of individual plants in BSCs with recovery time could optimize the structure of BSCs toward the state of a stable community (Deng et al. 2020; Shen et al. 2018; Zhu 1995, 2011). With the reproduction of microorganisms and the secretion of extracellular polymeric substances, as well as aggregation of soil particles, BSCs would be thickened and broadened (Lu et al. 2022a; Sokol et al. 2022). On the other hand, the appearance of tiny pits brought by weathering with recovery time might promote star-shaped BSC growth on relatively flat surfaces at RCSs, which may lead to BSCs expanding away from the crevices (Fig. 2).

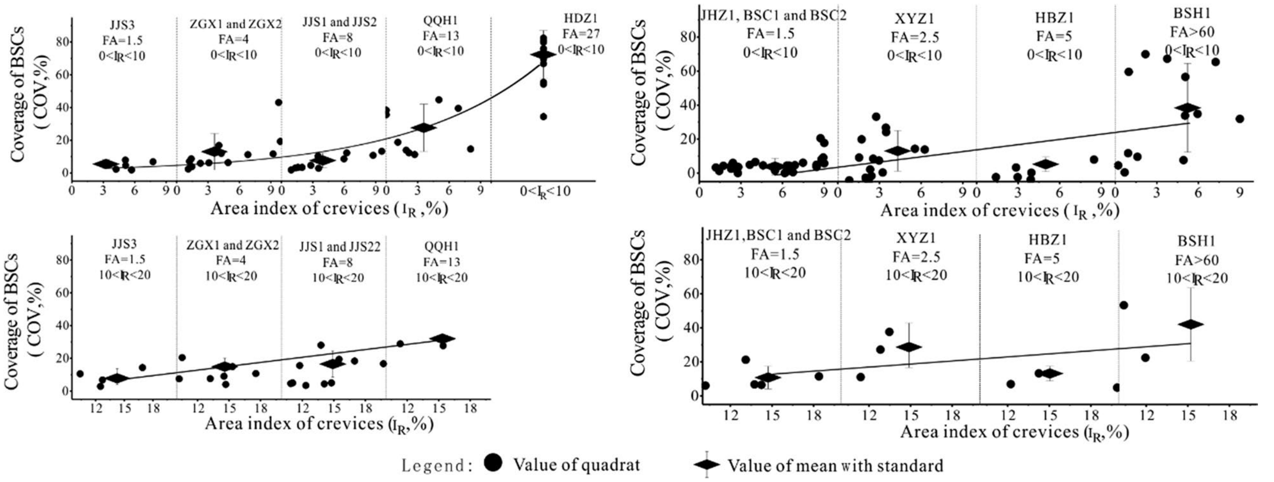

Fig. 9 Relationship of COV with small I_R on rock cut slopes at sampling sites. FA and I_R in the figure represent the formation age and crevice density of RCSs, respectively

Recovery rates of BSCs are highly variable with the age from less than 5 years (very fast) to more than 250 years (very slow) (Concostrina-Zubiri et al. 2019; Deng et al. 2020; Xiao et al. 2019a; Zhao et al. 2020). Our results also showed that the recovery time of BSCs appears and distributes extensively on sampling RCSs that lack water and soil is 1.5 and 27 years after disturbance, respectively, indicating a faster recovery rate of BSCs on RCSs.

The recovery rate of BSCs is largely dependent on the environmental conditions, especially the high soil moisture, soil fertile and microorganisms activity and diversity (Belnap et al. 2001, 2016; Belnap 2010; Karimi et al. 2022; Lucieer et al. 2014; Margolis et al. 2022; Tian et al. 2022a; Wang et al. 2022a, b; Zhang et al. 2002). Higher precipitation and humidity are also beneficial for the development of BSCs (Bu et al. 2015b; Karger et al. 2012; Langhans et al. 2010; Oishi 2019; Peng et al. 2022; Zaady et al. 2007; Zhang et al. 2002; Zhang et al. 2005b). Obviously, crevices could also increase humidity, which is beneficial to BSCs development, by collecting water and capturing fine and fertile soils with microorganisms on rock surfaces (Yuan et al. 2006). Meanwhile, the large mean annual precipitation of the studied regions in the western mountainous area of Sichuan Province, China, is ~ 1000 mm (Xiao et al. 2019b). Thus, the humid environment created by the climate and crevices might explain the faster development of BSCs at the sampling sites.

Nonlinear variation in properties of soils with FA

With the increase in recovery time and the development of vegetation and BSCs, soils on rock surfaces generally might accumulate and gradually become fertile (Lu et al. 2022a; Kato et al. 2010; Zhu 1995). However, our results showed that the averaged SW and major soil nutrient contents under similar environments (e.g., altitude, bedrock, slope aspect, and gradient) were not positively correlated with the increase in recovery time (Tables 3, 4). A couple of agents, e.g., BSCs and crevice, might affect soil accumulation at the sampling sites.

With respect to the low formation rate of soils developed on hard rock surfaces in alpine regions (Kato et al. 2010; Wells et al. 2008; Zhu 1995), the soil accumulation is derived mainly from the capability and capacity of trap formed soils lying on the upper position of RCSs and airborne fine particles, dependent on the features of BSCs (e.g., coverage and thickness) (Lu et al. 2022a) and crevices features (e.g., density, and width). Unfortunately, in our study, the crevice density and COV (especially on the sampling sites with an age of less than 13 years) on the RCSs vary unsystematically with formation age and accordingly result in irregular accumulation of soils.

Furthermore, in the process of ecological restoration, plant community structure can be optimized with time, and thus, more litter is input into soils (Deng et al. 2020; Feng et al. 2011; Nyenda et al. 2019; Zhao et al. 2015). The increase in litter directly transports organic matter and nutrient elements into the soil, resulting in the increase in major soil nutrients with time (Feng et al. 2011; He et al. 2022; Li et al. 2018b; Liu et al. 2022; Sokol et al. 2022; Tian et al. 2022b; Tonello et al. 2022; Zhao et al. 2015). Nevertheless, in our study, OC, TN and TP contents in soils on RCSs vary irregularly, possibly attributed to the interaction between the contents in the grains trapped from the slope soils and air, BSC biomass accumulation, decomposition of organic

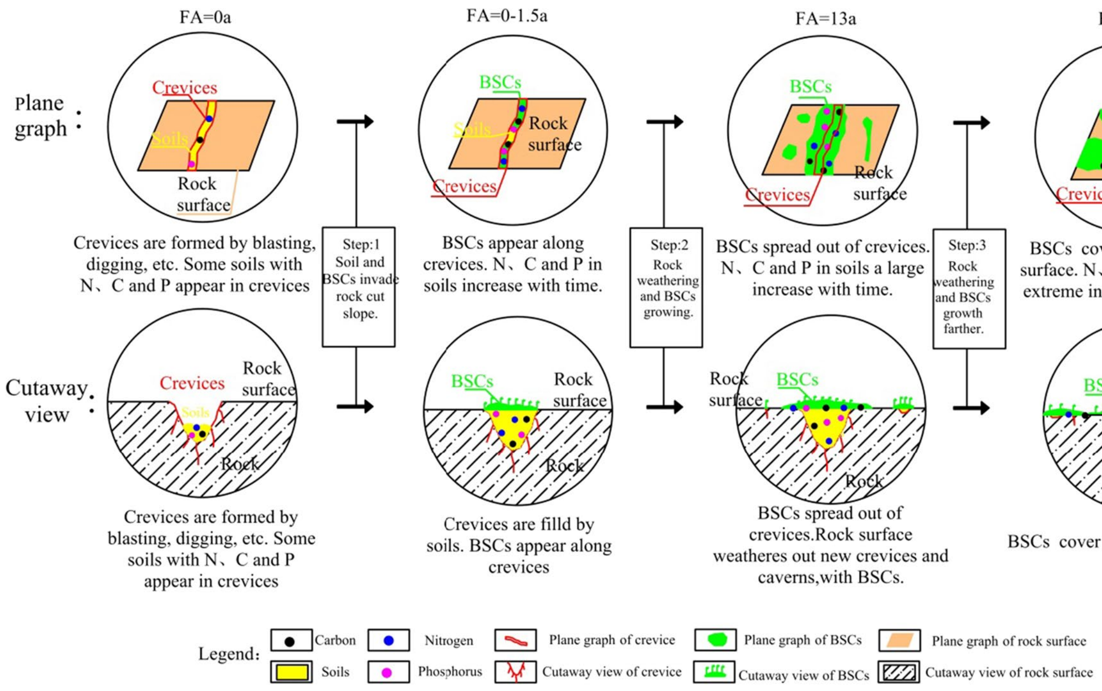

Fig. 10 Sketch diagram on ecological restoration processes of BSCs on RCSs in mountainous regions

matter, erosion intensity by water and air, etc. (Elbert et al. 2009; Lu et al. 2022b; Peng et al. 2022; Wu et al. 2001; Yuan et al. 2006; Zhang et al. 2022).

Conclusions

Our study provided a basis for exploring the effect of crevices and formation time on BSC development on RCSs in the west mountainous regions of Sichuan, Southwest China.

In summary, the contents of major nutrients in soils sampled from BSCs on RCSs are higher. The area index of the crevices (crevice density) and formation time could promote BSC development on RCSs. When the recovery time or formation time of RCSs was less than 13 years, BSCs were distributed generally and first along the crevices. Within an age of 1.5 years of RCS formation, the BSCs banded with fine soils with high nutrient contents could appear within the crevices. When the recovery time was over 27 years, under favorable conditions, the BSCs may even cover rock surfaces fully on RCSs, including the relatively smooth part (Fig. 10).

In alpine areas with stable rock strata and a low risk of geological disasters (e.g., landslides and rockfalls), the purposeful addition of the density of crevices on RCSs may effectively accelerate the formation and development of the soil–bryophyte system and the natural recovery on RCSs.

Abbreviations

BSC	Biological soil crust
BSCs	Biological soil crusts
RCS	Rock cut slope
RCSs	Rock cut slopes
I_R	Area index of crevices
COV	Coverage of BSCs
BM	Biomass of BSCs
SW	Soil weight
OC	Organic carbon
TN	Total nitrogen
TP	Total phosphorus
FA	Formation age of each RCS
CK	References or natural slope
SR1	The study region 1 in the eastern slope of the Jiajinshan Mountainous Range
SR2	The study region 2 in the eastern slope of the northern section of the Jiudinshan Mountainous Range

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Author contributions

CMH, MQZ, JD, and YWA designed the research. MQZ and CMH prepared the manuscript and revised this paper. MQZ, WQP, QZ, LX and WHL participated in fieldwork and sample collection. MQZ, WQP, QZ and YML participated in laboratory tests. MQZ, and QZ prepared tables and figures. All authors read and approved the final manuscript.

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Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Availability of data and materials
The datasets used and analyzed in this study are available from the corresponding author upon reasonable request.

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